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Autor(en): **Schwendinger, Peter J.**

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Liphistius thaleri, a new mesothelid spider species from southern Thailand (Araneae: Liphistiidae)

Peter J. Schwendinger

ABSTRACT Contrib. Nat. Hist. 12: 1253–1268.

***Liphistius thaleri* sp. nov. is described from male and female specimens collected on Ko Libong, a small island off the western coast of southern Thailand. The new species is closely related to *L. langkawi* Platnick & Sedgwick, 1984, for which new material is illustrated. Their closest relative is *L. murphyorum* Platnick & Sedgwick, 1984, the male pedipalpus of which is also illustrated from new material. These three species form a distinct phylogenetic lineage within the *Liphistius trang*-group. Notes on the biology of *Liphistius thaleri* sp. nov. and *L. langkawi* are given. Island endemism in *Liphistius* is discussed and a hypothesis for the Euramerican origin of mesothelid spiders is proposed.**

Keywords: Taxonomy, Mesothelae, *Liphistius langkawi, L. murphyorum,* superspecies, biology, biogeography, Ko Libong, Euramerica.

Introduction

When I approached Konrad Thaler in 1985 with my request that he supervise a thesis on orthognathous spiders of northern Thailand, he was rather sceptical, but then decided to take the risk and I was off for the following two and a half years. As enthusiastic progress reports were sent back, he became curious and visited me in Chiang Mai in February 1987. Together we had several exciting field-trips to my main collecting sites in Chiang Mai Province on my old second-hand motorbike. During these excursions we encountered exotic arachnids like *Perania* (Tetrablemmidae, Araneae) and *Gnomulus* (Oncopodomorphi, Opiliones) upon which I subsequently focused more attention. One of the highlights of his visit was the discovery of brown widow spiders, *Latrodectus geometricus* C. L. Koch, 1841, on a nearby mountain (Knoflach & van

Harten 2002: 340) and under the chair of his guest room. So, whilst I had not found him the most luxurious accommodation in town, at least it was of arachnological interest. I still do not know of anybody else who has found *Latrodectus* in northern Thailand.

As a part of my thesis, I was able to study several species of the most prominent spider genus in that region, the living fossil spider *Liphistius*. Since then I have paid special attention to mesothelid spiders when collecting in Southeast Asia, and my material of this spider group (deposited in the MHNG) has become quite extensive. Several new species and unknown males of nominal species are now available and await taxonomic treatment. It was in July 2005, nine days after the untimely death of Konrad Thaler, that I found a *Liphistius* population on a small island in southern Thailand, which turned out to belong to an undescribed species. I owe the opportunity to take up research on this fascinating group of animals to him. For this, as well as in gratitude for his help and encouragement over many years, and in appreciation of his arachnological work, I dedicate the new species described here to Konrad Thaler.

Material and Methods

Abbreviations, technical terms and methodology: AME, ALE, PME, PLE anterior (posterior) median (lateral) eyes; MOQ median ocular quadrangle. Terminology of genital structures follows Schwendinger (1990, 1995). Measurements were taken on the dorsal side, between midpoint of anterior and posterior margin. Total length includes chelicerae and anal tubercle. Female genitalia were drawn from exuviae. All specimens examined were collected by me and are deposited in the Muséum d'histoire naturelle de la Ville de Genève, Switzerland (MHNG) and in the Naturhistorisches Museum Wien, Austria (NHMW).

Taxonomy

Liphistiidae Thorell, 1869
Liphistius Schiödte, 1849

Liphistius thaleri sp. nov. (Figs. 1–12)

Type material: Male holotype (MHNG), Thailand, Trang Province, Ko (= Island) Libong (also called Ko Talibong), near Ao Tokae (= Gekko Bay) (7° 16' 04" N, 99° 22' 38" E), 30 m (remnant patch of evergreen forest), collected on 20 July 2005 (matured on 7 September 2005). Paratypes: From the type locality, all collected on 20 July 2005, five males [matured on 5 September 2005 (MHNG); 1 October 2005 (NHMW); 10 October 2005 (MHNG); 5 November 2005 (MHNG); 8 September 2006 (MHNG)], eight females [moulted 14 September 2005 and 22 June 2005 ("allotype"; MHNG); 17 September 2005, 3 March 2006, 29 July 2006, 30 January 2007 and 16 June 2007 (MHNG); 29 September 2005, 23 March 2006, 14 July 2006, 2 December 2006 and 22 May 2007 (NHMW); 15 October 2005, 5 May 2006 and 11 March 2007 (MHNG); 10 March 2006, 18 August 2006 and 14 June 2007 (MHNG); 30 March 2006, 6 August 2006 and 20 June 2007 (MHNG); 24 March 2006, 2 July 2006 and 30 March 2007 (MHNG)].

