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A taxonomic revision of the *Liphistius birmanicus*-group (Araneae: Liphistiidae) with the description of five new species

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Abstract: Most of the species of the *Liphistius birmanicus*-group are revised on the basis of genital morphology and an identification key to all species is given. Twelve species are recognized: seven previously known, five new. *Liphistius metopiae* Schwendinger, sp. nov. from northern Thailand, and *L. tung* Schwendinger, sp. nov., *L. ferox* Schwendinger & Huber, sp. nov., *L. cupreus* Schwendinger & Huber, sp. nov. and *L. platnicki* Schwendinger & Huber, sp. nov. from eastern Myanmar are described from both sexes. New males and females of *L. birmanicus* Thorell, 1897, *L. pinlaung* Aung *et al*., 2019 and *L. pyinoolwin* Xu *et al*., 2021 from the type localities are illustrated. A new locality each for *L. birmanicus* and for *L. pinlaung* is reported; additional taxonomic characters of the type specimens of *L. lahu* Schwendinger, 1998 are shown. Illustrations of intraspecific variation among the new specimens and information on their biology are given. The presumed relationships within the *birmanicus*-group and between this group and other species groups in *Liphistius* are discussed. Lateral pockets in the uterus externus, a previously overlooked structure of unknown function in the female genitalia of *Liphistius* species, are illustrated.

Keywords: Arachnida - Mesothelae - trapdoor spiders - morphology - variation - biology - Myanmar - Thailand.

INTRODUCTION

The *Liphistius birmanicus*-group, established by Schwendinger (1998: 28), previously contained seven species: *L. birmanicus* Thorell, 1897, *L. lordae* Platnick & Sedgwick, 1984, *L. pinlaung* Aung, Xu, Lwin, Sang, Yu, Liu, Liu & Li, 2019, *L. hpruso* Aung, Xu, Lwin, Sang, Yu, Liu, Liu & Li, 2019 and *L. pyinoolwin* Xu, Yu, Aung, Yu, Liu, Lwin, Sang & Li, 2021 from Myanmar, *L. lahu* Schwendinger, 1998 from Thailand and *L. nabang* Yu, Zhang & Zhang, 2021 from China (World Spider Catalog, 2022). The recent discovery of a *Liphistius* in southern China, the northernmost species known so far in this genus, was surprising but not unexpected. Congeneric species from territories in Myanmar that lie not very far south of the Chinese type locality were already known to us and are described here. *Liphistius tanakai* Ono & Aung, 2020, known only from the female holotype collected on an island off the coast of southern Myanmar, appears to belong to the *trang*-group. Many more undescribed species presumably live in the mountainous parts of the eastern half of Myanmar. It is a challenge to find out how far to the west in Myanmar *Liphistius* occurs. In the east the mighty Mekong River appears to be an important, though not absolute biogeographical barrier for the genus (Schwendinger, 2013). The Sittoung (= Sittang) River in Myanmar, and possibly the Ayeyarwady (= Irrawaddy) River to the north of it, currently appears to mark the western limits of the geographical range of *Liphistius*. Does the species also occur in the Bago Yoma Mountain Range between these two rivers? No liphistiid spiders were discovered there during a one-day visit to the Bago Yoma Mountains by the first two authors (PJS and SH) in 2014, nor during an expedition to that region by members of the Japanese National Museum of Nature and Science in August 2018 (Ono & Aung, 2020: 89). How far north does *Liphistius* occur? The type locality of *L. nabang* in

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China is so far the northernmost locality for the genus, but mesothelid fossils from Cretacious amber have been found much further north in the Hukaung Valley of the Kachin State (Wunderlich, 2017). They belong to extinct families, but it is likely that their modern descendants still live there today.
Since the publication of a comprehensive synopsis by Pocock (1900), not much substantial information on extant spiders (in contrast to fossil spiders in Burmese amber) of Myanmar has come out, which is mostly due to political issues in the country. Renewed collecting efforts during the last years (see Aung *et al*., 2019; Ono & Aung, 2020; Xu *et al*., 2021; Ono & Aung, 2022; this paper) will hopefully lead to a renaissance in research and publications on the spider fauna of Myanmar. There is so much more to be discovered in this biologically rich and diverse country.

MATERIAL AND METHODS

Morphological methods: Morphological characters were studied and drawn with a Zeiss SV11 stereomicroscope and an attached drawing tube. Whenever possible, female copulatory organs were drawn and examined from exuviae. Vulvae of alcohol-preserved specimens were cleared of soft tissue with fine forceps, insect pins and a paintbrush. Clearing in KOH was avoided, because it often leads to some degree of deformation (bulging) of the vulval plate. The ventral cuticular wall of the female genital region was cut off with micro-scissors to allow an unimpeded view of the ventral side of the vulval plate. Photos of vulval plates were taken with a video camera attached to a Zeiss SV6 stereomicroscope and stacked with the Automontage©System. Terminology of genital structures follows Schwendinger & Ono (2011) and Schwendinger (2017). Opisthosomal tergites are numbered from anterior to posterior, with the anterior-most being tergite I. Body measurements are all in mm (for other measurements the units are given) and were taken on the dorsal side, between the midpoints of the anterior and posterior margins. Total length includes chelicerae and anal tubercle. The carapace length was measured with the carapace in a slightly forward-inclined position so that the anterior and posterior margins were at the same focal plane. Leg and palp lengths are given in the following manner: total length (femur + patella + tibia + metatarsus + tarsus). In the paragraph "Variation" only characters that are considered to be taxonomically relevant are mentioned. In a few drawings some of the strong bristles on the cumulus and on the palpal tarsus were cut off virtually above the base to make the underlying structures better visible and to reduce the size of the figures. On the corresponding specimens these bristles remain intact. In the figure legends references to illustrations that are to the same scale are separated by commas, references to illustrations of different scales by semi-colons.
The type specimens of *L. birmanicus*, *L. lordae* and *L. pyinoolwin* were not re-examined because new material of both sexes is available from the corresponding type localities. The female syntypes (one of them meanwhile the lectotype) of *L. birmanicus* were re-described (also re-examined in all cases?) by Pocock (1900: 156), Bristowe (1933: figs 6, 7b, 8d, 9a), Haupt (1983: 280, figs 5C, 6C) and by Xu *et al*. (2021: 51, fig. 10G-H).

Map: The distribution map (Fig. 1) was created with simplemappr (www.simplemappr.net).

Museum acronyms: AMNH = American Museum of Natural History, New York, USA; BRCM = Biodiversity Research Centre of Myanmar, Nay Pyi Taw, Myanmar (note: until this collection is fully operational, all specimens destined to be deposited there will be temporarily stored in the NMNS); CBEE = Centre for Behavioural Ecology and Evolution, College of Life Sciences, Hubei University, Wuhan, Hubei Province, China; MCSNG = Museo Civico di Storia Naturale, Genova, Italy; MHBU = Museum of the Hebei University, Baoding, China; MHNG = Muséum d'histoire naturelle de la Ville de Genève, Switzerland; NMNS = National Museum of Nature and Science (formerly National Science Museum), Ibaraki, Japan; THNHM = Thailand Natural History Museum, Pathumthani, Thailand.

Other abbreviations used in the text: AME = anterior median eyes; CDO = central dorsal opening (macro-pore) of poreplate; CL = carapace length; CW = carapace width. Additional abbreviations are explained in the corresponding figure legends.

Arrangement of species: The presentation of species in this text is more or less in geographical order, from south to north, starting with the species in Thailand (Fig. 1).

TAXONOMIC PART

The *birmanicus*-group

When this species group was defined by Schwendinger in 1998 it contained only three species (*L. birmanicus, L. lordae* and *L. lahu*). As four additional species were added later and five are newly described here, a refined diagnosis and description of this group is necessary and given in the following.

Diagnosis: Essentially distinguished by the following four characters: (1) Contrategular area below (proximal of) tegulum completely unpigmented (e.g. Figs 8F, H-I, 13F-G, 21K, M, 23L-M). In males of all other species groups this area is more or less extensively pigmented. (2) A more or less distinct (least so in *L. platnicki* sp. nov., Fig. 23F) proximal ledge on retrodorsal side of contrategulum (e.g. Fig. 4A-C, G). A similar ledge is present only in *L. desultor* Schiödte, 1849, but there it is situated medially, not proximally, and its most prominent part is on the proventral side, not on the retroventral side (Schwendinger *et al*., 2019: fig. 5F-G, I-K). (3) Embolus proper narrowly divided, with a longer sclerotised part and a distinctly shorter membranous part lying close to each other (e.g. Fig. 4C-D, G). This is also found in the *bristowei*- (e.g. Schwendinger, 1990: figs 57-59), *malayanus*- (e.g. Schwendinger, 2017: fig. 3B, D, F, H), *tioman*-, *linang*- and *batuensis*-group, whereas in the *trang*-group the embolus is widely divided, with both parts clearly apart from each other (Schwendinger, 1990: figs 60-62; Schwendinger, 2017: fig. 3A, C, E, G). (4) Poreplate with a pair of more or less developed (least so in *L. nabang* and *L. cupreus* sp. nov., Yu *et al*., 2021: fig. 4 and Fig. 22) anterior lobes (e.g. Fig. 5). The females of several species in the *malayanus*-, *tioman*-, *linang*- and *batuensis*-group also have pronounced anterior lobes on their poreplates, but these co-occur with either a very large receptacular cluster, a very large CDO or a reduced sclerotisation of the posterior part of the poreplate and/or of the posterior stalk (see various illustrations in Schwendinger, 2017).

Additions to description: Medium-sized to very large species (CL of males 4.92-12.67, CW 4.56-11.47). All males and the females of most species with a brown to almost black body colouration, often with annulated legs (Figs 2, 3A-D); only in *L. birmanicus* and *L. hpruso* females with yellow or orange-coloured areas on carapace and proximal portions of legs and palps (Fig. 3E-I). Males with medium-sized tibial apophysis, triangular in ventral view, usually not much set back from distal margin of palpal tibia (e.g. Fig. 6K, N; except in *L. tung* sp. nov., Fig. 8B), carrying four long tapering apical megaspines (e.g. Fig. 4F). Paracymbium rather short, moderately deep, with indistinctly conical, almost plane distal side (e.g. 4H-J), or with distinctly conical distal side (only in *L. cupreus* sp. nov., *L. platnicki* sp. nov. and *L. nabang*, Figs 21A, 23A, Yu *et al*., 2021: fig. 3D-F), and with (e.g. Fig. 6L) or without (e.g. 10A) a retrolateral-proximal heel; the latter widely (e.g. Figs 4H-I, 15G) or narrowly rounded (e.g. Figs 6L, 19F), in *L. lordae* heel protruding proximally (Fig. 17G), in all other cases retrolaterally (e.g. Fig. 6J, L-N); cumulus not or only indistinctly elevated (e.g. Fig. 4H-J), or distinctly elevated (only in *L. cupreus* sp. nov., *L. platnicki* sp. nov. and *L. nabang*, Figs 21B, 23A-B, Yu *et al*., 2021: fig. 3D-F), carrying several long, strong bristles. Ventral side of palpal tarsus with a distinct subdistal suture (Figs 21A, 23A), with a subdistal trench or without any depression there; distal margin of palpal tarsus widely but shallowly invaginated (e.g. Fig. 4G). Subtegulum with (e.g. Fig. 10A, G) or without (e.g. Fig. 21A, K, M) a small apophysis, never with a large one. Tegulum well-developed and wide; its distal margin not elevated in most species (e.g. Fig. 8F-G), only in *L. nabang* and *L. platnicki* sp. nov. distinctly elevated into a short wide keel (Yu *et al*., 2021: fig. 3A-B, D-E and Fig. 23I-M); proximal margin of tegulum with a wide, finely to coarsely dentate edge, in most species more or less bent and overhanging the unpigmented membranous contrategular area below it (e.g. Fig. 6F) or adpressed to it (e.g. Fig. 10B), only in *L. platnicki* sp. nov. straight and strongly salient (Fig. 23M). Pigmented bridge between tegulum and contrategulum on retrodorsal side of palpal organ well developed. Contrategulum carrying a medium-sized, more or less conical proventral process with a rounded (e.g. Fig. 4A-C) or widely truncate apex (Fig. 17A, C), in most species at a roughly 45-90° angle to the axis of the palpal organ (e.g. Fig. 4G), in *L. birmanicus* and *L. pinlaung* distad-directed, almost parallel to axis of palpal organ (Figs 13D, F, 15C, E); distal edge of contrategulum narrow (e.g. Fig. 21E) to wide (e.g. Fig. 19A), its prolateral part with a more (e.g. Fig. 6I) or less (e.g. Fig. 4G) elevated keel, its prodorsal part evenly arched (e.g. 4A-C), or with an angular (in *L. cupreus* sp. nov., Fig. 21A, E-F, H-I) or arched protrusion (in *L. nabang,* Yu *et al*., 2021: fig. 3B); retrodorsal side of contrategulum with a pronounced (e.g. Fig. 4A-C, G) or rather small (only in *L. cupreus* sp. nov., *L. platnicki* sp. nov. and *L. nabang*, Figs 21E-F, H-I, N, 23F, H-I, Yu *et al*., 2021: fig. 3A-B) proximal ledge; contrategular area proximal of tegulum completely unpigmented (e.g. Fig. 8F-I). Para-embolic plate short in most species, with (e.g. Fig. 6F-H) or without (e.g. Fig. 4C-D) a slight indentation between it and keel-shaped retroventral edge of embolus complex; in *L. tung* sp. nov. and *L. ferox* sp. nov. para-embolic plate long and tounge-shaped (Figs 8A, I-H, 10A-D). Retrolateral margin of embolus complex unpigmented and overhanging distal margin of tegulum (e.g. Fig. 8F-G); prolateral margin of embolus complex with a lobate protrusion in *L. pyinoolwin* (Fig. 19A-B), unmodified in all other species of the group. Embolus proper narrowly divided; its sclerotised part strengthened by 2-6 ribs reaching apex; only in *L. ferox* sp. nov. with 2 ribs, one of them carrying a triangular distal protrusion (Fig. 10E-H); in distal view retrolateral side of sclerotised embolus part rounded and concave in most species, only in *L. ferox* sp. nov. angular (Fig. 10H); membranous part of embolus proper distinctly shorter than sclerotised part, at its base a more or less strongly pigmented area with longitudinal or inclined wrinkles (e.g. Figs 6I, 13D). Females with lateral folds of vulval plate well developed, glabrous or carrying few to several hairs; no hairs in genital atrium, and only exceptionally a single hair on poreplate or on posterior stalk (Figs 16I, 18E). Poreplates mostly wider than long (with only very few exceptions, e.g. Fig. 22N), with a more or less strongly invaginated anterior margin (slightly arched only in one documented female of *L. nabang*, Yu *et al*. 2021: fig. 4E-F) carrying a pair of anterior lobes ranging from large and wide (in *L. lordae*, Fig. 18) to small and reduced to 1-2 clusters of vesicles (in *L. cupre*us sp. nov., Fig. 22 and *L. nabang*, Yu *et al*., 2021: fig. 4); lateral margins of poreplate ventrally with (e.g. Fig. 7) or without small, knob-shaped antero-lateral processes (e.g. Fig. 5); CDO mostly small (e.g. Fig. 5A), slightly larger only in *L. tung* sp. nov. (Fig. 9A, C, E), distinctly larger only in juveniles (Fig. 9G), mostly rounded (e.g. Fig. 5A, D), rarely slit-like (Fig. 14D); receptacular cluster always racemose (never digitiform as in some *trang*-group species), moderately large, only in a few females slightly surpassing anterior margin of poreplate (e.g. Figs 5A-B, 18D, G-H). Poreplate and posterior stalk always fully sclerotised and connected to each other. The latter ranging from very short (e.g. Fig. 22K) to quite long (e.g. Fig. 9C and Aung *et al*., 2019: fig. 3B-E), and from much narrower than poreplate (e.g. Fig. 20) to distinctly wider than poreplate (e.g. Fig. 24D and Yu *et al*., 2021: fig. 4C-F), from widely eliptically (e.g. Fig. 9A) to quadrangular (e.g. Fig. 14B) and axe-blade-shaped (e.g. Fig. 16A), with a short and indistinct (e.g. Figs 22, 24) to long and pronounced (e.g. Fig. 20F-G) constriction in its anterior part.

Species included (n = 12): *Liphistius birmanicus* Thorell, 1897 (Myanmar), *L. cupreus* sp. nov. (Myanmar), *L. ferox* sp. nov. (Myanmar), *L. hpruso* Aung *et al.*, 2019 (Myanmar), *L. lahu* Schwendinger, 1998 (Thailand), *L. lordae* Platnick & Sedgwick, 1984 (Myanmar), *L. metopiae* sp. nov. (Thailand), *L. nabang* Yu *et al*., 2021 (China), *L. pinlaung* Aung *et al.*, 2019 (Myanmar), *L. platnicki* sp. nov. (Myanmar), *L. pyinoolwin* Xu *et al.,* 2021 (Myanmar), *L. tung* sp. nov. (Myanmar).

Distribution: All species known so far occur in the mountainous area that lies roughly between the Ayeyarwady (= Irrawaddy) River in the west, the Mekong River in the east and the Thai-Burmese border in the south (Fig. 1). At least two of these species (*L. lahu* and *L. ferox* sp. nov.) occur together with or very close to species of the *bristowei*-group.

Key to the species:

1 Males (unknown for *L. hpruso*) 2
\- Females........ 12
2(*1*) Proventral process of contrategulum strongly distad-directed, almost parallel to axis of palpal organ (Figs 13D, F, 15C) 3
\- Proventral process of contrategulum inclined from axis of palpal organ at an angle of roughly 45-90° (Figs 4G, 6I, 8I, 10F, 17E, 19C, 21N, 23H) 4
3(*2*) Large spiders (CL and CW of males 7.79-9.30 and 7.29-8.48, respectively); paracymbium without retrolateral-proximal heel (Fig. 13H) .... *L. birmanicus* (Myanmar)
\- Medium-sized spiders (CL and CW of males 4.92-6.27 and 4.56-5.40, respectively); paracymbium with retrolateral-proximal heel (Fig. 15G) .... *L. pinlaung* (Myanmar)
4(*2*) Para-embolic plate much longer than retroventral edge of embolus complex (Figs 8A, H-I, 10A-D 5
\- Para-embolic plate as long as or only slightly longer than retroventral edge of embolus complex (Figs 4D, 6F, 13E, 15D, 17D, 19D, 21A, 23A) 6
5(*4*) Medium-sized spiders (CL and CW of males 6.30-6.70 and 5.70-6.26, respectively); sclerotised part of embolus proper strengthened by 3 longitudinal ribs reaching the apex, none of them with an angular distal protrusion (Fig. 8A, C-D, F-I); proximal edge of tegulum salient, distinctly protruding from surface of palpal organ (Fig. 8H-J); tibial apophysis distinctly set back from anterior margin of tibia (Fig. 8B) .... *L. tung* sp. nov. (Thailand)
\- Very large spiders (CL and CW of males 11.47-12.67 and 10.45-11.47, respectively); sclerotised part of embolus proper strengthened by only 2 longitudinal ribs reaching the apex, one of them carrying an angular distal protrusion (Fig. 10E-H); proximal edge of tegulum adpressed to surface of palpal organ (Fig. 10B); tibial apophysis only slightly set back from anterior margin of tibia (Fig. 10J) .... *L. ferox* sp. nov. (Myanmar)
6(*4*) Cumulus distinctly elevated (Figs 21B, 23B, Yu *et al*., 2021: fig. 3D-F); paracymbium with distinctly conical distal side (21A, 23A, Yu *et al*., 2021: fig. 3D-F); proximal ledge on retrodorsal side of contrategulum indistinct or small (Figs 21E-F, H-I, L-N, 23F, H-I) 7
\- Cumulus not or only slightly elevated (Figs 4H-J, 6J, L-N, 17G, 19E-F); paracymbium with indistinctly conical, almost plane distal side (Figs 4H-J, 6J, L-N, 17G, 19E-F); proximal ledge on retrodorsal side of contrategulum pronounced (Figs 4A-C, 6A-D, 17A, C, 19A) 9
7(*6*) Distal edge of contrategulum evenly rounded, without a prodorsal protrusion in distal view (Fig. 23E-F); distal margin of tegulum distinctly elevated, developed as a short and wide keel (Fig. 23I-M); paracymbium without a retrolateral-proximal heel (Fig. 23A) .... *L. platnicki* sp. nov. (Myanmar)

- Distal edge of contrategulum with an angular or arched prodorsal protrusion in distal view (Fig. 21A, E-F, H-I, L, Yu *et al*., 2021: fig. 3B); distal margin of tegulum distinctly, indistinctly or not elevated (Fig. 21K, M, Yu *et al*., 2021: fig. 3A-B, D-E); paracymbium with or without a retrolateral-proximal heel (Yu *et al*., 2021: fig. 3E, Fig. 21A) 8

8(*7*) Distal edge of contrategulum with an angular prodorsal protrusion (Fig. 21A, E-F, H-I, L) and with a narrowly rounded dorsal apex (Fig. 21E-G); distal edge of tegulum not or only indistinctly elevated (Fig. 21K, M); paracymbium without a retrolateral-proximal heel (Fig. 21A) .... *L. cupreus* sp. nov. (Myanmar)

- Distal edge of contrategulum with an arched prodorsal protrusion and with a pointed dorsal apex (Yu *et al*., 2021: fig. 3B); distal edge of tegulum distinctly elevated, developed as a short, wide keel (Yu *et al*., 2021: fig. 3A-B, D-E); paracymbium with a retrolateral-proximal heel (Yu *et al*., 2021: fig. 3E) .... *L. nabang* (China)

9(*6*) Proventral process of contrategulum very wide, with widely truncate apex in distal view (Fig. 17A, C); heel of paracymbium protruding proximally (Fig. 17G) .... *L. lordae* (Myanmar)

- Proventral process of contrategulum conical, with narrowly rounded or narrowly and obliquely truncate apex in distal view (Figs 4A-C, 6A-D, 19A); heel of paracymbium protruding retrolaterally (Figs 4H-J, 6J, L-N, 19E-F) 10

10(*9*) Retrolateral-proximal heel of paracymbium carrying 2-3 enlarged spicules (Fig. 19E-F); base of embolus complex with a lobate prolateral protrusion in distal view (Fig. 19A-B) .... *L. pyinoolwin* (Myanmar)

- Retrolateral-proximal heel of paracymbium without enlarged spicules but normal spicules or stiff bristles instead (Fig. 4H-J, 6J, L-N); base of embolus complex without prolateral protrusion in distal view (Fig. 4C, 6A) 11

11(*10*) Depth/length ratio of tibial apophysis of palp ~ 1.4 (Fig. 4F); retrolateral-proximal heel of paracymbium widely rounded (Fig. 4H-J); prolateral part of distal edge of contrategulum indistinctly elevated (Fig. 4E, G); no invagination between para-embolic plate and retroventral edge of embolus complex (Fig. 4C-D) ... *L. lahu* (Thailand)

- Depth/length ratio of tibial apophysis of palp ~ 2.2 (Fig. 6O); retrolateral-proximal heel of paracymbium narrowly rounded (Fig. 6J, L-N); prolateral part of distal edge of contrategulum distinctly elevated (Fig. 6H-I); a shallow invagination between para-embolic plate and retroventral edge of embolus complex (Fig. 6F-H) .... *L. metopiae* sp. nov. (Thailand)

12(*1*) Portions of carapace, legs and palps of females and of last immature instars of males orange-coloured (Fig. 3E-I) 13

- Body and legs uniformly dark, or body brown and legs more or less distinctly annulated (Figs 2, 3A-C) 14

13(*12*) Large spiders (CL and CW of females up to 14.73 and 13.27, respectively); posterior stalk of vulval plate usually wider than long or rarely as wide as long, its posterior margin usually straight, rarely widely rounded (Fig. 14) .... *L. birmanicus* (Myanmar)

- Medium-sized spiders [CL and CW of female holotype (fully grown?) 7.02 and 6.16, respectively]; posterior stalk of vulval plate clearly longer than wide, its posterior margin narrowly rounded or angular (Aung *et al*., 2019: fig. 3B-E) .... *L. hpruso* (Myanmar)

14(*12*) Very large spiders (CL and CW in females up to 18.32 and 16.61, respectively); anterior lobes of poreplate folded ventrad (Figs 11-12); body and legs uniformly very dark, without annulations (Fig. 3A-B) .... *L. ferox* sp. nov. (Myanmar)

- Medium-sized spiders [CL and CW in females up to 8.50 and 7.90, respectively (for *L. lordae*)]; anterior lobes of poreplate not folded ventrad (Figs 5, 7, 9, 16A-J, 18, 20, 22, 24, Yu *et al*., 2021: fig. 4); body brown to dark, legs annulated or not 15

15(*14*) Posterior stalk as wide as or wider than poreplate; anterior lobes of poreplate reduced to 1-2 clusters of vesicles on each side (Figs 22, 24, Yu *et al*., 2021: fig. 4) 16

- Posterior stalk narrower than poreplate; anterior lobes of poreplate fully developed (Figs 5, 7, 9, 16A-J, 18, 20) 18

16(*15*) Ventral side of vulval plate with a widely separated pair of "bulging margins" laterally between poreplate and posterior stalk; posterior part of genital atrium strongly curved ventrad (Yu *et al*., 2021: fig. 4) .... *L. nabang* (China)

- "Bulging margins" absent; posterior part of genital atrium not strongly curved ventrad 17

17(*16*) Anterior margin of poreplate with 1-2 rather small clusters of vesicles on each side; lateral margins of poreplate without anterolateral processes; posterior stalk much shorter than poreplate (Fig. 22); prefoveal setae on carapace absent .... *L. cupreus* sp. nov. (Myanmar)

- Anterior margin of poreplate with only one rather large cluster of vesicles on each side; lateral margin of poreplate with a small knob-shaped anterolateral process on each side; posterior stalk almost as long as poreplate (Fig. 24); prefoveal setae present .... *L. platnicki* sp. nov. (Myanmar)

18(*15*) No knob-shaped anterolateral processes on ventral side of poreplate (Figs 5, 9, 18) 19

- Each lateral side of poreplate ventrally with a knob-shaped anterolateral process (Figs 7, 16A-J, 20) 21

19(*18*) Anterior lobes of poreplate very wide and continuous with lateral poreplate margins, no step between them step (Fig. 18); no annulations on legs and palps .... *L. lordae* (Myanmar)
- Anterior lobes of poreplate mostly rather narrow, with a more or less distinct step between them and lateral poreplate margins (Figs 5, 9); legs and palps with or without annulations 20
20(*19*) Step between anterior lobes and lateral margins of poreplate pronounced; length of posterior stalk clearly more than half of poreplate length (Fig. 9); legs and palps not annulated .... *L. tung* sp. nov. (Myanmar)
- Step between anterior lobes and lateral margins of poreplate rather indistinct; length of posterior stalk less than or little more than half of poreplate length (Fig. 5); legs and palps annulated .... *L. lahu* (Thailand)
21(*18*) Posterior stalk of vulval plate clearly longer than wide or only slightly wider than long, its anterior portion with a long constriction (Fig. 20; Xu *et al*., 2021: figs 5-7) .... *L. pyinoolwin* (Myanmar)
- Posterior stalk of vulval plate clearly wider than long, its anterior portion with a short constriction (Figs 7, 16A-J; Aung *et al*., 2019: fig. 5) 22
22(*21*) Anterior margin of poreplate mostly with a deep and narrowly U-shaped invagination between anterior lobes (indistinct in Fig. 7E); posterior stalk of vulval plate small in comparison with poreplate (Fig. 7); legs and palps annulated .... *L. metopiae* sp. nov. (Thailand)
- Anterior margin of poreplate with a less deep, more widely U-shaped or widely V-shaped invagination between anterior lobes; posterior stalk of vulval plate distinctly larger in comparison with poreplate (Fig. 16A-J, Aung *et al*., 2019: fig. 5); legs and palps not annulated .... *L. pinlaung* (Myanmar)

Detailed presentation of species:

***Liphistius lahu* Schwendinger, 1998**
Figs 1, 4-5

Liphistius lahu Schwendinger, 1998: 17-19, fig. 1A-H (description of males and females). – Schwendinger, 1999: fig. 1A-H (reprint of illustrations in Schwendinger, 1998).

Holotype: MHNG-ARTO-0024737; male; Thailand, Chiang Mai Province, Fang District, Doi Angkhang, 1540 m, 19°55'10"N, 99°02'55"E; 27.VIII.1990; leg. P.J. Schwendinger.

Paratypes: MHNG-ARTO-0024739; 1 male; collected together with the holotype. – MHNG-ARTO-0024740 to 24745; 6 female paratypes; collected at the type locality; 27.VIII.1990 and 25.IX.1986; leg. P.J. Schwendinger.

Other material: MHNG; 1 female; Thailand, Chiang Mai Province, Fang District, Doi Pha Luang, 1600 m, 20°02'37"N, 99°06'14"E; 3.XI.1990; leg. P.J. Schwendinger. No new material available.

Diagnosis: Males distinguished by a moderately deep tibial apophysis (depth/length ratio ~ 1.4, Fig. 4F), by a widely rounded retrolateral-proximal heel on paracymbium (Fig. 4H-J), by an indistinctly elevated prolateral part of the distal contrategular edge (Fig. 4E, G), and by short para-embolic plate not separated by an invagination from retroventral edge of embolus complex (Fig. 4C-E). Females distinguished by ventral side of poreplate without anterolateral processes and by an indistinct step between anterior lobes and lateral poreplate margins; posterior stalk axe-blade-shaped, about half as long as poreplate (Fig. 5).

