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A revision of the trapdoor spider genus *Liphistius* (Mesothelae: Liphistiidae) in peninsular Malaysia; part 1

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Abstract: The currently known *Liphistius* species of peninsular Malaysia are assigned to five species-groups: the *trang*-group, the *malayanus*-group, the *batuensis*-group, the *tioman*-group and the *linang*-group. The latter four are defined and treated here. They are composed of eleven species. Four of them, *L. negara* sp. nov., *L. gracilis* sp. nov., *L. priceae* sp. nov. and *L. linang* sp. nov., are new and here described from males and females. *Liphistius indra* sp. nov., very closely related to *L. linang* sp. nov., is additionally described from the deep south of Thailand. The previously unknown males of *L. endau* Sedgwick & Platnick, 1987 and of *L. tempurung* Platnick in Platnick *et al.*, 1997 are presented for the first time. *Liphistius malayanus cameroni* Haupt, 1983 is placed in the synonymy of *L. malayanus* Abraham, 1923b. Information and illustrations of intraspecific variation in most species of these groups (except for *L. johore* Platnick & Sedgwick, 1984, for which no new material is available) is given together with data on biology and distribution. Taxonomic characters and biogeography are discussed.

Keywords: Arachnida - morphology - taxonomy - revision - variation - biology.

INTRODUCTION

The first ever *Liphistius* described and type species of the genus, *L. desultor* Schiödte, 1849, was found on Penang Island, off the western coast of peninsular Malaysia. Subsequently twelve additional *Liphistius* species (*L. batuensis* Abraham, 1923a; *L. malayanus* Abraham, 1923b; *L. johore* Platnick & Sedgwick, 1984; *L. langkawi* Platnick & Sedgwick, 1984; *L. murphyorum* Platnick & Sedgwick, 1984; *L. panching* Platnick & Sedgwick, 1984; *L. tioman* Platnick & Sedgwick, 1984; *L. yangae* Platnick & Sedgwick, 1984; *L. endau* Sedgwick & Platnick, 1987; *L. kanthan* Platnick in Platnick *et al.*, 1997; *L. tempurung* Platnick in Platnick *et al.*, 1997; *L. laruticus* Schwendinger in Platnick *et al.*, 1997) and one subspecies (*Lipistius malayanus cameroni* Haupt, 1983) were described from that country and are so far known only from there. A fifteenth taxon, *L. rufipes* Schwendinger, 1995, is known from both sides of the Thai-Malaysian border (Schwendinger, 1995; World Spider Catalog, 2017). Five of these species (*L. endau, L. johore, L. kanthan, L. tempurung* and *L. yangae*) were previously known only from females (as *L. johore* still is).

A first compilation of the knowledge (though without regard to taxonomy) on *Liphistius* of Malaysia was given by Yong (1978), a second by Platnick & Sedgwick (1984) in the context of a generic revision. During the last years considerable new *Liphistius* material (most of it deposited in the Natural History Museum of Geneva) has become available, which allows improved diagnoses for most species from Malaysia, documentation of their interspecific variation, descriptions of unknown males and the reporting of new localities. All this will be presented in two papers, starting here with the species which are assigned to four newly established species groups (distribution given in Fig. 1). The Malaysian species of the species-rich and widely distributed *trang*-group (defined in Schwendinger, 1990) will be treated in the second part of this revision.

MATERIAL AND METHODS

Morphology was studied and drawn mostly with a Zeiss SV11 stereomicroscope and an attached drawing tube, the ventral side of the *L. malayanus cameroni* vulval plate with a Nikon Optiphot compound microscope with an attached drawing tube. Whenever possible, female copulatory organs were drawn and examined from exuviae. Vulvae of alcohol-preserved specimens were cleared of soft tissue with fine forceps, insect pins

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and a paint brush with stiff bristles. Clearing in KOH was avoided, because it often leads to more or less pronounced deformation (bulging) of the vulval plate. With the exception of the paratype of *L. malayanus cameroni*, the ventral cuticular wall of the female genital region was cut off with microscissors to allow an unimpeded view of the ventral side of the vulval plate. Terminology of genital structures follows Schwendinger & Ono (2011), which, with regard to some parts of the male palpal organ, differs considerably from the terminology used in earlier publications on *Liphistius*. The term "embolus proper" refers to the distal portion of the embolus complex (= sclerite III *sensu* Kraus, 1978) which is more or less deeply divided into a sclerotized part and into a membranous (hyaline, hyaloid) part between which lies the opening of the spermophore. The embolus proper is distinguished from the wide base of the embolus complex which carries the more or less distinctly developed para-embolic plate (a homologue of the conductor in Heptathelinae). The term "vulval plate" is here used to describe the sclerotised ventral wall of the vulva (as opposed to the thin membranous dorsal wall). It is composed of an anterior portion (i.e. the poreplate, perforated by pores that lead to ampulliform vesicles and to a receptacular cluster on its ventral side) and a posterior portion (i.e. the unpigmented or lightly pigmented genital atrium within which lies the strongly pigmented posterior stalk). Opisthosomal tergites are numbered from anterior to posterior, with the anteriormost 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 its anterior and posterior margin 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 relevant taxonomic characters 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.

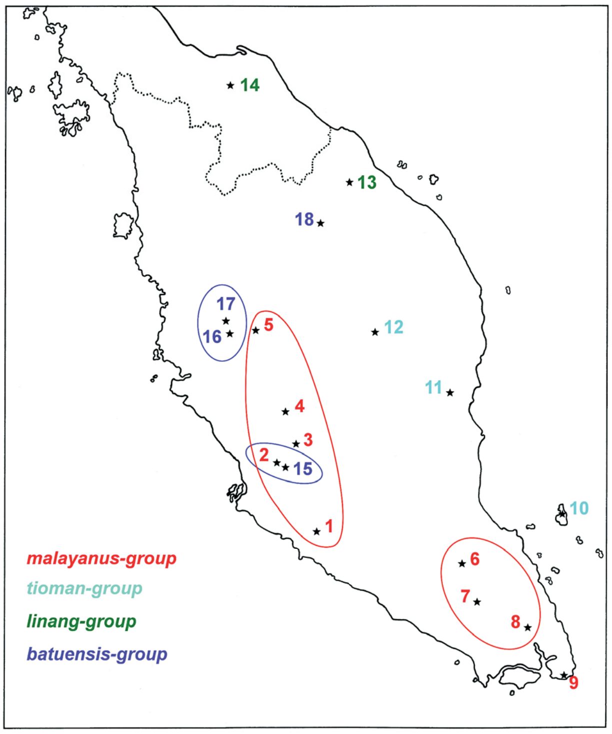

Fig. 1. Localities of *Liphistius* species of the *malayanus*-group, *tioman*-group, *linang*-group and *batuenis*-group in peninsular Malaysia and southern Thailand (coast of Sumatra omitted): 1 - Gunung Angsi (type locality of *L. malayanus*); 2 - Templer Park and Gua Anak Takun (*L. malayanus*, *L. batuensis*); 3 - Genting Highlands (*L. malayanus*); 4 - Fraser's Hill (*L. malayanus*); 5 - Cameron Highlands (type locality of *L. malayanus cameroni*); 6 - Sungai Jasin in Endau Rompin National Park (type locality of *L. endau*); 7 - Gunung Belumut (*L. endau*); 8 - Gunung Muntahak (*L. endau*; type locality of *L. gracilis* sp. nov.); 9 - Sungai Rengit (type locality of *L. johore*); 10 - Gunung Kajang on Tioman Island (type locality of *L. tioman*); 11 - Gua Charas in Bukit Charas (type locality of *L. panching*); 12 - Nusa Camp in Taman Negara (type locality of *L. negara* sp. nov.); 13 - Jeram Linang Waterfall (type locality of *L. linang* sp. nov.); 14 - Sankalakhierie Mountains (type locality of *L. indra*); 15 - Batu Caves (type locality of *L. batuensis*); 16 - Gua Tempurung (type locality of *L. tempurung*); 17 - Gua Cicak (*L. tempurung*); 18 - Gua Keris (type locality of *L. priceae* sp. nov). Localities with conspecific populations are encircled. Colours distinguish species groups.

The type specimens of most taxa treated here were not re-examined because: (a) those of the "old species" (*L. malayanus*, *L. batuensis*) were redescribed and illustrated in Haupt (1983) and Platnick & Sedgwick (1984); (b) the descriptions and illustrations of the other taxa (except for *L. malayanus cameroni*) are considered sufficient and reliable, and thus a re-examination of the types is not necessary; (c) some of the new specimens presented here were collected at (or very close to) the type localities of their respective species (*L. batuensis*, *L. endau*, *L. panching*, *L. tempurung*, *L. tioman*), and no second *Liphistius* species is known to occur at these localities.

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; ZMH = Centrum für Naturkunde (formerly Zoologisches Museum) of the University of Hamburg, Germany; ZRC = Zoological Reference Collection of the National University of Singapore (now housed in the

Lee Kong Chian Natural History Museum, Singapore). Other abbreviations used in the text are: AME = anterior median eyes, CDO = dorsal central opening (macropore) of poreplate. Additional abbreviations are explained in the figure legends.

TAXONOMIC PART

Liphistius Schiödte, 1849

Type species: *Liphistius desultor* Schiödte, 1849, described from female holotype deposited in the Natural History Museum of Denmark (= Zoological Museum of the University of Copenhagen).

Diagnosis and characterisation: See Platnick & Sedgwick (1984); habitus as in Fig. 2A-B.

The *malayanus*-group

Diagnosis: Distinguished from the *trang*-group by an indistinctly split embolus proper (Fig. 3B, D, F, H) and from all other species groups by distal edge of contrategulum proventrally ending in a V-shaped or U-shaped row of denticles (the clearest synapomorphy of this group; Figs 4C; 6A, C; 8A, D). Vulval plate strongly sclerotised, with a large, undivided CDO and with a large, undivided receptacular cluster (Figs 5, 7, 9).

Key to the species-groups in peninsular Malaysia:

1 Embolus proper deeply split, distal portion of sclerotised and membranous part disconnected from each other on both sides (on retrodorsal side more widely so than on proventral side); ventrolateral wall of sclerotised part and of membranous part basally running into a short but very wide, mostly dorsad-directed fold (called "dorsal lamella" in Schwendinger, 1990: figs 60-62) (Fig. 3A, C, E, G); distal margin of tegulum (corresponding to marginal tegular apophysis of Heptathelinae; see Schwendinger & Ono, 2011) drawn into a more or less distinctly prominent edge; subtegulum with or without apophysis. Poreplate with small CDO and rather small and simple receptacular cluster; mediolateral processes on ventral rim of poreplate present or absent (e.g. Schwendinger, 1990: figs 37-39, 43-45, 47-49, 53-56) .... *trang*-group

\- Embolus proper much less distinctly split, sclerotised and membranous part touching each other on both sides and forming a closed tube; connecting fold mostly long and narrow, indistinct and running prolaterad (Fig. 3B, D, F, H) (in *L. endau* and *L. negara* sp. nov. bent prodorsad instead of running straight proventrad or prolaterad; Figs 6F, H; 8F-G); distal margin of tegulum indistinct, never developed as an edge; subtegular apophysis never present. Poreplate with very large quadrangular, pentangular or trapezium-shaped CDO (see Fig. 5), or (rarely) with small or medium-sized circular CDO (see Fig. 24F), or with indistinct slit-like CDO (see Figs 16A, C-D; 22A, C, E, G); receptacular cluster large or medium-sized, always complex, never simple and digitiform; mediolateral processes on ventral rim of poreplate always absent 2

2 Contrategulum with distal edge proventrally ending in a downward-curved, U-shaped or V-shaped row of denticles (Figs 4C; 6A, C; 8A, D); para-embolic plate short or absent. Vulval plate strongly sclerotised; CDO large, of various shapes; receptacular cluster large, always undivided .... *malayanus*-group

\- Distal edge of contrategulum proventrally not ending in a U-shaped or V-shaped row of denticles; para-embolic plate short or long. Vulval plate completely or only partially scerotised; CDO small to large, rounded, angular or slit-like, entire, medially divided by a longitudinal septum (Fig. 13G), or completely divided into two paramedian openings (Figs 13A, C-D; 14I); receptacular cluster entire or divided into two paramedian halves (Figs 13B, E-F, H; 14J) 3

3 Contrategulum with more or less distinct ventral process (Figs 10B, 11F, 14C-D). Vulval plate completely scerotised; CDO rounded or angular, entire (Fig. 12A, C, F), medially divided by a longitudinal septum (Fig. 13G), or completely divided into two paramedian openings (Figs 13A, C-D; 14I); receptacular cluster always divided into two paramedian halves (Figs 12B, D, G; 13B, E-F, H; 14J) .... *tioman*-group

\- Contrategulum always without ventral process. Posterior portion of vulval plate only partially scerotised; CDO and receptacular cluster never divided longitudinally 4

4 Para-embolic plate long, its distal margin coarsely serrate (Figs 15B-D, 17B-D); dorsal apex of contrategulum narrow and pointed (Figs 15E-F, 17G-H); distal margin of cymbium with two indistinct, subequal lobes (Figs 15B, 17B); tibial apophysis divided into a long part carrying three megaspines and a short part with only one megaspine, all these megaspines short and bent (Figs 15A, G-I; 17A, I-K). Vulval plate with posterior stalk reduced to a small sclerite at posterior margin, far apart from poreplate (Figs 16A-E, 18A-F) .... *linang*-group

\- Para-embolic plate short, its distal margin smooth; dorsal apex of contrategulum wider, tounge-shaped, with rounded or pointed tip (Figs 19D, 21I-L, 23D-G); distal margin of cymbium with prodorsal lobe distinctly longer than proventral one (Figs 19C, 21H, 23J); tibial apophysis undivided, its megaspines long or short, curved but not bent. Posterior stalk wide, close to poreplate, not or only partially connected to poreplate (Figs 20, 22, 24) .... *batuensis*-group

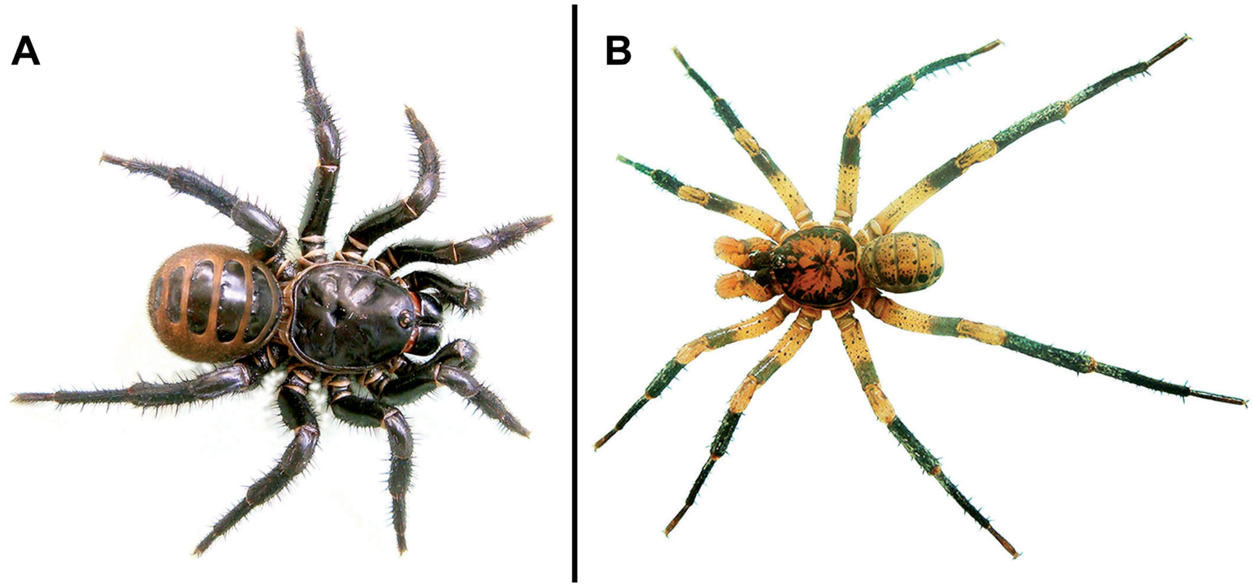

Fig. 2. Habitus of two *Liphistius* species from peninsular Malaysia and southern Thailand. (A) *Liphistius endau*, female from Kota Tinggi (Malaysia), dorsal view. (B) *Liphistius indra* sp. nov., male paratype from the Sankalakhierie Mountains (Thailand), same view.

Description: Small to large species (carapace length of males 4.36-12.04, carapace width 3.64-10.99); body colouration uniformly dark (in large species: *L. malayanus* and *L. endau*; Fig. 2A) or brown with annulated legs and palps (in smaller species: *L. johore* and *L. gracilis* sp. nov.). Male palp with membranous and sclerotised part of embolus proper in close contact with each other (both distinctly separated in *trang*-group), together forming a closed tube; dorsal wall of sclerotized part of embolus proper straight and directed proventrad (*L. malayanus*; Fig. 4G-H), curved prodorsad (*L. endau*; Fig. 6F, H) or bent prodosad (*L. gracilis* sp. nov.; Fig. 8F-G); para-embolic plate short or absent (Figs 4D, 6E); tegulum with coarsely dentate proximal edge (corresponding to dorsal extension of terminal apophysis in Heptathelinae; see Schwendinger & Ono, 2011), distal margin (corresponding to marginal apophysis) indistinct, not drawn into a prominent edge (Figs 4D-F, 6D-E, 8E); contrategulum with indistinct ventral process or without, distal edge carrying several teeth, prolateral ones numerous, tiny and forming a serrate crest (*L. gracilis* sp. nov.; Fig. 8D-G), few and small (*L. malayanus*; Fig. 4G-L), or only represented by a single large triangular tooth (*L. endau*; Fig. 6F, H-O), proventral denticles of distal edge forming a downward-curved V-shaped (Fig. 4C) or U-shaped row (Figs 6A, C; 8D), dorsal apex of contrategulum widely to narrowly tongue-shaped (Figs 4G-L; 6F, H-O; 8F-G); subtegulum always without apophysis; paracymbium quite small and shallow to large and deep (Figs 4A, 6B, 8B); cumulus very low, indistinct, carrying several long, thick bristles; retrolateral tibial apophysis relatively short and carrying long apical megaspines (*L. malayanus* and *L. endau*; Figs 4A-B, 6A-B) or quite long and carrying distinctly shorter megaspines (*L. gracilis* sp. nov.; Fig. 8A-C, I-J); both apical lobes of cymbium weakly developed (Fig. 8D). Vulva (Figs 5, 7, 9, 10A): poreplate strongly pigmented and sclerotised, wider than long, its anterior margin more or less distinctly recurved, with or without anterolateral lobes or processes, never with mediolateral processes; CDO and ventral receptacular cluster large to very large, both undivided; posterior stalk wide (in *L. endau* even covering entire width of genital atrium; Fig. 7), somewhat trapezium-shaped or almost triangular (Fig. 10A); genital atrium with few to many lateral hairs and with no, few or numerous median hairs.

Species included: *Liphistius endau, L. malayanus, L. gracilis* sp. nov. and presumably also *L. johore* (male still unknown).

Relationships: Species of the *malayanus*-group are most similar and probably closely related to species of the *tioman*-group. The two large species, *L. malayanus* and *L. endau,* are closer to each other than to the much smaller *L. gracilis* sp. nov. (distinguished by serrate distal edge of contrategulum and by sharp bend in wide dorsal wall of sclerotised part of embolus proper). Small size, details of the vulval plate and geographical proximity suggest a close relationship between *L. gracilis* sp. nov. and *L. johore*, but this can only be confirmed when the male of the latter species is discovered.

Key to the species of the *malayanus*-group:

1 Small spiders (carapace length of mature males and females 4.36-5.34, carapace width 3.64-4.22) with brown body colouration and annulated limbs; lateral and posterolateral margins on ventral side of poreplate not bulging (Fig. 9B, D, F; Platnick & Sedgwick, 1984: fig. 80)..2

\- Large (carapace lengths in males 7.90-12.04, carapace width 7.0-10.99), uniformly dark-coloured spiders; lateral and posterolateral margins of poreplate on ventral side of vulval plate bulging (Figs 5B, J; 7B, E, G)..................3

2 Vulval plate with indistinct transition between poreplate and posterior stalk, the latter wide in transition zone; anterior margin of poreplate without or with only indistinct anterolateral invaginations; genital atrium with numerous lateral and median hairs (Fig. 9A, C, E)..*L. gracilis* sp. nov.

\- Vulval plate with distinct transition between poreplate and posterior stalk, the latter very narrow in transition zone; anterior margin of poreplate with pronounced anterolateral invaginations; genital atrium without hairs (Fig. 10A) (male unknown)..*L. johore*

3 Dorsal and ventral wall of sclerotised part of embolus proper equally wide, both ends facing proventrad (Fig. 4G-H), dorsal wall ending in indistinct rounded lobe (Fig. 4C-F); membranous part of embolus proper distally narrow (Figs 3F, H; 4C); distal edge of contrategulum with one to several small denticles (Fig. 4C, G-L); paracymbium about as deep as wide (Fig. 4A). Dorsal side of vulval plate with anterolateral corners of genital atrium not bulged and elevated above level of poreplate; usually no median hairs in genital atrium (Fig. 5A, C-H, but see Fig. 5I); receptacular cluster not divided into subclusters (Fig. 5B, J)..*L. malayanus*

\- Dorsal wall of sclerotised part of embolus proper wider than ventral wall, end of dorsal wall bent prodorsad (Fig. 6F, H) and forming pronounced lobe (Fig. 6C-E); membranous part of embolus proper distally wide (Fig. 6C, F-H); distal edge of contrategulum with a single large triangular tooth (Fig. 6F, H-O); paracymbium much deeper than wide (Fig. 6B). Dorsal side of vulval plate with anterolateral corners of genital atrium bulged and elevated above level of poreplate; median hairs usually present in genital atrium (Fig. 7A, C-D, F); receptacular cluster divided into three more or less distinct subclusters (Fig. 7B, E, G)..*L. endau*

Distribution: All described species of this group occur in the western and southern part of peninsular Malaysia (Fig. 1, localities 1-9); an undescribed species appears to be present in the northeastern corner of the country (Fig. 1, locality 13).

Liphistius malayanus Abraham, 1923

Figs 3B, D, F, H; 4-5

Liphistius malayanus Abraham, 1923b: 770-774, text-fig. 1a-b (description of female). – Abraham (1929: 674-676, pl. 1, figs 3-4, pl. 2, figs 11-16; first description of male). For synonymy and other taxonomically relevant publications see the World Spider Catalog, 2017.

Liphistius malayanus cameroni Haupt, 1983: 282, figs 3e, 4d, 5f, 6f (description of male and female). **New synonym**

Type material: BMNH; female holotype of *L. malayanus* (not examined); Negri Sembilan, Gunung Angsi near Seremban; XII.1922; leg. F. de la Mare Norris. – ZMH (A16/84); male holotype and female paratype of *L. malayanus cameroni* (examined); Pahang, Cameron Highlands, Berinchang; 4.III.1981; leg. J. Haupt & T. Dach.

Remark: A *L. malayanus* male (not examined) from Fraser's Hill was described by Abraham (1929) and deposited in the BMNH. Haupt (1983: 281, figs 3d, 4c) re-described this specimen and referred to it as the paratype, but it has no type status, having been collected in November 1928, after the publication of the original description of the species.

Material examined: ZMH (A16/84); male holotype [left palp detached, macerated and partly collapsed, cymbium and hematodocha cut open to expose tendons inside, all strong spines deformed; right palp without tegulum, contrategulum and embolus complex] (matured VII.1981) and female paratype of *Liphistius malayanus cameroni*; Pahang, Cameron Highlands, Berinchang; 4.III.1981; leg. J. Haupt & T. Dach. – Collection of Joseph Koh, n° JK.14.10.05.0001; 1 male; Pahang, Cameron Highlands, Taman Tringkap NE of Brinchang, 4°28'26"N, 101°22'58"E; 5.X.2014; leg. N. Bay. – MHNG; 1 female, 1 juv. male; Perak, Cameron Highlands, ca 1 km SW of Ringlet, 1060 m; 21.I.1995; leg. P.J. Schwendinger. – MHNG (sample TM-15); 1 juv. male; Pahang, Cameron Highlands, Tanah Rata, trail n° 9, 4°27.620'N, 101°23.400'E, 1210 m; 29.IX.2001; leg. L. Monod. – SMF 7425/2 (ex coll. C. F. Roewer); 2 juv. females (labelled as "1 male and 1 female, det. Roewer, 1935"); Pahang, "Ginting Kial Highlands" [probably a peak in the Cameron Highlands]. – SMF 40602; 1 male; Pahang, Fraser's Hill, roadside at Jalan Girdle; 19.XII.2001; leg. S. Huber. – SMF 56206; 1 female; Pahang, Fraser's Hill, roadside at Jalan Girdle; 19.XII.2001; leg. S. Huber. – MHNG (ex coll. S. Huber, sample O-4, C); 1 male (matured end March 2002), 1 female (moulted 24.VI.2002); Pahang, Fraser's Hill, Jalan Guillemard; 18.XII.2001; leg. S. Huber. – SMF 64093; 1 female; Pahang, Fraser's Hill, 1300 m, 3°43.105'N, 101°45.164'E; 17.VI.2013; leg. P. Jäger. – MHNG

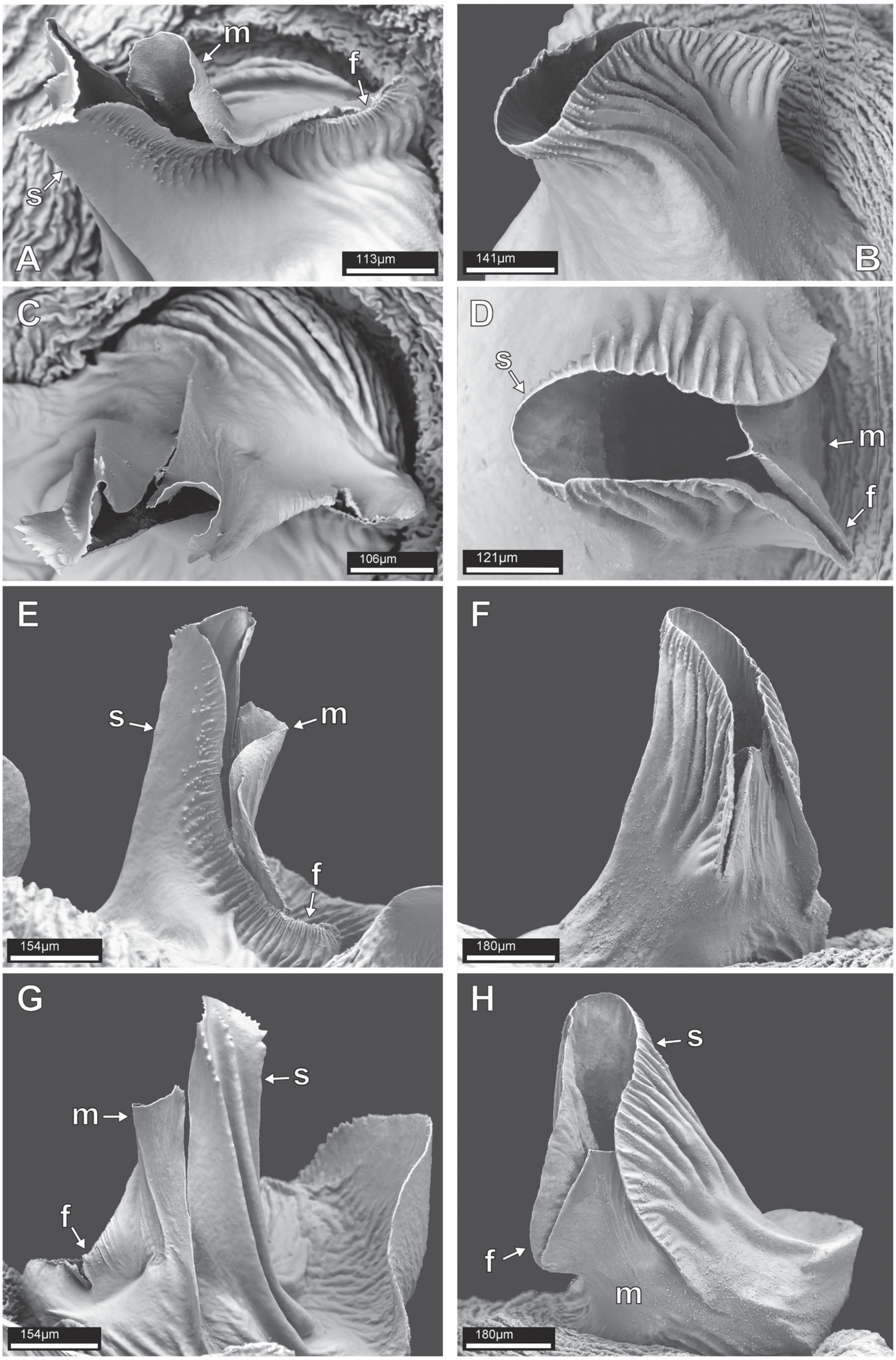

Fig. 3. SEM-micrographs of embolus proper of left palpal organ of two males: *Liphistius desultor* from Penang Hill (A, C, E, G) and *Liphistius malayanus* from Fraser's Hill (B, D, F, H). (A) Retroventral-distal view. (B) Dorsal-distal view. (C) Distal view (dorsal side to the right). (D) Distal view (prolateral side to the right). (E) Retrodorsal view. (F) Prodorsal view. (G) Proventral view. (H) Prolateral view. Abbreviations: f - major embolic fold; m - membranous part of embolus proper; s - sclerotised part of embolus proper.

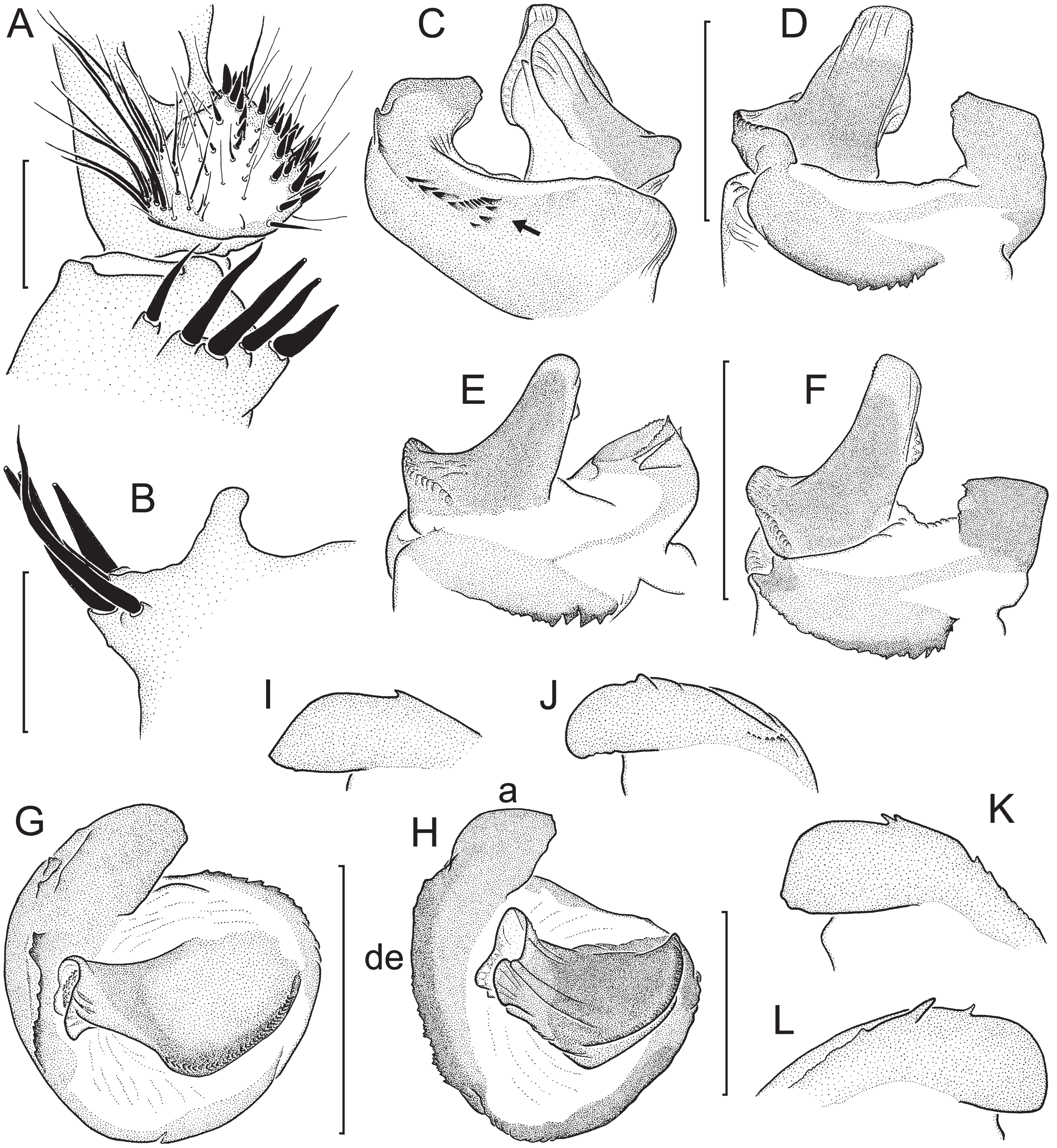

Fig. 4. *Liphistius malayanus*, details of palp of four males: Templer Park (A, C-D, H-I); holotype of *L. malayanus cameroni* (B, E, G); Cameron Highlands, ZRC (F, J), Fraser's Hill, MHNG (K-L). (A) Paracymbium and tibial apophysis of left palp, retroventral view. (B) Tibial apophysis of right palp, ventral view. (C) Distal part of left palpal organ, proventral view (arrow indicating V-shaped row of denticles at proventral end of distal edge of contrategulum). (D, F) Same, retrodorsal and slightly proximal view. (E) Same, retrodorsal view. (G-H) Left palpal organ, distal view (dorsal side up). (I, K) Distal edge of contrategulum of right palp, distal view (dorsal side to the left). (J) Same, distal and slighly prolateral view. (L) Same of left palp, distal and slighly prolateral view (dorsal side to the right). Abbreviations: a - dorsal apex of contrategulum; de - distal edge of contrategulum. Scale lines: 1.0 mm (A; B; C-D; E, G; F; H-L).

(sample MAL-04/02); 1 male (matured 18.IX.2004), 2 females (moulted 30.VII.2004, 24.I., 28.VIII., 8.XII.2005; 19.X.2004, 30.VII.2005), 4 juveniles; Pahang, Genting Highlands, 3°25'42"N, 101°47'41"E, 1650 m; 18.-19.V.2004; leg. P.J. Schwendinger. – SMF 21946/1; 1 female; without locality data; 10.XI.1933; ex coll. Wiehle, don. W. S. Bristowe. – SMF 60037; 1 female; "Selangor" [should be Pahang], Genting Highlands, 1800 m; 3.II.1989; leg. U. Maschwitz, don. H. Steiner. – SMF 40016; 1 female; Pahang, Genting Highlands, 1200 m; 27.VII.2001; leg. A. Kovac. – MHNG (sample SIM-01/14); 1 male (matured end VIII.2003), 1 female (moulted 31.XII.2001), 1 juvenile; Selangor, Templer Park, 3°17'55"N, 101°37'13"E, 230 m; 13.VII.2001; leg. P.J. Schwendinger.