Etymology: The new species is named after the highly esteemed Austrian arachnologist, myriapodologist and entomologist, the late Konrad Thaler.

Diagnosis: Similar to *Liphistius langkawi* Platnick & Sedgwick, 1984, but with different colour pattern on carapace. Males distinguished by: Spines on paracymbium longer and stronger; subtegular apophysis distally broader; tegular process small and conical, not connected to dorsodistal edge of tegulum; proximal ledge and distal edge on dorsal side of tegulum coarsely dentate, not running into each other; para-embolic plate quite long, triangular and undivided, without spatulate ventral part; embolus longer. Females with six instead of five knobs on ventral rim of pore plate and with lateral hairs in genital atrium.

Description: Male (holotype). Colouration in alcohol: Ground colour of carapace light orange, with grey pattern behind eye tubercle and around fovea; dark brown pattern along margin (Fig. 1). Opisthosoma cream, mottled with light grey; tergites light orange-cream, with paired dark brown patches, these confluent on anterior tergites, increasingly isolated from each other on posterior tergites (Fig. 1). Chelicerae grey distally, cream proximally. Pedipalpi light brown, with dark brown annulations distally on femur and proximally and dis-

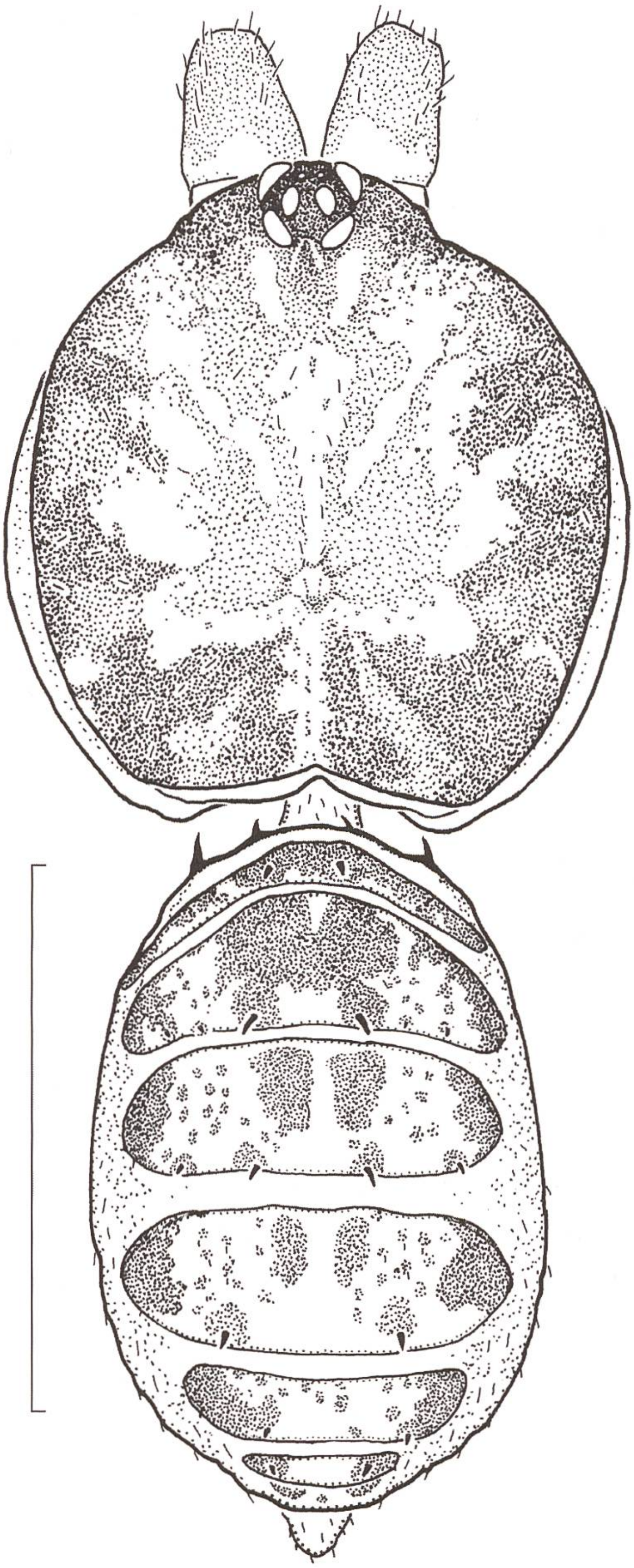


Fig. 1. ***Liphistius thaleri*** **sp. nov., male holotype, body without limbs, dorsal view. Scale line 5.0 mm.**

tally on tibia (extending onto tibial apophysis). Legs light brown, with dark brown annulations distally on femora, proximally on all tibiae, subdistally on tibiae I and II, subproximally on metatarsi I–III (indistinct on III), distally on metatarsi I and II (indistinct on II), proximally on tarsi I–III (indistinct on III); dark brown patches dorsally on patellae of legs and pedipalpi; dark brown spots ventrally on femora of legs and pedipalpi.

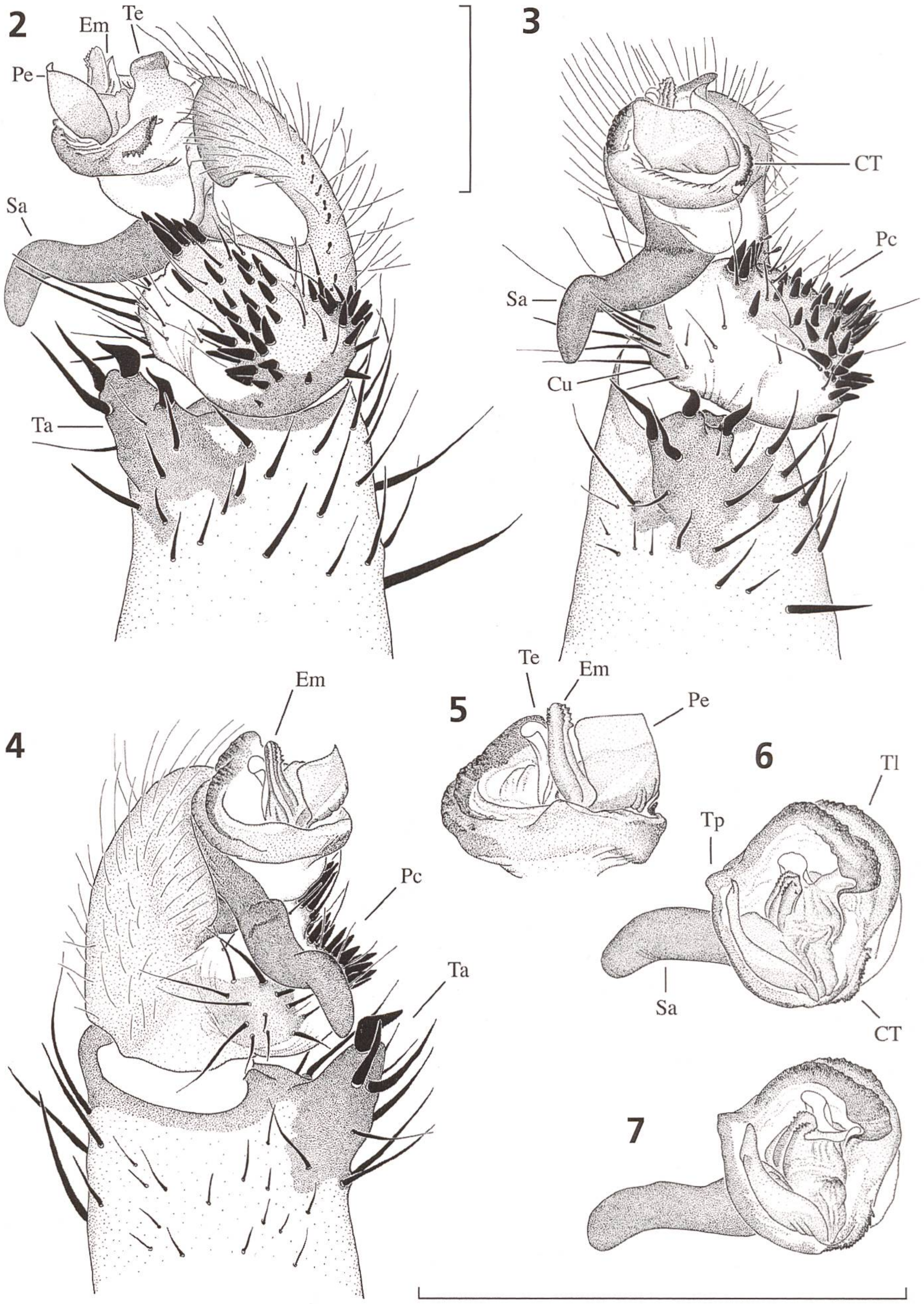
	Leg I	Leg II	Leg III	Leg IV	Pedipalpus
Femur	4.5 (4.4)	4.5 (4.4)	4.6 (4.4)	6.0 (5.6)	2.7 (3.7)
Patella	2.3 (2.4)	2.4 (2.5)	2.4 (2.5)	2.5 (2.7)	1.7 (2.0)
Tibia	3.5 (2.8)	3.6 (2.9)	3.8 (3.0)	4.9 (4.2)	3.2 (2.6)
Metatarsus	3.9 (2.7)	4.3 (3.0)	5.2 (3.5)	7.2 (5.4)	–
Tarsus	1.8 (1.4)	2.0 (1.5)	2.3 (1.8)	3.1 (2.4)	1.7 (2.7)
Total	16.0 (13.7)	16.8 (14.3)	18.3 (15.2)	23.7 (20.3)	9.3 (11.0)

