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A revision of the trapdoor spider genus *Liphistius* (Mesothelae: Liphistiidae) in Peninsular Malaysia; part 2

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Abstract: The currently known species of the *Liphistius trang*-group in Peninsular Malaysia are revised on the basis of genital morphology and an identification key is given. *Liphistius thaleban* Schwendinger, 1990 and *L. rufipes* Schwendinger, 1995 are placed in the synonymy of *L. yangae* Platnick & Sedgwick, 1984. The previously unknown male of *L. kanthan* Platnick, in Platnick *et al.*, 1997 is described for the first time. *Liphistius kanthan* and *L. tempurung* Platnick, in Platnick *et al.*, 1997 are reported to occur together at the Tempurung Cave. *Liphistius buran* Schwendinger, sp. nov., an island species with a novel character of the palpal organ, is described from males and females. Information on and illustrations of intraspecific variation in most of these species is given together with data on biology and distribution. For selected *Liphistius* species in Malaysia a phylogenetic tree based on an analysis of COI sequences is presented and discussed in comparison with relationships inferred from morphological characters. Molecular data confirm the distinction between the *malayanus*-group and the *trang*-group in Malaysia, but, unlike an earlier interpretation of morphological evolution of genitalia, place species of the *trang*-group as basal to the *malayanus*-group.

Keywords: Arachnida - morphology - taxonomy - variation - biology - cave species - COI.

INTRODUCTION

The Malaysian *Liphistius* species belonging to the *malayanus*, *batuensis*, *tioman* and *linang* species-groups were treated in the first part of this revision (Schwendinger, 2017), here those of the *trang*-group follow. The *trang*-group was defined by Schwendinger (1990: 349) and later subdivided into six informal subgroups (species complexes) on the basis of genital characters (A: *L. dangrek, L. isan, L. nesioticus, L. ornatus, L. owadai, L. phileion, L. sayam, L. suwat*; B: *L. erawan, L. laoticus, L. ochraceus, L. onoi, L. pusohm, L. tham, L. thoranie*; C: *L. fuscus, L. phuketensis, L. schwendingeri*; D: *L. albipes, L. bicoloripes, L. buran* sp. nov., *L. castaneus, L. desultor, L. kanthan, L. laruticus, L. niphanae, L. sumatranus, L. trang, L. yangae*; E: *L. langkawi, L. murphyorum, L. thaleri*; F: *L. tenuis*. For species authorities and their references see the World Spider Catalog, 2019). This group is species-rich (currently 33 species, excluding the two new synonyms and including the new species described here) and widely distributed in the northern part of Malaysia, in southern, western, central and eastern Thailand, in southwestern Laos and in western Cambodia (unpublished data for the latter country). In addition to the single new species from Malaysia described here, several more from other SE-Asian countries await description.

In parallel to and independently from the morphology-based study of Malaysian *Liphistius* species by Schwendinger (2017), the second author carried out a study of selected *Liphistius* species of Malaysia for her M. Sc. thesis (Syuhadah, 2016) which included morphological and molecular data. The results of this study are presented here and compared with interspecies relationships inferred from morphological characters.

MATERIAL AND METHODS

Morphological methods: Morphological characters were studied and drawn mainly with a Zeiss SV11 stereomicroscope and an attached drawing tube, the vulval plates of the *L. yangae* paratypes with a Nikon Optiphot compound microscope and an attached drawing tube. SEM-micrographs of a critical-point-dried and

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gold-sputtered male palp were taken with a Zeiss DSM-940-A scanning electron microscope. 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 with stiff bristles. Clearing in KOH was avoided, because it often leads to more or less pronounced 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. Terminology of genital structures follows Schwendinger & Ono (2011) and Schwendinger (2017); it partly differs from the terminology used in earlier publications on *Liphistius*. 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 midpoint of anterior and posterior margin. 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 measurement are given in the following manner: total length (femur + patella + tibia + metatarsus + tarsus). In the paragraph "Variation" only taxonomic characters considered to be relevant are mentioned. 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 primary type specimens of several taxa treated here were not re-examined because: (a) those of the "old species" (*L. desultor*) were redescribed and illustrated in Haupt (1983) and Platnick & Sedgwick (1984); (b) the descriptions and illustrations of the other taxa (*L. kanthan, L. langkawi, L. laruticus, L. murphyorum, L. yangae*) are considered sufficient and reliable, and thus a re-examination of the types is not regarded as necessary; (c) some of the new specimens presented here were collected at (or very close to) the type localities of their respective species (*L. kanthan, L. langkawi*, *L. muphyorum*, *L. yangae*).

Male spiders of the genus *Liphistius* possess a unique character: an embolus (here called "embolus proper") that is deeply split into a thick sclerotised part (strengthened by longitudinal ribs) and a thin membranous (hyaline) part. On one side (the prolateral or proventral side) the split reaches down to the base of the embolus proper. On the other (retrodorsal or prodorsal) side the split does not reach the base of the embolus proper but is drawn out into a more or less widely extended membranous fold, the major embolic fold (Fig. 14F-G; Schwendinger, 2017: fig. 3). This condition we call a deeply split embolus, and to our knowledge it is not found in any other spiders. In the *trang*-group males both embolic parts are distinctly apart and the division is wide (Schwendinger, 1990: figs 60-62; Schwendinger, 2017: fig. 3A, C, E, G), whereas in other species groups both parts are close to each other and the division is narrow [however, embolus morphology is not uniform in these species groups – compare e.g. *bristowei*-group (Schwendinger, 1990: figs 57-59) with *malayanus*-group (Schwendinger, 2017: fig. 3B, D, F, H) – and thus these are not necessarily most closely related to each other]. In the Heptathelinae the embolus is similar to that of *Liphistius* and certainly homologous, but of different build. Most importantly: the entire embolus is sclerotised, there is no membranous part. The thin apical rim of the heptatheline embolus opening is usually hyaline or partly hyaline (e.g. Logunov & Vahtera, 2017: figs 14, 17), but there is no separate membranous embolic part. In a few Heptathelinae and in most Opisthothelae the opening of the spermophor is a simple round pore (e.g. Haupt, 2003: fig. 51C-E), in many others the embolus is compressed and the opening is a long thin slit (e.g. Schwendinger & Ono, 2011: figs 6, 8-9). In some species this slit has a straight apical margin (e.g. Haupt, 2003: fig. 48C; Schwendinger & Ono, 2011: figs 6, 26), in others the distal margin is more or less distinctly invaginated (e.g. Haupt, 2003: fig. 49A-B; Logunov & Vahtera, 2017: figs 7, 9, 12, 14, 17, 20), but judging from heptatheline males we have examined it is not split. What appears to be a deep split down to the base on one side of the embolus in heptatheline males shown in Ono (1997: figs 1, 15; 1998: figs 6, 21) needs to be re-examined; it may be a step and not a split.

Consequently our character state coding for embolus morphology (see Table 1 and Fig. 17) is: (A, white) entirely sclerotised, undivided and tube-like; (B, blue) entirely sclerotised, undivided and compressed, with straight distal margin; (C, green) entirely sclerotised, undivided and compressed, with more or less strongly invaginated distal margin; (D, yellow) partly sclerotised, narrowly divided into sclerotised and membranous parts; (E, black) partly sclerotised, widely divided into sclerotised and membranous parts.

Molecular methods: The molecular analysis includes COI sequence data from 45 ingroup terminals: sequences from 40 *Liphistius* specimens from Peninsular Malaysia were generated during the course of the second author's research work for her M. Sc. (Syuhadah, 2016), and sequences from five additional *Liphistius* specimens from Laos, Malaysia and Thailand were obtained from GenBank (see Table 1 for detailed data and references). Thirty-six specimens of the closely related sub-family Heptathelinae, as well as seven specimens of the mygalomorph families Atypidae (2 spp.), Halonoproctidae (4 spp.) and Ctenizidae (1 sp.) were selected as out-groups. The data for these species were also downloaded from GenBank (see Table 1 for references).

DNA extraction, polymerase chain reaction and sequencing: The specimens sequenced in the course of this study were collected in Peninsular Malaysia and preserved in 70% ethanol at room temperature, except

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for the dissected right fourth leg of each specimen which was preserved in absolute ethanol at minus 20°C. One to three legs of each specimen were stored individually in microcentrifuge tubes filled with absolute ethanol and kept at minus 20°C prior to DNA analysis.

The whole genomic DNA was extracted from one or two legs per individual using the I-genomic CTB DNA Extraction Kit protocol for animal tissue (iNtRON Biotechnology, Seongnam, South Korea). A fragment of the mitochondrial cytochrome c oxidase subunit I gene (COI) was amplified using the universal primer pair LCO1490, HCO2180 (Folmer *et al.*, 1994). Amplifications of the COI was performed in a final volume of 30 µL containing 2.40 µL dNTPs, 3.00 µL of 10X i-Taq PCR buffer, 0.60 µL of i-Taq™ plus DNA Polymerase (iNtRON Biotechnology, Seongnam, South Korea); 15.0 µL ultra-pure water; 10 pmol of each forward and reverse primer; and 7.5 µL genomic DNA.

Table 1. Detailed data of the specimens included in the phylogenetic analysis, with GenBank registration numbers for COI sequences (Fig. 16) and character coding for embolus types (Fig. 17).

	FAMILY/SUB-FAMILY	Specimen Code	Genus	Species	Sex	Locality	GenBank accession no.	Reference	Embolus type
INGROUP	LIPHISTIINAE	LS013	*Liphistius*	*malayanus*	♀	Ampang Forest Reserve, Selangor	KR017711	this study	D
INGROUP	LIPHISTIINAE	LS014	*Liphistius*	*malayanus*	♀	Ampang Forest Reserve, Selangor	KR017712	this study	D
INGROUP	LIPHISTIINAE	LS020	*Liphistius*	*malayanus*	♀	Ulu Bendul Amenity Forest, Negeri Sembilan	KR028500	this study	D
INGROUP	LIPHISTIINAE	LS114	*Liphistius*	*malayanus*	♀	Ulu Bendul Amenity Forest, Negeri Sembilan	KR017713	this study	D
INGROUP	LIPHISTIINAE	LS012	*Liphistius*	*malayanus*	♀	Fraser's Hill, Pahang	KR028501	this study	D
INGROUP	LIPHISTIINAE	LS008	*Liphistius*	*malayanus*	♀	Fraser's Hill, Pahang	KR028502	this study	D
INGROUP	LIPHISTIINAE	LS009	*Liphistius*	*malayanus*	♂	Genting Highland, Pahang	KR028504	this study	D
INGROUP	LIPHISTIINAE	LS011	*Liphistius*	*malayanus*	♀	Genting Highland, Pahang	KR028503	this study	D
INGROUP	LIPHISTIINAE	LS010	*Liphistius*	*malayanus*	♀	Genting Highland, Pahang	KR028505	this study	D
INGROUP	LIPHISTIINAE	LS001	*Liphistius*	*malayanus*	♀	Ulu Gombak Forest Reserve, Selangor	KR028506	this study	D
INGROUP	LIPHISTIINAE	LS018	*Liphistius*	*malayanus*	♀	Ulu Gombak Forest Reserve, Selangor	KR028507	this study	D
INGROUP	LIPHISTIINAE	LS019	*Liphistius*	*malayanus*	♀	Ulu Gombak Forest Reserve, Selangor	KR028508	this study	D
INGROUP	LIPHISTIINAE	LS098	*Liphistius*	*malayanus*	juvenile	Kemensah Waterfall, Selangor	KR028537	this study	D
INGROUP	LIPHISTIINAE	LS021	*Liphistius*	*desultor*	♀	Penang Botanic Gardens, Penang	KR028514	this study	E
INGROUP	LIPHISTIINAE	LS034	*Liphistius*	*desultor*	♀	Penang Botanic Gardens, Penang	KR028515	this study	E
INGROUP	LIPHISTIINAE	LS036	*Liphistius*	*desultor*	♀	Penang Botanic Gardens, Penang	KR028516	this study	E
INGROUP	LIPHISTIINAE	LS053	*Liphistius*	*desultor*	♀	Teluk Bahang Amenity Forest, Penang	KR028517	this study	E
INGROUP	LIPHISTIINAE	LS054	*Liphistius*	*desultor*	juvenile	Teluk Bahang Amenity Forest, Penang	KR028518	this study	E
INGROUP	LIPHISTIINAE	LS022	*Liphistius*	*murphyorum*	♂	Teluk Bahang Amenity Forest, Penang	KR028519	this study	E
INGROUP	LIPHISTIINAE	LS035	*Liphistius*	*murphyorum*	♀	Teluk Bahang Amenity Forest, Penang	KR028520	this study	E

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	FAMILY/SUB-FAMILY	Specimen Code	Genus	Species	Sex	Locality	GenBank accession no.	Reference	Embolus type
INGROUP	LIPHISTIINAE	LS037	*Liphistius*	*murphyorum*	♀	Teluk Bahang Amenity Forest, Penang	KR028521	this study	E
INGROUP	LIPHISTIINAE	LS093	*Liphistius*	*endau*	juvenile	Endau-Rompin National Park, Johor	KR028522	this study	D
INGROUP	LIPHISTIINAE	LS094	*Liphistius*	*endau*	♀	Endau-Rompin National Park, Johor	KR028523	this study	D
INGROUP	LIPHISTIINAE	LS148	*Liphistius*	*endau*	♀	Endau-Rompin National Park, Johor	KR028524	this study	D
INGROUP	LIPHISTIINAE	LS140	*Liphistius*	*endau*	♀	Kota Tinggi Waterfall, Johor	KR028525	this study	D
INGROUP	LIPHISTIINAE	LS141	*Liphistius*	*endau*	♀	Kota Tinggi Waterfall, Johor	KR028526	this study	D
INGROUP	LIPHISTIINAE	LS125	*Liphistius*	*laruticus*	♀	Maxwell Hill, Perak	KR028527	this study	E
INGROUP	LIPHISTIINAE	LS128	*Liphistius*	*laruticus*	♀	Maxwell Hill, Perak	KR028528	this study	E
INGROUP	LIPHISTIINAE	LS136	*Liphistius*	*laruticus*	♀	Maxwell Hill, Perak	KR028529	this study	E
INGROUP	LIPHISTIINAE	LS142	*Liphistius*	sp.	♀	Lake Kenyir, Terengganu	KR028530	this study	?
INGROUP	LIPHISTIINAE	LS143	*Liphistius*	sp.	♂	Lake Kenyir, Terengganu	KR028531	this study	D
INGROUP	LIPHISTIINAE	LS049	*Liphistius*	sp.	juvenile	Pasir Raja Forest Reserve, Terengganu	KR028535	this study	?
INGROUP	LIPHISTIINAE	LS051	*Liphistius*	sp.	juvenile	Pasir Raja Forest Reserve, Terengganu	KR028536	this study	?
INGROUP	LIPHISTIINAE	LS059	*Liphistius*	sp.	juvenile	Felda Tekam, Pahang	KR028538	this study	?
INGROUP	LIPHISTIINAE	LS067	*Liphistius*	sp.	juvenile	Felda Tekam, Pahang	KR028539	this study	?
INGROUP	LIPHISTIINAE	LS080	*Liphistius*	cf. *desultor*	juvenile	Ulu Kinta Amenity Forest, Perak	KR028532	this study	E
INGROUP	LIPHISTIINAE	LS081	*Liphistius*	cf. *desultor*	♀	Ulu Kinta Amenity Forest, Perak	KR028533	this study	E
INGROUP	LIPHISTIINAE	LS082	*Liphistius*	cf. *desultor*	♀	Ulu Kinta Amenity Forest, Perak	KR028534	this study	E
INGROUP	LIPHISTIINAE	LS002	*Liphistius*	sp.	♂	Parit Falls Forest Eco Park, Cameron Hl., Pahang	KR028511	this study	D
INGROUP	LIPHISTIINAE	LS003	*Liphistius*	sp.	♂	Parit Falls Forest Eco Park, Cameron Hl., Pahang	KR028512	this study	D
INGROUP	LIPHISTIINAE	-	*Liphistius*	*laoticus*	-	Laos, Champasak, Etu Waterfall	KP229833	Xu *et al*., 2015b	E
INGROUP	LIPHISTIINAE	-	*Liphistius*	*laoticus*	-	Laos, Champasak, Fane Waterfall	KP229884	Xu *et al*., 2015b	E
INGROUP	LIPHISTIINAE	-	*Liphistius*	*erawan*	-	Thailand	JQ407803	Podsiadlowski *et al.* (unpublished)	E
INGROUP	LIPHISTIINAE	-	*Liphistius*	*malayanus*	-	Malaysia, Pahang, Genting Highlands	KP229904	Xu *et al.*, 2015b	D
INGROUP	LIPHISTIINAE	-	*Liphistius*	*malayanus*	-	Malaysia, Pahang, Genting Highlands	KP229862	Xu *et al*., 2015b	D
OUTGROUP	HEPTATHELINAE	-	*Ganthela*	*cipingensis*	-	China, Jingganshan, Jiangxi	KP229886	Xu *et al.*, 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Ganthela*	sp.	-	China, Wangjiangshan, Fujian	KP229899	Xu *et al.*, 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Heptathela*	*amamiensis*	-	Japan, Amami, Kyushu	KP229858	Xu *et al*., 2015b	C
OUTGROUP	HEPTATHELINAE	-	*Heptathela*	*higoensis*	-	Japan, Miyazaki, Kyushu	KP229890	Xu *et al.*, 2015b	C
OUTGROUP	HEPTATHELINAE	-	*Heptathela*	*kimurai*	-	Japan, Shiroyama, Kyushu	KP229828	Xu *et al*., 2015b	C