Diagnosis: Large, dark-coloured species in both sexes. Males distinguished from those of other species in the *malayanus*-group by tibial apophysis situated distinctly lower (more proximal) than distal margin of palpal tibia (Fig. 4B); distal edge of contrategulum carrying a series of small denticles (Fig. 4G-L), those at proventral end arranged in a V-shaped row (Fig. 4C), 1-2 at prodorsal end isolated and slightly enlarged; dorsal apex of contrategulum large, wide, tounge-shaped and asymmetrical, its prolateral margin more strongly arched than retrolateral margin (Fig. 4G-L); dorsal wall of embolus proper as wide as ventral wall (Fig. 4G-H); membranous part of embolus proper distally narrower than proximally (Figs 3F, H, 4C). Females distinguished by vulval plate (Fig. 5) with widely trapezium-shaped (posteriorly widest) posterior stalk not connected to pigmented lateral patches in genital atrium; poreplate with distinct anterolateral lobes; CDO large, very variable in shape, mostly longer than wide; receptacular cluster very large, in most cases protruding beyond straight or procurved anterior margin of poreplate.

Additions to description of male: *Scopula*: See paragraph "Variation".

Palp: Both apical lobes of cymbium equally short, dorsal one usually slightly more pointed than ventral one. Retrolateral apophysis of palpal tibia entire, situated at a clearly more proximal level than distal margin of article (Fig. 4B), carrying four long apical megaspines (Fig. 4A-B). Paracymbium relatively small and shallow, about as deep as cymbium in retroventral view (Fig. 4A; Platnick & Sedgwick, 1984: fig. 64); cumulus low, carrying a compact group of moderately long thick bristles. Subtegulum without apophysis. Tegulum with quite few small teeth only in retrodorsal portion of proximal edge, distal margin not drawn into an edge (Fig. 4D-F). Contrategulum with very indistinct, widely rounded ventral process (Fig. 4G-H); distal edge with a series of small denticles, those at proventral end arranged in a V-shaped row (Fig. 4C), 1-2 enlarged denticles or a sharp keel in prolateral to prodorsal section of distal edge (Fig. 4G-L); dorsal apex of contrategulum developed as a large, linguiform, strongly projecting horizontal plate, its prolateral margin being more strongly arched than its retrolateral margin (Fig. 4G-L). Embolus complex with para-embolic plate developed as a more or less distinctly elevated, rounded edge (Fig. 4D-F); below it a second small edge present in some cases (Fig. 4D); sclerotised and membranous part of embolus proper in contact for almost their entire length (Fig. 3D, F, H); sclerotized part with numerous longitudinal ribs carrying tiny denticles distally (Fig. 3B, D, F, H), its dorsal and ventral walls equally wide and parallel to each other (Figs 3D; 4G-H), dorsal wall ending in indistinct rounded lobe (Fig. 4C-F); membranous part distally narrower than proximally (Fig. 3D, F, H), its proximal portion essentially unpigmented.

Additions to description of female: Vulval plate (Fig. 5) always with few to many hairs laterally in genital atrium, rarely also posteromedially (Fig. 5I). Posterior stalk more or less distinctly trapezium-shaped (posteriorly wider than anteriorly), densely pitted in posterior portion. Poreplate wider than long, with a pair of anterolateral lobes projecting anteriad and slightly bent ventrad; several of these lobes more or less distinctly constricted at base (Fig. 5A-C, E); anterior margin of poreplate straight to procurved; lateral and posterolateral margins on ventral side of pore plate bulging (Fig. 5B, J). CDO large and of variable shape, mostly longer than wide, rarely wider than long (Fig. 5E). Receptacular cluster large and strongly racemose, in most cases protruding beyond anterior margin of poreplate, rarely not (Fig. 5G).

Taxonomic remarks: *Liphistius malayanus cameroni* has been the only subspecies in the genus *Liphistius*. As specimens later collected near the type locality show no relevant differences from specimens of the nominal subspecies, this case became doubtful. Thus a re-examination of the types of *Liphistius malayanus cameroni* was necessary, and it revealed that they differ considerably from the illustrations and explanations given in the original description of this subspecies. The vulva of the female paratype was cleared of tissue, but the ventral wall of the genital region (with bristles still attached) was not removed, thus not allowing a clear view of the ventral side of the poreplate. It therefore appears that Haupt's (1983) illustrations were made with the help of a compound microscope without using a drawing tube, which would explain why the poreplate in the original illustrations is wider than in reality and why the outlines of the posterior stalk are too rounded. The same is probably also the case in the dorsal view of the same poreplate, it being too wide, with a triangular CDO leading to the receptacular cluster and with a peculiar double posterior margin of the posterior stalk (see Haupt, 1983: figs 5f, 6f). In fact the vulva of the paratype of *L. malayanus cameroni* does not differ from the vulvae of the other *L. malayanus* females examined (Fig. 5A-B cf. Fig. 5C-J) in any way that would warrant a distinct taxonomic status.

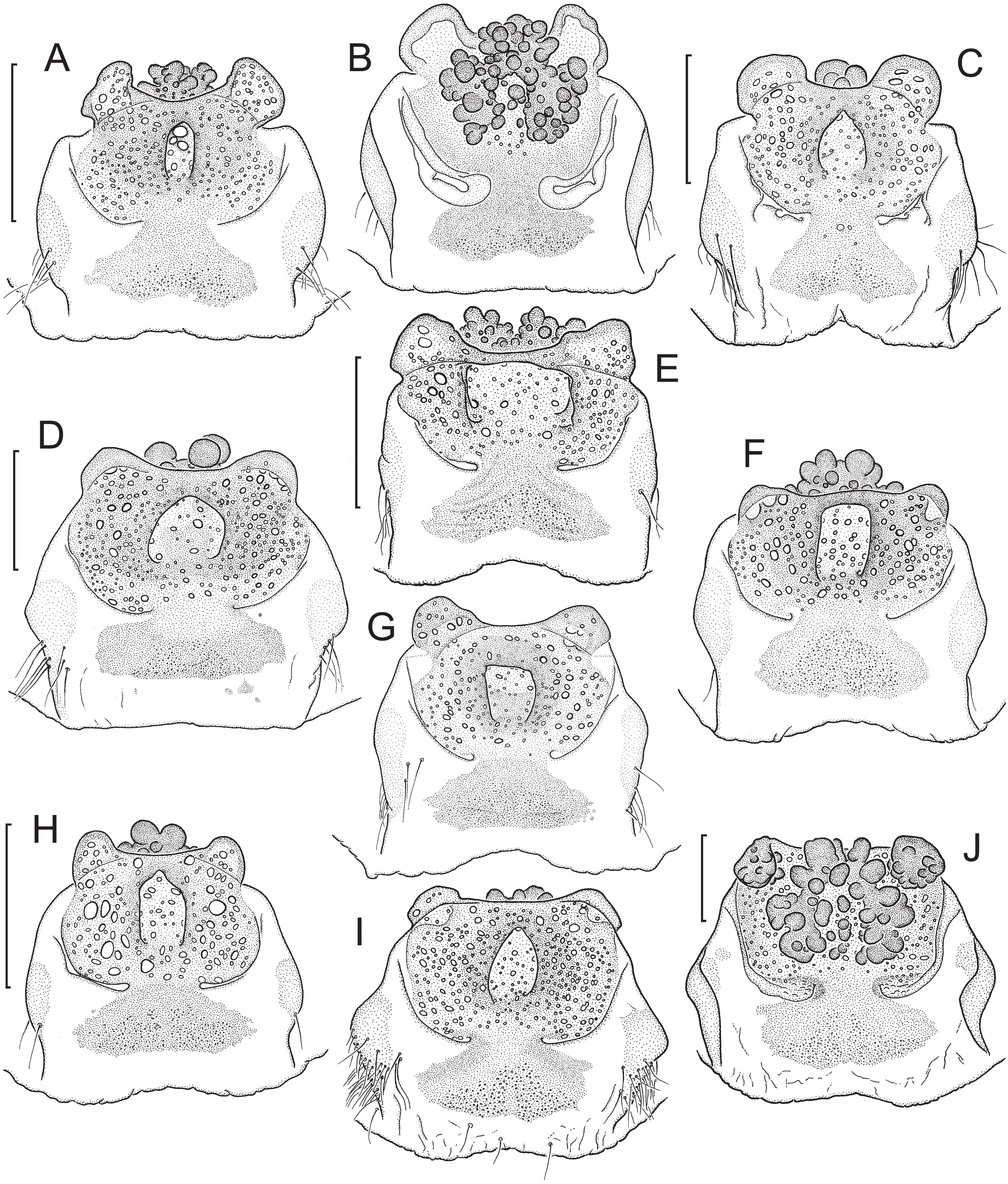

Fig. 5. *Liphistius malayanus*, vulval plate of eight females: paratype of *L. m. cameroni* from Berinchang, Cameron Highlands (A-B); exuvia of female from Ringlet, Cameron Highlands (C); female (SMF 64093) from Fraser's Hill (D); female (moulted 24.VI.2002) from Fraser's Hill; poreplate slightly deformed by brief immersion in cold KOH (E); female (SMF 56206) from Fraser's Hill (F); female (SMF 60037) from Genting Highlands (G); female (moulted 8.XII.2005) from Genting Highlands (H); exuvia of female from Templer Park (I-J). (A, C-I) Dorsal view. (B, J) Ventral view. Scale lines: 1.0 mm (A-B; C, F; D; E, G; H; I-J).

The illustrated differences between the male holotype of *L. malayanus cameroni* and the male that Haupt incorrectly referred to as a paratype of *L. malayanus* (in BMNH, not examined) are mostly due to a slightly different view of the palp and due to the fact that the palpal organ of the BMNH male is expanded (turned clockwise by about 90°) (Haupt, 1983: figs 3D, 4C cf. figs 3E, 4D). None of the *L. malayanus* males examined has the tibial apophysis of the male palp situated as far distally as illustrated by Haupt (1983: figs 3D, 4C), therefore this may also be due to a different view. The embolus proper of the left palp of the *L. m. cameroni* holotype (that of the right palp is missing, together with tegulum and contrategulum) is slightly narrower than that of the second male from the Cameron Highlands and that of other conspecific males examined. This difference is presumably connected to size: the *L. m. cameroni* holotype is the smallest among the *L. malayanus* males examined. The character in which the holotype of *L. m. cameroni* most visibly differs from other conspecific males is a slightly elevated para-embolic plate (Fig. 4E), which is also present in the second male from the Cameron Highlands (Fig. 4F). However, an indistinctly elevated para-embolic plate is present in one of the two males from the Fraser's Hill, whereas all other conspecific males possess only a distinct edge at this place (Fig. 4D). Thus the holotype of *L. m. cameroni* differs from other conspecific males examined in possessing the most extreme states of three quite variable characters, but it is not representative for the population in the Cameron Highlands. I consequently place *Liphistius malayanus cameroni* in the synonymy of *Liphistius malayanus* which makes the species monotypic again.

Variation: Carapace lengths in males (n=6; including the holotype of *L. m. cameroni*) 7.90-11.23, carapace widths 7.04-9.69; in the largest female from each locality (n=4; not including the paratype of *L. m. cameroni*) 10.86-16.67 and 10.00-14.07, respectively. The holotype of *L. m. cameroni* is the smallest male examined, with carapace length 7.90, width 7.04; in the second male from the Cameron Highlands it is 9.63 and 8.40, respectively. The largest female is from the Templer Park, measuring 16.67 and 14.07; the second largest female is from the Fraser's Hill, measuring 16.54 and 14.07. The female paratype of *L. m. cameroni* measures 9.26 and 7.53, the second female from the Cameron Highlands 10.86 and 10.12.

The apical megaspines on the tibial apophysis are quite variable in length, but not as thin as illustrated in Murphy & Platnick (1981: figs 8, 11, 14, 17, 20) and in Platnick & Sedgwick (1984: figs 63-67); the ventral-most of them is mostly bent distad and has a thin, long apex (Fig. 4A-B). The ventral megaspine is bent in the male from the Templer Park (Fig. 4A), whereas in the holotype of *L. m. cameroni* (Fig. 4B), in a male from the Genting Highlands, and also in a second male from the Cameron Highlands it is slightly sigmoid.

The distal edge of the contrategulum carries one or two slightly enlarged dorsal denticles at some distance from the projecting dorsal apex (Fig. 4G, I-L); in two males there is a sharp edge at the same place (Fig. 4H), but only on one palp. These larger denticles are followed by a variable number of smaller proventral denticles.

The para-embolic plate is always low, most visibly elevated (but not with a sharp edge) in the holotype of *L. m. cameroni* (Fig. 4E), in a second male from the Cameron Highlands (Fig. 4F) and in a male from the Fraser's Hill. In the second male from the Fraser's Hill it is not elevated; the remaining males examined are intermediate (Fig. 4D). An indistinct second edge, situated below the indistinct para-embolic plate, is found in the only available male from the Genting Highlands and in the only available male from the Templer Park (Fig. 4D), but not in other males examined (Fig. 4E-F).

The size of the embolus proper varies from relatively thick in the male from the Templer Park (Fig. 4D) to distinctly more slender in the holotype of *L. m. cameroni* (Fig. 4E); the other males are intermediate (Fig. 4F). The longitudinal ribs on the sclerotised part of the embolus proper vary from indistinct to distinct (Fig. 3B, D, F, H), so do the denticles on them.

There is considerable variation in the extent of the tarsal scopulae in males. The scopula on tarsus I is always thin and undivided, covering two-thirds of the ventral side in most males, only one half in the male from the Genting Highlands. The scopula on tarsus II is slightly denser than on tarsus I, undivided and covering two-thirds of the ventral side in all males. Tarsal scopula III is like tarsal scopula II in most males, in the non-type male from the Cameron Highlands it is light. Tarsal scopula IV is dense in all males except for the non-type male from the Cameron Highlands (light), undivided in all males except for the same male from the Cameron Highlands (distinctly divided) and for the male from the Genting Highlands (indistinctly divided), covering two-thirds of the ventral surface in most males except for a male from the Cameron Highlands (covering only half of the surface) and the male from the Templer Park (covering three-quarters). The male holotype of *L. malayanus cameroni* had already been returned to its depository when the tarsal scopulae were examined. Even if both males from the Cameron Highlands differed from those of other localities in shape and extent of their tarsal scopulae (especially on tarsus IV), this would not warrant a subspecific distinction. The tarsal scopula in this species is too variable to be of high taxonomic value.

The vulval plates of large females have more lateral hairs in the genital atrium than those of small females (Fig. 5I cf. Fig. 5H). In the largest female (from the Templer Park) hairs are also present posteromedially in the genital atrium (Fig. 5I). The shape of the posterior stalk is quite variable but mostly trapezium-shaped (Fig. 5). Even more variable is the size and shape of the CDO of the poreplate, ranging from (mostly) longer than wide to (rarely) wider than long, from quadrangular to pentangular and from near-triangular to near-circular (Fig. 5A, C-I). The receptacular cluster is always large, undivided and has a complex structure, covering most of the ventral side of the poreplate (Fig. 5B, J); only in one female examined (from the Genting Highlands) does it not protrude beyond the anterior margin of the poreplate (Fig. 5G). The anterior poreplate margin varies from more or less strongly invaginated (in most cases; Fig. 5A-E, G-J) to slightly arched medially (Fig. 5F).

Distribution: *Liphistius malayanus* is known from several lowland and upland localities in the western part of central Malaysia (Perak, Pahang, Selangor and Negeri Sembilan; Fig. 1, localities 1-5). See also Platnick & Sedgwick (1984: 24). *Liphistius* records from other localties near Kuala Lumpur (e.g. Klang Gates; Murphy & Murphy, 2000: plate 2.5) can also be attributed to *L. malayanus*. This species has a relatively wide geographical range (the northernmost localitiy, in the Cameron Highlands, is about 280 km away from the southernmost locality, Gunung Angsi) and a large vertical distribution (from 230 to 1800 m altitude).

Biology: Spiders were collected from quite different habitats: soil on exposed sides of roads and trails inside and outside forests (but never very far from a forest), sides of erosion gullies, sloping forest floor, and in decomposing wood of logs lying on the forest floor. Trapdoors of females were up to 3.8 cm long and 6.5 cm wide. Signal lines (not more than eight) were usually about 10 cm long, in one immature male even 24 cm long. The longest burrow measured was 20 cm long. Two penultimate males had trapdoors with a length of 1.9-2.2 cm and a width of 3.0-3.4 cm, which is probably normal. A juvenile male (moulted again but died before reaching maturity) from near Ringlet in the Cameron Highlands had a surprising 2.9 cm long and 5.0 cm wide trapdoor.

The female paratype of *L. m. cameroni* and two other females (from Fraser's Hill and Templer Park) show bite marks on their carapaces and chelicerae. These were probably caused by specimens of *Ljunghia bristowi*, a species of ectoparasitic laelapid mites originally described from *L. malayanus* (see Halliday & Juvara-Bals, 2016: 837-845).

Mature males were collected in the field in October and December; in captivity males matured between July and March. The mating period in *L. malayanus* appears to be much longer than in other congeneric species. I did not find any egg cases.

Liphistius endau Sedgwick & Platnick, 1987

Figs 2A, 6-7

Liphistius endau Sedgwick & Platnick, 1987: 361-363 (description of female). – Foelix & Erb, 2010 (study on venom gland openings on cheliceral fangs). – Foelix *et al*., 2010 (study on scopula hairs of male).

Type material: AMNH; juvenile female holotype (not examined; see paragraph "Variation" below); Malaysia, Johore [sic], Ulu Endau area, from the banks of Sungai Jasin; 10.XI.1985; leg. W.C. Sedgwick.

Material examined: MHNG, sample SIM-01/10; 2 males (matured 1.II.2002, 27.II.2003), 2 females (moulted 27.IV.2002, 28.IV.2002), 2 juvenile males, 3 juvenile females; Johor, Endau-Rompin National Park, between Kuala Jasin and Kuala Marong (2°31'44"N, 103°22'02"E), 40 m (rain forest along stream); 3.-5. VII.2001; leg. P.J. Schwendinger. – MHNG; left palp of mature male; Johor, near Gunung Belumut; leg. C. Sainsbury, don. R. Foelix. – MHNG (sample Sum-00/02); 2 females; Johor, Gunung Muntahak, Kota Tinggi Waterfalls (1°49'51"N, 103°49'56"E), 170 m (rainforest near stream); 5.II.2000; leg. P.J. Schwendinger. – MHNG (sample SIM-01/07); 2 penultimate males, 4 females, 1 juvenile; same locality, 170 m; 24.-26.VI.2001; leg. P.J. Schwendinger. – MHNG (sample MAL-04/05); 2 penultimate males, 2 females, 1 juvenile; same locality, 170 m; 26.-27.V.2004; leg. P.J. Schwendinger. – MHNG (sample TM-14/02); 3 males (matured 20.VIII., 22.X., 6.XI.2014), 2 females; same locality, 120 m; 21.-22.VI.2014; leg. P.J. Schwendinger. – MHNG, SMF; 2 males (one killed 30.IX.2010, the other died 22.III.2012), 1 female; Malaysia, locality and collector unknown; don J. Kral.

Diagnosis: Large, dark-coloured species. Males distinguished from those of the similar *L. malayanus* by tibial apophysis of male palp situated more distally (Fig. 6A cf. Fig. 4B); paracymbium much deeper (Fig. 6B cf. Fig. 4A); tegulum with more teeth on proximal margin (Fig. 6D-E cf. Fig. 4D-F); distal edge of contrategulum with only one very large, triangular tooth prolaterally; dorsal apex of contrategulum more symmetrical, both lateral margins almost equally arched (Fig. 6F, H-O cf. Fig. 4G-L); dorsal wall of sclerotized part of embolus proper much wider than ventral wall and curved prodorsad (Fig. 6F, H cf. Fig. 4G-H), with a large lobate extension prodorsally (Fig. 6C-E cf. Fig. 4D-F); adpressed membranous part of embolus proper distally much wider than proximally (Fig. 6C cf. Fig. 4C); opening of spermophore a long and narrow slot (Fig. 6F-H cf. Fig. 4G-H). Females distinguished from those of *L. malayanus* by median portion of genital atrium clearly sunk below lateral portions and usually carrying more hairs (mostly no hairs in *L. malayanus*); posterior stalk usually (except in small females) fused

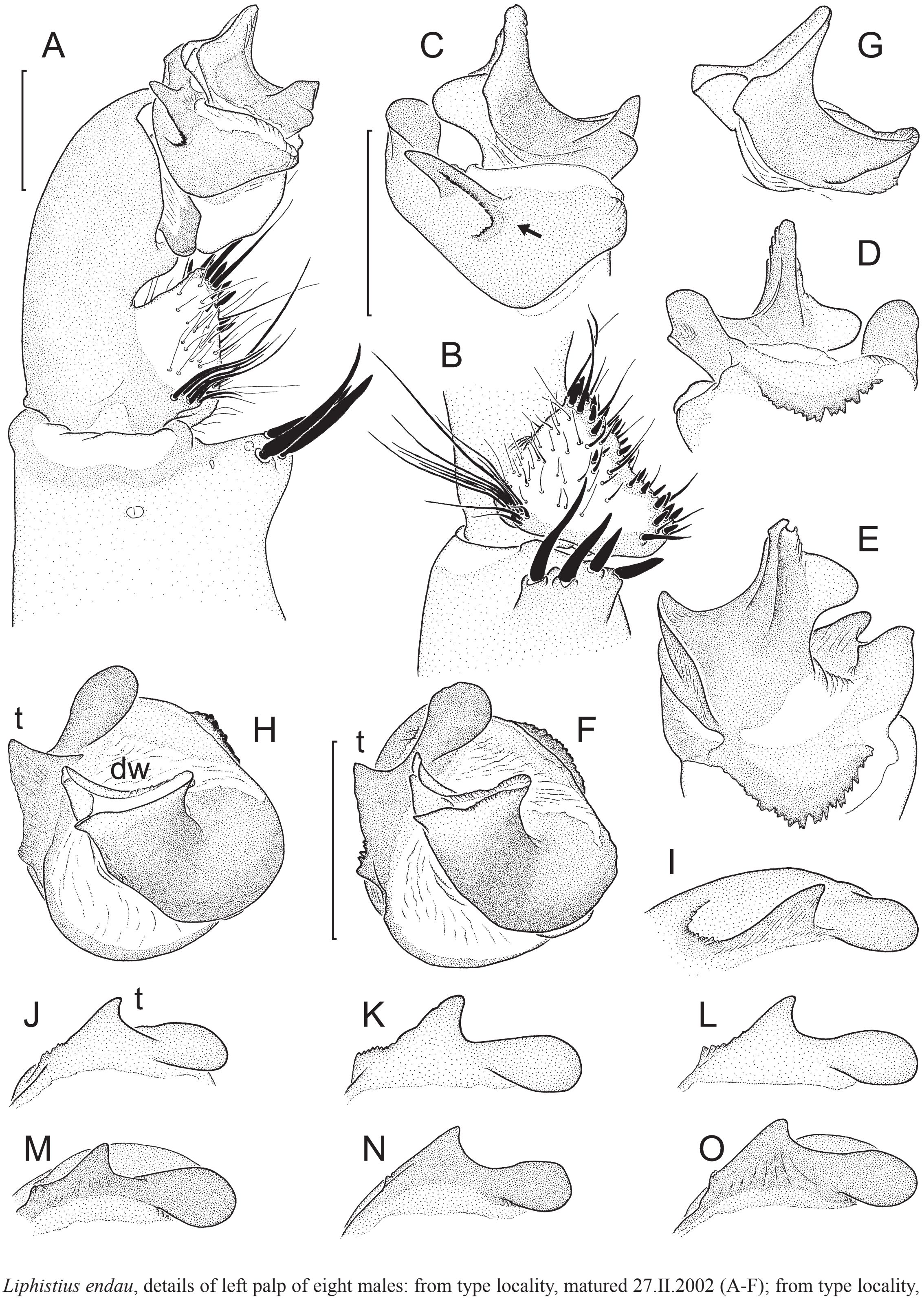

Fig. 6. *Liphistius endau*, details of left palp of eight males: from type locality, matured 27.II.2002 (A-F); from type locality, matured 1.II.2002 (G-I); from unknown locality, died 22.III.2012 (J); from unknown locality, killed 30.IX.2010 (K); from Gunung Belumut (L); from Kota Tinggi, matured 22.X.2014 (M); same place, matured 20.VIII.2014 (N); same place, matured 6.XI.2014 (O). (A) Distal part of palp, ventral view. (B) Paracymbium and tibial apophysis, retroventral view. (C) Palpal organ, proventral view (arrow indicating U-shaped row of denticles at proventral end of distal edge of contrategulum). (D) Same, retrodorsal and slightly proximal view. (E) Same, retrodorsal view. (F, H) Same, distal view (dorsal side up). (G) Embolus complex, proventral and slightly distal view. (I) Distal edge of contrategulum, distal and slighly prolateral view (dorsal side to the right). (J-O) Same, distal view. Abbreviations: dw - dorsal wall of sclerotized part of embolus proper; t - tooth on distal edge of contrategulum. Scale lines: 1.0 mm (A-B; C-E, G-H; F, I-O).

with pigmented lateral patches in genital atrium (Fig. 7A, C-D, F, H-I cf. Fig. 5A, C-I); receptacular cluster not or only slightly protruding beyond anterior margin of poreplate, divided into three more or less distinct subclusters (Fig. 7B, E, G cf. Fig. 5B, J).

Description of male (matured 27.II.2003): *Colour in alcohol* (much darker in life; colouration as in female, Fig. 2A): All sclerotised parts uniformly brown, except for cream-coloured proximal portion of chelicerae, cream-coloured membranes of prosoma and light brown opisthosomal membranes.

Bristles on carapace: Short bristles along all margins (strongest on posterior margin, longest behind, on and in front of eye mound); none on coxal elevations; five short bristles anterior to fovea.

Scopula: Tarsus I with thin scopula in distal half of ventral side, divided for its entire length by narrow, pale, glabrous longitudinal median stripe and by some

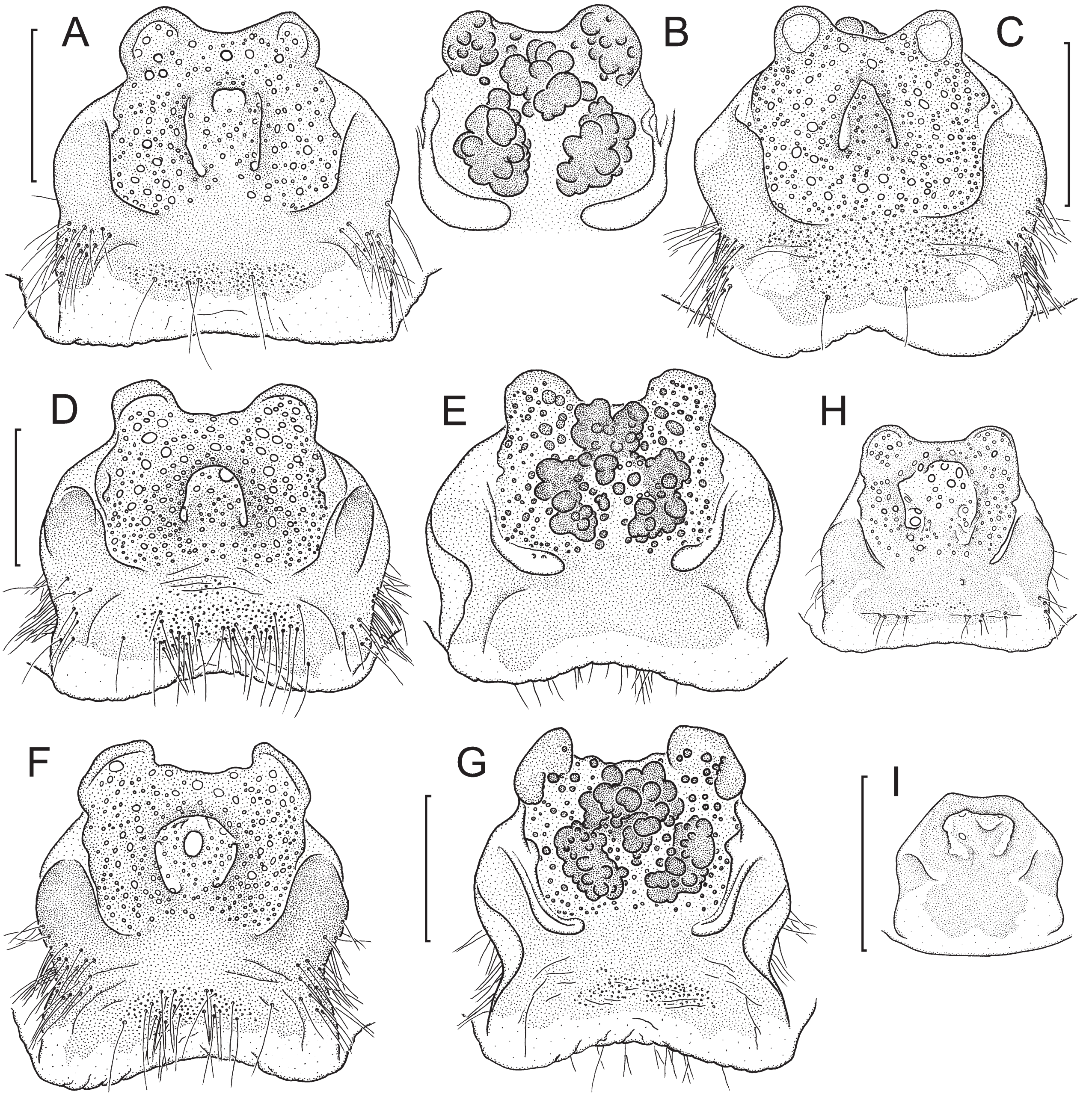

Fig. 7. *Liphistius endau*, vulval plate of six females: adult from unknown locality (A-B); largest female from Kota Tinggi (C); exuvia of reproductive female (moulted 27.IV.2002) from type locality (D-E); exuvia of reproductive female (moulted 28.IV.2002) from type locality (F-G); medium-sized juvenile from type locality (H); small juvenile from type locality (I). (A, C-D, F, H-I) Entire vulval plate, dorsal view. (B) Poreplate, ventral view. (E, G) Entire vulval plate, ventral view. Scale lines: 1.0 mm (A-B; C; D-E; F-G; H-I).

bristles; tarsus II with slightly denser scopula in distal three-quarters, only distally divided by median stripe; tarsi III-IV with dense scopula covering distal four-fifths, only distally divided by median stripe.

Cheliceral teeth: Eleven small ones on promargin of cheliceral groove on both sides.

Palp: Tibial apophysis situated distally, not clearly set back from distal margin of tibia, carrying four moderately long (dorsal ones shorter than ventral ones) megaspines (Fig. 6A-B). Both apical lobes of cymbium very short and equally rounded. Paracymbium basally very deep (Fig. 6B), its cumulus only slightly elevated, carrying stiff bristles reaching base of contrategulum (looking shorter in Fig. 6A because pointing ventrad rather than distad). Subtegulum without apophysis. Tegulum short and wide, coarsely dentate along entire proximal margin (Fig. 6D-E). Contrategulum with indistinct, widely arched proventral process (Fig. 6F); distal edge with denticles at proventral end distinctly elevated on a U-shaped ridge (Fig. 6A, C), with a single large triangular tooth prolaterally and with spatulate, quite symmetrical dorsal apex (Fig. 6F). Para-embolic plate only little elevated (Fig. 6A, C-E); sclerotised part of embolus proper strongly compressed dorso-ventrally, its dorsal wall distinctly wider than its ventral wall, curved prodorsad (Fig. 6F) and ending in a pronounced, prodorsad-directed, rounded lobe (Fig. 6C-E); membranous part of embolus proper distally much wider than proximally (Fig. 6C), its proximal portion slightly pigmented.

Measurements: Total length 22.30; carapace 9.26 long, 8.40 wide; opisthosoma 10.33 long, 7.62 wide; eye mound 1.34 long, 1.50 wide; palpal coxa 2.97 long, 1.98 wide; labium 0.69 long, 1.58 wide; sternum 4.06 long, 2.48 wide (1.29 on ventral surface); palp 15.83 long (4.43 + 2.79 + 5.74 + 2.87); leg I 27.21 long (7.21 + 3.61 + 5.90 + 7.05 + 3.44); leg II 28.11 long (7.21 + 3.61 + 6.15 + 7.62 + 3.52); leg III 30.99 long (7.54 + 3.77 + 6.56 + 9.02 + 4.10); leg IV 38.27 long (9.34 + 3.93 + 7.54 + 12.21 + 5.25).

Additions to description of female: Posterior margin of genital sternite more or less distinctly invaginated (Fig. 7A, C-H; 7I is a very small juvenile). Vulval plate (Fig. 7) strongly sclerotised and pigmented, roughly as long as wide, with a more or less distinct lateral constriction in posterior third. Genital atrium with many lateral hairs and in many cases also with additional median hairs; median zone of genital atrium clearly sunken below lateral zones (indistinct in small females). Posterior stalk wide, completely fused with poreplate and with strongly pigmented, buldging lateral parts of genital atrium (Fig. 7A, C-H). Poreplate entirely and strongly pigmented, its anterior margin slightly invaginated, with a pair of pronounced anterolateral lobes. CDO large to very large, its posterior margin not sunken, giving the opening the shape of a horseshoe (Fig. 7C-D, F) or of an open quadrangle (Fig. 7A, H); enlarged pores inside CDO leading to receptacular cluster (Fig. 7A, C-D, F); the latter large and complex but not or only slightly protruding beyond anterior margin of poreplate, divided into three more or less distinct subclusters (Fig. 7B, E, G).

Variation: Carapace lengths in males (n=7) 9.26-12.04, in the largest females (n=4) 13.33-14.94; carapace widths 8.09-10.99 and 10.74-12.84, respectively. The three males from Kota Tinggi have a shorter scopula on their anterior legs (I: very thin, medially divided, covering only distal quarter; II: slightly denser, only apically divided, covering distal half; III: dense, undivided, covering three-quarters; IV: dense, undivided, covering distal four-fifths) than males from the type locality and from an unknown locality (I: thin, divided, distal half; II: slightly denser, apically divided, distal tree-quarters; III-IV: dense, undivided, distal four-fifths).

Variation in the shape of the distal edge of the contrategulum is shown in Fig. 6F, H-O, variation in the shape of the vulval plate in Fig. 7. With age (and body size) the number of hairs in the genital atrium of females increases.

All females from Kota Tinggi have fewer hairs in the genital atrium than females from other localities. Among six medium to large-sized females from that locality only one large female has two hairs in a median position (Fig. 7C), all others (including another large female) have none.