Tab. 1. *Liphistius thaleri* sp. nov. Leg and pedipalpus measurements (in mm) of male holotype and female "allotype" (in parentheses).

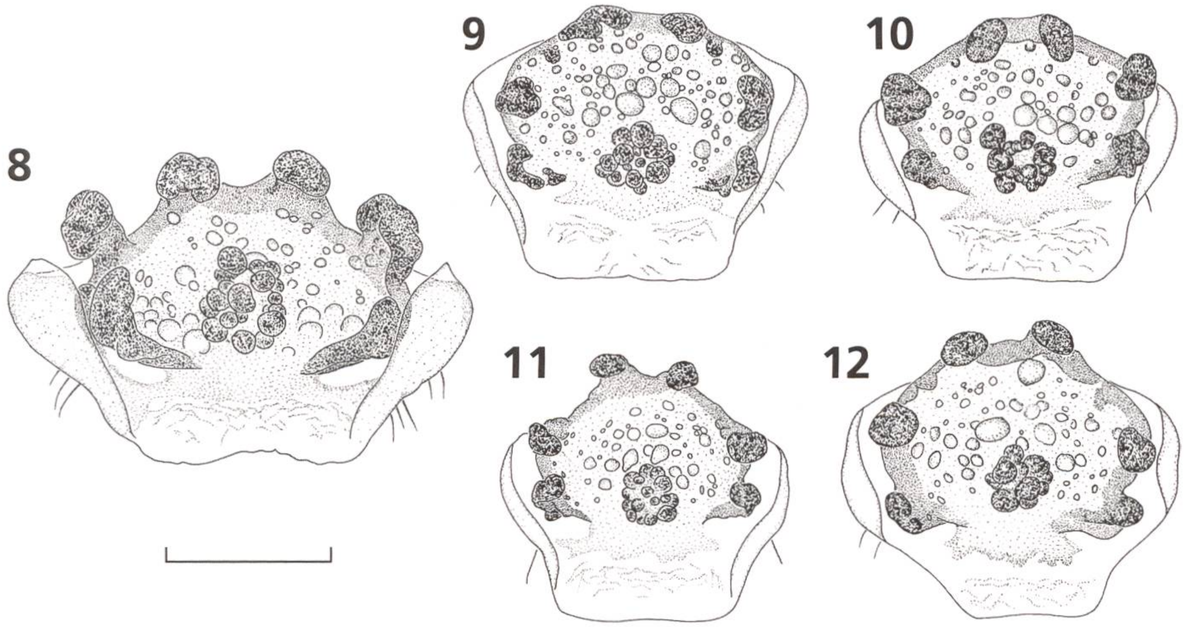
Total length 13.9 mm. Carapace 5.7 mm long, 5.1 mm wide, set with several short hairs scattered over entire surface. Ocular tubercle 0.86 mm long, 0.96 mm wide. Eye sizes and interdistances: AME 0.07 mm on left side, 0.04 mm on right side, ALE 0.52 mm, PME 0.31 mm, PLE 0.53 mm; AME-AME 0.09 mm, AME-ALE 0.10 mm, PME-PME 0.03 mm, PME-PLE 0.10 mm, ALE-PLE 0.04 mm. MOQ 0.41 mm long, front width 0.21 mm, back width 0.50 mm. Labium 0.5 mm long, 1.0 mm wide. Sternum 2.7 mm long, 1.8 mm wide (1.0 mm on ventral surface). Maxillae 1.9 mm long, 1.2 mm wide. Promargin of cheliceral groove with eight small teeth on each side. Paired tarsal claws of anterior legs with four to six teeth, of posterior legs with three to five teeth; unpaired claw with zero to two tiny denticles. Measurements of legs and pedipalpus, see Tab. 1. Opisthosoma 6.3 mm long, 4.1 mm wide.