Additions to description: Medium-sized spiders with brown colouration in both sexes and annulated legs and palps in females and juveniles (in large spiders less distinct than in small ones, annulations thus fading as females become older and larger). Males with scopula weak on tarsi I-II, slightly denser on tarsi III-IV, covering distal 4/5 of tarsus I and distal 5/6 of tarsi II-IV. Male palps with moderately deep tibial apophysis (depth/length ratio ~ 1.4), not set back from distal margin of tibia, carrying four long, pointed apical megaspines (Fig. 4F; Schwendinger, 1998: fig. 1A-C; Schwendinger, 1999: fig. 1A-C); paracymbium short, with an almost flat distal surface and with a widely arched retrolateral-proximal heel (Fig. 4H-J); cumulus indistinct, carrying a group of 5-6 long, strong bristles (Fig. 4H-J; Schwendinger, 1998: fig. 1B-C; Schwendinger, 1999: fig. 1B-C); subtegulum without apophysis (Fig. 4E); proventral process of contrategulum conical, with narrowly rounded apex in dorsal view (Fig. 4A-C); prolateral part of distal edge of contrategulum developed as a low (not elevated as in *L. metopiae* sp. nov.) keel (Fig. 4E, G); no wrinkles on dorsal side of contrategulum, a pronounced proximal ledge on its retrodorsal side (Fig. 4A-C); distal edge of contrategulum very wide, with narrowly rounded dorsal apex (Fig. 4A-C; Schwendinger, 1998: fig. 1D-E; Schwendinger, 1999: fig. 1D-E); tegulum large, its distal margin not elevated, its proximal edge widely arched, coarsely serrate, bent and distinctly overhanging membranous area of contrategulum below it (Fig. 4C-D; Schwendinger, 1998: fig. 1A-B; Schwendinger, 1999: fig. 1A-B); para-embolic plate very short, not separated from retroventral edge of embolus complex by an invagination (Fig. 4C-E); sclerotised part of embolus proper strengthened by 3-4 distally dentate longitudinal ribs reaching apex, narrowly divided from distinctly shorter membranous embolus part; at base of membranous embolus part a weakly pigmented area with only 3-4 longitudinal wrinkles and with a wide and

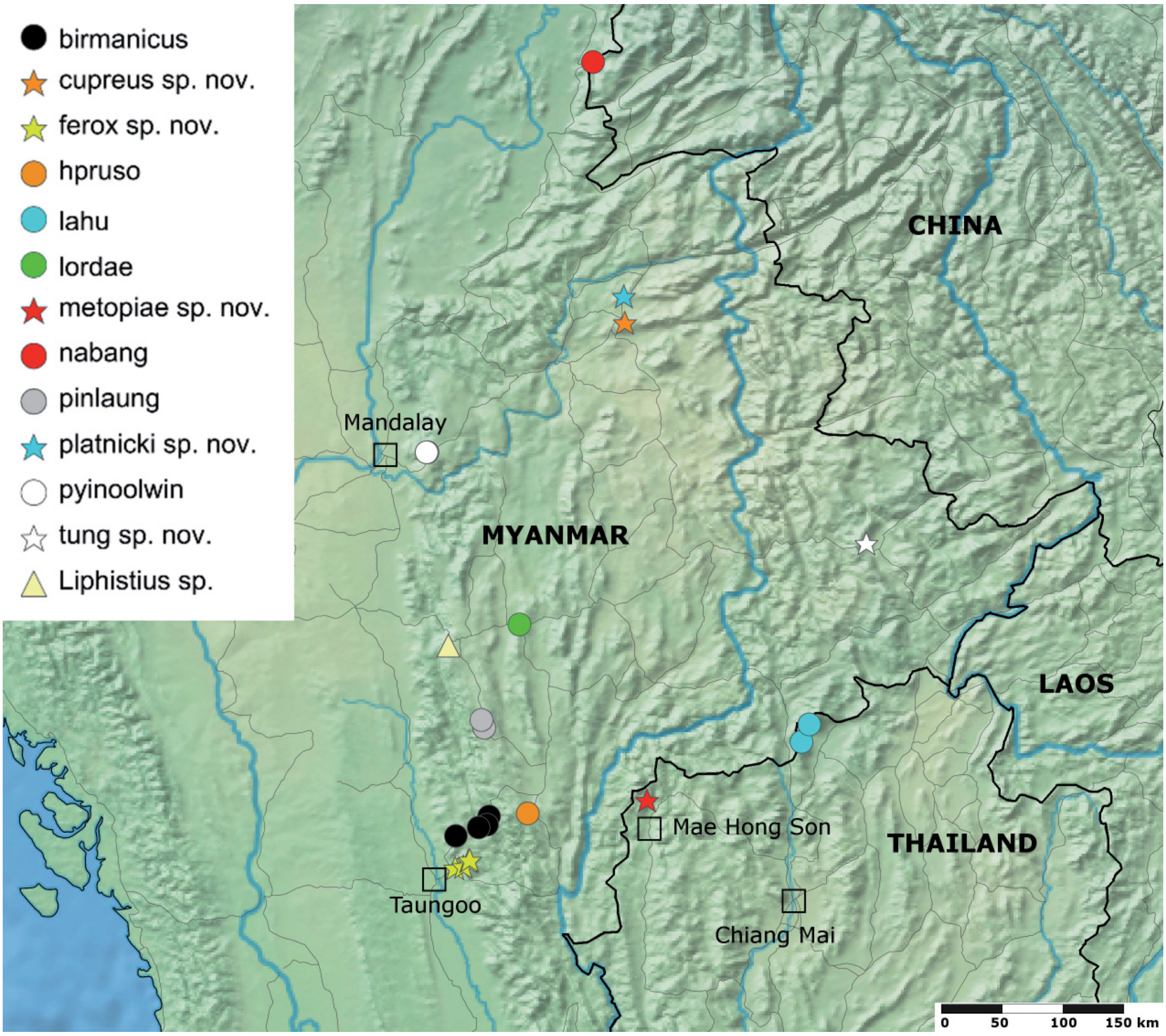


Fig. 1. Localities of species in the *Liphistius birmanicus*-group in northern Thailand, eastern Myanmar and southern China. Blue lines indicate major rivers, black lines national borders, grey lines major roads.

asymmetrical distal margin (Fig. 4C-D, G). Females with more or less distinctly annulated legs and palps; uterus externus with a small pair of lateral pockets (as illustrated for *L. ferox* sp. nov., Fig. 11I-J, N, P and Fig 12D, F); vulval plate with several hairs on lateral folds; poreplate wider than long, with a pair of pronounced, rounded lobes on anterior margin, without anterolateral processes; an indistinct step between anterior lobes and lateral poreplate margins (Fig. 5E-F, H); receptacular cluster racemose, quite long, almost reaching or slightly surpassing anterior margin of poreplate (Fig. 5; Schwendinger, 1998: fig. 1F-H; Schwendinger, 1999: fig. 1F-H); posterior stalk axe-blade-shaped, its anterior portion narrow, its posterior margin wide and arched, narrower than poreplate.

Variation: For carapace measurements and prefoveal setae counts see Table 1. All specimens examined have well-developed AME. Variation in the shape of the paracymbium and of the distal edge plus the proventral process of the contrategulum of males is shown in Fig. 4H-J and Fig. 4A-C, respectively. Variation in the shape of the vulval plates of five females is shown in Fig. 5.

Relationships: Palp morphology of males is very similar in *L. lahu* and *L. metopiae* sp. nov., indicating that these two species are not only geographically but also phylogenetically close to each other.

Distribution: *Liphistius lahu* is known from two localities in the mountains of the northern Thai province of Chiang Mai, at and close to the border with the Shan State of Myanmar (Fig. 1). This species can probably be found on both sides of that border.

Biology: Information is given in the original description (Schwendinger, 1998: 19). No new specimens or new biological information are available.

Liphistius metopiae Schwendinger, sp. nov.
Figs 1, 6-7

Liphistius sp.: Schwendinger & Pape, 2000: 353, figs 4-5 (report on predation by fly).

Holotype: MHNG-ARTO-0028249; male (matured 17.VII.1998; right tarsus IV, and to a lesser extent also right tarsus III, bent due to deformation in final moult); Thailand, Mae Hong Son Province and District, near Pang Tong Palace (19°30'10"N, 97°56'56"E), 870 m; 27.XII.1997; leg. P.J. Schwendinger.

Paratypes: MHNG-ARTO-0028250; 1 male (matured 7.VII.1998); collected together with the holotype. – MHNG-ARTO-0028251, MHNG-ARTO-0028265, MHNG-ARTO-0028266; 3 females (allotype, MHNG-ARTO-0028251); same locality; 2.XII.1998; leg. P.J. Schwendinger. – MHNG-ARTO-28252; 1 female; same locality; 21.X.2000; leg. P.J. Schwendinger. – THNHM; 1 female; same locality; 21.X.2000; leg. P.J. Schwendinger.

Etymology: The species epithet is a name in the genitive case referring to the sarcophagid fly *Metopia*

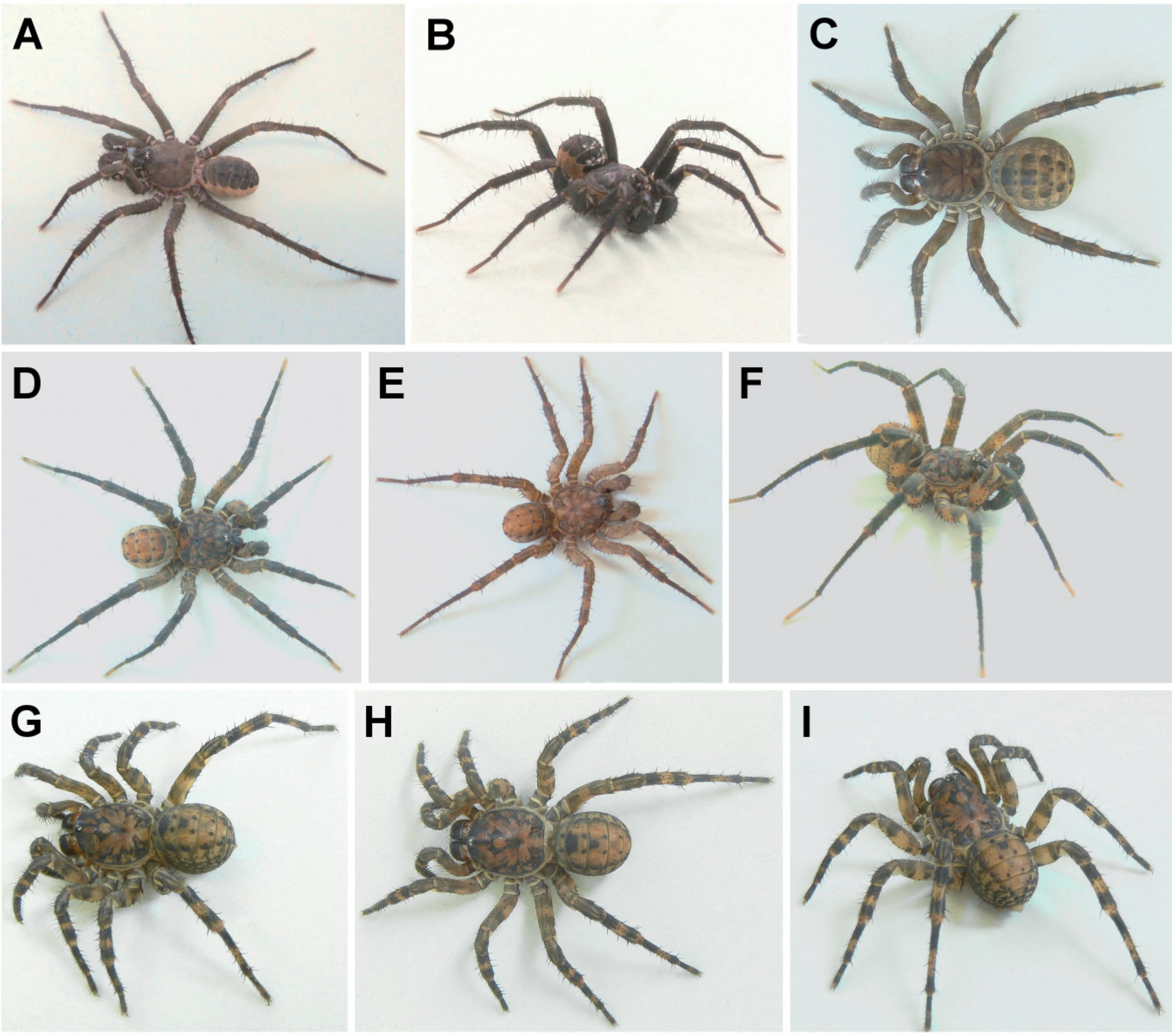


Fig. 2. Habitus of some species of the *Liphistius birmanicus*-group. (A) *Liphistius tung* sp. nov., male holotype. (B) *Liphistius pyinoolwin*, male (matured 1.X.2014) from the Anisakan Falls; note exuviae of ectoparasitic mites (*Ljunghia* sp.) on the opisthosoma. (C) *Liphistius platnicki* sp. nov., female paratype (moulted 10.III.2021) from near Loi Kan Village. (D, F) *Liphistius cupreus* sp. nov., male paratype from near Kong Nyaung Village. (E) Same species, different male paratype. (G) Same species, female paratype (moulted 13.II.2021). (H-I) Same species, different female paratype (moulted 21.V.2021). Not to scale.

sinensis Pape, 1986 whose larvae were observed devouring a female of the new species (Schwendinger & Pape, 2000).

Diagnosis: Medium-sized species with annulated legs and palps in females and juveniles. Similar to *L. lahu*, males distinguished by a relatively deeper tibial apophysis (depth/length ratio ~ 2.2 versus ~ 1.4 in *L. lahu*; Fig. 6O cf. Fig. 4F), by a more pronounced retrolateral-proximal heel on paracymbium (Fig. 6J, L-N cf. Fig. 4H-J), by prolateral part of distal edge of the contrategulum more distinctly elevated (indistinctly elevated in *L. lahu*; Fig. 6H-I cf. Fig. 4E, G), and by short para-embolic plate and retroventral edge of embolus complex separated by a very shallow invagination (Fig. 6F-H; no invagination in *L. lahu*, Fig. 4C-E). Females distinguished from those of *L. lahu* by ventral side of poreplates carrying distinct anterolateral processes and by a smaller receptacular cluster (Fig. 7 cf. Fig. 5).

Fig. 3. Habitus of some species of the *Liphistius birmanicus*-group. (A) *Liphistius ferox* sp. nov., male paratype (matured 1.IX.2014) from Pathi Village. (B) Same species, female paratype from Thandaung Gyi. (C) *Liphistius pinlaung*, female from near Tong Htiwaw Temple. (D) *Liphistius birmanicus* from Yado, male (matured 20.IX.2017). (E) Same species, large female n°1. (F, H) Same species, large female n°2. (G) Same species, small female. (I) Same species, large female n°3. Not to scale.

Description of male (holotype): *Colour in alcohol* (darker in life): Mostly light brown, with some lighter spots on patellae and tibiae of legs and palps (remnants of median and distal annulation). Some light spots also on opisthosomal tergites III-X; on tergites VI-VII most of median portion very light, with only a few dark spots. Most of ventral surface of leg femora and of palpal tibia very light. Palpal tarsus, sclerites of palpal organ and cheliceral fangs dark reddish brown. Most of ventral side of palpal coxae and proximal portion of proximal cheliceral article cream-coloured. Opisthosomal membranes very light brown, speckled with dark brown. Eye mound very dark.

Setae on carapace: A few setae remote from margin; none anterior to fovea.

Cheliceral teeth: 12 and 13 (including a tiny one) small teeth of different sizes on promargin of right and left cheliceral groove, respectively.

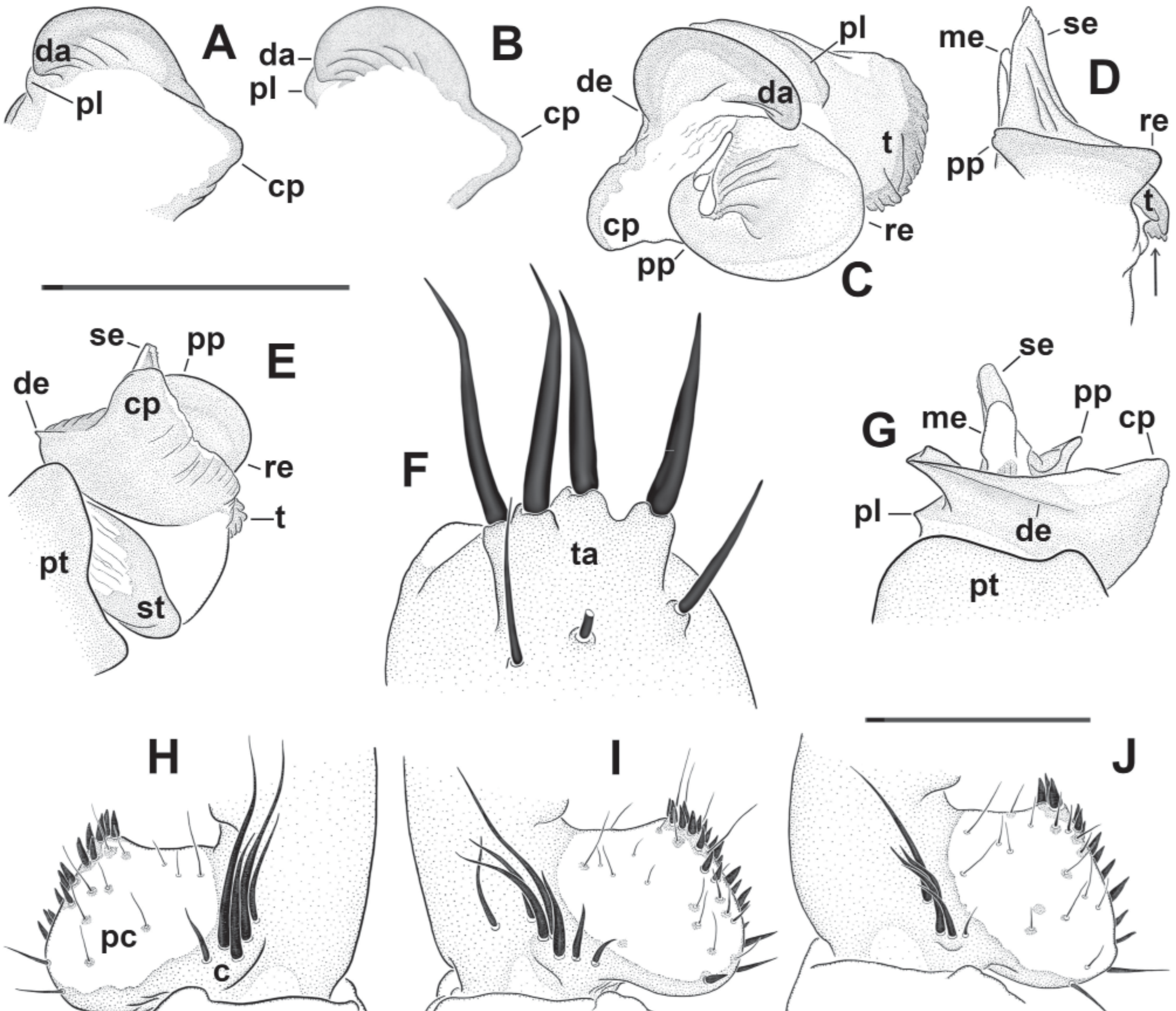


Fig. 4. *Liphistius lahu*, palp of male holotype (B-I) and of male paratype (A, J). (A-B) Contrategulum of right palp, distal view (dorsal side up). (C) Left palpal organ, distal and slightly retrodorsal view (dorsal side up). (D) Distal part of left palpal organ, retroventral and slightly distal view; bent proximal edge of tegulum indicated by arrow. (E) Distal part of left palp, vental and slightly proximal view. (F) Distal part of left tibia, retrolateral and slightly proximal view. (G) Palpal organ and distal margin of tibia of left palp, prolateral and slightly proximal view. (H) Proximal part of tarsus of right palp, ventral view. (I-J) Same of left palp. Scale lines 1.0 mm (A-G; H-J). Abbreviations: c - cumulus; cp - proventral contrategular process; da - dorsal apex of distal contrategular edge; de - prolateral part of distal edge of contrategulum; me - membranous part of embolus proper; pc - paracymbium; pl - proximal ledge on retrodorsal side of contrategulum; pp - para-embolic plate; pt - palpal tarsus; re - retroventral edge of embolus complex; se - sclerotised part of embolus proper; st - subtegulum; t - tegulum; ta - tibial apophysis.

Scopula: Distally divided by a short glabrous longitudinal stripe and proximally with a median row of stiff bristles on all tarsi; quite thin and not clearly outlined in distal 3/4 of ventral side of leg tarsi I-II; dense and clearly outlined, covering 4/5 of ventral side of tarsi III-IV.

Tarsal claws: Paired claws with 3-4 teeth on tarsus I, 4 teeth on tarsi II-III, 4-5 teeth on tarsus IV; unpaired claw of tarsi II-III with 0-1 denticle, of tarsi I and IV without denticle.

Palp: Tibial apophysis basally wide in ventral view (Fig. 6K) and deep in retrolateral view (depth/length ratio ~ 2.2, Fig. 6O), not set back from distal margin of tibia (Fig. 6K), carrying four apical megaspines with tapering tips, the ventral two longer than the dorsal two (Fig. 6K, O). Distal margin of tarsus widely but shallowly invaginated (Fig. 6I). Paracymbium short, wider than long in ventral view, moderately deep, with an almost flat distal surface and a pronounced, narrowly arched retrolateral-proximal heel (Fig. 6J, M); indistinctly elevated cumulus carrying a group of 4-5 long strong bristles (Fig. 6J, M). Subtegulum with an indistinct apophysis (Fig. 6J, see also Fig. 6L for paratype). Tegulum wide, with long and strongly bent, coarsely serrate proximal edge and with a long transverse median ridge; distal margin not elevated (Fig. 6E-F). Pigmented bridge between tegulum and contrategulum on retrodorsal side of palpal organ narrow (Fig. 6E). Contrategulum with short, quite wide proventral process ending in a narrow, truncate apex (Fig.

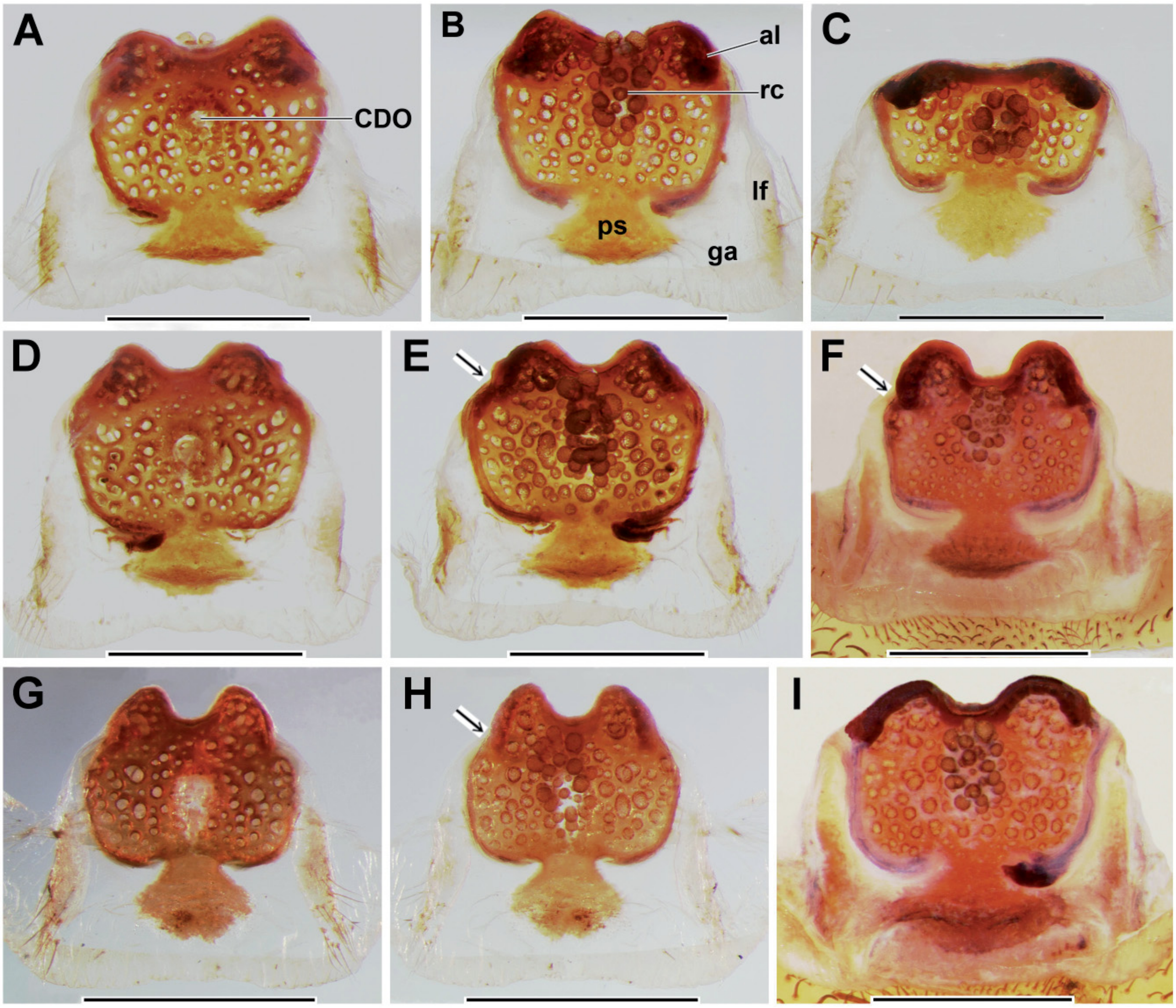
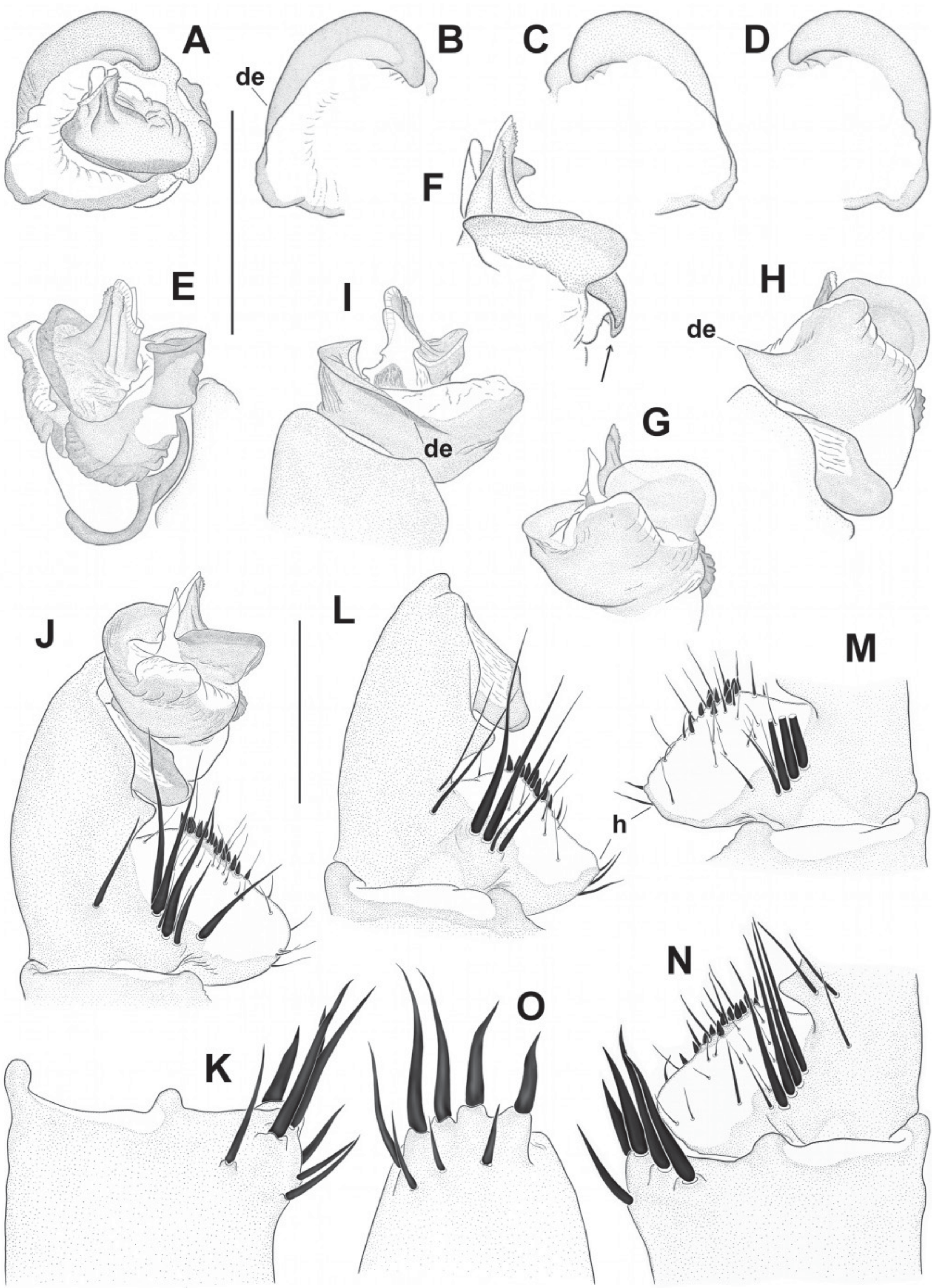


Fig. 5. *Liphistius lahu*, vulval plates of five females; dorsal view (A, D, G), ventral view (B, E-F, H-I) and anteroventral view (C). (A-C) Paratype MHNG-ARTO-0024744 (taken from specimen). (D-E) Paratype MHNG-ARTO-0024741 (from exuvia). (F) Paratype MHNG-ARTO-0024745 (from specimen). (G-H) Paratype MHNG-ARTO-0024742 (from exuvia). (I) Female from Doi Pa Luang (from specimen). Scale lines 1.0 mm. Arrows indicating indistinct step between anterior lobes and lateral margin of poreplate. Abbreviations: al - anterior lobe of poreplate; CDO - central dorsal opening of poreplate; ga - genital atrium; lf - lateral fold of vulval plate; ps - posterior stalk; rc - receptacular cluster.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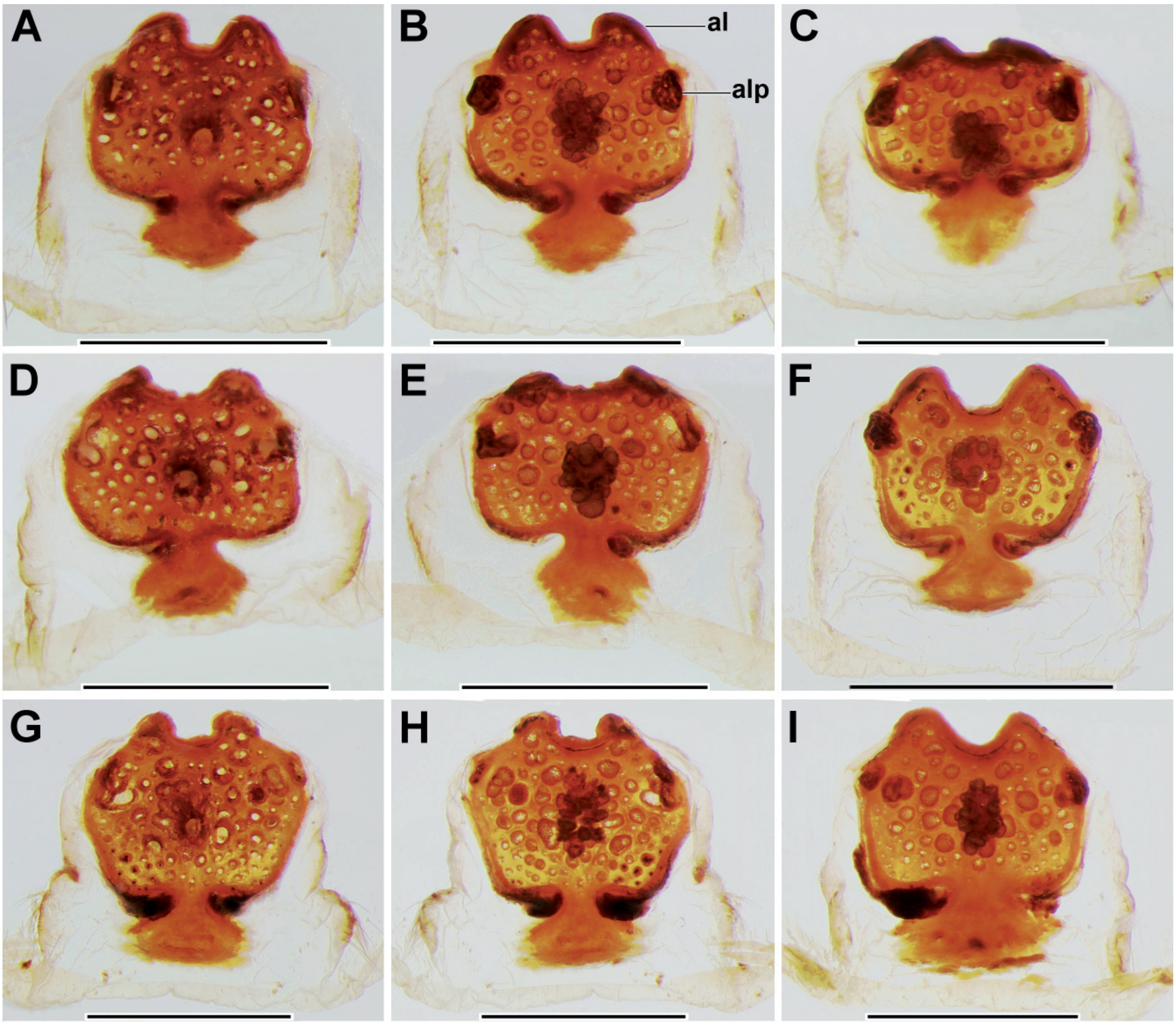

Fig. 7. *Liphistius metopiae* sp. nov., vulval plates of five female paratypes (all taken from exuviae); dorsal view (A, D, G), ventral view (B, E-F, H-I) and anteroventral view (C). (A-C) Allotype; moult of 23.IV.1998. (D-E) Moult of 16.IV.1999. (E) Moult of 24.II.2000. (G-H) Moult of 28.VI.2001. (I) Moult of 4.III.1999. Scale lines 1.0 mm. Abbreviations: al - anterior lobe of poreplate; alp - anterolateral process of poreplate.