The female holotype (in AMNH, not examined) has a carapace length of 7.5 and a width of 6.6, and is thus only about half the size of the three largest females examined. The illustrations of the holotype vulva (Sedgwick & Platnick, 1987: figs 1-2) differ from the vulvae examined by lacking distinct anterolateral lobes on the poreplate (also absent in the smallest juvenile female examined; Fig. 7I). The posterior stalk of the holotype vulva is not yet fused with the pigmented lateral zones of the genital atrium (as it is also the case in the two juvenile females examined; Fig. 7H-I) and it appears to lack lateral hairs (as it is the case in the smallest female examined; Fig. 7I). The holotype is therefore a juvenile female with a not fully developed vulval plate. As (according to the original description) its vulval plate corresponds quite well with vulval plates of juveniles examined from the same area (possibly even from the same locality), and as no other *Liphistius* species is known from that area, there is no doubt that these specimens are conspecific.

Distribution: Known from three localities in the northern and western part of Johor State (Fig. 1, localities 6-8).

Relationships: Large size, details of the male palp (e. g. shape of distal edge of contrategulum and its dorsal apex; shape of tibial apophysis) and details of the vulval plate (bulging lateral and posterolateral margins on ventral side of poreplate forming a distinct boundary between poreplate and posterior stalk) indicate that *L. endau* and *L. malayanus* are more closely related to each other than to *L. johore* and *L. gracilis* sp. nov.

Biology: The new specimens from the type locality or from very close to it (in the Endau-Rompin N.P.) were found on the banks of a stream in a rain forest; specimens from the Kota Tinggi Waterfall were collected from the sloping forest floor and soil banks on both sides of rain forest stream running over a series of falls. Most burrows were in the soil, but at the Kota Tinggi Waterfall two medium-sized burrows were constructed in the rotten wood of a fallen tree, with the signal lines spread over the wood surface. At the type locality the burrow entrance of a large female had nine signal threads, at the Kota Tinggi Waterfall four burrows (of three large females and one penultimate male) were equipped with nine signal lines; all other burrows had a maximum of eight lines running over rock, soil and tree roots. The longest signal line (of the largest female) was 34 m long, those of other burrows examined were not more than 21 cm long. Trapdoors of four penultimate males were 2.6-3.2 cm long and 4.0-4.7 cm wide; that of the largest female 3.3 and 5.9, respectively. The latter spider lived in a 35 cm long burrow. Males became mature in August, October and November (after 2-5 months in captivity) and in February (after one and a half years in captivity, therefore probably not corresponding to conditions in nature). One male (from the Kota Tinggi Waterfall) ate a half-dead cricket a few days after its last moult but not again later. I also observed this in newly matured males of *L. dangrek* Schwendinger, 1996, and it had been reported for males of *L. desultor* by Murphy & Platnick (1981: 46), but it occurs only rarely and probably only in large species. Usually *Liphistius* males cease feeding when becoming adult.

Egg cases were constructed (all of them in captivity or during transport) in June and July. One egg case built in Geneva by a female from the type locality was 5.0 cm long, 4.7 cm wide, 2.8 cm high and contained 453 eggs. Another female from the same locality built during the transport an egg case of tissue paper, with a 3 cm diameter, containing 331 eggs. A third, old and empty egg case at the Kota Tinggi Waterfall was 4.0 cm long, 54.6 cm wide, 1.8 cm high. A fourth female from the same locality built a tissue paper egg case of 4.2 cm diameter and 2.0 cm height, containing 395 light orange-coloured eggs.

Liphistius gracilis sp. nov.

Figs 8-9

Types: MHNG, sample SIM-01/07; male holotype (matured 13.VIII.2001), 5 male paratypes (matured 18.IX., 19.IX.2001, 5.I., 24.III., 3.VI.2002), 5 female paratypes; Malaysia, Johor, Kota Tinggi Waterfalls at foot of Gunung Muntahak, 170 m (evergreen rain forest); 24.-26.VI.2001, leg. P.J. Schwendinger. – SMF, sample TM-14/02; 1 male paratype (matured 5.XI.2016); same locality; 21.-22.VI.2014; leg. P.J. Schwendinger. – MHNG, SMF, sample Sum-00/01; 3 female paratypes [moulted 3.V. (allotype); early VIII.; 26.XII.2000; 16.V., 6.X.2001]; same locality; 4.II.2000; leg. P.J. Schwendinger.

Etymology: The species epithet is a Latin adjective meaning “gracile”, “slender”, “slim”, referring to the small body size of this species in comparison with *L. malayanus* and *L. endau*.

Diagnosis: Similar to *L. malayanus* and *L. endau* but much smaller in body size, with lighter body colouration and annulated legs and palps. Males distinguished from those of *L. malayanus* (Fig. 4) and *L. endau* (Fig. 6) by tibial apophysis of palp longer and directed more distad (Fig. 8A, C), carrying shorter megaspines, the dorsal one sitting clearly lower than the rest (Fig. 8B, H-J); paracymbium relatively deeper than in *L. malayanus* and shallower than in *L. endau* (Fig. 8A-C cf. Fig. 4A and Fig. 6B, respectively); distal edge of contrategulum serrate (Fig. 8A, D-G), its apex distinctly smaller (Fig. 8F-G cf. Fig. 4G-L and Fig. 6F, H-O); dorsal wall of sclerotised part of embolus proper ending in a sharply prodorsad-bent lobe (Fig. 8D-G) [both walls equally wide in *L. malayanus* (Fig. 4G-H); dorsal wall prodorsal-curved (not sharply bent) in *L. endau* (Fig. 6F, H)]. Vulva of *L. gracilis* sp. nov. (Fig. 9) different from vulvae of *L. malayanus* (Fig. 5) and *L. endau* (Fig. 7) by ventral side of poreplate without bulging lateral and posterolateral margins, thus transition between poreplate and posterior stalk much less marked; anterior margin of poreplate with less distinct anterolateral lobes; receptacular cluster wider than long, more distinctly protruding beyond anterior margin of poreplate. Vulva different from that of *L. johore* (Fig. 10A) by lacking pronounced anterolateral invatinations in the margin of the poreplate, by having a wide and indistinct transition between poreplate and posterior stalk (narrow and distinct in *L. johore*), any by possessing hairs in the genital atrium.

Description of male (holotype): *Colour in alcohol* (darker in life): Carapace mostly light brown, with darker patches along margins (medially broken on posterior margin), extending between coxal elevations; dark anterior margin enclosing very dark eye mound; dark W-shaped pattern behind eye mound indistinct; a few small dark spots on pars cephalica; a paramedian pair of dark patches anterior to fovea; chelicerae cream-coloured proximally, grey-brown distally; legs and palps mostly light brown, with darker zone proximally on

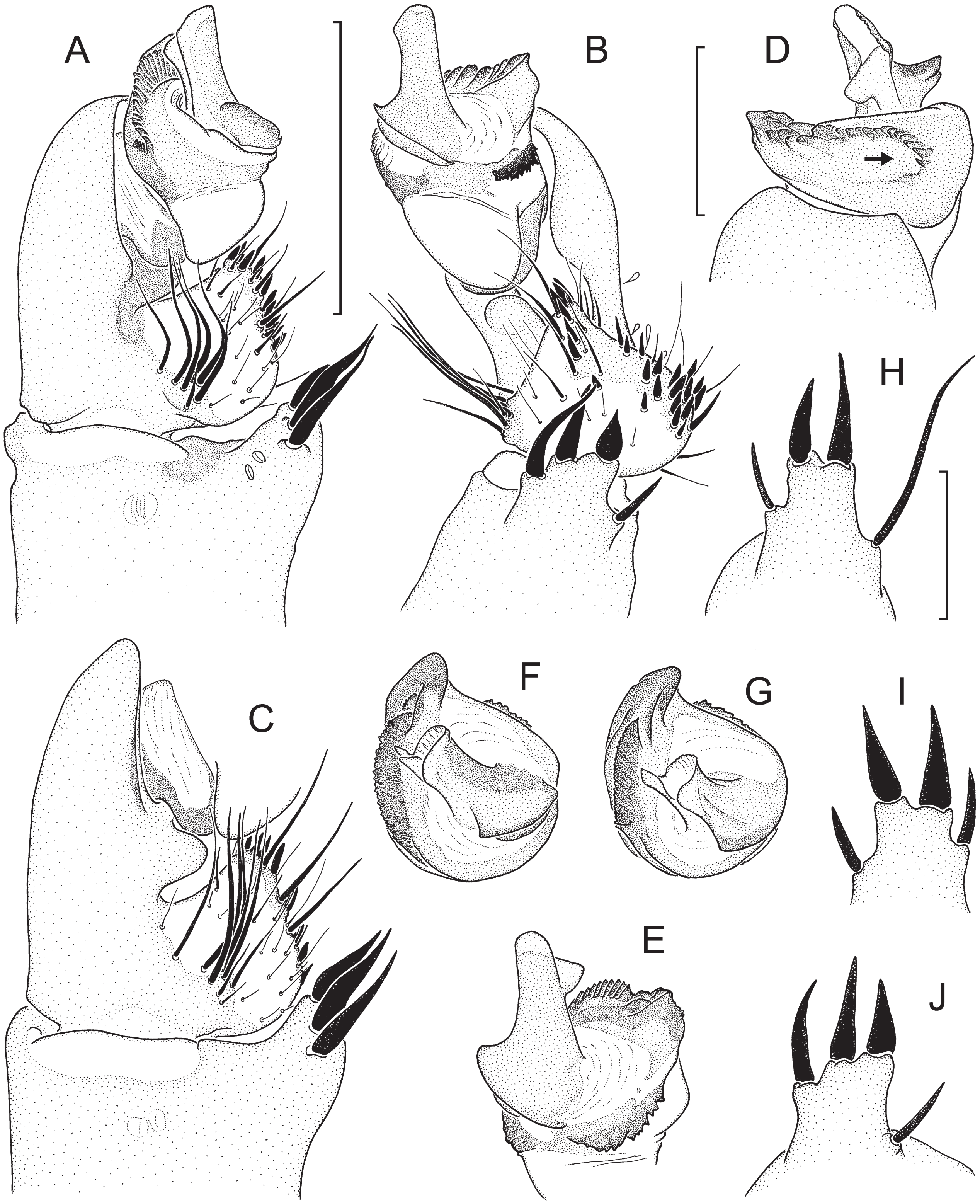

Fig. 8. *Liphistius gracilis* sp. nov., details of palp of three males: paratype, matured 5.I.2002 (A-B, H); holotype (C-F, I-J); paratype, matured 19.IX.2001 (G). (A) Distal part of palp, ventral view. (B) Same, retrolateral view. (C) Subtegulum, cymbium and distal part of palpal tibia, ventral view. (D) Distal part of cymbium and palpal organ, proventral view (arrow indicating U-shaped row of denticles at proventral end of distal edge of contrategulum). (E) Same, retrodorsal view. (F-G) Same, distal view (dorsal side up). (H-I) Right tibial apophysis, retrolateral and slightly proximal view. (J) Left tibial apophysis, same view. Scale lines: 1.0 mm (A-C), 0.5 mm (D-G; H-J).

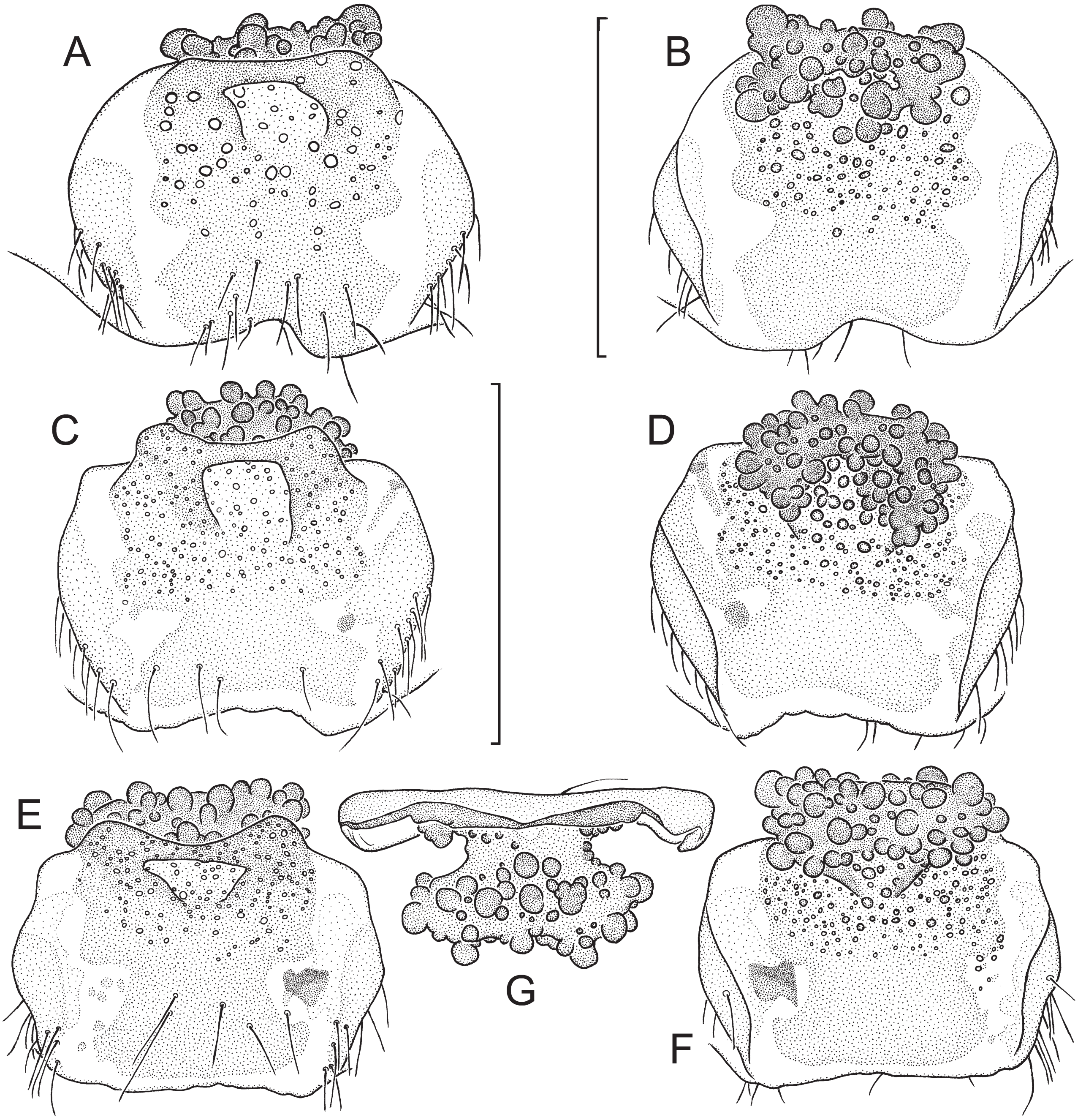

Fig. 9. *Liphistius gracilis* sp. nov., vulval plate of three females (all from exuviae): allotype (A-B); paratype, moult 31.VIII.2001 (C-D); paratype, moult 27.IX.2001 (E-G). (A, C, E) Vulval plate, dorsal view. (B, D, F) Same, ventral view. (G) Same, anterior view. Scale lines: 1.0 mm (A-B; C-G).

patellae and tibiae of legs III-IV, and in proximal half of all metatarsi. Opisthosomal tergites cream-coloured, with dark marginal and central patches on tergite I, other tergites only with lateral and anterolateral patches; membranous part of opisthosoma cream-coloured. Sclerotised parts of ventral side of body light brown.

Bristles on carapace: Short bristles along all margins (strongest on posterior margin, longest behind, on and in front of eye mound), on coxal elevations and in area behind fovea, none anterior to fovea.

Cheliceral teeth: Ten and eleven small ones on promargin of cheliceral groove of right and left chelicera, respectively.

Scopula: Tarsus I with very thin scopula confined to distal fifth of ventral side, divided for its entire length by narrow pale, glabrous longitudinal median stripe and by some bristles; tarsus II with very thin scopula in distal quarter, only distally divided by median stripe; tarsus III with dense scopula covering distal half, only distally divided by median stripe; tarsus IV with dense scopula covering distal three-fifths, only distally divided by median stripe.

Claws: Paired tarsal claws on anterior legs with 4-6 denticles, on posterior legs with 5-6 denticles; unpaired claws in most cases with a single denticle on anterior legs, none on posterior legs.

Palp: Tibial apophysis relatively long, situated at distal margin of tibia, inclined distad [Fig. 8A (showing paratype matured 5.I.2002), C], carrying four quite short megaspines, the dorsal one rising from a clearly more proximal position than the others [Fig. 8B, H (showing paratype matured 5.I.2002), I-J]. Both apical lobes of cymbium indistinct, prodorsal one more rounded than retrodorsal one (Fig. 8D). Paracymbium relatively large and basally deep [Fig. 8A-B (showing paratype matured 5.I.2002), C-D], its cumulus indistinctly elevated, carrying moderately long stiff bristles [Fig. 8A-B (showing paratype matured 5.I.2002), C]. Subtegulum without apophysis. Tegulum short and wide, coarsely dentate along entire proximal margin, not or only indistinctly connected to contrategulum on retrodorsal side (Fig. 8E). Contrategulum without ventral process; distal edge finely serrate, proventrally ending in a U-shaped row of denticles (Fig. 8D), dorsally ending in a spatulate asymmetrical apex (Fig. 8F). Para-embolic plate only little elevated (Fig. 8B, showing paratype matured 5.I.2002); sclerotized part of embolus proper without longitudinal keels or ribs and not carrying denticles (Fig. 8A-B, showing paratype matured 5.I.2002), its dorsal wall distinctly wider than its ventral wall, abruptly bent prodorsad approximately at a right angle (Fig. 8F) and ending in a pronounced angular lobe (Fig. 8D-E); membranous part of embolus proper apically widened and lying on lobe of dorsal wall of sclerotised part (Fig. 8D).

Measurements: Total length 11.32; carapace 4.67 long, 3.96 wide; opisthosoma 4.83 long, 3.64 wide; eye mound 0.68 long, 0.80 wide, AME well-developed; palpal coxae 1.38 long, 0.95 wide; labium 0.40 long, 0.79 wide; sternum 2.37 long, 1.50 wide (0.83 on ventral surface); palp 7.99 long (2.53 + 1.34 + 2.81 + 1.31); leg I 15.97 long (4.35 + 1.90 + 3.40 + 4.03 + 2.29); leg II 17.01 long (4.43 + 1.90 + 3.56 + 4.63 + 2.49); leg III 18.92 long (4.55 + 1.90 + 4.00 + 5.78 + 2.69); leg IV 23.89 long (5.38 + 2.06 + 5.10 + 8.03 + 3.32).

Description of female (allotype): *Colour in alcohol* (darker in life): As in male but with a more pronounced dark pattern on carapace, resulting in a more distinct W-shaped pattern behind eye mound, and with a pronounced, light brown, flower-shaped pattern on pars thoracica; all opisthosomal tergites with larger dark patches, tergites II-V additionally with dark anteromedian patches. Legs light brown, with dark proximal and subapical annulations on femora (also on palpal femur), tibiae, metatarsi (indistinct on posterior legs) and on tarsi (indistinct on posterior legs). Palpal tibia with dark proximal and apical annulation; tarsus mostly dark, proventral-distal area lighter.

Bristles on carapace: Slightly stronger and longer (especially in front of eye mound) than in male.

Cheliceral teeth: Eleven strong cheliceral teeth on promargin of cheliceral groove on both sides.

Claws: Paired tarsal claws on legs with mostly 4-5 denticles (one claw with only two); unpaired claws with two denticles on legs I-III, 1-2 on leg IV. Tarsi without scopula.

Vulva: Vulval plate (Fig. 9A-B) distinctly sclerotised and pigmented, wider than long. Genital atrium uniformly flat, its lateral parts not bulging on dorsal side, with several lateral and median hairs. Posterior stalk wide, indistinctly perforated with tiny micropores; transition to poreplate indistinct, only slightly constricted. Anterior margin of poreplate slightly to distinctly invaginated, with indistinct anterolateral lobes, without anterolateral invaginations; ventral side of poreplate without bulging lateral and posterolateral margins. CDO large, undivided, irregularly quadrangular, close to anterior margin of poreplate. Receptacular cluster clearly wider than long, deep, distinctly projecting beyond anterior margin of poreplate.

Measurements: Total length 13.53; carapace 5.34 long, 4.19 wide; opisthosoma 5.70 long, 4.15 wide; eye mound 0.74 long, 0.83 wide; palpal coxae 1.74 long, 1.27 wide; labium 0.63 long, 1.27 wide; sternum 2.53 long, 1.86 wide (0.91 on ventral surface); palp 8.98 long (3.01 + 1.58 + 2.14 + 2.25); leg I 11.82 long (3.56 + 1.94 + 2.73 + 2.25 + 1.34); leg II 12.22 long (3.60 + 1.98 + 2.73 + 2.49 + 1.42); leg III 12.74 long (3.60 + 1.98 + 2.45 + 3.05 + 1.66); leg IV 16.41 long (4.27 + 2.10 + 3.24 + 4.55 + 2.25).

Variation: Carapace lengths in males (n=7) 4.36-4.75, in females with a well-developed vulval plate (n=9) 4.29-5.34, in the smallest female with an egg case 4.66. Carapace widths 3.64-4.06, 3.11-4.22 and 3.51, respectively.

In four males (including the holotype) the scopula extends over the distal half of the ventral side of tarsus III and over the distal three-fifths of tarsus IV, in the other three males it extends over the distal three-fifths of tarsus III and over the distal two-thirds of tarsus IV; on legs I-II the extent of the scopula is the same in all males. Variation in the shape of the tibial apophysis of the male palp is shown in Fig. 8A-C, H-J; variation in the shape of the distal edge of the contrategulum in Fig. 8F-G; variation in the shape of vulval plates of the females examined in Fig. 9. Two female paratypes (Fig. 9C, E), but not the allotype (Fig. 9A), have a moderately pronounced anterolateral lobe followed by a slight anterolateral invagination on each side of the poreplate. The largest (oldest) female (Fig. 9A) has more hairs in the genital atrium than smaller (younger) females (Fig. 9E). The posterior margin of the genital sternite of females is almost straight to distinctly invaginated (Fig. 9A-F).

Distribution: The types were collected from the surroundings of the Kota Tinggi Waterfall, at the foot of Gunung Muntahak, north of Kota Tinggi, in Johor State (Fig. 1, locality 8). Burrows of probably the same species were seen along the trail to the nearby Pelepah Waterfall. Two juveniles (don J. Kral) from Gunung Belumut, about 32 km further northwest, may also belong to this species.

Biology: At the Kota Tinggi Waterfall *L. gracilis* sp. nov. occurs together with the much larger *L. endau* which belongs to the same species-group. Burrows of the two species were seen only a few centimetres from each other. *Liphistius endau* was exclusively found very close to the waterfall and to the stream, *L. gracilis* sp. nov. also further away, but both were absent from high earthbanks (old road sides) in a palm oil plantation adjacent to the rain forest. Most burrows were simple, equipped with a single trapdoor and dug into the soil; a few small ones were sac-like nests with two trapdoors, constructed on the moss-covered surface of rock (as also known from cave species and from juveniles of forest-dwelling species; see Schwendinger, 1987). The trapdoors of seven penultimate males were 1.1-1.3 cm long and 1.6-1.9 cm wide; that of the largest female 1.3 and 2.0, respectively. All burrows had a maximum of eight, relatively long signal lines running over soil, stones and tree roots; the longest signal line (of the largest female) was 21 cm long.
Four males collected in June became adult in August to November of the same year; two males reached maturity in January and February after over 1.5 years in captivity (thus probably not corresponding to conditions in nature). In early July and early August two females built egg cases in captivity, 1.7-2.0 cm in diameter and 1.1-1.4 cm high, containing 30 and 36 eggs suspended on a thin layer of fine silk strands. Adult females moulted twice per year, in May and again in August to November.

Liphistius johore Platnick & Sedgwick, 1984

Fig. 10A

Liphistius johore Platnick & Sedgwick, 1984: 30, figs 79-80 (description of female).

Type material: Bernice Pauahi Bishop Museum, Honolulu, USA; female holotype (not examined); Malaysia, Johore [sic], Sungai Rengit, Pengarang; 19.XII.1961; leg. K.J. Kunchuna.

Material examined: None.

Diagnosis: Seemingly a fairly small species (carapace length of female holotype 5.15, carapace width 4.00). Female with annulated legs and yellow-coloured to orange-coloured carapace and opisthosomal tergites (Platnick & Sedgwick, 1984: 30); vulva with a wide poreplate with a distinct anterolateral invagination on each side of anterior margin, seemingly without bulging lateral and posterolateral margins on ventral side (Platnick & Sedgwick, 1984: fig. 80), with relatively large pores on dorsal side, with a large CDO (at its posterior margin level with the poreplate), and with a large receptacular cluster projecting far beyond anterior margin of poreplate; genital atrium without hairs, including a strongly trapezium-shaped (posteriorly wide, anteriorly very narrow, posterior margin almost straight) posterior stalk (Fig. 10A; Platnick & Sedgwick, 1984: figs 79-80).

Male: Unknown.

Female: This species was described on the basis of only the female holotype. For an easy comparison with other species treated here, the dorsal aspect of the vulval plate was re-drawn from Platnick & Sedgwick (1984: fig. 79) and is shown in Fig. 10A.

Relationships: The vulval plate (with a large CDO, with a huge receptacular cluster projecting far beyond the anterior margin of the well-sclerotised poreplate and with a well-sclerotised posterior stalk fully connected to the poreplate) indicates that *L. johore* is a member of the *malayanus*-group. Relatively small size, the presence of anterolateral invaginations on the poreplate (also present, but less distinct, in some females of *L. gracilis* sp. nov.; Fig. 9C, E) and the apparent absence of bulged lateral and posterolateral margins on the ventral side of the poreplate (not clearly evident from original illustrations of the vulval plate of the holotype, see Platnick & Sedgwick, 1984: fig. 80) indicate that *L. johore* and *L. gracilis* sp. nov. are more closely related to each other than to *L. malayanus* and *L. endau*.

Distribution and remarks: The type locality is given as "Sungai Rengit, Pengarang" (Fig. 1, locality 9). Kampung Sungai Rengit and the Pengarang ferry

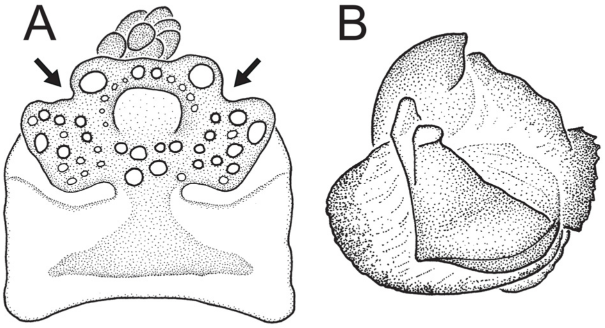

Fig. 10. *Liphistius johore*, female holotype (A); *Liphistius panching*, male from type locality (B). (A) Dorsal view of vulval plate (redrawn from Platnick & Sedgwick, 1984: fig. 79) (arrows indicating anterolateral invaginations in margin of poreplate). (B) Distal view of left palpal organ (dorsal side up) (redrawn from Sedgwick & Platnick, 1986: fig. 5).

terminal and immigration post (with nearby remains of the "Pengarang Battery", a British defence post overrun by the Japanese Army during the fall of Singapore in World War II) are about 15 km apart. I spent a full day searching in both the fairly undisturbed forest on the publicly accessible little hill next to the Pengarang ferry terminal (the nearby, distinctly higher and nicely forested Bukit Pengarang lies on the land of a large Malaysian naval base and is off limits to civilians and foreigners) and in the strongly disturbed forest of Bukit Pelali, about 5 km north of Kampung Sungai Rengit, but found no traces (not even empty burrows) of *Liphistius*.

Liphistius sp.

A single female (in MHNG; leg. P.J. Schwendinger), large (carapace length 12.45, carapace width 11.02) and uniformly dark-coloured, was collected close to the Jeram Linang Waterfall (Fig. 1, locality 13), south of Kota Baharu in the Kelantan State, together with the types of *L. linang* sp. nov. It produced an egg case in late January. Judging from the shape of its vulval plate, this specimen belongs to an undescribed species in the *malayanus*-group,

The *tioman*-group

Diagnosis: Medium-sized to large (carapace length of males 6.23-11.30, carapace length 6.01-10.04), uniformly dark-coloured spiders. Similar to species of the *malayanus*-group, distinguished by distal edge of contrategulum proventrally not ending in a V-shaped or U-shaped row of denticles; ventral process of contrategulum well-developed, basally wide (Figs 10B, 11F, 14C-D); para-embolic plate more elevated (Figs 11B-E, 14E-F); poreplate with CDO medium-sized and undivided (Fig. 12A, C, F) or large and divided by a more or less distinctly developed longitudinal bridge (Figs 13A, C-D, G; 14I); receptacular cluster medium-sized, more or less distinctly divided into two halves by a longitudinal trench (Figs 12B, D-E, G; 13B, E-F, H; 14J).

Species included: *Liphistius negara* sp. nov., *L. panching* and *L. tioman.*

Relationships: Species of the *tioman*-group are similar and probably closely related to species of the *malayanus*-group. *Liphistius panching* and *L. negara* sp. nov. from the mainland are more similar to each other than they are to the very distinct island-dwelling *L. tioman*.

Distribution: Eastern part of peninsular Malaysia and an offlying island (Fig. 1, localities 10-12).

Liphistius tioman Platnick & Sedgwick, 1984

Figs 11-12

Liphistius tioman Platnick & Sedgwick, 1984: 28-29, figs 81-87 (description of male and female).

Type material: AMHN; male holotype and female paratype (not examined); Malaysia, Pahang, Tioman Island, Gua Sinah and Gua Panah, 2600 ft. altitude; 29.VII.1982; leg. W.C. Sedgwick.

Material examined: MHNG, sample SIM-01/09; 1 male (matured 3.I.2002), 7 females (moulted 17.XII.2001; 2.IX.2001, 6.III., 4.X.2002, 7.VI.2003; 8.IX.2001, 16.II., 23.VI.2002), 1 penultimate male;

Key to the species of the *tioman*-group:

1 Tibial apophysis of male palp deeply divided, both parts equally long and carrying very short megaspines (Fig. 11A, H-I); tegulum very narrow, with few denticles on proximal edge (Fig. 11B); para-embolic plate long and distally pointed (Fig. 11C-E). Vulval plate with very wide, indistinctly outlined transition between poreplate and posterior stalk, lateral and posterolateral margins on ventral side of poreplate not bulging; genital atrium without median hairs (Fig. 12)... *L. tioman*

\- Tibial apophysis undivided, carrying long megaspines (Fig. 14G; Sedgwick & Platnick, 1986: figs 1-2, 5); tegulum wide, with numerous denticles on proximal edge (Fig. 14F; Sedgwick & Platnick, 1986: figs 1-2); para-embolic plate short and widely rounded (Fig. 14E-F; Sedgwick & Platnick, 1986: figs 1-2). Vulval plate with narrow, distinctly outlined transition between poreplate and posterior stalk, lateral and posterolateral margins on ventral side of poreplate bulging; genital atrium without median hairs (Figs 13, 14I-J) 2

2 Paracymbium longer than deep (Sedgwick & Platnick, 1986: figs 2-3); ventral process of contrategulum short, its apex widely rounded; distal edge of contrategulum smooth (Sedgwick & Platnick, 1986: fig. 5; Fig. 10B). Vulval plate slightly longer than wide or as long as wide; poreplate anteriorly wider than posteriorly, its anterior margin usually clearly invaginated (Fig. 13) .... *L. panching*

\- Paracymbium deeper than long (Fig. 14A-B); ventral process of contrategulum moderately long, its apex narrowly rounded (Fig. 14C-D); distal edge of contrategulum prodorsally with a single large triangular tooth (Fig. 14C-D). Vulval plate clearly wider than long; poreplate anteriorly narrower than posteriorly, its anterior margin only indistinctly invaginated (Fig. 14I-J) ....*L. negara* sp. nov.

Pahang, Tioman Island, Gunung Kajang (2°45'45''N, 104°08'43''E), 820-850 m; 30.VI.2001; leg. P.J. Schwendinger.

Diagnosis: Males distinguished from those of all other *Liphistius* species by a deeply and widely divided retrolateral apophysis on palpal tibia, both parts being equally long (Fig. 11A, H-I). Males distinguished from those of other species in the *tioman*-group additionally by a long and pointed para-embolic plate (Fig. 11C-E) and by a very narrow tegulum with few denticles on proximal edge, situated very close to dorsal apex of contrategulum (Fig. 11B, F). Females with poreplate widely fused with posterior stalk; receptacular cluster medially more or less distinctly divided; CDO undivided (Fig. 12).

Additions to description of male: *Scopula*: In distal two-thirds of ventral side of tarsus I, in distal three-quarters of tarsus II, in distal two-thirds of tarsus III, in distal half of tarsus IV (narrower than on other tarsi). All scopulae thin and only distally (behind the claws) divided by a glabrous longitudinal median stripe.
Palp: Tibial apophysis situated apically, not set back from anterior margin of palp (Fig. 11G), deeply divided: retrolateral part deeper, aligned with axis of tibia and carrying three very short pointed megaspines; retrodorsal part much narrower, pointing away from axis of tibia, carrying a single, slightly longer pointed magaspine (Fig. 11A, G-I). Distal margin of cymbium with very indistinct lobes (Fig. 11C). Paracymbium relatively short and moderately deep (Fig. 11A); cumulus indistinct, carrying a fairly compact group of long stiff bristles (Fig. 11A). Subtegulum without apophysis. Tegulum very narrow, its proximal edge carrying few overlapping scale-like denticles, situated close to dorsal apex of contrategulum (Fig. 11B, F). Contrategulum with large, conical ventral process being slightly constricted at base (Fig. 11F); distal edge of contrategulum distinctly elevated and composed of numerous parallel ribs instead of teeth (Fig. 11B-F), dorsal apex relatively small and narrowly rounded, only slighly elevated above underlying surface (Fig. 11B, F). Para-embolic plate long, narrow and asymmetrically triangular (Fig. 11B-E); embolus proper strongly inclined prolaterad (Fig. 11B), distally widened; dorsal wall of sclerotised part distinctly wider than ventral wall, ending in a quadrangular lobe (Fig. 11B-C, F), retrolateral wall not enforced by ridges but only with an indistinct, short distal keel (Fig. 11B, F); membranous part of embolus proper slightly widened distally (Fig. 11C).

Additions to description of female: Genital atrium of vulval plate (Fig. 12) without median hairs, few to several lateral hairs present in some females; lateral margin of genital atrium not forming flaps bending ventrad and inwards (as usual in *Liphistius*) but only indistinct mounds on the dorsal (not the ventral) side (Fig. 12A, C, F). Posterior stalk relatively short and wide, fused with poreplate without recognizable transition, reaching lateral margins of vulval plate in some females. Poreplate of variable shape, in most females examined anteriorly slightly narrower than posteriorly, its anterior margin indistinctly invaginated, without lobes; CDO quite large, undivided, anteriorly deep, posteriorly level with rest of poreplate (Fig. 12A, C, F; but see illustration of paratype in Platnick & Sedgwick, 1984: fig. 86); receptacular cluster quite large and wide, more or less distinctly divided into two paramedian subclusters (Fig. 12B, D-E, G).