Pedipalpi (Figs. 2–6) with fairly short spines on distinct tibial apophysis (Ta); paracymbium (Pc) large and massive, carrying long stiff bristles scattered on low, widely rounded cumulus (Cu). Subtegular apophysis (Sa) very long, vermiform, its apex bent proximad. Tegulum (Te) with dentate dorsodistal edge rising to a rounded angle; dorsal side of tegulum with dentate proximal ledge (Tl); tegular process (Tp) small, pointed; contrategulum (CT) narrow, its ventral edge finely dentate and sigmoid, its dorsal edge indistinct, straight. Para-embolic plate (Pe) quite large, somewhat obliquely triangular, narrowly rounded distally; embolus (Em) fairly short, divided into two distinctly detached parts, sclerotized part strengthened by one short proximal ridge and three longer longitudinal ridges reaching apex.

Female ("allotype"). Colouration as in male, except for: Distinct dark annulations distally on all leg metatarsi, and subproximally (weak on legs III–IV) and distally on all leg tarsi and pedipalpal tarsi; ventral side of all leg coxae darkened; ventral side of pedipalpal coxae mostly orange-brown, with darkened retrolateral border (wide anteriorly, narrow posteriorly); genital region darkened.



Figs. 2–7. ***Liphistius thaleri*** **sp. nov., 2–6, male holotype; 7, male paratype (matured 5 September 2005). – 2: distal part of pedipalpus, retrolateral view; – 3: idem, retroventral view; – 4: idem, ventral view; – 5: distal part of pedipalpal organ, ventral view; – 6–7: pedipalpal organ, distal view. Abbreviations: Em = embolus, Cu = cumulus, CT = contrategulum, Pc = paracymbium, Pe = para-embolic plate, Sa = subtegular apophysis, Ta = tibial apophysis, Te = dorsodistal edge of tegulum, Tl = proximal ledge on dorsal side of tegulum, Tp = tegular process. Scale line 1.0 mm (2–4 and 5–7 same scale).**



Figs. 8–12. ***Liphistius thaleri*** **sp. nov., vulvae of five female paratypes (9, "allotype"). – 8: proximo-ventral view; – 9–12: ventral view. Scale line 0.5 mm.**