Fig. 6. *Liphistius metopiae* sp. nov., palps of male holotype (A, D-K, M, O) and of male paratype (B-C, L, N). (A) Left palpal organ, distal view (dorsal side up). (B) Distal edge of contrategulum and proventral process of left palp, distal view. (C-D) Same of right palp, distal view. (E) Left palpal organ, retrolateral view. (F) Distal part of left palpal organ, retroventral and slightly distal view; bent proximal edge of tegulum indicated by arrow. (G) Same, ventral and slightly proximal view. (H) Entire palpal organ and distal margin of tibia, ventral and more proximal view than in G. (I) Same, prolateral view. (J) Left tarsus and palpal organ, ventral view. (K) Distal part of left tibia, ventral view. (L) Left tarsus and subtegulum, ventral view. (M) Right paracymbium, ventral view. (N) Right paracymbium and distal part of tibia, ventral view. (O) Distal part of tibia, retrolateral and slightly proximal view. Scale line 1.0 mm (A-I; J-O). Abbreviations: de - prolateral part of distal contrategular edge; h - retrolateral-proximal heel of paracymbium.

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6A, D); with several wrinkles on dorsal surface (Fig. 6I) and with a distinct proximal ledge on retrodorsal side (Fig. 6A, D); distal edge of contrategulum quite wide and widely arched, its prolateral part distinctly elevated into a keel (Fig. 6H-I), its dorsal apex narrowly rounded (Fig. 6A, D). Para-embolic plate short and widely arched, separated from keel-shaped retroventral edge of embolus complex by an indistinct invagination (Fig. 6F-H). Embolus proper with sclerotised part strengthened by 3-4 longitudinal ribs reaching apex and carrying tiny denticles distally (Fig. 6A, E-J); membranous part of embolus proper distinctly shorter than sclerotised part, both narrowly divided; at base of membranous embolus part a short weakly pigmented area with numerous (distinctly more than in *L. lahu*) longitudinal wrinkles and with a widely and asymmetrically angular distal margin (Fig. 6I); embolic folds (connecting membranous and sclerotised parts of embolus proper) short and indistinct (Fig. 6A, I).

Measurements: Total length 14.68; CL 6.03, CW 5.44; opisthosoma 6.27 long, 3.89 wide; eye mound 0.81 long, 1.01 wide; palpal coxa 1.90 long, 1.35 wide; labium 0.60 long, 1.15 wide; sternum 2.90 long, 1.75 wide (0.95 on ventral surface); palp 10.60 long (3.17 + 1.83 + 3.77 + 1.83); leg I 17.73 long (5.00 + 2.38 + 3.81 + 4.40 + 2.14); leg II 19.13 long (5.16 + 2.38 + 3.97 + 5.16 + 2.46); leg III 20.76 long (5.24 + 2.42 + 4.21 + 6.19 + 2.70); leg IV 27.47 long (6.55 + 2.66 + 5.56 + 8.89 + 3.81).

Description of female (allotype): *Colour in alcohol* (distinctly darker in life): Mostly light brown. Eye mound very dark. Chelicerae brown distally, cream-coloured proximally. Carapace with dark pattern including torch-shaped marking between eye mound and fovea. Palpal coxae only slightly lighter than leg coxae (in contrast to males); labium and sternum distinctly lighter than leg coxae. Legs light brown, with indistinct dark annulations proximally and subdistally on tibiae of legs and palps; tarsi I-II uniformly brown, tarsi III-IV with a light median zone. Membranous cuticle of opisthosoma light greyish brown with dark spots; tergites I-II uniformly brown, the following tergites with increasingly larger light areas, on tergites V-X brown areas reduced to lateral marks.

Setae on carapace: Few (only slightly more than in males) short, blunt setae on posterior and lateral margins and on coxal elevations of carapace; 10 setae in two parallel rows anterior to fovea.

Cheliceral teeth: 12 strong teeth on promargin of each cheliceral groove.

Claws: Palpal claws with 2 and 4 indistinct denticles. Paired tarsal claws of all legs with 3 teeth; unpaired claws of legs I-II with 1 denticle, none on legs III-IV (left tarsus IV missing). All tarsi without scopula.

Vulva (Fig. 7A-C): Uterus externus not examined; presumably small lateral pockets present. Vulval plate slightly wider than long, its lateral folds well developed, carrying several hairs. Anterior margin of poreplate with a quite large pair of arched lobes separated by a deep U-shaped invagination; lateral margins of poreplate ventrally with a knob-shaped anterolateral process on each side; posterior margins of poreplate distinctly bulged; CDO moderately developed, situated slightly posterior to centre of poreplate; receptacular cluster racemose, longer than wide, not reaching anterior margin of poreplate. Posterior stalk relatively short, axe-blade-shaped, clearly narrower than poreplate.

Measurements: Total length 20.99; CL 7.82, CW 6.73; opisthosoma 9.41 long, 7.82 wide; eye mound 1.04 long, 1.23 wide; palpal coxa 2.67 long, 1.78 wide; labium 0.89 long, 1.88 wide; sternum 3.86 long, 2.38 wide (1.48 on ventral surface); palp 12.83 long (4.16 + 2.38 + 3.22 + 3.07); leg I 15.54 long (4.75 + 2.67 + 3.27 + 3.27 + 1.58); leg II 16.48 long (5.05 + 2.77 + 3.37 + 3.61 + 1.68); leg III 18.02 long (5.10 + 2.92 + 3.56 + 4.36 + 2.08); leg IV 24.70 long (6.63 + 3.27 + 4.90 + 7.13 + 2.77).

Variation: For carapace measurements and prefoveal setae counts see Table 1. In all specimens examined the AME are well developed. In both males examined extent and density of the scopulae are the same. Variation in the shape of the dorsal apex of the distal contrategular edge and of the proventral contrategular process is shown in Fig. 6A-D; variation in the shape of the paracymbium in Fig. 6J, L-N. The male paratype has two long transverse median ridges on the tegulum, the holotype has only one (Fig. 6E). The holotype has one of the ventral bristles on the palpal tarsus distinctly stronger than the other bristles there (Fig. 6J); in the paratype two of these bristles are strengthened (Fig. 6L). The pigmented area at the base of the membranous part of the embolus has either a widely and obliquely truncate distal margin, giving the area an upside-down panflute-like shape, or its distal margin is widely and obliquely angular, like an asymmetrical roof (Fig. 6I). Females have more or less distinctly annulated legs and palps. In two of the females the dark pattern on the pars cephalica of the carapace is less distinct than in the other three females examined. Variation in the shape of the vulval plate is shown in Fig. 7. Intraspecific variation in the shape of the vulval plates (particularly concerning anterior lobes and posterior stalk) is considerable, but all females examined possess distinct anterolateral processes, which clearly distinguish them from females of the closely related *L. lahu*.

Relationships: *Liphistius metopiae* sp. nov. is morphologically similar and geographically close to *L. lahu*, which occurs about 130 km to the northeast (Fig. 1). Looking only at male genital characters, both species are difficult to distinguish, but the differences in female genital characters are more obvious. Both species appear to be most closely related to each other.

Distribution: The new species is only known from its type locality in Mae Hong Son Province, northern Thailand (Fig. 1). Since this is only 6-7 km away from the Thailand-Myanmar border, it is quite likely that *L. metopiae* sp. nov. also occurs in Myanmar.

Biology: Most small burrows (inhabited by juveniles) are T-shaped and equipped with two trapdoors; most large burrows are simple and have only one trapdoor. The largest door (of a female; n=7) observed in the field was 2.2 cm long and 3.2 cm wide; the front doors of the two males examined were 1.2-1.4 cm long and 1.8-2.0 cm wide. In the field many doors had moss growing on them. There were up to eight signal lines attached to the front entrance of the burrows; the longest line measured 6.5 cm. Four fresh egg cases, 2.1-2.8 cm long, 2.1-3.2 cm wide, 1.4-2.0 cm high, were collected in early and late December; an additional egg case (2.8, 3.0, 2.0 cm respectively) was constructed in captivity in early January. The cases contained 80, 113, 180, 210, 231 and 231 eggs suspended on a fine sheet of thin silken treads. In captivity the two males examined matured in early and late July, about half a year after being collected. In early December several females had egg cases in their burrows in the field. Females moulted between February and June.
Three females have pitlike bitemarks on the carapace and on the proximal part of the chelicerae. These were most likely caused by parasitic mites of the genus *Ljunghia* Oudemans, 1932 (see Halliday & Juvara-Bals, 2016).
Sarcophagid flies of the species *Metopia sinensis* raised from *L. lahu* carcasses in burrows at the type locality were initially interpreted as a case of carrion feeding (Schwendinger, 1998: 19). Later Schwendinger & Pape (2000) reported about empty puparia in burrows of *L. metopiae* sp. nov. (then already recognized as being different from *L. lahu*) and about six *M. sinensis* larvae that were slowly devouring a fully active female at the Pang Tong site. This predatory interaction between *Liphistius* and *M. sinensis* appears to be a rather widespread (but not common) phenomenon in northern Thailand. Circumstantial evidence indicates that larvae of this fly also feed on *L. bristowei* (Bristowe, 1976: 5; Schwendinger, 1990: 339; Schwendinger & Pape, 2000: 355). To our knowledge, this has not been observed for other *Liphistius* species.

Liphistius tung Schwendinger, sp. nov.
Figs 1, 2A, 8-9

Holotype: MHNG-ARTO-0028284 (sample THMY-10/08); male (matured 23.I.2014); Myanmar, Shan State, near Kong Paek Village (21°19'55"N, 99°30'37"E), NW of Kyaing Tong (= Kengtung, Keng Tong, Chieng Tung, Chiang Tung), 1300 m; 7.-8.I.2011; leg. P.J. Schwendinger.

Paratypes: MHNG-ARTO-0028285 (sample THMY-10/08); 1 male (matured 10.I.2013); collected together with the holotype. – MHNG-ARTO-0028286 to ARTO-28290, BRCM (sample THMY-10/08); 6 females (allotype, MHNG-ARTO-0028286); collected together with the holotype.

Other material: MHNG (sample THMY-10/08); 1 penultimate male collected together with the types.

Etymology: The species epithet is a name in apposition taken from "Tungkalasi", a mythical hermit who is said to have founded the city of Kengtung, the capital of a former Shan principality.

Diagnosis: Medium-sized species with no annulations on legs and palps in either sex. Similar to *L. lahu*, males distinguished by para-embolic plate much longer (Fig. 8H-I, cf. Fig. 4D); slightly bent proximal edge of tegulum more strongly salient (Fig. 8H-I cf. Fig. 4D); paracymbium without retrolateral-proximal heel, rectangular in ventral view (Fig. 8A-B cf. Fig. 4H-J). Females distinguished from those of *L. lahu* by lacking dark rings (annulations) on legs and palps and by vulval plates having a relatively longer posterior stalk, a larger CDO, a relatively shorter receptacular cluster, and anterior lobes closer to each other (Fig. 9 cf. Fig. 5).

Description of male (holotype): *Colour in alcohol* (see Fig. 2A): Mostly uniformly brown; ventral side of body slightly lighter than dorsal side; palpal coxae cream-coloured; proximal part of chelicerae and membranous cuticle of opisthosoma equally cream-coloured; opisthosomal tergites III-VI with indistinct light marks in centre of each lateral half; legs and palps without annulations; palpal tarsus and sclerites of palpal organ dark brown; eye mound very dark.
Setae on carapace: In posterior half distinctly more short, blunt-tipped setae than in anterior half; 4+5 setae in two parallel rows anterior to fovea.
Cheliceral teeth: 11 and 12 small teeth of different sizes on promargin of left and right cheliceral groove, respectively.
Scopula: Distally divided by a short glabrous longitudinal stripe and proximally with a median row of stiff bristles on all tarsi; quite thin and not clearly outlined in distal 2/3 of ventral side of leg tarsus I; equally developed and covering distal 3/4 of tarsus II; dense and clearly outlined, covering 4/5 of tarsi III-IV.
Tarsal claws: Paired claws with 4-5 teeth on tarsi I-II, 4-6 teeth on tarsus III, 5 teeth on tarsus IV; unpaired claw of tarsi I-II with 3-4 denticles, of tarsus III with 3 denticles, of tarsus IV with 1 denticle.
Palp: Tibial apophysis basally quite narrow in ventral view, distinctly set back from distal margin of tibia (Fig. 8B), carrying 4 long and tapering apical megaspines, the ventral two weaker and longer than the two dorsal ones (Fig. 8B). Distal margin of tarsus widely but shallowly invaginated (Fig. 8J). Paracymbium relatively short and moderately deep, quadrangular, longer than wide in ventral view, its distal side domed (not conical), without a retrolateral-proximal heel (Fig. 8A-B); slightly

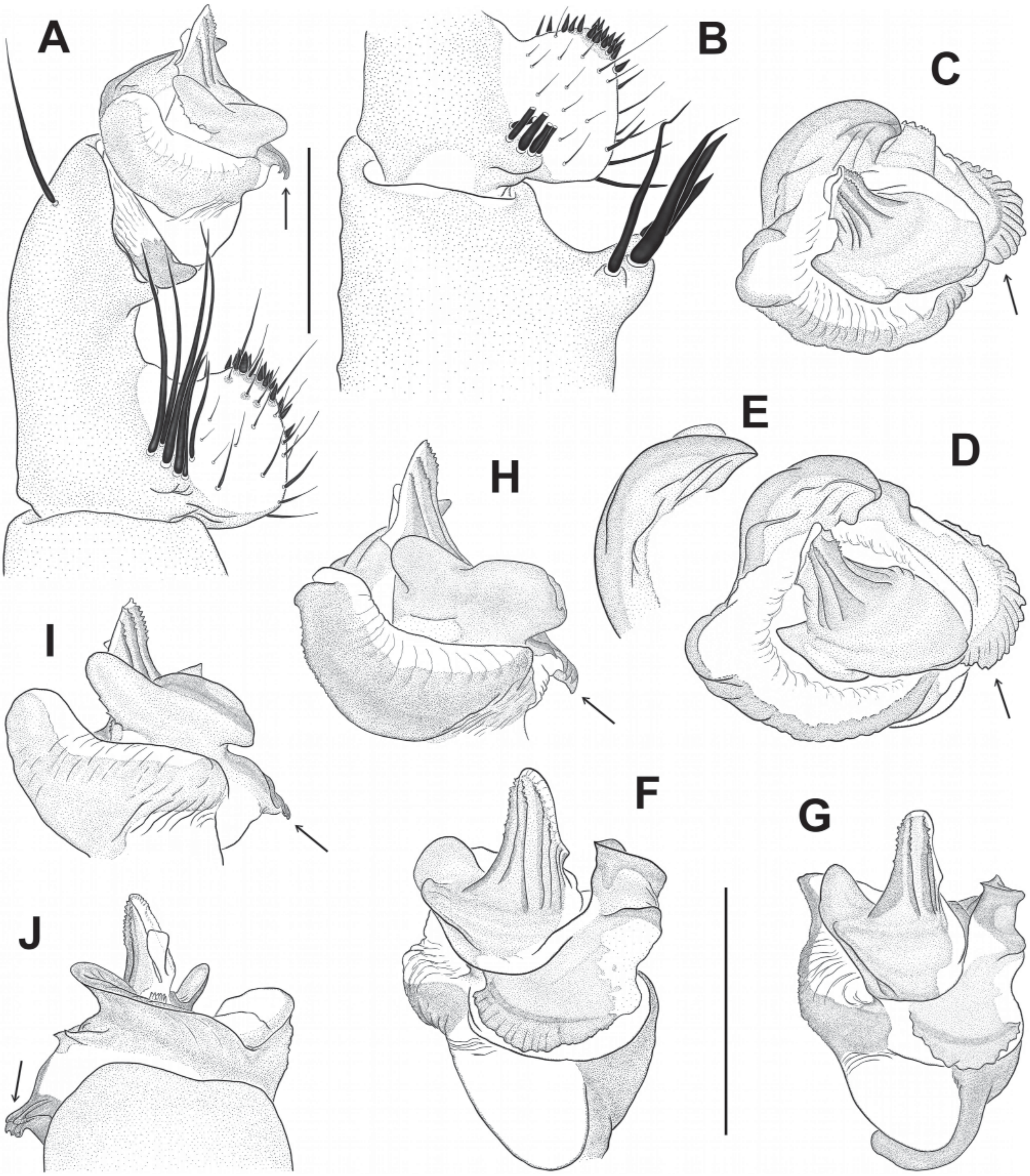


Fig. 8. *Liphistius tung* sp. nov., left palps of male holotype (A-C, G, I-J) and of male paratype (D-F, H). (A) Tarsus and palpal organ, ventral view. (B) Distal part of tibia and proximal part of tarsus, ventral view. (C-D) Palpal organ, distal view (dorsal side up). (E) Distal edge of contrategulum, distal and slightly prodorsal view. (F) Palpal organ, retrolateral view. (G) Same, retroventral view. (H-I) Distal part of palpal organ, ventral and slightly proximal view. (J) Distal part of tarsus and palpal organ, prolateral view. Arrows indicating bent and salient proximal edge of tegulum. Scale lines 1.0 mm (A-B; C-J).

elevated cumulus carrying a densely packed group of 5 long strong bristles (Fig. 8A-B). Subtegulum without apophysis (Fig. 8A, G). Tegulum wide, with long and slightly bent, moderately serrate proximal edge strongly protruding from surface of palpal organ (Fig. 8A, C, I-J); distal margin not elevated (Fig. 8G). Tegulum and contrategulum connected by a well-developed pigmented bridge on retrodorsal side of palpal organ (Fig. 8G). Contrategulum with short, blunt conical proventral process (Fig. 8C); no wrinkles on dorsal surface, a distinctly developed proximal ledge on retrodorsal side (Fig. 8C, G, J); distal edge of contrategulum widely arched and carrying pronounced ridges, its dorsal apex narrowly rounded (Fig. 8C), appearing pointed when slightly inclined prodorsad (Fig. 8E, showing male paratype). Para-embolic plate long, tounge-shaped, inclinded prodorsad, with rounded distal margin, its prodorsal margin weakly dentate (Fig. 8A, I). Retroventral edge of embolus complex distinctly elevated into a short, widely arched keel (Fig. 8I). Sclerotised part of embolus proper strengthened by 4 longitudinal ribs reaching apex and carrying denticles distally (Fig. 8A, C, G, I); membranous part of embolus proper distinctly shorter than sclerotised part, both narrowly divided; at base of membranous embolus part a short and weakly pigmented area with numerous longitudinal wrinkles, its distal margin horizontal and fairly straight (Fig. 8J); embolic folds short and indistinct.

Measurements: Total length 16.35; CL 6.30, CW 5.70; opisthosoma 7.18 long, 5.26 wide; eye mound 0.90 long, 1.21 wide; palpal coxa 2.23 long, 1.36 wide; labium 0.64 long, 1.32 wide; sternum 2.87 long, 2.15 wide (1.16 on ventral surface); palp 11.72 long (3.43 + 2.07 + 3.99 + 2.23); leg I 19.06 long (5.42 + 2.63 + 4.23 + 4.47 + 2.31); leg II 20.41 long (5.54 + 2.71 + 4.43 + 5.18 + 2.55); leg III 23.64 long (6.06 + 2.71 + 4.78 + 6.86 + 3.23); leg IV 29.31 long (6.90 + 2.79 + 5.90 + 9.33 + 4.39).

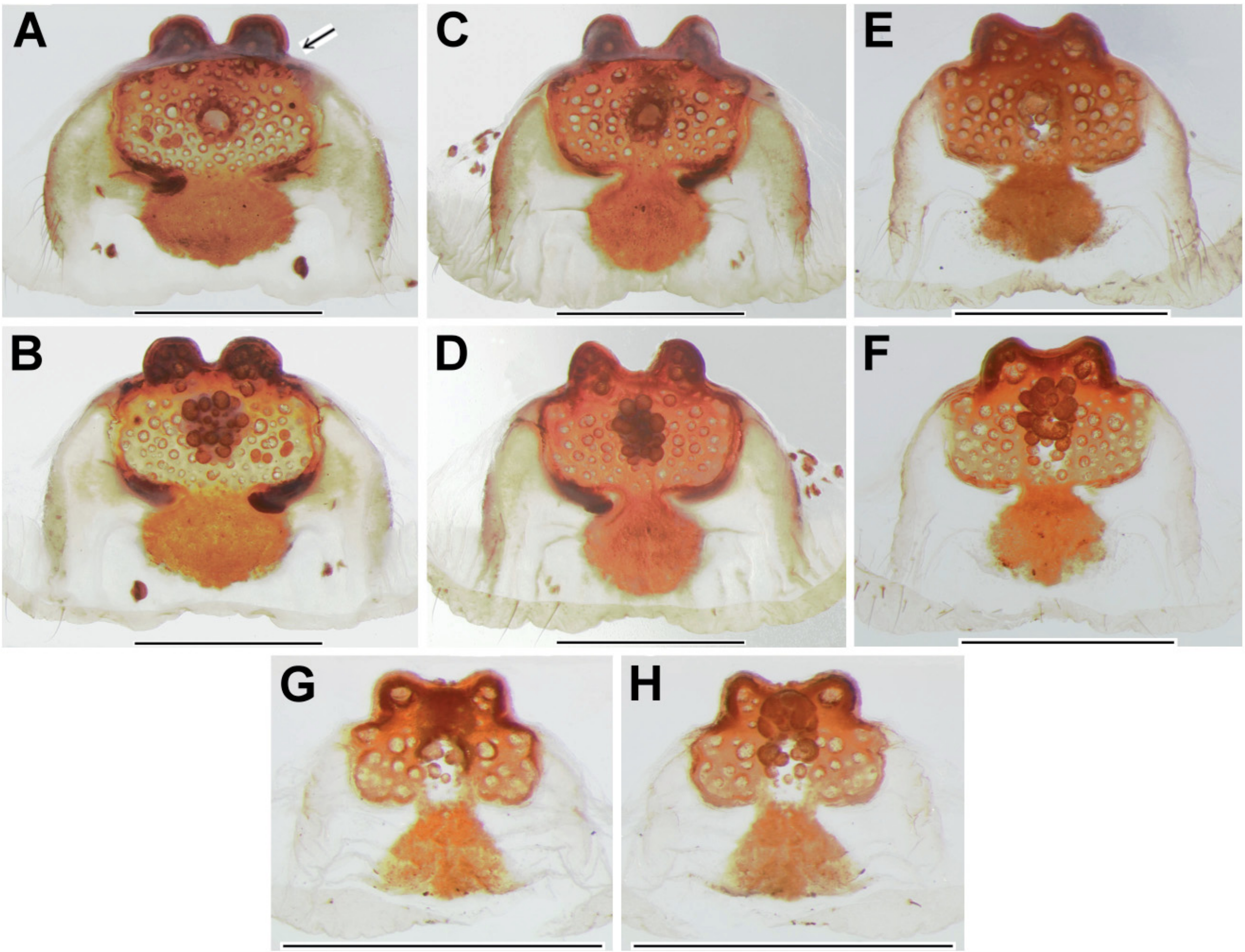


Fig. 9. *Liphistius tung* sp. nov., vulval plates of four females; dorsal view (A, C, E, G) and ventral view (B, D, F, H). (A-B) Allotype (taken from specimen). (C-D) Large paratype (taken from specimen). (E-F) Medium-sized paratype (from exuvia 18.IV.2013). (G-H) Small paratype (from exuvia 28.III.2012). Arrow indicating pronounced step between anterior lobes and lateral margin of poreplate. Scale lines 1.0 mm.

Description of female (allotype): *Colour in alcohol* (darker in life): Mostly dark brown. Eye mound and anterior margin of carapace black. Chelicerae dark brown distally, light brown proximally. Carapace with dark pattern including torch-shaped marking between eye mound and fovea. No dark annulations on legs and palps. Membranous cuticle of opisthosoma light greyish brown; tergites dark greyish brown. Ventral sclerites lighter than dorsal ones.
Setae on carapace: Several (more than in males) short, blunt setae on posterior and lateral margins and on coxal elevations of carapace; 10+14 setae in two parallel rows anterior to fovea.
Cheliceral teeth: 13 strong teeth on promargin of right cheliceral groove, 15 on left groove.
Claws: Palpal claws with 2 and 4 worn denticles. Paired tarsal claws of leg I with 3 teeth, of legs II-IV with 3-4 teeth; unpaired claws of legs I-II with 3 denticles, of leg III with 2-4 denticles, of leg IV with 1-2 denticles. All tarsi without scopula.
Vulva (Fig. 9A-B): Uterus externus with a distinct pair of lateral pockets on dorsal side (as illustrated for *L. ferox* sp. nov., Figs 11I-J, N, P, 12D, F). Vulval plate wider than long; its lateral folds well developed, carrying several hairs. Anterior margin of poreplate with a pair of strongly arched lobes, these close to each other and separated by a narrow and deep invagination; posterior margins of poreplate distinctly bulged; CDO slightly larger than in females of other species in same group, situated in centre of poreplate; receptacular cluster racemose, relatively small, slightly longer than wide, not reaching anterior margin of poreplate. Posterior stalk large, widely oval, narrower than poreplate.
Measurements: Total length 19.48; CL 7.85, CW 7.06; opisthosoma 8.65 long, 7.16 wide; eye mound 1.15 long, 1.31 wide; palpal coxa 2.73 long, 1.59 wide; labium 0.89 long, 1.99 wide; sternum 3.93 long, 2.04 wide (1.79 on ventral surface); palp 13.96 long (4.57 + 2.58 + 3.28 + 3.53); leg I 16.75 long (5.17 + 2.98 + 3.43 + 3.38 + 1.79); leg II 17.35 long (5.17 + 3.08 + 3.53 + 3.58 + 1.99); leg III 18.94 long (5.37 + 3.13 + 3.73 + 4.37 + 2.34); leg IV 26.05 long (7.06 + 3.38 + 5.22 + 7.06 + 3.33).

Variation: For carapace measurements and prefoveal setae counts see Table 1. In one female the left AME is missing, in another one it is indistinctly developed. In both males examined extent and density of the scopulae are the same. Variation in details of the male palp is illustrated in Fig. 8. The holotype has one of the proventral-distal bristles on the left palpal tarsus distinctly stronger than the other bristles (Fig. 8A). In contrast to the holotype, the male paratype has a smooth prodorsal margin of the para-embolic plate (Fig. 8H; dentate in the holotype, Fig. 8A, I). The number of longitudinal ribs reaching the apex of the sclerotised embolus part ranges from four to five. The pigmented area at the base of the membranous part of the embolus has a horizontal and fairly straight distal margin in the holotype, whereas in the male paratype it is widely and asymmetrically angular. Small females have distinctly annulated legs and palps, whereas in large females the annulations are indistinct to absent, obviously having faded as the spiders became older and larger. Variation in the shape of the vulval plates is shown in Fig. 9. The vulval plates of small (immature?) females have less pronounced anterior lobes, less bulging posterior poreplate margins, a relatively larger CDO, a relatively larger receptacular cluster with a partly unsclerotised base, and an anteriorly narrower posterior stalk than large females (Fig. 9E-H cf. Fig. 9A-D).

Relationships: Among males of the *birmanicus*-group a large para-embolic plate (common in species of the *trang*-group) is only found in *L. tung* sp. nov. and *L. ferox* sp. nov. (Fig. 8H-I and Fig. 10A-D). This appears to be a synapomorphy, but considering the wide geographical separation of both species (Fig. 1) it may actually be a homoplasy.

Distribution: The new species is only known from its type locality in the south-eastern part of the Shan State (Fig. 1).

Biology: The spiders examined were collected from the banks of a small stream running through fallow fields on a steep mountain side. All burrows were simple and unbranched, with a single trapdoor up to 2.0 cm long and 3.3 cm wide, and with up to eight signal lines, the longest measuring 8 cm. In captivity the two males became adult in burrows with 2.4-2.9 cm long and 1.8-2.0 wide trapdoors. Three egg cases, 2.2-3.0 cm long, 2.3-3.3 cm wide, 1.7-2.3 cm high, were found at the type locality in early January. They contained 56, 97 and 110 light yellow eggs suspended in a fine mesh of silken threads. The males matured in early January, after two and three years in captivity. Since at that period of the year egg cases were found in the wild, the mating dates of the males in captivity were obviously later than in nature.

Liphistius ferox Schwendinger & Huber, sp. nov.

Figs 1, 3A-B, 10-12

Holotype: MHNG-ARTO-0028317 (sample MT-14/10); male (matured 2.X.2014); Myanmar, Kayin State, Thandaung Lay (19°01'15"N, 96°35'00"E), 140 m; 16.VII.2014; leg. P.J. Schwendinger & S. Huber.