Taxonomic remarks: The tibial apophysis of the male palp of *L. tioman* is unique and distinctly autapomorhic. A similar divided tibial apophysis is found in males of the *linang*-group, but that is considered to have evolved convergently (see also Discussion). The wide ventral process of the contrategulum, the wide posterior stalk and the divided receptacular cluster indicate a close relationship with *L. panching* and *L. negara* sp. nov.

Variation: Carapace lengths in males (n=2; values of the holotype are taken from Platnick & Sedgwick, 1984: 29) 6.23-6.93, carapace widths 6.01-6.34. In females with fully developed copulatory organs (n=7) the carapace length is 5.54-7.92 and the carapace width 5.15-7.38. Variation in the shape of poreplates of the females examined is shown in Fig. 12. The retrolateral tibial apophyses of the left and right palp of the examined male are shown in Fig. 11A and Fig. 11I, respectively.

Distribution: Known only from higher altitudes on Tioman Island (Fig. 1, locality 10).

Biology: Spiders of this species were found under and between huge granite boulders (some of them touching each other and forming recesses) in a lush rain forest. These recesses probably correspond to the Gua Sinah or Gua Panah which is the exact type locality and which were described as not being real caves (like their Malay names suggest) but just overhung caverns (Platnick & Sedgwick, 1984: 29). Burrows were mostly dug into loamy soil at the base and between the bolders (a few small spiders had silken nests on the surface of bolders just above the ground, as described for juvenile spiders of *L. trang*, see Schwendinger, 1987: fig. 5), and they had up to eight exceptionally long (up to 34 cm) signal lines spread over soil or rock surface. The trapdoor of the adult male (before its final moult) was 1.8 cm long and 3.2 cm wide, that of the largest female was 1.9 cm and 3.2 cm, respectively. When collected at the end of June, four females had egg cases: one was not opened, another was empty, the remaining two were 2.2-2.7 cm long, 2.8-2.9 cm wide and 1.9 cm high; they contained 3rd instar spiderlings (not collected, not counted).

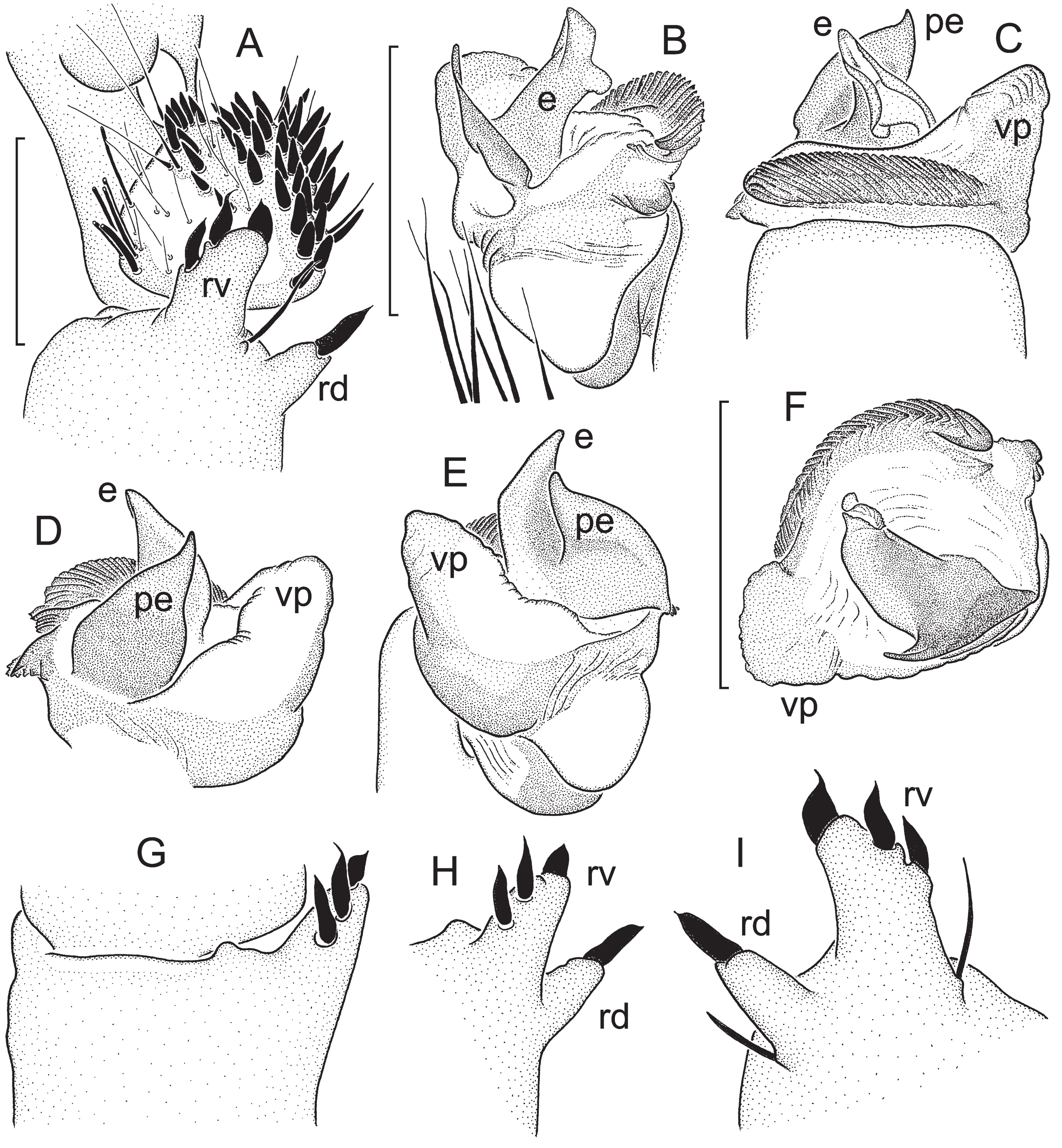

Fig. 11. *Liphistius tioman*, details of left and right palp of a male (matured 3.I.2002) from the type locality; left palp (A-C, E-H) and right palp (D, I). (A) Distal part of tibia and base of tarsus, retroventral view. (B) Palpal organ and tips of bristles on cumulus, retrolateral view. (C) Distal part of cymbium and palpal organ, prolateral view. (D) Palpal organ, retrolateral view. (E) Same, retroventral view. (F) Same, distal view (dorsal side at 1 o'clock). (G) Tibial apophysis, ventral view. (H) Same, retroventral view. (I) Same, retrolateral and slightly proximal view. Abbreviations: e - embolus proper; pe - para-embolic plate; rd - retrodorsal part of tibial apophysis; rv - retroventral part of tibial apophysis; vp - ventral process of contrategulum. Scale lines: 1.0 mm (A, G-H; B-E, I; F).

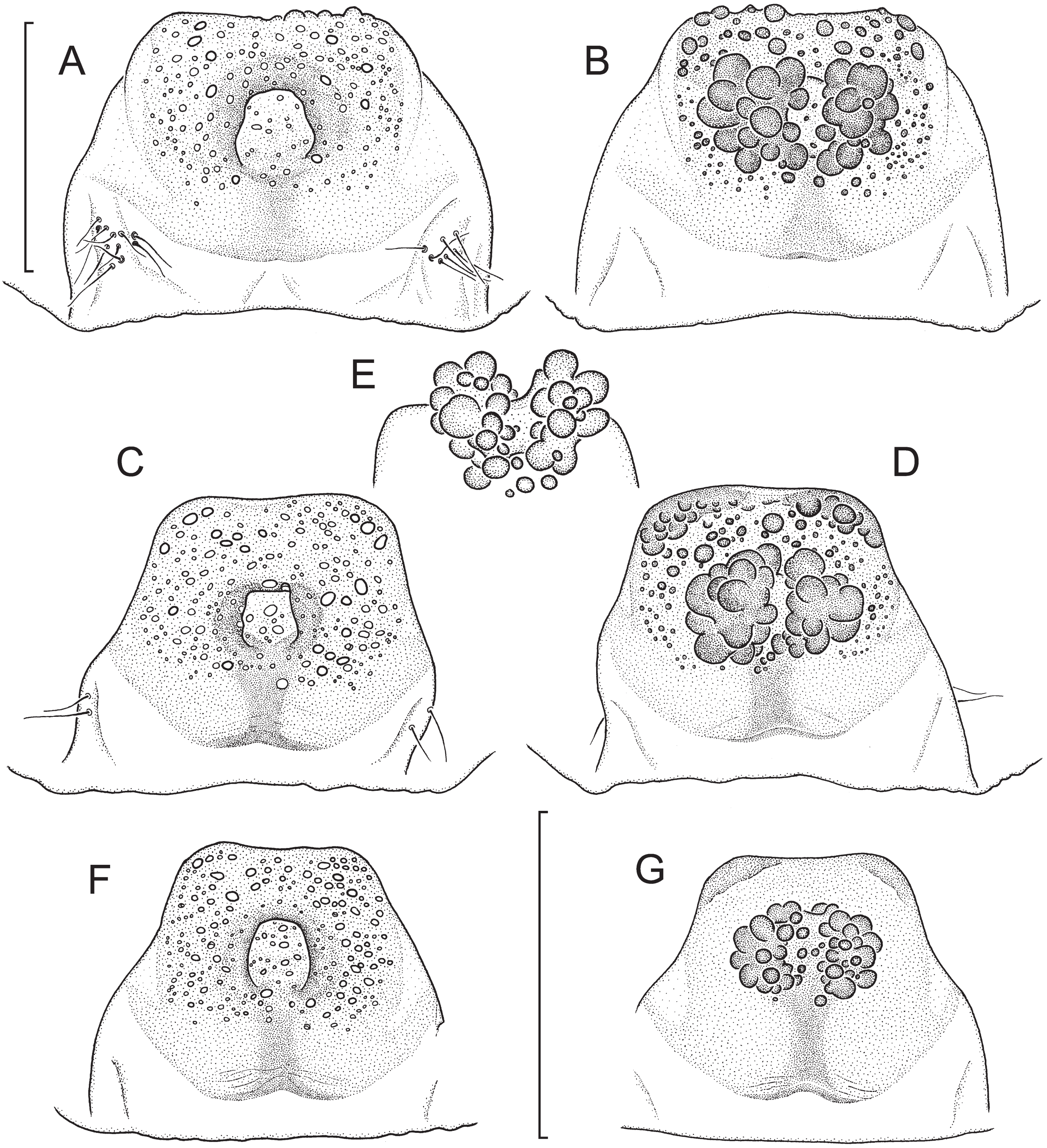

Fig. 12. *Liphistius tioman*, vulval plate of three females from the type locality: specimen moulted 17.XII.2001 (A-B); exuvia, moult 7.VI.2003 (C-E); exuvia, moult 16.II.2002 (F-G). (A, C, F) Entire structure, dorsal view. (B, D, G) Same, ventral view (vesicles in G omitted). (E) Receptacular cluster, ventral and slightly posterior view. Scale lines: 1.0 mm (A-B; C-G).

Liphistius panching Platnick & Sedgwick, 1984
Figs 10B, 13

Liphistius panching Platnick & Sedgwick, 1984: 27-28, figs 77-78 (description of female). – Sedgwick & Platnick (1986: 205-206, figs 1-8; description of male).

Type: AMHN; female holotype (not examined); Malaysia, Pahang, Gua Panching [= Gua Charas; see paragraph "Distribution"], 24 km N of Kuantan; 31.VII.1982; leg. W.C. Sedgwick.

Material examined: MHNG, sample MAL-04/07; 3 females (moulted 30.X.2004, 26.III., 7.IX.2005, 19.II.2006; 8.XII.2004, 30.XII.2005); Pahang, about 1 km north of Kampung Panching, Gua Charas, 3°54'41"N, 103°08'50"E, 120 m; 1.-2.VI.2004; leg. P.J. Schwendinger. – MHNG, sample SIM-01/11; 6 females (moulted 7.VII.2001, XII.2002; 8.VII.2001; 27.II., 16.X.2002), 4 juveniles; same locality; 7./8. VII.2001; leg. P.J. Schwendinger.

Diagnosis: Male (see Sedgwick & Platnick, 1986: figs 1-8 and Fig. 10B) distinguished by retrolateral apophysis of palpal tibia in ventral view very wide at base, only little set back from anterior margin of article (Sedgwick & Platnick, 1986: fig. 3); distal margin of

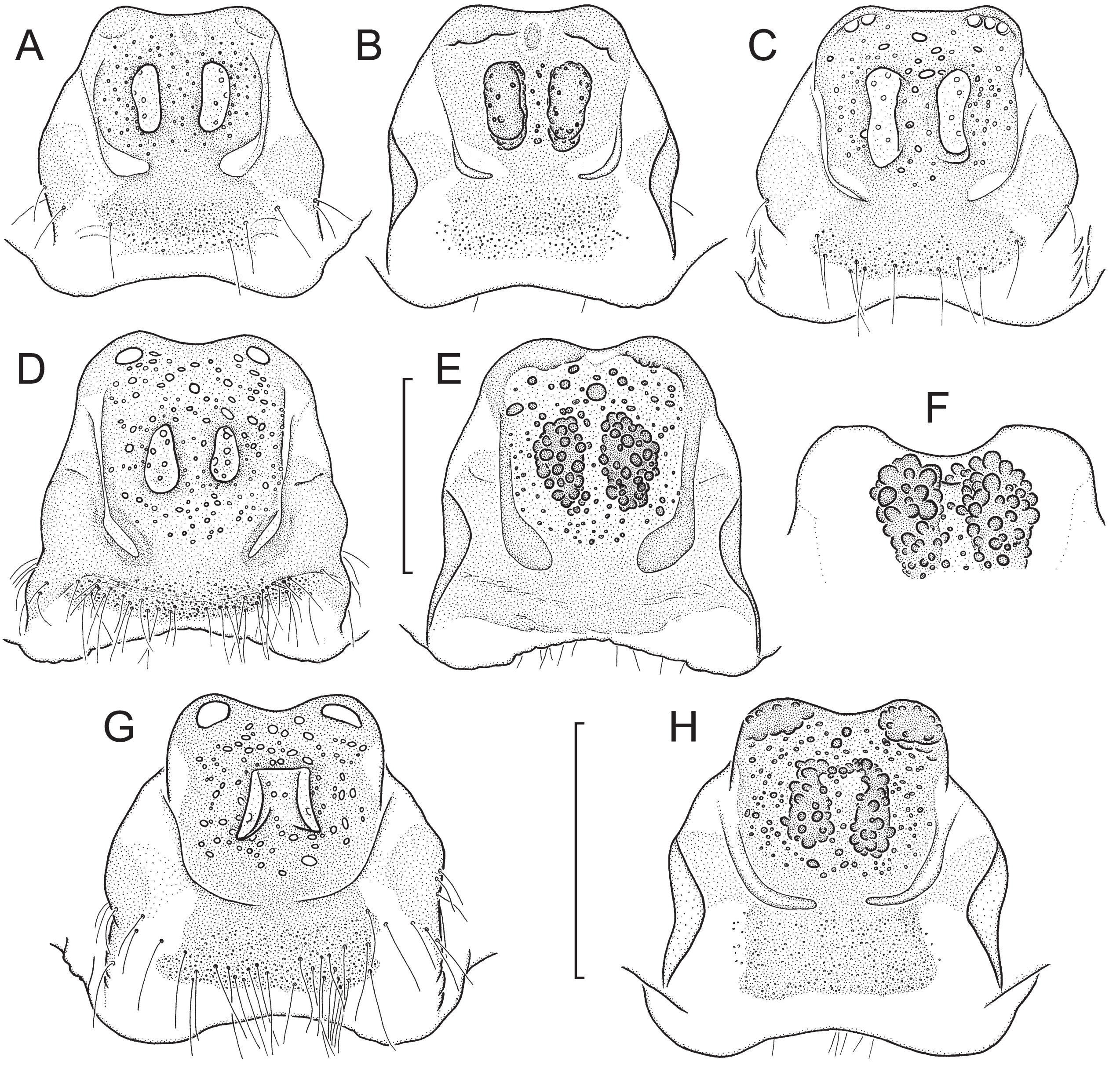

Fig. 13. *Liphistius panching*, vulval plate of four female specimens from the type locality: specimen moulted 16.X.2002 (A-B), moulted VIII.2005 (C), built egg case 16.VII.2001 (D-F), moulted 30.XII.2005 (G-H). (A, C-D, G) Entire structure, dorsal view. (B, E, H) Same, ventral view. (F) Receptacular cluster, ventral and slightly posterior view. Scale lines 1.0 mm: (A-C, F-H; D-E).

cymbium with indistinct lobes (Sedgwick & Platnick, 1986: fig. 4); paracymbium quite shallow, without retrolateral-proximal heel; cumulus indistinct, with moderately long bristles (Sedgwick & Platnick, 1986: figs 1-5); tegulum with many teeth on proximal edge (Sedgwick & Platnick, 1986: figs 1-2); contrategulum with short, very widely arched ventral process pointing proventrad and with pointed dorsal apex (Fig. 10B; Sedgwick & Platnick, 1986: fig. 5); para-embolic plate short (Sedgwick & Platnick, 1986: figs 1-4); embolus proper apically wide (Sedgwick & Platnick, 1986: fig. 3; Fig. 10B), dorsal wall of sclerotized part apparently long and sharply bent prodorsad (Sedgwick & Platnick, 1986: fig. 5). Females (see Platnick & Sedgwick, 1984: figs 77-78 and Fig. 13) distinguished by vulva with few to many lateral and median hairs in genital atrium; posterior stalk wide, quadrangular to trapezium-shaped; poreplate anteriorly wider than posteriorly, with a more or less distinctly invaginated anterior margin and with bulging lateral and posterolateral margins on ventral side; two central dorsal openings (CDO) separated by a wide longitudinal bridge (Fig. 13A, C-D, G); two longitudinal receptacular clusters more or less completely separated from each other by a longitudinal trench (Fig. 13B, E-F, H).

Remarks: According to information from Lorenzo Prendini, the current curator of the arachnid collections at the AMNH, the normally developed male of *L. panching* (deposited together with a malformed male) cannot be found at the moment. To my knowledge, this is the only useful male specimen of *L. panching* in any public scientific collection, and a re-examination of details of the palpal organ of this species was therefore not possible. For an easy comparison with other species, the distal aspect of the palpal organ was re-drawn from Sedgwick & Platnick (1986: fig. 5) and is shown in Fig. 10B.

Unlike in any other *Liphistius* species examined, the vulval plates on the exuviae of *L. panching* females (much more than other sclerotised parts of the exuviae) have become partially depigmented; some have almost completely lost their pigmentation. This is probably due to alcohol preservation. In undissected females the vulval plates have retained their original pigmentation.

Variation: Sedgwick & Platnick (1986: 205) give the carapace length 9.8 and the carapace width 8.4 for the normally developed male, but no measurements for the teratological male with an incompletely developed palp. Carapace lengths in females with fully developed copulatory organs (n=8) 7.62-8.71, carapace widths 6.63-8.12.

Variation in the shape of the vulval plates examined is shown in Fig. 13. In one female the two receptacular clusters and the two central dorsal openings (CDO) are anteriorly connected with each other (Fig. 13G-H). The larger (older) a female is, the more hair it has in its genital atrium (Fig. 13D cf. Fig. 13A).

Distribution: The type locality is given as “Gua Panching [= Panching Cave], a cave 24 km north of Kuantan”. This is identical with Gua Charas (Fig. 1, locality 11) in Bukit Charas (= Charas Hill) near Kampung Panching (= Panching Village), which is actually a bit over 20 km northwest of Kuantan. This should not be confused with Bukit Panching, which did not have any caves, was situated about 1.5 km southwest of Bukit Charas and has been completely removed by quarrying in the 1990s. Today only a water-filled depression shows where the hill once stood (Liz Price, personal communication).

Biology: All spiders examined were collected from sloping loamy soil in the oligophic zone at the entrance area of the Charas Cave. In captivity one female built an egg case (2.7 cm long, 2.8 m wide and 1.4 cm high) in late July 2001. The eggs (more than 21) were found partially rotten when the egg case was opened.

***Liphistius negara* sp. nov.**

Fig. 14

Types: MHNG, sample MAL-04/14; male holotype (matured 9.VII.2006), 1 male paratype (matured end of July 2005), female allotype, 2 juv. males; Malaysia, Pahang, Taman Negara, trail from Nusa Camp to Abai Waterfall, 4°23’49”N, 102°25’50”E, 110 m; 16.-17. VI.2004; leg. P.J. Schwendinger.

Etymology: The species epithet, a name in apposition, is taken from the Malay name of the type locality: taman (= park), negara (= national).

Diagnosis: Large, uniformly dark-coloured species in both sexes. Similar to *L. panching*, distinguished by slightly larger size (carapace length of males 10.28-11.30, width 8.70-10.04 versus 9.8 and 8.4, respectively, in male of *L. panching*, see Sedgwick & Platnick (1986: 205). Males with tibial apophysis in ventral view narrower at base, more distinctly set back from anterior margin of tibia (Fig. 14A cf. Sedgwick & Platnick, 1986: fig. 3); paracymbium deeper (Fig. 14B cf. Sedgwick & Platnick, 1986: fig. 2); ventral process of contrategulum narrower and more pointed (Fig. 14C-D cf. Fig. 10B and Sedgwick & Platnick, 1986: fig. 5); distal edge of contrategulum with a large triangular tooth, dorsal apex rounded instead of pointed (Fig. 14C-D cf. Fig. 10B and Sedgwick & Platnick, 1986: fig. 5). Female distinguished from those of *L. panching* by vulval plate wider than long; poreplate anteriorly distinctly narrower than posteriorly instead of anteriorly wider than posteriorly (Fig. 14I-J cf. Fig. 13 and Platnick & Sedgwick, 1984: figs 77-78).

Description of male (holotype): *Colour in alcohol* (much darker in life): Most sclerotised parts uniformly chestnut-brown, on ventral side slightly lighter than on

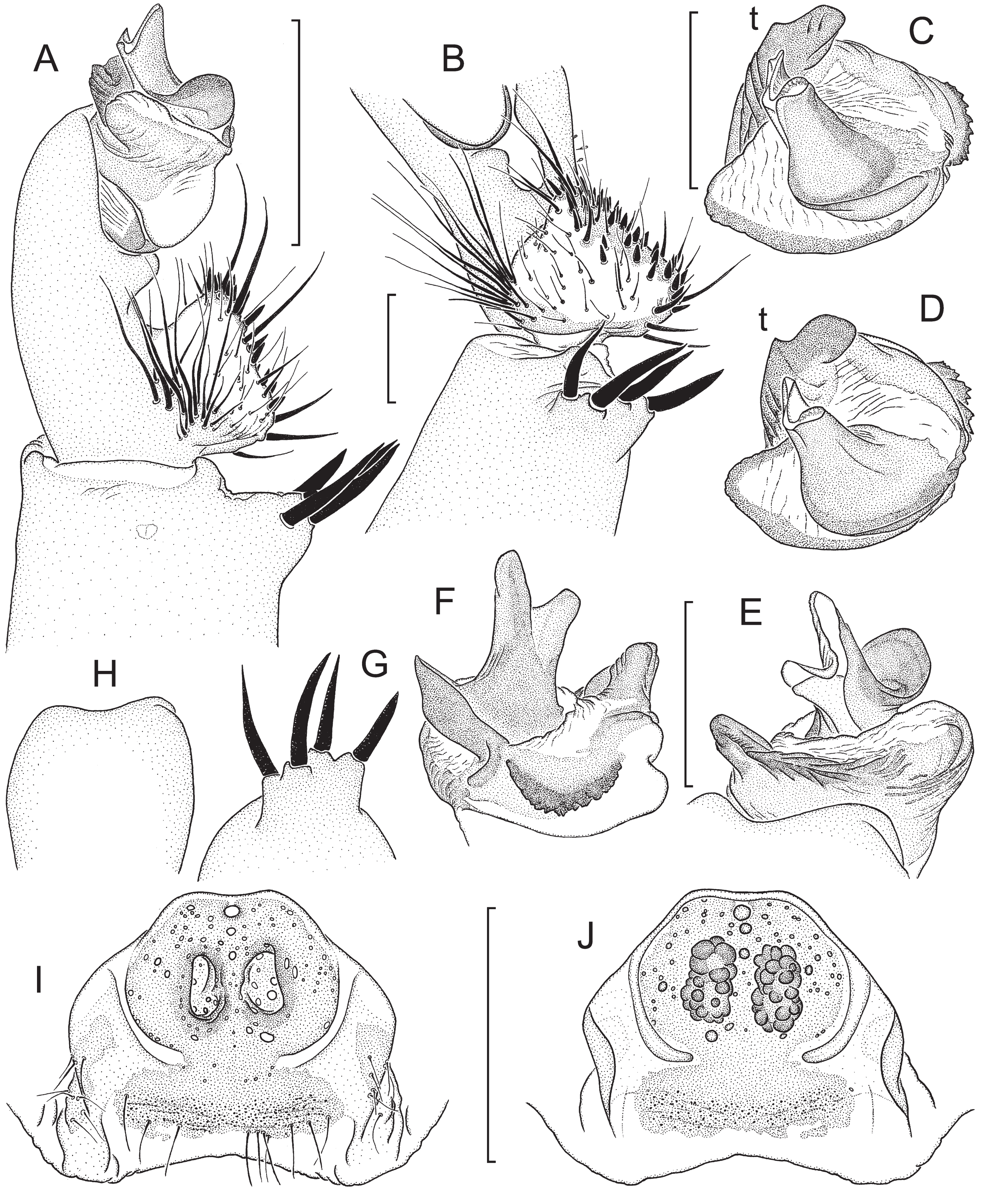

Fig. 14. *Liphistius negara* sp. nov., details of left palp of male holotype (A-C, E-H) and of male paratype (D); vulval plate of female allotype (I-J). (A) Distal part of palp, ventral view. (B) Distal part of tibia and base of tarsus, retroventral view. (C-D) Palpal organ, distal view (dorsal side up). (E) Same, proventral view. (F) Same, retrodorsal view. (G) Tibial apophysis, retrolateral and slightly proximal view. (H) Distal part of cymbium, prolateral view. (I) Vulval plate, dorsal view. (J) Same, ventral view. Abbreviation: t - tooth on distal edge of contrategulum. Scale lines: 1.0 mm (A; B, G-H; C-D; E-F; I-J).

dorsal side; carapace reddish chestnut-brown; proximal portion of chelicerae cream-coloured; membranes of opisthosoma greyish cream, other membranes white.

Bristles on carapace: Stiff bristles along all margins (longest anteriorly); many weaker and shorter ones on coxal elevations and behind fovea, fewer of them on both sides of eye mound and in a W-shaped arrangement behind it.

Cheliceral teeth: Eleven and twelve small ones on promargin of cheliceral groove on right and left chelicera, respectively.

Scopula: Tarsus I with thin scopula confined to distal third of ventral side, divided for its entire length by narrow pale, glabrous longitudinal median stripe and by some bristles; tarsus II with thin scopula in distal half, only distally divided by median stripe; tarsi III-IV with dense scopula covering distal four-fifths, only distally divided by median stripe.

Claws: Paired tarsal claws on anterior legs with 4-5 denticles, on posterior legs with 4-6 denticles; unpaired claws in most cases carrying a single denticle.

Palp: Tibial apophysis slightly set back from distal margin of tibia (Fig. 14A), carrying four medium-sized pointed megaspines (Fig. 14B, G). Both apical lobes of cymbium indistinct and equally rounded (Fig. 14E, H). Paracymbium basally deep (Fig. 14B), its cumulus indistinctly elevated, carrying moderately long stiff bristles (Fig. 14A-B). Subtegulum without apophysis. Tegulum short and wide, coarsely dentate along entire proximal margin (Fig. 14F). Contrategulum with distinct conical ventral process, its rounded apex directed proventrad (Fig. 14C); distal edge with several oblique ribs and with a large triangular tooth prodorsally, ending in spatulate asymmetrical dorsal apex (Fig. 14C). Paraembolic plate short (Fig. 14A, E-F); retrolateral side of sclerotised part of embolus proper without longitudinal keels or ribs and not carrying denticles, dorsal wall much wider than ventral wall and sharply bent prodorsad, thus opening of spermophor forming an L (Fig. 14A, C, E); membranous part of embolus proper distally wider than proximally, with only slightly pigmented proximal portion (Fig. 14E).

Measurements: Total length 27.94; carapace 11.30 long, 10.04 wide; opisthosoma 11.55 long, 9.04 wide; eye mound 1.51 long, 1.61 wide, AME well-developed; palpal coxae 3.68 long, 2.26 wide; labium 1.00 long, 2.01 wide; sternum 5.35 long, 3.01 wide (1.34 on ventral surface); palp 18.76 long (5.69 + 3.18 + 6.44 + 3.45); leg I 32.80 long (9.20 + 4.69 + 7.20 + 8.28 + 3.43); leg II 35.06 long (9.45 + 4.69 + 7.70 + 9.54 + 3.68); leg III 38.66 long (9.45 + 4.69 + 8.20 + 12.05 + 4.27); leg IV 47.53 long (11.55 + 4.85 + 9.79 + 15.48 + 5.86).

Description of female (allotype): Colour in alcohol (much darker in life) as in male. Carapace with stiff bristles as in male, plus a pair of bristles anterior of fovea. Eleven strong teeth on promargin of cheliceral groove on both sides. Paired tarsal claws on anterior legs with three denticles, on posterior claws with 3-4 denticles; unpaired claws in most cases with a single denticle (claws worn on all limbs). Tarsi without scopula.

Vulva (Fig. 14I-J): Posterior margin of genital sternite slightly and widely invaginated. Vulval plate distinctly sclerotised and pigmented, wider than long. Genital atrium with several lateral and median hairs. Posterior stalk wide, with micropores, fused with poreplate. Poreplate entirely and distinctly pigmented, its anterior margin indistinctly invaginated and clearly narrower than posterior margin. Two central dorsal openings (CDO) separated by a longitudinal bridge; two longitudinal receptacular clusters on ventral side completely separated from each other.

Measurements: Total length 22.00; carapace 9.62 long, 8.28 wide; opisthosoma 10.29 long, 8.62 wide; eye mound 1.22 long, 1.42 wide; palpal coxae 3.18 long, 2.01 wide; labium 1.17 long, 2.18 wide; sternum 4.35 long, 2.59 wide (1.59 on ventral surface); palp 16.23 long (5.35 + 3.01 + 4.02 + 3.85); leg I 19.76 long (5.86 + 3.60 + 4.27 + 4.02 + 2.01); leg II 20.57 long (6.02 + 3.68 + 4.35 + 4.43 + 2.09); leg III 22.25 long (6.19 + 3.68 + 4.52 + 5.35 + 2.51); leg IV 30.37 long (8.03 + 3.85 + 6.11 + 8.70 + 3.68).

Variation: Carapace lengths in males (n=2) 10.28-11.30, widths 8.70-10.04. The male paratype has the same reduced scopula on anterior legs (especially on tarsus I) as the holotype. Variation in the shape of the palpal organ, see Fig. 14C-D.

Distribution: Known only from the type locality in central peninsular Malaysia (Fig. 1, locality 12).

Biology: The types were collected from sloping soil and from decaying wood in a rain forest. The largest burrow (of juvenile male, not yet penultimate) had a 2.6 cm long ad 4.1 cm wide trapdoor. The trapdoors of old females thus must be of similar size as those of *L. malayanus* and *L. endau*. The female allotype of *L. negara* sp. nov. appears to be mature (judging from the degree of sclerotisation of its vulval plate), but not yet fully grown. Most burrow entrances had eight signal lines, one had nine. Both males became mature in July, after one and two years of captivity, respectively.

The male paratype has a pronounced pathological outgrowth on the right cheliceral fang, and bite marks of parasitic *Ljungia bristowi* mites on its carapace (many) and opisthosomal tergites (few), but not elsewhere.

The linang-group

Diagnosis: Small to medium-sized spiders (carapace length of males 4.50-6.83, carapace width 3.98-6.21) with a colour pattern on carapace, limbs and opisthosomal tergites (Fig. 2B). Distinguished from the *malayanus*-

Key to the species of the *linang*-group:

1 Males without scopula on tarsus IV; long bristle retroventrally at base of tibial apophysis thin (Fig. 15A, G-I); paracymbium quite long (Fig. 15A); distal edge of contrategulum with wide gap behind distinctly bent dorsal apex (Fig. 15B). Poreplate with anterior margin distinctly invaginated (Fig. 16A-E); CDO a transverse slit or triangle without enlarged pores lateral to it (Fig. 16A, C-D); receptacular cluster indistinctly divided into lateral halves, its vesicles quite short (Fig. 16B, E) .... *L. linang* sp. nov. (in Malaysia)

\- Males with scopula on tarsus IV; long bristle retroventrally at base of tibial apophysis thick, spine-like (Fig. 17A, I-K); paracymbium short (Fig. 17A); distal edge of contrategulum without gap behind only slightly or not bent dorsal apex (Fig. 17B, G-H). Poreplate with anterior margin only indistinctly invaginated (Fig. 18); CDO a longitudinal slit or semicircular hole with an enlarged pore on each lateral side (Fig. 18A, C, E, G); receptacular cluster not divided into lateral halves, its vesicles quite long (Fig. 18B, D, F, H) .... *L. indra* sp. nov. (in Thailand)

group and the *tioman*-group by males possessing a large para-embolic plate with a coarsely serrate distal margin (Figs 15A-D, 17A-D), a narrow and pointed dorsal apex of the contrategulum (Figs 15E-F, 17G-H), and a retrolateral tibial apophysis deeply divided into a long, deep retroventral part and a very short, small retrodorsal part (Figs 15G-I, 17I-K) (tibial apophysis also deeply divided in *L. tioman* but in that species both parts equally long; Fig. 11A, G-I); three megaspines on retroventral part short and bent, single megaspine on retrodorsal part short, curved and weaker than other megaspines (Figs 15A, G-I; 17A, I-K). Females distinguished by a peculiar vulval plate with an only partially sclerotised poreplate widely separated from small remnant of posterior stalk situated at posterior margin of vulva (Figs 16A-E, 18); CDO small, in many cases slit-like (Figs 16A, C-D; 18A, C, E, G).

Species included: *Liphistius linang* sp. nov., *L. indra* sp. nov.

Relationships: The *linang*-group is morphologically intermediate between the *tioman*-group and the *batuensis*-group. Sharing with *L. tioman* a deeply divided tibial apophysis with the retrodorsal-apical megaspine distinctly separated from the other three megaspines, and sharing with this and other species in the *tioman*-group a distinctly elevated para-embolic plate. Females of the *linang*-group show strong resemblance with those of the *batuensis*-group by possessing an only partially sclerotised poreplate. However, females of *L. linang* sp. nov. have a divided receptacular cluster, as do females of all *tioman*-group species. The relationships of the linang-group are therefore not clear.