Total length 16.5 mm. Carapace 6.4 mm long, 5.6 mm wide. Ocular tubercle 0.80 mm long, 1.00 mm wide. Eye sizes and interdistances: AME 0.06 mm, ALE 0.52 mm, PME 0.28 mm, PLE 0.44 mm; AME-AME 0.15 mm, AME-ALE 0.10 mm, PME-PME 0.06 mm, PME-PLE 0.06 mm, ALE-PLE 0.07 mm. MOQ 0.41 mm long, front width 0.25 mm, back width 0.53 mm. Labium 0.7 mm long, 1.5 mm wide. Sternum 3.1 mm long, 2.0 mm wide (1.4 mm on ventral surface). Maxillae 2.7 mm long, 1.5 mm wide. Opisthosoma 7.4 mm long, 5.4 mm wide. Promargin of cheliceral groove with nine teeth on each side. Paired tarsal claws of legs I–II with four teeth, of legs III–IV with four to five teeth, unpaired claw with three denticles on legs I, III, three to four denticles on leg II, and two denticles on leg IV; pedipalpal claws bare. Hairs on ventral side of labium, sternum, limb coxae and opisthosoma distinctly longer than in males. Measurements of legs and pedipalpus, see Table 1.

Vulva (Fig. 9)with poreplate bearing six strongly sclerotized and pigmented protuberances (called "lobes" in Platnick & Sedgwick 1984: 16) on strengthened rim. Receptacular cluster moderately developed, racemose, situated in posterior half of poreplate. Posterior stalk of poreplate short, wide, with indistinctly outlined posterior border. Genital atrium with two lateral hairs on each side.

Variation: Range of measurements in males (n=6): Body length 8.8–13.9 mm, carapace length 4.4–5.7 mm, width 3.9–5.2 mm. Maximal measurements in females (n=8): Body length 18.2 mm, carapace length 7.2 mm, width 6.3

mm. Variation in shape of pedipalpal organ, see Figs. 6–7 (distal view). Variation in poreplate shape, see Figs. 8–12. Larger (and older) females have more hairs laterally in the genital atrium than smaller specimens.

Relationships: *L. thaleri* sp. nov. is most closely related to *L. langkawi* from Langkawi Island, Malaysia. The strongly elongated subtegular apophysis of the pedipalpal organ and the presence of protuberances on the anterior and lateral rim of the poreplate indicate that of both species are in the same phylogenetic lineage as *L. murphyorum* PLATNICK & SEDGWICK, 1984.

Distribution: Known only from Ko Libong, an island about 1–2 km off the western coast of southern Thailand.

Natural history: All *L. thaleri* sp. nov. types were collected from a roadside bank in a remnant patch of rainforest adjacent to a small rubber-tree plantation, only about 30 m away from the seashore.