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	FAMILY/SUB-FAMILY	Specimen Code	Genus	Species	Sex	Locality	GenBank accession no.	Reference	Embolus type
OUTGROUP	HEPTATHELINAE	-	*Qiongthela*	*baishensis*	-	China, Baisha, Hainan	KP229805	Xu *et al*., 2015b	B
OUTGROUP	HEPTATHELINAE	-	*Qiongthela*	sp.	-	China, Bawangling, Hainan	KP229897	Xu *et al*., 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Qiongthela*	sp.	-	China, Hainan, Jianfeng	KP229901	Xu *et a*l., 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Ryuthela*	*ishigakiensis*	-	Japan, Okinawa, Iriomotejima	KP229823	Xu *et al*., 2015b	B
OUTGROUP	HEPTATHELINAE	-	*Ryuthela*	*nishihirai*	-	Japan, Taira, Okinawa	KP229830	Xu *et al*., 2015b	C
OUTGROUP	HEPTATHELINAE	-	*Ryuthela*	*sasakii*	-	Japan, Tokashiki, Okinawa	KP229813	Xu *et al.*, 2015b	C
OUTGROUP	HEPTATHELINAE	-	*Sinothela*	*heyangensis*	-	China, Shanxi	KP229846	Xu *et al.*, 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Sinothela*	*luotianensis*	-	China, Luotian, Hubei	KP229881	Xu *et al.*, 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Songthela*	*goulouensis*	-	China, Gouloufeng, Hunan	KP229824	Xu *et al.*, 2015b	B
OUTGROUP	HEPTATHELINAE	-	*Songthela*	*hangzhouensis*	-	China, Hengshan, Hunan	KP229802	Xu *et al*., 2015b	B
OUTGROUP	HEPTATHELINAE	-	*Songthela*	*sapana*	-	Vietnam, Sa Pa	KP229882	Xu *et al*., 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Sinothela*	*sinensis*	-	China, Yiyuan, Shandong	KP229871	Xu *et al.*, 2015b	B
OUTGROUP	HEPTATHELINAE	-	*Songthela*	*wosanensis*	-	China, Eschan, Yunnan	KP229836	Xu *et al*., 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Songthela*	sp.	-	China, Chengxi, Anjiang, Hunan	KP229850	Xu *et al*., 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Songthela*	sp.	-	China, Dali, Hunan	KP229818	Xu *et a*l., 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Songthela*	sp.	-	China, Kumming, Yunnan	KP229883	Xu *et al*., 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Songthela*	sp.	-	China, Lichuan, Hubei	KP229851	Xu *et al*., 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Songthela*	sp.	-	China, Western Hill, Yunan	KP229906	Xu *et al.*, 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	*abca*	-	Vietnam, Lao Cai	KP229817	Xu *et al*., 2015b	C
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	*cucphuongensis*	-	Vietnam, Cuc Phuong	KT767580	Xu *et al*., 2016	C
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	*cucphuongen*sis	-	Vietnam, Cuc Phuong	KP229855	Xu *et al*., 2015b	C
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	*hongkong*	-	China, Hong Kong	KP229867	Xu *et al*., 2015b	A
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	*nahang*	-	Vietnam, Tuyen Quang, Na Hang	KY417118	Vahtera & Logunov, 2017	C
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	*nahang*	-	Vietnam, Tuyen Quang, Na Hang	KY417119	Vahtera & Logunov, 2017	C
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	*tomokunii*	-	Vietnam, Tam Dao	KP229912	Xu *et al*., 2015b	C
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	*tonkinensis*	-	Vietnam, Luc Nam	KP229840	Xu *et al.*, 2015b	C
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	sp.	-	China, Mt Yuelu, Hunan	KP229841	Xu *et al*., 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	sp.	-	Vietnam, Yenbai	KP229853	Xu *et al.*, 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	sp.	-	China, Chenzhou, Hunan	KP229905	Xu *et al.*, 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	sp.	-	China, Ji'an, Jiangxi	KP229856	Xu *et al.*, 2015b	?
OUTGROUP	HEPTATHELINAE	-	*Vinathela*	sp.	-	China, Jinggangshan, Jiangxi	KP229915	Xu *et al.*, 2015b	?
OUTGROUP	ATYPIDAE	-	*Atypu*s	*yajuni*	-	China, Mojiang, Yunnan	KP208887	Xu *et al.*, 2015b	A
OUTGROUP	ATYPIDAE	-	*Atypus*	*heterothecus*	-	China, Luohu, Shenzhen	KP208882	Xu *et al.*, 2015b	A
OUTGROUP	HALONOPROCTIDAE	-	*Conothele*	*taiwanensis*	-	Laos, Oudom Xai Province	KP208890	Xu *et al*., 2015b	A
OUTGROUP	HALONOPROCTIDAE	-	*Cyclocosmia*	*ricketti*	-	China, Hangzhou, Zhejiang	KP208889	Xu *et al*., 2015b	A
OUTGROUP	CTENIZIDAE	-	*Cyrtocarenum*	*grajum*	-	-	KU854132	Kornilios *et al*., 2016	A
OUTGROUP	HALONOPROCTIDAE	-	*Latouchia*	*typica*	-	China, Shenzhen	KP208888	Xu *et al*., 2015b	A
OUTGROUP	HALONOPROCTIDAE	-	*Ummidia*	*picea*	-	Spain, Murcia, Alberca, El Valle	KT756335	Opatova *et al*. (unpublished)	A

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PCR parameters included an initial 95°C denaturation followed by 35 cycles of 45 seconds at 95°C, 45 seconds at 56.3°C, 45 seconds at 72°C with a final 5 minute extension at 72°C. The PCR products were purified and directly sequenced using 3730XL Genetic Analyzer (Applied Biosystems).

Prior to data analysis all sequence reads were checked against chromatograph data using the Sequence Scanner v1.0 (Applied Biosystem™, California, USA) to ensure a high quality of the sequence and to remove ambiguous bases. Each chromatogram for the forward and reverse sequence for each sample was checked by eye for errors and assembled using MEGA 5.2 (Tamura *et al.*, 2011). All nucleotide sequences were then aligned using the Clustal W algorithm included in MEGA and were trimmed to a length of 552 bp. The aligned COI sequences were submitted to the GenBank database (see Table 1 for accession numbers and detailed data).

Phylogenetic analysis: The COI sequences were divided into three partitions corresponding to the three codon positions. The substitution model GTR+I+G, chosen on the basis of the Bayesian information criterion (BIC) in jMODELTEST 2.1.10 (Darriba *et al.*, 2012), was applied to the three partitions independently. We conducted Bayesian-inference (BI) analysis (Huelsenbeck & Ronquist, 2001) in MrBayes 3.2.7 (Ronquist *et al.*, 2012) by running Markov chain Monte Carlo (MCMC) in two independent runs of four chains. Trees were sampled every 1000 generations and the two runs converged after 7,202,000 generations. The first 25% of the generated trees were discarded, as confirmed by visualisation of the log likelihood trace and the average standard deviation of the split frequencies being <0.01. Posterior probabilities were calculated and reported on a 50% majority-rule consensus tree of the post-burnin sample.

Usefulness of COI: Mitochondrial DNA evolves more rapidly (two to more than twenty time faster) than nuclear DNA throughout the animal kingdom (Allio *et al*., 2017). It is thus generally regarded as a poor candidate to evaluate phylogenetic relationships at the deeper hierarchical levels, but can still be considered for studies of recently evolved taxonomic groups (Moore, 1995). For instance, Hwang & Kim (1999) consider COI loci suitable to infer intrafamilial and intrageneric phylogenetic relationships in Arthropoda. Nevertheless, evaluating phylogenies based on a single mitochondrial gene is questionable, and a multilocus analysis including both mitochondrial and nuclear markers is always more appropriate for inferring a phylogeny (Rubinoff & Holland, 2005). However, in the present case our aim was not to provide an accurate assessment of the phylogenetic relationships within Liphistiidae, but rather to determine if molecular data will recover clades congruent with species groups diagnosed by embolus morphology. The DNA barcoding region of the mitochondrial cytochrome *c* oxidase subunit I has already been used with success to delimit species in Liphistiidae (Xu *et al.*, 2015a) as well as in other spider groups (Hamilton *et al*., 2011; Čandek & Kuntner, 2015), and thus appears to be a suitable tool for confirming the phylogenetic importance of embolus morphology in the genus *Liphistius*.

Character optimization: Character states pertaining to the morphology of the embolus were mapped onto the Bayesian cladogram with Mesquite version 2.75 (Maddison & Maddison, 2011) using the parsimony criterion. The characters were treated as ordered because there is a clear evolutionary sequence from a simple tube-like, completely sclerotised embolus developing into more complex and divided structures with a sclerotised and a membranous part. The consistency index and retention index were calculated and are provided in the corresponding figure.

Museum acronyms: AMNH = American Museum of Natural History, New York, USA; BMNH = Natural History Museum, London, UK (formerly British Museum of Natural History); MHNG = Muséum d'histoire naturelle de la Ville de Genève, Switzerland; SMF = Senckenberg Museum, Frankfurt, Germany; NHMS = Lee Kong Chian Natural History Museum, Singapore; ZMC = Zoological Museum, University of Copenhagen, Denmark.

Other abbreviations used in the text: AME = anterior median eyes, CDO = central dorsal opening (macropore) of poreplate. Additional abbreviations are explained in the corresponding figure legends.

TAXONOMIC PART

The *trang*-group

Diagnosis: Small to large species (carapace length of males 4.36-12.04, carapace width 3.64-10.99). Males are distinguished from those of all other species groups in *Liphistius* by a deeply split embolus proper with the sclerotised part (strengthened by three longitudinal ridges) and the membranous part being widely divided and connected by a short but very wide major embolic fold on the retrolateral side (Schwendinger, 2017: fig. 3A, C, E, G), as well as by a pronounced, usually quite long para-embolic plate which is not or only slightly inclined from the axis of the embolus proper. Fully grown females (but not all small ones) are distinguished from those of other species groups in Malaysia by possessing a small CDO, a small receptacular cluster (never protruding beyond the anterior margin of the poreplate), more or less pronounced (in some species reduced or absent) lateral processes on the ventral rim of the poreplate, and a quite short posterior stalk which is rarely wider than the poreplate and rarely constricted at its base. Females and large juvenile males of some species possess orange-coloured proximal limb articles (i.e. always the femora; in at least one species in Thailand also the patellae and tibiae) and parts of the carapace (Fig. 1A).

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Species included: *Liphistius albipes, L. bicoloripes, L. buran* sp. nov., *L. castaneus, L. dangrek, L. desultor, L. erawan, L. fuscus, L. isan, L. kanthan, L. langkawi, L. laoticus, L. laruticus, L. murphyorum, L. nesioticus, L. niphanae, L. ochraceus, L. onoi, L. ornatus, L. owadai, L. phileion, L. phuketensis, L. pusohm, L. sayam, L. schwendingeri, L. sumatranus, L. suwat, L. tenuis, L. thaleri, L. tham, L. thoranie, L. trang, L. yangae*. For species authorities and their references see the World Spider Catalog (2019).

Relationships: The relationships with other species groups are unclear. Widely divided embolic parts as present in species of this group are neither found in other congeners nor in other spiders, and this character state is thus possibly a synapomorphy. Similarities in the shape of the vulval plates indicate a close relationship with species of the *bristowei*-group. In contrast to embolus morphology, COI data indicate that the *trang*-group is parapyletic and that the *malayanus*-group is nested in it (see Figs 16-17 and paragraph "Molecular part").

Distribution: In Malaysia all known species of this group are only found in the northern and northwestern parts of the country, from the Thai-Malaysian border in Perlis in the north to Gunung Stong in Kelantan in the east to Pangkor Island in Perak in the south (Fig. 2, localities 1, 6-7, 10-18). In Thailand this group is widely distributed and species-rich in the southern, central and eastern regions of the country. In Laos at least two species (one of them also occurring in Thailand; Schwendinger, 2013) are found in the south, and in Cambodia at least two species occur in the west (Schwendinger, unpublished data).

Liphistius yangae Platnick & Sedgwick, 1984

Figs 3-4

Liphistius yangae Platnick & Sedgwick, 1984: 14, figs 22-23 (description of female).
Liphistius thaleban Schwendinger, 1990: 345-347, figs 50-56 (description of male and female). **New synonym.**
Liphistius rufipes Schwendinger, 1995: 143-144, figs 1-6, 9-11 (description of male and female). **New synonym.**

Types: NHMS (previously deposited in the Zoological Reference Collection of the National University of Singapore); female holotype (not examined); Malaysia, Perlis, Kaki Bukit; collector unknown; December 1938. – NHMS and AMNH; 13 mostly young female paratypes (4 of them, NHMS ZRC.1983.11.11.1, examined); same data as for holotype. – MHNG; male holotype and 4 female paratypes of *L. thaleban* syn. nov. (examined); Thailand, Thaleban N.P.; 20.VIII.1986; leg. P.J. Schwendinger. – MHNG; male holotype, 3 female paratypes of *L. rufipes* syn. nov. (examined); Thailand, Than To Waterfall.; 2.II.1991 and 19.I.1994; leg. P.J. Schwendinger. – 1 male paratype of *L. rufipes* syn. nov. (examined); Malaysia, Perak, E of Bukit Baring; 8.II.1991; leg. P.J. Schwendinger.

Other material examined: MHNG; 1 male (matured 20.XII.1995), 1 juv. male, 1 female; Thailand, Songkhla Prov., Tone Nga Chang Waterfall, about 15 km W of Had Yai, 160 m; 2.II.1995; leg. P.J. Schwendinger. – MHNG, sample THA-99/4; 2 males (matured 20.IV.2003 and 19.IV.2004, respectively), 1 penultimate male, 2 females (last moulted 16.X.2002 and 7.II.2003, respectively); Thailand, Pattani Prov., Sankhalakhierie Mountains; 22.X.1999; leg. P.J. Schwendinger. – MHNG, sample THA-11/08; 1 female



Fig. 1. *Liphistius* spp. females in front of burrow with door closed (A) and at burrow entrance with door open (B). (A) Not fully-grown spider, probably belonging to *L. desultor*, at an undisclosed locality near Ipoh (© Fletcher & Baylis). (B) *L. kanthan* inside Kanthan Cave (© N. Syuhadah).

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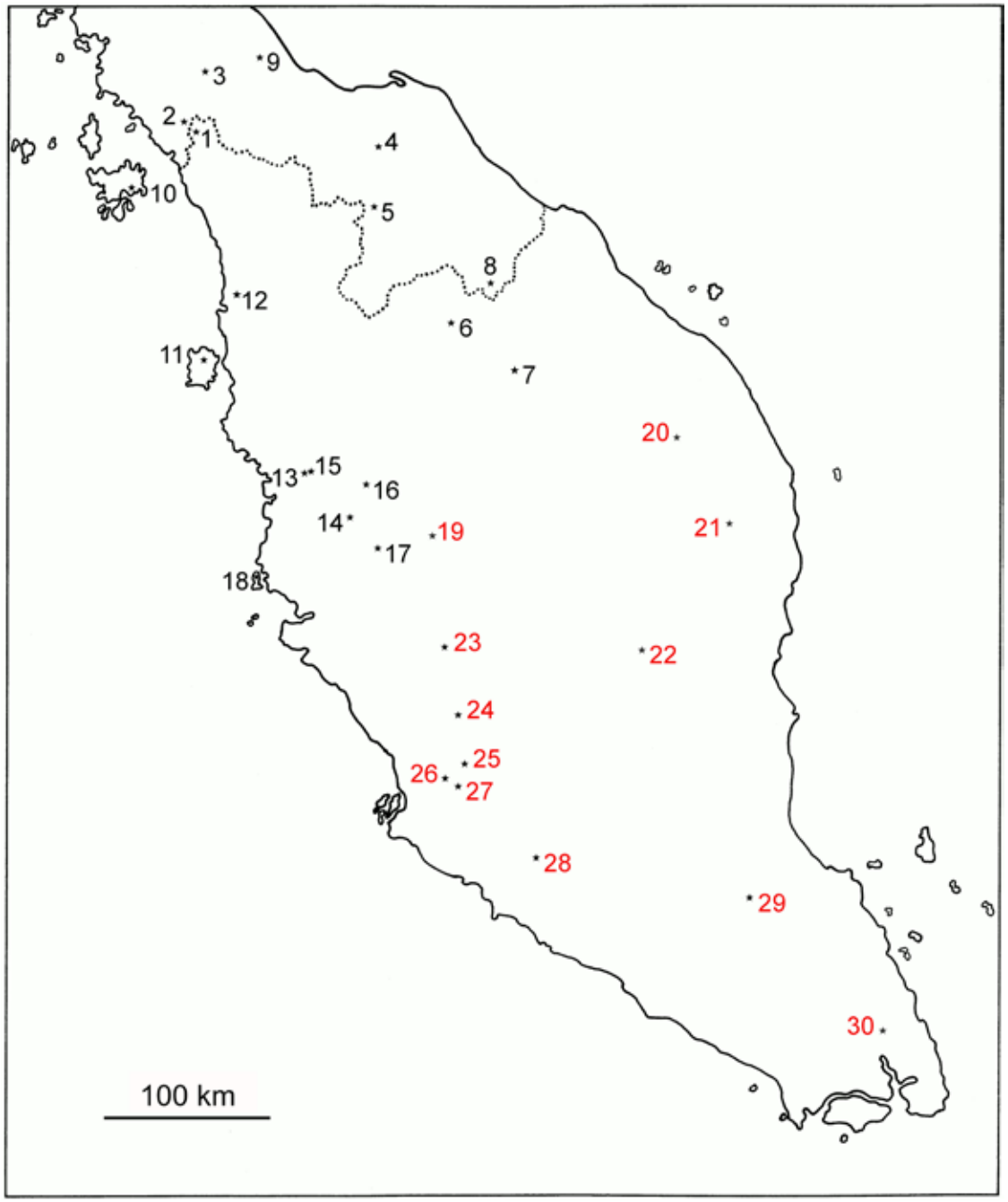


Fig. 2. Localities of *Liphistius* specimens of the *trang*-group in Peninsular Malaysia and southern Thailand used for morphological examination (in black) and of specimens of at least two species groups in Peninsular Malaysia used for molecular analysis (in red on the map, with an asterisk here in the figure caption). The coast of Sumatra is omitted. 1 - Kaki Bukit (type locality of *L. yangae*); 2 - Thaleban N.P. (*L. yangae*; type locality of *L. thaleban* syn. nov.); 3 - Tone Nga Chang Waterfall (*L. yangae*); 4 - Sankalakhierie Mountains (*L. yangae*); 5 - Than To Waterfall (*L. yangae*; type locality of *L. rufipes* syn. nov.); 6 - Bukit Baring (*L. yangae*, reported under *L. rufipes* syn. nov.); 7 - Gunung Stong (*L. yangae*); 8 - Hala-Bala W.S. (*Liphistius* cf. *yangae*); 9 - Had Yai (*Liphistius* cf. *yangae*); 10 - Langkawi Island (type locality of *L. langkawi*); 11 - Penang Island, including Telok Bahang and Penang Botanic Gardens (type locality of *L. desultor* and of *L. murphyorum*); 12 - Gunung Jerai (= Kedah Peak) (*L. desultor*); 13 - foot of Maxwell Hill (*L. desultor*); 14 - Ulu Kinta and undisclosed locality near Ipoh (*Liphistius* cf. *desultor*); 15 - high altitudes of Maxwell Hill (type locality of *L. laruticus*); 16 - Gua Kanthan (type locality of *L. kanthan*); 17 - Gua Tempurung (type locality of *L. tempurung*; *L. kanthan*); 18 - Pangkor Island (type locality of *L. buran* sp. nov.); 19* Parit Falls (*Liphistius* sp.); 20*- Lake Kenyir (*Liphistius* sp.); 21* - Pasir Raja (*Liphistius* sp.); 22* - Felda Tekam (*Liphistius* sp.); 23* - Fraser's Hill (*L. malayanus*); 24* - Genting Highland (*L. malayanus*); 25* - Ulu Gombak Forest Reserve (*L. malayanus*); 26* - Kemensah Waterfall (*L. malayanus*); 27* - Ampang Forest Reserve (*L. malayanus*); 28* - Ulu Bendul Amenity Forest (*L. malayanus*); 29* - Endau-Rompin National Park (type locality of *L. endau*); 30* - Kota Tinggi Waterfall (*L. endau*).