Distribution: Northeastern peninsular Malaysia and southern Thailand (Fig. 1, localities 13-14).

Liphistius linang sp. nov.
Figs 15-16

Types: MHNG; male holotype (matured end XII.2001), 4 male paratypes (matured 14.IX., 1.X.1999, early XI.2000, end XII.2001) and 4 female paratypes (including allotype, moulted 12.II.2002); Malaysia, Kelantan, about 15 km E of Machang, Jeram Linang Waterfall, 5°44’34”N, 102°22’29”E, 50 m; 12.I.1999; leg. P.J. Schwendinger.

Etymology: Name in apposition, taken from the Malay name of the type locality: jeram (= rapids), linang (tearful, weeping).

Diagnosis: Medium-sized, bicoloured species in both sexes. Similar to *L. tioman*, males distinguished by retroventral part of bipartite tibial apophysis carrying longer and bent megaspines; retrodorsal part of tibial apophysis developed as a small tubercle carrying a weaker megaspine (Fig. 15A, G-I cf. Fig. 11A, G-I); tegulum with wide, distinctly dentate proximal edge (Fig. 15D cf. Fig. 11B); contrategulum without (or with very indistinct) ventral process, its distal edge finely dentate instead of ribbed, prodorsally with a wide gap before reaching hook-shaped dorsal apex (Fig. 15B, E-F cf. Fig. 11C, F); para-embolic plate large, distally wide, with coarsely dentate margins (Fig. 15A-F cf. Fig. 11C-E); dorsal wall of sclerotised part of embolus proper not ending in protruding lobe, as wide as ventral wall (Fig. 15B, E-F cf. Fig. 11B-C, F); scopula on tarsi IV absent.

Description of male (holotype): *Colour in alcohol* (much darker in life): Carapace mostly light brown; pars cephalica brown except for indistinct grey-brown W-shaped pattern behind eye mound and light brown medial patch between eye mound and fovea; brown area on pars cephalica connected to brown flower-shaped area around fovea; long brown patches along lateral (wide) and posterior (very narrow) margins of pars thoracica and between coxal elevations. Chelicerae with proximal portion cream-coloured, distal portion dark brown. Palps in proximal half of femur and tibia and in distal half of patella light brown, mottled with dark spots, other parts dark brown; cymbium entirely very dark reddish brown. Legs mostly dark brown except for light brown distal half of all patellae and light brown proximal half of all femora (mottled with dark spots); leg tibiae (in contrast to those of palp) to tarsi entirely dark brown. Opisthosoma mostly light brown, mottled

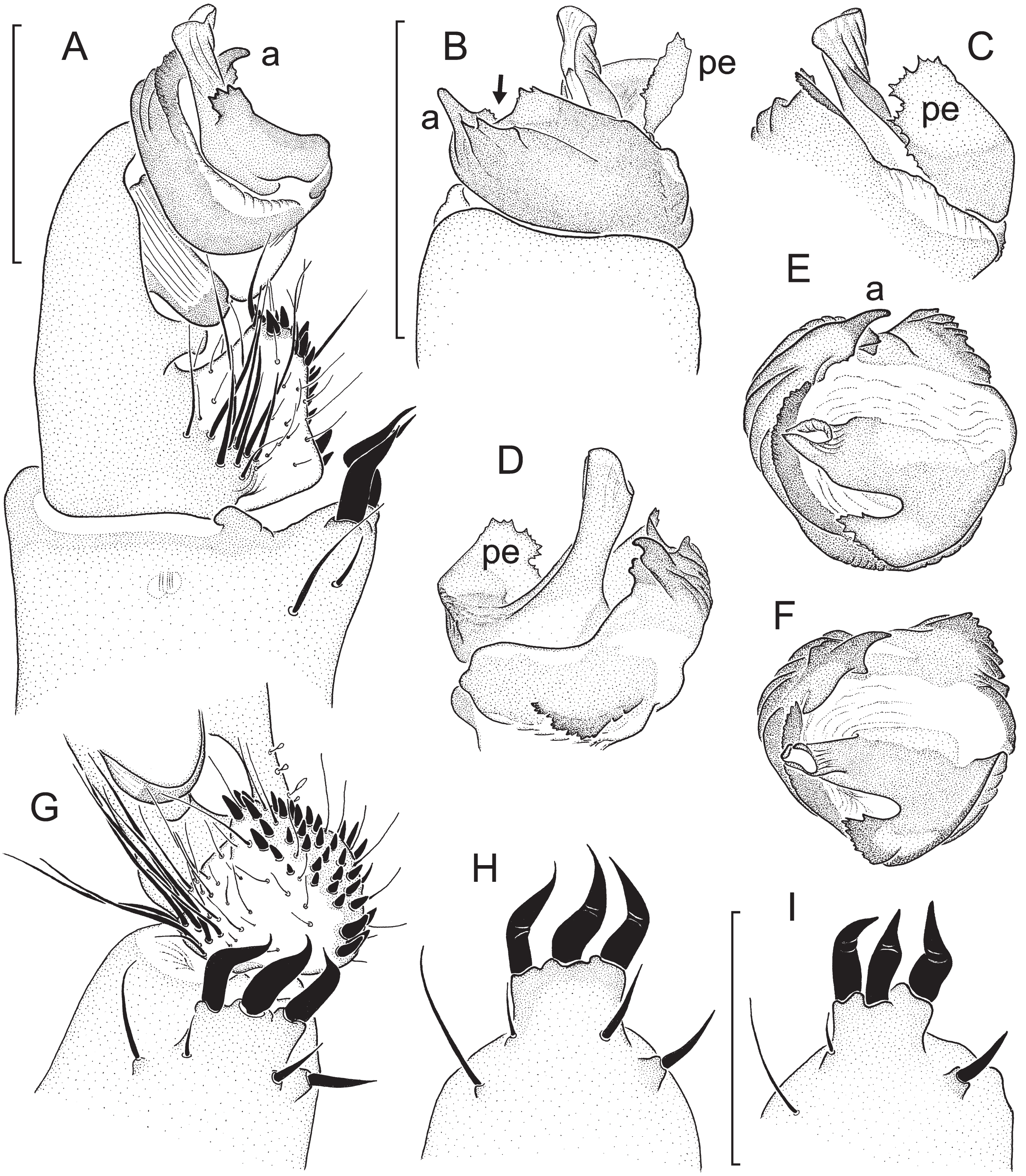

Fig. 15. *Liphistius linang* sp. nov., details of left palp of two males; holotype (A-E, G-H), paratype matured 14.IX.1999 (F, I). (A) Distal part of palp, ventral view. (B) Distal part of cymbium and palpal organ, prolateral view (arrow indicating gap in distal edge of contrategulum). (C) Palpal organ, proventral and slightly proximal view. (D) Same, retrodorsal view. (E-F) Same, distal view (dorsal side up). (G) Paracymbium and tibial apophysis, retrolateral view. (H-I) Tibial apophysis, retrolateral and slightly proximal view. Abbreviations: a - dorsal apex of contrategulum; pe - para-embolic plate. Scale lines: 1.0 mm (A, G; B-F; H-I).

with dark spots laterally; tergites I-II almost entirely dark brown, tergite III light brown with extensive dark lateral and median patches, following tergites with distinct dark lateral spots and increasingly indistinct median spots, last two tergites tiny and entirely dark brown.

Bristles on carapace: Few short, weak bristles along all margins except posterior one, on coxal elevations, in front and behind fovea; longer, stronger bristles on, behind and in front of eye mound.

Cheliceral teeth: Ten small ones on promargin of cheliceral groove of each chelicera.

Scopula: Tarsi I-III with moderately dense scopula in distal two-thirds of ventral side, only distally divided by a short median stripe; tarsus IV entirely without scopula.

Claws: Paired tarsal claws on anterior legs with 3-5 denticles, on posterior legs with 4-5 denticles; unpaired claws with one indistinct denticle or without.

Palp: Tibial apophysis situated distally, only slightly set back from anterior margin of palp (Fig. 15A), deeply divided: (a) retroventral part long and deep, pointing slightly away from axis of tibia, carrying three medium-sized, bent megaspines; (b) retrodorsal part much smaller and shorter, shaped like a low tubercle, carrying a single bent, relatively weak spine (i.e. a reduced megaspine); long bristle retroventrally below tibial apophysis weak (Fig. 15A, G-H). Distal margin of cymbium with indistinct lobes (Fig. 15B). Paracymbium quite long and moderately deep, with an indistinct retrolateral-proximal heel (Fig. 15A, G); cumulus indistinct, carrying a moderately compact group of long stiff bristles (Fig. 15A, G). Subtegulum without apophysis. Tegulum with wide, distinctly dentate proximal edge (Fig. 15D). Contrategulum without recognizable ventral process; prolateral surface with a few ribs, distal edge sharp in proventral part, finely dentate in prolateral part, with a deep gap in prodorsal part before reaching very narrow, slightly hook-shaped dorsal apex (Fig. 15B, E). Para-embolic plate large, its distal margin wide, strongly dentate and directed proventrad-distad (Fig. 15B-E); embolus proper relatively narrow, inclined prolaterad (Fig. 15A-D), dorsal and ventral walls of sclerotised part equally wide and lying close to each other, retrolateral wall enforced by five weak ridges (Fig. 15E); membranous part of embolus proper narrow, indistinct (Fig. 15B).

Measurements: Total length 14.22; carapace 5.83 long, 5.05 wide; opisthosoma 6.86 long, 4.31 wide; eye mound 0.91 long, 1.12 wide; palpal coxae 1.76 long, 1.23 wide; labium 0.49 long, 1.08 wide; sternum 2.55 long, 1.81 wide (1.03 on ventral surface); palp 9.66 long (2.55 + 1.91 + 3.53 + 1.67); leg I 17.64 long (4.80 + 2.30 + 3.82 + 4.61 + 2.11); leg II 18.67 long (4.80 + 2.30 + 4.02 + 5.20 + 2.35); leg III 20.48 long (4.95 + 2.35 + 4.26 + 6.27 + 2.65); leg IV 26.72 long (6.27 + 2.65 + 5.74 + 8.58 + 3.48).

Description of female (allotype): *Colour in alcohol* (much darker in life): As in male, except for carapace with more extensive dark areas, all of them interconnected; W-shaped pattern behind eye mound distinct; metatarsi of legs and palps mostly dark, with a small light zone at base; tibiae with dark proximal and subdistal annulations; light brown femora with indistinct (in comparison to tibiae) dark proximal and subdistal annulations; opisthosomal tergites III-VII with more extensive dark median patches; genital area darker than surrounding parts of genital sternite, with a white, bell-shaped posterior zone (Fig. 16F).

Bristles on carapace: Stiff bristles as in male, plus an additional pair just anterior to fovea.

Cheliceral teeth: Nine strong teeth on promargin of left cheliceral groove, ten on right side.

Claws: Palpal claw with three denticles on right side, none on left side. Paired claws with two denticles on anterior legs, 2-3 denticles on posterior legs; unpaired claws with 1-2 denticles on legs I-III, none on leg IV. All tarsi without scopula.

Vulva: Posterior margin of genital sterite invaginated (Fig. 16F). Vulval plate (Fig. 16A-E, illustrations of paratypes) with pigmentation and sclerotisation completely lost in median zone. Posterior stalk reduced to a small isolated, ventrad-bent posterior sclerite at some distance from or on posterior margin of genital sternite; posterior stalk and poreplate widely separated from each other. Genital atrium slightly sunken below level of poreplate, carrying numerous hairs on both sides of remnant of posterior stalk. Poreplate with indistinctly outlined lateral and posterior margins, these not bulging from ventral side of plate; anterior margin distinctly and widely invaginated, forming two more or less pronounced anterolateral lobes. CDO relatively small, wider than long, transversally slit-like or triangular, situated in unpigmented or weakly pigmented area of poreplate (Fig. 16A, C-D, paratypes). Ventral receptacular cluster quite large and racemose, longitudinally divided into two lateral subclusters, its individual vesicles globular, about as long as wide (Fig. 16B, E, paratypes).

Measurements: Total length 17.25; carapace 5.93 long, 5.00 wide; opisthosoma 7.89 long, 6.13 wide; eye mound 0.82 long, 1.04 wide; palpal coxae 1.91 long, 1.37 wide; labium 0.64 long, 1.37 wide; sternum 2.65 long, 2.11 wide (1.27 on ventral surface); palp 10.00 long (3.24 + 1.86 + 2.30 + 2.60); leg I 12.40 long (3.77 + 2.16 + 2.50 + 2.50 + 1.47); leg II 12.90 long (3.82 + 2.21 + 2.55 + 2.75 + 1.57); leg III 13.73 long (3.92 + 2.25 + 2.60 + 3.24 + 1.72); leg IV 19.71 long (5.10 + 2.55 + 4.07 + 5.54 + 2.45).

Remark: In the female allotype the long spinnerets (anterior and posterior laterals) are bent anteriad, which is an artefact resulting from having been pressed against the wall of the vial in that position for some time.

Variation: Carapace lengths in males (n=5) 4.91-6.15, carapace widths 4.19-5.09; in females with well-developed vulval plates (n=4) 5.53-5.90 and 4.29-5.03,

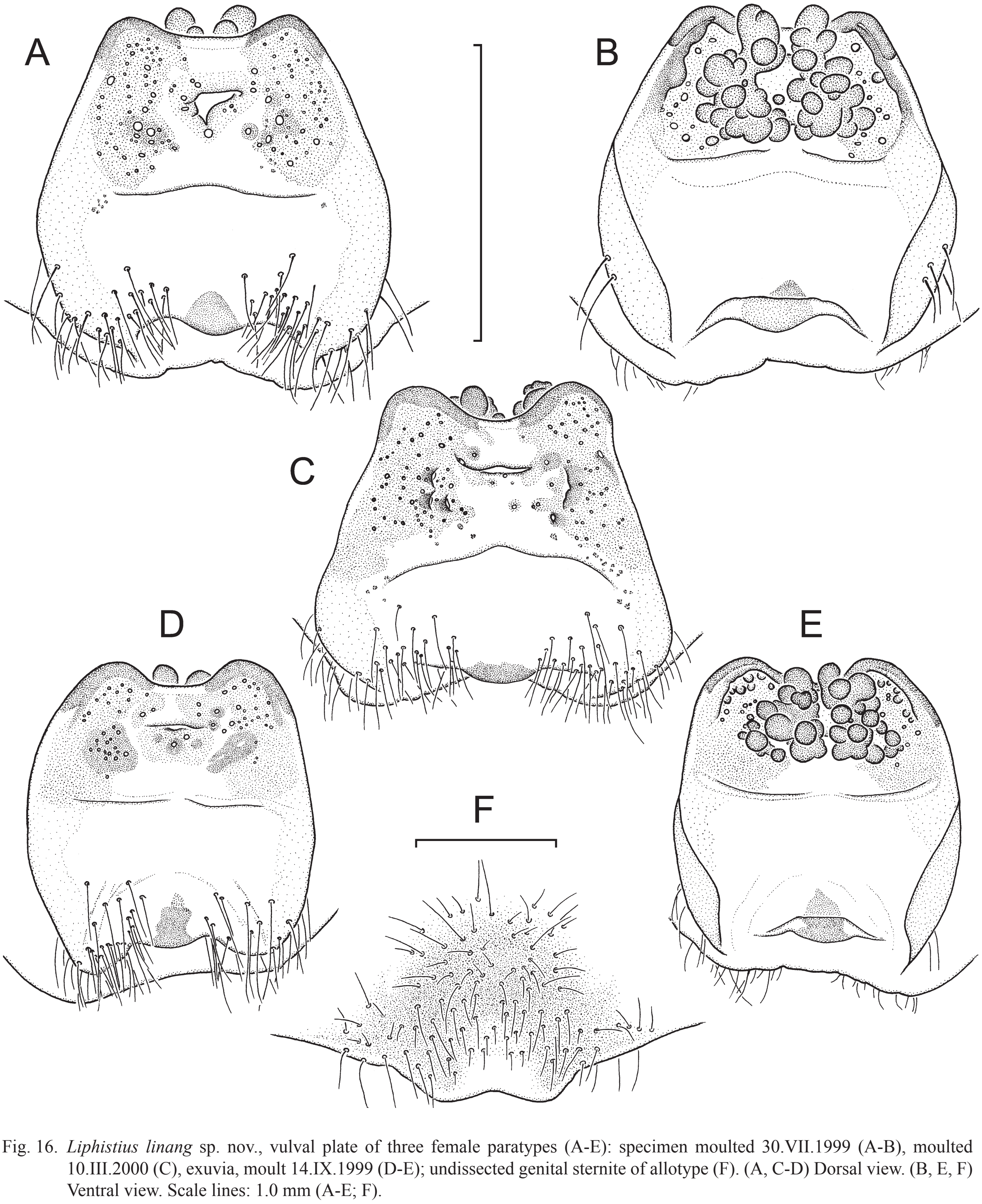

Fig. 16. *Liphistius linang* sp. nov., vulval plate of three female paratypes (A-E): specimen moulted 30.VII.1999 (A-B), moulted 10.III.2000 (C), exuvia, moult 14.IX.1999 (D-E); undissected genital sternite of allotype (F). (A, C-D) Dorsal view. (B, E, F) Ventral view. Scale lines: 1.0 mm (A-E; F).

respectively. All males lack a scopula on tarsus IV. Variation in the shape of the retrolateral tibial apophysis of the male palp is shown in Fig. 15G-I; variation in the shape of the prolateral-distal edge of the contrategulum in Fig. 15E-F; variation in the shape of the vulval plate in Fig. 16A-E.

Distribution: Known only from the type locality (Fig. 1, locality 13) in the northeastern corner of peninsular Malaysia. At the same locality, only metres away from burrows of *L. linang* sp. nov., a single female of another, much larger, dark-coloured *Liphistius* species was found. This female (mentioned under

Liphistius sp. at the end of the presentation of the *malayanus*-group) appears to be more closely related to *L. endau* than to the geographically closer *L. negara* sp. nov.

Biology: Spiders of this species were quite abundant in a lush rain forest along the stream above the Jeram Linang Waterfall. The burrows had a single trapdoor and mostly nine signal lines (up to 4 cm long) spread over soil surface. Trapdoors of penultimate males (n=5) were 1.2-2.0 cm long and 1.8-2.3 cm wide, those of reproductive females (with egg case; n=5) 1.2-1.7 cm and 1.8-2.3 cm, respectively.
Two males matured in mid-September and at the beginning of October of the year when they were collected. The three other males were raised from eggs (hatched in late May); one of them matured in November of the following year, the other two one year later in December. Less than one and a half years from hatching to maturation is exceptionally short for a *Liphistius* male, and this may be due to conditions in captivity in Geneva. Three females built egg cases in captivity between early February and early March, two of them were 1.7-1.9 in diameter, 1.25-1.3 cm high, and contained 40 and 84 light beige-yellow eggs suspended on a thin mesh of fine silk threads. The first generation females in captivity moulted in April, July and September.

Liphistius indra sp. nov.

Figs 2B, 17-18

Types: MHNG; male holotype (matured 27.IX.2011), 8 male (matured 24.VIII., 7.IX., 10.IX., 17.IX., 25.IX., 26.X.2011, 30.IX., 4.X.2012) and 13 female paratypes (including allotype which did not moult); Thailand, Pattani Province, about 20 km NW of Yala, Sankalakhierie Mountains, 6°39'09"N, 101°05'55"E, 200 m; 12.VII.2011; leg. P.J. Schwendinger. – MHNG, SMF; 1 male (matured 17.XI.2000) and 5 female paratypes; same locality, 260 m; 22.X.1999; leg. P.J. Schwendinger.

Etymology: The species epithet refers to one of the two old names of the type locality: Indragiri (= Indra's mountain) and Bukit Besar (= big mountain) (Skeat, 1953: 21). Indra ("Phra In" in Thai mythology) is the king of the Vedic gods. Name in apposition.

Diagnosis: Medium-sized, light brown-coloured species in both sexes. Very similar to *L. linang* sp. nov., distinguished by males with a ventral scopula on tarsus IV; long bristle retroventrally below tibial apophysis much stronger, resembling a megaspine (Fig. 17A, I-K cf. Fig. 15A, G-I); paracymbium distinctly shorter, more globular (Fig. 17A, I cf. Fig. 15A, G); distal edge of contrategulum without dentate gap, ending in a beak-like rather than a hook-like dorsal apex (Fig. 17B, G-H cf. Fig. 15B, E-F). Females distinguished from those of *L. linang* sp. nov. by anterior margin of poreplate less deeply and less widely invaginated; very weak pigmentation (in contrast to none) in anterior part of genital atrium (corresponding to reduced anterior part of posterior stalk); CDO semicircular or longitudinally slit-like instead of transversally slit-like, flanked by an enlarged pore on each side (Fig. 18A, C, E, G cf. Fig. 16A, C-D); receptacular cluster larger, not divided into two lateral subclusters, its individual vesicles (especially posterior ones) longer (Fig. 18B, D, F, H cf. Fig. 16B, E).

Description of male (holotype): *Colour in alcohol* (much darker in life; see Fig. 2B for paratype): Carapace with wide grey-brown margin (broken posteromedially) including most of pars cephalica and connected to flower-shaped patch of same colour around fovea; three very light brown areas between eye mound and fovea (anterior two small, kidney-shaped and in a pair, posterior one larger, inverted lanceolate) and light patches between darker central and marginal areas. Chelicerae with proximal portion cream-coloured, distal portion grey-brown. Palps in proximal half of femur and tibia and in distal half of patella light brown, mottled with dark spots, other parts grey-brown; cymbium entirely reddish brown. Legs mostly grey-brown except for light brown distal half of all patellae and light brown proximal half of all femora (mottled with dark spots); leg tibiae (in contrast to those of palp) to tarsi entirely dark brown. Membranous parts of opisthosoma light brown; tergite I almost entirely grey-brown, tergite II with extensive dark lateral and median patches, following tergites with distinct dark lateral spots and increasingly indistinct median ones, last two tergites tiny and mostly grey-brown.
Bristles on carapace: Few short, weak bristles along most of its margins (completely absent posteriorly and largely absent laterally), on coxal elevations and in front of fovea (not behind); longer, stronger bristles on, behind and in front of eye mound.
Cheliceral teeth: Eleven small ones on promargin of cheliceral groove of each chelicera.
Scopula: Tarsi I-III with moderately dense scopula in distal half of ventral side, only distally divided by a short median stripe; tarsus IV with weak scopula in distal quarter, medially divided for its entire length.
Claws: Paired tarsal claws with 3-4 denticles on anterior legs, 2-4 denticles on posterior legs; unpaired claws with 1-2 indistinct denticles on tarsi I-III, none on tarsus IV.
Palp: Tibial apophysis situated distally, only slightly set back from anterior margin of tibia (Fig. 17A), deeply divided: (a) long and deep retrolateral part pointing slightly away from axis of tibia, carrying three medium-long and bent megaspines; (b) short and small retrodorsal part carrying a single, slightly curved megaspine (Fig. 17I); long bristle retroventrally below tibial apophysis very strong, almost as thick as megaspines (Fig. 17A, I). Distal margin of cymbium with short lobes (Fig. 17B, showing paratype matured 4.X.2012). Paracymbium

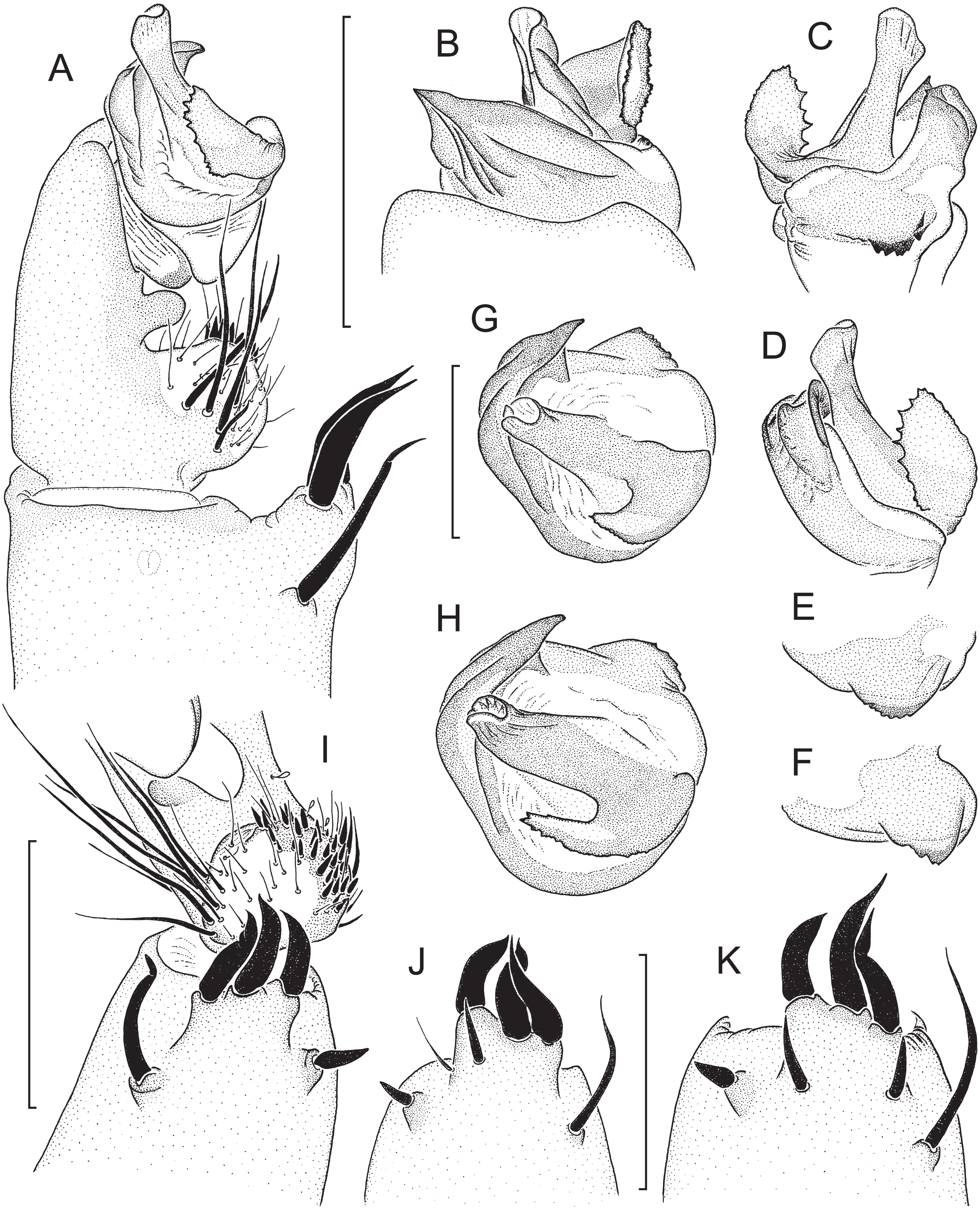

Fig. 17. *Liphistius indra* sp. nov., details of left (A-I) and right (J-K) palp of three males; holotype (A, C-D, G, I), paratype matured 4.X.2012 (B, F, H, K), paratype matured 24.VIII.2011 (E, J). (A) Distal part of palp, ventral view. (B) Distal part of cymbium and palpal organ, prolateral view. (C) Palpal organ, retrodorsal view. (D) Same, proventral and slightly proximal view. (E-F) Tegulum, retrodorsal view. (G-H) Palpal organ, distal view (dorsal side up). (I) Paracymbium and tibial apophysis, retrolateral view. (J-K) Tibial apophysis, retrolateral and slightly proximal view. Scale lines: 1.0 mm (A, I; B-F, H; J-K), 0.5 mm (G).

globular, quite short and shallow, without retrolateral heel (Fig. 17A, I); cumulus indistinct, carrying a group of long stiff bristles (Fig. 17A, I). Subtegulum without apophysis. Tegulum with moderately wide, strongly dentate proximal edge (Fig. 17C). Contrategulum without recognizable ventral process; prolateral surface with a few ribs; distal edge sharp throughout, with an indistinct, very short and wide invagination (not a gap) prodorsally (Fig. 17B, showing paratype matured 4.X.2012) before reaching very narrow, beak-shaped dorsal apex (Fig. 17G). Para-embolic plate large, its distal margin wide, strongly dentate (Fig. 17A, C, G); embolus proper slightly inclined prolaterad, relatively narrow (Fig. 17A, C-D), dorsal and ventral walls of sclerotised part equally wide and lying close to each other, retrolateral wall with few indistinct longitudinal ridges (Fig. 17G);

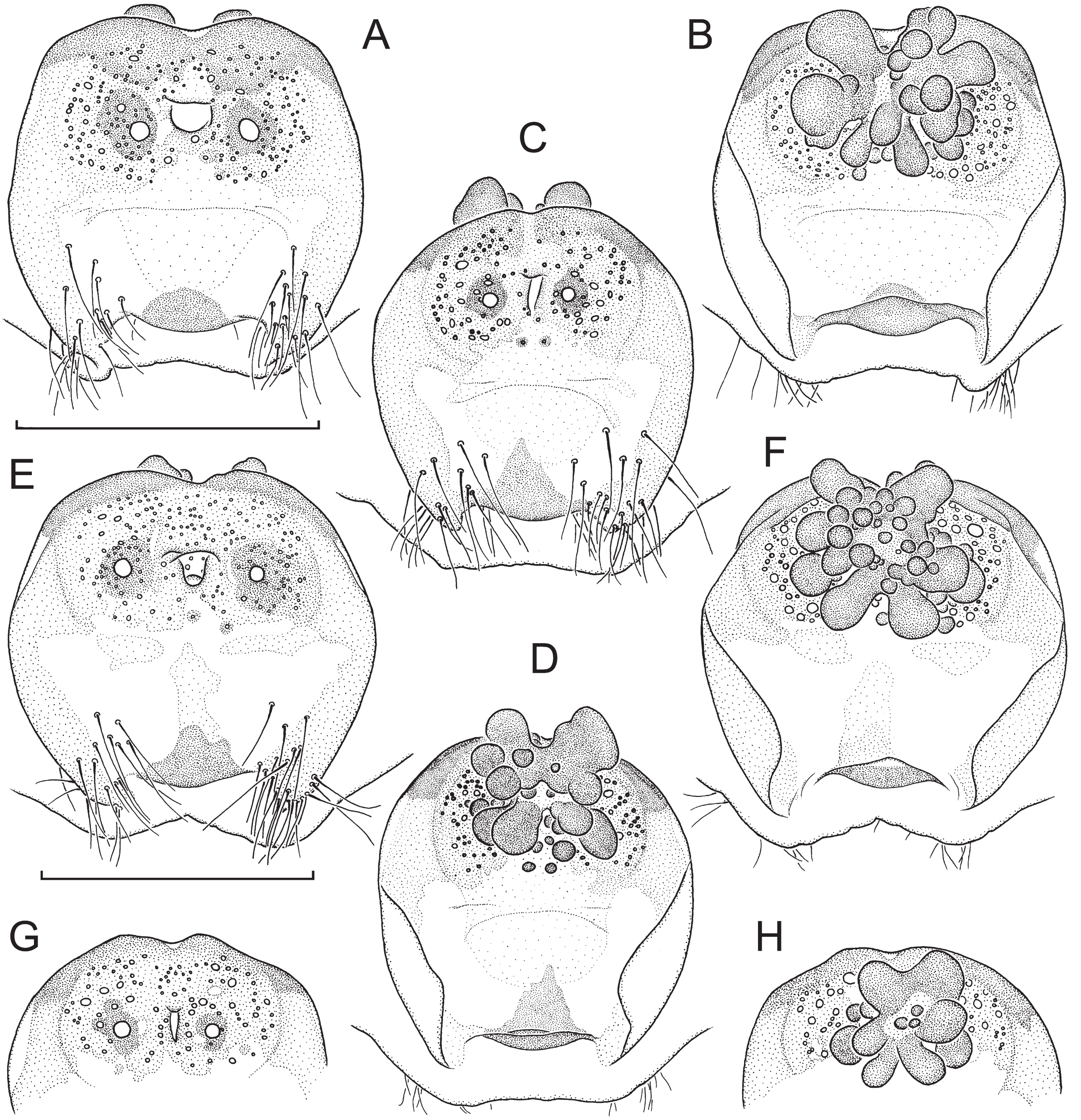

Fig. 18. *Liphistius indra* sp. nov., vulval plate of four female paratypes (all from exuviae): moult 15.III.2012 (A-B), moult 10.II.2001 (C-D), moult 15.VIII.2002 (E-F), moult 3.XI.2001 (G-H). (A, C, E) Entire structure, dorsal view. (B, D, F) Same, ventral view. (G) Anterior part of vulval plate, ventral view. (H) Receptacular cluster, ventral view. Scale lines: 1.0 mm (A-D, G-H; E-F).

membranous part of embolus proper narrow, indistinct (Fig. 17B, showing paratype matured 4.X.2012).

Measurements: Total length 11.57; carapace 5.08 long, 4.49 wide; opisthosoma 4.25 long, 2.91 wide; eye mound 0.80 long, 0.97 wide; palpal coxae 1.61 long, 1.10 wide; labium 0.43 long, 0.98 wide; sternum 2.24 long, 1.57 wide (0.87 on ventral surface); palp 9.10 long (2.72 + 1.65 + 3.31 + 1.42); leg I 15.36 long (4.13 + 1.97 + 3.31 + 3.98 + 1.97); leg II 15.83 long (4.17 + 2.01 + 3.31 + 4.33 + 2.01); leg III 17.32 long (4.41+ 2.05 + 3.46 + 5.04 + 2.36); leg IV 22.91 long (5.67 + 2.20 + 4.88 + 7.01 + 3.15).

Description of female (allotype): *Colour in alcohol* (much darker in life): Generally darker reddish-brown than male; light areas on carapace mottled with dark brown spots, flower-shaped area around fovea less clearly outlined; tarsi and metatarsi of legs and palps mostly dark, with a small light zone at base of palpal tarsi and leg metatarsi; all tibiae with dark proximal and subdistal annulations; femora with indistinct (in comparison to tibiae) and broken proximal and subdistal annulations; opisthosomal tergites II-V with larger dark median patches; genital area darker than surrounding parts of genital sternite, with a light posterior margin.

Bristles on carapace: As in male, plus several tiny bristles behind fovea.

Cheliceral teeth: Eleven mostly strong cheliceral teeth on promargin of left cheliceral groove, nine on right.

Claws: Palpal claws with two denticles. Paired claws with 2-3 denticles on anterior legs, 2-4 denticles on posterior legs; unpaired claws with two denticles on tarsi I-III, none on tarsus IV. All tarsi without scopula.

Vulva: Posterior margin of genital sternite slightly and widely invaginated. Vulval plate (Fig. 18, illustrations of paratypes) with pigmentation much reduced but still discernible in median zone. Posterior stalk reduced to a very weakly pigmented, wide to narrow anterior part and a small, strongly pigmented, ventrad-bent posterior sclerite at some distance from posterior margin of genital sternite. Genital atrium with numerous hairs on both sides of remnant of posterior stalk. Lateral and posterior margins of poreplate indistinctly outlined, not bulging from ventral side; anterior margin only slightly invaginated at midpoint, not forming anterolateral lobes. CDO relatively small, longitudinally slit-like or semicircular, lying in weakly pigmented area of poreplate (Fig. 18A, C, E, G, showing paratypes). Ventral receptacular cluster quite large and racemose, not divided into two lateral subclusters, its individual vesicles mostly digitiform, longer than wide (Fig. 18B, D, F, H, showing paratypes).