Paratypes: MHNG-ARTO-0028318 and MHNG-ARTO-0028319 (sample MT-14/10); 1 male (matured 1.IX.2014) and 1 female (allotype, MHNG-ARTO-0028319); collected together with the holotype. – BRCM, MHNG-ARTO-0028321 and MHNG-ARTO-0028322; 2 males (matured 7.X.2014, 18.IX.2016) and 1 female (sample MT-14/04);

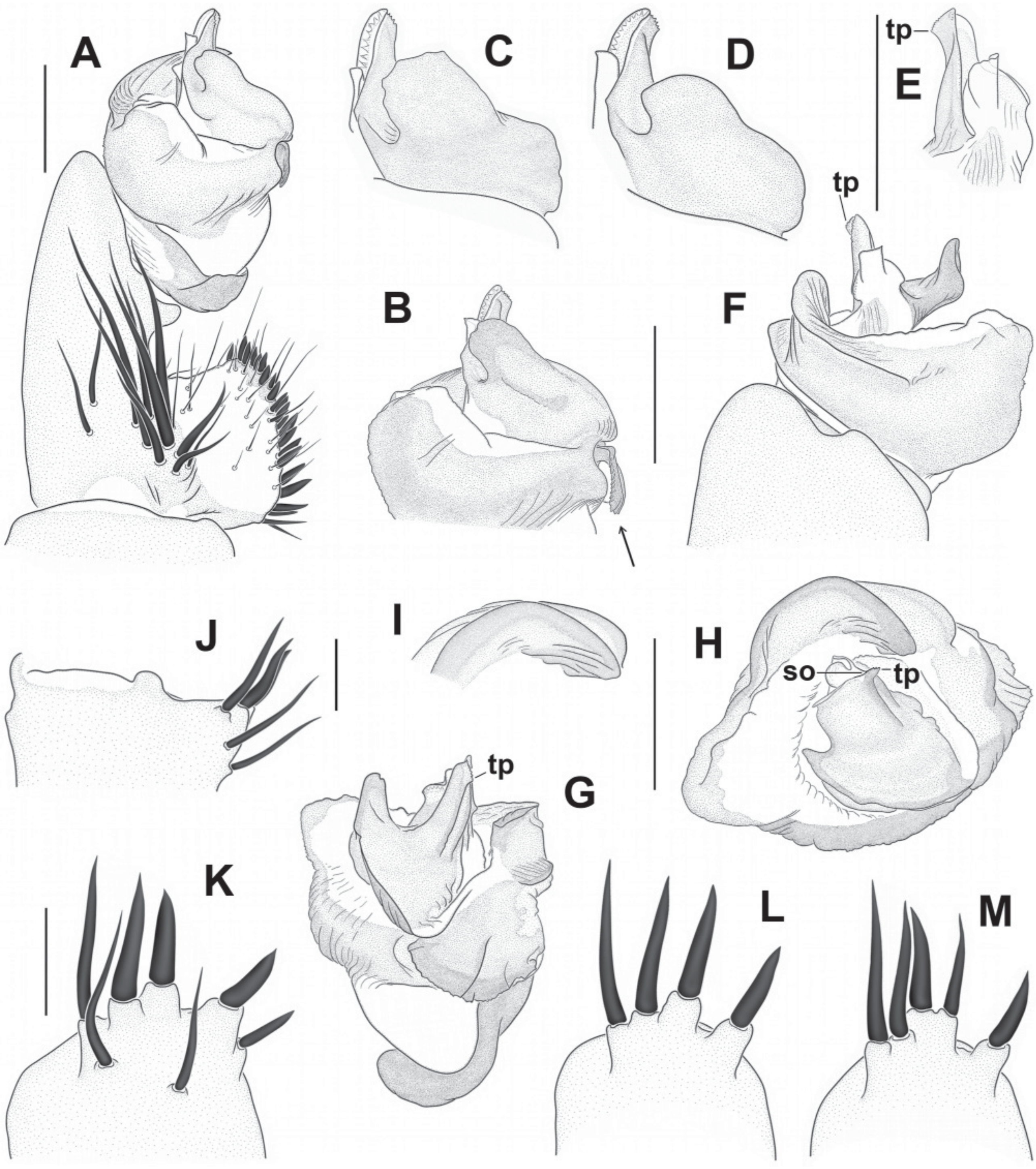
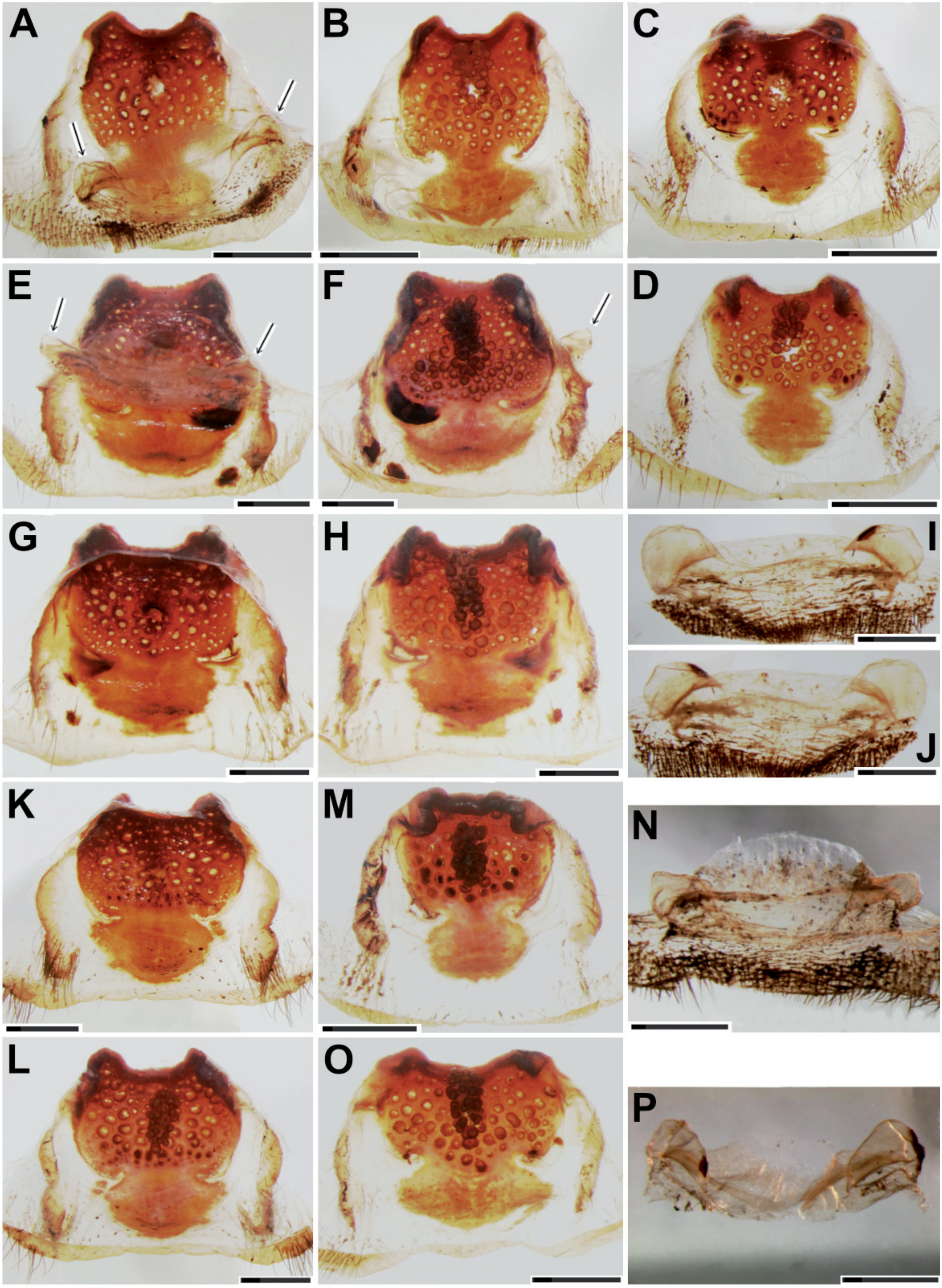


Fig. 10. *Liphistius ferox* sp. nov., left palps of four males; holotype (A-B, E-K), male from Naw Bubaw, matured IV.2019 (C, M), male from Thandaung Gyi, matured 7.X.2014 (D), male from Thandaung Gyi, matured 18.IX.2016 (L). (A) Tarsus and palpal organ, ventral view. (B) Distal part of palpal organ, ventral view; bent and adpressed proximal edge of tegulum indicated by arrow. (C-D) Embolus complex, ventral view. (F) Embolus proper, prodorsal view. (G) Palpal organ, retroventral view. (H) Palpal organ, distal view (dorsal side up). (I) Dorsal part of contrategulum, distal and slightly prolateral view. (J) Distal part of tarsus, ventral view. (K-M) Same, retrolateral and slightly proximal view. Scale lines 1.0 mm (A; B, F-G; C-E; H-I; J; K-M). Abbreviations: tp - triangular distal protrusion of longitudinal rib on sclerotised part of embolus proper; so - angular retrolateral side of sperm duct opening.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Myanmar, Kayin State, along road from Thandaung Lay to Thandaung Gyi, 850 m (19°01'54"N, 96°38'29"E); 12./14./16.VII.2014; leg. P.J. Schwendinger & S. Huber. – MHNG-ARTO-0028323 to MHNG-ARTO-0028333, BRCM (samples MT-14/07); 1 male (matured 10.IX.2014) and 11 females (samples MT-14/05 and MT-14/06); along same road, 1150 m (19°04'15"N, 96°40'37"E); 12./14./16.VII.2014; leg. P.J. Schwendinger & S. Huber. – MHNG-ARTO-0028335 to MHNG-ARTO-0028340 (samples O-234A and MT-14/07); 1 male (matured IV.2019) and 5 females; Myanmar, Kayin State, Mt Naw Bubaw (19°04'39"N, 96°41'12"E), 1350-1410 m; 12./14.VII.2014; leg. P.J. Schwendinger & S. Huber.

Other material: MHNG (sample MT-14/07); 3 juveniles; Myanmar, Kayin State, Mt Naw Bubaw (19°04'39"N, 96°41'12"E), 1350-1410 m; 12./14. VII.2014; leg. P.J. Schwendinger & S. Huber. – BRCM; 1 female; Myanmar, Kayin State, on roadside about 7 km E from border between Bago Region and Kayin State, Thaundaung Gyi Township (19°01'56.3"N, 96°38'39.2"E), 850 m; 6.VIII.2018; leg. H. Ono. – BRCM; 1 female; Myanmar, Kayin State, 21 miles E of Taungoo, Thaundaung Gyi Township, near Taw Pya Gyi Village (19°02'35.5"N, 96°39'38.1"E), 940 m; 6.VIII.2018; leg. H. Ono.

Etymology: The Latin adjective "ferox" (= wild, ferocious) refers to the exceptionally aggressive behaviour of these spiders.

Diagnosis: Distinguished from all other species of the *birmanicus*-group by the combination of very large size and uniformly dark body colouration in both sexes. Genital morphology similar to that of *L. tung*

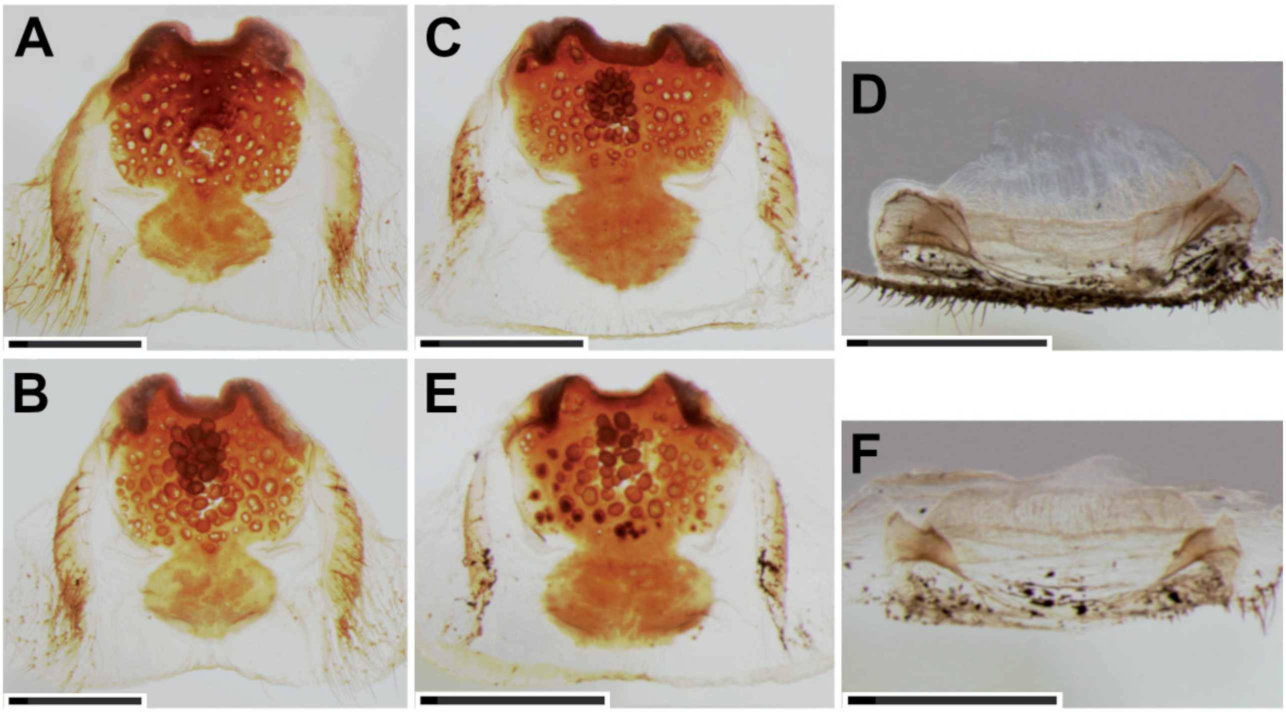

Fig. 12. *Liphistius ferox*, vulvae of three females; dorsal view (A, D, F), ventral view (B-C, E). (A-B) Thandaung Gyi, moulted 26.X.2014; vulval plate. (C) Thandaung Gyi, moulted 11.1.2015; vulval plate. (D) Same female; isolated uterus externus. (E) Thandaung Gyi, moulted 6.XII.2014; vulval plate. (F) Same female; isolated uterus externus. Scale lines 1.0 mm.

Fig. 11. *Liphistius ferox*, vulvae of seven females; dorsal view (A, C, E, G, I, K, N, P), ventral view (B, D, F, H, J, L-M, O). (A-B) Thandaung Gyi, moulted 21.VII.2015; with uterus externus attached (in B hidden on other side). (C-D) Thandaung Gyi, moulted 8.1.2015. (E-F) Thandaung Gyi, moulted 15.VII.2015; with uterus externus attached (in F only pocket of one side visible). (G-H) Thandaung Gyi, moulted 16.VII.2015; vulval plate. (I-J) Same female; isolated uterus externus. (K-L) Naw Bubaw, moulted 26.II.2015. (M) Allotype; Thandaung Lay, moulted 10.VII.2015, vulval plate. (N) Same female; isolated uterus externus. (O) Thandaung Gyi, moulted 20.IX.2014; vulval plate. (P) Same female; isolated uterus externus. Arrows indicating paired lateral pockets of still attached membranous uterus externus. Scale lines 1.0 mm.

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sp. nov., i.e. both species possessing a long para-embolic plate in males (Fig. 10A-D and Fig. 8A, H-I; short in other species of the *birmanicus*-group) and lacking anterolateral processes on the ventral side of the poreplate in females (Figs 11-12 and Fig. 9). Different from *L. tung* sp. nov. by much larger body size (CL in males 11.47-12.67, CW 10.45-11.47 versus 6.30-6.70 and 5.70-6.26 in *L. tung* sp. nov.); sclerotised embolus part with only 2 longitudinal ribs reaching apex, one of them with a triangular distal protrusion pointing retrodorsad (Fig. 10E-H); retrolateral side of sperm duct opening angular in distal view (Fig. 10H; in *L. tung* sp. nov. with 4-5 normal ribs and concave retrolateral side of sperm duct opening, Fig. 8C-D, F-I); proventral process of contrategulum relatively larger than in *L. tung* sp. nov. (Fig. 10H cf. Fig. 8C-D); tibial apophysis only slightly set back from distal margin of tibia (Fig. 10J; much further set back in *L. tung* sp. nov., Fig. 8B). Females different from those of *L. tung* sp. nov. by anterior lobes of poreplate folded ventrad and more widely separated from each other (Figs 11-12 cf. Fig. 9).

Description of male (holotype): *Colour in alcohol* (much darker in life, as in Fig. 3A): Mostly uniformly brown, ventral side of body slightly lighter than dorsal side; prolateral part of palpal coxae, proximal part of chelicerae and membranous cuticle of opisthosoma light brown; all opisthosomal tergites uniformly dark brown; legs and palps without annulations; palpal tarsus and sclerites of palpal organ dark brown; eye mound very dark.

Setae on carapace: Few short, blunt-tipped setae on coxal elevations and on lateral margin of carapace; strongest setae on posterior margin, longest setae on and behind eye mound; no setae anterior to fovea.

Cheliceral teeth: 12 small teeth of different sizes on promargin of each cheliceral groove.

Scopula: Distally divided by a short glabrous longitudinal stripe and proximally with a median row of stiff bristles on all tarsi; distinct but weak in distal 3/4 of ventral side of leg tarsus I; equally weak and covering distal 4/5 of tarsus II; slightly denser and more clearly outlined, covering 5/6 of tarsi III-IV.

Tarsal claws: Paired claws with 4-5 teeth on tarsi I-III, 3-5 teeth on tarsus IV; unpaired claw of tarsus I with 1 denticle, of tarsi II-III with 1-2 denticles, of tarsus IV bare.

Palp: Tibial apophysis of moderate size, widely triangular in ventral view, slightly set back from distal margin of tibia (Fig. 10J), carrying 5 apical megaspines: ventral one rather weak, longer than the others and ending in a filiform tip, following 3 megaspines shorter and stronger, dorsalmost megaspine shortest and weakest; 3 ventral megaspines situated on a common base, 2 dorsal ones each on a separate base (Fig. 10K; see also Variation). Distal margin of tarsus slightly invaginated (Fig. 10F). Paracymbium quite short, somewhat quadrangular, longer than wide in ventral view, moderately deep, its distal side only indistinctly conical, no retrolateral-proximal heel (Fig. 10A); cumulus developed as a slightly elevated and quite long, low mound carrying a densely packed group of 9 long strong bristles (Fig. 10A). Subtegulum with indistinct but recognizable apophysis (Fig. 10A, G). Tegulum wide, with slightly bent, adpressed, moderately serrate proximal edge (Fig. 10B, G); distal margin not elevated, overhung by unpigmented retroventral margin of embolus complex; with a short subdistal ridge (not to be misinterpreted as an elevated distal tegular edge) and two longer more proximal ridges (Fig. 10G). Pigmented bridge between tegulum and contrategulum on retrodorsal side of palpal organ well developed (Fig. 10G-H). Contrategulum with quite large (in comparison with other species of the same group), conical proventral process ending in a rounded apex in distal view (Fig. 10H); a few wrinkles on dorsal surface and a well-developed proximal ledge on retrodorsal side (Fig. 10F, H-I); distal edge of contrategulum widely arched and carrying pronounced ridges below narrowly rounded dorsal apex (Fig. 10H-I). Para-embolic plate large, toungue-shaped, inclinded prodorsad, its widely rounded apex with a small indentation (Fig. 10A-B; see also Variation). Retroventral edge of embolus complex elevated into a short, widely arched keel (Fig. 10A-B). Embolus proper with sclerotised part strengthened by only 2 longitudinal ribs reaching apex and carrying tiny denticles distally, ventral rib with a triangular distal protrusion pointing prodorsad (Fig. 10E-H); retrolateral side of sperm duct opening (i.e. inner side of sclerotised embolus part) angular in distal view (Fig. 10H; concave in other congeners, e.g. Fig. 15A); membranous part of embolus proper distinctly shorter than sclerotised part, both narrowly divided; at base of membranous embolus part a fairly long and strongly pigmented area with numerous longitudinal wrinkles, its distal margin strongly oblique; embolic folds short and indistinct (Fig. 10E-F).

Measurements: Total length 28.97; CL 12.59, CW 11.81; opisthosoma 13.28 long, 8.97 wide; eye mound 1.37 long, 1.80 wide; palpal coxa 3.62 long, 2.50 wide; labium 1.12 long, 2.24 wide; sternum 6.03 long, 3.45 wide (1.72 on ventral surface); palp 21.90 long (6.21 + 4.05 + 7.76 + 3.88); leg I 35.09 long (9.66 + 5.17 + 7.41 + 8.88 + 3.97); leg II 36.72 long (9.83 + 5.34 + 7.67 + 9.74 + 4.14); leg III 39.57 long (9.83 + 5.43 +7.93 + 11.55 + 4.83); leg IV 48.45 long (12.07 + 5.69 + 9.57 + 15.09 + 6.03).

Description of female (allotype): *Colour in alcohol* (distinctly darker in life, as in Fig. 3B): Mostly dark brown. Eye mound and anterior margin of carapace very dark. Chelicerae dark brown distally, orange-coloured proximally. Carapace without pattern; legs and palps without annulation. Tergites and membranous cuticle of opisthosoma almost equally dark greyish brown. Ventral side of palpal coxae, distal part of labium, ventral plates

of opisthosomal segments II-III, and spinnerets orange-coloured. Sternum greyish orange-coloured.
Setae on carapace: Mostly as in male, but setae on posterior margin longer and thinner; 3+4 setae (some very small) in two parallel rows anterior to fovea.
Cheliceral teeth: 14 strong teeth on promargin of right cheliceral groove, 15 on left groove.
Claws: Palpal claws with 2 and 3 worn denticles. Paired tarsal claws of legs I-II with 3 teeth, of leg II with 4 teeth, of legs III-IV with 3-4 teeth; unpaired claw of leg I with 1 denticle, of leg II with 2, of leg III with 1-2 denticles, of leg IV with 0-1 denticle. All tarsi without scopula.
Vulva (Fig. 11M-N): Uterus externus with a pair of quite large lateral pockets on dorsal side (see Fig. 11N; see also Figs 11I-J, P, 12D, F for other females). Vulval plate slightly wider than long; its lateral folds well-developed and carrying several hairs. Anterior margin of poreplate thick, with a pair of narrow anterior lobes bent ventrad and separated by a shallow, mostly horizontal invagination (but see Variation); no anterolateral processes; posterior margins of poreplate not bulged; CDO small, situated in centre of poreplate; receptacular cluster racemose, distinctly longer than wide, not reaching anterior margin of poreplate. Posterior stalk large and widely oval, narrower than poreplate.
Measurements: Total length 35.34; CL 15.26, CW 13.97; opisthosoma 15.34 long, 13.28 wide; eye mound 1.75 long, 2.13 wide; palpal coxa 5.34 long, 3.79 wide; labium 1.81 long, 3.45 wide; sternum 7.93 long, 4.31 wide (2.59 on ventral surface); palp 25.95 long (8.19 + 5.00 + 6.55 + 6.21); leg I 31.46 long (9.83 + 6.03 + 6.38 + 6.81 + 2.41); leg II 32.93 long (10.17 + 6.21 + 6.38 + 7.41 + 2.76); leg III 35.94 long (10.34 + 6.55 + 6.72 + 8.97 + 3.36); leg IV 47.94 long (13.10 + 6.90 + 9.31 + 13.97 + 4.66).

Variation: For carapace measurements and prefoveal setae counts see Table 1. All spiders examined have well-developed AME. Large and small specimens of both sexes lack annulations on legs and palps. In all males examined the extent and density of the scopulae are the same; all have a very similar shape of their proventral contrategular process, all have only two longitudinal ribs reaching the apex of the sclerotised embolus part (one of the ribs with a triangular distal protrusion), and all have an angular inner side of the sclerotised embolus part. The ventral part of the tibial apophysis carries a group of 3-4 rather long apical megaspines on a common base, the dorsal part a group of 1-2 rather short megaspines on a separate base; both bases are separated by a distinct invagination (Fig. 10K-M). The indistinctly elevated cumulus carries 6-9 long and very strong bristles (some of them almost as thick as the megaspines on the tibial apophysis). All but one male (matured 1.IX.2014) have a more or less distinctly developed, short subdistal ridge on the tegulum that can be misinterpreted as an elevated distal margin (Fig. 10G). There is some variation in the number of ridges on the surface of the tegulum and in their lengths. The distal margin of the large para-embolic plate is widely rounded or has one or more angles in most specimens (Fig. 10C-D); it is slightly invaginated on the left palp of the holotype (Fig. 10A-B). The pigmented area at the base of the membranous embolus part has a distal margin that varies between straight, slightly invaginated, slightly inclined and asymmetrically angular. Variation in details of the male palp is illustrated in Fig. 10. Variation in the shape of the vulval plate is considerable and shown in Figs 11-12. The anterior lobes of the poreplate (which are mostly quite small) are completely bent ventrad, towards the receptular cluster, in the allotype (Fig. 11M), less distinctly so in other females examined (Figs 11B, D, F, H, L, O, 12B-C, E), and the invagination between these lobes is more or less straight and horizontal, but always wide and shallow; all females lack anterolateral processes on the poreplate; the posterior margins of the poreplate are mostly indistinct, bulging only in one female and there probably deformed on one side (Fig. 11F), therefore not typical for the species. The receptacular cluster is much longer than wide in most females, in one specimen even reaching the anterior margin of poreplate (Fig. 11H); only in one of the females examined is the receptacular cluster only slightly longer than wide (Fig. 12C). The posterior stalk usually has a short anterior constriction, except for one female which obviously has deformed posterior poreplate margins (Fig. 11E-F; the same appears to be the case, but only on one side and therefore probably also representing a deformation or an excessive sclerotisation, in a second female, Fig. 11G-H). The shape of the posterior stalk varies from widely oval (e.g. Fig. 11M) to narrowly (e.g. Fig. 12C) or widely axe-blade-shaped (e.g. Fig. 11O). The lateral folds of the vulval plate carry few to many hairs.

Relationships: The new species possesses unique and autapomorphic characters on the sclerotised part of its embolus proper, i.e. only two longitudinal ribs, one of them with a triangular distal protrusion (Fig. 10E-H); the retrolateral surface of sperm duct opening compressed and angular in distal view (Fig. 10H). It clearly is not very closely related to *L. birmanicus*, despite close geographical proximity and similar body size. Similarities in the morphology of male and female copulatory organs (especially the presence of a large para-embolic plate and the absence of anterolateral processes on the poreplate) indicate a much closer relationship between *L. ferox* sp. nov. and *L. tung* sp. nov. than between *L. ferox* sp. nov. and *L. birmanicus*. However, the geographical separation of *L. ferox* sp. nov. and *L. tung* sp. nov. by about 400 km severely challenges a possible sister relationship between these two species.

Distribution: The type specimens were collected along the road from Thandaung Lay (also called Pathi

Village) in the lowlands at 140 m altitude, past a station at 850 m, to Thandaung Gyi Village at about 1150 m, and further up to below the summit of Mount Naw Bubaw at 1350-1410 m (Fig. 1). This is the largest known altitudinal range for any *Liphistius* species. The paralectotypes of *L. birmanicus* from the Biapo Mountains near Leiktho (spelled "Leito" in Fea, 1896), about 15 km north of Thandaung Gyi and Naw Bubaw, presumably also belong to *L. ferox* sp. nov. (see Remarks under *L. birmanicus*).

Biology: The specimens examined were collected from earth banks on both sides of a road running through secondary forest and evergreen hill forest. All burrows were simple and unbranched, closed by a single trapdoor. The largest trapdoor in females was 4.3 cm long and 6.5 cm wide, those of penultimate males 2.8-3.5 cm long and 3.9-5.0 cm wide. Most burrow entrances had 6-8 signal lines attached, the longest measuring 8 cm, a single burrow was equipped with nine signal lines.

Males matured in captivity between early September and early October, only a few months after being captured. The maturation date in June 2019, after almost five years of captive rearing, is not likely to correspond to conditions in nature. No egg cases were found in mid-July; they are presumably constructed in December (as in conspecific species in northern Thailand). Large females usually moulted once per year, between July and February; smaller females moulted for a second time between March and May. Two spiders, a female from Thandaung Gyi at 1150 m and a juvenile male from Naw Bubaw at 1400 m, carried ectoparasitic mites of the genus *Ljunghia* (see Halliday & Juvara-Bals, 2016) on them. The mites left bite marks on the carapace and chelicerae (in the proximal and distal portions) as observed in other *Liphistius* spp., and additionally also on the soft and flexible membranes between coxae, trochanters and femora of the palps and of the first pair of legs. The latter has not been observed in other such cases. Previously there was only evidence that these mites pierce strongly sclerotised parts of the spider exoskeleton to feed, an unusual behaviour so far unexplained.

Liphistius birmanicus Thorell, 1897

Figs 1, 3D-I, 13-14

Liphistius birmanicus Thorell, 1897: 162-169 (description of females). – Pocock, 1900: 156 (English summary of Thorell's lengthy original description in Latin). – Bristowe, 1933: 1025, figs 6, 7b, 8d, 9a (comparison and illustration of characters of female). – Bristowe, 1938: 661 (misidentification; description of immature male of an unnamed *Liphistius* species from Moulmein). – Bristowe, 1975: 166-167 (new report based on misidentied specimen belonging to *L. bristowei* Platnick & Sedgwick, 1984). – Haupt, 1983: 280, figs 5c, 6c (illustration of vulval plate of female erroneously referred to as the holotype and later selected as the lectotype by Platnick & Sedgwich, 1984). – Platnick & Sedgwick, 1984: 8-10, figs 7-13 (designation of lectotype; description of incorrectly identified males and females belonging to *L. pyinoolwin*). – Schwendinger, 1990: 331-332, figs 1-4 (illustration of copulatory organs of incorrectly identified male and female *L. pyinoolwin* specimens in AMNH).

Types: MCSNG; female lectotype of *L. birmanicus*; Myanmar, Kayin State, Yadò (spelled Ja-dò in Fea, 1896: 457-458, fig. 149), in montibus Carin Asciuii Chebà, 1200-1300 m; 1885-1888; leg L. Fea. – MCSNG; 2 immature paralectotypes of *L. birmanicus*; Myanmar, Kayin State, in montibus Carin Chebà sive Biapò, 1000-1200 m; 1885-1888; leg. L. Fea. Not examined.

Remarks: Leonardo Fea (1852-1903) collected the types of *L. birmanicus* between December 1887 and January 1889 (Fea, 1897: 391). The original description states that the two juvenile specimens (the paralectotypes from Biapò, given as situated at 900 m altitude in Fea, 1896: 391) have entirely dark legs and palps ("toti nigricantes vel sordide fusci"), whereas the adult female (the lectotype from Yadò) has a carapace that is partly brick-red and partly dark ("cephalothorax praesertim in parte thoracica paullo testaceo-fusco-variatus") as well as bicoloured legs and palps: mostly dark ("ad maximam partem… nigricantes vel sordide fusci"), with dark brick-red femora and dark brick-red annulations on patellae, tibiae and metatarsi ("patellae, tibiae et metatarsi, et etiam femora supra, vestigiis annuli vel annulorum binorum testaceo-fuscorum praedita"; Thorell, 1897: 166). This indicates that the paralectotypes from Biapò are not conspecific with the lectotype from Yadò, because small females from Yadò have bicoloured legs and palps as do the corresponding large females (Fig. 3G cf. Fig. 3E-F, H-I). It is quite likely that the paralectotypes belong to *L. ferox* sp. nov., because Biapò is much closer to Thandaung Gyi than to Yadò (Fea, 1896: pl. 3), and because *L. ferox* sp. nov. has an exceptionally large vertical distribution (from 140 m to 1400 m). It presumably also has a correspondingly large geographical range.

New material: MHNG, BRCM (sample MT-14/33); 6 males (matured 24.IX.2014, 30.X.2014, 15.XI.2014, 27.I.2016, 28.II.2016, 9.XI.2017) and 10 females; Myanmar, Kayin State, farmland and rice fields in the southern part of the Yado (= Yadò) Valley, near the southernmost village called "Preisciò" in Fea (1896: 458, pl. 3), 19°19'50"N, 96°48'29"E, 1100 m; 18.-19. VI.2014; leg. P. Schwendinger & S. Huber. – MHNG (sample MT-14/35); 1 female; Myanmar, Shan State, roadside about 3 km NE of the northern end of the Yado Valley, 19°23'20"N, 96°49'29"E, 1130 m; 19.VI.2014; leg. P. Schwendinger.