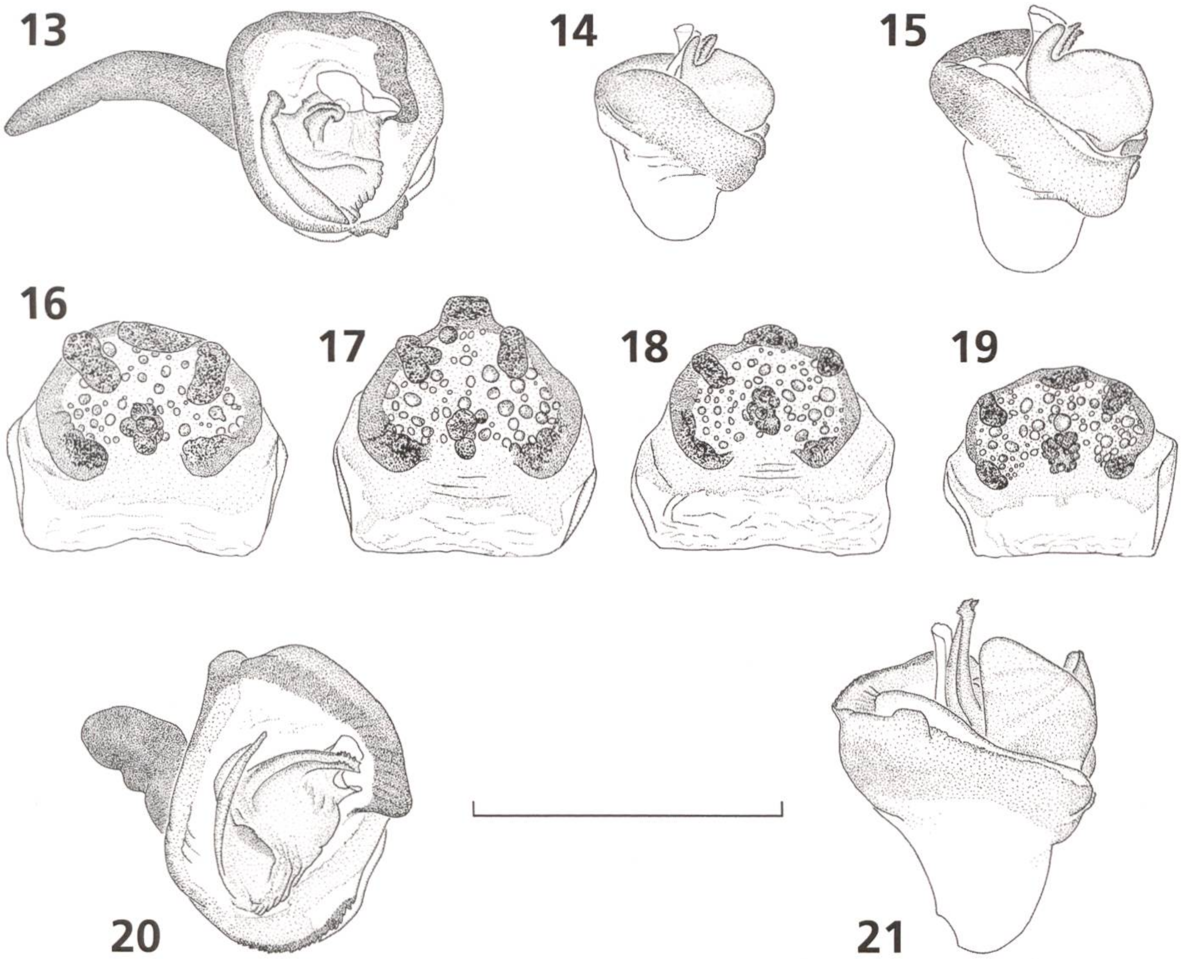
The burrows examined were up to 10 cm long, mostly Y-shaped (a few, mostly large burrows were unbranched), with two entrances closed by trapdoors. Main doors (entrance with signal lines) were up to 1.6 cm long and 2.9 cm wide in females, 1.1–1.3 cm long and 1.6–2.1 cm wide in penultimate males. Back doors (without signal lines) were slightly smaller. From the main entrance six to eight silken signal lines (up to 10 cm long) were spread over the soil surface, roots and stones. The spiders were sitting behind the main door during the daytime (on a rainy day) and reacted to disturbance by retreating to the bottom of the burrow or behind the back door. From there they withdrew outside upon further disturbance.

Five males reached maturity between September and November 2005, after one and a half to three and a half months in captivity; one male in early September 2006, after over 13 months in captivity. Egg laying (no observations) presumably takes place in December and January.

***Liphistius langkawi* PLATNICK & SEDGWICK, 1984 (Figs. 13–19)**

Liphistius langkawi; Platnick & Sedgwick (1984): 14–16, figs. 31–37; description of male and female. – Haupt (2003): 71; listing.

Material examined: West Malaysia, Kedah State, Pulau (= Island) Langkawi, specimens from three localities: 1) Gua Landak (= Porcupine Cave; probably the type locality; 6° 18' 14" N, 99° 51' 29" E), 60 m, east of Kuah; 2) road side near Beringin Beach, 10–30 m; 3) Temurun Waterfall (6° 26' 04" N, 99° 42'30" E), 60 m, north of Kuala Terian; collected 29 November to 3 December 2001: Five males (matured 29 June 2002, 8 October 2002, 18 October 2002, 9 July 2003, 28 July 2003); 12 females (moulted in September, October 2005, March,



Figs. 13–21: 13–19, *Liphistius langkawi* Platnick & Sedgwick (13, 14, male matured 9 September 2003; 15, male matured 8 October 2002); 20–21, *Liphistius murphyorum* Platnick & Sedgwick (male matured October 1985). – 13, 20: pedipalpal organ, distal view; – 14–15, 21: distal part of pedipalpal organ, ventral view; – 16–19: vulvae of four females, ventral view. Scale line 1.0 mm.