Measurements: Total length 19.45; carapace 6.61 long, 5.67 wide; opisthosoma 8.27 long, 6.69 wide; eye mound 0.95 long, 1.01 wide; palpal coxae 2.20 long, 1.54 wide; labium 0.75 long, 1.73 wide; sternum 3.15 long, 2.20 wide (1.26 on ventral surface); palp 11.61 long (3.78 + 2.20 + 2.83 + 2.80); leg I 14.25 long (4.49 + 2.48 + 2.95 + 2.87 + 1.46); leg II 14.68 long (4.49 + 2.56 + 2.95 + 3.11 + 1.57); leg III 15.43 long (4.57 + 2.56 + 2.99 + 3.58 + 1.73); leg IV 22.44 long (6.30 + 2.91 + 4.57 + 6.14 + 2.52).

Variation: Carapace lengths in males (n=10) 4.50-6.83, carapace widths 3.98-6.21; in females with well-developed vulval plates (n=18) 5.55-7.24 and 4.80-6.30, respectively. All ten males possess a weak ventral scopula on tarsus IV; it is medially divided in three of them (including the holotype), undivided in the others. Three males have more or less distinct remnants of "tibial spurs" (*sensu* Platnick & Goloboff, 1985) on legs I-III. A male lacks one of its AME; in all other specimens examined both AME are well-developed. Variation in details of the male palp, see Fig. 17G-H, I-K; variation in the morphology of the vulval plate, see Fig. 18. One of the larger females examined has a small knob-like sclerite in the membranous dorsal wall of its vulva which fits into the CDO of the ventral wall (= vulval plate). Such a structure was also observed in some (but only few) vulvae of large females of other species. This is an unlikely (because inefficient) plugging device and more probably a by-product of increased sclerotisation of the vulval plate in old females.

Distribution: Known only from the type locality (Fig. 1, locality 14) in the deep south of Thailand. This area lies in the former Sultanate of Pattani which was an independent Malay kingdom until 1785, then became a tributary of the kingdom of Siam, and in 1909 formally a Siamese province. A second species, *Liphistius* cf. *thaleban* Schwendinger, 1990, occurs at the same locality. That species is much larger, has orange-coloured femora in larger juveniles and adult females, and belongs to the *trang*-group.

Biology: The spiders examined were collected in an evergreen rain forest, close to a stream. Their burrows had a single trapdoor, usually opening downwards, and 8-10 (mostly nine) relatively short signal lines (up to 4 cm long) spread over soil surface. Trapdoors of penultimate males (n=8) were 1.25-1.8 cm long and 1.65-2.3 cm wide, those of females (n=17) up to 2.1 cm long and 3.0 cm wide.

Males matured in captivity between August and November, most (six out of ten) in September. Adult females in captivity usually moulted twice per year, in January to April and in June to November. As all females were collected in July and October (outside the breeding season), no egg cases were observed.

Upon being provoked, one mature male and one large female displayed "tiptoing" but without the pumping movements (raising and lowering the body above the surface) usually observed in large *Liphistius* spiders.

Two females carried mites of the genus *Ljunghia* (see Halliday & Juvara-Bals, 2016: 857) which left clearly visible dark bite marks on the carapace and on the light proximal portion of the chelicerae, but not on other parts of the body. The mites were seen to aggregate in the fovea, around the sternum, under the spinnerets and on the ventral side of the leg femora of the spiders. One mite was seen inserting its gnathosoma into one of the bite marks on the carapace, obviously taking in food.

Two immature males (with swollen palpal tarsi and thus possibly penultimate; not paratypes) had a swollen, light-coloured (like porcelain) opisthosoma when collected and died soon afterwards. This indicates an infection with Rickettsiales (see Haupt, 2003: 66-67, fig. 41D). Haupt (2003: 67, figs 24A, 25A) reported rickettsia-like microorganisms in the spermophore of the mesothelid *Ryuthela nishihirai* (Haupt, 1979) and assumed that infection can occur through copulation. This was certainly not the case in the two immature males of *L. indra* sp. nov.

At the type locality, *L. indra* sp. nov. occurs together with *Liphistius* cf. *thaleban*. Burrows of both species were found side by side.

The *batuensis*-group

Diagnosis: Small to medium-sized spiders (carapace length of males 4.42-6.46, carapace width 4.02-5.87). Distinguished from species of other groups by males with a strongly reduced proximal edge on the tegulum (Figs 19H, 21B, 23I) and with an elongated prodorsal-apical lobe on the cymbium (Figs 19C, 21H, 23J). Females similar to those of the *linang*-group in possessing a vulval plate with reduced pigmentation and sclerotisation, distinguished by a relatively wider vulval plate with the poreplate only partially connected to the large and wide posterior stalk or separated by a short distance (Figs 20, 22, 24).

Species included: *Liphistius batuensis*, *L. tempurung* and *L. priceae* sp. nov.

Relationships: The reduced pigmentation and sclerotisation of the vulval plate and the reduced posterior edge of the tegulum point to a close relationship with the *linang*-group, but a loss or reduction is only a weak indication for common ancestry. At present the relationships of the *batuensis*-group with other groups are unclear, but there is strong morphological evidence for close relationship among the species of the *batuensis*-group. Moreover, all three species have a strong association with caves (much more so than in species of the *tioman*-group).

Distribution: Western and central part of peninsular Malaysia (Fig. 1, localities 15-18). All species are known exclusively from limestone caves.

Liphistius batuensis Abraham, 1923
Figs 19-20

Liphistius batuensis Abraham, 1923a: 15-21, pl. 1, figs 1-9 (description of male and female). Synonymy and taxonomic literature, see World Spider Catalog (2017).

Types: BMNH; male lectotype (designated by Haupt, 1983: 282) and 11 female plus 4 juvenile paralectotypes (all not examined); Malaysia, Selangor, Batu Caves; XII.1921-I.1922; leg. H.C. Abraham.

Material examined: MHNG; 1 male; Selangor, Kuala Lumpur, Batu Caves; 24.VII.1969; leg. R. Pilet. – MHNG; 2 females; Batu Caves, près de Kuala Lumpur;

Key to the species of the *batuensis*-group:

1 Tibial apophysis of male palp carrying long megaspines (Fig. 19A); distal edge of contrategulum with quite long parallel ridges pointing towards dorsal apex (Fig. 19D-E, I); para-embolic plate medium-long (19E-I); dorsal wall of sclerotised part of embolus proper wider than ventral wall, its end sharply bent proventrad (Fig. 19D-F, I). Poreplate with very wide CDO (Fig. 20A, C-D, F-G) .... *L. batuensis*

\- Tibial apophysis with medium-long or short megaspines (Figs 21E-G; 23B, K-O); para-embolic plate short (Figs 21A-B; 23A, H-I); distal edge of contrategulum with quite short parallel ridges pointing towards embolus (Fig. 21C, I-L; 23D-E, H); dorsal wall of sclerotised part of embolus proper as wide as ventral wall, not bent ventrad (Figs 21I-L, 23D-E). Poreplate with rounded and moderately wide, or slit-like or drop-like CDO (Figs 22A, C, E, G, K, I; 24A, C, E-F) 2

2 Scopula covering only one-third of ventral side of male tarsus IV. Tibial apophysis short and basally wide in ventral view (Fig. 21E), carrying medium-long megaspines (Fig. 21E-G); paracymbium quite small (Fig. 21A, D); dorsal apex of contrategulum wide, tounge-shaped (Fig. 21I-L). Poreplate of vulva with distinctly invaginated anterior margin (Fig. 22A-I); CDO slit-like or drop-like, sitting in a posteriorly indistinctly outlined hollow (Fig. 22A, C, E, G, I) .... *L. tempurung*

\- Scopula covering two-thirds of ventral side of male tarsus IV. Tibial apophysis quite long and basally narrow in ventral view (Fig. 23B), carrying short megaspines (Fig. 23B, K-O); paracymbium quite large (Fig. 23A-B); dorsal apex of contrategulum narrow, spatulate (Fig. 23D-G). Poreplate with indistinctly or not invaginated anterior margin (Fig. 24A, C-F); CDO round or angular, distinctly outlined on all sides (Fig. 24A, C, E-F) .... *L. priceae* sp. nov.

XI.1976 ; leg. B. Koepchen. – MHNG, sample SIM-01/13; 2 males (matured 18.X.2001, 8.II.2002), 2 females (moulted 13.I.2002; 24.I.2002), exuviae of 3rd female (spider not collected); Selangor, Batu Caves, Dark Cave, Caverns B, C, D (3°14'12.7"N, 101°41'00.0"E), 100 m; 12.VII.2001; leg. P.J. Schwendinger. – SMF-13907, n° 3; 2 females, 1 juv. male; Selangor, Batu Caves; leg. Clark, det. Roewer, 1962 (identified as 3 females). – SMF-13908, n° 4; macerated remains of 2 specimens (one a juvenile male, the other without opisthosoma); Selangor, Batu Caves; leg. Clark, det. Roewer, 1962. – SMF-21945/1; 1 female; no locality data; 19.XI.1933; det. W. S. Bristowe.

Diagnosis: Medium-sized, light brown-coloured species in both sexes. Males characterized by cumulus carrying a group of very long, thick bristles (Fig. 19A-B); tegulum with exceptionally small and narrow proximal edge carrying few denticles (Fig. 19H); distal edge of contrategulum with 2-4 quite long parallel ridges pointing towards dorsal apex, without denticles (Fig. 19D-E, I); para-embolic plate distinctly elevated (Fig. 19E-I), with sharp proventral angle at base (Fig. 19D-E, G; see arrows); apex of embolus proper wide in prolateral and retrolateral view (Fig. 19E-F, H), its dorsal wall much wider than its ventral wall, end of dorsal wall sharply bent proventrad (Fig. 19D-F, I). Females characterized by poreplate largely unpigmented in its posterior portion, more or less distinctly separated from short, wide posterior stalk; posterior portion of genital atrium not markedly bent ventrad; no anterolateral lobes on poreplate; CDO very wide, its anterior margin sunken and clearly outlined, its posterior margin at level of poreplate and not clearly outlined; genital atrium in most cases without hairs, its lateral folds weakly developed (Fig. 20).

Additions to description of male: *Scopula*: Tarsus I with thin scopula in distal half of ventral side, divided for its entire length by a narrow pale, glabrous longitudinal median stripe and by some bristles; tarsus II likewise, scopula only distally divided; tarsus III with thin scopula in distal three-fifths, only distally divided; tarsus IV with thin scopula (narrower than on other tarsi) in distal half, only distally divided.

Palp: Tibial apophysis basally wide in ventral view, moderately long, slightly set back from distal margin of tibia (Fig. 19A), its apical megaspines relatively long and thin (but not as thin as illustrated in Murphy & Platnick, 1981: figs 9, 12, 15, 21 and in Platnick & Sedgwick, 1984: figs 70-72, 74), dorsal ones longer than ventral ones. Prodorsal-apical lobe of cymbium distinctly longer and more pointed than proventral-apical one (Fig. 19C). Paracymbium of average size and depth (Fig. 19A-B), carrying very long (longest ones reaching base of embolus complex), thick bristles in a loose group on non-elevated cumulus (Fig. 19A). Subtegulum without apophysis. Tegulum with very small proximal edge carrying only few denticles (Fig. 19H). Pigmented bridge between tegulum and contrategulum on retrolateral side of palpal organ disconnected (Fig. 19H). Contrategulum with indistinct, short and wide ventral process; distal edge with 2-4 parallel ridges pointing towards tongue-shaped dorsal apex (Fig. 19D-E, I). Para-embolic plate distinctly elevated (Fig. 19E-I), with sharp proventral angle at its base (Fig. 19D-G, see arrows). Embolus proper with wide apex (Fig. 19E-F, H); dorsal wall of sclerotised part much wider than ventral wall, end of former sharply bent ventrad and partly overlapping membranous part of embolus proper (Fig. 19D-F, I); sclerotised part of embolus proper retrolaterally with a single longitudinal distal keel (Fig. 19D-F, G); membranous part of embolus proper unpigmented throughout.

Additions to description of female: Posterior margin of genital sternite straight or indistinctly invaginated (Fig. 20). Vulval plate (Fig. 20) short, wide; posterior portion and lateral margins of poreplate largely unpigmented, more or less distinctly separated from short, wide, well-pigmented posterior stalk; posterior part of genital atrium only slightly and gradually curved ventrad; anterior margin of poreplate slightly and widely invaginated, without anterolateral lobes; CDO very wide, its anterior margin sunken and clearly outlined, its posterior margin level with poreplate and not clearly outlined (Fig. 20A, C-D, F-G); receptacular cluster very large, strongly protruding anteroventrad, reaching beyond anterior margin of poreplate; genital atrium without lateral hairs and in most cases without median hairs, its lateral folds indistinctly developed (Fig. 20B, E, H).

Remarks: The apical megaspines on the tibial apophysis of the male palp are not as thin as illustrated by Platnick and Sedgwick, and the one situated most dorsally is not as long as shown by these authors (Platnick & Sedgwick, 1984: figs 70-72, 74).

It is not clear what Platnick & Sedgwick (1984: 25) mean with their diagnostic character "short, erect tegular apophysis".

Variation: Carapace lengths in males (n=3) 5.24-5.99, in females with fully developed vulval plate (n=7) 4.76-6.67; carapace widths 4.60-5.56 and 4.09-5.56, respectively. The scopula on tarsus I is divided for its entire length in two males, only distally so in the third; the scopula on tarsus IV extends over the distal half in two males, over the distal three-fifths in the third. One mature male retains a proventral "tibial spur" (*sensu* Platnick & Goloboff, 1985) on its right leg I. Variation in the shape of the vulval plate of females examined is shown in Fig. 20 (see also Murphy & Platnick, 1981: figs 26-27 and Platnick & Sedgwick, 1984: figs 75-76). One female has a single median hair in its genital atrium (Fig. 20D); in all other females examined the genital atrium is completely devoid of hairs (Fig. 20A-C, E-H). Most specimens examined have fully developed anterior median eyes; only one small female has a reduced (but cornea present) AME on one side.

Distribution: First reported from the Batu Caves by Ridley (1899: 580), this specis is only known from the Dark Cave and the Rift Cave which are part of the Batu Cave system (Lim & Yussof, 2009: 127-128; Fig. 1, locality 15) north of Kuala Lumpur, and from the

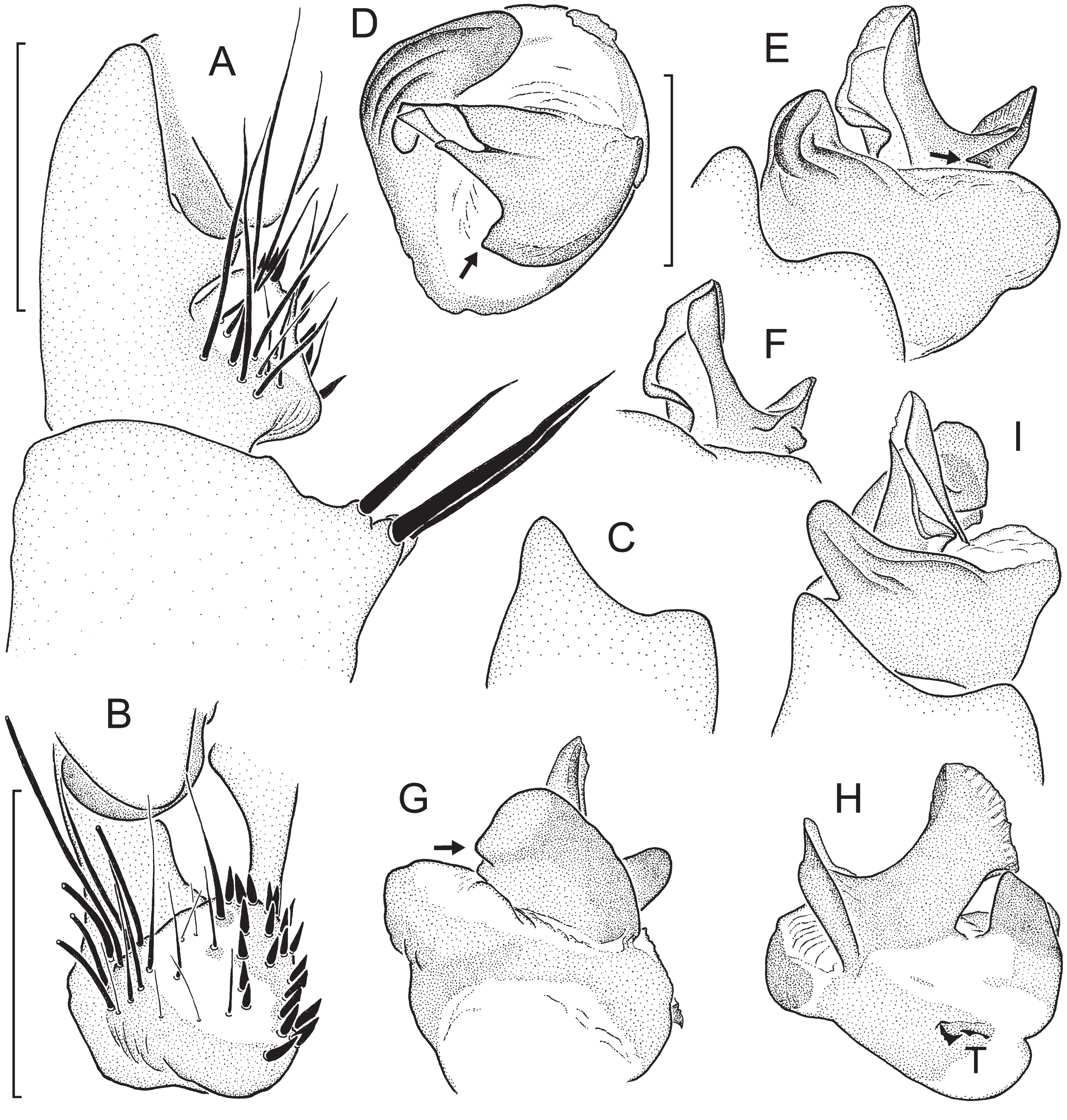

Fig. 19. *Liphistius batuensis*, details of left palp of two males from type locality: specimen collected 24.VII.1969 (A-B, F, I), specimen matured 8.II.2002 (C-E, G-H). (A) Distal part of palp (palpal organ not indicated), ventral view. (B) Paracymbium, retrolateral view. (C) Distal part of cymbium, prolateral view. (D) Palpal organ, distal view (dorsal side up; arrow indicating proventral angle at base of para-embolic plate). (E) Palpal organ, proventral view (arrow indicating same structure as in D). (F) Embolus complex, proventral view. (G) Palpal organ, retroventral and slightly proximal view (arrow indicating same structure as in D-E). (H) Same, retrodorsal view. (I) Same, prolateral view. Abbreviation: T - tegulum. Scale lines: 1.0 mm (A, C; B) and 0.5 mm (D-I).

Anak Takun Cave in the Templer Park which lies about 9 km further north (Fig. 1, locality 2). The latter record is based only on females and juveniles (Platnick & Sedgwick, 1984: 26). The Gua Anak Takun population was reported to contain hundreds of burrows in 1961 (McClure *et al*., 1967), only one in 1986 (Yussof, 1987), three in 2006 (Lim & Yussof, 2009). Steiner (1998: 148) reported that the Gua Anak Takun population had probably become extinct, which fortunately proved to be incorrect. Neverthess the future of this population, which no longer receives legal protection, is bleak (Lim & Yussof, 2009: 131). Fortunately the Batu Cave populations are doing much better (Lim & Yussof, 2009: 125-126).

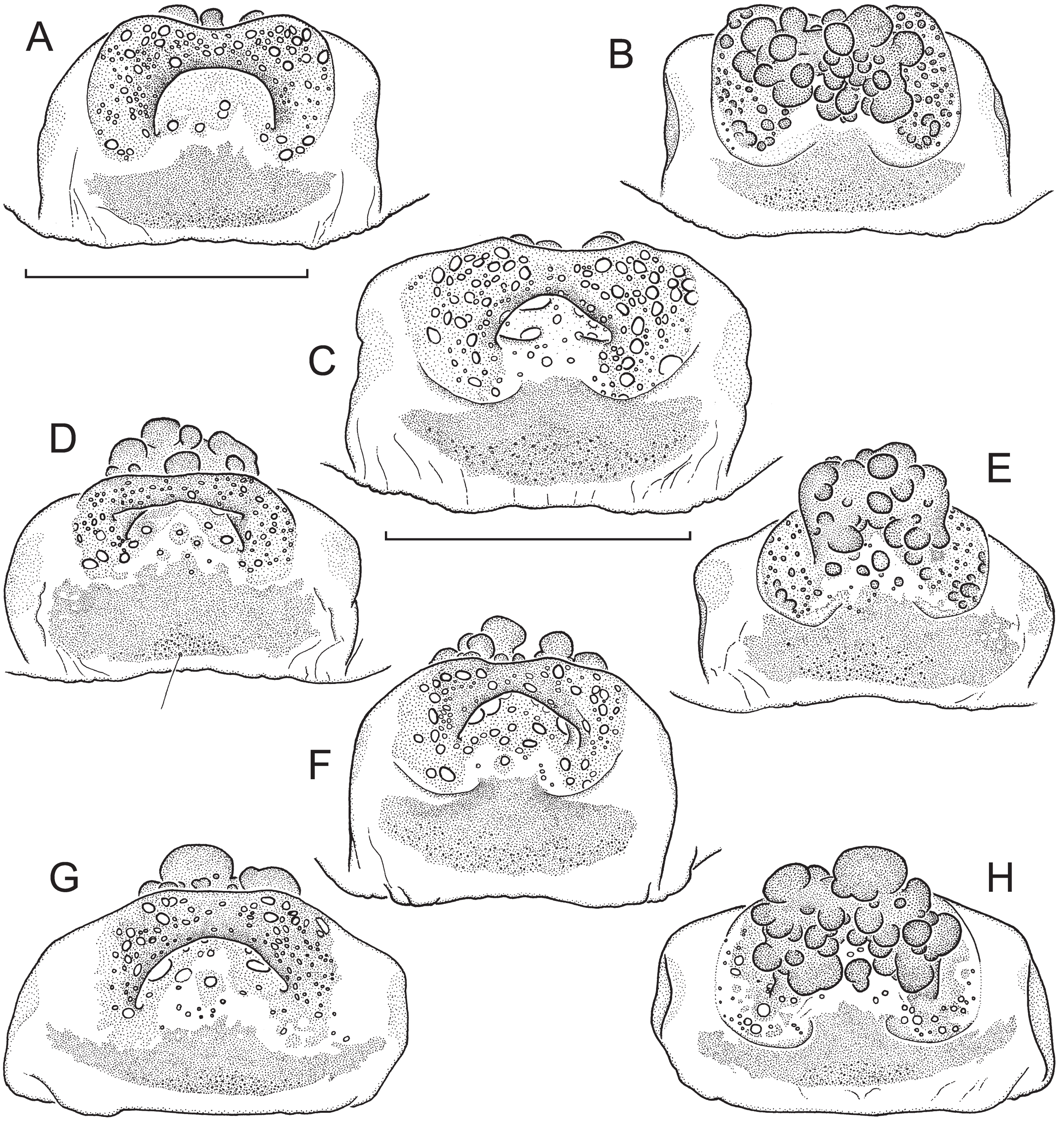

Fig. 20. *Liphistius batuensis*, vulval plate of five females from the type locality: exuvia, moult 24.I.2002 (A-B); specimen SMF 13907 (C); exuvia, moult 12.VII.2001 (D-E); specimen leg. XI.1976 (F); exuvia, moult 13.I.2002 (G-H). (A, C-D, F-G) Dorsal view. (B, E, H) Ventral view. Scale lines: 1.0 mm (A-B, D-E, G-H; C, F).

Biology: I collected spiders of this species only from sac-like nests on cave walls in the aphotic zone of the Batu Caves. No burrows were seen in the soil. The largest nest inspected (of a female) was 6 cm long and had a 1.9 cm long and 3.0 cm wide front door, as well as a 1.2 cm long and 1.9 wide back door. Penultimate males in captivity built nests with 1.6-1.8 cm long and 2.4 cm wide trapdoors. An egg sac of 1.8 cm diameter and 0.9 cm depth was found in the cave; it contained no eggs. One mature male was collected (by R. Pilet) in the cave in late July; two males matured in captivity (three and six and a half months after capture) in late October and early February. The mating period of *L. batuensis* appears to be relatively long, as it is the case in other congeneric species in peninsular Malaysia. Despite the fact that all specimens examined were found in the dark portions of caves, no troglobiomorphic adaptations are visible apart from a relatively light body colouration in living spiders.

An excellent and very detailed account of the biology of *L. batuensis* was given by Klingel (1967). Similar but shorter presentations of this species and its habitat appeared in Abraham (1923a), Bristowe (1933, 1952) and McClure *et al*. (1967). Lim & Yussof (2009) gave a detailed account of the state of the three known populations of this species.

Liphistius tempurung Platnick, 1997

Figs 21-22

Liphistius tempurung Platnick in Platnick, Schwendinger & Steiner, 1997: 4-6, figs 10-11 (description of female).

Type: AMNH; female holotype (not examined); Malaysia, Perak, Gua Tempurung; 18.V.1996; leg. H. Steiner.

Material examined: MHNG, sample MAL-04/17; 3 males (matured 25.IX., 26.IX.2004, 13.XI.2005), 6 females (moulted 21.X.2004; 9.XII.2004; 19.XI.2004 and 3.IV.2005; 30.XII.2004 and 17.X.2005 and 24.V.2006 and 22.I.2007; IX.2004 and 13.IX.2005 and 8.II.2006; 8.X.2004 and 1.III.2005); Perak, 25 km south of Ipoh, Gua Tempurung, 4°24’58”N, 101°11’15”E, 90 m (limestone cave, dark zone); 22.VI.2004; leg. P.J. Schwendinger. – MHNG, sample 200/01; 1 juvenile; Perak, Gunung Lanno, Gua Cicak, 80 m; 16.XI.2001; leg. H. Steiner. – MHNG, sample MAL-04/16; 3 males (matured 31.XII.2004, 23.I.2005, 17.VI.2005), 3 females (moulted 8.I.2005; 17.I.2005); Perak, Gunung Lanno, Gua Cicak; 21.VI.2004; leg. P.J. Schwendinger.

Diagnosis: Medium-sized, light brown-coloured species in both sexes. Similar to *L. batuensis,* males distinguished by much shorter and stouter megaspines on tibial apophysis of palp (Fig. 21E-G cf. Fig. 19A); proximal edge of tegulum without denticles (Fig. 21B cf. Fig. 19H); retrolateral bridge between tegulum and contrategulum unbroken (Fig. 21B cf. Fig. 19H); contrategulum with more pronounced, rather conical ventral process; distal edge with several short parallel ridges situated near base of ventral process and directed towards embolus; dorsal apex of contrategulum wider, without ridges (Fig. 21I-L cf. Fig. 19D); embolus proper more slender (Fig. 21A-B cf. Fig. 19E, H), dorsal wall of its sclerotised part without sharply bent end overlapping membranous part (Fig. 21C, I-L cf. Fig. 19D-F, I); base of embolus complex without sharp proventral angle (Fig. 21I-L cf. Fig. 19D-E, G), para-embolic plate less elevated (Fig. 21B cf. Fig. 19H). Females distinguished from those of *L. batuensis* by anterior and posterior margins of vulval plate distinctly invaginated (Fig. 22 cf. Fig. 20); posterior part of genital atrium more strongly curved ventrad, clearly visible on female specimen when viewed from posteroventrally (Fig. 22M-N); poreplate with much smaller CDO (Fig. 22A, C, E, G, I, K cf. Fig. 20A, C-D, F-G).

Description of male (matured 26.IX.2004): *Colour in alcohol* (slightly darker in life): Sclerotised parts light brown, except for cream-coloured proximal portion of chelicerae, whitish membranes of prosoma and cream-coloured membranes of opisthosoma.

Bristles on carapace: Short bristles along all margins (longest and strongest in front of eye mound); few on coxal elevations; four short bristles anterior to fovea; thick (spinelike) bristles on eye mound.

Scopula: Thin (weakest and narrowest on tarsus IV) and only distally divided by median stripe on all leg tarsi; covering distal half of ventral side of tarsi I-III, only distal one-third of tarsus IV.

Cheliceral teeth: Eleven small teeth of different sizes on promargin of right cheliceral groove, twelve on left cheliceral groove.

Palp (illustrations mostly of male matured 13.XI.2005): Tibial apophysis basally quite wide in ventral view, distinctly set back from distal margin of tibia (Fig. 21E), carrying four medium-long apical megaspines, the second from ventral situated clearly lower (more proximal) than others (Fig. 21E-F). Apical lobes of cymbium distinct, prodorsal one longer and narrower than proventral one (Fig. 21H). Paracymbium of average length but quite shallow (Fig. 21A, D), carrying long thick bristles in a widely spaced group on non-elevated cumulus (Fig. 21A, D). Subtegulum without apophysis. Tegulum with proximal edge indistinct and completely without denticles, distinguished from rest of tegulum only by a stronger pigmentation (Fig. 21B). Pigmented bridge between tegulum and contrategulum on retrolateral side of palpal organ unbroken (Fig. 21B). Contrategulum with distinct, somewhat conical (in distal view) ventral process, with several parallel ridges directed towards embolus and situated near base of ventral process; dorsal apex of contrategulum large and widely tounge-

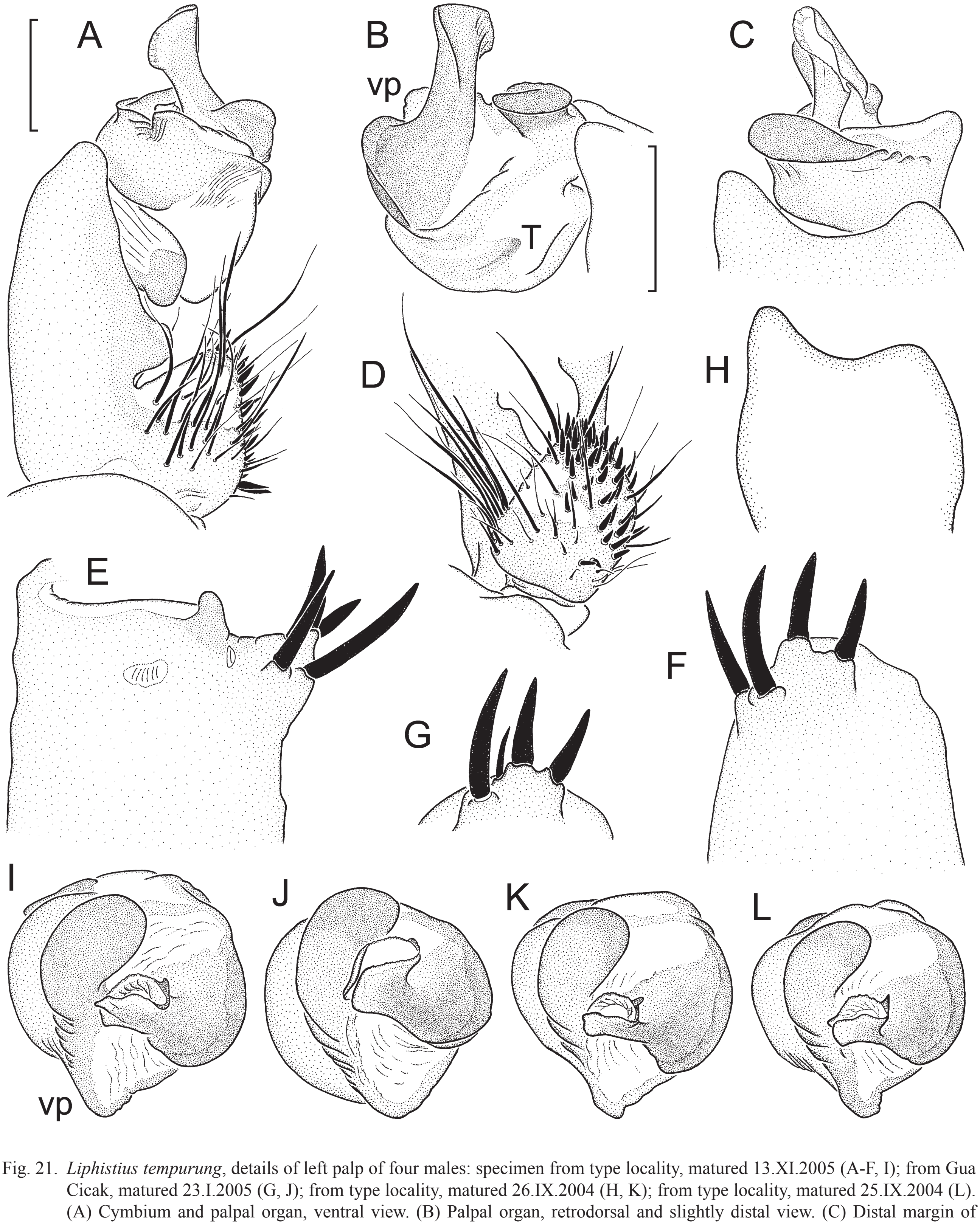

Fig. 21. *Liphistius tempurung*, details of left palp of four males: specimen from type locality, matured 13.XI.2005 (A-F, I); from Gua Cicak, matured 23.I.2005 (G, J); from type locality, matured 26.IX.2004 (H, K); from type locality, matured 25.IX.2004 (L). (A) Cymbium and palpal organ, ventral view. (B) Palpal organ, retrodorsal and slightly distal view. (C) Distal margin of cymbium and palpal organ, prolateral view. (D) Paracymbium, retrolateral view. (E) Distal part of palpal tibia, ventral view. (F) Tibial apophysis, retrodorsal and slightly proximal view. (G) Same, retrolateral and slightly proximal view. (H) Distal part of cymbium, prolateral view. (I-L) Palpal organ, distal view (dorsal side up). Abbreviations: T - tegulum; vp - ventral process of contrategulum. Scale lines: 0.5 mm (A, D-G; B-C, H-L).