Diagnosis: Quite large spiders (CL in males 7.79-9.50, in the largest female 14.73, CW in males 7.29-9.45, in the largest female 13.27) with parts of legs, palps and carapace (especially pars cephalica) of females and late instar juvenile males yellow or orange-coloured (Fig. 3E-I; Xu *et al*., 2021: fig. 2I). Palp of male similar to that of much smaller *L. pinlaung* male, both possessing a distad-directed proventral contrategular process (Fig. 13D, F and Fig. 15C). Different from *L. pinlaung* by a more oval palpal organ in distal view (Fig. 13A cf. Fig. 15A), a wider and shorter pigmented area at base of membranous embolus part (Fig. 13D cf. Fig. 15C) and a widely arched retrolateral paracymbium side lacking a proximal heel (Fig. 13H cf. Fig. 15G). Vulval plate distinguished from that of uniformly dark brown *L. pinlaung* female by anterior lobes of poreplate closer to each other and posterior stalk more angular in shape (Fig. 14 cf. Fig. 16).

Additions to description: Males mostly with uniformly dark brown sclerites (Fig. 3D; Xu *et al*., 2021: fig. 2J), apart from an orange-coloured area in posterior portion of cephalic carapace part in some males (see Variation), and with weak scopulae on tarsi I-II, slightly denser ones on tarsi III-IV, covering only distal 1/2 of tarsus I, distal 2/3 of tarsus II, distal 3/4 of tarsus III and distal 4/5 of tarsus IV in most males (see also Variation). Male palp with moderately deep tibial apophysis (depth/length ratio ~ 1.8), relatively small and triangular in ventral view, only slightly set back from distal margin of tibia (illustrated as distinctly set back in Xu *et al*., 2021: fig. 8A), carrying four long pointed apical megaspines; distal margin of palpal tarsus widely but shallowly invaginated, with a small knob-shaped process on distodorsal corner (Fig. 13C); paracymbium short, somewhat globular in ventral view, its retrolateral surface widely and evenly arched, without a proximal heel (Fig. 13H); cumulus slightly elevated, carrying a dense group of several long strong bristles close to each other and arranged in two rows (Fig. 13H); subtegulum without apophysis (Fig. 13E); tegulum large, its distal margin not elevated, its proximal edge widely arched, finely dentate, bent and overhanging membranous area below it (Fig. 13E-G); contrategulum with proventral process conical and inclined distad (almost parallel to axis of embolus proper), its apex narrowly rounded (Fig. 13A, D-F; Xu *et al*., 2021: fig. 8D-F); a few oblique wrinkles on dorsal surface (Fig. 13D) and a pronounced proximal ledge on retrodorsal side (Fig. 13A, D, G); distal edge of contrategulum moderately wide, with a few ridges and a narrowly rounded dorsal apex (Fig. 13A-B), prolateral part of edge elevated and developed as a distinct keel (Fig. 13D); para-embolic plate short, about as long as retroventral edge of embolus complex and separated from it by a shallow invagination (Fig. 13E-F); embolus proper with sclerotised part strengthened by 5-6 longitudinal ribs reaching apex and carrying denticles distally, narrowly divided from distinctly shorter membranous embolus part; short area at base of membranous part strongly pigmented, with numerous longitudinal wrinkles, its distal margin wide and slightly oblique (Fig. 13D). Females with few to several hairs on lateral folds of vulval plate; poreplate as long as wide (Fig. 14N-O), or wider than long (Fig. 14A-M), posteriorly wider than anteriorly, with a pair of rather indistinct (Fig. 14L) to very wide, rounded lobes (Fig. 14N-O) on anterior margin, and with a small pair of anterolateral processes; CDO fairly small, round, quadrangular or triangular (Fig. 14A, D, G, J, N); receptacular cluster racemose, slightly to distinctly longer than wide, not reaching anterior margin of poreplate (Fig. 14B-C, E-F, H-I, K-M, O; Xu *et al*., 2021: figs 9-10); posterior stalk narrower than poreplate, axe-blade-shaped, with posterior margin widely arched (Fig. 14G-I, L) or trapezoidal, in the latter case posterior margin straight and narrower than median part of posterior stalk (Fig. 14A-F, J-K, M-O); transition from poreplate to posterior stalk usually distinctly constricted (see also Variation).

Variation: For carapace measurements and prefoveal setae counts see Table 1. In all specimens the AME are distinctly developed. The number of setae anterior to the fovea ranges 11-25 in males and it is over 40 (continuous with other setae on pars cephalica of carapace) in all females. Three males have a distinct orange-coloured area in the posterior portion of the pars cephalica; in one male this area is only indistinct; in the remaining two males it is not visible. In the female from the Shan State the carapace has a larger orange-coloured area than in females from Yado, with the W-shaped dark marking behind its eye mound only continuous in the middle, the lateral parts developed as series of dark spots. In males the extent of the tarsal scopulae is slightly variable: I - 1/2-2/3, II - 2/3-3/4, III - 3/4-4/5, IV - 4/5. Variation in details of the male palp is given in Fig. 13. In one of the males examined the tibial apophysis is slightly further set back from the distal margin of the palpal tibia than in other males, but not as far as illustrated in Xu *et al.,* 2021: fig. 8A. Variation in the shape of the vulval plate is considerable (see Fig. 14; Xu *et al*., 2021: figs 9-10). The anterior margin of the poreplate is indistinctly (Fig. 14J-K) to deeply invaginated (Fig. 14N-O); the poreplate is usually clearly wider than long (Fig. 14A-M), in one female as long as wide (Fig. 14N-O); the anterior lobes of the poreplate are indistinct (Fig. 14J-K) to very distinct (Fig. 14N-O); the CDO is small (Fig. 14A) to very small (Fig. 14N), round in most females, developed as a longitudinal slit or triangle in two specimens (Fig. 14D, G); the pores on the dorsal side of the poreplate are quite large (Fig. 14A, J) to small (Fig. 14N); the lateral margins of the poreplate vary from widely arched (Fig. 14J-K) to almost straight

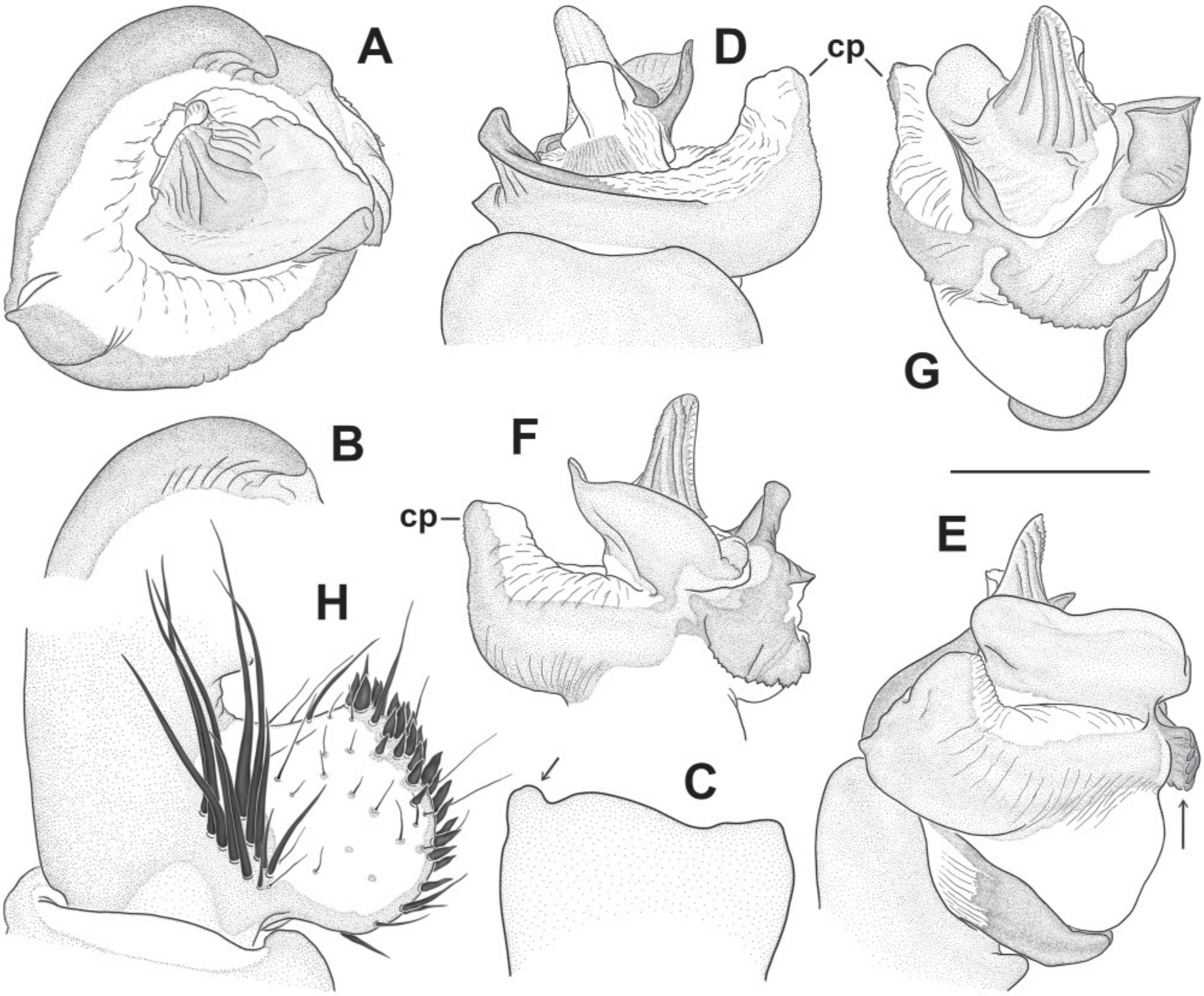

Fig. 13. *Liphistius birmanicus*, left palps of two males from the type locality; male matured 27.I.2016 (A-B), male matured 15.XI.2014 (C-H). (A) Palpal organ, distal view (dorsal side up). (B) Dorsal part of contrategulum, distal and slightly prolateral view. (C) Distal part of tarsus, prodorsal view; knob-shaped process on distodorsal corner indicated by short arrow. (D) Palpal organ and distal margin of tarsus, prolateral view. (E) Same, ventral view; bent proximal edge of tegulum indicated by long arrow. (F) Distal part of palpal organ, retroventral and slightly proximal view. (G) Palpal organ, retrolateral view. (H) Proximal part of tarsus, ventral view. Scale line 1.0 mm. Abbreviation: cp - proventral contrategular process.

Fig. 14. *Liphistius birmanicus*, vulval plates (all taken from exuviae) of ten females from the type locality (A-M) and of one female from the Shan State (N-O); dorsal view [A, D (with uterus externus attached), G, J, N], ventral view (B-C, E-F, H-I, K-M, O). (A-B) Moult of 6.II.2021. (C) Moult of 27.XII.2020. (D) Moult of 20.XI.2021. (E) Moult of 19.II.2021 (same specimen as D). (F) Moult of 21.II.2021. (G-H) Moult of 25.XII.2020. (I) Moult of 14.V.2021. (J-K) Moult of 20.III.2021. (L) Moult of 26.X.2017. (M) Moult of 24.VIII.2017. (N-O) Moult of 2.IV.2018. Arrows indicating paired lateral pockets of membranous uterus externus. Scale lines 1.0 mm.

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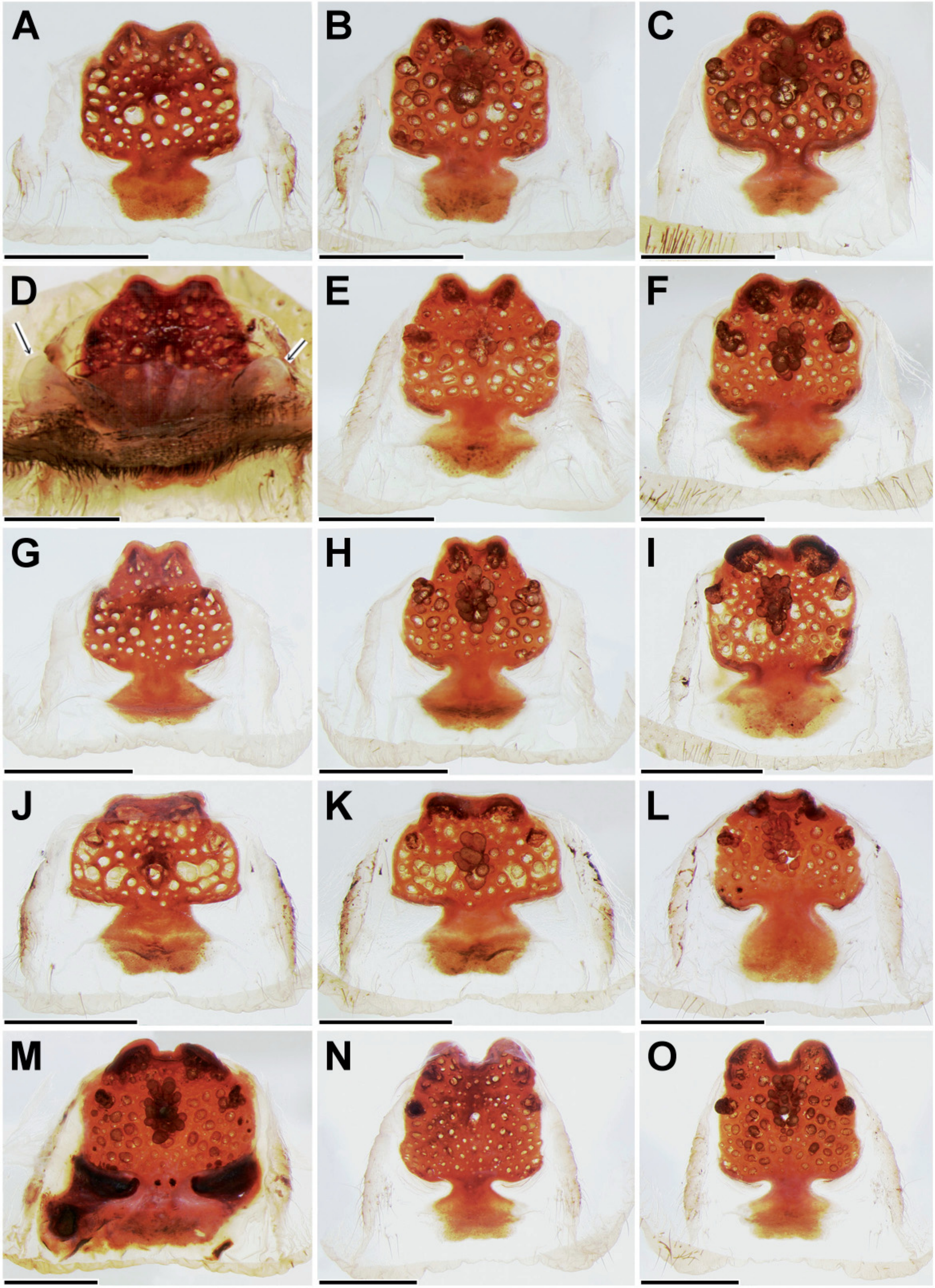
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(Fig. 14N-O); the posterior stalk is constricted at the base, trapezoidal, posteriorly narrower than medially in most females, axe-blade-shaped in two specimens (Fig. 14G, L), or widely connected to the poreplate without a constriction in another specimen (Fig. 14M, presumably deformed). It should be noted that almost all vulval plates had more or less distinct dark soiling, especially along the posterior margins of the poreplate (removed by forceps in the illustrated vulvae). These are remnants of old cuticle, and the older the spider, the denser and thicker these remaining fragments of old cuticle are. In one of the large females this presumably caused deformation at the posterior poreplate margin and at the base of the posterior stalk (Fig. 14M; see also Xu *et al*., 2021: fig. 9F, I). Tiny fragments of old cuticle are also visible inside the lateral folds of the vulval plate in some specimens (e.g. Fig. 14B, I-M). The anterolateral processes on the ventral side of the poreplate are always present, but not always very pronounced (Fig. 14B).

Relationships: Males of *L. birmanicus* and *L. pinlaung* share a strongly distad-directed proventral process of the contrategulum, which is unique within the genus and indicates a close phylogenetic relationship (in addition to geographical proximity) between these two species despite pronounced differences in body size and colouration. Judging from the body colouration of females and juveniles and from vulval plate morphology it is quite likely that *L. birmanicus* is even more closely related to *L. hpruso* than to *L. pinlaung*. However, as long as the male of *L. hpruso* remains unknown or until molecular data of these three species are available for comparison, the relationship between these species cannot be confirmed. For a morphological distinction between *L. birmanicus* and *L. hpruso* see Taxonomic remarks under the latter species.

Distribution: *Liphistius birmanicus* is known from the mountainous area where the Kayin State, the Kayah State and the Shan State meet (Fig. 1). The report of a damaged immature *L. birmanicus* male from Moulmein (= Mawlawmyine) by Gravely (1915: 260; see also Bristowe, 1938: 661) is most likely incorrect. *Liphistius* males and females collected at two localities near Mawlawmyine belong to the *bristowei*-group.

Biology: The specimens examined were collected from earth banks on the sides of rice fields, vegetable fields and ditches. Most burrows were simple and unbranched, closed by a single trapdoor; one penultimate male had two doors. The largest trapdoor in females was 3.5 cm long and 5.1 cm wide, those of penultimate males 2.0-2.4 cm long and 3.2-3.6 cm wide. Burrow entrances had 6-8 relatively thick and short signal lines attached, the longest measuring 6 cm.

The first three males matured in captivity between early September and mid-November, only a few months after being captured. Two maturations of males, in January and February, occurred about 1.5 years after capture and presumably do not correspond with such events in nature. No egg cases were found in the field in late June; they are presumably constructed in December (as in conspecific species in northern Thailand). Most large females moulted twice per year.

One of the males examined (matured 30.X.2014) had parasitic mites (*Ljunghia* sp.) sitting on its carapace (especially in the fovea), on the membranous cuticle behind the carapace, on opisthosomal tergites I-II (where mite exuviae were attached) and on the labium and sternum. As usual, the mites left numerous bite marks on the carapace, but not on the chelicerae (or on any other body parts).

Liphistius hpruso Aung, Xu, Lwin, Sang, Yu, Liu, Liu & Li, 2019

Fig. 1

Liphistius hpruso Aung *et al*., 2019: 32-34, fig. 3A-E (description of females).

Types: CBEE; female holotype (XUX-2018-151) and 1 female paratype (XUX-2018-152); Myanmar, Kayah State, Loikaw District, Hpruso, Dokhule, 19.41°N, 97.10°E, 1157 m; 17.VII.2018; D. Li, F.X. Liu, X. Xu & L. Yu. Types not examined; no new material available.

Taxonomic remarks: Judging from illustrations in the original description, this species appears to be closely related to *L. birmanicus* and *L. pinlaung* from which it can be distinguished by a distinctly longer and narrower posterior stalk of the vulval plate (Aung *et al*., 2019: fig. 3B-E cf. Figs 14, 16). The body colouration of the female holotype (Aung *et al*., 2019: fig. 3A; however, carapace colouration given as “light brown” and leg colouration as “brown”, see p. 33 in same paper) is similar to that of young (not fully grown) females of *L. birmanicus* (Fig. 3G). In addition to close geographical proximity, this indicates a very close phylogenetic relationship between *L. hpruso* and *L. birmanicus*. We thus assume that the not yet known male of *L. hpruso* also possesses a distad-directed proventral contrategular process.

Distribution: This species is only known from its type locality (Fig. 1), about 30 km to the east of the known localities of *L. birmanicus* and roughly at the same altitude.

Liphistius pinlaung Aung, Xu, Lwin, Sang, Yu, Liu, Liu & Li, 2019

Figs 1, 3C, 15, 16A-J

Liphistius pinlaung Aung, Xu, Lwin, Sang, Yu, Liu, Liu & Li, 2019: 34-37, figs 4-5 (description of males and females).

Types: CBEE; male holotype (XUX-2018-164), 1 male and 5 female paratypes (XUX-2018-162, 167, 169, 169A, 169B, 169J); Myanmar, Shan State, Pinlaung Township, about 14 km to Pinlaung from Pekon, 20.02°N, 96.79°E, 1410 m; 19.VII. 2018; leg. D. Li, F.X. Liu, X. Xu and L. Yu.

New material: MHNG, BRCM (sample MT-14/31); 10 males (matured 20.VI., 21.VI., 28.VI., 20.VIII., 17.IX., 23.IX.2014, 23.XI., 2x end of XII.2014, 4.VII.2015) and 10 females; Myanmar, Shan State, 1.5 km W of Pinlaung, near Wingabar Taung and Tong Htiwaw (= Taung Hti Bwar) Temple, 20°04'29"N, 96°46'13"E, 1470 m; 16.VI.2014; leg. P. Schwendinger & S. Huber.

Diagnosis: Medium-sized species with uniformly dark body in both sexes. Copulatory organs quite similar to those of *L. birmanicus*. Palpal organ distinguished by having a fairly circular outline in distal view (Fig. 15A; in *L. birmanicus* oval and relatively wider, Fig. 13A) and a relatively longer and narrower pigmented area with a more steeply inclined distal margin at base of membranous embolus part (Fig. 15C; in *L. birmanicus* much wider, its distal margin horizontal or only slightly inclined, Fig. 13D). Vulval plates usually, but not in all cases, with a relatively wider poreplate than in *L. birmanicus* and with an axe-blade-shaped or widely elliptical posterior stalk with a widely arched posterior margin (Fig. 16; posterior stalk angular, mostly with a straight posterior margin in *L. birmanicus*, Fig. 14).

Additions to description of male: Tarsal scopulae: I - thin, covering 3/4 of ventral side, distinct in distal half, more or less distinct in proximal half; II - thin but slightly denser than on tarsus I, covering distal 5/6 of ventral side; III-IV - denser than on tarsi I-II, covering 5/6 of ventral side. Male palps with tibial apophysis quite distinctly set back from distal margin of tibia (more so than in the *L. birmanicus* males examined; but see Xu *et al.*, 2021: fig. 8A-B), triangular in ventral view, depth/length ratio ~ 1.9 (see Aung *et al.*, 2019: fig. 4D-E); paracymbium quite short, its distal surface indistinctly conical, its retrolateral surface flat, with a moderately developed, widely rounded retrolateral-proximal heel (Fig. 15G); very strong bristles on low cumulus overlapping strong bristles on ventral side of palpal tarsus (Fig. 15G); contrategulum with quite large, distad-directed proventral process (Fig. 15A, C-E; very similar to that of *L. birmanicus*, Fig. 13A, D-F), with a pronounced proximal ledge on retrodorsal side (Fig. 15A), and with a moderately wide distal edge with a few weak ridges and a narrowly rounded dorsal apex (Fig. 15A-B); tegulum large, with finely dentate and bent proximal edge (Fig. 15D, F), distal margin not elevated [in some specimens a fairly long ridge is present just below the distal margin (in addition to a long median ridge) which can be misinterpreted as an elevated edge, Fig. 15F]; para-embolic plate short, about as long as retroventral edge of embolus complex and separated from it by a shallow invagination (Fig. 15D); embolus proper narrowly divided, its sclerotised part strengthened by 4-5 longitudinal ribs reaching apex and carrying denticles distally; area at base of membranous embolus part quite long and narrow, distinctly pigmented, with numerous longitudinal wrinkles, its distal margin widely truncate and steeply inclined (this area is much wider in *L. birmanicus*, its distal margin is not or only slightly inclined, Fig. 13D).

Taxonomic remarks: As can be seen from the relatively light body colouration and from the partly collapsed paracymbium, the male holotype was obviously killed and preserved very soon after its final moult. Metatarsus and tarsus of both its legs IV were very pale when still alive, and additionally deformed (due to a weak sclerotisation of the new cuticle) in the preserved specimen (Aung *et al.*, 2019: figs 2D, 4B). These leg articles obviously got stuck in the exuvia during the final moult, and were not able to become fully pigmented and sclerotised before the spider was killed. Therefore the light-coloured left metatarsus and tarsus IV of the holotype are an artefact caused by a moulting accident, and they are not a diagnostic character of the species as incorrectly stated by Yu *et al.* (2021: 37, incorrectly spelled "*L. pinglaung*"). The fact that the proventral process of the contrategulum is distad-directed, which is characteristic for *L. pinlaung* as well as *L. birmanicus*, is not mentioned in the original description or visible in the corresponding illustrations (Aung *et al.*, 2019: 36, fig. 4).

Variation: For carapace measurements and prefoveal setae counts see Table 1. In all specimens the AME are distinctly developed. In all males examined the extent of the tarsal scopulae is essentially the same, but in some specimens the proximal borders of the scopulae are less distinctly outlined than in others. Variation in details of the male palp is given in Fig. 15. The number of very strong bristles on the cumulus ranges 4-7: in most males examined (apart from one) they overlap strong bristles on the ventral side of the palpal tarsus (Fig. 15G). In five males examined there is a more or less distinct ridge below the distal margin of the tegulum of both palps (and in one male on only one palp; Fig. 15F), which can be misinterpreted as an elevated distal edge. A real elevated distal tegular edge is present in *L. platnicki* sp. nov. (Fig. 23I-M), in *L. nabang* (Yu *et al.*, 2021: fig. 3A-B, D-E) and in males of other species groups. Small females have distinctly annulated legs, in large females the annulations have become indistinct. Variation in the shape of the vulval plate is considerable, especially in shape and size of the anterior lobes and the distance between them, and in the shape of the posterior stalk (Fig. 16A-J; Aung *et al.*, 2019: fig. 5). The posterior margin of the posterior stalk is mostly straight in all three female paratypes illustrated in Aung *et al.* (2019: fig. 5), much like in females of *L. birmanicus* (Fig. 14), whereas in the females examined by us it ranges from straight (Fig. 16D-E), to widely rounded

(Fig. 16I-J) and very widely V-shaped (Fig. 16C). The poreplate of the smallest female examined has an exceptionally small receptacular cluster and relatively large pores (some much larger than the CDO; Fig. 16I-J). This appears to be a general feature of young (immature?) females rather than a case of individual variation in this species. The same female also has a single hair between the poreplate and the posterior stalk, which is unusual for species of the *birmanicus*-group (but see vulval plates of some species in Peninsular Malaysia, Schwendinger, 2017: figs 7, 9, 13, 14I-J).

Relationships: Despite pronounced differences in body colouration of females and juveniles, similarities in male (especially in the distad-directed proventral contrategular process) and female copulatory organs indicate a close relationship between *L. pinlaung* and *L. birmanicus*. *Liphistius hpruso* may also be very closely related, but that needs to be confirmed by the discovery of its male or by genetic analysis.

Distribution: *Liphistius pinlaung* is known from two localities near Pinlaung Village in the western part of the Shan State (Fig. 1).

Biology: The specimens examined were collected from earth banks on the sides of a road and of rice fields. All burrows were simple and unbranched, closed by a single trapdoor. The largest trapdoor in females was 2.0 cm long and 2.5 cm wide, those of penultimate males 1.2-1.7 cm long and 1.7-2.4 cm wide. Burrow entrances had 6-8 signal lines attached, the longest measuring 5 cm. The first three males matured within two weeks after being captured, a fourth one over three months later; maturation in November of the following year and of July of the year after that are presumably due to conditions in captivity. Most females moulted twice per year, in June to July and again in October to December; old females moulted only once per year.

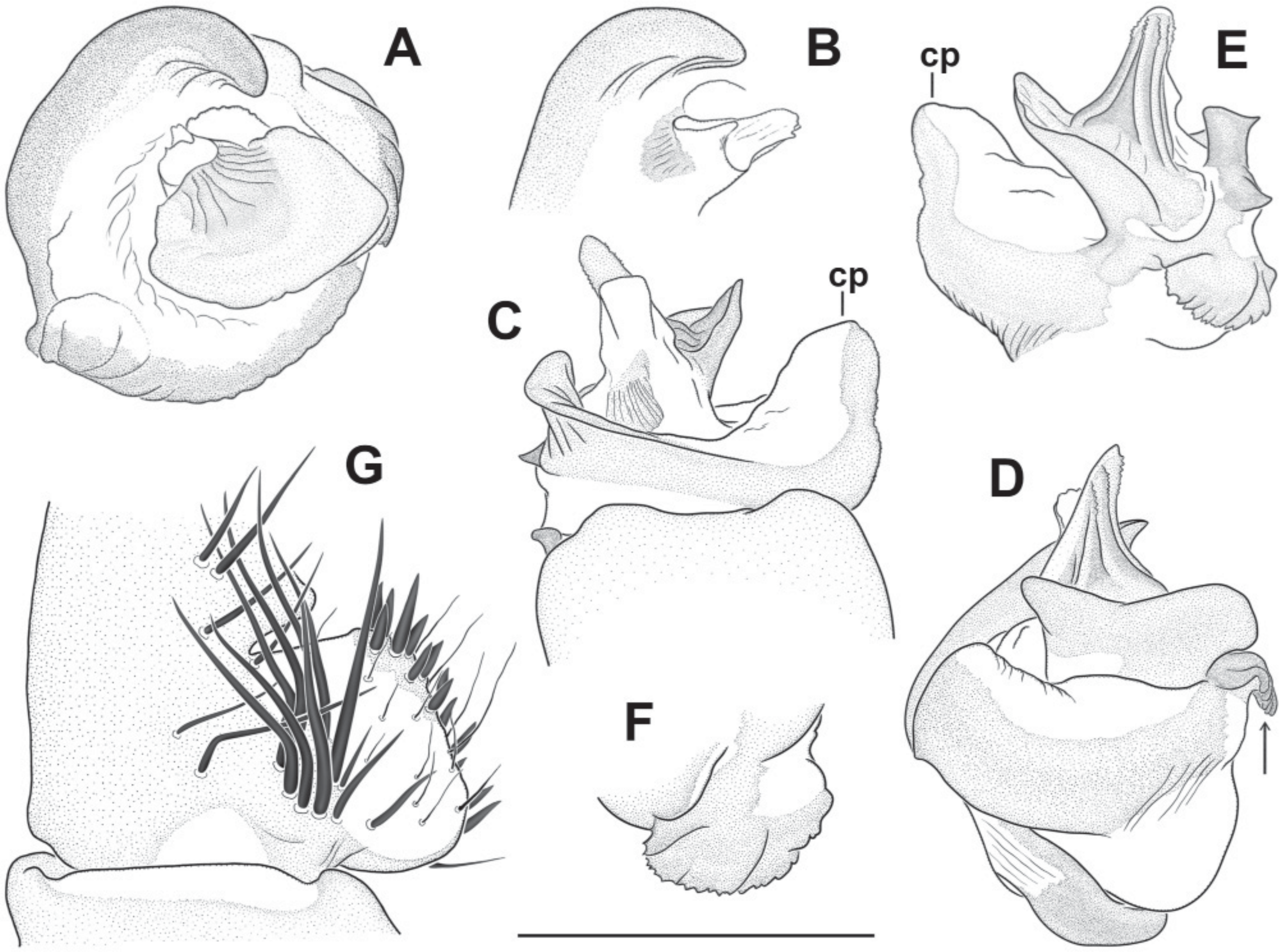

Fig. 15. *Liphistius pinlaung*, left palps of two males: matured 23.XI.2014 (A-B), matured 4.VII.2015 (C-G). (A) Palpal organ, distal view (dorsal side up). (B) Dorsal part of contrategulum and embolus proper, distal and slightly prolateral view. (C) Palpal organ and distal margin of tarsus, prolateral view. (D) Palpal organ, ventral view; bent proximal edge of tegulum indicated by arrow. (E) Distal part of palpal organ, retroventral view. (F) Tegulum, retrolateral view. (G) Proximal part of tarsus, ventral view. All to same scale; scale line 1.0 mm. Abbreviation: cp - proventral process of contrategulum.