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Key to the species of the *trang*-group in Malaysia:

1 Large spiders [carapace lengths in males (largest female in parentheses) 8.4-12.9 (15.6), carapace width 7.4-11.4 (13.9)]; parts of carapace and proximal articles of legs and palps in females and large immature males[1] orange-coloured (Fig. 1A). Uniformly dark-coloured adult males of carapace length 8.4-8.5 and carapace width 7.4-8.0 with widely rounded or widely triangular para-embolic plate 2

- Small to medium-sized spiders [carapace lengths in males (largest female in parentheses) 4.0-8.5 (8.1), carapace width 3.6-8.0 (7.4)]; body colouration of adult spiders light brown (Fig. 1B) or dark brown, limb articles uniformly dark or brown with more or less distinct dark annulations. Uniformly dark-coloured adult males of carapace length 8.4-8.5 and carapace width 7.4-8.0 (at present only applying to *L. laruticus*) with narrowly arched (subtegular apophysis present) or obliquely truncate (subtegular apophysis absent) para-embolic plate..... 3

2 Male palp always with basally wide tibial apophysis, deep paracymbium, longer than wide cumulus, medium-long proventral process of contrategulum, without ledge on prolateral side of contrategulum, and with narrowly arched, narrowly truncate or triangular para-embolic plate (Fig. 3); females with posterior stalk of vulval plate narrower than poreplate, in some (mostly young) specimens with light longitudinal median band, receptacular cluster as wide as long or only slightly longer, CDO situated in centre of poreplate (Fig. 4) ..... *L. yangae*

- Male palp mostly with basally narrow tibial apophysis, with shallow paracymbium, wider than long cumulus, short proventral process of contrategulum, with distinct ledge on prolateral side of contrategulum, and with widely arched para-embolic plate (Fig. 5); females with posterior stalk clearly wider than poreplate, never with light median band, receptacular cluster distinctly longer than wide, CDO situated slightly posterior to centre of poreplate (Fig. 6)..... *L. desultor*

3 Medium-sized spiders [carapace lengths in males (largest female in parentheses) 7.8-8.5 (8.1), carapace width 6.8-8.0 (7.4)]; body of adult spiders of both sexes uniformly dark-coloured; males with large, wide, obliquely truncate para-embolic plate, its proventral-distal corner protruding further than its retroventral-distal corner (Fig. 7A, E); females with rounded poreplate (Fig. 7J)..... *L. laruticus*

- Small spiders [carapace lengths in males (largest female in parentheses) 4.0-7.5 (7.8), carapace width 3.6-7.2 (7.1)]; body of adult spiders of both sexes brown, with more or less distinctly annulated limbs; males with para-embolic plate narrow (Figs 8B-D) or obliquely truncate, its retroventral-distal corner protruding further than its proventral-distal corner (Figs 10G, H, I); adult females with quadrangular poreplate 4

4 Palpal organ with distinct subtegular apophysis (Figs 8A-D, 9A, C, E, F); tegulum well developed; scopula on tarsi of anterior legs of males indistinct and not clearly delimited; poreplates with paired or unpaired processes on anterior margin (Figs 8E-I, 9H)..... 5

- Palpal organ without subtegular apophysis; tegulum reduced (Figs 10J-K, 13E); scopula on tarsi of anterior legs of males distinct and quite clearly delimited; poreplates without processes on anterior margin (Figs 11, 15) 6

5 Males with normal paracymbium and with moderately long (less than twice as long as wide) subtegular apophysis, its apex widely rounded; para-embolic plate undivided, subtriangular; retrolateral edge of embolic base (not connected to para-embolic plate) elevated to form a distinct, subtriangular plate (Fig. 8A-D). Females with ventral rim of poreplate carrying four (two anterior and two anterolateral) processes (Fig. 8E-I). Both sexes without short setae anterior to fovea..... *L. murphyorum*

- Males with voluminous, basally very wide paracymbium and with very long (three times longer than width at base) and tapering subtegular apophysis; para-embolic plate divided into narrow, spatulate proventral part and widely arched retroventral part; retrolateral edge of embolic base developed as an indistinct ledge (Fig. 9B, D, G). Females with ventral rim of poreplate carrying five (one anteromedian, two anterolateral and two posterolateral) processes (Fig. 9H). Both sexes with numerous short setae anterior to fovea ..... *L. langkawi*

6 Males with proximal-retrolateral heel of paracymbium carrying two enlarged spinules; proventral process of contrategulum indistinct; membrane at base of embolus complex without microtrichia; major embolic fold (see Schwendinger, 2017: fig. 3) narrow, normally developed (Fig. 10E-F, K). Females with poreplate possessing a well-developed posterior stalk (Fig 11). Both sexes without a pair of dark paramedian bands anterior to fovea .... *L. kanthan*

- Males with heel of paracymbium carrying only one enlarged spinule; proventral process of contrategulum pronounced; membrane at base of embolus complex densely covered with microtrichia (Fig. 14A-E); major embolic fold basally wide, urn-shaped (Fig. 13E-F, H-I). Poreplate without posterior stalk (Fig. 15). Both sexes with a pair of dark paramedian bands anterior to fovea (Fig. 12A-B) ..... *L. buran* sp. nov.

1 Small juveniles of all *Liphistius* species look the same and are indistinguishable on the basis of morphological characters.

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(last moulted 16.VII.2011); Sankhalakhierie Mountains; 12.VII.2011; leg. P.J. Schwendinger. – MHNG, sample THMA-00/13a; 2 males (matured 10.VIII.2001 and 29.VIII.2002, respectively), 1 juv. male, 1 penultimate male, 7 females (last moulted 20.II.2001, 8.III.2002, 9.III.2001, 10.III.2001, 14.III.2001, 6.IV.2002, VII.2002, respectively); Malaysia, Perlis, Wan Tangga Valley (behind Gua Kelam), about 1 km W of Kaki Bukit village, 6°38'48"N, 100°11'51"E, 70 m; 8.VIII.2000; leg. P.J. Schwendinger. – MHNG, sample MAL-04/11; 1 male (matured 22.I.2007), 3 females (last moulted 12.I.2006, 31.XII.2006 and 5.I.2007, respectively); Malaysia, Kelatan, Gunung Stong (= Setong), 5°20'22"N, 101°58'15"E, 200 m, rainforest near stream; 10.VI.2004; leg. P.J. Schwendinger.

Diagnosis: Large spiders. Females and immature males of at least one year of age with orange-coloured femora and carapace. Distinguished from *L. bicoloripes* Ono, 1988 (occurring north of the range of *L. yangae*) by dark tibiae and patellae (orange-coloured in *L. bicoloripes*) in females and immature males. Females different by genital atrium with fewer or no lateral hairs, and poreplate posteriorly equally wide or wider than anteriorly (equally wide or narrower in *L. bicoloripes*) (Fig. 4; Schwendinger, 1995: figs 9-11 cf. Schwendinger, 1995: figs 38-41). Males different by a narrowly rounded or triangular, scale-like paraembolic plate (obliquely truncate in *L. bicoloripes*), by a shorter proventral process on contrategulum, by a tegulum with a pronounced distal edge and a sigmoid row of teeth on proximal edge (distal tegular edge indistinct and proximal edge with curved row of teeth in *L. bicoloripes*) and by a longer paracymbium with a slightly more elevated cumulus (Fig. 3; Schwendinger, 1995: figs 1-7 cf. Schwendinger, 1995: figs 32-37). Distinguished from *L. desultor* (occurring south of the range of *L. yangae*) by males with a longer, apically rounded proventral process on contrategulum (Fig. 3E-H cf. Fig. 5F-G), without an elevated ridge on prolateral side of contrategulum (Fig. 3E cf. Fig. 5F-G, I-K), with a narrower (longer than wide) and less distinctly elevated cumulus carrying weaker and more scattered bristles (Fig. 3C-D cf. Fig. 5A-B, D-E), and usually with a basally wider tibial apophysis (Fig. 3A-B cf. Fig. 5A-B; but see Fig. 5C and paragraph "Variation"). Females very difficult to distinguish from females of *L. desultor*: usually without or with only indistinct median processes on lateral margin of poreplate and with a not much longer than wide receptacular cluster (Fig. 4 cf. Fig. 6); some specimens with an arched distal margin of the poreplate and with very few or no median and lateral hairs in genital atrium (Fig. 4; Schwendinger, 1990: figs 53-56; Schwendinger, 1995: figs 9-11 cf. Fig. 6; Murphy & Platnick, 1981: figs 22-23; Platnick & Sedgwick, 1984: figs 50-51; Platnick *et al*., 1997: fig. 28; Haupt, 2003: fig. 43A-B).

Additions to description of male: Scopula weak on tarsi I-II, denser on tarsi III-IV; only distally divided by median stripe on all leg tarsi; covering distal third of ventral side of tarsus I, distal half of tarsus II, distal two-thirds to three-fourths of tarsus III and distal two-thirds to four-fifths (in largest male, the *L. rufipes* syn. nov. paratype from Bukit Baring) of tarsus IV.

Variation: Carapace length in males (n=9) ranges 8.36-12.88, carapace width 7.42-11.43. The largest female (from Than To Waterfall; a paratype of *L. rufipes* syn. nov.) has a 15.61 long and 13.91 wide carapace. In the four obviously juvenile female paratypes examined the carapace length is 5.20-5.79, the carapace width 4.37-4.92; in the female holotype (not examined; probably also not fully grown) it is 6.41 and 5.53, respectively (Platnick & Sedgwick, 1984: 14). The number of short setae anterior to the fovea ranges from zero to six.
The shape of the vulva is very variable (Fig. 4) and consequently a clear distinction between females of *L. yangae* and *L. desultor* is not always possible. Variation in characters of the male palp is shown in Fig. 3.

Remarks: The type series of *L. yangae* consists of quite small, juvenile females, as shown by the incompletely developed and weakly sclerotised vulval plates with a relatively large but not clearly outlined CDO, by a low, indistinct receptacular cluster and by an indistinctly outlined, lightly pigmented/sclerotised posterior stalk (Fig. 4A-C). None of the new female specimens examined has a poreplate as illustrated in Platnick & Sedgwick (1984: figs 22-23; presumably the holotype, but not identified as such; anteriorly distinctly narrower than posteriorly, anterior margin straight, lateral processes on ventral rim absent). However, the smallest vulval plates of non-type females examined (from an exuvia of a specimen from the Sankalakhierie Mts and from Gunung Stong), although about double the size of the largest *L. yangae* paratype examined, are quite similar (Fig. 4D-E). These differences are probably due to different body sizes and interspecific variation (see paragraph "Variation"). A relatively large CDO appears to be a juvenile character state in females of this species (as perhaps in others). This character state seems to be retained in fully-grown females of the *malayanus*-, *timan*- and *batuensis*-groups (see Schwendinger, 2017) but not in other species groups. A relatively large CDO may be plesiomorphic.
Another reason for placing *L. thaleban* syn. nov. in the synonymy of *L. yangae* is the fact that adult male and female spiders collected at Kaki Bukit (the type locality of *L. yangae*) are very similar to and obviously conspecific with the types of *L. thaleban* syn. nov. (its holotype is an exceptionally small male). The type localities of both nominal species are only about 6 km apart (see Fig. 2, localities 1 and 2). Since the female holotype of *L. yangae* obviously has bicoloured legs (femora given as yellow

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in the original description of 1984, probably orange-coloured when the specimen was collected in 1938), as have females of *L. thaleban* syn. nov. and *L. rufipes* syn. nov. which occur in the same area, it is very likely that these three names in fact refer to one single species. Other large *Liphistius* species with orange-coloured leg articles (*L. bicoloripes, L. dangrek* Schwendinger, 1996, *L. desultor, L. isan* Schwendinger, 1998*, L. ornatus* Ono & Schwendinger, 1990, *L. sumatranus* Thorell, 1890) have relatively large geographical ranges. This also appears to be the case in *L. yangae*.

Relationships: *Liphistius yangae* belongs to species complex D (see Schwendinger, 1998: 29, table 2) due to the following combination of characters: cumulus plane

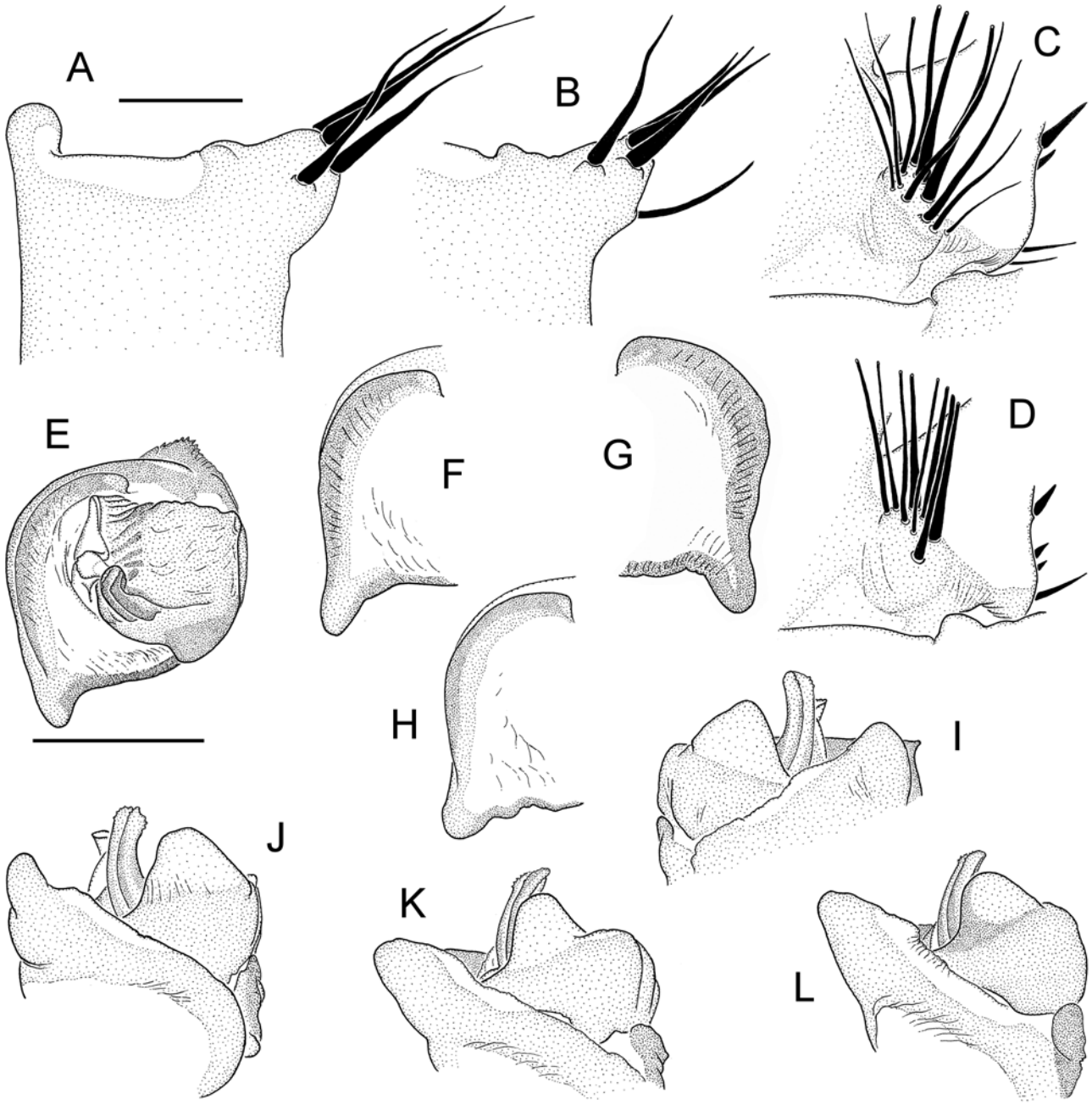


Fig. 3. *Liphistius yangae*, details of six males: from Kaki Bukit, matured 29.VIII.2002 (A, C, K), from Kaki Bukit, matured 10.VIII.2001 (B, D-E, L), from Gunung Stong (F, J), from the Sankalakhierie Mts (H), from Bukit Baring (paratype of *L. rufipes* syn. nov.; G) and from Than To Waterfall (holotype of *L. rufipes* syn. nov.; I). (A) Distal part of left tibia, ventral view. (B) Tibial apophysis of left palp, ventral view. (C-D) Cumulus on left palp, ventral view. (E) Left palpal organ, distal view (dorsal side up). (F, H) Distal edge of contrategulum of left palp, distal view. (G) Same of right palp. (I) Distal part of right palpal organ, ventral view. (J) Same of left palp. (K-L) Same of left palp, retroventral view. Scale lines 1.0 mm (A-B; C-L).

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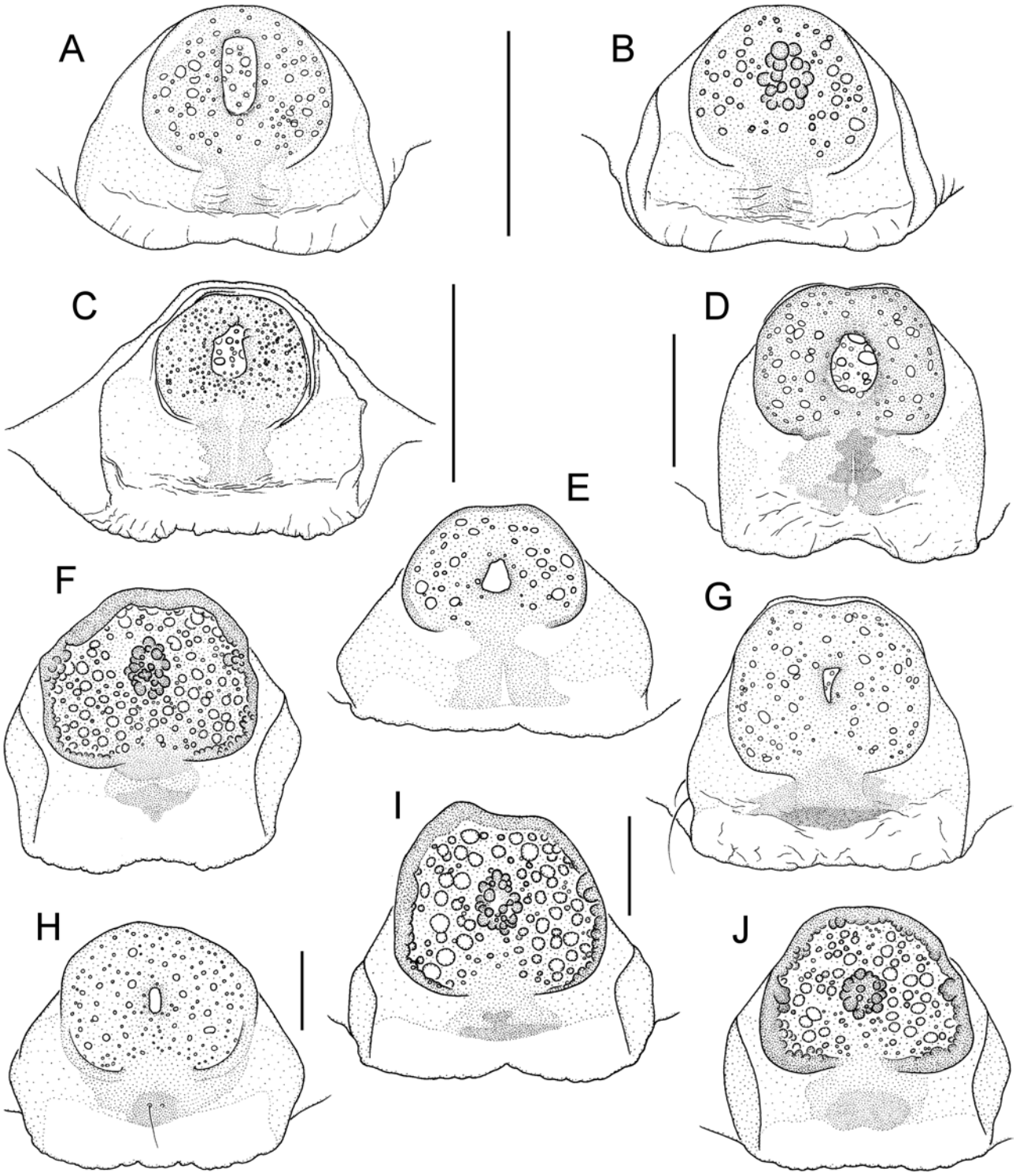


Fig. 4. *Liphistius yangae*, details of vulval plate of nine females; dorsal view (A, C-E, G-H), ventral view (B, F, I-J). (A-B) First juvenile paratype. (C) Second juvenile paratype. (D) Juvenile from Gunung Stong. (E) Juvenile from the Sangkalakhierie Mts. (F) Mature specimen (moulted 20.II.2001) from Kaki Bukit. (G) Different specimen from Kaki Bukit (moulted 17.VIII.2000). (H) Different specimen from Kaki Bukit (moulted 14.III.2001). (I) Different specimen from Kaki Bukit (moulted 9.III.2001). (J) Mature specimen (moulted 16.VII.2011) from the Sangkalakhierie Mts. Scale lines 0.5 mm (A-B; C; D-G; H, J; I).