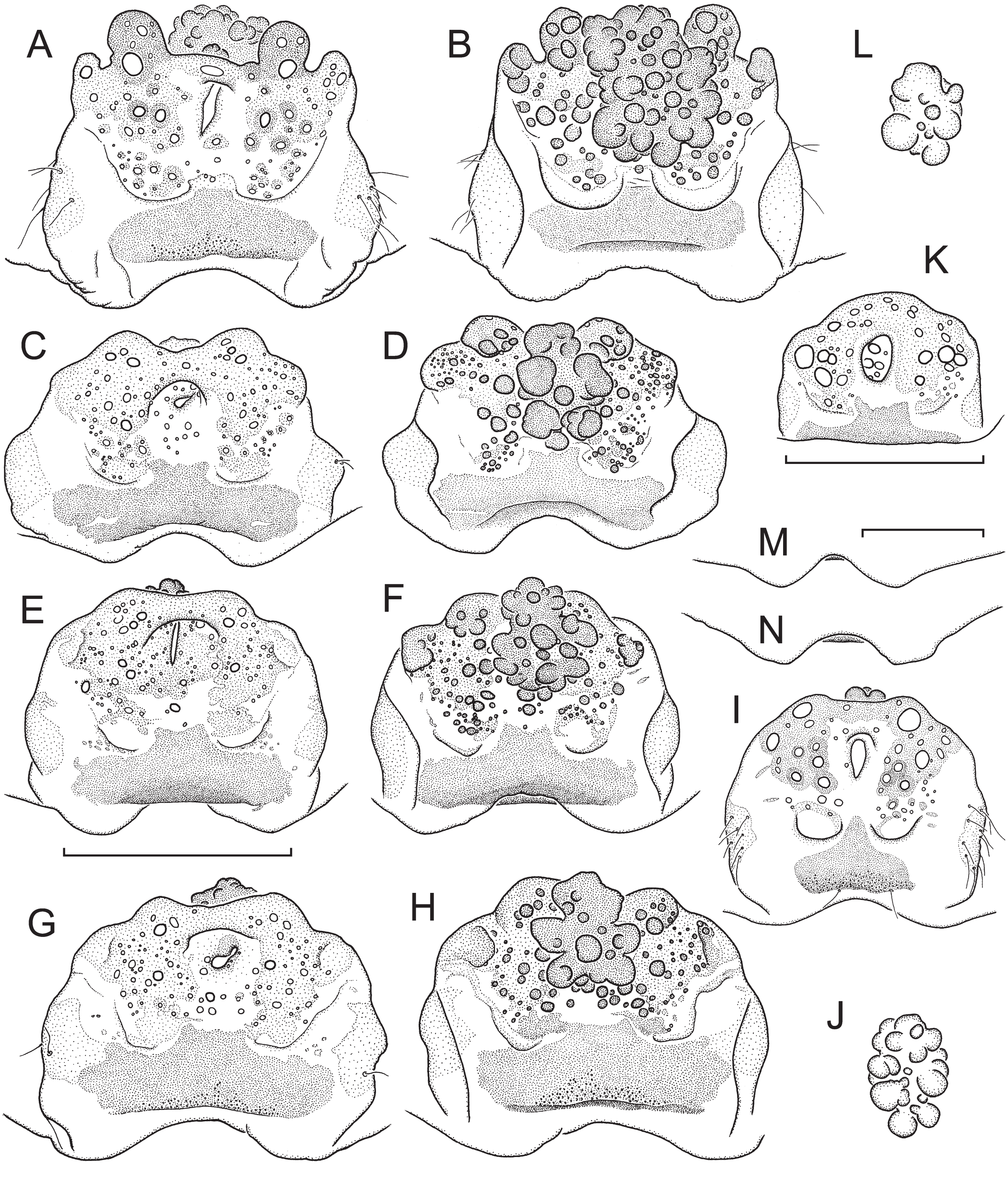

Fig. 22. *Liphistius tempurung*, details of copulatory organ and genital sternite of six females: Gua Cicak, specimen moulted 8.I.2005 (A-B, N); Gua Tempurung, exuvia, moult 22.I.2007 (C-D, M); Gua Tempurung, exuvia, moult 9.XII.2004 (E-F); Gua Tempurung, exuvia, moult 21.X.2004 (G-H); medium-sized female from Gua Cicak (I-J); small female from Gua Tempurung (K-L). (A, C, E, G, I, K) Vulval plate, dorsal view. (B, D, F, H) Same, ventral view. (J, L) Receptacular cluster, ventral view. (M-N) Posterior margin of genital sternite, ventral view. Scale lines: 1.0 mm (A-D, I-L; E-H; M-N).

shaped (Fig. 21I). Para-embolic plate short (Fig. 21B); no sharp proventral angle on and no sharp edge below para-embolic plate. Embolus proper with moderately wide apex (Fig. 21A-B); dorsal and ventral walls of sclerotised part equally wide, without modification (Fig. 21I), retrolateral wall carrying a distinct distal keel (Fig. 21B); membranous part of embolus proper narrow, unpigmented throughout (Fig. 21C).

Measurements: Total length 14.55; carapace 5.69 long, 5.25 wide; opisthosoma 6.04 long, 5.15 wide; eye mound 0.67 long, 0.83 wide; palpal coxae 1.68 long, 1.19 wide; labium 0.45 long, 0.99 wide; sternum 2.52 long, 1.68 wide (on ventral surface 0.79); palp 9.80 long (2.97 + 1.73 + 3.47 + 1.63); leg I 16.78 long (4.85 + 2.13 + 3.61 +4.16 + 2.03); leg II 18.07 long (4.95 + 2.13 + 3.96 + 4.65 + 2.38); leg III 19.65 long (5.00 + 2.13 + 4.21 + 5.64 + 2.67); leg IV 25.45 long (6.04 + 2.38 + 5.25 + 8.12 + 3.66).

Additions to description of female: Posterior margin of genital sternite widely W-shaped (Fig. 22A-I), in slightly posteroventral view posterior edge of posterior stalk of vulval plate clearly visible between paramedian lobes (Fig. 22M-N). Vulval plate (Fig. 22A-I, K) moderately wide; large parts of poreplate unpigmented, particularly central area around CDO; CDO indistinct, composed of a small drop-shaped or longitudinally slit-shaped opening lying within a larger hollow with a distinct, sunken anterior margin and an indistinct (level with poreplate) posterior margin (Fig. 22A, C, E, G, I); receptacular cluster large and complex (Fig. 22B, D, F, H), slightly protruding beyond widely invaginated anterior margin of poreplate; posterior stalk strongly pigmented, more or less completely separated from pigmented areas of poreplate, its posterior portion finely pitted and bent ventrad at right angles; genital atrium with few or without lateral hairs, most vulvae without posterior hairs (Fig. 22A, C, E, G, I, K).

Variation: Carapace lengths in males (n=6) 5.51-6.46, carapace widths 4.92-5.87; in the largest females with a well-developed vulval plate (n=9) 5.94-7.87 and 4.80-6.69, respectively. In two females from Gua Tempurung both AME are completely absent, in other specimens they are reduced (without cornea), tiny (smaller than the pits from which nearby bristles arise) or normally developed. There is only minor variation in the tarsal scopula of males: covering distal two-thirds of tarsus II in two males (both from Gua Cicak), only distal half in all other males; being very thin (in two males from Gua Cicak) or thin (in remaining males) on tarsus IV, always weaker than on tarsi I-III.

Variation in the shape of the ventral process of the contrategulum is shown in Fig. 21I-L, variation in the shape of vulval plates in Fig. 22A-I, K. One male from the Gua Cicak has one of the four apical megaspines on its tibial apophysis weakly developed on both palps (Fig. 21G). The number of lateral hairs in the genital atrium of females ranges from a few to none (Fig. 22A-I); one female (from Gua Cicak) has additionally two paramedian hairs in the posterior part of its genital atrium (Fig. 22I). Females from Gua Cicak have more hairs in the genital atrium than females from the type locality. The CDO is relatively large and clearly discernible only in the two smallest females from each locality (Fig. 22I, K); in all larger females examined it is small and lies in a depression (Fig. 22A, C, E, G).

Biology: All specimens examined were collected from burrows in sandy or loamy soil on the floor in the aphotic zone of two caves. Unlike in *L. batuensis*, no nests were found on cave walls. Most burrows ran into the depth of the soil and were closed by a single trapdoor. Only one burrow ran under the soil surface and had a second door at the opposite end, about six centimetres away from the first door. From the main entrance up to eight quite long (as usual in cave-dwelling *Liphistius*) signal lines (the longest 20 cm) ran over the soil surface (in a few cases also over nearby rock). The trapdoor of the largest female was 1.8 cm long and 3.0 cm wide, in penultimate males trapdoors were 1.2-1.8 long and 2.0-2.8 wide.

Despite the fact that all spiders examined were found in the dark portions of these two caves, no noteworthy troglobiomorphic adaptations are visible, apart from a relatively light body colouration in all living spiders and a more or less distinct reduction of the AME in some spiders.

An illustrated presentation of *L. tempurung* (together with *L. kanthan*) and its habitat is given in Steiner (1998). An extensive bibliography on *Lipistius* and many other animals in caves of Malaysia can be found on Liz Price's website (Price, 2017).

Distribution: Known only from inside two limestone caves (Fig. 1, localities 16-17), about 13 km apart, southeast of Ipoh in the Perak State. A short description of Gua Tempurung and photographs of the cave and some spider nests are given in Platnick *et al*. (1997: 2-3, figs 1-3).

Remarks: First reported from a "cave in Gunong Tempurong" by Bullock (1972: 138) under *L. batuensis*, this is a narrowly endemic species restricted to caves. Like the other cave-living *Liphistius* species in Malaysia [*L. batuensis*, *L. kanthan* (currently on the IUCN list of critically endangered species; http://www.iucnredlist.org/search?page=52) and *L. priceae* sp. nov.], *L. tempurung* is at great risk of becoming extinct if overcollected, or if their habitats change or are destroyed. Quarrying of limestone hills for cement production is widespread in Malaysia and elsewhere in Southeast Asia, and poses the greatest danger for these species.

Liphistius priceae sp. nov.

Figs 23-24

Types: MHNG (most types, including the holotype), SMF (1 male and 1 female paratypes), sample MAL-04/10; male holotype (matured late VIII.2004), 8 male paratypes (matured 20.VII., 1.VIII., 18.IX. 2004, mid-VII.; 11.VIII.2005; 3 male paratypes collected mature at the site) and 11 female paratypes (including allotype, moulted 24.XI.2004); Malaysia, Kelantan, about 5 km S of Dabong, Gua Keris (= Kris Cave) and Gua Pagar (locally also called Gua King Kong), 130 m; 8.-9. VI.2004; leg. P.J. Schwendinger. The precise type locality is Gua Keris.

Etymology: The new species is named in honour of Liz Price (London, UK), a former long-time resident in Kuala Lumpur, and a very active speleologist who over 30 years explored and published on caves and cave faunas all over Southeast Asia. She was also involved in conservation and trying to save some caves from destruction by quarrying in Malaysia.

Diagnosis: Small to medium-sized, light-brown-coloured species, similar and closely related to *L. tempurung*. Both sexes slightly smaller than those of *L. tempurung* (carapace length of males 4.42-5.23 versus 5.51-6.46 in *L. tempurung*). Males distinguished by scopula on tarsus IV more extensive; palpal tibia with a longer retrolateral apophysis carrying much shorter megaspines (Fig. 23B, K-O cf. Fig. 21E-G); paracymbium larger, with a more prominent retrolateral-proximal part (Fig. 23A cf. Fig. 21A); tegulum with more clearly outlined proximal edge (Fig. 23I cf. Fig. 21B); contrategulum with series of oblique ribs on distal edge extending further prolaterally, dorsal apex much smaller and narrower, with a more pointed tip (Fig. 23D-G cf. Fig. 21I-L); para-embolic plate with more prominent, angular distal margin (Fig. 23A, D-E cf. Fig. 21A, I-L); sclerotised part of embolus proper with more pointed apex (Fig. 23A, I cf. Fig. 21A-B). Females distinguished from those of *L. tempurung* by larger and more prominent receptacular cluster (Fig. 24 cf. Fig. 22); CDO much wider and more distinctly outlined, not sitting in a hollow (Fig. 24A, C, E-F cf. Fig. 22A, C, E, G, I); anterior margin of poreplate not or only indistinctly invaginated; posterior stalk anteriorly narrower.

Description of male (holotype): *Colour in alcohol* (slightly darker in life): Body mostly light brown, carapace with indistinct cream-coloured and flower-shaped area around fovea. Chelicerae with proximal portion cream-coloured, distal portion light brown. Cheliceral fangs, palpal tarsi and sclerites of palpal organ reddish brown (darker than rest of body). Legs with indistinct annulations (light median rings) on all tibiae and metatarsi; legs and palps with a light distal zone on patellae. Opisthosomal tergite I uniformly light brown, following tergites with increasingly larger light areas in posterior part (except for bases of paired para-median spines); membranous part of opisthosoma cream-coloured.

Bristles on carapace: Stiff bristles on anterior and posterior margins, as well as on and behind eye mound; fewer weaker bristles on lateral margins and on posterior coxal elevations; no bristles anterior to fovea.

Cheliceral teeth: Twelve small teeth on promargin of cheliceral groove of each chelicera.

Scopula: All tarsi with indistinctly outlined scopula on roughly distal two-thirds of ventral side, only behind claw divided by a short median stripe; scopula on tarsus I very thin and its proximal limit difficult to identify; scopula on other tarsi denser and and more clearly delimited.

Claws: Paired tarsal claws with 3-4 denticles on anterior legs, 4-5 denticles on posterior legs; unpaired claws with one indistinct denticle or without.

Palp: Tibial apophysis well-developed and quite long, slightly set back from anterior margin of tibia, distinctly pointing away from axis of tibia (Fig. 23B), carrying four very short megaspines, the ventral one being longest, a median one set back from distal margin (Fig. 23K). Distal margin of cymbium with elongate prodorsal lobe (Fig. 23J). Paracymbium quite large and moderately deep, with a distinct retrolateral-proximal bulge (Fig. 23A, C); cumulus indistinctly elevated, carrying few long stiff bristles (Fig. 23A, C). Subtegulum without apophysis. Tegulum with wide, sharp, non-dentate proximal edge (Fig. 23I). Contrategulum with somewhat widely conical (its apex narrowly rounded) ventral process; distal edge with long row of oblique parallel ridges pointing towards embolus; dorsal apex asymmetrical, quite small and narrow, with narrowly rounded tip (Fig. 23D). Para-embolic plate low, its distal margin angular (Fig. 23A, D, I); embolus proper with slightly widened and obliquely truncate apex (Fig. 23A, I), dorsal and ventral walls of sclerotised part equally wide and lying close to each other (Fig. 23D), retrolateral side enforced by a long, distinct keel (Fig. 23D, I); membranous part of embolus proper narrow, indistinct (Fig. 23H).

Measurements: Total length 9.96; carapace 4.51 long, 4.24 wide; opisthosoma 3.96 long, 2.61 wide; eye mound 0.64 long, 0.76 wide, AME well-developed; palpal coxae 0.99 long, 0.95 wide; labium 0.40 long, 0.87 wide; sternum 2.02 long, 1.47 wide (0.75 on ventral surface); palp 7.77 long (2.46 + 1.39 + 2.69 + 1.23); leg I 14.69 long (3.96 + 1.82 + 3.17 + 3.64 + 2.10); leg II 15.61 long (4.08 + 1.82 + 3.29 + 4.08 + 2.34); leg III 17.18 long (4.16 + 1.86 + 3.56 + 4.91 + 2.69); leg IV 21.62 long (5.07 + 1.90 + 4.51 + 6.69 + 3.45).

Description of female (allotype): *Colour in alcohol* (slightly darker in life): Mostly as in male, annulations on tibiae and metatarsi of legs slightly more distinct; palpal tarsus reddish brown only at tip. Opisthosomal tergites generally darker, light patches smaller.

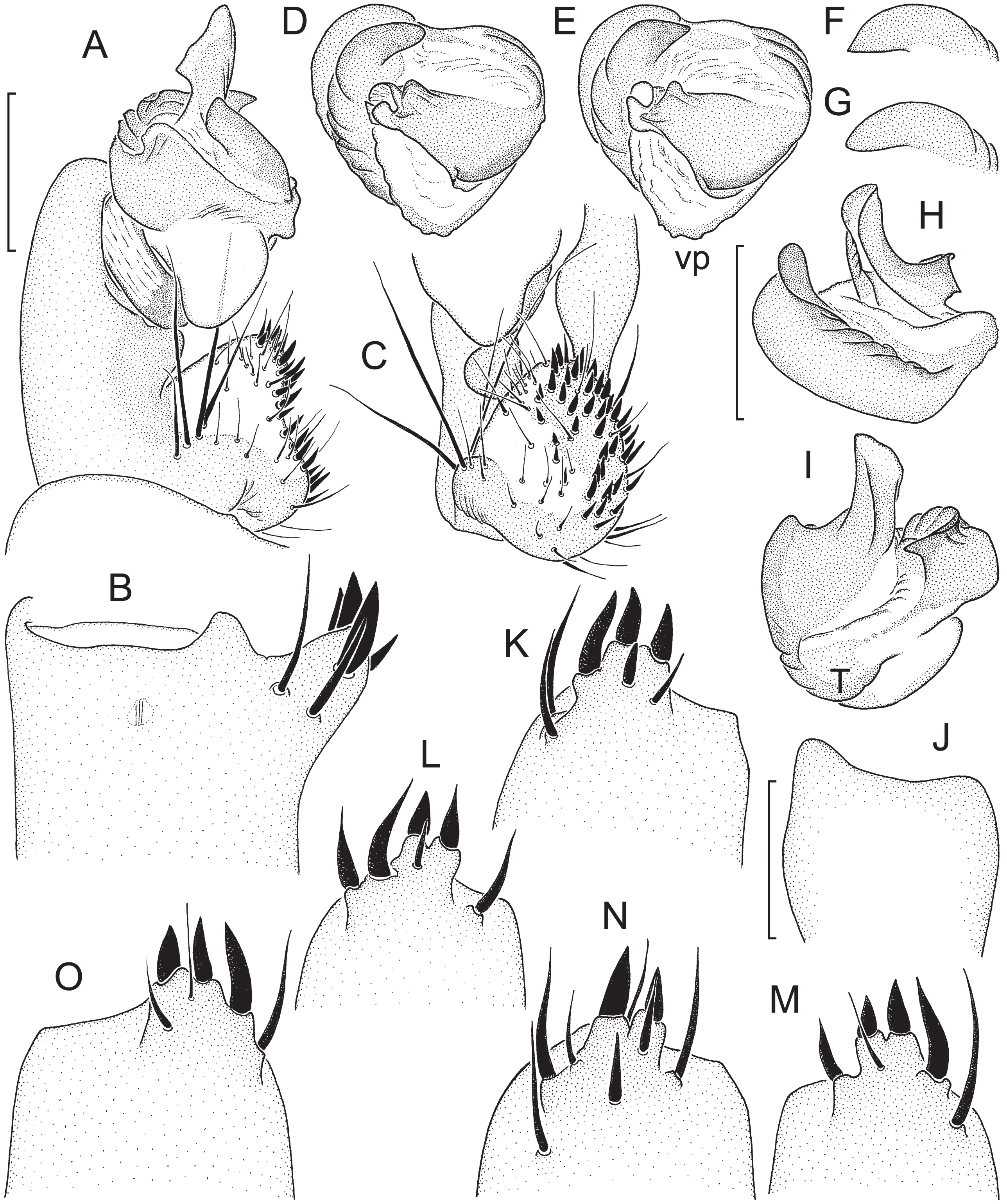

Fig. 23. *Liphistius priceae* sp. nov., details of palp of six males; holotype (A-D, H-K), male paratype collected mature (E), paratype matured 20.VII.2004 (F), paratype matured 1.VIII.2004 (G), paratype matured 18.IX.2004 (L-M) and paratype matured 11.VIII.2005 (N-O). (A) Left cymbium and palpal organ, ventral view. (B) Distal part of left tibia, ventral view. (C) Left paracymbium, retrolateral view. (D-E) Left palpal organ, distal view (dorsal side up). (F-G) Dorsal apex of contrategulum of right palpal organ, distal view (dorsal side to the left). (H) Distal part of left palpal organ, prolateral view. (I) Same, retrodorsal and slightly distal view. (J) Distal part of cymbium, prolateral view. (K-L, N) Left tibial apophysis, retrolateral and slightly proximal view. (M, O) Right tibial apophysis, same view. Abbreviations: T - tegulum; vp - ventral process of contrategulum. Scale lines: 1.0 mm (A-C, K-O), 0.5 mm (D-I; J).

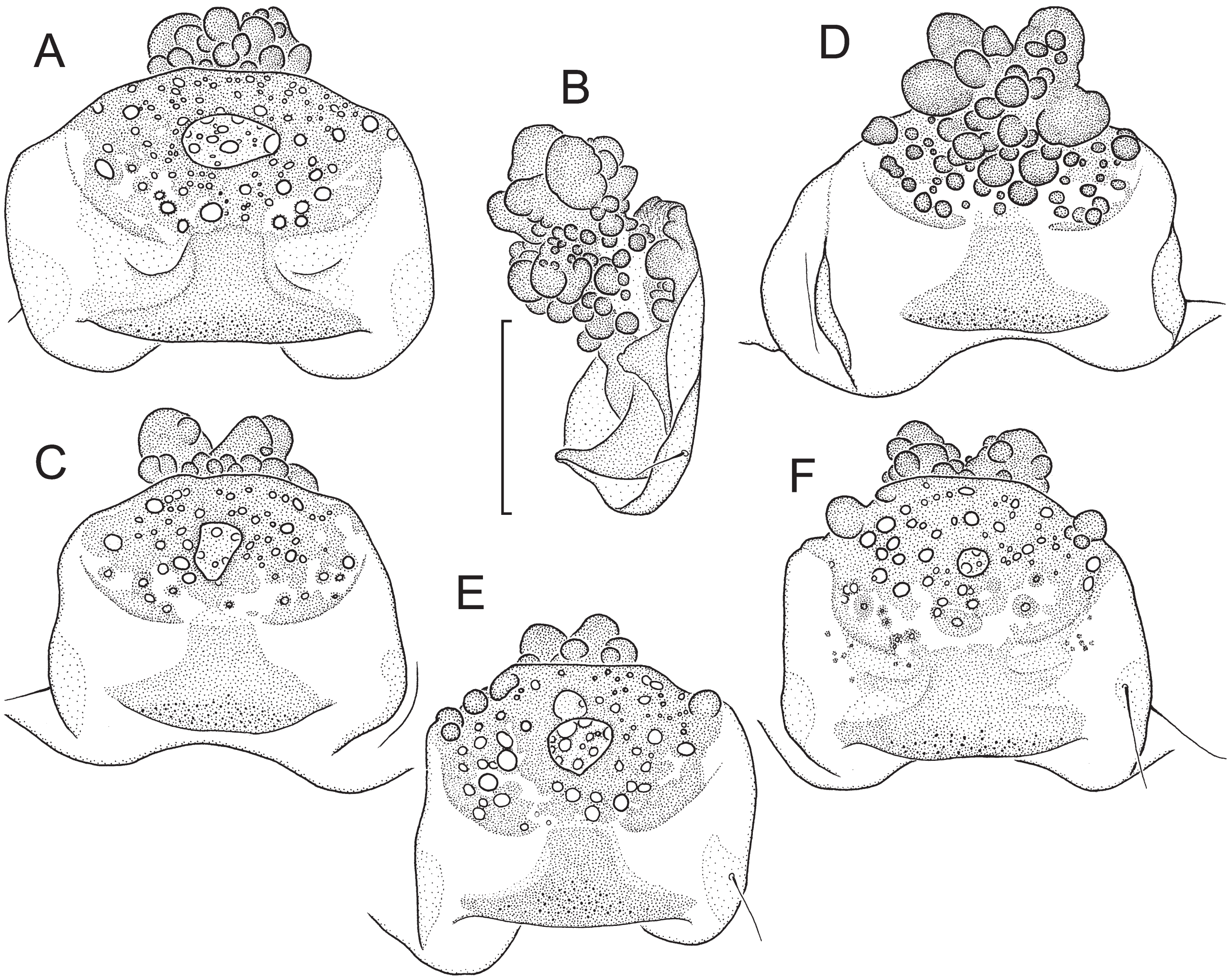

Fig. 24. *Liphistius priceae* sp. nov., vulval plate of four female paratypes (all from exuviae): paratype, moult 1.I.2006 (A-B), allotype, moult 24.XI.2004 (C-D), paratype, moult 13.XI.2005 (E), paratype, moult 2.IV.2005 (F). (A, C, E-F) Dorsal view. (B) Lateral view. (D) Ventral view. Scale lines: 0.5 mm (A-F).

Bristles on carapace: Mostly as in male, additionally with very few tiny bristles on anterior coxal elevations.

Cheliceral teeth: Eleven strong teeth on promargin of left cheliceral groove, twelve on right side.

Claws: Each palpal claw with three worn denticles. Paired leg claws with 2-4 denticles; unpaired claws of legs I-III with 2-3 denticles, leg IV with 0-2. All tarsi without scopula.

Vulva: Posterior margin of genital sternite widely W-shaped (Fig. 24C-D), in slightly posteroventral view posterior edge of posterior stalk clearly visible between paramedian lobes. Vulval plate (Fig. 24C-D) wider than long; posterior part of poreplate partly unpigmented; CDO distinctly outlined, somewhat quadrangular, longer than wide (Fig. 24C), leading into large and complex receptacular cluster (Fig. 24D); the latter strongly protruding beyond slightly arched anterior margin of poreplate (Fig. 24C); posterior stalk strongly pigmented, trapezium-shaped, anteriorly much narrower than posteriorly, indistinctly separated from pigmented areas of poreplate, its posterior portion finely pitted and bent ventrad at right angles (Fig. 24B, showing paratype).

Measurements: Total length 15.38; carapace 6.18 long, 4.91 wide; opisthosoma 6.49 long, 4.83 wide; eye mound 0.69 long, 0.82 wide; palpal coxae 1.90 long, 1.43 wide; labium 0.63 long, 1.43 wide; sternum 2.85 long, 1.90 wide (1.11 on ventral surface); palp 10.26 long (3.33 + 1.82 + 2.65 + 2.46); leg I 12.91 long (4.12 + 2.06 + 2.81 + 2.61 + 1.31); leg II 13.42 long (4.12 + 2.10 + 2.85 + 2.81 + 1.54); leg III 14.30 long (4.20 + 2.14 + 2.93 + 3.33 + 1.70); leg IV 19.46 long (5.23 + 2.38 + 4.08 + 5.39 + 2.38).

Variation: Carapace lengths in males (n=9) 4.42-5.23, carapace width 4.02-4.76; in females with well-developed copulatory organs (n=9) 5.54-5.85 and 4.61-5.04, respectively. In a male and in a female one of the two AME is absent, in all other specimens both are distinct. In two males (including the holotype) the W-shaped marking behind the eye mound is indiscernible, in the other males it is more or less well-developed. No noteworthy variation in size and density of the tarsal scopula of males was detected. The arrangement of distal megaspines on the tibial apophysis of the male palp is quite variable (Fig. 23K-O). A male paratype has fewer bristles on the cumulus of both palps than the other males; one of the cumulus bristles of the illustrated holotype palp runs to the dorsal side of the palpal organ (Fig. 23A, C). The dorsal apex of the contrategulum is narrowly rounded to pointed (Fig. 23D-G). Variation in the shape of the vulval plates is shown in Fig. 24. The CDO is small to large, wider than long or longer than wide, circular, elliptical or quadrangular (Fig. 24A, C, E-F). The posterior stalk is more or less distinctly separated from the pigmented area of the poreplate. The lateral walls of the genital atrium are developed as narrow folds (Fig. 24D) or as simple trenches. Three of the females examined have 1-2 lateral hairs on only one side of the genital atrium (Fig. 24A-B, E-F), the allotype has none (Fig. 24C-D).

Distribution: Known only from two caves in the same limestone hill (Fig. 1, locality 18) in the north of peninsular Malaysia.

Biology: The spiders examined were all collected in different zones (from the euphotic entrance area to the aphotic interior) of both caves. No such spiders were found in the adjacent degraded rain forest. Despite apparently being confined to these caves, *L. priceae* sp. nov. shows no noteworthy cave adaptations in its morphology.

Quite short burrows with a single door and relatively long signal lines (no measurements were taken), as usual for cave-dwelling *Liphistius*, were built in horizontal or sloping loam at or near the cave entrance, as well as in cracks and holes of the walls at the entrance and in deeper portions of the caves. No sac-like retreats on rock surface, as constructed by some other cave-dwelling *Liphistius*, were seen. The trapdoor of the largest female was 1.4 cm long and 2.4 cm wide, in penultimate and adult males they were 1.15-1.6 long and 1.55-2.0 wide.

Three males were adult when collected in early June 2004; four others matured not long afterwards, between late July and late September; the remaining two males matured in mid-July and late August of the following year. Adult females usually moulted twice per year: between March and August and again between September and January. No egg cases were found in the field and no eggs were laid in captivity, which means that the females had not yet mated when collected in early June.

DISCUSSION

Morphological characters: The polarity (plesiomorphy versus apomorphy) of genital characters in liphistiid spiders is difficult to assess. No other animals than the Araneae have the palps of males modified as gonopods, and no other living spiders are more primitive than the Liphistiidae. An outgroup comparison for male copulatory characters is therefore not possible. However, we have indications of the possible evolution of female copulatory organs in spiders from ingroup comparison. Schwendinger & Ono (2011: 626-628) discussed five hypotheses given in the literature and concluded that the female copulatory organs of Heptathelinae are much closer to a hypothetical ancestral form than those of the Liphistiinae (which are quite unique within the Araneae). If female copulatory organs of a given group are primitive, then it can be assumed that this also holds true for the corresponding male copulatory organs. Exciting new fossil evidence supports this assumption. Wunderlich (2017a: 97-99, figs 17-18, 20) very recently described and illustrated the male palps of two mid-Cretaceous mesothelid species which suggest (unfortunately not all details are visible) that these are more similar to heptatheline palps than to liphistiinae palps. Micro-CT scans will one day hopefully reveal more details of these fossil palps. They may not belong to species that are ancestors of the Liphistiidae, but we now have proof – for the first time – that male mesothelids already had complex palps (with an incrassate tibia, a large paracymbium carrying spinules, and with a cymbium as typical for extant liphistiids) about 100 million years ago. As these fossil palps lack a retrolateral tibial apophysis, they strongly resemble male palps of extant Heptathelinae. On this basis, genital characters of the *Liphistius* species treated here – and of the Liphistiidae in general – are interpreted as follows (this interpretation is not based on a phylogenetic analysis):

- The embolus proper of Heptathelinae is undivided and wholly sclerotized, without a membranous part but with some light pigmentation and a small groove-like fold in the dorsal embolic wall of some species; see Haupt, 2003: figs 48-50, 52; Schwendinger & Ono, 2011: fig. 5; also observed in males of *Qiongthela australis* (Ono, 2002), *Q. nui* (Schwendinger & Ono, 2011), *Vinathela abca* (Ono, 1999) (male not yet described but palp illustrated in Logunov & Vahtera, 2017: figs 17-19), *V. tomokunii* (Ono, 1997), *V. tonkinensis* (Bristowe, 1933) and in two undescribed heptatheline species from Vietnam. Therefore the bipartite embolus proper of *Liphistius* (unique among spiders) is believed to be derived. The deeply split embolus proper of the *trang*-group is consequently more derived than the rather closed embolus proper in other groups of *Liphistius* species.
- The orientation of the embolus complex on the palpal organ differs by an angle of about 90°. In most *trang*-

group species the major embolic fold (marked "f" in Fig. 3; called "dorsal lamella" in Schwendinger, 1990: 347, figs 58, 61) that connects the retrolateral wall of the sclerotised part with the membranous part is wide (Fig. 3A, C, E, G) and essentially directed dorsad (in males examined ranging from prodorsad to retrodorsad; see e.g. Schwendinger, 1996: figs 6-7). A second, always very short and indistinct minor embolic fold (called "ventral lamella" in Schwendinger, 1990: 347, figs 59, 62) is also present and connects both embolic parts on the opposite side. In all other species groups (including the ones treated here) the major embolic fold is very narrow (Fig. 3B, D, F, H) and always points proventrad or prolaterad (e.g. Fig. 4G-H). The latter is similar to the situation in the Heptathelinae. Heptatheline spiders do not have a membranous part of the embolus proper, but the narrow end of the spermophore opening (seen in distal view), where the membranous part is situated in *Liphistius*, is directed prolaterad. This position is therefore considered as plesiomorphic. Males of *L. tenuis* Schwendinger, 1996 (Schwendinger, 1996: figs 16-17) and of an undescribed, closely related species from Cambodia (both belonging to the *trang*-group and both also unusual in other ways) are exceptions: their major embolic fold (although relatively wide and short as in all other *trang*-group species) clearly points prolaterad, and this may be plesiomorphic.

- The displacement of the para-embolic plate (considered homologous with the conductor of Heptathelinae which lies very close to the embolus; Schwendinger & Ono, 2011: 618) away from the embolus proper to the ventral/retroventral edge of the embolic base is presumably derived. So is the reduction of the para-embolic plate.
- Modifications on the distal edge of the contrategulum (e.g. in the form of parallel ridges or teeth) are found in *Liphistius* and in the Heptathelinae and have probably evolved several times in parallel. The V-shaped or U-shaped row of denticles at the proventral end of this edge (Figs 4C, 6C, 8D) is a clear synapomorphy of the *malayanus*-group and unique to these species.
- A ventral process on the contrategulum is absent in the Heptathelinae. The spindle-shaped, distad-directed process on the contrategulum of *Ganthela yundingensis* Xu (in Xu *et al.*, 2015a: figs 10-12) is more likely homologous with the strongly elongate, spine-like, distad-directed contrategular denticle of species in *Ryuthela* Haupt, 1983 than with the ventrad- or proventrad-directed, blunt process in many *Liphistius* species. A distinct contrategular process is present in some (but not all) species of all groups except for the *bristowei*-group and the *linang*-group; *L. malayanus* and *L. endau* (in the *malayanus*-group) appear to have an indistinct, very low and wide contrategular process. This structure may be a synapomorphy for the genus *Liphistius* that has become lost many times, or it may be a synapomorphy for certain species groups (with subsequent loss in some of their species).
- The usually well-developed and very prominent marginal and terminal apophyses of the tegulum in Heptathelinae are much reduced in the Liphistiinae. The distal edge of the *Liphistius* tegulum (corresponding to the marginal apohysis in Heptathelinae) is completely reduced in all species treated here, but still visible as a more or less distinct and prominent edge in other species groups. The dentate proximal edge of the *Liphistius* tegulum (corresponding to the dentate edge on the dorsal extension of the terminal apophysis in Heptathelinae; Schwendinger & Ono, 2011: 619, fig. 52) is strongly or completely reduced in the *batuensis*-group, but more or less well-developed in other species groups. These different degrees of reduction are considered as apomorphic.
- The presence of a subtegular apophysis (absent in the Heptathelinae) is most likely a synapomorphy of *Liphistius* which has been independently reduced or lost in many species of all groups, completely so in all species treated here.
- A more or less elevated cumulus (often indiscernible but always identifiable by the presence of a group of bristles that are distinct from nearby bristles) is quite unique within spiders, not present in the Heptathelinae, and a clear synapomorphy for *Liphistius*. Whether the elevated or the non-elevated cumulus is apomorphic remains unclear.
- The presence of a retrolateral apophysis on the palpal tibia of males distinguishes *Liphistius* from the Heptathelinae (Platnick & Sedgwick, 1984: 3) and it is a synapomorphy for *Liphistius*, probably evolved convergently to the retrolateral tibial apophysis in other spider families. This is supported by fossil evidence. The surprisingly well-preserved male palps of *Parvithele muelleri* Wunderlich, 2017 and of *P. spinipes* Wunderlich, 2017 from mid-Cretaceous amber of northern Myanmar (= Burma) lack a tibial apophysis, and they – at least the palp of the former species – look quite similar to male palps of extant Heptathelinae (see Wunderlich, 2017a: 98-99, figs 17-18, 20). As mentioned above, this is a strong indication that copulatory organs of Heptathelinae are more primitive than those of *Liphistius*.
- The deeply divided tibial apophysis of *L. tioman* (*tioman*-group) on one hand, and that of *L. linang* sp. nov. and *L. indra* sp. nov. (*linang*-group) on the other, are unique and highly derived. Their different shapes (different length of dorsal part of apophysis), in connection with different types of female copulatory organs, show that they probably evolved in convergence. Female genital characters (which are often more conservative than male genital characters) indicate that the *tioman*-group is closer to the *malayanus*-group than to the *linang*-group.
- The vulval plate of *Liphistius* is unique among spiders and a clear synapomorphy for the genus (Platnick & Sedgwick, 1984: 3). It starts off as a small, slightly

sclerotised and lightly pigmented structure in juvenile females and becomes larger and increasingly sclerotised and pigmented with each moult. For me it is not possible to tell if the female is still immature or already adult from just looking at a vulval plate. Surprisingly small females (clearly smaller than the conspecific males) were observed to produce eggs. The only partially pigmented (and sclerotised) vulval plate of the *linang*-group and the *batuensis*-group thus suggests neoteny or an atavism linking these species to the Heptathelinae with an unsclerotised, leathery bursa copulatrix (Schwendinger & Ono, 2011: 621, figs 55-57). However, the fact that the unpigmented parts of the vulval plates in the *linang*-group and in the *batuensis*-group are found in its centre, around the base of the receptacular cluster and between the poreplate and the posterior stalk, not at the periphery as in juvenile females, is a strong indication that this is a case of apomorphic reduction. This is not just a matter of reduced pigmentation, but also of reduced sclerotisation. Cleared vulval plates dissected from specimens of these species or vulval plates on exuviae (without the surrounding tissue that keep them straight) often fold along a horizontal axis that runs through the desclerotised areas. It is thus a clear synapomorphy for the species in the *linang*-group and for the species in the *batuensis*-group, but it remains to be established if it is also a synapomorphy for both groups together.