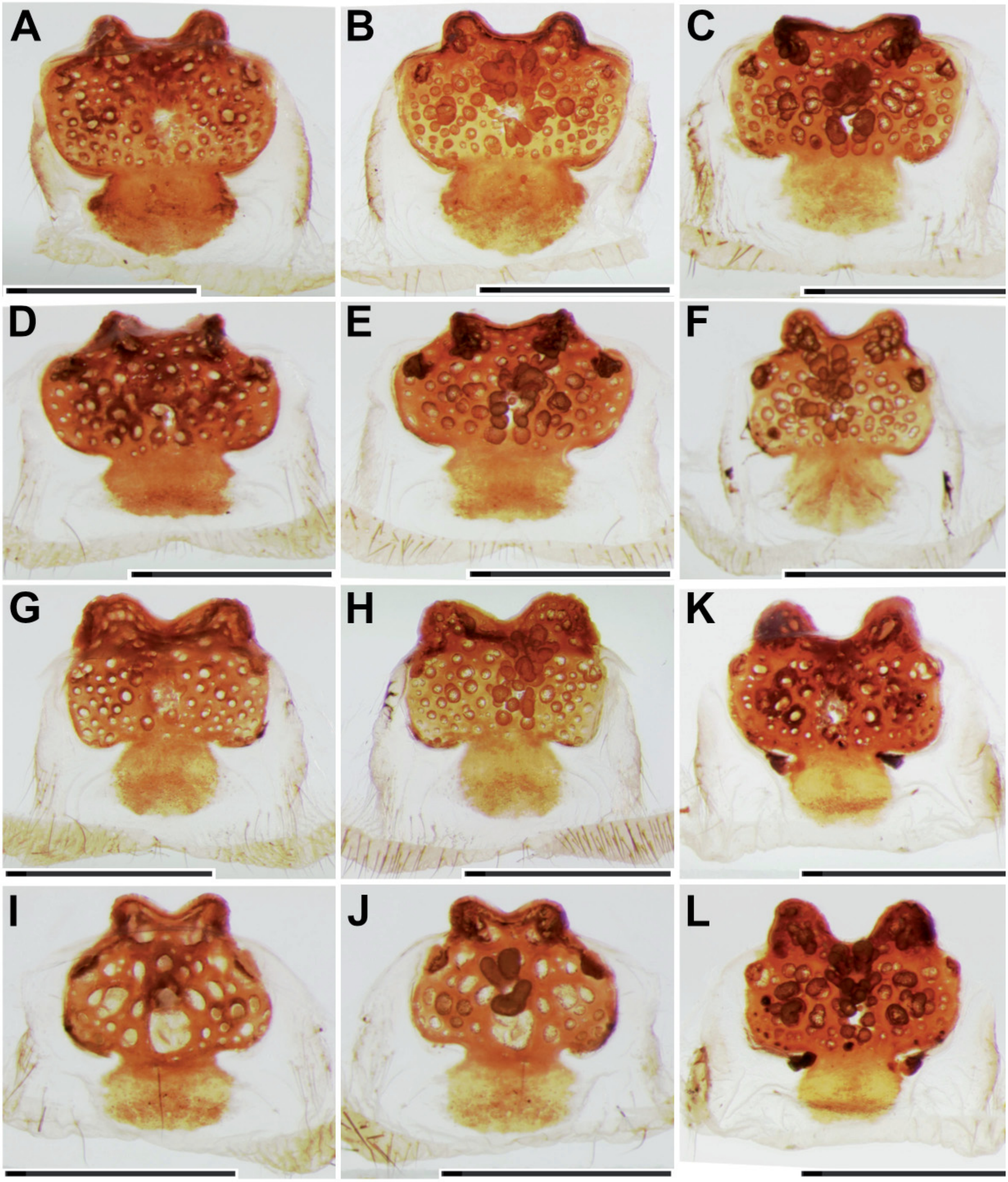

Fig. 16. *Liphistius pinlaung* (A-J) and *Liphistius* sp. (specimen from Kalaw; K-L), vulval plates of seven females (all taken from exuviae), dorsal view (A, D, G, I, K) and ventral view (B-C, E-F, H, J, L). (A-B) Moult of 10.II.2019. (C) Moult of 7.XII.2018. (D-E) Moult of 10.IV.2021. (F) Moult of 21.X.2018. (G-H) Moult of 16.V.2020. (I-J) Moult of 8.III.2020. (K-L) Moult of 15.VIII.2017. Scale lines 1.0 mm.

Liphistius sp.
Figs 1, 16K-L

Material: MHNG (sample MT-14/29); 1 female; Myanmar, Shan State, 3 km SW of Kalaw, along road to water reservoir, 20°36'16"N, 96°32'06"E, 1400 m; 14.VI.2014; leg. P. Schwendinger & S. Huber.

Taxonomic remarks: Body size and colouration and the shape of the vulval plate of this female is quite similar to that of *L. pinlaung* females (Fig. 16K-L cf. Fig. 16A-J). The vulval plate differs by larger and more deeply separated anterior lobes, by a longer receptacular cluster (reaching anterior margin of poreplate), and by a relatively shorter posterior stalk. This female (CL 7.34, CW 6.15 and thus within the size range of *L. pinlaung* females) either belongs to a different species, or it is a specimen at the far end of intraspecific variability in females of *L. pinlaung*.

Distribution and biology: The locality of this female lies about 50 km north of the known localities of *L. pinlaung* (Fig. 1), at roughly the same altitude. This form or species appears to be locally rare. Despite intensive search in the area around Kalaw for two full days, only a single spider was found. It was extracted from a simple burrow, closed by a 2.8 cm wide and 2.12 cm long trapdoor, with an old (filled with mould), 2.2 cm wide, 2.1 cm long and 1.3 cm high egg case at its end. In captivity the spider moulted two months after capture.

Liphistius lordae Platnick & Sedgwick, 1984
Figs 1, 17-18

Liphistius lordae Platnick & Sedgwick, 1984: 10-11, figs 18-19 (description of female). – Schwendinger, 1990: 332-334, figs 5-10 (description of males and females). – Schwendinger, 1998: fig. 1I (illustration of palpal organ). – Schwendinger, 1999: fig. 1I (reprint of illustration in Schwendinger, 1998).

Type: AMNH; female holotype (not examined); Myanmar, Shan State, west of Taunggyi Mountain, 5000 feet; 15.VII.1982; leg. W.C. Sedgwick.

Other material: MHNG; 2 males (one collected adult, the other matured 26.IX.1987) and 4 females; outskirts of Taunggyi City, 20°45'17"N, 97°02'27"E, 1560 m; 22.IX.1987; leg P. Schwendinger. No new material available.

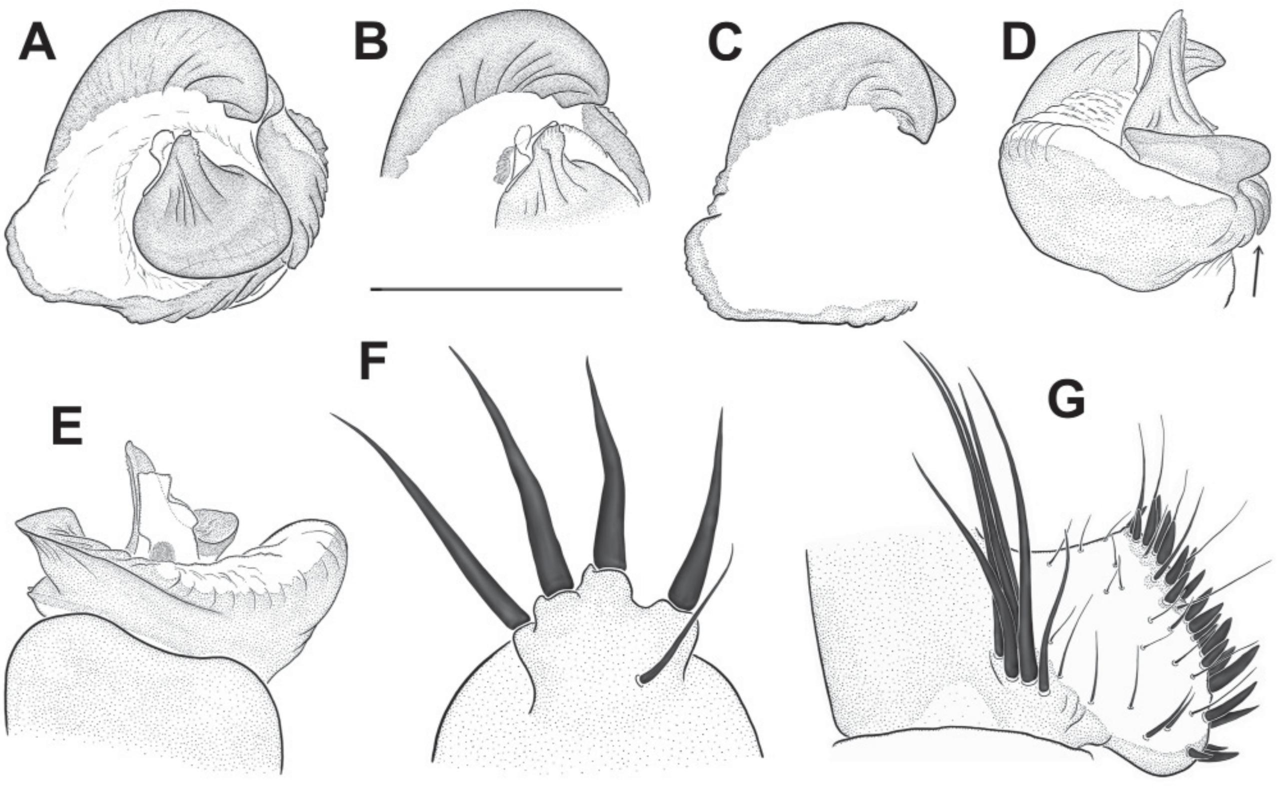

Fig. 17. *Liphistius lordae*, left palps of two males: male n°1 (A-B, D-G), male n°2 (C). (A) Palpal organ, distal view (dorsal side up). (B) Dorsal part of contrategulum and embolus proper, distal and slightly prolateral view. (C) Contrategulum, distal view. (D) Distal part of palpal organ, ventral view; bent and adpressed proximal edge of tegulum indicated by arrow. (E) Palpal organ and distal margin of tarsus, prolateral view. (F) Tibial apophysis, retrolateral and slightly proximal view. (G) Proximal part of tarsus, ventral view. Scale line 1.0 mm.

Diagnosis: Medium-sized spiders with uniformly dark brown body colouration in both sexes, without recognizable annulations on legs and palps. Males distinguished from those of other species in the *birmanicus*-group by short paracymbium with a proximally protruding, rounded proximal-retrolateral heel (Fig. 17G) and by proventral contrategular process exceptionally wide, with a widely truncate apex in distal view (Fig. 17A, C). Females different from those of the same group by having exceptionally wide anterior lobes, no anterolateral processes on poreplate, posterior stalk with a medium-long constriction in its anterior part (Fig. 18).

Additions to description: Males with scopulae weak on tarsi I-II, slightly denser on tarsi III-IV, covering distal 2/3 of tarsus I, distal 3/4 of tarsi II-III and distal 4/5 of tarsus IV. Male palps with moderately deep tibial apophysis (depth/length ratio ~ 1.5), only slightly set back from distal margin of tibia, carrying four long, pointed apical megaspines (Fig. 17F; Schwendinger, 1990: figs 5-7); paracymbium short, carrying fairly long retrodorsal spicules (distinctly longer than in *L. lahu*, *L. metopiae* sp. nov. and *L. tung* sp. nov.) and a large, arched retrolateral-proximal heel distinctly inclined proximad instead of pointing retrolaterad (Fig. 17G); cumulus indistinct, carrying a group of about 6 long

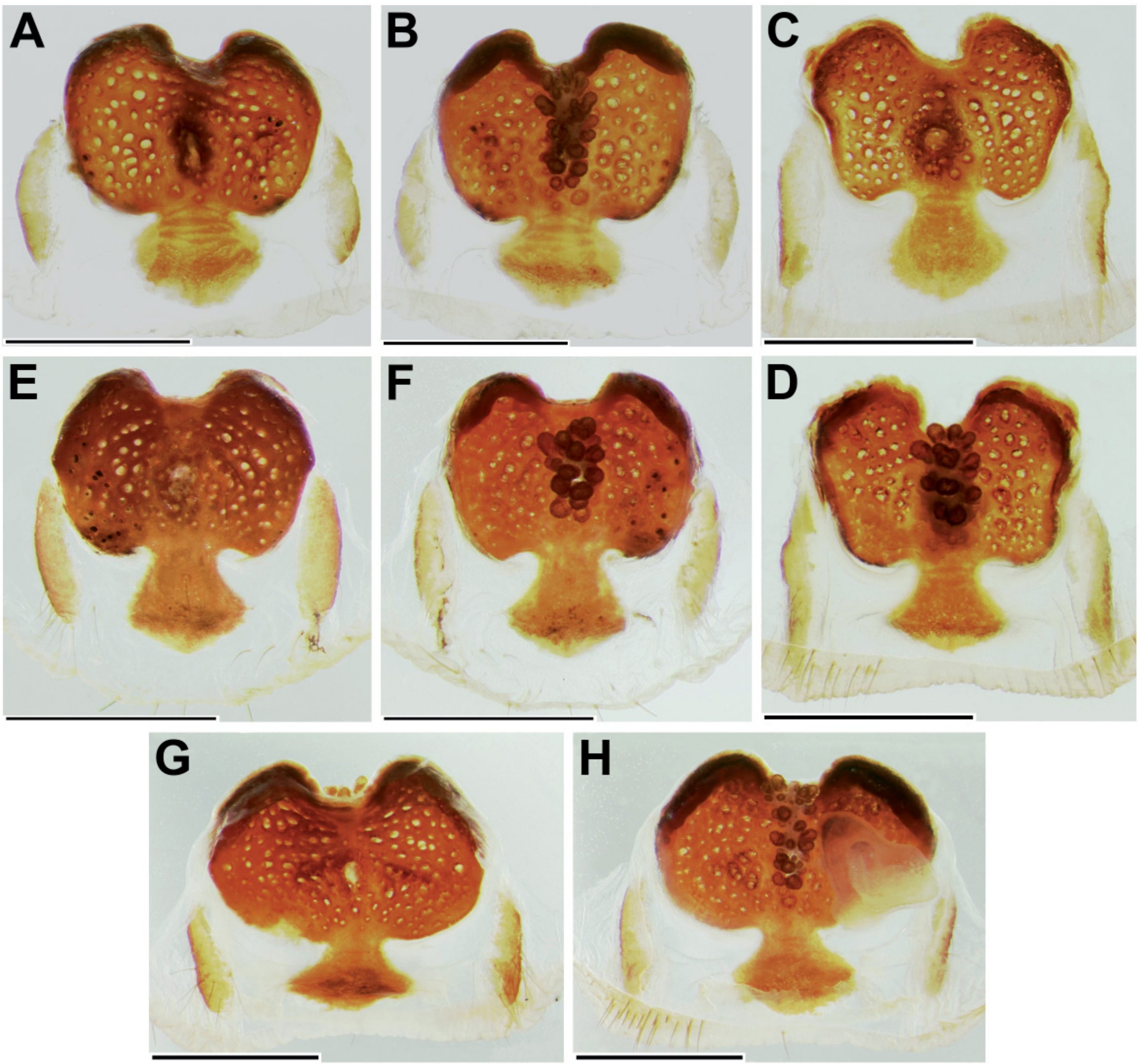

Fig. 18. *Liphistius lordae*, vulval plates of four females; dorsal view (A, C, E, G) and ventral view (B, D, F, H); all taken from exuviae. (A-B) Female n°1. (C-D) Female n°2. (E-F) Female n°3. (G-H) Female n°4; note pathologically enlarged vesicle on left side of poreplate. Scale lines 1.0 mm.

strong bristles (Fig. 17G; Schwendinger, 1990: figs 6-7); subtegulum with indistinct apophysis; tegulum large, its distal margin not elevated, its proximal edge widely arched, finely serrate, distinctly bent and adpressed to membranous area below it (Fig. 17D; Schwendinger, 1990: figs 5-6); contrategulum with very wide proventral process ending in a widely truncate apex (Fig. 17A, C; Schwendinger, 1990: fig. 7); prolateral part of distal contrategular edge sharp but not elevated into a pronounced keel (Fig. 17E); proximal ledge on retrodorsal side of contrategulum pronounced (Fig. 17A, C, E); distal edge of contrategulum very wide and carrying ridges, its dorsal apex very narrowly rounded, almost pointed in distal view (Fig. 17A-C); para-embolic plate short, about as long as retroventral edge of embolus complex and not separated from it by an invagination (Fig. 17A, D); embolus proper narrowly divided, its sclerotised part strengthened by 3 longitudinal ribs reaching apex and carrying denticles distally; membranous embolus part distinctly shorter than sclerotised part, short area at its base strongly pigmented, with numerous longitudinal wrinkles and with fairly straight or widely and strongly asymmetrically angular distal margin (Fig. 17E). Females with uniformly dark legs and palps without annulations; vulval plates (Fig. 18; Schwendinger, 1990: figs 8-10) with several hairs on lateral folds, one female even with a single hair on posterior stalk (Fig. 18E); poreplate wider than long, anteriorly wider than posteriorly, with a pair of very wide lobes on anterior margin, without anterolateral processes, posterior margins not bulged; CDO fairly small, quite variable in shape; receptacular cluster racemose, much longer than wide, reaching or almost reaching anterior margin of poreplate; posterior stalk clearly narrower than poreplate, axe-blade-shaped, with distinct anterior constriction, posterior margin wide and more or less strongly arched.

Variation: For carapace measurements and prefoveal setae counts see Table 1. All specimens examined have well-developed AME. Variation in the shape of the proventral contrategular process is shown in Fig. 17, variation in the shape of the vulval plates in Fig. 18.

Relationships: *Liphistius lordae* possesses some quite unusual characters in the male and female copulatory organs that make it difficult to establish its relationships on a morphological basis. It clearly belongs to the *birmanicus*-group and it is apparently not very closely related to the geographically close *Liphistius* sp. that occurs near Kalaw or to *L. pinlaung*. Within the *birmanicus*-group a very wide distal contrategular margin is otherwise only found in *L. pyinoolwin* (Fig. 17A-C cf. Fig. 19A-B), and both also share an adpressed posterior tegular edge, which are not very strong indications that both are more closely related to each other than each of them with any other known species. However, we believe that unknown species exist that are more closely related to either of these two species.

Distribution: *Liphistius lordae* is known only from the type locality in the mountains of the Shan State (Fig. 1).

Liphistius pyinoolwin Xu, Yu, Aung, Yu, Liu, Lwin, Sang & Li, 2021

Figs 1, 2B, 19-20

Liphistius birmanicus Thorell, 1897 (misidentification): Platnick & Sedgwick, 1984: 8-10, figs 7-15 (description of males and females in AMNH under *L. birmanicus*). – Schwendinger, 1990: 331-332, figs 1-4 (illustration of copulatory organs of 1 male and 3 females in AMNH misidentified as *L. birmanicus*).

Liphistius pyinoolwin Xu, Yu, Aung, Yu, Liu, Lwin, Sang & Li, 2021: 45-50, figs 2D-E, 3-7 (description of males and females).

Type material: CBEE (XUX-2018-089 to XUX-2018-111A); male holotype, 7 male paratypes and 15 female paratypes (not examined); Myanmar, Mandalay Region, Pyin Oo Lwin District, Dat Taw Gyaint Waterfall (= Anisakan Falls), 908 m, 21.98°N, 96.38°E; l3.VII.2018; leg. Li, Liu, Xu and Yu.

Material examined: MHNG, BRCM (sample MT-14/31); 12 males (matured 4.IX., 11.IX., 24.IX., 25.IX., 1.X., 4X., 5.X., 16.X.2014, 19.X., 20.X.2014, 3.IX., 5.X.2015) and 3 females; Myanmar, Mandalay Division, Pyin U Lwin (= Pyin Oo Lwin) District, Anisakan Waterfalls (21°58’50”N, 96°23’11”E), 600 m; 8.VII.2014; leg. P.J. Schwendinger & S. Huber. – AMNH; 2 males (matured 14.X.1982 and 23.X.1982; one of them illustrated in Platnick & Sedgwick, 1984: figs 7-11, 14 and in Schwendinger, 1990: fig. 1) and 5 females (one of them illustrated in Platnick & Sedgwick, 1984: figs 12-13, 15, three of them in Schwendinger, 1990: figs 2-4); gorge near Maymyo (= Pyin U Lwin = Pyin Oo Lwin), 3500 feet; 13.VII.1982; leg. W.C. Sedgwick.

Diagnosis: Medium-sized, dark spiders with annulated legs and palps (on posterior legs more distinctly so than on anteriors) in females and juvenile males. Males distinguished from those of other species in the *birmanicus*-group by paracymbium carrying 2-3 enlarged spicules (longer than the ones distal to them) on a narrowly rounded retrolateral-proximal heel (Fig. 19E-F); base of embolus complex prolaterally with a lobate protrusion (Fig. 19A-B). Females similar to those of *L. lordae*, distinguished by having annulated legs and palps; poreplate with a pair of anterolateral processes (absent in *L. lordae*); anterior lobes of poreplate quite narrow (very wide in *L. lordae*); posterior stalk posteriorly narrower than in *L. lordae* (Fig. 20 cf. Fig. 18).

Additions to description: Males with scopulae very weak on tarsus I (especially in proximal half),

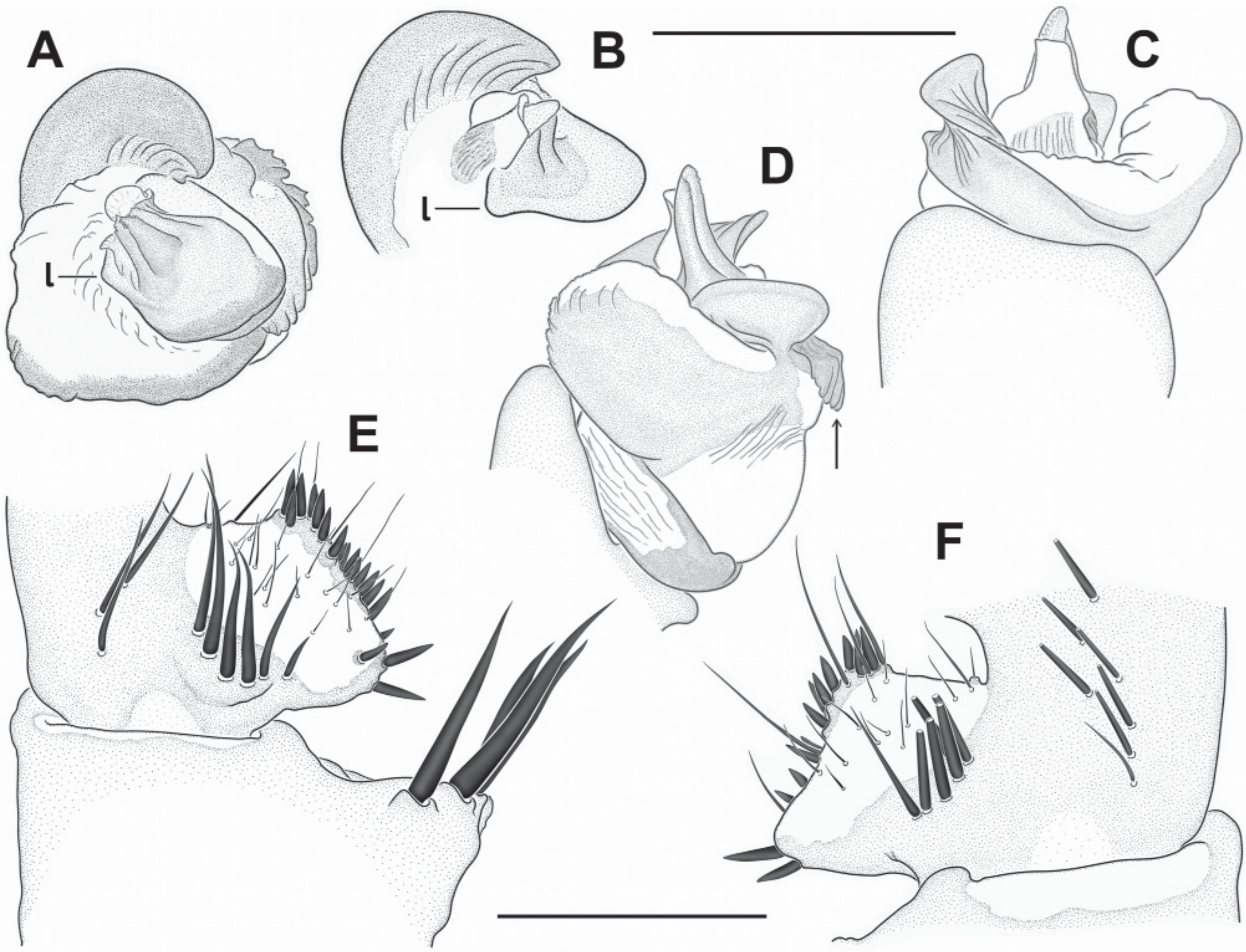

Fig. 19. *Liphistius pyinoolwin*, palps of two males: matured 16.X.2014 (A-E), matured 24.IX.2014 (F). (A) Left palpal organ, distal view (dorsal side up). (B) Left embolus complex and dorsal part of contrategulum, distal and slightly proventral view. (C) Left palpal organ and distal margin of tarsus, prolateral view. (D) Left palpal organ, ventral and slightly proximal view; bent and adpressed proximal edge of tegulum indicated by arrow. (E) Distal part of left tibia and proximal part of tarsus, ventral view. (F) Distal margin of right tibia and proximal part of tarsus, ventral view. Scale lines 1.0 mm (A-D; E-F). Abbreviation: l - lobate prolateral protrusion on base of embolus complex.

increasingly denser on tarsi III-IV, covering distal 3/4 of tarsus I, distal 4/5 of tarsus II and distal 5/6 of tarsi III-IV. Male palp with tibial apophysis slightly set back from anterior margin of tibia (Fig. 19E); paracymbium with a moderately to narrowly rounded retrolateral-proximal heel, always carrying 2-3 elongate spinules (longer than those situated more distally; Fig. 19E-F); distal margin of tegulum not elevated, proximal edge coarsely dentate, bent and adpressed to contrategular surface below it (Fig. 19D); contrategulum with short, widely conical proventral process with a rounded apex (Fig. 19A); distal edge of contrategulum very wide (Fig. 19A), its prolateral part long, slightly elevated to a keel (Fig. 19C), its dorsal apex narrowly rounded (Fig. 19A-B); base of embolus complex with a lobate prolateral protrusion (Fig. 19A-B); para-embolic plate short and indistinct, not separated by an invagination from retroventral edge of embolus complex (Fig. 19D); embolus proper narrowly divided, its sclerotised part strengthened by 3 longitudinal ribs reaching apex and carrying denticles distally (Fig. 19A-B, D); area at base of membranous embolus part wide, distinctly sclerotised and furnished with numerous quite long and deep wrinkles, its distal margin oblique (Fig. 19B-C). Females with a pair of light marks half way between ocular mound and fovea; poreplates wider than long, with distinct, quite narrow (distinctly narrower than in *L. lordae*) anterior lobes and with anterolateral processes; posterior stalk mostly axe-blade-shaped, with an exceptionally long and narrow constriction in its anterior part (Fig. 20, Xu *et al*., 2021: figs 5-7, see also Variation).

Variation: For carapace measurements and prefoveal setae counts see Table 1. All specimens examined

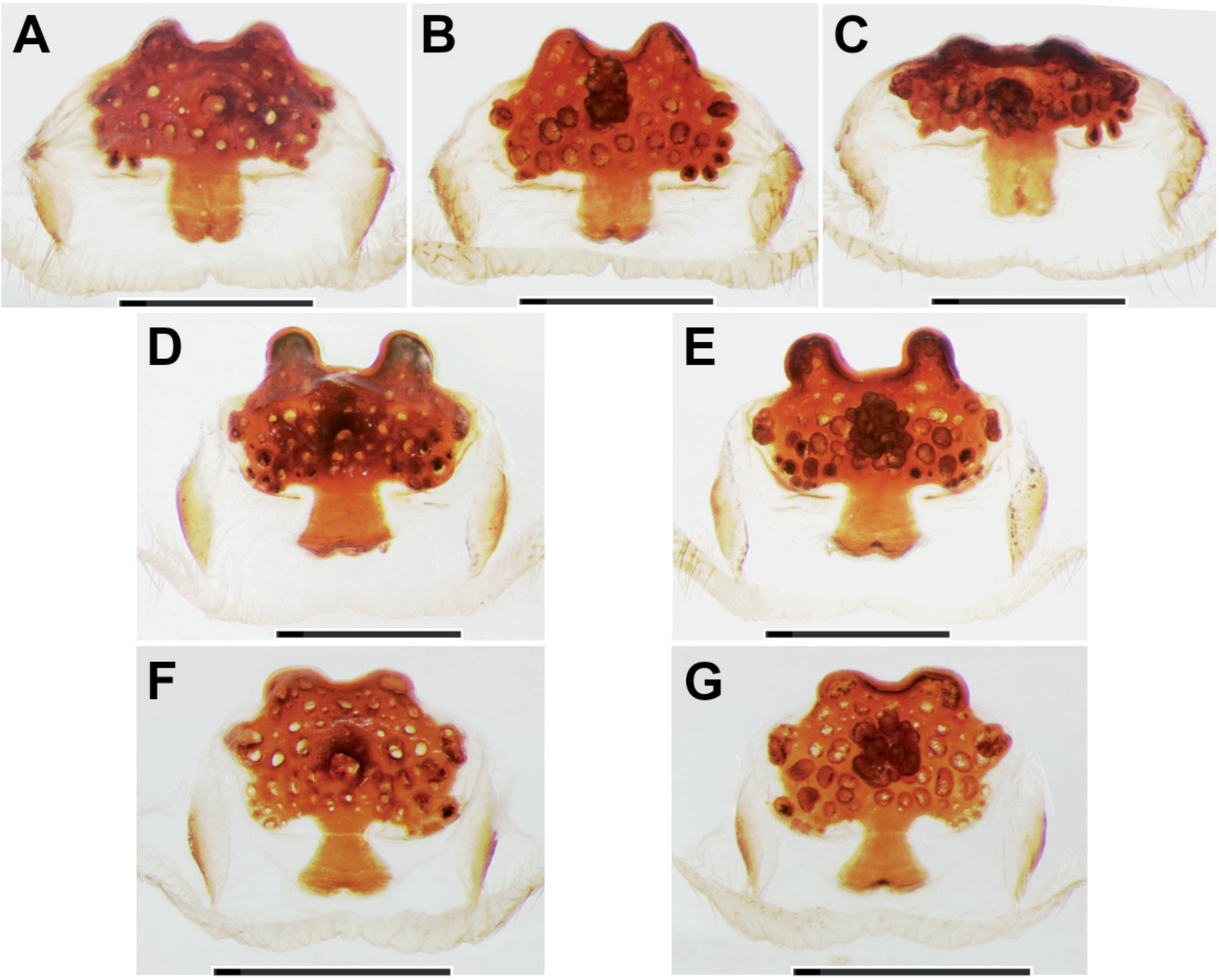

Fig. 20. *Liphistius pyinoolwin*, vulval plates of three females (all taken from exuviae), dorsal view (A, D, F), ventral view (B, E, G) and ventral and slightly anterior view (C). (A-C) Moult of 1.IX.2017. (D-E) Moult of 15.X.2017. (F-G) Moult of 22.I.2016. Scale lines 1.0 mm.

have well-developed AME. Variation in the shape of the male palp is shown in Fig. 19. In distal view the apex of the proventral contrategular process is widely rounded in most specimens (Fig. 19A), in one it is very widely triangular. The unusually deep apex of this process shown in prolateral view (Fig. 19C) is due to an artificial swelling (caused by alcohol preservation?) of the membrane on its distal side. This is not so in illustrations by Xu *et al*. (2021: figs 3-4). The distinctly pigmented area at the base of the membranous embolus part has an oblique distal margin (Fig. 19C), in some specimens with a small median spike or a longer spike at the higher end. In illustrations of male palps by Xu *et al*. (2021: figs 3-4) two characteristic features (elongate spicules on lower retrolateral corner of paracymbium; bent and adpressed proximal edge of tegulum) are not clearly visible or not visible at all; a third characteristic feature (lobate prolateral protrusion of embolus complex) is recognizable (Xu *et al*., 2021: fig. 3B, I). Variation in the shape of the vulval plates of three females examined is shown in Fig. 20. One of these specimens has wart-like ventral vesicles on the posterior margin of the poreplate and a very narrow posterior stalk (with roughly parallel lateral margins; Fig. 20A-C). This is presumably abnormal, as is the vulval plate illustrated by Xu *et al*. (2021: fig. 6F, I) which completely lacks a posterior stalk. The posterior margin of the posterior stalk is straight (Xu *et al*., 2021: fig. 5E, H) or more or less widely arched, with a small median invagination (Fig. 20), with a very small median lobe (Xu *et al*., 2021: figs 6E, 7D-E, G-H) or with neither (Xu *et al*., 2021: figs 5D, G, 6D, G, 7B-C, F, I). The receptacular cluster of this species is also quite variable, not or only barely reaching the anterior margin of the poreplate in the three females examined (Fig. 20B, E, G), reaching the margin or surpassing it in six females illustrated by Xu *et al.* (2021: figs 5G-I, 6G-I, 7C, G-I). The CDO is mostly circular, small to medium-sized (Fig. 20A, D, F), in some females longer than wide, elliptical or teardrop-shaped (Xu *et al*., 2021: figs 5D, F, 6D, 7F).