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or slightly elevated and bearing long stiff bristles, dark patch with spinules on paracymbium not isolated by a pale band, sclerotised part of embolus with 2-3 ridges running into pointed apex. Only in species complex D (in southern Thailand, western Malaysia and Sumatra) and in species complex A (in eastern Thailand; both probably more closely related to each other than to other species complexes) we have species with a large body and with an orange-coloured carapace and orange-coloured proximal leg and palp segments.

Distribution: *Liphistius yangae* appears to have a wide distribution on both sides of the border between Malaysia and Thailand. For three localities in northern Malaysia and four from southern Thailand mature males are available, and these records are therefore quite reliable. Additional spiders, which presumably also belong to this species, were seen (but not collected) in Thailand: inside the campus of the Prince of Songkhla University in Had Yai (Songkhla Province) and near the Sirinthon (= Sirindhorn) Waterfall in the Hala-Bala Wildlife Sanctuary (Narathiwat Province). See Fig. 2, localities 1-9.

Biology: Males in captivity became mature in July, August, December, January and February. Females usually moulted twice per year. Further information on the biology of this species is given in Schwendinger (1990: 347, under *L. thaleban* syn. nov.) and in Schwendinger (1995: 144-145, under *L. rufipes* syn. nov.).

Liphistius desultor Schiödte, 1849

Figs 1A, 5-6

Liphistius desultor Schiödte, 1849: 621-623, pl. 5, figs 1-7 (description of female). – Kraus, 1978: 237-239, figs 2-4 (first illustration of male palp under *L. batuensis* Abraham, 1923a).

For synonyms and further relevant taxonomic literature, see World Spider Catalog (2019).

Type material: ZMC; female holotype (not examined); "Pinang insula"; van Teylingen.

Material examined: MHNG; 1 male (matured 23.VIII.1992); Penang Hill (= Bukit Bendera), 700 m; 1.XII.1991; leg. P.J. Schwendinger. – SMF (no inventory number; ex coll. O. Kraus); 1 male without palps; Penang Island; 1.X.1961; leg. H. Klingel. – SMF (no inventory number; ex coll. O. Kraus); right palp (metal-coated for SEM), probably belonging to male without palps. – BMNH 1975.1.24.4 (ex. coll. W.S. Bristowe); 2 females (1 large, 1 small), 3 juv. males (2 of them penultimate); Penang; 6.XI.1974; leg. W.S. Bristowe. – BMNH (no inventory number; ex. coll. W.S. Bristowe); 1 female; Kedah Peak; I.1932; leg. W.S. Bristowe. – MHNG; 1 male (matured 26.X.1995); Gunung Jerai (= Kedah Peak), 170 m; 1.II.1995; leg. P.J. Schwendinger. – MHNG; 1 male (matured 10.X.1996); Bukit Larut (= Maxwell Hill), 50 m; 8.I.1996; leg. P.J. Schwendinger.

Diagnosis: Large species, adult females and large juveniles of both sexes with orange-coloured femora on legs and palps (Fig. 1A). Similar to *L. yangae*, males distinguished by basally narrower tibial apophysis (Fig. 5A-B cf. Fig. 3A-B, but see Fig. 5C and paragraph "Variation"), by shallower paracymbium, by wider than long cumulus with bristles arranged in one row (Fig. 5A-B, D-E cf. Fig. 3C-D), by basally wide and almost symmetrical proventral process of contrategulum (Fig. 5F-G cf. Fig. 3E-H), by prolateral side of contrategulum with a pronounced ledge (the most obvious distinction; Fig. 5F-G, I-K, see arrows), by proximal edge of tegulum with stronger teeth, and by more widely rounded para-embolic plate (Fig. 5H, K cf. Fig. 3I-L). Females difficult to distinguish from those of *L. yangae*; quadrangular poreplate generally with only very slightly arched to slightly invaginated anterior margin and thick lateral margins carrying indistinct anterolateral processes; receptacular cluster quite long and bent anteriad (Fig. 6C), distinctly longer than wide in ventral view (Fig. 6A, D cf. Fig. 4F, I-J); CDO in a slightly more posterior position (behind centre of poreplate; Fig. 6B, E cf. Fig. 4G-H for adult specimens); posterior stalk short, wider than poreplate (Fig. 6A-B, D-E cf. Fig. 4).

Additions to description of male: Scopula weak on tarsi I-II, denser on tarsi III-IV, only distally divided by median stripe on all leg tarsi; covering distal third of ventral side of tarsus I, distal half or slightly less of tarsus II, three-fifths to two-thirds (only in male from Gunung Jerai) of tarsus III, and distal two-thirds of tarsus IV.

Variation: Carapace length in males (n=5), including the one described in Platnick & Sedgwick, 1984: 20), is 9.49-11.16, carapace width 8.05-9.94; in the largest female (described in Platnick & Sedgwick, 1984: 18-20) it is 14.62 and 12.46, respectively. Variation in details of the male palp are given in Fig. 5; variation in the vulval plate of two females in Fig. 6. Most males examined and a male illustrated in the literature have a basally narrow tibial apophysis (Fig. 5A-B; Platnick & Sedgwick, 1984: fig. 47). However, the male from Gunung Jerai (Fig. 5C) has a basally wide tibial apophysis on both palps, as is the case in *L. yangae* males, but otherwise corresponds to *L. desultor*, especially in possessing a distinct (but slightly smaller than in other conspecific males) ledge on the prolateral surface of the contrategulum (Fig. 5K). Only two of the females examined or illustrated in the literature have a single hair on one of the lateral folds of the genital atrium (Fig. 6D; Platnick *et al*., 1997: fig. 28), all other females are without hairs inside the vulva (Fig. 6A; Murphy & Platnick, 1981: fig. 23; Platnick & Sedgwick, 1984: fig. 51).

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Relationships: *Liphistius desultor* appears to be most closely related to *L. yangae*. Both belong to species complex D.

Distribution: *Liphistius desultor* is known from several lowland and upland localities on Penang Island, and from low altitudes on the nearby mainland: Kedah Peak (= Gunung Jerai) and Maxwell's Hill (= Bukit Larut). The species probably also occurs at an undisclosed locality near Ipoh (unconfirmed record documented in photos by Kenneth Fletcher, see Fig. 1A) and, according to molecular data, also at Ulu Kinta near Ipoh. See Fig. 2, localities 11-14.

Biology: The spiders examined were collected from sides of roads and trails inside and close to rainforests. They were locally quite abundant on Penang Hill, but much less so on Gunung Jerai and at the foot of Maxwell's Hill. In captivity two males became mature in late August and late October. A mature male was collected on Penang Hill in late July (Platnick & Sedgwick, 1984: 20). An egg case containing 509 eggs was found on Penang Hill at the beginning of December (Platnick *et al*., 1997: 12). Further information on the biology of this species (and its burrow structure) is found in Yong (1978), Murphy & Platnick (1981) and Platnick *et al*. (1997).

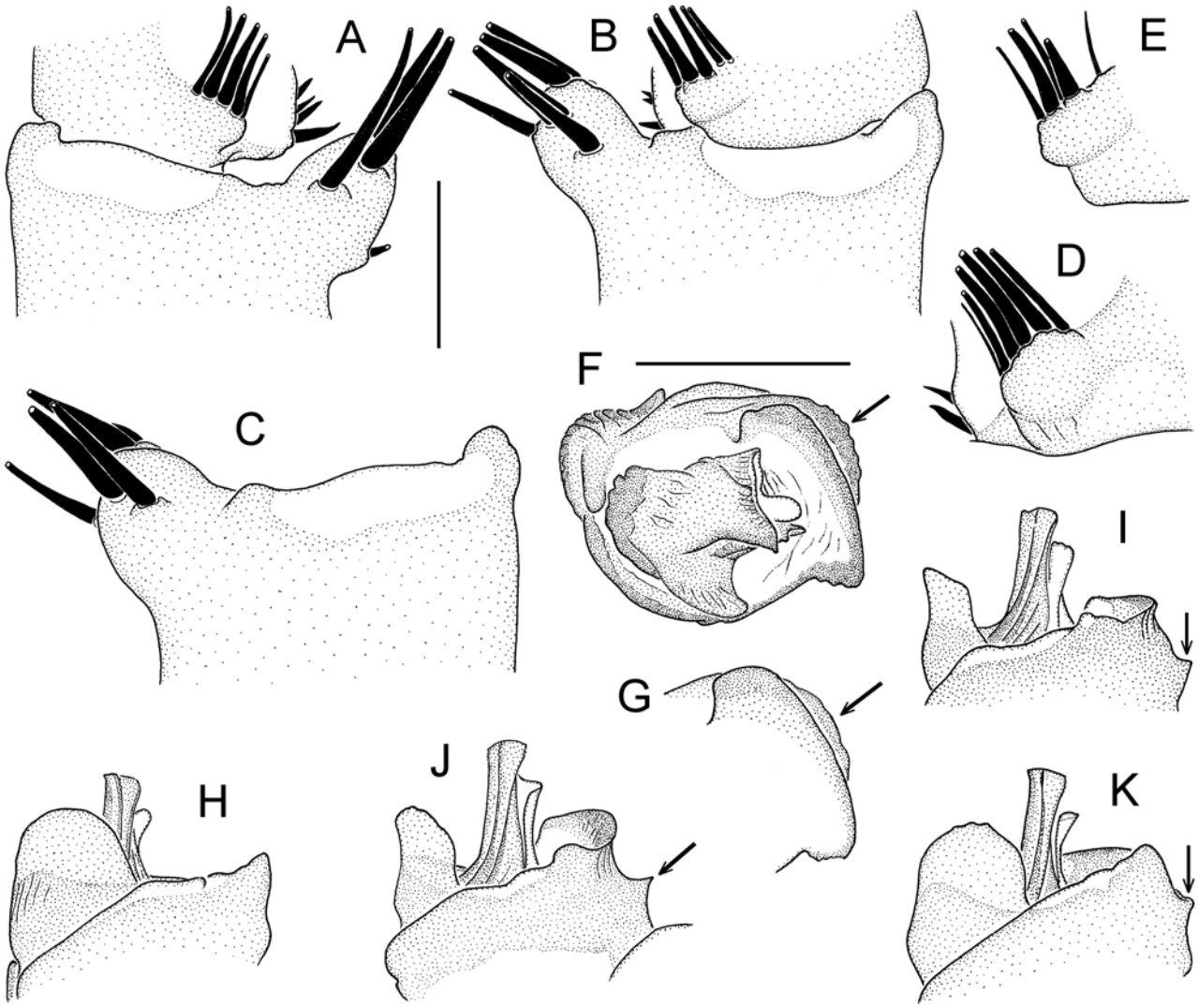


Fig. 5. *Liphistius desultor*, details of palp of four males: from Penang Hill (in MHNG; A, H-I), from Penang Island (in SMF; E, G), from Maxwell Hill (B, F, J), from Gunung Jerai (= Kedah Peak) (C-D, K). (A) Distal part of tibia and base of left tarsus, ventral view. (B-C) Same of right palp. (D-E) Cumulus of right palp, ventral view. (F) Palpal organ, distal view; arrow indicating ledge on prolateral side of contrategulum. (G) Distal edge and prolateral ledge (indicated by arrow) of contrategulum, distal view. (H, K) Distal part of right palpal organ, retroventral view. (I-J) Same, ventral view; arrow indicating ledge on prolateral side of contrategulum (also in K). Scale lines 1.0 mm (A-C; D-K).

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Liphistius laruticus Schwendinger, in Platnick, Schwendinger & Steiner, 1997

Fig. 7

Liphistius laruticus Schwendinger, in Platnick, Schwendinger & Steiner, 1997: 9-11, figs 14-21 (description of male and female).

Types: MHNG; male holotype (matured 3.VIII.1995), male paratype (matured 30.VIII.1994) and 2 female paratypes (all examined); Malaysia, Maxwell Hill, 1380 m, 4°51'31"N, 100°48'07"E; 20.I.1994; leg. P.J. Schwendinger.

Other material examined: MHNG; 1 male (matured 28.VII.2002); Maxwell Hill (4°51.694'N, 100°47.631'E), 1000-1300 m; 24.IX.2001; leg. L. Monod.

Diagnosis: Similar and probably closely related to *L. desultor*, distinguished by uniformly dark colour in females and large juvenile males. Males different by a basally wider tibial apophysis, by the lack of a prominent ledge on prolateral side of contrategulum, by a narrower dorsal apex of the distal contrategular edge (Fig. 7F-H cf. Fig. 5F-G), and by a quadrangular, widely and obliquely truncate para-embolic plate with its proventral-distal corner more protruding than its retroventral-distal corner (the most obvious distinction; Fig. 7A, E cf. Fig. 5H, K). Females with poreplate rounded rather than rectangular, with arching anterior margin (Fig. 7I-J; Platnick *et al*., 1997: figs 20-21 cf. Fig. 6). Scopula on tarsus IV of males distinctly thinner and shorter than in *L. desultor*.

Additions to description of male: Scopula thin on tarsi I and IV, slightly denser on tarsi II and III; only distally divided by median stripe on all leg tarsi; covering distal third of ventral side of tarsus I, distal two-fifths of tarsus II, distal half of tarsus III and distal two-fifths

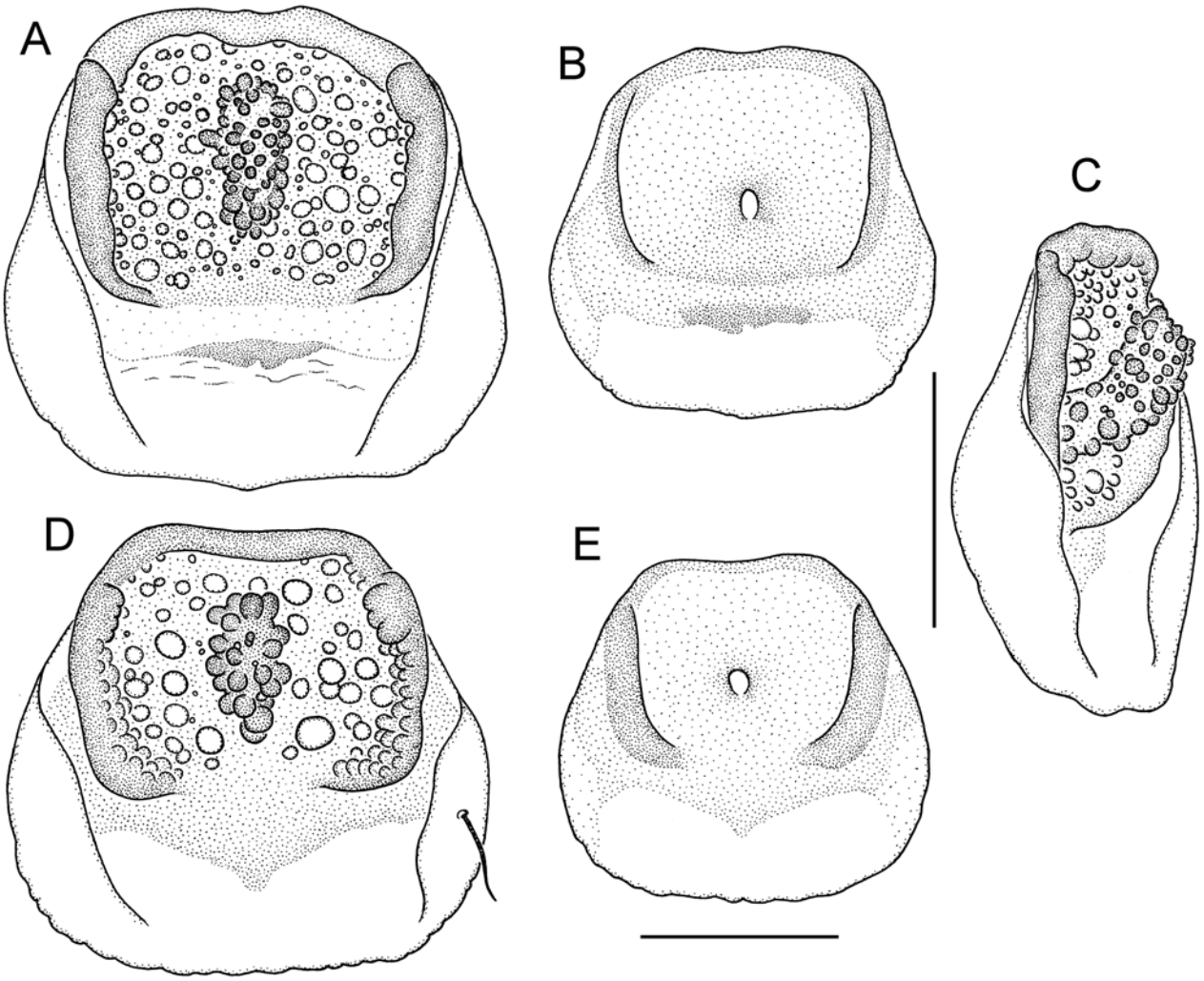


Fig. 6. *Liphistius desultor*, vulval plate of female (BMNH 175.1.24.4) from Penang Island (A-C) and of female (BMNH) from Gunung Jerai (= Kedah Peak) (D-E). (A, D) Ventral view. (B, E) Dorsal view, pores not illustrated. (C) Lateral view showing shape of receptacular cluster. Scale lines 1.0 mm (A, C-D; B, E).