- The unpaired receptacular cluster of *Liphistius* is most likely a derivate of the four receptacles present in primitive Heptathelinae (and in primitive Mygalomorphae). In the Heptathelinae the two pairs of receptacles show a tendency towards fusion into a single pair and further into a single receptacle, and a tendency for displacement away from the anterior margin of the bursa copulatrix onto the dorsal or onto the ventral side (less pronounced and less frequent) of the bursa (Schwendinger & Ono, 2011: 621-624). The simple digitiform receptacular cluster of a few species in the *trang*-group are most likely derived simplifications (also present in heptathelines; Schwendinger & Ono, 2011: 621, figs 42-43) of the complex receptacular cluster found in the species treated here.
- The divided receptacular cluster of the *tioman*-group is probably also derived. Considering that the divided receptacular cluster arises from a well-developed poreplate, it is unlikely to be a plesiomorphic link between the unpaired receptacular cluster in *Liphistius* and the paired receptacles of heptathelines. Early stages of a subdivision of the receptacular cluster into subclusters can be found in some females of *L. malayanus* (Fig. 5B) and *L. endau* (Fig. 7B, E, G), which indicates an evolutionary trend within the *tioman*-group and the *malayanus*-group and suggests that both are closely related.
- A character not previously recognised as being of taxonomic value in *Liphistius* is the extent and density of the ventral scopula on leg tarsi of males (not present in females). It allows some species to be distinguished from similar (closely related) ones, e.g. *L. linang* sp. nov. from *L. indra* sp. nov., and *L. tempurung* from *L. batuensis* and from *L. priceae* sp. nov. However, the most distinctive characters in males of extant liphistiids are found in the morphology of the palp. In females there are fewer valuable morphological characters for species distinction. Most of them are found in details of the vulva, but as these show relatively high degrees of intraspecific (even within-population) variability, an identification of females based on morphology and in the absence of corresponding males is still quite unreliable. Therefore the description of new species from females without the corresponding males, or – even worse – from a single female, should be avoided. It is advisable to illustrate the copulatory organs of more than just a single female per species. If a larger series of specimens is studied, then the typical as well as the most aberrant ones should be illustrated in order to avoid somebody else later describing a "new species" from an aberrant specimen.
- As in all other *Liphistius* species, those treated here possess "tibial spurs" (*sensu* Platnick & Goloboff, 1985) in juveniles and adult females, whereas adult males (except for quite rare cases in which individual "spurs" are retained) have lost them. The statement by Wunderlich (2017a: 90), with reference to Schwendinger & Ono (2011: 603), that "tibial spurs" are absent in *Qiongthela australis* (Ono, 2002) is incorrect. The corresponding observation by Schwendinger & Ono refers to males only; for females of this species "tibial spurs" are reported as "present on legs I-III".

Paleobiogeography: The oldest unambiguous mesothelid fossil is *Palaeothele montceauensis* (Selden, 1996) from a late Carboniferous Lagerstätte in France. Additional fossils that clearly belong to the Mesothelae were recently described (and placed in three extinct families) from mid-Createaceous amber of northern Myanmar by Wunderlich (2015, 2017a). Extant mesothelids (all belonging to the family Liphistiidae) are only known from East and Southeast Asia. These are the undisputed facts. Other Palaeozoic fossil taxa currently placed under "mesotheles" may not be true spiders and need re-evaluation (Dunlop *et al.*, 2017; Garwood *et al.*, 2016: 6; Penney & Selden, 2011). A discussion of these facts is given in the following.

In the late Carboniferous, when *P. montceauensis* lived, France was part of northwestern Pangaea and it was situated near the equator (Scotese, 2002). Mesothelid spiders may have originated in this period and in this region. Or they could have originated earlier, on the minor supercontinent of Euramerica, which was isolated and continuously situated at the equator (Scotese, 2002) or just south of the equator (Streel *et al.,* 2000) during the Devonian and the early Carboniferous, whereas northwestern Gondwana was slowly moving northward from southern temperate to subtropical latitudes during the same periods. Climatic conditions for the ancestors of *P. montceauensis* would have been more favourable on Euramerica than on Gondwana, unless global temperatures in the Palaeozoic and Mesozoic were indeed much more balanced than they are today (i.e. only warm temperate and subtropical zones but no tropical zone existed) and unless the geographical ranges of animal and plant taxa in these eras were almost pan-continental (Razumovsky, 1971; Zherikhin, 1978; Eskov & Golovatch, 1986). The fossil record supports an Euramerican origin of mesothelid spiders: Devonian Uraraneida (an extinct arachnid order close to the Araneae; considered as an suborder of the Araneae by Wunderlich, 2015: 46-48) in North America and western Russia (see Dunlop *et al.*, 2017); Carboniferous *Idmonarachne brasieri* Garwood, Dunlop, Selden, Spencer, Atwood, Vo & Drakopoulos, 2016 (an extinct arachnid of an unspecified order; considered as the sister group of the Araneae by Garwood *et al.*, 2016) in France; Carboniferous Arthrolycosidae, Arthromygalidae and Pyritaraneidae (which may or may not represent mesothelid spiders) in North America, England, France, the Czech Republic, Poland, Ukraine – all former parts of Euramerica – but also in Siberia (see Dunlop *et al.*, 2017). No Palaeozoic spider fossils are known from areas that then belonged to Gondwana.

Whatever happened before, in the late Carboniferous mesothelid spiders were evidently present in northwestern Pangaea. In the Mesozoic this region slowly drifted further north, out of tropical and subtropical latitudes. The alternatives for tropical spiders were adaptation to the new climatic conditions (something only few extant atypid and antrodiaetid species among the primitive spiders have achieved) or gradual dispersal while tracking suitable conditions which results in a shift in the geographical range. The latter would lead to only local extinction. Too rapid or too drastic changes in climatic conditions, or new barriers to dispersal, would lead to total extinction. This happened quite often, as the fossil record clearly shows: e.g. various tropical spider families in Baltic amber, see Wunderlich, 2004; Ricinulei fossils in North America, Europe and Burma, see Selden, 1992 and Wunderlich, 2012; Onychophora in Baltic and Burmese amber, see Poinar, 1996 and Murienne *et al.*, 2014.

How did mesothelid spiders get from northwestern Pangaea to East and Southeast Asia in between the late Carboniferous and today? Four hypotheses try to explain this:

1) Schwendinger (2009: 1265-1266) postulates that the mesothelid spiders originated in a tropical or subtropical part of Euramerica before the late Carboniferous, possibly before it was integrated into Pangea. When this region drifted northwards and became too cold to sustain these spiders, they migrated from their ancestral region into warmer zones. Those that stayed behind and those that spread southward became extinct (possibly due to large-scale aridification of this region during the late Palaeozoic and Mesozoic, see Rees *et al.*, 1999 and Rees *et al.*, 2000), whereas those that migrated eastwards along the southern margin of northeastern Pangea onto accreting terranes continued to exist and evolve until today. This hypothesis, called the "northern route" by Schwendinger (2009: 1265), was called the "stepping on Middle East" hypothesis by Xu *et al*. (2015b: 7-8), who also provided molecular-based dating of the diversification events for the family Liphistiidae and its genera. All known fossils that clearly belong to the Mesothelae support this hypothesis. Long-distance migration of animals with low powers of dispersal, as in the case of mesothelid spiders, should by no means be considered as something that happened relatively quickly. It would have taken many millions of years. In this case mesothelids had about 200 million years to get from France to northern Myanmar, and about another 100 million years to get from northern Myanmar to the present locations. That is a minimal pace of about 40 mm per year, which is certainly not beyond the capability of such spiders. It is quite likely (and not in contradiction with this hypothesis) that ancestral mesothelids dispersed slightly more quickly and were already widely distributed in southeastern Laurasia by the mid-Cretaceous.
2) A second hypothesis implies migration from tropical and subtropical areas of western Pangea eastwards along the northern margin of Gondwana, followed by rafting on a Cimmerian terrane that detached from the northeastern margin of Gondwana in the early Permian, drifing northwards through the Paleo-Tethys Ocean and accreting to the southern margin of eastern Laurasia in the early Jurassic. This was called the "southern route" by Schwendinger (2009: 1265) and the "out of Gondwana" hypothesis by Xu *et al.* (2015b: 7). This scenario is rather improbable, since, in order to "catch the raft", the spiders would have had to migrate through cold southern latitudes in a relatively short period of time. There are no fossils to support this.
3) Xu *et al.* (2015b: 7) proposed a third hypothesis, called the "silk road". It puts the eastward migration route further north, through northern Laurasia, onto the North China craton. As that would have gone through quite high northern latitudes and thus through a quite cold climate, it appears less likely than the first hypothesis. It is also not supported by any fossil evidence.
4) Wunderlich (2017a, b) indicates that during the Palaeozoic and Mesozoic mesothelid spiders were widespread in large parts of the world ["I suppose that East Asian Palaeozoic fossils of the Mesothelae will be discovered in the future" Wunderlich, 2017a: 88; "The Mesothelae did not invade South East

> Asia in the Palaeogene for the first time (see my corresponding comment below) but their members lived already in this region for million (sic) of years", "the report of (Mesothelae) fossils from the Southern Hemisphere should be only a matter of time", "I expect the discovery of fossil Mesothelae in the Southern Hemisphere in the future" Wunderlich, 2017b: 285-286] and that the extant species are relicts of that once vast distribution. This "relict" hypothesis would require large-scale extinction and the presence of mesothelid fossils in almost all known Palaeozoic and Mesozoic Lagerstätten. So far such fossils are only known from one locality in France (Palaeozoic) and from one locality in northern Myanmar (Mesozoic) and therefore support for this hypothesis is very weak.

In his recent publication, which also gives the description of mesothelid spiders (placed in three extinct families) from mid-Cretaceous amber of northern Myanmar, Wunderlich (2017a: 91; 2017b: 285) rejects the "stepping on Middle East" (Euramerican origin and eastward migration) hypotheses of Xu *et al.* (2015b), without referring to the same hypothesis by Schwendinger (2009). Wunderlich further states that "Mesothelae did not invade South East Asia in the Palaeogene for the first time" (Wunderlich, 2017b: 285). Yet, nobody has ever suggested that. Xu *et al.* (2015b: 4) placed the origin of the family Liphistiidae in the Palaeogene and in Southeast and East Asia, which does not exclude that now-extinct mesothelid families (as the ones described by Wunderlich) were present in this region earlier. Actually the discovery of mid-Cretaceous mesothelid fossils from northern Myanmar nicely supports the "stepping on Middle East" hypothesis, because northern Myanmar lies on the postulated migration route and it would have been suitable for accommodating mesothelid spiders. About 100 million years ago (in the mid-Createaceous) the land that is now northern Myanmar had already accreted to the southern margin of eastern Laurasia and was lying in warm (at least subtropical) latitudes (Scotese, 2002).

The answer to the question of how and from where mesothelid spiders did get to Southeast Asia lies in the ground. The discovery of a mesothelid fossil of any age in Australia or on other islands of the Sahul Shelf would disprove the "stepping on Middle East" hypothesis. So would a find of Palaeozoic mesothelid fossils in East Asia (predicted by Wunderlich, 2017a: 88). However, the discovery of mesothelid fossils in former western Gondwana would not disprove this hypothesis, providing that they were from northern South America or from northern Africa. These lands were adjacent to former Euramerica, situated in warm latitudes during the existence of Pangea, and could have been colonized by mesothelid spiders that later became extinct.

Biogeography: If the paleobiogeographical hypothesis advocated above is correct, then mesothelid spiders have come as far as they can: to the eastern and southeastern shores of tropical and subtropical Asia. Ancestors of species found on remote islands were already there before they separated from mainland Asia, as in the case of Japan (habouring *Heptathela* Kishida, 1923 and *Ryuthela* Haupt, 1983) (see Rogers & Santosh, 2004) and Hainan (harbouring *Qiongthela* Xu & Kuntner in Xu *et al.*, 2015a) (see Zhu, 2016). Taiwan, which has no mesothelids, was never connected to the mainland (Sibuet & Hsu, 2004). Islands close to the mainland were probably colonized from the mainland during one of the periods of lowered sea level in the Caenozoic. Several of these islands harbour liphistiid species, many of them are endemics (e.g. the Malaysian island of Penang even has two species: *L. desultor* which also occurs on the mainland and *L. murphyorum* which is an endemic; Platnick & Sedgwick, 1984: 16-20). The well-investigated island of Singapore, on the other hand, which is only about 1 km away from the mainland and which is much larger than Penang Island, has no resident *Liphistius* species. The same appears to be the case with less well-investigated Indonesian islands (several of which I have visited) south of Singapore. Extinction most likely occurred there, and one can expect to find Caenozoic fossils of liphistiid spiders on these and many other islands near mainland East and Southeast Asia.

Among the islands harbouring *Liphistius* species, Sumatra is the one furthest away from the mainland. It is important to note that *L. sumatranus* Thorell, 1890 is not a primitive relict species, but clearly a member of the derived and species-rich *trang*-group. It is morphologically similar to *L. desultor* (occurring on Penang Island and mainland northwestern Malaysia, facing the east coast of Sumatra), but sufficiently distinct (with a strongly autapomorphic plate-like elevation at the retrodorsal corner of the embolus complex in addition to an only slightly elevated para-embolic plate) to give evidence for a long separation from related species on the mainland. The Straight of Malacca (between Malaysia and Sumatra), which is only 65 km wide in the south and for the most part only 27 m deep (rarely more than 37 m), was probably largely dry during several periods of lowered global sea levels; not just during the Pleistocene glacial periods, but also earlier, during the Pliocene, Miocene and Oligocene (Miller *et al.*, 2005). This is a sufficiently large time frame (about 33 million years) for speciation to take place. Surprisingly no adaptive radiation appears to have occurred; but it may have, with *L. sumatranus* the only survivor.

It is suggestive that islands of the Sunda Shelf which are further away from mainland Southeast Asia harbour no liphistiid spiders. Had they ever made it to the very large and remote island of Borneo, they should have been able to successfully establish themselves and, given enough time, to radiate into a number of descendant species. One would also expect to find extant (and fossil) mesothelids on Borneo if they had arrived from northeastern Gondwana (see "out of Gondwana" hypothesis) or if they had been present on Borneo in the Mesozoic (see "relict" hypothesis). No mesothelids (extant or fossil) are known from Borneo, and I too failed to find any there.

Most species in the Malay Peninsula appear to be short-range endemics (according to Harvey, 2002). Among the species treated here, *L. gracilis* sp. nov., *L. indra* sp. nov., *L. johore*, *L. linang* sp. nov., *L. negara* sp. nov., *L. panching* and *L. tioman* are currently only known from their type localities (the presence of *L. gracilis* sp. nov. on Gunung Belumut needs to be confirmed; *L. johore* was not found again). *Liphistius endau* is known from three localities (Fig. 1, localities 6-8) and thus has a relatively wide distribution in the southern part of peninsular Malaysia, but the most widely distributed *Liphistius* species in the country clearly is *L. malayanus.* It is confirmed from five localities which are relatively far from each other [Fig. 1, localities 1-5; additional localties near Kuala Lumpur, e.g. Klang Gates (Murphy & Murphy, 2000: pl. 2.5), need confirmation but most likely also belong to this species]. This is an exceptionally large geographical range (very few congeners in northern and northeastern Thailand may have wider ranges) and also an exceptionally large vertical distribution. *Liphistius malayanus* occurs between altitudes of 230 m near Kuala Lumpur and about 1800 m in the Genting Highlands. It was also recorded from three other localities on mountains: Gunung Angsi, Fraser's Hill and the Cameron Highlands. This surpasses all other congeners and makes *L. malayanus* the ecologically most successful of the known *Liphistius* species.

The "cave species" have, as usual, very small geographical ranges, and their association with caves is more or less close. The "caves" in which *L. tioman* were found are not real caves but crevices under and between large boulders. Nevertheless, I could only find spiders of this species there, not anywhere else in the nearby forest, although this may just be a snapshot impression due to limited sampling. *Liphistius panching* was found in a quite large limestone cave, but only in the oligophotic zone behind the entrance and not in the completely dark portions. It was also collected at the entrance of the cave (Platnick & Sedgwick, 1984: 27-28). The quite large size and dark body colouration of this species is untypical for true cave spiders and therefore I assume that it also lives outside caves though I have not found them anywhere on Bukit Charas apart from the Caras Cave (not even in one of several smaller caves in the same hill). All three species of the *batuensis*-group have a very close association with limestone caves and have never been collected away from the entrance or the interior of caves. These are rather small spiders with a light body colouration (though without true cave adaptations) and thus they are in their somatic morphology very similar to *L. tham* Sedgwick & Schwendinger, 1990 which is only know from the dark interior of a limestone cave in central Thailand. *Liphistius priceae* sp. nov. has the least pronounced cave association of these three species. The types were found in the dark portions of the caves and at the cave entrances, some trapdoors were actually exposed to full sunlight for a short period of the day. Such spiders were not found in the nearby forest, nor in crevices of limestone bolders away from the cliffs, nor on the steep cliffs of the hill away from the cave entrances. *Liphistius batuensis* is well-investigated and much has been written about this species. It is most probably confined to the dark portions of limestone caves, and so is *L. tempurung* (in contrast to *L. kanthan* which will be treated in the second part of this revision). Due to their very localised occurrences and to their threatened (by quarrying and tourism) habitat, *L. batuensis* and *L. tempurung* are the rarest and most vulnerable liphistiids in Malaysia.

Syntopic occurrences of two *Liphistius* species in the Malay Peninsula are not uncommon, but a locality in Malaysia with three species (as at Khlong Nakha in southern Thailand; Schwendinger, 1995: 155) is not known. *Liphistius gracilis* sp. nov. and *L. endau* can be found at the Kota Tinggi Waterfall (Fig. 1, locality 8), with burrows of both species occurring side by side. The same is the case with *L. linang* sp. nov. and *Liphistius* sp. at the Jeram Linang Waterfall (Fig. 1, locality 13), and with *L. indra* sp. nov. and *Liphistius* cf. *thaleban* in the Sankalakhierie Mountains of southern Thailand (Fig. 1, locality 14). There is a sympatric occurence of two *Liphistius* species near Kuala Lumpur: *L. batuensis* lives in the dark portions of the Batu Cave (Fig. 1, locality 15) and of the Anak Takun Cave in the Templer Park (Fig. 1, localities 2), and *L. malayanus* lives in the nearby forests. Populations of both species may only be (or better: were before the forest around the limestone hills were cleared; Lim & Yussof, 2009: 130) hundreds of metres apart, but the habitats are very diffent. Two *Liphistius* species are found near Dabong (Fig. 1, locality 18): *L. priceae* sp. nov. in the Keris Cave and the Pagar Cave, *Liphistius* cf. *rufipes* a few kilometres away in the forest at the foot of Gunung Stong. A most remarkable co-occurrence of two cave species will be reported in the second part of this revision.

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REFERENCES

Abraham H.C. 1923a. A new spider of the genus *Liphistius*. *Journal of the Malayan Branch of the Royal Asiatic Society* 1: 13-21, pl. 1.

Abraham H.C. 1923b. A new spider of the genus *Liphistius* from the Malay Peninsula, and some observations on its habits. *Proceedings of the Zoological Society of London* 1923: 769-774, pl. 1.

Abraham H.C. 1929. The male of the spider *Liphistius malayanus* H. C. Abr., with further notes on the female and on its habits. *Proceedings of the Zoological Society of London* 1929: 671-677, pls 1-3.

Bristowe W.S. 1933. The liphistiid spiders. With an appendix on their internal anatomy by J. Millot. *Proceedings of the Zoological Society of London* 102(4): 1015-1057.

Bristowe W.S. 1952. The arachnid fauna of the Batu Caves in Malaya. *Annals and Magazine of Natural History* (ser. 12) 5: 697-707.

Bullock J.A. 1972. Cave biology in Malaysia. *Malayan Nature Journal* 25: 135-141.

Dunlop J., Penney D., Jekel D. 2017. A summary list of fossil spiders and their relatives. *In*: World Spider Catalog. Version 18.5. Natural History Museum Bern. Available from http://wsc.nmbe.ch (accessed in July 2017).

Eskov K.Y., Golovatch S.I. 1986. On the origin of trans-Pacific disjunctions. *Zoologische Jahrbücher: Abteilung für Systematik, Geographie und Biologie der Tiere* 113: 265-285.

Foelix R., Erb B. 2010. Mesothelae have venom glands. *The Journal of Arachnology* 38: 596-598.

Foelix R., Erb B., Michalik P. 2010. Scopula hairs in male *Liphistius* spiders: probable contact chemoreceptors. *The Journal of Arachnology* 38: 599-603.

Garwood R.J., Dunlop J.A., Selden P.A., Spencer A.R.T, Atwood R.C., Vo N.T., Drakopoulos M. 2016. Almost a spider: a 305-million-year-old fossil arachnid and spider origins. *Proceedings of the Royal Society, B (Biological Sciences)* 283: 20160125. DOI: 10.1098/rspb.2016.0125

Halliday B., Juvara-Bals I. 2016. Systematics and biology of the mite genus *Ljungia* Oudemans in Southeast Asia (Acari: Laelapidae). *Systematic and Applied Acarology* 21(6): 830-864.

Harvey M.S. 2002. Short-range endemism amongst the Australian fauna: some examples from non-marine environments. *Invertebrate Systematics* 16(4): 555-570.

Haupt J. 1979. Lebensweise und Sexualverhalten der mesothelen Spinne *Heptathela nishihirai* n. sp. (Araneae, Liphistiidae). *Zoologischer Anzeiger* 202(5/6): 348-374.

Haupt J. 1983. Vergleichende Morphologie der Genitalorgane und Phylogenie der liphistiomorphen Webspinnen (Araneae: Mesothelae). I. Revision der bisher bekannten Arten. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 21: 275-293.

Haupt J. 2003. The Mesothelae - a monograph of an exceptional group of spiders (Araneae: Mesothelae). *Zoologica* 154: 1-102.

Kishida K. 1923. *Heptathela*, a new genus of liphistiid spiders. *Annotationes Zoologicae Japonenses*10: 235-242.

Klingel H. 1967. Beobachtungen an *Liphistius batuensis* Abr. (Araneae, Mesothelae). *Zoologischer Anzeiger*, Supplement 30 (= Verhandlungen der deutschen zoologischen Gesellschaft 1966): 246-253.

Kraus O. 1978. *Liphistius* and the evolution of spider genitalia [pp. 235-254]. *In*: Merret P. (ed.). Arachnology. Symposia of the Zoological Society of London, n° 42. *Academic Press, London*, 530 pp.

Lim T.W., Yussof S.S. 2009. Conservation status of the Batu Caves trapdoor spider (*Liphistius batuensis* Abraham (Araneae, Mesothelae)): a preliminary survey. *Malayan Nature Journal* 61(2): 121-132.

Logunov D.V., Vahtera V. 2017. Description of a new species of *Vinathela* Ono, 2000 (Araneae: Mesothelae: Liphistiidae), based on morphological and molecular characters. *Arachnology* 17(5): 229-237.

McClure H.E., Lim B.-L., Winn S.E. 1967. Fauna of the Dark Cave, Batu Caves, Kuala Lumpur, Malaysia. *Pacific Insects* 9(3): 399-428.

Miller K.G., Kominz M.A., Browning J.V., Wright J.D., Mountain G.S., Katz M.E., Sugarman P.J., Cramer B.S., Christie-Blick N., Pekar S.F. 2005. The Phanerozoic record of global sea-level change. *Science* 310: 1293-1298.

Murienne J., Daniels S.R., Buckley T.R., Mayer G., Giribet G. 2014. A living fossil tale of Pangaea biogeography. *Proceedings of the Royal Society, B (Biological Sciences)* 281(1775): 20132648. DOI: 10.1098/rspb.2013.2648

Murphy F., Murphy J. 2000. An introduction to the spiders of South East Asia with notes on all the genera. *Malaysian Nature Society, Kuala Lumpur*, 625 pp., 32 colour plates.

Murphy J.A., Platnick N.I. 1981. On *Liphistius desultor* Schiödte (Araneae, Liphistiidae). *Bulletin of the American Museum of Natural History* 170: 46-56.

Ono H. 1997. A new species of the genus *Heptathela* (Araneae: Liphistiidae) from Vietnam. *Acta Arachnologica* 46(1): 23-28.

Ono H. 1999. Spiders of the genus *Heptathela* (Araneae, Liphistiidae) from Vietnam, with notes on their natural history. *The Journal of Arachnology* 27: 37-43.

Ono H. 2002. Occurrence of a heptatheline spider (Araneae, Liphistiidae) in Lam Dong Province, Vietnam. *Bulletin of the National Science Museum, Tokyo* (series A, Zoology) 28(3): 119-122.

Penney D., Selden P.A. 2011. Fossil spiders - the evolutionary history of a mega-divers order. Monograph series, volume 1. *Siri Scientific Press*, *Manchester*, 128 pp., 87 photos.

Platnick N.I., Goloboff P.A. 1985. On the monophyly of the spider suborder Mesothelae (Arachnida: Araneae). *Journal of the New York Entomological Society* 93(4): 1265-1270.

Platnick N.I., Sedgwick W.C. 1984. A revision of the spider genus *Liphistius* (Araneae, Mesothelae). *American Museum Novitates* 2781: 1-31.

Platnick N.I., Schwendinger P.J., Steiner H. 1997. Three new species of the spider genus *Liphistius* (Araneae, Mesothelae) from Malaysia. *American Museum Novitates* 3209: 1-13.

Poinar G. 1996. Fossil velvet worms in Baltic and Dominican amber: Onychophoran evolution and biogeography. *Science* 273: 1370-1371.

Price L. 2017. Malaysian biospeleology bibliography. Available at http://www.cavesofmalaysia.com/newspage3.htm (accessed in July 2017).

Razumovsky S.M. 1971. On the origin and age of tropical and laurel-leaved floras. *Bulletin of the Main Botanical Garden of the Academy of Sciences of the USSR (Moscow)* 82: 43-51. [In Russian]

Rees P.M., Gibbs M.T., Ziegler A.M., Kutzbach J.E., Behling P.J. 1999. Permian climates: evaluating model predictions using global paleobotanical data. *Geology* 27(10): 891-894.

Rees P.M., Ziegler A.M., Valdes P.J. 2000. Jurassic phytogeography and climates: new data and model comparisons [pp. 297-318]. *In*: Huber B.T., Macleod K.G., Wing S.L. (eds). Warm climates in earth history. *Cambridge University Press*, *Cambridge*, 426 pp.

Ridley H.N. 1899. Caves in the Malay Peninsula. Appendix. *Report of the sixty-eighth meeting of the British Association for the Advancement of Science held at Bristol in September 1898*: 572-583.

Rogers J.J.W., Santosh M. 2004. Continents and supercontinents. *Oxford University Press, New York*, 289 pp.

Schiödte J.C. 1849. Om en afvigende Slægt af Spindlernes Orden. *Naturhistorisk Tidsskrift* 2: 617-624.

Schwendinger P.J. 1987. On the male of *Liphistius trang* (Araneae: Mesothelae), with notes on the natural history of the species. *Natural History Bulletin of the Siam Society* 35: 19-25.

Schwendinger P.J. 1990. On the spider genus *Liphistius* (Araneae: Mesothelae) in Thailand and Burma. *Zoologica Scripta* 19(3): 331-351.

Schwendinger P.J. 1995. New *Liphistius* species (Araneae, Mesothelae) from southern Thailand and northern Malaysia. *Zoologica Scripta* 24(2): 143-156.

Schwendinger P.J. 1996. New *Liphistius* species (Araneae, Mesothelae) from western and eastern Thailand. *Zoologica Scripta* 25(2): 123-141.

Schwendinger P.J. 2009. *Liphistius thaleri*, a new mesothelid spider species from southern Thailand (Araneae, Liphistiidae). *Contributions to Natural History* 12(3): 1253-1268.

Schwendinger P.J., Ono H. 2011. On two *Heptathela* species from southern Vietnam, with a discussion of copulatory organs and systematics of the Liphistiidae (Araneae; Mesothelae). *Revue suisse de Zoologie* 118(4): 599-637.

Scotese C.R. 2002. Plate tectonics map and continental drift animations. Paleomap Project. Available from http://www.scotese.com/earth.htm (accessed in July 2017).

Sedgwick W.C., Platnick N.I. 1986. On the male of *Liphistius panching* (Araneae, Mesothelae). *Malayan Nature Journal* 39: 203-206.

Sedgwick W.C., Platnick N.I. 1987. A new species of *Liphistius* (Araneae, Mesothelae) from Johore, Malaysia. *Malayan Nature Journal* 41: 361-363.

Sedgwick W.C., Schwendinger P.J. 1990. On a cave-dwelling *Liphistius* from Thailand (Araneae: Liphistiidae). *Bulletin of the British arachnological Society* 8(4): 109-112.

Selden P.A. 1992. Revision of the fossil ricinuleids. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 83: 595-634.

Selden P.A. 1996. First fossil mesothele spider, from the Carboniferous of France. *In*: Mahnert V. (ed.). Proceedings of the 13th International Congress of Arachnology, Geneva, 3-8 September 1995. *Revue suisse de Zoologie* special volume 2: 585-596.

Sibuet J.-C., Hsu S.-K. 2004. How was Taiwan created? *Tectonophysics* 379: 159-181.

Skeat M.A. 1953. Reminiscences of the Cambridge University expedition to the north-east Malay states. *In*: Gibson-Hill C.A. (ed.). The Cambridge University Expedition to the North-East Malay States, and to upper Perak, 1899-1900. *Journal of the Malayan Branch of the Royal Asiatic Society* 26(4): 9-147.

Steiner H. 1998. Lebende Fossilien aus den Höhlen Malaysias. *Mitteilungen des Verbandes der deutschen Höhlen- und Karstforscher e.V. München* 44(4): 148-150.

Streel M., Caputo M.C., Loboziak S., Melo J.H.G. 2000. Late Frasnian-Famennian climates based on palynomorph analyses and the question of the Late Devonian glaciations. *Earth-Science Reviews* 52: 121-173.

Thorell T. 1890. Studi sui ragni Malesi e Papuani. IV, 1. *Annali del Museo Civico di Storia Naturale di Genova* (series 2) 8: 1-419.

World Spider Catalog 2017. World Spider Catalog. Version 18.5. Natural History Museum Bern. Available from http://wsc.nmbe.ch (accessed in July 2017).

Wunderlich J. 2004. Fossil spiders in amber and copal. *Beiträge zur Araneologie* 3A+B: 1-1908.

Wunderlich J. 2012. Description of the first fossil Ricinulei in amber from Burma (Myanmar), the first report of this arachnid order from the Mesozoic and from Asia, with notes on the related extinct order Trigonotarbida. *Beiträge zur Araneologie* 7: 233-244.

Wunderlich J. 2015. On the evolution and the classification of spiders, the Mesozoic spider faunas, and the descriptions of new Cretaceous taxa mainly in amber from Myanmar (Burma) (Arachnida: Araneae). *Beiträge zur Araneologie* 9: 21-408, 481-512.

Wunderlich J. 2017a. New and rare fossil spiders (Araneae) in mid Cretaceous amber from Myanmar (Burma), including the description of new extinct families of the suborders Mesothelae and Opisthothelae, as well as notes on the taxonomy, the evolution and the biogeography of the Mesothelae. *Beiträge zur Araneologie* 10: 72-279.

Wunderlich J. 2017b. Palaebiogeography and phylogenomics - fossil proofs contra results from molecular genetic: the case of Mesozoic segmented spiders (Araneae: Mesothelae). *Beiträge zur Araneologie* 10: 285-288.

Xu X., Liu F., Chen J., Ono H., Li D., Kuntner M. 2015a. A genus-level taxonomic review of primitively segmented spiders (Mesothelae, Liphistiidae). *ZooKeys* 488: 121-151.

Xu X., Liu F., Cheng R.-C., Chen J., Xu X., Zhang Z., Ono H., Pham D.S., Norma-Rashid Y., Arnedo M.A., Kuntner M., Li D. 2015b. Extant primitively segmented spiders have recently diversified from an ancient lineage. *Proceedings of the Royal Society, B (Biological Sciences)* 282: 20142486.

Yong H.-S. 1978. Living fossil spiders. *Nature Malaysiana* 3(1): 32-39.

Yussof S. 1987. Gua Anak Takun revisited. *Malayan Naturalist* 40: 12-16.

Zherikhin V.V. 1978. Development and changes of Cretaceous and Cenozoic faunistic complexes (Tracheata and Chelicerata). *Proceedings of the Paleontological Institute of the USSR Academy of Sciences (Moscow)* 165: 1-200. [In Russian]

Zhu H. 2016. Biogeographical evidences help revealing the origin of Hainan Island. *PLoS One* 11(4): e0151941. DOI: 10.1371/journal.pone.0151941