Relationships: Similarities in the shape of the vulval plate (anteriorly narrow posterior stalk; Fig. 20 cf. Fig. 18) and in the palpal organ (very wide distal edge of contrategulum, adpressed proximal edge of tegulum; Fig. 19A-B, D cf. Fig. 17A-D) suggest a fairly close relationship between *L. pyinoolwin* and *L. lordae*.

Distribution: This species is currently only known from the type locality near the western edge of the Shan Plateau (Fig. 1).

Biology: Most of the specimens examined were collected from earth banks at the bottom of a waterfall, a few on the sides of a trail. Most burrows were simple and undivided, closed by a single trapdoor; one burrow was Y-shaped and equipped with two doors close to each other; two burrows were sac-like, with two doors, built in the depression of a rock bolder, as know from cave-dwelling *Liphistius* species (see e.g. Klingel, 1967). Most burrows had 6-8 signal lines radiating from the entrance; only one had nine lines. The largest female had a 2.0 cm long and 2.9 wide trapdoor; penultimate males had 1.3-1.9 cm long and 2.1-2.8 cm wide trapdoors. Males matured between early September and late October, only a few months after being captured. No egg cases were found in the field in early July. Eggs are presumable laid in December, as it is the case in congeneric species in the mountains of northern Thailand (Schwendinger, 1990). In captivity large females moulted once per year, between September and October. One of the males carried parasitic mites of the genus *Ljunghia* (see Halliday & Juvara-Bals, 2016) which discarded their exuviae on the dorsal side of the spider opisthosoma (Fig. 2B). Another male fed on a cricket after reaching maturity, which is rather unusual because most adult *Liphistius* males stop feeding.

Liphistius cupreus Schwendinger & Huber, sp. nov.
Figs 1, 2D-I, 21-22

Holotype: MHNG-ARTO-0028341 (sample MT-14/21); male (matured 18.V.2017); Myanmar, Shan State, SE of Lashio, near Kong Nyaung Village (22°54’07”N, 97°47’27”E), 1130 m; 8.-9.VI.2014; leg. P.J. Schwendinger & S. Huber.

Paratypes: MHNG-ARTO-0028342 to MHNG-ARTO-0028347, BRCM (sample MT-14/21); 7 males (matured mid-VI.2015, two at end of VI.2015, 5.V.2016, 27.V.2016, 30.VI.2016, 1.VII.2016); collected together with the holotype. – MHNG-ARTO-0028349 to MHNG-ARTO-0028359, BRCM (sample MT-14/21); 12 females (allotype, MHNG-ARTO-0028349, last moulted 19.I.2019); collected together with the holotype.

Other material: MHNG; 2 small, badly preserved females, 1 juvenile; same data as for type specimens.

Etymology: The Latin adjective “cupreus” (= copper-coloured) refers to the colouration of the opisthosomal tergites in both sexes.

Diagnosis: Medium-sized spiders; both sexes with annulated legs (in females more distinct than in males) and without prefoveal setae. Most similar to *L. nabang* and *L. platnicki* sp. nov. by males sharing a distinctly elevated cumulus and a paracymbium with a distinctly conical distal side (Fig. 21A-B cf. Yu *et al*., 2021: fig. 3D-F and 23A-B); females sharing a similar vulval plate with more or less strongly reduced anterior poreplate lobes and with a short and wide posterior stalk widely connected to the popeplate (Fig. 22 cf. Yu *et al*., 2021: fig. 4 and Fig. 24). Males distinguished from those of *L. nabang* by tegulum lacking a distinctly elevated distal edge (Fig. 21K, M; present in *L. nabang*, Yu *et al*., 2021: fig. 3A-B, D-E) and having a widely rounded proximal edge (Fig. 21K; bent in *L. nabang*, giving the tegulum a triangular shape, Yu *et al*., 2021: fig. 3A); distal edge of contrategulum with an angular and finely dentate projection prodorsally (Fig. 21A, E-F, H-I; in *L. nabang* widely arched and not dentate, Yu *et al*., 2021: fig. 3B); paracymbium without a retrolateral-proximal heel (Fig. 21A cf. Yu *et al*., 2021: fig. 3E). Females distinguished from those of *L. nabang* by poreplates with 1-2 clusters of vesicles on each side of anterior margin (in *L. nabang* only 1) and without bulging posterolateral margins; posterior part of genital atrium not bent ventrad (Fig. 22 cf. Yu *et al*., 2021: fig. 4). Males distinguished from those of *L. platnicki* sp. nov. by tegulum lacking a distinctly elevated distal edge (Fig. 21K, M cf. Fig. 23I-M), proximal tegular edge only slightly protruding (Fig. 21J; strongly protruding in *L. platnicki* sp. nov., Fig. 23M); distal edge of contrategulum with an angular prodorsal projection (Fig. 21A, E-F, H-I; no projection in *L. platnicki* sp. nov., Fig. 23A, E-F). Females distinguished from those of *L. platnicki* sp. nov. by poreplate lacking anterolateral processes and by a relatively shorter posterior stalk (Fig. 22 cf. Fig. 24).

Description of male (holotype): *Colour in alcohol* (darker in life; as in Fig. 2D-F): Carapace with orange background colour and dark lateral and anterior margins; pars cephalica grey-brown except for a pair of light brown lateral marks and an unpaired light posteromedian mark; eye mound black; pars thoracica with irregularly shaped dark marks on coxal elevations and with a light brown posteromedian mark. Chelicerae cream-coloured proximally and prolaterally, grey-brown medially, light orange-coloured distally. Ventral side of palpal coxae and of sternum light orange-coloured, contrasting with slightly darker labium and leg coxae. Legs and palps mostly dark brown on dorsal side, apart from distal half of tarsi I-II slightly lighter than proximal half and apart from an indistinct light median mark on leg tibiae; ventral side of legs with distinct light median mark on tibiae I-II and with an indistinct one on tibiae III-IV; ventral side of leg femora with distinct light median and proximal marks (remnants of annulations; see also Variation), plus scattered dark spots; ventral side of palpal tibia and femur light, with scattered dark spots; palpal tarsus and cheliceral claw dark reddish brown. Opisthosoma with light greyish brown membranous cuticle and with light orange-coloured sternites; tergite I entirely dark brown; tergite II mostly dark brown, with orange-coloured paramedian-posterior marks; tergites III-VII mostly light orange-coloured, with large dark marks, with a pair of dark paramedian-posterior marks and with scattered small dark spots; tergite VIII very small, entirely dark.

Setae on carapace: Few short setae (with wide gaps between them) on lateral margins; none on posterior margin; isolated setae on anterior coxal elevations, groups of 7-10 setae on posterior coxal elevations. No setae anterior to fovea.

Cheliceral teeth: 12 small teeth of different sizes on promargin of each cheliceral groove.

Scopula: Only distally divided by a median stripe on all tarsi; weak, posteriorly very thin and not clearly outlined in distal 4/5 of ventral side of leg tarsus I; equally thin and covering distal 5/6 of tarsus II; distinctly denser, more clearly outlined, covering 5/6 of tarsus III; equally dense and covering 4/5 of tarsus IV.

Tarsal claws: Paired claws with 4-5 teeth on tarsi I-III, 5 teeth on tarsus IV; unpaired claw of all leg tarsi without denticles.

Palp: Tibial apophysis short, triangular and basally wide in ventral view, not set back from distal margin of tibia (Fig. 21C), carrying 4 long apical megaspines, ventral 2 longer than dorsal 2; dorsal to apophysis a quite long spine on a slightly elevated base (Fig. 21C-D). Palpal tarsus with a pronounced subdistal suture on ventral side (Fig. 21A) and with a widely but shallowly invaginated distal margin (Fig. 21N). Paracymbium moderately deep (Fig. 21B), longer than wide, with a distinctly conical distal side and a widely arched retrolateral side in ventral view, lacking a retrolateral-proximal heel (Fig. 21A); cumulus quite large, distinctly elevated, carrying a densely packed group of about 10 long, strong bristles (Fig. 21A-B). Subtegulum without apophysis (Fig. 21A, M). Tegulum wide, axe-blade-shaped, its distal margin not elevated (Fig. 21M), its proximal edge short, widely rounded and finely dentate (see Fig. 21K showing paratype), only slightly bent and protruding, only little overhanging membranous contrategular area below it (Fig. 21J). Pigmented bridge between tegulum and contrategulum on retrodorsal side of palpal organ well developed (Fig. 21E, M). Contrategulum with moderately developed conical proventral process ending in a rounded apex in distal view (Fig. 21H-I); a few fine wrinkles on dorsal surface and a small proximal ledge on retrodorsal side (Fig. 21H, L-N, see also Fig. 21E-F for paratype); distal edge of contrategulum narrow, carrying a widely angular and finely dentate projection prodorsally (Fig. 21A, H-I, see also Fig. 21E-F for paratype), dorsal apex of contrategulum quite long and beak-like, very narrowly rounded (Fig. 21H-I, L, see also Fig. 21E-G for paratype). Para-embolic plate short, about as long as retroventral edge of embolus complex and not visibly separated from it by an invagination (Fig. 21A). Membranous prolateral-proximal zone of embolus complex distinctly swollen (Fig. 21A); embolus proper narrowly divided, its sclerotised part strengthened by 2 thick and 1 thin longitudinal ribs reaching apex and carrying denticles distally (Fig. 21A, M, see also Fig. 21E-F, K for paratypes); membranous part of embolus proper distinctly shorter than sclerotised part, at its base a short, proximally wide and weakly pigmented area with numerous longitudinal wrinkles and with a concave distal margin; embolic folds short (Fig. 21N).

Measurements: Total length 15.55; CL 6.03, CW 5.55; opisthosoma 6.90 long, 5.55 wide; eye mound 0.86 long, 0.97 wide; palpal coxa 2.02 long, 1.43 wide; labium 0.52 long, 1.15 wide; sternum 3.06 long, 2.14 wide (1.03 on ventral surface); palp 9.65 long (2.94 + 1.79 + 3.21 + 1.71); leg I 16.82 long (4.68 + 2.38 + 3.41 +4.29 + 2.06); leg II 17.85 long (4.68 + 2.42 + 3.57 + 4.88 + 2.30); leg III 20.16 long (5.00 + 2.54 + 3.89 + 5.95 + 2.78); leg IV 24.64 long (5.99 + 2.70 + 4.88 + 7.58 + 3.49).

Description of female (allotype): *Colour in alcohol* (darker in life, as in Fig. 2G-I): Mostly as in male, but generally slightly lighter (due to longer preservation in alcohol). Light distal area on chelicerae much smaller than in male and divided into a small median spot and a

Fig. 21. *Liphistius cupreus* sp. nov., palps of three males; holotype (A-D, H-J, L-N), paratype matured end VI.2018 (E-G), paratype matured mid VI.2018 (K). (A) Left tarsus and palpal organ, ventral view. (B) Left paracymbium and distal margin of tibia, retrolateral view. (C) Distal part of left tibia, ventral view. (D) Same, retrolateral and slightly proximal view. (E) Left palpal organ, distal view (dorsal side up). (F) Dorsal part of left contrategulum and embolus proper, distal and slightly ventral view. (G) Dorsal part of left contrategulum, distal and slightly dorsal view. (H) Left contrategulum, distal and slightly ventral view. (I) Right contrategulum, same view. (J) Part of left palpal organ, retroventral view; slightly bent proximal edge of tegulum indicated by arrow. (K) Right palpal organ, retrolateral and slightly distal view. (L) Left palpal organ and distal margin of tarsus, dorsal and slightly proximal view. (M) Left palpal organ, retrolateral and slightly distal view. (N) Left palpal organ and distal margin of tarsus, prodorsal and slightly proximal view. Scale lines 1.0 mm (A-B, E-N; C-D). Abbreviation: a - angular prodorsal protrusion at base of distal edge of contrategulum.

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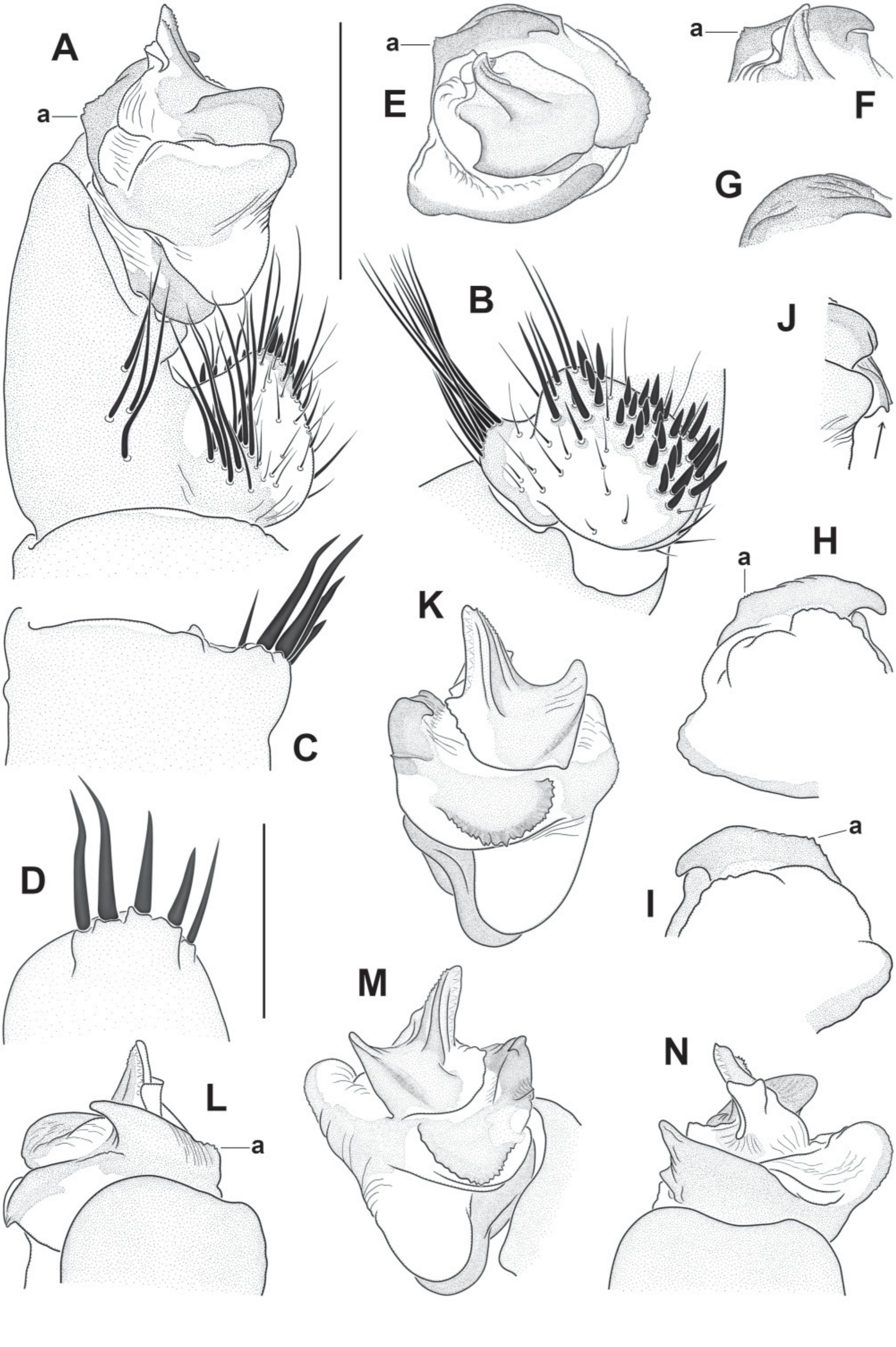
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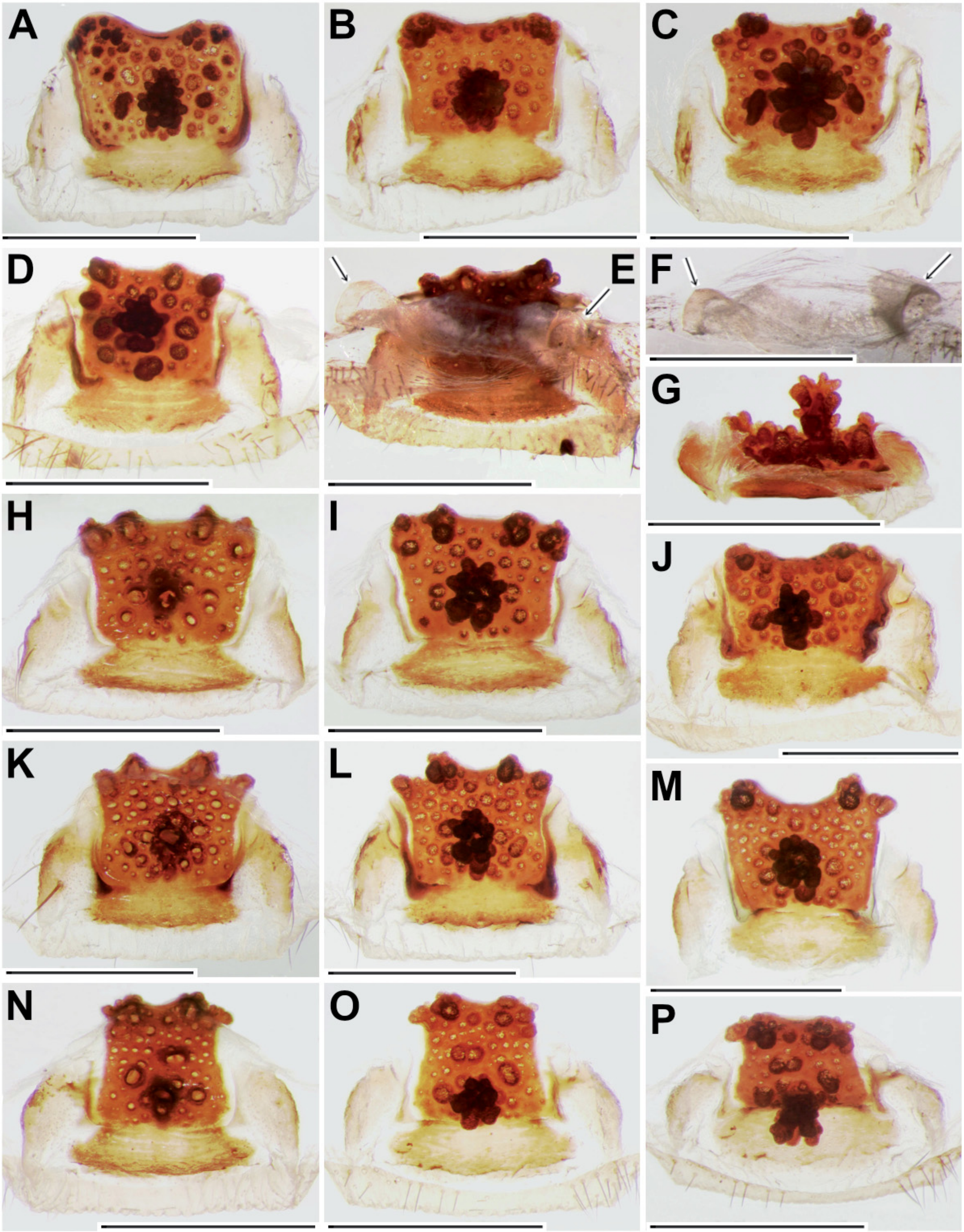

Fig. 22. *Liphistius cupreus* sp. nov., vulval plates of ten females (all taken from exuviae), dorsal view (E with uterus externus attached, H, K, N), ventral view (A-D, I-J, L-M, O), ventral and slightly anterior view (P), posterior view (G), and isolated uterus externus (F). (A) Moult of 10.II.2019. (B) Moult of 12.V.2020. (C) Moult of 5.VII.2019. (D-F) Moult of 22.XI.2020. (G) Moult of VI.2019. (H-I) Moult of 13.II.2021. (J) Allotype; moult of 19.I.2019. (K-L) Moult of 14.II.2021. (M) Moult of 1.V.2021. (N-P) Moult of 23.X.2021. Arrows indicating paired lateral pockets of membranous uterus externus. Scale lines 1.0 mm.

longitudinal retrodorsal stripe. Three light marks on pars cephalica and posteromedian light mark on pars thoracica of carapace less conspicuous. Palpal coxae darker than in males, almost of same colour as leg coxae I-II (leg coxae III-IV slightly lighter). Annulation of legs and palps more distinct than in males, clearly visible dorsally on all tibiae and on metatarsi III-IV, less clearly so on all femora and on tarsi III-IV. Distal 1/4 of palpal tarsus dark reddish brown.

Setae on carapace: Mostly as in male, but even fewer short setae on lateral margin; no setae anterior to fovea.

Cheliceral teeth: 11 strong teeth on promargin of right cheliceral groove; 11 strong teeth and 1 tiny denticle on left chelicera.

Claws: Palpal claws with 4 denticles each. Paired claws of legs I-II with 4 teeth, of leg III with 4-5 teeth, of leg IV with 5-6 teeth; unpaired claws of legs I-II with 1 denticle, of leg III with 0-1 denticle, of leg IV bare. All tarsi without scopulae.

Vulva (Fig. 22J): Membranous uterus externus with a distinct pair of lateral pockets (see Fig. 22E-F for another female). Vulval plate wider than long; only one hair on lateral fold of one side. Poreplate with widely but shallowly invaginated anterior margin carrying a single small process or cluster of vesicles (probably reduced anterior lobes) on one side and two small processes on other side, with inconspicuous lateral and posterior margins and with small CDO; receptacular cluster racemose but rather simple, longer than wide, not reaching anterior margin of poreplate, very deep (see Fig. 22G, P for other females). Posterior stalk short, as wide as poreplate, axe-blade-shaped, anteriorly only slightly narrower than posteriorly, with a widely arched posterior margin.

Measurements: Total length 20.08; CL 7.62, CW 6.90; opisthosoma 8.65 long, 6.35 wide; eye mound 0.98 long, 1.12 wide; palpal coxa 2.54 long, 1.79 wide; labium 0.63 long, 1.67 wide; sternum 4.37 long, 2.62 wide (1.39 on ventral surface); palp 12.39 long (4.05 + 2.38 + 3.02 + 2.94); leg I 15.91 long (5.04 + 2.78 + 3.25 + 3.25 + 1.59); leg II 16.59 long (5.04 + 2.90 + 3.25 + 3.57 + 1.83); leg III 18.49 long (5.16 + 3.06 + 3.49 + 4.48 + 2.30); leg IV 25.04 long (6.83 + 3.29 + 4.92 + 7.06 + 2.94).

Variation: For carapace measurements and prefoveal setae counts see Table 1. When still alive, at least one of the mature males examined showed light annulations on its leg femora, which are clearly visible not only on the ventral but also on the dorsal side (Fig. 2D, F); in alcohol these annulations are difficult to see. All specimens examined lack setae anterior to the fovea, and all specimens have both AME well developed. The extent of the scopulae differs among males: covering 3/4-5/6 of the ventral side of the leg tarsi (most often 4/5), rarely equally on all legs, in most specimens covering a larger portion on tarsi II-III that on tarsus I and tarsus IV. Variation in details of the male palp is given in Fig. 21. The angular prodorsal protrusion at the base of the distal contrategular edge is more or less prominent but always clearly visible (Fig. 21A, E-F, H-I, L). The proventral contrategular process in distal view is asymmetrically conical on the right palp of the holotype (Fig. 21I). Three male paratypes have a short subdistal ridge at the distoventral corner of their tegulum (Fig. 21K), which is very different in shape from but presumably homologous to the elevated distal tegular edge in *L. nabang* and *L. platnicki* sp. nov. (Yu *et al.*, 2021: fig. 3A-B, D-E and Fig. 23I-M). All males examined have: three ridges (two thick and one thin) reaching the apex of the sclerotised embolus part; a swollen membranous area prolaterally-proximally on the embolus complex; a beak-like dorsal apex of the distal contrategular edge; a rather indistinct proximal ledge on the retrodorsal side of the contrategulum; a short and only slightly bent proximal tegular edge. In the largest female (the allotype) the annulation (a light median ring) of metatarsi I-II is completely broken on the dorsal side (being entirely dark); in medium-sized females there are small light spots on the dorsal side of metatarsi I-II (i.e. a partially broken annulation); in smaller females the annulation of metatarsi I-II is entire, as it is on metatarsi III-IV and on all tibiae. Variation in the shape of the vulval plate is considerable (Fig. 22): the anterior poreplate margin bears one or two small processes on each side (often different numbers on both sides; these are probably reduced anterior lobes, as indicated by only little reduced lobes in two females, Fig. 22A-B); the CDO is in the centre of the poreplate (Fig. 22H) or distinctly posterior to it (Fig. 22N); the shape of the receptacular cluster ranges from fairly small and simple (Fig. 22O) to quite large and complex (Fig. 22C), but it never reaches the anterior margin of the poreplate; most vulval plates have no hairs on their lateral folds, if present, there are only 1-2 and usually only on one side, in one specimen one of these hairs is unusually thick (Fig. 22K).

Relationships and biogeography: *Liphistius cupreus* sp. nov. is very similar and presumably most closely related to *L. nabang*. Considering how far the localities of both nominal species are apart, it is very unlikely that they are actually conspecific. All species in the *birmanicus*-group appear to have quite small geographical ranges. In *Liphistius* it is generally large-sized species in the lowlands (e.g. *L. yangae* Platnick & Sedgwick, 1984; see Schwendinger *et al.*, 2019: 333, fig. 2) that are known to have relatively large geographical ranges, not small or medium-sized species in the mountains. The type locality of *L. nabang* lies about 190 km north of that of *L. cupreus* sp. nov. (both in the mountains of the Shan-Yunnan Plateau), whereas the morphologically less similar but geographically much closer *L. platnicki* sp. nov. was found only 17 km north of the type locality of *L. cupreus* sp.

nov. (Fig. 1). These three species form a well-defined subgroup within the *bristowei*-group (see Discussion - Relationships).

Biology: The spiders were found on earth banks on the side of a rural road and on the sides of a stream in a disturbed evergreen hill forest. All burrows were closed by a single trapdoor and had up to eight signal lines attached to the entrance. Penultimate males had the front door 1.45-1.9 cm long and 2.2-2.5 cm wide. The largest female had a 2.1 cm long and 2.9 cm wide door. Males matured in captivity between mid and end-June in the first year after capture (on June 8 and 9), between early May and the beginning of July in the second year, and in late May of the third year. The mating period in nature appears to be in May to June; possibly even much earlier, as indicated by the find of 3rd instar spiderlings in the burrow of a female when it was captured in early June. In captivity another female built an egg case, 2.8 cm long, 3.0 cm wide and 2.0 cm high, containing 39 light yellow eggs suspended on a layer of fine silk, about 2.5 months after being captured. Mature females usually moulted twice per year: between November and March and again between May and July. The female that built an egg case subsequently moulted in December.

Liphistius platnicki Schwendinger & Huber, sp. nov.

Figs 1, 2C, 23-24

Holotype: MHNG-ARTO-0028361 (sample MT-14/25); male (matured 1.VIII.2016); Myanmar, Shan State, N of Lashio, near Loi Kan Village (23°05'23"N, 97°47'02"E), 1140 m; 10.VI.2014; leg. P.J. Schwendinger & S. Huber.

Paratypes: MHNG-ARTO-0028362 to MHNG-ARTO-0028366, BRCM (sample MT-14/25); 6 males (matured 10.IX.2015; 26.V.2016; 2.VII.2016; 3.VII.2016; 26.VII.2016; 8.VIII.2016); collected together with the holotype. – BRCM, MHNG-ARTO-0028369 to MHNG-ARTO-0028377 (sample MT-14/25); 10 female paratypes (allotype, MHNG-ARTO-0028377, last moulted 10.III.2021); collected together with the holotype.

Etymology: We name this species in honour of the renowned American arachnologist Norman I. Platnick (1951-2020) who, together with Walter C. Sedgwick, revised and properly defined the genus *Liphistius* in 1984 and described several species (also from Myanmar) in this genus. Initially we wanted to name after him the species that he misidentified as *L. birmanicus* and that he described and illustrated from both sexes in much detail, but that meanwhile was named *L. pyinoolwin* in 2021.

Diagnosis: Medium-sized, mostly brown species with indistinctly annulated legs in females (but not in males). Most similar to *L. nabang*. Males different by distal contrategular edge in distal view without a prodorsal protrusion (Fig. 23A, E-F, I; present in *L. nabang*, Yu *et al.*, 2021: fig. 3B) and with a narrowly rounded apex (Fig. 23E-G; pointed in *L. nabang*, Yu *et al.*, 2021: fig. 3B); proximal edge of tegulum widely rounded (Fig. 23J-L; angular in *L. nabang*, Yu *et al.*, 2021: fig. 3A); paracymbium without retrolateral-proximal heel (Fig. 23A; present in *L. nabang*, Yu *et al.*, 2021: fig. 3E). Females distinguished from those of *L. nabang* by poreplate anteriorly wider than posteriorly (in *L. nabang* anteriorly narrower than posteriorly or equally wide), its anterior margin more strongly invaginated (in *L. nabang* slightly invaginated to arched); posterior stalk relatively longer and slightly constricted in anterior portion, without "bulging margins" between poreplate and posterior stalk (in *L. nabang* transition between poreplate and posterior stalk very wide and carrying widely separated "bulging margins"); posterior part of genital atrium not strongly curved ventrad (Fig. 24 cf. Yu *et al.*, 2021: fig. 4).