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of tarsus IV. Obliquely truncate para-embolic plate with its proventral-distal corner more protruding than its retroventral-distal corner (Fig. 7A, E).

Variation: Carapace length in males (n=3) is 7.84-8.53, carapace width 6.81-7.99; in the largest female (the allotype) it is 8.14 and 7.35, respectively.

Distribution: *Liphistius laruticus* is only known from altitudes above 1000 m on Maxwell Hill (= Bukit Larut). See Fig. 2, locality 15. *Liphistius desultor* occurs at the foot of the same mountain (Fig. 2, locality 13). Considering that both species are probably closely related, we assume that they are separated by different microclimatic conditions at different altitudes of Maxwell Hill, which receives the highest rainfall in Peninsular Malaysia.

Relationships: *Liphistius laruticus* appears to be more closely related to *L. desultor* than to *L. yangae*. All three belong to species complex D.

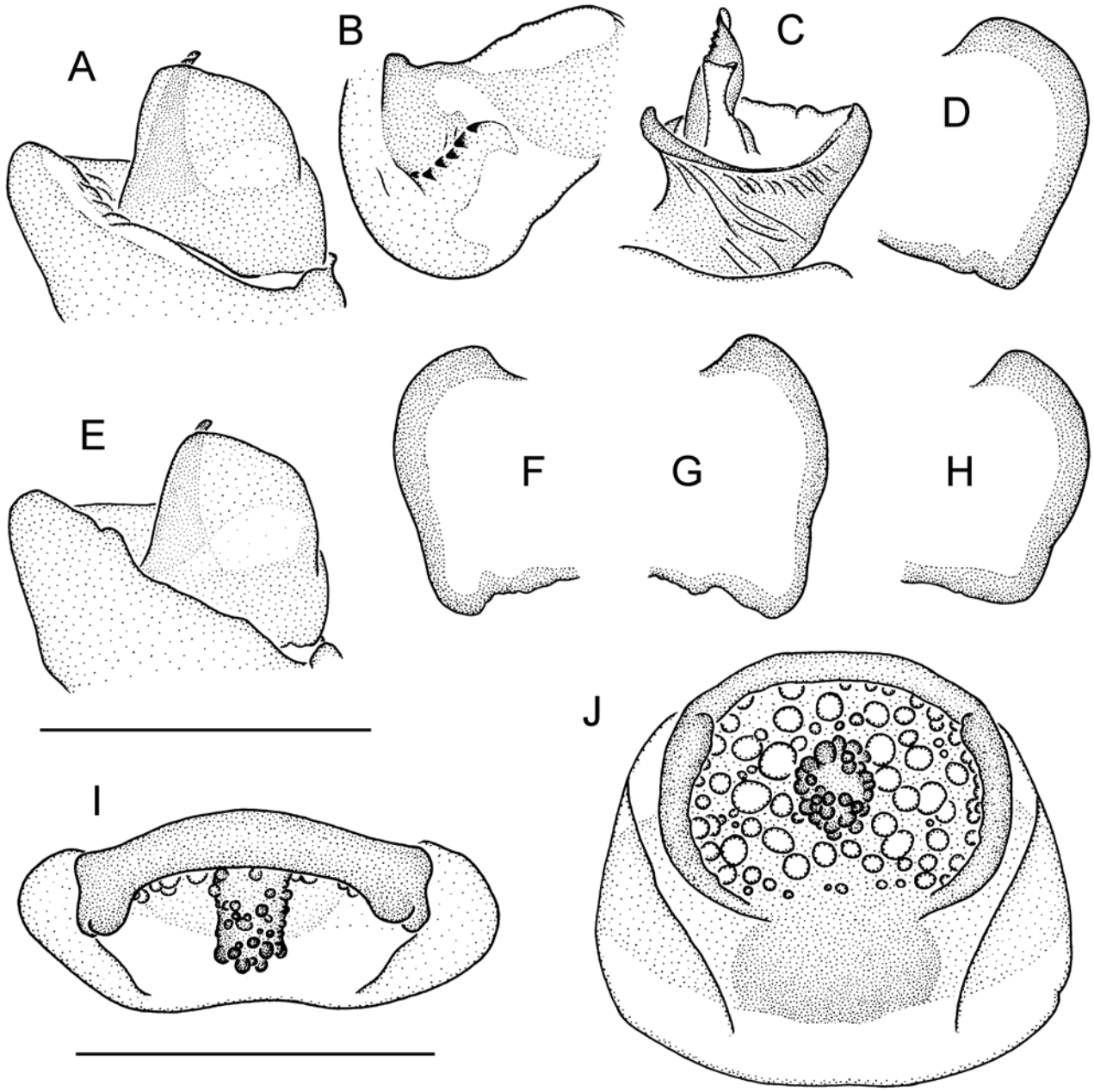


Fig. 7. *Liphistius laruticus*, details of male (A-H) and female genitalia (I-J); male holotype (A-D), new male (matured 28.VII.2002) (E-G), male paratype (H), female allotype (I-J). (A, E) Distal part of left palpal organ, retroventral view. (B) Left tegulum, retrolateral view. (C) Distal part of left palpal organ, prodorsal view. (D, G-H) Distal edge and proventral process of contrategulum of right palp, distal view. (F) Same of left palp. (I) Vulval plate (of exuvia), anterior and slightly ventral view. (J) Same, ventral view. Scale lines 1.0 mm (A-H; I-J).

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Liphistius murphyorum Platnick & Sedgwick, 1984
Fig. 8

Liphistius desultor Schiödte, 1849. – Murphy & Platnick, 1981: 51-55, figs 7, 10, 13, 16, 19 (misidentification of male).

Liphistius n. sp. A. – Haupt, 1983: 279, fig. 3a (description of male without giving an available species name).

Liphistius murphyorum Platnick & Sedgwick, 1984: 16-18, figs 16, 38-44 (description of male and female, provision of available species name). – Haupt, 2003: 71, figs 44C, 46A-B (photo of male and SEM of male palp). – Schwendinger, 2009: 1262-1263, figs 20-21 (illustration of palpal organ).

Types: AMNH; male holotype and female paratype (not examined); Malaysia, Penang Island; 20.VII.1982; leg. W.C. Sedgwick.

Material examined: MHNG; 1 male (matured X.1985); Malaysia; Penang Island, Penang Hill, about 700 m; XII.1984; leg. P.J. Schwendinger. – SMF (ex coll. O. Kraus); 1 male, 2 females; Penang Island; 1.X.1961; leg. H. Klingel. – MHNG (ex coll. O. Kraus; received in exchange from SMF); 1 male; Penang Island; 1.X.1961; leg. H. Klingel. – SMF; 1 male, 1 female; Penang Island; 1.X.1961; leg. H. Klingel. – SMF; 3 females, 3 juveniles; Penang Island; 30.IX. (no year given, presumably 1961); leg. H. Klingel. – MHNG (received in exchange from SMF); 1 female; Penang Island; 30.IX. (no year given, presumably 1961); leg. H. Klingel. – SMF (ex coll. O. Kraus); 1 isolated male palp; no locality, date or collector given.

Diagnosis: Relatively small species, distinguished from all other *Liphistius* species by the combination of a long and strong subtegular apophysis with a domed apex, and a quite long, subtriangular (with narrowly rounded apex) para-embolic plate next to a more or less long (but always shorter than para-embolic plate), subtriangular plate (i.e. an extension of the retrolateral edge of the embolus complex) at a very narrow angle to the para-embolic plate in males (Fig. 8A-D; Platnick & Sedgwick, 1984: figs 38-42; Schwendinger, 2009: figs 20-21), and by four (two anterior and two anterolateral) protuberances on the ventral rim of the poreplate in females (Fig. 8E-F, H; Platnick & Sedgwick, 1984: fig. 44).

Additions to description: Scopula of males very thin, indistinct and not clearly delimited on tarsi I-II, dense and clearly delimited on tarsi III-IV; spread over distal four-fifths of ventral side and only distally divided by median stripe on all leg tarsi. No setae anterior to fovea in either sex.

Variation: Carapace length in males (n=5, including measurements of holotype given in Platnick & Sedgwick, 1984: 18) ranges 5.05-6.03, carapace width 4.25-5.43. In the largest female (out of four examined plus the female described by Platnick & Sedgwick, 1984: 16) it is 6.96 and 6.08, respectively.

Relationships: The pronounced subtegular apophysis of the palpal organ and the presence of processes on the anterior margin of the poreplate clearly show that *L. murphyorum* belongs to species complex E (Schwendinger, 2009: 1263, there incorrectly called "superspecies D"). *Liphistius langkawi* from Langkawi Island (Malaysia) and *L. thaleri* from Libong Island (Thailand), both off the west coast of the Thai-Malay Peninsula, also belong to this very distinct subgroup.

Distribution: *Liphistius murphyorum* is only known from Penang Island, having been collected at the foot and at higher altitudes of Penang Hill (Fig. 2, locality 11). On this mountain *L. murphyorum* occurs together with *L. desultor*, and the two species seemingly share the same habitat.

Liphistius langkawi Platnick & Sedgwick, 1984
Fig. 9

Liphistius langkawi Platnick & Sedgwick, 1984: 14-16, figs 31-37 (description of male and female). – Schwendinger, 2009: 1260-1262, figs 13-19 (illustration of palpal organs and vulvae).

Material examined: Same material (5 males and 12 females from Langkawi Island; leg. P.J. Schwendinger) as mentioned in Schwendinger (2009: 1260-1261). One male and one female from this lot now deposited in SMF (exchange of specimens). No new material available.

Diagnosis: Relatively small species. Males distinguished from those of all other *Liphistius* species by the unique combination of a voluminous, basally very wide paracymbium, an extremely long, tapering subtegular apophysis, a narrowly rounded dorsal contrategular apex with a trench-like depression flanking and sheltering the major embolic fold on one side (Fig. 9A, C, E, F, see arrows), a para-embolic plate divided into a very narrow, spatulate proventral part and a widely arched retroventral part, and a not or only slightly elevated ledge on retrolateral edge of embolus complex at a wide (about 60°) angle to the para-embolic plate (Fig. 9A-G; Platnick & Sedgwick, 1984: figs 31-35; Schwendinger, 2009: figs 13-15). Females distinguished by five (one anteromedian, two anterolateral and two posterolateral) protuberances on ventral rim of poreplate (Fig. 9H; Platnick & Sedgwick, 1984: figs 36-37; Schwendinger, 2009: figs 16-19).

Additions to description: Scopula on all legs very thin, indistinct and not clearly delimited, composed of hairs scattered over distal four-fifths of ventral side of tarsi, decreasing in density from distal to proximal. Both sexes with numerous short setae anterior to fovea.

Variation: Carapace length in males (n=6, including measurements of the holotype given in Platnick &

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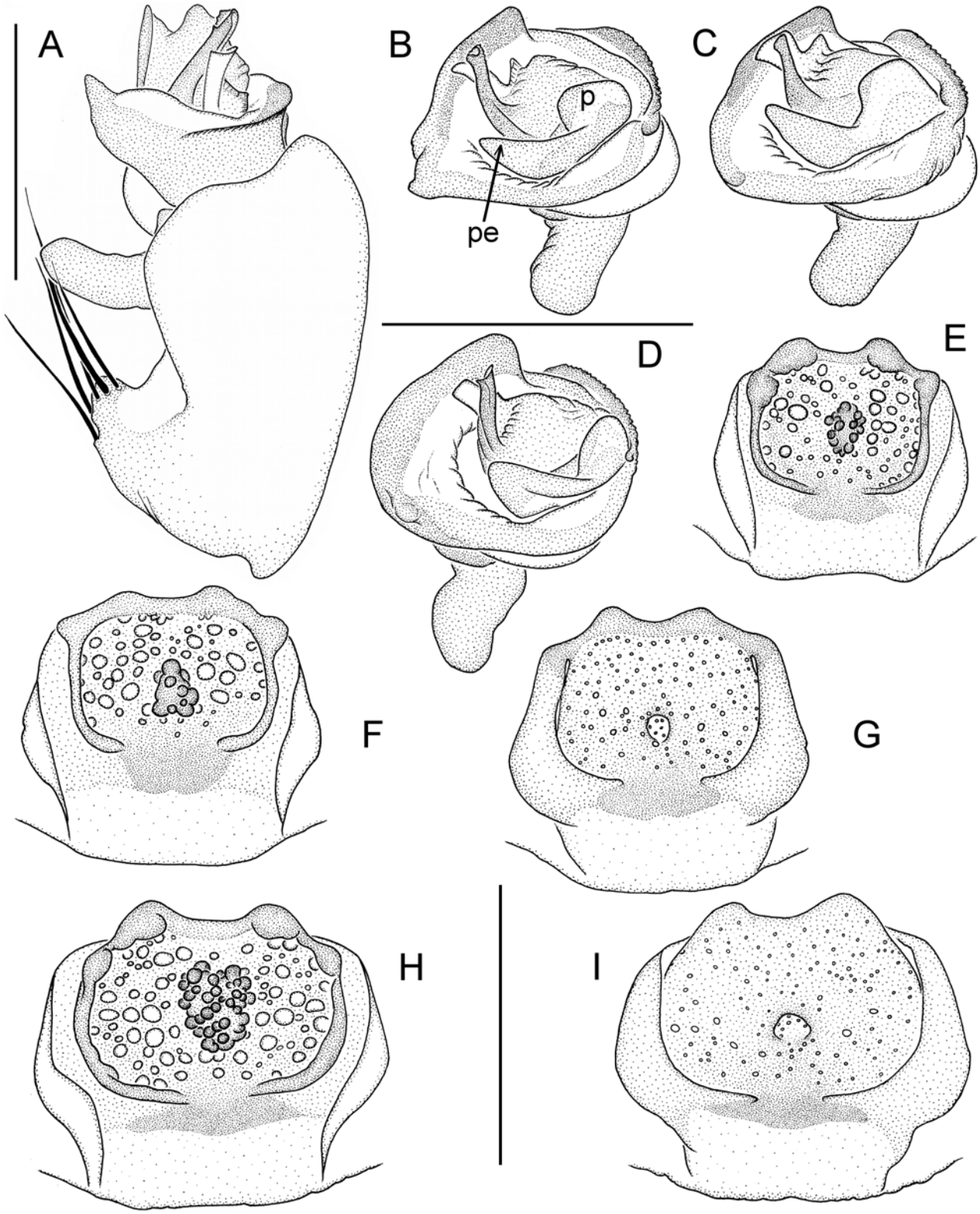


Fig. 8. *Liphistius murphyorum*, details of right palp of four males (A-D; A in MHNG, B-D in SMF) and vulval plate of three females (E-I; E in MHNG, F-I in SMF). (A) Tarsus and palpal organ, prolateral view. (B-D) Palpal organ, distal view (dorsal side up). (E-F, H) Vulval plate, ventral view. (G, I) Same, dorsal view. Abbreviations: pe = para-embolic plate; p = plate on retrolateral edge of embolus complex. Scale lines 1.0 mm (A; B-D; E-I).

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Sedgwick, 1984: 16) ranges 4.02-5.69, carapace width 3.47-5.29; in the largest female (out of twelve examined) it is 7.21 and 6.27, respectively. Variation in the shape of the vulva is illustrated for the paratype in Platnick & Sedgwick (1984: figs 36-37) and for four non-type females in Schwendinger (2009: figs 16-19). The palpal organ of the holotype and of two non-type males is illustrated in Platnick & Sedgwick (1984: 31-35) and Schwendinger (2009: figs 13-15), respectively. Figure 9A-G shows the shape of the subtegular apophysis and of the structures on the ventral to retroventral edge of the embolus complex of another four non-type males; Fig. 9H shows the vulval plate of an additional non-type female. Five to ten short setae are present anterior to the fovea in both sexes. These are more or less clearly continuous with numerous short setae behind the eye tubercle. The AME in two males and three females are reduced or completely absent on one side.

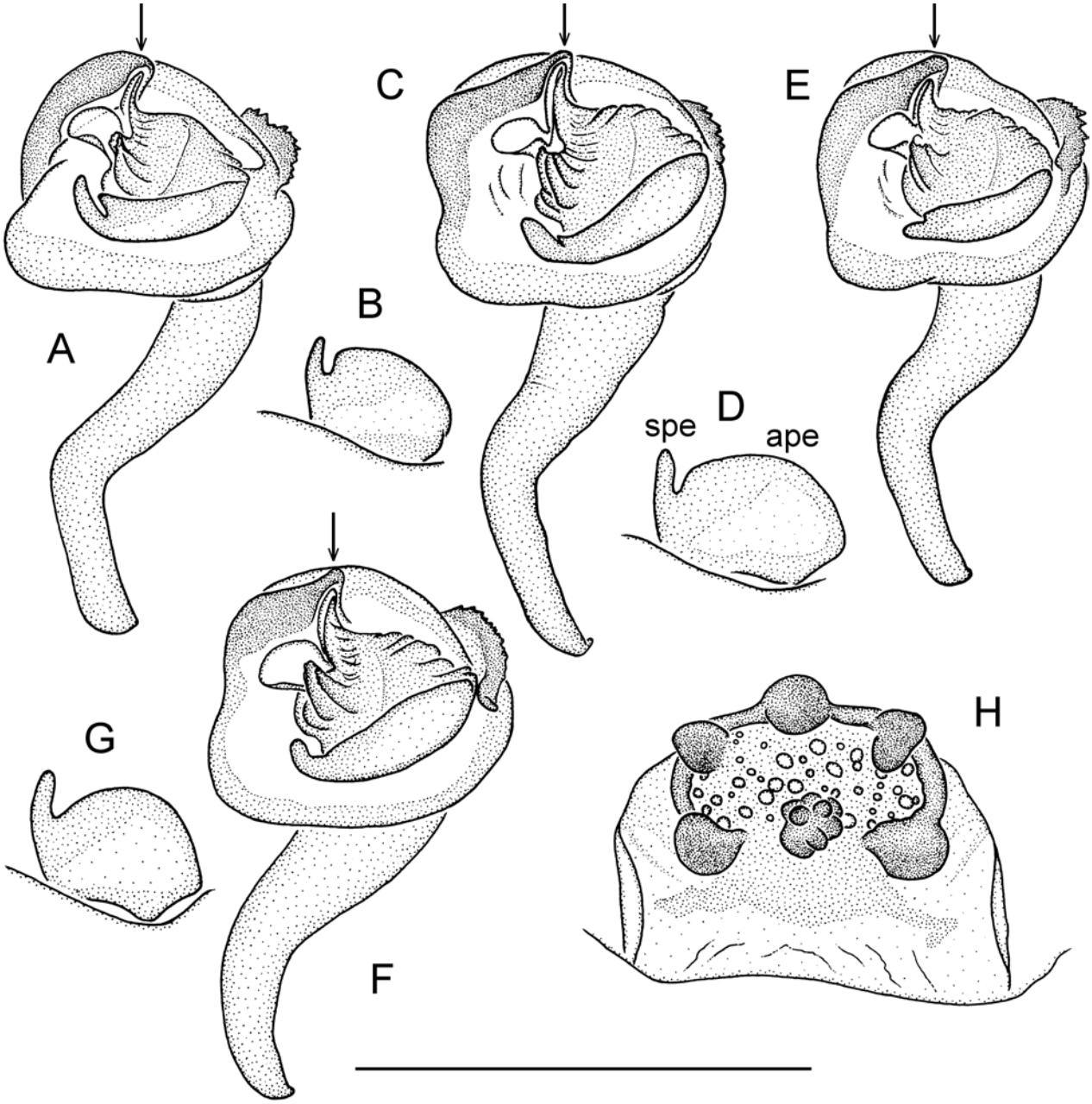


Fig. 9. *Liphistius langkawi*, details of genitalia of four males (A-B, C-D, E, F-G) and of one female from Langkawi Island. (A, C, E-F) Palpal organ of left palp, distal view (dorsal side up; arrows indicating trench-like depression in dorsal apex of contrategular edge). (B, D, G) Para-embolic plate of left palp, retroventral view. (H) Vulval plate, ventral view. Abbreviations: ape = arched retroventral part of para-embolic plate; spe = spatulate proventral part of para-embolic plate. Scale line 1.0 mm (A-H).