Description of male (holotype): *Colour in alcohol* (darker in life): Mostly light brown. Carapace with slightly darkened, large, orchid-shaped pattern on pars thoracica; eye mound black. Chelicerae cream-coloured proximally, light brown distally. Ventral side of palps and legs slightly lighter than dorsal side; most of ventral side of palpal coxae and leg tarsi cream-coloured. Legs and palps mostly light brown, without annulations; palpal tarsus and sclerotised parts of palpal organ dark brown. Membranous cuticle of opisthosoma cream-coloured and finely mottled with grey. Sternites of opisthosoma slightly darker than membranous cuticle; tergite I entirely dark brown, tergites II-VI mostly light yellow-brown, with darker spots laterally and on

Fig. 23. *Liphistius platnicki* sp. nov., palps of three males; holotype (A-D, H-J, M), paratype matured 26.VII.2019 (E-G), paratype matured 8.VIII.2016 (K-L). (A) Left tarsus and palpal organ, ventral view. (B) Left paracymbium and distal margin of tibia, retrolateral view. (C) Distal part of left tibia, ventral view. (D) Same, retrolateral and slightly proximal view. (E) Left palpal organ, distal view (dorsal side up). (F) Dorsal part of left contrategulum and embolus proper, distal and slightly ventral view. (G) Dorsal part of left contrategulum, distal and slightly dorsal view. (H) Left palpal organ and distal margin of tarsus, prodorsal and slightly proximal view. (I) Same, dorsal and slightly proximal view. (J) Same, retrolateral and slightly distal view. (K) Left palpal organ, retrolateral view. (L) Tegulum and nearby parts of right palpal organ, same view. (M) Part of left palpal organ, retroventral view; elevated distal edge of tegulum indicated by short arrow, straight, salient proximal tegular edge indicated by long arrow. Scale lines 1.0 mm (A-B; C-D; E-M).

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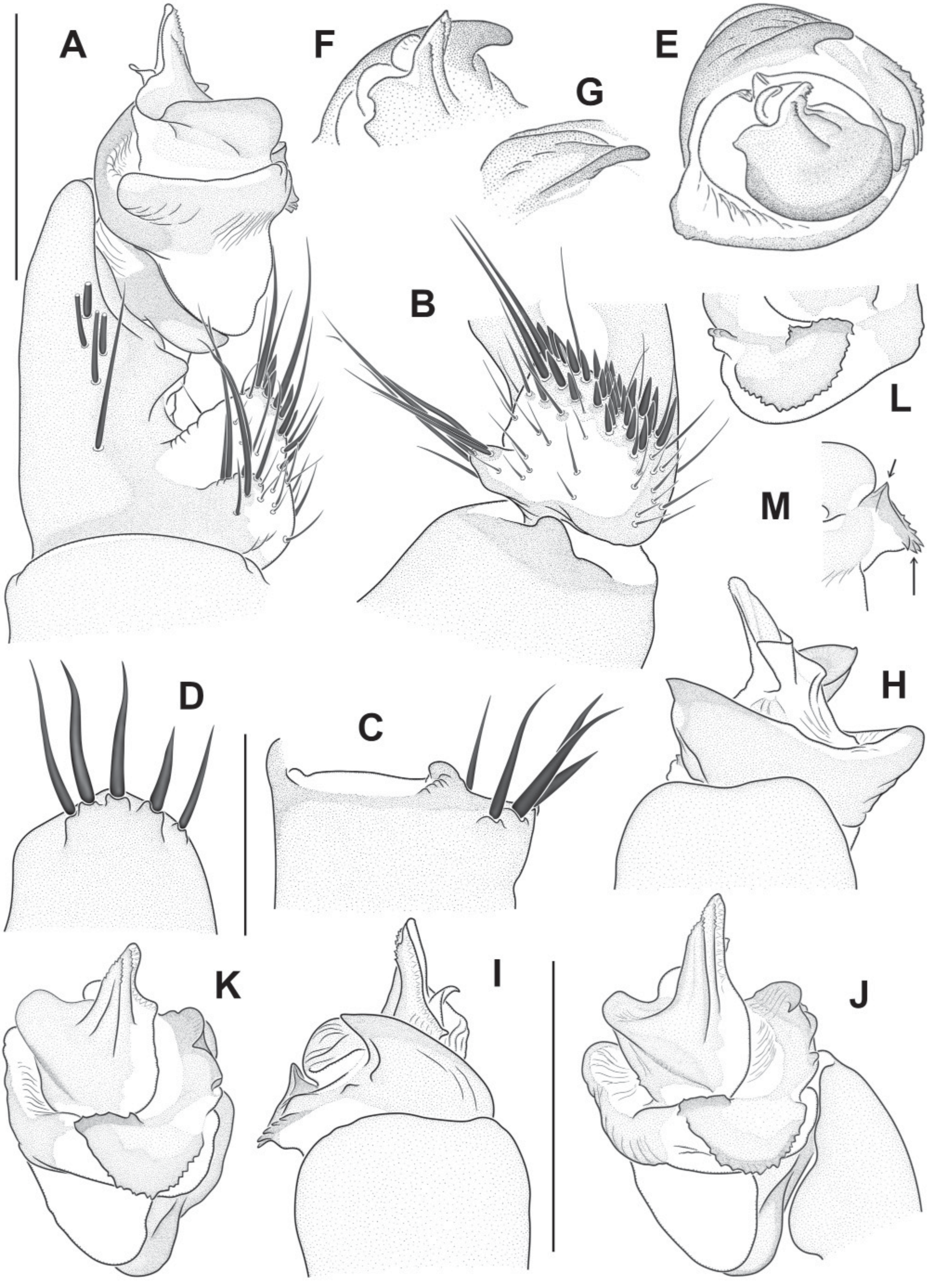
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posterior margin, tergites VII-X light yellow-brown medially and dark brown laterally.
Setae on carapace: Several small setae around eye mound, including one closely spaced enlarged pair side by side behind eye mound; few small setae on lateral margins of carapace and on coxal elevations; 1 enlarged seta on each posterolateral corner; no setae on posterior margin; 2 small setae anterior to fovea.
Cheliceral teeth: 12 small teeth of different sizes on promargin of each cheliceral groove.
Scopula: Only distally divided by median stripe on all tarsi; quite weak on tarsus I, only slightly denser on other tarsi; covering distal 5/6 of tarsi I-III, distal 4/5 of tarsus IV.
Tarsal claws: Paired claws with 3 teeth on tarsus I, 3-4 on tarsus II, 4 on tarsus III, 5-6 on tarsus IV; unpaired claw with 1-2 (mostly 2) denticles on tarsi I-III, 1 and 3 on tarsus IV.
Palp: Tibial apophysis short, triangular and basally wide in ventral view, not set back from distal margin of tibia (Fig. 23C), carrying 4 long apical megaspines, the ventral 3 distinctly longer than the dorsal one; dorsal to apophysis a quite long spine on a slightly elevated base (Fig. 23C-D). Palpal tarsus with a pronounced subdistal suture on ventral side (Fig. 23A) and with a widely but shallowly invaginated distal margin (Fig. 23H-I). Paracymbium moderately deep (Fig. 23B), in ventral view clearly longer than wide, with a distinctly conical distal side, without a retrolateral-proximal heel (Fig. 23A); cumulus distinctly elevated, unpigmented on its retroventral side, carrying a group of 5 long, strong bristles (Fig. 23A-B). Subtegulum without apophysis (Fig. 23A, J). Tegulum wide, axe-blade-shaped; its distal margin elevated, developed as a short, wide keel with a quite straight margin (Fig. 23I-J, M); its proximal edge widely rounded and finely dentate, straight (not bent proximad) and strongly protruding from surface of palpal organ (Fig. 23I-J, M). Pigmented bridge between tegulum and contrategulum on retrodorsal side of palpal organ well developed (Fig. 23J). Contrategulum with moderately developed, conical proventral process (Fig. 23E, showing paratype); essentially only a single strong wrinkle on prolateral surface and a very indistinct proximal ledge on retrodorsal side (Fig. 23H-J, see also Fig. 23F, K for paratype); distal edge of contrategulum narrow and evenly arched, without protrusion prodorsally; dorsal apex of contrategulum quite long and very narrowly rounded (Fig. 23I, see also Fig. 23E-G for paratype). Para-embolic plate short, about as long as retroventral edge of embolus complex and not clearly separated from it by an invagination (Fig. 23A). Membranous prolateral-proximal zone of embolus complex not swollen (Fig. 23 A; swollen in *L. cupreus* sp. nov., Fig. 21A); embolus proper narrowly divided, its sclerotised part strengthened by 3 longitudinal ribs reaching apex and carrying denticles distally (Fig. 23J, see also Fig. 23E-F, K for paratypes); membranous part of embolus proper distinctly shorter than sclerotised part, at its base a short, weakly pigmented area with only a few longitudinal wrinkles and with a very narrow and concave distal margin; embolic folds short (Fig. 23H).
Measurements: Total length 13.12; CL 5.45, CW 4.93; opisthosoma 5.56 long, 3.82 wide; eye mound 0.90 long, 0.96 wide; palpal coxa 1.91 long, 1.19 wide; labium 0.40 long, 0.95 wide; sternum 2.70 long, 1.91 wide (0.95 on ventral surface); palp 9.14 long (2.74 + 1.67 + 3.18 + 1.55); leg I 16.10 long (4.41 + 2.23 + 3.34 +3.97 + 2.15); leg II 17.01 long (4.45 + 2.23 + 3.46 + 4.49 + 2.38); leg III 19.12 long (4.77 + 2.23 + 3.78 + 5.52 + 2.82); leg IV 23.48 long (5.80 + 2.38 + 4.77 + 7.03 + 3.50).

Description of female (allotype): *Colour in alcohol* (darker in life, as in Fig. 2C): Mostly as in male, but generally darker, distal part of chelicerae much darker. Legs and palps with indistinct annulations, i.e. faint and broken light median rings on all tibiae of legs and palps, plus on metatarsi of legs II-IV, and very faint on tarsi II-IV; a faint light proximal ring on all leg metatarsi. Membranous cuticle of opisthosoma more distinctly mottled with grey-brown than in male; tergites II-VI with much larger dark portions, extending from anterior to posterior margins, leaving rather small paramedian pairs of longitudinal bands.
Setae on carapace: Slightly more than in the holotype; pair of stiff bristles in front of eye mound much larger; pair of enlarged setae behind eye mound situated behind each other (in male side by side); 5 small setae anterior to fovea.
Cheliceral teeth: 12 strong teeth on promargin of each cheliceral groove.
Claws: Left palpal claw with 2 denticles, right claw with 3 denticles. Paired tarsal claws of legs I-II with 3 teeth, of leg III with 4 teeth, of leg IV with 3-4 teeth; unpaired claws of leg I with 3 denticles, of leg II with 3-4 denticles, of leg III with 2 denticles, of leg IV with 1-2 denticles. All tarsi without scopula.
Vulva (Fig. 24C, F): Membranous uterus externus with a small but distinct pair of lateral pockets (see Fig. 24G for another female). Vulval plate slightly longer than wide, with a few hairs on lateral folds. Poreplate with widely and quite deeply invaginated anterior margin carrying a

Fig. 24. *Liphistius platnicki* sp. nov., vulval plates of ten females (all from exuviae), dorsal view (A, D, K, O), ventral view (B-C, E, H-J, L-N, P), anterior view (F), and isolated uterus externus (G). (A-B) Moult of 29.I.2021. (C, F) Moult of 10.III.2021 (allotype). (D-E) Moult of 25.IV.2020. (G, N) Moult of 14.X.2021. (H) Moult of 14.V.2020. (I) Moult of 20.XI.2021. (J) Moult of 13.X.2021. (K-L) Moult of 2.IV.2021. (M) Moult of 7.I.2021. (O-P) Moult of 3.X.2021. Arrows indicating paired lateral pockets of membranous uterus externus. Scale lines 1.0 mm.

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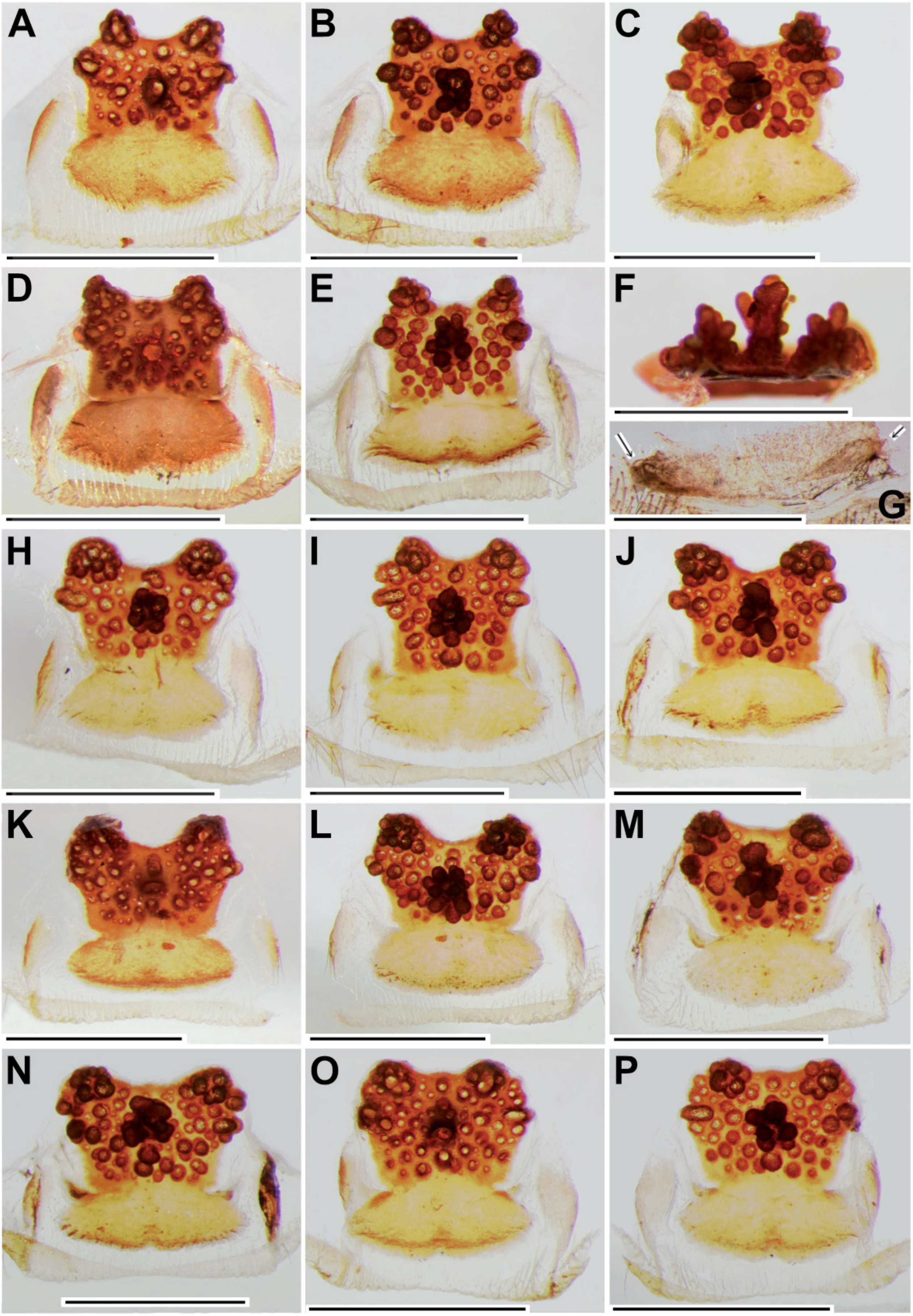
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fairly large and widely separated pair of vesicle clusters (corresponding to anterior lobes); anterolateral processes on each side of poreplate small, composed of only one vesicle (on one side) or a few vesicles (on other side). CDO small; receptacular cluster racemose, slightly longer than wide, not reaching anterior margin of poreplate, very deep (Fig. 24F). Posterior stalk quite long, wider than poreplate, with a slight constriction at transition from poreplate to posterior stalk; axe-blade-shaped, anteriorly narrower than posteriorly, with a widely arched posterior margin (Fig. 24C).

Measurements: Total length 18.56; CL 6.68, CW 5.84; opisthosoma 8.62 long, 6.92 wide; eye mound 0.97 long, 1.00 wide; palpal coxa 2.42 long, 1.55 wide; labium 0.64 long, 1.55 wide; sternum 3.54 long, 2.34 wide (1.43 on ventral surface); palp 10.61 long (3.38 + 2.03 + 2.54 + 2.66); leg I 13.59 long (4.21 + 2.42 + 2.74 + 2.70 + 1.52); leg II 14.06 long (4.21 + 2.46 + 2.74 + 2.98 + 1.67); leg III 15.30 long (4.25 + 2.54 + 2.94 + 3.66 + 1.91); leg IV 21.09 long (5.68 + 2.82 + 4.17 + 5.76 + 2.66).

Variation: For carapace measurements and prefoveal setae counts see Table 1. All specimens have both AME well developed. In four specimens the prefoveal setae are situated relatively far away from the fovea. Most females have two enlarged bristles behind the eye mound, one specimen has only one. In most males the scopula covers 5/6 of the ventral side of tarsi I-III and 4/5 of tarsus IV, in one male it covers 4/5 of tarsus I. Variation in details of the male palp is given in Fig. 23. None of the males has a prodorsal protrusion at the base of the distal contrategular edge (present in *L. nabang* and *L. cupreus* sp. nov.). The apex of the proventral contrategular process is narrowly rounded or obliquely truncate (Fig. 23E) in distal view. All males have a distinctly elevated distal tegular edge which is dentate (Fig. 23K-L) or quite smooth (Fig. 23J). All males examined have three ridges reaching the apex of the sclerotised embolus part. The lightly pigmented area at the base of the membranous embolus part has wrinkles that are more or less strongly inclined, in some specimens being almost horizontal. In small females the annulations (light median rings) on the legs and palps are more pronounced than in the allotype (the largest female examined). Variation in the shape of the vulval plate is shown in Fig. 24: the lateral folds carry no or only very few hairs; the anterior margin of the poreplate is slightly to deeply invaginated, widely concave to straight; the anterior lobes (vesicle clusters) are narrow to wide; the anterolateral processes are small and composed of one to only a few vesicles; the receptacular cluster is small to medium-sized, always racemose, never reaching the anterior poreplate margin; the posterior stalk is axe-blade-shaped to almost elliptical.

Relationships: The new species appears most closely related to *L. nabang* + *L. cupreus* sp. nov. with which it shares characters explained further below (see Discussion - Relationships). These three species form the most distinct subgroup within the *birmanicus*-group.

Distribution: This species is only known from the type locality near Lashio, about 17 km north of the type locality of *L. cupreus* sp. nov. (Fig. 1).

Biology: No mature spiders and no egg cases were found at the type locality, but the dates at which males matured in captivity (especially the first date after capture) indicate that this species has a phenology very similar to other congeneric species in Myanmar and northern Thailand.

Table 1. Carapace measurements (in mm; including data from the literature) and prefoveal setae counts of *Liphistius birmanicus* group species.

Liphistius	N of males	CL in males	CW in males	Prefoveal setae in males	N of females	CL in females	CW in females	Prefoveal setae in females
lahu	2	6.0-6.3	5.5-5.9	3-6	7	6.3-8.0	5.3-7.3	9-13
metopiae sp. nov.	2	6.03-6.19	5.44-5.50	0-4	5	7.48-8.37	6.73-7.43	2-10
tung sp. nov.	2	6.30-6.70	5.70-6.26	9-10	6	up to 7.42	up to 6.62	11-24
ferox sp. nov.	6	11.47-12.67	10.45-11.47	0-2	18	up to 18.32	16.61	0-22 (mostly 0-7)
birmanicus	8	7.79-9.50	7.29-9.45	11-25	22	6.41-14.73	5.45-13.27	over 40
hpruso					2	up to 7.02	up to 6.16	?
pinlaung	12	4.92-6.54	4.56-6.34	0-4	15	up to 7.62	up to 6.66	7-14
lordae	2	6.3-6.5	5.9-6.1	2-4	4	7.3-8.5	6.2-7.9	13-22
pyinoolwin	20	4.23-7.48	4.87-7.13	9-14	18	up to 8.42	up to 7.87	24-28
cupreus sp. nov.	8	5.67-6.11	5.00-5.63	0	12	up to 7.70	up to 6.90	0
platnicki sp. nov.	7	5.21-6.21	4.82-5.77	1-4	10	up to 6.68	up to 5.84	3-5
nabang	2	up to 4.89	up to 5.11	0?	3	up to 7.48	up to 6.52	0?

Liphistius nabang Yu, Zhang & Zhang, 2021

Liphistius nabang Yu, Zhang & Zhang, 2021: 36-40, figs 1-4 (description of males and females).

Types: MHBU-ARA-00020000 to MHBU-ARA-00020004; male holotype, 1 male and 3 female paratypes; China, Yunnan Province, Yingjiang County, Nabang (24°45'07.64"N, 97°33'47.02"E and 24°45'27.13"N, 97°33'52.86"E), 265-283 m; 2.VIII.2019 and 2.X.2019; leg. Q. Ji and K. Yu, C. Zhang & S.Y. Zhang. Types not examined; no additional material available.

Diagnosis: Distinguished by the following combination of characters: tegulum somewhat triangular in shape, with distinctly elevated distal edge and V-shaped proximal edge; distal contrategular edge with widely rounded prodorsal protrusion and pointed apex; paracymbium with retrolateral-proximal heel; cumulus distinctly elevated (Yu *et al*., 2021: fig. 3); vulval plate strongly bent ventrad in proximal part; poreplate with reduced anterior lobes and without anterolateral processes; posterior stalk short, wider than poreplate; a pair of lateral "bulging margins" between poreplate and posterior stalk (Yu *et al*., 2021: fig. 4).

Additions to description and taxonomic remarks: This species is most similar and probably very closely related to *L. cupreus* sp. nov. and *L. platnicki* sp. nov., which are also geographically the closest congeners. *Liphistius nabang* shares with these two species a number of characters which are taxonomically more or less important. These are: an enlarged spine on an elevated base dorsal of the tibial apophysis (Yu *et al*., 2021: fig. 3D; Figs 21C-D, 23C-D), a relatively long and narrow paracymbium with a distinctly conical distal side and a distinctly elevated cumulus (Yu *et al*., 2021: fig. 3D-F; Fig. 21A-B; Fig. 23A-B), a more or less distinctly elevated distal edge of the tegulum (Yu *et al*., 2021: fig. 3A-B, D-E; Fig. 21K; Fig. 23I-M; absent in some males of *L. cupreus* sp. nov., Fig. 21M) and a reduced proximal ledge on the dorsal side of the contrategulum (Yu *et al*., 2021: fig. 3A-B; Figs 21E-F, H-I, K-N, 23F, I-K) in males, plus a similar vulval plate with more or less strongly reduced anterior poreplate lobes and with a wide (at least as wide as poreplate) posterior stalk in females (Yu *et al*., 2021: fig. 4; Figs 22, 24). It is not clear from the original description and illustrations if *L. nabang* also shares with these two new species a pronounced subdistal suture on the ventral side of the palpal tarsus. *Liphistius nabang* differs from these two similar species by possessing a rather triangular tegulum (Yu *et al*., 2021: fig. 3A cf. Figs 21K, 23J-L) and a retrolateral-proximal heel on the paracymbium (Yu *et al*., 2021: fig. 3E; absent in *L. cupreus* and *L. platnicki* sp. nov., Figs 21A, 23A) in males, as well as by a wider posterior stalk and a shallowly invaginated or slightly arched distal poreplate margin (instead of always invaginated, in most cases more deeply so than on *L. nabang*) (Yu *et al*., 2021: fig. 4 cf. Figs 22, 24). The widely separated lateral pair of "bulging margins" of *L. nabang*, situated on the ventral side of the vulval plate between the poreplate and the posterior stalk (Yu *et al*., 2021: fig. 4), is a structure that we have not observed in any other congeners and which appears to be autapomorphic. We assume that these "bulging margins" are exceptionally widely separated, thickened posterior poreplate margins.
CL and CW of the male holotype are given as 4.89 and 5.11 (Yu *et al*., 2021: 37; no measurements are given for the male paratype), which suggests that this structure is wider than long, something we have not observed in any other *Liphistius* species. This odd ratio is not evident from the corresponding photo (Yu *et al*., 2021: fig. 2A), where the carapace looks clearly longer than wide. If measured in a position with the anterior and posterior carapace margin at the same focal plane, the measurements are probably different.
Although not mentioned in the original description of *L. nabang*, photos of the male holotype and of a female paratype therein (Yu *et al*., 2021: fig. 2A-B) indicate that prefoveal setae are missing in both sexes. Within the *birmanicus*-group this unusual lack (if confirmed) is only shared with the closely related *L. cupreus* sp. nov.

Variation: See Yu *et al*., 2021: 37, 40. For carapace measurements see Table 1.

Distribution: This species is known only from the type locality, which lies at low altitudes right at the border between the Yunnan Province of China and the Kachin State of Myanmar. It presumably occurs on both sides of the border.

DISCUSSION

New character: The lateral pockets of the membranous uterus externus of *Liphistius* females have previously been overlooked. They are best visible on exuviae; in entire specimens the uterus externus usually gets removed or destroyed during dissection. These pockets are quite pronounced and well visible in large species like *L. ferox* sp. nov. and *L. birmanicus* (see Figs 11I-J, N, P, 12D, F, 14D), whereas in smaller species like *L. lahu*, *L. cupreus* sp. nov. (Fig. 22E-F) and *L. platnicki* sp. nov. (Fig. 24G) they are rather small or indistinct. These pockets are presumably present in all species of the *birmanicus*-group. They also were found in *L. marginatus* Schwendinger, 1990 (*bristowei*-group), *L. ornatus* Ono & Schwendinger, 1990 (*trang*-group) and *L. malayanus* Abraham, 1923 (*malayanus*-group) and thus probably are part of the groundplan of female genitalia in *Liphistius*. This character appears to be of only minor taxonomic value on the species level, and its function is unclear. Under a compound microscope numerous tiny pores can be seen in the membranous dorsal and ventral walls of the uterus externus between these pockets, but not in the the walls of the pockets themselves. Through these pores presumably glands empty into the uterus externus (as other glands empty into the vulva through pores in the poreplate; Schwendinger & Ono, 2011: figs 59-64) and keep sperm that the female receives during copulation viable (or flush it out?). Thus in *Liphistius* the entire vulva, not only its receptacular cluster and vesicles, is a spermstoring organ. However, it is surprising that there are no pores in the walls of the lateral pockets.

Relationships: Some similarities in male and female copulatory organs (narrowly divided embolus proper, unpigmented retrolateral margin of embolus complex) and geographic proximity indicate a close relationship between the *birmanicus*-group and the *bristowei*-group. The geographical ranges of both groups are very close to each other, and there is even evidence for co-occurrence (see below). The *trang*-group is currently known to be geographically separated from the *birmanicus*-group by about 600 km (the distance between localities of *L. ferox* sp. nov. in eastern Myanmar and *L. erawan* Schwendinger, 1996 in western Thailand). Clear differences in genital morphology, especially the widely divided embolus proper in *trang*-group males (see Schwendinger, 1990: figs 60-62, Schwendinger, 2017: fig. 3A, C, E, G), do not suggest a close phylogenetic relationship between the *birmanicus*-group and the *trang*-group. The remaining currently recognized species groups (*malayanus*-, *tioman*-, *linang*-, *batuensis*-group; Schwendinger, 2017) all occur far from the geographical range of the *birmanicus*-group, in Peninsular Malaysia or on the Thai side of the Thai-Malaysian border. Little in the genital morphology of these species indicates a close relationship with *birmanicus*-group species. Among the few characters they have in common are the presence of anterior lobes on the poreplates of some species, and a quite short major embolic fold between the sclerotised and the membranous part of the embolus proper. The major embolic fold is long in *bristowei*-group males (see e.g. Schwendinger, 1990: figs 57-59) and it is a diagnostic character for that species group. Of course, this morphology-based interpretation needs to be confirmed by molecular data.

Within the *birmanicus*-group we can distinguish four more or less clearly defined subgroups on the basis of morphological characters. 1) The three northernmost species (*L. cupreus* sp. nov., *L. platnicki* sp. nov. and *L. nabang*) share a posterior stalk that is as wide or wider than the poreplate, and more or less strongly reduced anterior lobes on the poreplate in females, as well as five genital characters in males [i.e. a relatively long and narrow apex of the distal contrategular edge, a more or less distinctly elevated distal tegular edge (indistinct or absent in *L. cupreus* sp. nov.), a distinctly elevated cumulus, a relatively long paracymbium with a distinctly conical distal side, a quite strong spine on an elevated base dorsal of the tibial apophysis; Figs 21, 23, Yu *et al.*, 2021: fig. 3] that are not found in other species of this group. These three species thus form a quite well-defined subgroup. 2) *Liphistius birmanicus* and *L. pinlaung* occur close to each other and share a peculiar and probably synapomorphic distad-directed proventral contrategular process (Figs 13D, F, 15C, E; this is inclined at an angle of about 45-90° from the axis of the palpal organ in all other congeners, e.g. Fig. 4G); their female genitalia are also quite similar to each other, having anterolateral processes on the poreplate and an axe-blade-shaped posterior stalk (Figs 14, 16). The male of *L. hpruso* is unknown, but close geographical proximity, a similar vulval plate and a body colouration similar to that of *L. birmanicus* suggest that *L. hpruso* also belongs to this quite well-defined subgroup. 3) *Liphistius lahu* and *L. metopiae* sp. nov. in Thailand have very similar male palps (Figs 4, 6), but their female genitalia are more distinct [*L. metopiae* sp. nov. with anterolateral processes (Fig. 7), *L. lahu* without (Fig. 5)]. We consider these two species to be closest relatives. 4) *Liphistius tung* sp. nov. and *L. ferox* sp. nov. share a long, tongue-shaped para-embolic plate (Figs 8A, H-I, 10A-D), which is very short in all other species of the group. However, the localities of both species are far apart, and these species have otherwise little else in common that is relevant. Either the similarities in the para-embolic plate of both species are due to homoplasy, or there are yet unknown species that provide a link. 5) The remaining two species, *L. lordae* and *L. pyinoolwin*, are geographically fairly close to each other (Fig. 1). Males of both species have an adpressed proximal tegular margin (Figs 17D, 19D) and a relatively narrow posterior stalk (Figs 18, 20). Morphology-based support for a very close relationship is not particularly strong, and it seems probable that there are yet unknown species which are more closely related to these two species than they are to each other.

Zoogeography: The *birmanicus*-group is the northernmost of the species groups in *Liphistius*. Most of its species occur in Myanmar, two in northern Thailand (*L. lahu* and *L. metopiae* sp. nov.) and one in southern China (*L. nabang*). The geographical range of the *birmanicus*-group borders on that of the *bristowei*-group roughly along the frontier between Myanmar and northern Thailand, but no overlap is yet known. *Liphistius lahu* and *L. lannaianus* Schwendinger, 1990 were found only about two kilometres away from each other, on either side of a mountain ridge at Doi Angkhang, on the Thai side of the border. We know of at least two true syntopic occurrences of *Liphistius* species in Myanmar: near Taungoo (= Toungoo) burrows of *L. ferox* sp. nov. were found together with those of an undescribed species in the *bristowei*-group. Based on molecular data, Ono & Aung (2020: 90, 94) reported the existence of two congeneric species (*L. tanakai* in the *trang*-group plus an undescribed species represented only by juveniles) on Lampi Island in southern Myanmar. All known *birmanicus*-group species are allotopic, which is also the case for the *bristowei*-group and for the species groups in Peninsular Malaysia, but not for the species-rich, widely distributed and ecologically very successful *trang*-group.

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