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Relationships: The extremely long subtegular apophysis of the male palp and the distinct anterior and anterolateral protuberances on the ventral rim of the poreplate clearly show that *L. langkawi* belongs to species complex E, together with *Liphistius murphyorum* and *L. thaleri*.

Biology: See Platnick & Sedgwick (1984: 16) and Schwendinger (2009: 1261-1262).

Distribution: *Liphistius langkawi* is only known from two localities on Pulau Langkawi. Since these localities are about 15 km apart and on opposite sides of the island, it is quite likely that these spiders can be found in suitable habitats all over the island.

Liphistius kanthan Platnick, in Platnick, Schwendinger & Steiner, 1997

Figs 1B, 10-11

Liphistius kanthan Platnick, in Platnick, Schwendinger & Steiner, 1997: 6-9, figs 12-13 (description of female).

Type: AMNH; female holotype (not examined); Malaysia, Perak, Gua (= cave) Kanthan; IX.1996; leg. H. Steiner.

Material examined: MHNG; 3 males (matured 9.VII.1998, 7.II.1999, 22.V.1999), 2 females, 2 immature males; Malaysia, Perak, Gua Kanthan, 60 m, 4°45'41"N, 101°07'15"E; 14.XII.1997; leg. P.J. Schwendinger & L. Price. – MHNG; 1 male (matured 14.IX.1998), 1 female, 1 immature male; Malaysia, Perak, Gua Tempurung, 4°25'02"N, 101°11'16"E; 13.XII.1997; leg. P.J. Schwendinger & L. Price.

Diagnosis: Similar to *L. laruticus*, distinguished by smaller body size and lighter body colouration; males different by much shorter, obliquely truncate para-embolic plate with retroventral-distal corner protruding further than proventral-distal corner (Fig. 10G-I cf. Fig. 7A, E), by less distinct proventral contrategular process (Fig. 10E-F cf. Fig. 7D, F-H), by less pronounced, shorter tegulum (distal edge smaller, proximal edge with fewer denticles; Fig. 10J cf. Fig. 7B), by having two enlarged spinules on retrolateral heel of paracymbium (Fig. 10A, C cf. Platnick *et al.*, 1997: figs 14-16), by more elevated cumulus with bristles less inclined from axis of palpal tarsus (Fig. 10A, C cf. Platnick *et al.*, 1997: figs 15-16), and by tibial apophysis being more slender (Fig. 10B, D cf. Platnick *et al.*, 1997: figs 14, 16). Females different from those of *L. laruticus* by poreplate with distinctly projecting processes on lateral margins in a more proximal position, by a distinctly more posteriorly situated CDO, by a longer and basally narrower receptacular cluster, and by a posteriorly much narrower posterior stalk (Fig. 11 cf. Fig. 7J).

Description of male (from Gua Kanthan, matured 9.VII.1998): *Colour in alcohol* (slightly darker in life): Sclerotised parts mostly light brown, except for: black eye mound, light paired patches on pars cephalica of carapace, cream-coloured proximal portion of chelicerae, reddish brown cheliceral fang and reddish brown palpal tarsus; ventral side of legs slightly lighter than dorsal side; membranes of prosoma whitish, membranes of opisthosoma greyish cream-coloured; opisthosomal tergites I-II light brown, others cream-coloured, with light brown spots (mostly along lateral and posterior margins).
Setae on carapace: Distinctly more setae in posterior half than in anterior half; six setae anterior to fovea.
Cheliceral teeth: Eleven small teeth of different sizes on promargin of each cheliceral groove.
Scopula: Only distally divided by a median stripe on all tarsi; very thin and covering distal two-fifths of ventral side of leg tarsus I; equally thin and covering two-thirds of tarsus II; distinctly denser and covering two-thirds of tarsus III; equally dense and covering three-fourths of tarsus IV.
Tarsal claws: Paired claws with 4-5 denticles; unpaired claws of anterior legs with 3-4 tiny denticles, those of posterior legs with 2-3 denticles.
Palp: Tibial apophysis quite wide at base, not set back from distal margin of tibia (Fig. 10B), carrying four very long apical megaspines with filiform tips (Fig. 10B-D). Apical lobes of tarsus little pronounced (Fig. 10L). Paracymbium fairly long and narrow in ventral view (Fig. 10A), moderately deep, its rounded retrolateral heel carrying two enlarged spinules (Fig. 10A, C); slightly elevated cumulus carrying three long thick bristles touching each other at base (Fig. 10A, C). Subtegulum without apophysis. Tegulum with indistinct proximal edge carrying few (4-5) weak denticles arranged in a curved row and pointing distad and ventrad instead of proximad; distal edge weakly pronounced, straight and only partly pigmented (Fig. 10J). Pigmented bridge between tegulum and contrategulum on retrodorsal side of palpal organ disconnected (Fig. 10J). Contrategulum with indistinct, rounded, proventrad- and slightly distad-directed process and with several fine, oblique parallel ridges on prolateral surface; dorsal apex of distal contrategular edge quite widely rounded and unmodified (i.e. without trench-like depression as in *L. langkawi*; Fig. 10E). Para-embolic plate short and obliquely truncate, its distal margin slightly invaginated, its retroventral-distal corner protruding further than its proventral-distal corner (Fig. 10G); no sharp ledge on prolateral side of contrategulum (as present in *L. desultor*). Sclerotised part of embolus proper long and narrow, strengthened by two pronounced longitudinal ribs, with more or less distinct denticles on apex (Fig. 10A, E); membranous part of embolus proper clearly shorter than sclerotised part.
Measurements: Total length 17.45; carapace 6.72 long, 6.42 wide; opisthosoma 7.55 long, 6.52 wide; eye mound 0.95 long, 1.20 wide; palpal coxae 2.16 long, 1.47 wide; labium 0.68 long, 1.37 wide; sternum 3.04 long, 2.25

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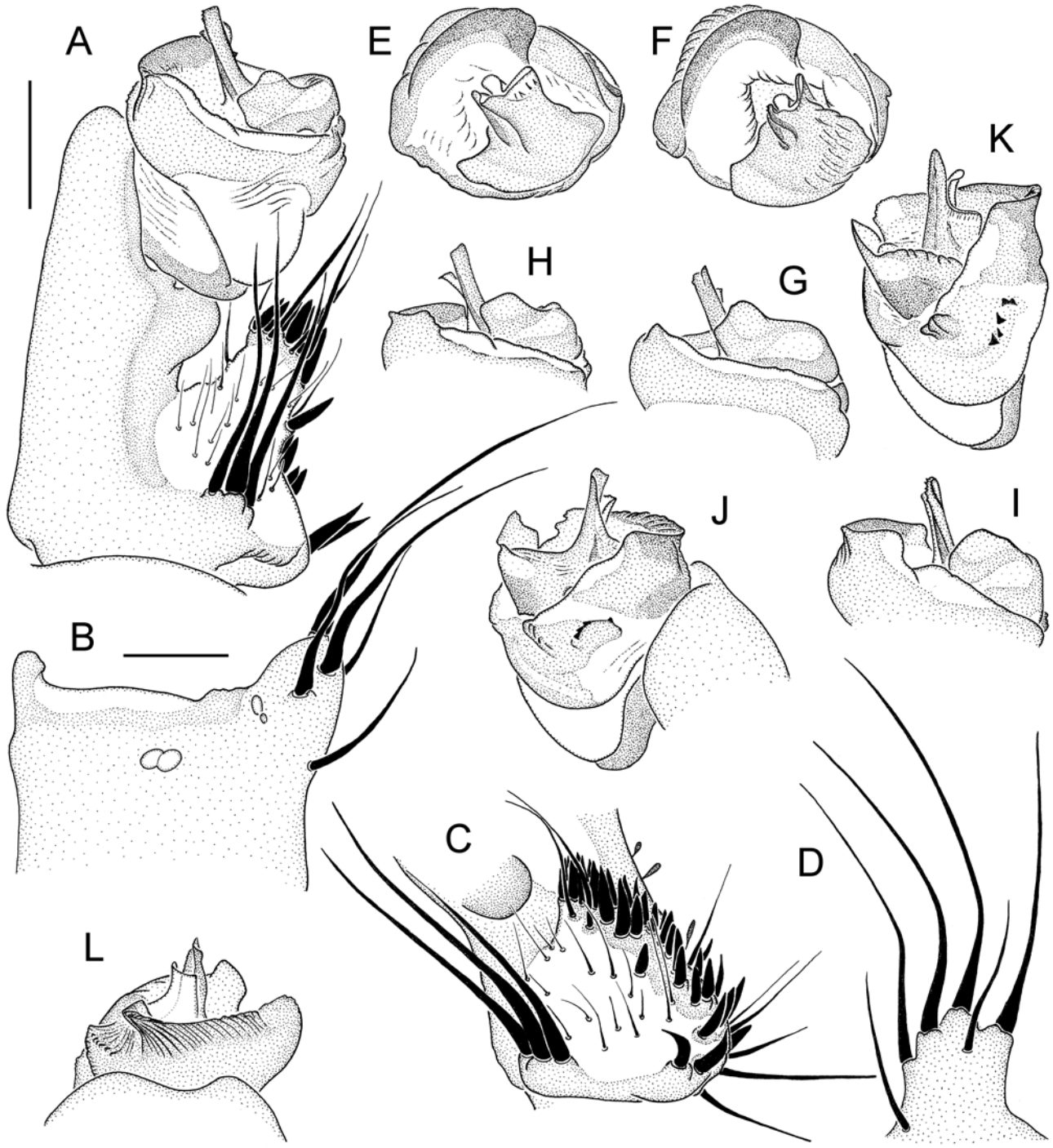


Fig. 10. *Liphistius kanthan*, details of left palp of two males from Kanthan Cave (A-E, G-H, J, L) and of one male from Tempurung Cave (F, I, K); male matured 9.VII.1998 (A-E, G, J, L), male matured 7.II.1999 (H), male matured 14.IX.1998 (F, I, K). (A) Tarsus and palpal organ, ventral view. (B) Distal part of tibia, ventral view. (C) Paracymbium, retrolateral view. (D) Tibial apophysis, retrolateral and slightly proximal view. (E-F) Palpal organ, distal view (dorsal side up). (G-I) Contrategulum and embolus complex, retroventral view. (J-K) Palpal organ, retrodorsal view. (L) Distal margin of tarsus and palpal organ, prodorsal view. Scale lines 0.5 mm (A, C, E-L; B, D).

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wide (on ventral surface 0.93); palp 11.67 long (3.73 + 2.16 + 3.92 + 1.86); leg I 23.48 long (6.67 + 2.94 + 5.39 +5.93 + 2.55); leg II 25.83 long (6.96 + 3.04 + 5.88 + 7.06 + 2.89); leg III 28.33 long (7.06 + 3.04 + 6.37 + 8.43 + 3.43); leg IV 35.89 long (8.43 + 3.14 + 8.04 + 11.57 + 4.71).

Additions to description of female: Vulval plate (Fig. 11) clearly wider than long, its posterior margin straight or indistinctly W-shaped. Ventral rim of poreplate with distinct lobes in a position between anterolateral and mediolateral; ventral side of poreplate with quite large vesicles (Fig. 11B, D-F); CDO small, situated in an unusual posterior position (Fig. 11A; see also Platnick *et al.*, 1997: fig. 12); receptacular cluster long, with a narrow stalk and a relatively small and little differentiated head (Fig. 11C); posterior stalk of poreplate strongly pigmented, anteriorly wide, posteriorly with a narrow truncate margin (Fig. 11B, D-F); genital atrium without lateral hairs.

Variation: Carapace length in males (n=4) ranges 6.72-7.54, carapace width 6.27-7.16; in the largest female (out of three examined) it is 7.84 and 7.06, and in the holotype 4.5 and 3.9, respectively. The holotype is thus a quite small female, but its vulva is nevertheless characteristic for the species (Platnick & Sedgwick, 1984: figs 12-13). The two large females from Gua Kanthan examined have protruding lateral processes on the ventral rim of the poreplate, whereas in two small females (holotype from Gua Kanthan and female from Gua Tempurung) these processes are only indicated by swellings (Fig. 11F and Platnick *et al.*, 1997: fig. 13). Variation in details of the male palp is given in Fig. 10. The single male from Gua Tempurung differs from three males from the type locality in a slightly arched distal margin of the para-embolic plate (straight or slightly invaginated in the others) (Fig. 10I cf. Fig. 10A, G-H), in an unbroken (though very narrow) retrodorsal bridge between tegulum and contrategulum, in stronger denticles in a slightly sigmoid row on proximal edge of the tegulum (Fig. 10K), and in both enlarged spinules on the retrolateral heel of the paracymbium with a longer filiform tip. In one male from the type locality the tips of these enlarged spinules are filiform only on one palp, in another male from the same locality only one of the two spinules (on both palps) has a filiform tip. The Gua Tempurung male has the scopula on its left tarsus II slightly shorter than on its right tarsus II. The number of setae anterior to the fovea varies from three to nine. One male from the type locality has lost both AME; another male and a female from the same locality have lost only one of them.

Relationships: Similarities in male and female genitalia show that *Liphistius kanthan* is most closely related to *L. buran* sp. nov. We attribute both species to complex D (see explanation under relationships of *L. buran* sp. nov.).

Distribution: *Liphistius kanthan* is known only from Gua Kanthan and Gua Tempurung (Fig. 2, localities 16 and 17), two limestone caves near Ipoh, in western Peninsular Malaysia. The two caves are 39 km apart. Gua Tempurung is the only know cave to harbour two *Liphistius* species. The limestone formation within which lies Gua Tempurung thus deserves high priority for conservation measures.

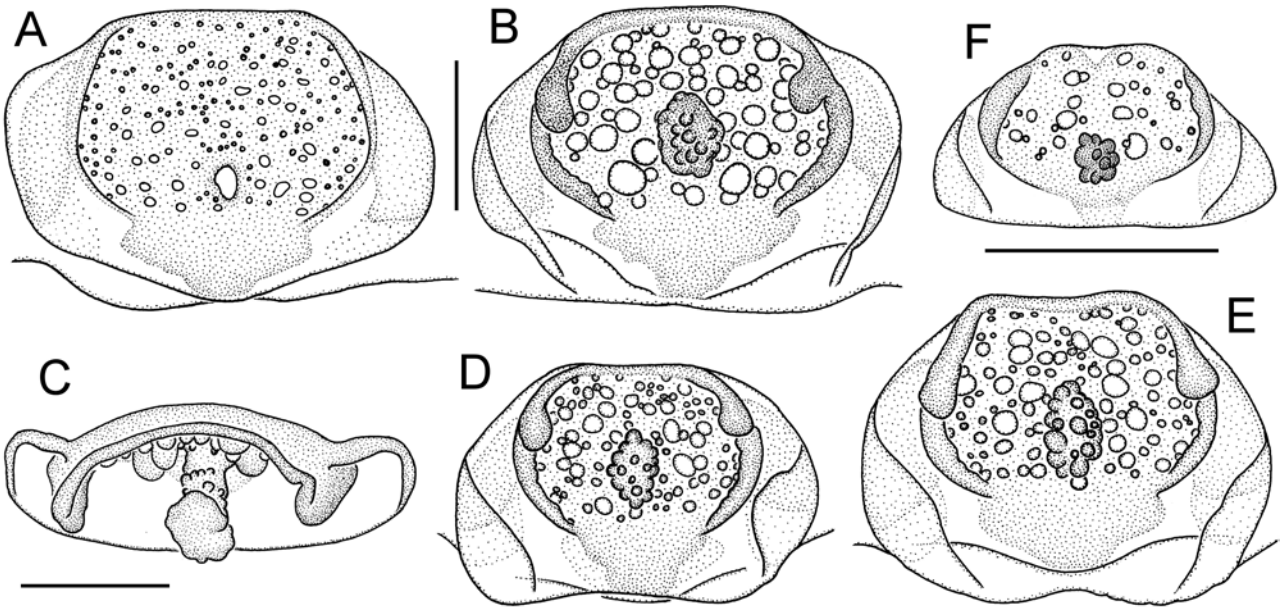


Fig. 11. *Liphistius kanthan*, vulval plate of three fully grown females from Kanthan Cave (A-C; D; E) and of one small female from Tempurung Cave (F). (A) Dorsal view. (B, D-F) Ventral view. (C) Anterior view. Scales 0.5 mm (A-B; C-E; F).

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Biology: The spiders examined were collected in the completely dark parts of Gua Kanthan (type locality of *L. kanthan*) and around the entrance of Gua Tempurung (type locality of *L. tempurung* Platnick, in Platnick, Schwendinger & Steiner, 1997, a species of the *batuensis*-group), in the euphotic and oligophotic parts of the cave. Steiner (1998a, b) also reported this species to be quite abundant at the entrance of Kanthan Cave and gave some information on its biology. Apart from a generally light body colouration and some degree of reduction in the AME (also present in many congeners not associated with caves), there is no indication of a morphological adaptation to permanent cave life. Since this species has never been collected away from limestone caves or cave entrances, is very likely to be restricted to such habitats, as it also is the case in *L. priceae* Schwendinger, 2017 (see Schwendinger, 2017: 437).

Males became mature in February, May, September and December, after 7-17 months in captivity, indicating that mating may take place all year round, without a specific mating period. However, this may not correspond to conditions in nature. The first two maturation dates (9.VII.1998 and 14.IX.1998, after seven and nine months in captivity) correspond well with the usual mating period of *Liphistius* species; the later dates (7.II.1999 and 22.V.1999, after 14 and 17 months in captivity) appear artificially delayed.

When collected in mid-December, one of the females had a 1.5 cm wide and 1.2 cm deep egg sac filled with already hatched (at least 2nd instar) spiderlings (not collected; see photos in Price, 1998). This female moulted two days later. The other two females examined (both adult) moulted in February to April, May and June, August and September, and in December, respectively, thus four times a year.

Two of the mature males had 2.9-3.0 cm wide and 1.7-2.0 cm long trapdoors. No other measurements of the burrows were taken.

Conservation status: *Liphistius kanthan* is currently listed by the International Union for Conservation of Nature (IUCN) as a critically endangered species (Whitten *et al*., 2013) and thus is considered as one of the rarest and most threatened spider species in the world. However, the new find from Gua Tempurung shows that it is not as restricted in its distribution as previously assumed. This species may also occur in and at the entrances of other caves in the area. Several limestone hills exist in the Kinta Valley, but unfortunately many of them are threatened by quarrying for cement production (Price, 1998, 2012, 2013). Thus *L. kanthan* continues to deserve a high degree of protection and its two know localities merit strong conservation efforts.

Liphistius buran **Schwendinger, sp. nov.**

Figs 12-15

Types: MHNG; male holotype (matured 29.III.1998), female allotype (constructed egg case 13.I.1998, moulted 26.III.1998), 3 males (matured 22.X.1998, 25.XI.1998, 22.XII.1998) and 6 female paratypes; Malaysia, Perak, Pangkor Island, Pangkor Hill (4°14’12”N, 100°34’07”E), 30-150 m; 15.-16.XII.1997; leg. P.J. Schwendinger.

Etymology: Malay: buran = sea anemone. The species epithet, a noun in apposition, refers to the shape of the strongly autapomorphic pad of microtrichia on the palpal organ of this species.

Diagnosis: Distinct from all other congeners by the presence of numerous microtrichia on the distal haematodocha (sensu Kraus, 1978) at the base of the embolus complex on the palpal organ (Figs 13H-I, 14A-E). Similar and apparently most closely related to *L. kanthan*. Both sexes distinguished from those of *L. kanthan* by a distinctly darker colour pattern, in particular by two paramedian bands in front of fovea (Fig. 12A-B). Males additionally different by one (two in *L. kanthan*) enlarged spinule on retrolateral-proximal heel of paracymbium (Fig. 13A, C cf. Fig. 10A, C), by less distinct denticles on distad-turned proximal margin of tegulum (Fig. 13E cf. Fig. 10J-K), by a long proventral contrategular process (indistinct in *L. kanthan*; Fig. 13H-I cf. Fig. 10E-F), by a slightly longer para-embolic plate (Fig. 13G cf. Fig. 10G-I) and by an urn-shaped major embolic fold (Figs 13E-F, H-I, 14A-C, F-G cf. Fig. 10E-F). Females distinguished from those of *L. kanthan* by the complete absence of a posterior stalk on vulval plate (Fig. 15 cf. Fig. 11) and by a less strongly raised receptacular cluster (Fig. 15C cf. Fig. 11C).

Description of male (holotype): *Colour in alcohol* (darker in life): Carapace with light brown basic colouration; anterior portion of pars cephalica with dark brown pattern around two parallel, lancelolate light paramedian patches behind very dark eye mound; posterior portion of pars cephalica with a conspicuous pair of brown paramedian bands anterior to brown fovea, these bands not reaching brown areas of pars cephalica and carrying six very short setae; pars thoracica mostly light brown, with a few dark specks in central part and with irregularly shaped brown lateral patches on coxal elevations (Fig. 12A). Chelicerae with proximal portion cream-coloured; distal portion light brown, with darker longitudinal bands. Annulated legs and palps with light brown basic colouration and dark brown rings: femora with proximal and subdistal rings (the latter indistinct on palps), tibiae only with proximal rings (indistinct on leg IV), metatarsi with indistinct proximal rings (hardly discernible on posterior legs), leg tarsi uniformly light brown, palpal tarsi reddish brown. Opisthosoma with

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cream-coloured membranous cuticle and mostly light brown tergites with lateral and paramedian pairs of irregular dark spots decreasing in size from anterior to posterior tergites: pair of dark paramedian spots large and medially confluent on tergite I, medially separated on tergite II, fragmented into two pairs on tergite III, rudimentary on tergite IV, absent on subsequent tergites.
Setae on carapace: Distinctly more setae in posterior half than in anterior half; six setae in two parallel rows (on brown bands) anterior to fovea.
Cheliceral teeth: Twelve and thirteen small teeth of different sizes (some hardly discernible) on promarginal groove of left and right chelicera, respectively.
Scopula: Only distally divided by median stripe on all tarsi; indistinct, not clearly outlined, composed of few scattered scopuliform setae in distal third of ventral side of leg tarsus I; equally thin and covering distal half of tarsus II; distinctly denser, clearly outlined, covering three-fourths of tarsus III and tarsus IV.
Tarsal claws: Paired claws with 3-4 denticles on tarsi I-II, three denticles on tarsus III, four denticles on tarsus IV; unpaired claw of tarsi I-III bare, of tarsus IV with one tiny denticle.
Palp: Tibial apophysis basally moderately wide in ventral view, not set back from distal margin of tibia (Fig. 13B), carrying five very long apical megaspines with filiform tips, all of them at different angles to axis of tibia (Fig. 13B, D). Apical lobes of tarsus little pronounced (Fig. 13F). Paracymbium fairly long and narrow in ventral view, moderately deep, its rounded retrolateral-proximal heel carrying one enlarged spinule (Fig. 13A, C); slightly elevated cumulus carrying five long thick bristles, most of them touching each other at the base (Fig. 13A, C). Subtegulum without apophysis. Tegulum little developed, with indistinct proximal edge turned distad and carrying a series of indistinct denticles in a curved row; distal edge distinct, widely arched and only partly pigmented (Fig. 13E). Pigmented bridge between tegulum and contrategulum on retrolateral side of palpal organ widely disconnected (Fig. 13E). Contrategulum with quite long and pointed proventral process (Fig. 13H); with a few very fine, oblique parallel ridges on prolateral surface (Fig. 13F); without a sharp ledge on prolateral surface (as present in *L. desultor*); dorsal apex of distal edge very narrowly rounded, almost triangular (Fig. 13H). Soft membrane (= distal haematodocha) at base of embolus complex densely covered with microtrichia of unknown function (Fig. 13H; see also Figs 13I, 14A-E for paratypes). Para-embolic plate with widely truncate apex, its retroventral-distal corner more protruding than its proventral-distal corner (Fig. 13H; see also Fig. 13G for paratype). Embolus proper narrow, sclerotised part strengthened by two longitudinal ribs, with more or less pronounced denticles on apex (Fig. 13A, H); membranous part of embolus proper only slightly shorter than sclerotised part; major embolic fold urn- or pitcher-shaped, with its two opposing walls widely separated at base (best seen in alcohol-preserved specimens; Fig. 13E-F, H; see also Figs 13I, 14A-C, F for paratypes and "Variation").
Measurements: Total length 11.73; carapace 5.20 long, 4.64 wide; opisthosoma 4.41 long, 3.19 wide; eye mound 0.83 long, 1.03 wide; palpal coxae 1.69 long, 1.10 wide; labium 0.47 long, 0.94 wide; sternum 2.32 long, 1.73 wide (on ventral surface 0.87); palp 9.06 long (2.68 + 2.05 + 2.83 + 1.50); leg I 15.68 long (4.33 + 2.17 + 3.39

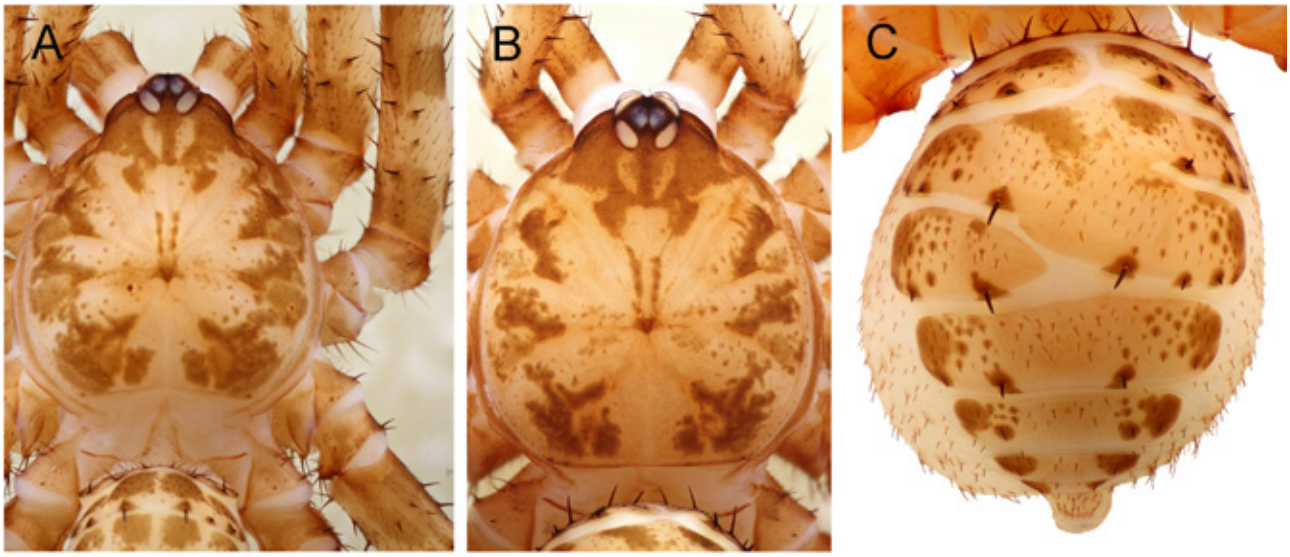


Fig. 12. *Liphistius buran* sp. nov. (A) Prosoma of male holotype, dorsal view (note bite marks on carapace). (B) Same of male paratype (matured 22.X.1998). (C) Opisthosoma of male paratype (matured 22.X.1998) with deformed tergites II-IV, dorsal view. Not to scale.

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+ 3.90 + 1.89); leg II 16.38 long (4.45 + 2.17 + 3.54 + 4.25 + 1.97); leg III 18.04 long (4.41 + 2.17 + 3.78 + 5.20 + 2.48); leg IV 23.98 long (5.59 + 2.36 + 5.20 + 7.40 + 3.43).

Description of female (allotype): *Colour in alcohol* (distinctly darker in life): Mostly as in male, but dark areas on pars cephalica and on coxal elevations of carapace smaller; two dark paramedian bands anterior to fovea indistinctly connected to dark pattern behind eye mound. Distal part of chelicerae distinctly darker; ventral side of body slightly darker. Dark annulations on all leg articles and on most palpal articles more distinct; palpal tarsus with light brown area in proximal two-thirds, rest of article dark brown.

Setae on carapace: Slightly longer than in male; eight setae in two parallel rows on dark bands anterior to fovea.

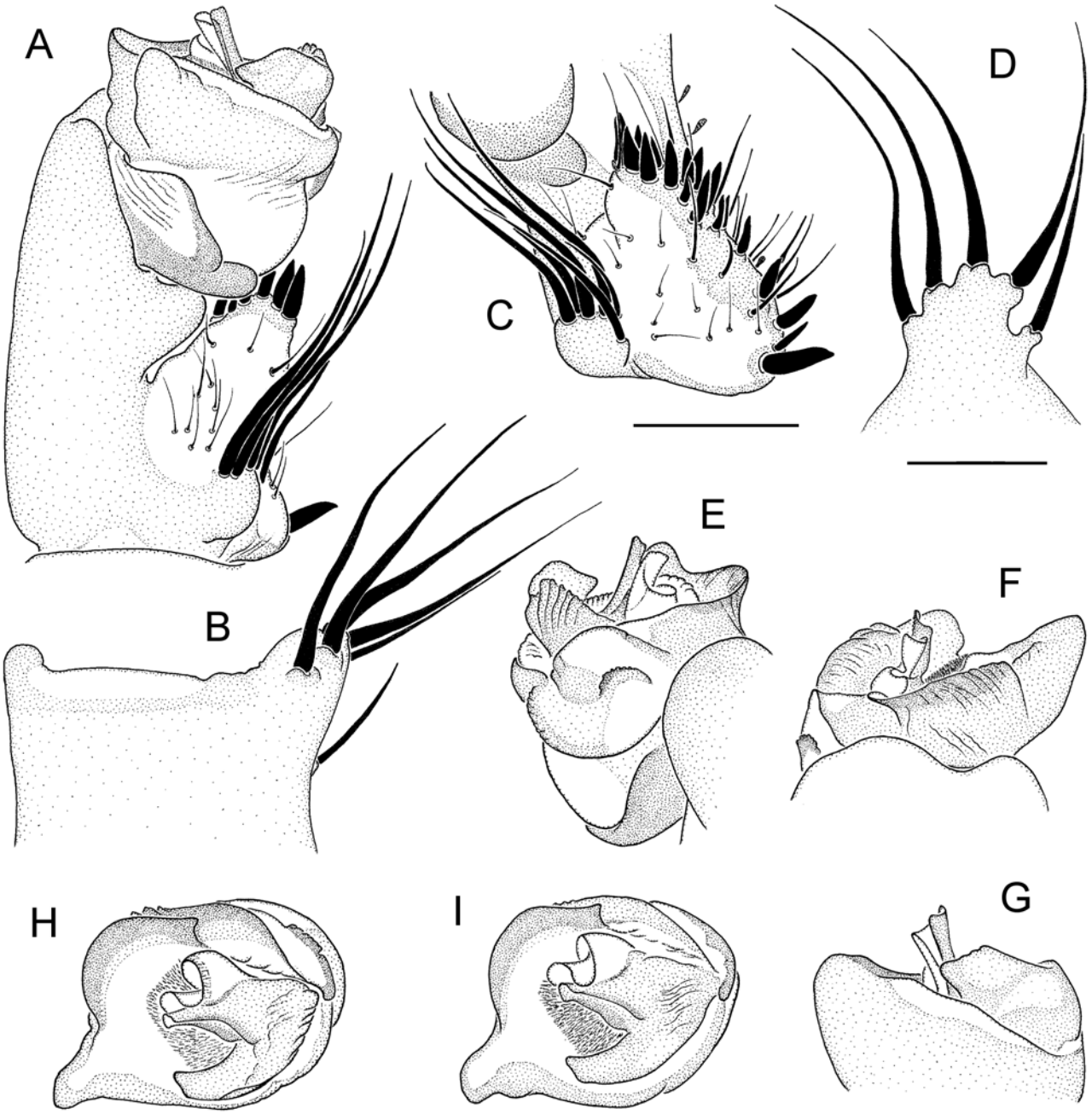


Fig. 13. *Liphistius buran* sp. nov., details of left male palp; holotype (A-F, H), paratype matured 22.XII.1998 (G), paratype matured 25.XI.1998 (I). (A) Tarsus and tarsal organ, ventral view. (B) Distal part of tibia, ventral view. (C) Paracymbium, retrolateral view. (D) Tibial apophysis, retrolateral and slightly proximal view. (E) Palpal organ, retrodorsal view. (F) Distal margin of tarsus and palpal organ, prodorsal view. (G) Contrategulum and embolus complex, retroventral view. (H-I) Palpal organ, distal view (dorsal side up). Scale lines 0.5 mm (A-C, E-I; D).

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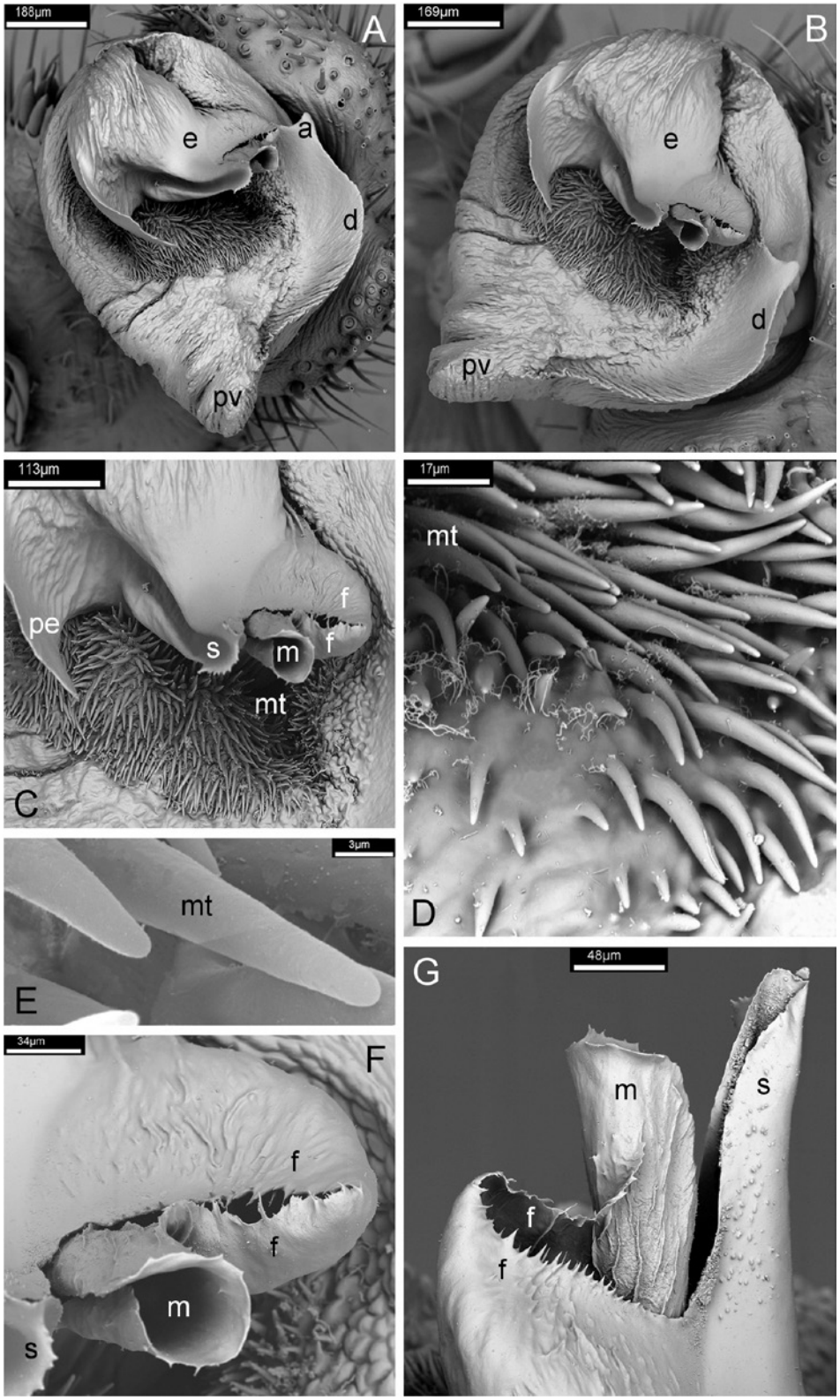


Fig. 14. *Liphistius buran* sp. nov., SEM-micrographs of right palpal organ of male paratype (matured 22.X.1998). (A) Whole palpal organ, distal view showing pad of microtrichia on membrane at base of embolus complex. (B) Same, rotated clockwise on longitudinal axis for about 50°. (C) Detail of embolus complex and microtrichia, approximately same view as in B. (D) Margin of microtrichia pad. (E) Apices of two microtrichia. (F) Part of embolus proper, approximately same view as in A. (G) Embolus proper, dorsal view. Abbreviations: a = dorsal apex of distal edge of contrategulum; d = distal edge of contrategulum; e = embolus complex; f = major embolic fold; m = membranous part of embolus proper; mt = microtrichium, microtrichia; pe = para-embolic plate; pv = proventral process of contrategulum; s = sclerotised part of embolus proper.

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Cheliceral teeth: Eleven strong teeth on promargin of groove of right chelicera, twelve on left chelicera.
Claws: Palpal claw with two denticles. Paired tarsal claws of anterior legs with 2-4 denticles, of posterior legs with 2-3 denticles; unpaired claws of anterior legs with 2-4 denticles, of posterior legs with 2-3 denticles. All tarsi without scopula.
Vulva (Fig. 15A-C): Vulval plate distinctly wider than long. Genital atrium remarkably short, strongly bent ventrad, without posterior stalk; lateral folds on ventral side of vulval plate well developed, without hairs. Poreplate with slightly and very widely invaginated, only slightly incrassate anterior margin and with strongly incrassate lateral margins ending in prominent, rounded anterolateral lobes; posterior margin of poreplate with irregular outline, situated just behind small CDO, the latter thus in an unusual posterior position on poreplate; receptacular cluster racemose, longer than wide.
Measurements: Total length 15.40; carapace 5.95 long, 5.00 wide; opisthosoma 5.99 long, 4.68 wide; eye mound 0.82 long, 0.97 wide; palpal coxae 2.06 long, 1.43 wide; labium 0.71 long, 1.43 wide; sternum 2.86 long, 2.38 wide (1.19 on ventral surface); palp 10.04 long (3.33 + 1.87 + 2.46 + 2.38); leg I 13.38 long (4.05 + 2.26 + 2.78 + 2.70 + 1.59); leg II 13.74 long (4.05 + 2.26 + 2.82 + 2.94 + 1.67); leg III 14.64 long (4.05 + 2.30 + 2.90 + 3.41 + 1.98); leg IV 19.65 long (5.24 + 2.46 + 4.13 + 5.28 + 2.54).

Variation: Carapace length in males (n=4) ranges 5.20-6.23, carapace width 4.64-5.52; in the largest female (out of six examined) it is 6.59 and 5.48, respectively. The number of setae anterior to the fovea varies from six to eight in males and from seven to ten in females. In all specimens examined both AME are well developed. In two males the scopula is slightly more distinct on tarsus II, and the scopula on tarsi III-IV is slightly more extensive (covering four-fifths of ventral side of article) than in the other two males (including the holotype; covering three-fourths). Variation in details of the male palp is given in Fig. 13. Three males have a single enlarged spinule (longer and thicker than others nearby) on the proximal-retrolateral heal of the paracymbium of both palps; in the fourth male that

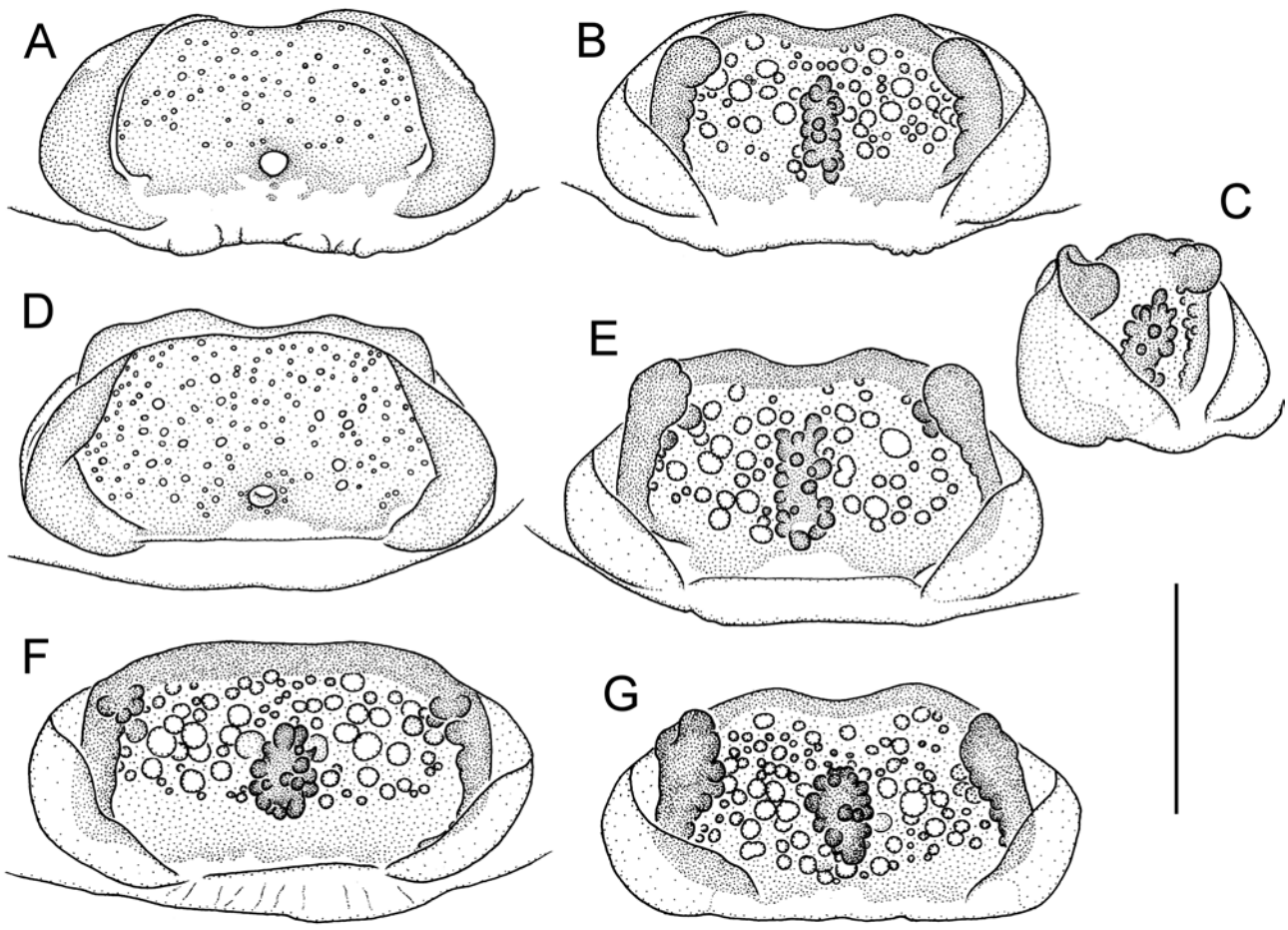


Fig. 15. *Liphistius buran* sp. nov., details of vulval plate from exuviae of four females; allotype (A-C), paratype moulted 3.VIII.1999 (D-E), paratype moulted 29.VIII.1998 (F), paratype moulted 24.V.1998 (G). (A, D) Dorsal view. (B, E-G) Ventral view. (C) Lateral view. Scale line 0.5 mm (A-G).

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modified spinule is recognizable only on one palp. In the dried palp used for SEM examination the distal margins of the major embolic fold (as well as the lateral margins of the membranous part of the embolus proper) are bent towards each other (Fig. 14B-C, F) and thus obscuring the urn-shaped form of the major embolic fold that is visible in alcohol-preserved palps (Fig. 13E-F, H-I). This is due to the deformation of thin, membranous cuticle caused by drying. Variation in the shape of the vulval plate is shown in Fig. 15. One of the male paratypes (matured 22.X.1998) shows a rare deformation of opisthosomal tergites II-IV (Fig. 12C).

Relationships: The vulval plate of this species strongly resembles that of species complex C (*L. fuscus, L. phuketensis* and *L. schwendingeri*) from southern Thailand in being wide and short, without a posterior stalk (Fig. 15 cf. Schwendinger, 1995: figs 18-20 and Schwendinger, 1998: fig. 5G-I), but it has distinct anterolateral lobes on the ventral rim of the poreplate. As males of *L. buran* sp. nov. do not possess a large tegulum and a distal contrategulum edge with a series of distinct wrinkles as characteristic for males of species complex C, we consider the new species more closely related to the species of complex D (*L. albipes, L. bicoloripes, L. castaneus, L. desultor, L. kanthan, L. laruticus, L. niphanae, L. sumatranus, L. trang, L. yangae*). This is also more consistent with biogeography: *L. kanthan*, which appears to be most closely related to *L. buran* sp. nov., is also geographically close (Fig. 2, localities 16-17 and 18). Both species share a similar vulval plate (with the CDO situated in a clearly more posterior position than in females of other congeners in Malaysia; presumably a synapomorphy) and a similar male palp (weakly developed tegulum, para-embolic plate with obliquely truncate distal margin, presence of 1-2 enlarged spinules on retrolateral heel of paracymbium).

Distribution: The new species is known only from Pangkor Island (= Pulau Pangkor) off the coast of Perak State, in the west of Peninsular Malaysia (Fig. 2, locality 18).

Biology: The spiders examined were found on sloping earth banks along an old logging road in a dense rainforest at the foot of Pangkor Hill (= Bukit Pangkor). Most burrows had only a single trapdoor, a few burrows were T-shaped and had two doors. Penultimate males had the front door 1.0-1.4 cm long and 1.6-2.1 cm wide (n = 4), and the back door (if present) 1.2-1.5 cm long and 1.7-2.1 cm wide (n = 2). The largest female had a single, 1.5 cm long and 2.1 cm wide door.

In captivity, in late January 1998, two of the females constructed egg cases, 1.9-2.1 cm in diameter and 1.3-1.5 cm deep, containing 33 and 56 light yellow eggs suspended on a fine mesh of silk threads. The spiders subsequently moulted in late March and in early April, respectively. The other three females moulted in April to May and again in August to September, twice per year.

Parasitic mites of the genus *Ljunghia* (see Halliday & Juvara-Bals, 2016: 853) were collected from three females and one male (the holotype). Bite marks were left on the carapace (see Fig. 12A) and on the dorsal side of the chelicerae but nowhere else on the body. The largest female has the most bite marks, the smallest female the fewest (only on the carapace).

MOLECULAR PART

Phylogenetic analysis and character optimization: Monophyly of the family Liphistiidae and of the genus *Liphistius* are recovered with a strong support (both with posterior probability = 1) (Fig. 16), but the evolutionary relationships between *Liphistius* and the remaining liphistiid genera remains unresolved. Within *Liphistius* two relatively well supported groupings were retrieved: (1) a clade comprising *L. desultor*, *L. laruticus* and specimens (not examined by the first author) from Ulu Kinta (near Ipoh), Telok Bahang (Penang Island) and the Penang Botanic Gardens, which probably all belong to *L. desultor* (posterior probability = 0.9993), and (2) a clade that includes *L. endau* Sedgwick & Platnick, 1987, *L. malayanus* Abraham, 1923b, as well as specimens (not examined by the first author) from the Parit Falls (in the Cameron Highlands), Felda Tekam, Pasir Raja and Lake Kenyir, which may belong to undescribed species (posterior probability = 0.9677). The latter group (= clade 2) corresponds to the *malayanus*-group and is characterized by a narrowly divided embolus, whereas the species in clade 1 possess a widely divided embolus. The non-Liphistiinae species (Heptathelinae, Atypidae, Halonoproctidae, Ctenizidae), on the other hand, have an undivided (no division into sclerotised and membranous part) embolus (see Fig. 17).

DISCUSSION

Zoogeography and vulnerability: The syntopic occurrence of two *Liphistius* species (*L. tempurung* and *L. kanthan*) in the interior and at the entrance of the same cave (Gua Tempurung in Perak State) is remarkable and not known from any other cave. On one hand this changes the status of *L. kanthan* as a critically endangered species (see Whitten *et al*., 2013), on the other hand it highlights the value of Tempurung Cave – and the limestone hill in which it is situated – for conservation. All *Liphistius* "cave species" in Malaysia (i.e. *L. batuensis, L. kanthan, L. panching* Platnick & Sedgwick, 1984*, L. priceae* and *L. tempurung*) are known exclusively from the entrance area (including cliff walls right outside the cave entrance) and from the interior of limestone caves. If a limestone hill with caves harbouring such spiders is quarried, the entire resident *Liphistius* population (or populations in

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Fig. 16. 50% majority-rule consensus tree computed from the Bayesian analysis of COI sequences of liphistiid and mygalomorph spiders. Posterior probabilities are indicated for each node.

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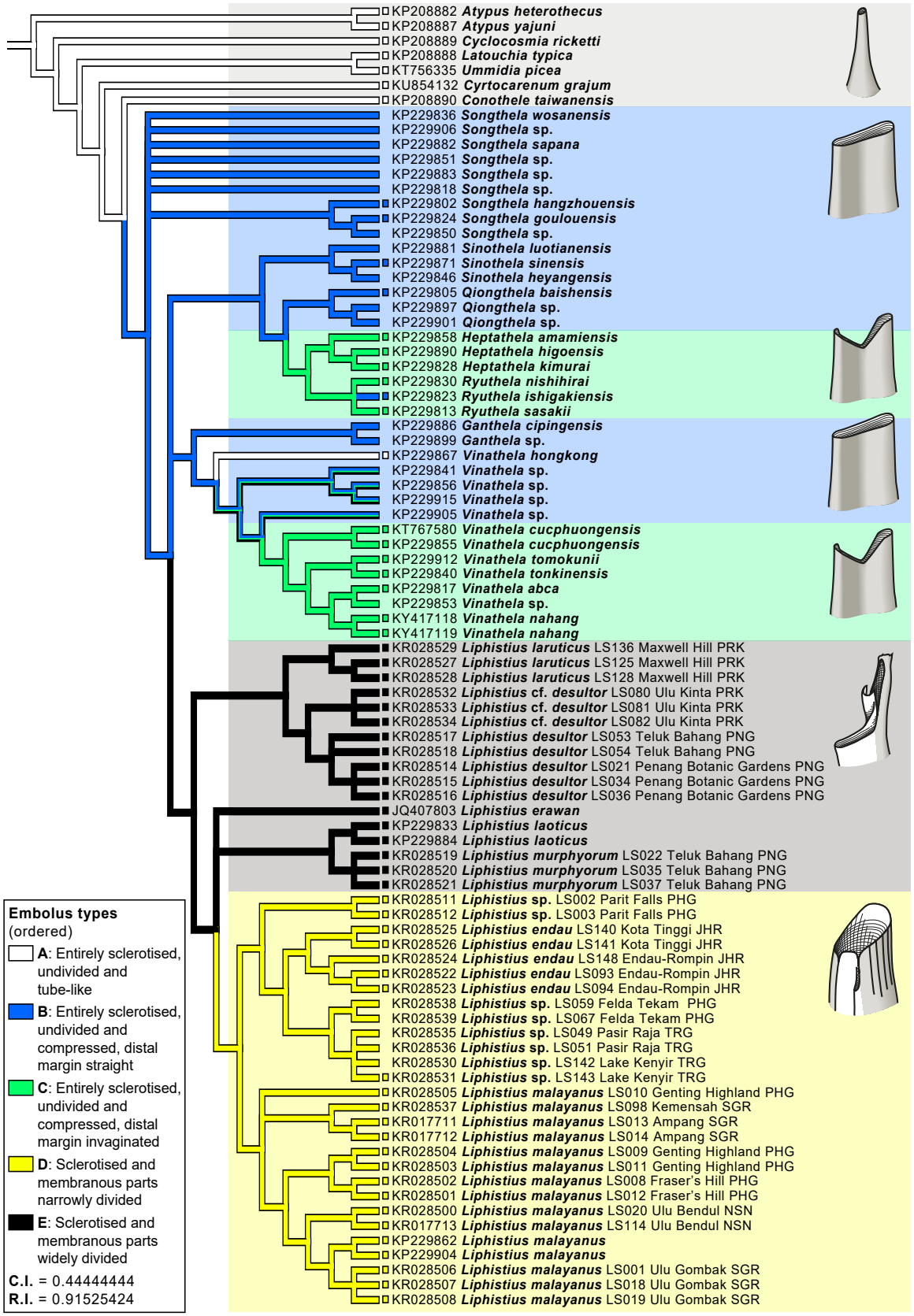


Fig. 17. Ancestral state reconstruction of embolus types: A = white, B = blue, C = green, D = yellow, E = black. Characters are mapped onto the maximum clade credibility tree from the Bayesian analysis. The consistency index and retention index, as well as schematic drawing for each character state are provided. Species in which the embolus type is known are marked with a small square at the end of the corresponding branches.

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the case of Gua Tempurung) will be wiped out and the already small genepool of the species will be further severely diminished. In the case of *L. priceae*, which is so far only known from two small caves close together in the same limestone hill (Schwendinger, 2017: 437), the entire species could go extinct. A special effort should be made to conserve these rare and charismatic species.

Phylogenetic analysis and character optimization: The gene COI alone does not provide enough signal to resolve the phylogenetic relationships between the various genera in the family Liphistiidae with confidence. Most of the nodes are poorly supported. Moreover, the topology retrieved here (Heptathelinae basal to *Liphistius*) is in contradiction with the phylogeny published by Xu *et al*. (2015b), which was computed from a much larger dataset (five genes, both nuclear and mitochondrial). Therefore only the relationships within *Liphistius* retrieved in our analysis are considered reliable and are discussed here.

The monophyly of *Liphistius* and the grouping of *L. endau*, *L. malayanus* and specimens with uncertain identity from four localities (all included in the monophyletic *malayanus*-group) are congruent with relationships inferred from embolus morphology. Although species of the *trang*-group do not form a monophyletic group, they are placed together as basal to the *malayanus*-group, which is also in congruence with embolus morphology. In the genus *Liphistius* this genital structure is most peculiar: it is split longitudinally on two opposing sides into distinct parts, one sclerotised, the other membranous (see Schwendinger, 2017: fig. 3), whereas in all other spiders, including the closely related Heptathelinae, it forms a closed, often compressed sclerotised tube (see paragraph "Material and methods - morphological methods"). Moreover, within *Liphistius* an undisputable morphological dichotomy clearly distinguishes species of the *trang*-group from the other congeners. Our molecular data show that the species of the *malayanus*-group, in which males possess a narrowly divided embolus, form a monophyletic group that is clearly distinct from species of the *trang*-group, in which males have a widely divided embolus. Although counterintuitive, the present molecular-based phylogeny suggests that the widely divided embolus (*trang*-group) is the primitive state. A more logical sequence would have been the gradual opening of an entire embolus (present in most spiders).

The molecular data also show another incongruence with the interpretation of morphological data. Schwendinger (2017: 395) placed *L. malayanus cameroni* Haupt, 1983, described from specimens collected in the Cameron Highlands, in the synonymy of *L. malayanus*. The two males from the Parit Falls in the Cameron Highlands, however, are quite distinct in their COI sequences from *L. malayanus* specimens collected at six localities outside the Cameron Highlands (Fig. 16). Either the two Parit Falls specimens belong to an undescribed species in the *malayanus*-group, which is quite unlikely, or the taxonomic status of *L. malayanus cameroni* needs to be re-evaluated.

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