April 2006). One male and one female deposited in NHMW, all others in MHNG.

Variation: Range of measurements in males (n=5): Body length 8.7–15.3 mm, carapace length 4.0–5.6 mm, width 3.6–5.2 mm. Maximal measurements in females (n=12): Body length 16.7 mm, carapace length 5.4 mm, width 4.8 mm.

Remarks: The divided para-embolic plate with a spatulate and slightly bent part on the ventral side of the pedipalpus (Figs. 14–15; clearly visible in the illustrations of Platnick & Sedgwick 1984: figs. 32–35) of *L. langkawi* is exceptional in *Liphistius*. A similar structure is only known from *L. phuketensis* Schwendinger, 1998 (see Schwendinger 1998: fig. 5C, D; Schwendinger 1999: fig. 5C, D), which belongs to the same species-group but not to the same superspecies as *L. langkawi*, *L. thaleri* sp. nov. and *L. murphyorum*.

Natural history: *L. langkawi* was quite abundant at the three sites mentioned. Burrows of these spiders were found in quite different habitats: In wet, loamy soil at the dead end of Landak Cave (in complete darkness); in dry forest soil; in rock fissures filled with soil and on the surface of rock at the cave entrance; in very hard and dry soil on roadside banks exposed to the sun; and in compact soil under large stones and boulders in a small shady valley with a stream and a waterfall. Most burrows (of relatively large specimens) were simple, unbranched and with only one trapdoor. Several burrows were T- or Y-shaped, with two trapdoors and a main tunnel running into the depth of the soil (as illustrated for *L. trang* PLATNICK & SEDGWICK, 1984 by Schwendinger 1987: figs. 2, 4). A few small juveniles were seen living in sac-like retreats attached to rock surface. This is known from cave-dwelling *Liphistius* (see Klingel 1967) and from juveniles of other surface-dwelling species (e.g., *L. trang*, see Schwendinger 1987: fig. 5). Near Temurun Waterfall three specimens were collected from V-shaped burrows with two trapdoors, their entrances were running into short tunnels that met 1–2 cm below the soil surface but did not continue further into a combined main tunnel. When these burrows were dug up, the spiders retreated to a slightly enlarged chamber at the deepest point of the burrow (the bottom of the "V"). I have never observed such a burrow structure in other *Liphistius* species.

Main trapdoors (entrance with six to eight signal lines) were up to 1.6 cm long and 2.1 cm wide in females and 1.0–1.7 cm long and 1.6–2.2 cm wide in penultimate males (in other species they are usually smaller than in females!). Back doors (without signal lines) were slightly smaller. Signal lines attached to burrows inside Landak Cave were distinctly longer (up to 14 cm) than those attached to burrows outside the cave.

In December 2001 an old egg case, 1.7 cm long, 1.9 cm wide and 1.2 cm high, was found with mouldy remnants of eggs inside. Egg laying presumably took place several weeks earlier. After 7–20 months in captivity males reached maturity between late June and late October. Mature females moulted twice per year.

Liphistius murphyorum **PLATNICK & SEDGWICK, 1984** (Figs. 20–21)

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

Liphistius n. sp. A; Haupt (1983): 279, fig. 3a; description of male.

Liphistius murphyorum; Platnick & Sedgwick (1984): 16–18, figs. 38–44; formal description of species from male and female. – Haupt (2003): 71 (listing), fig. 44C (photo of male), fig. 46A, B (SEM of male pedipalpus).

Material examined: West Malaysia, Penang Island, Penang Hill (= Bukit Bendera), about 700 m, one male (MHNG), XII.1984 (matured October 1985).

Remarks: The specimen examined largely corresponds to the description and illustrations of the male holotype (not examined) given in Platnick & Sedgwick (1984). It differs from the holotype by larger size (body length 13.2 mm, carapace length 6.0 mm and width 5.4 mm; in holotype 10.6, not including chelicerae, 5.11 and 4.3 mm, respectively) and by constrictions on the subtegular apophysis (Fig. 20, cf. Platnick & Sedgwick 1984: fig. 42). Such constrictions are also visible in the specimen illustrated by Haupt (2003: fig. 46B).

Discussion

Taxonomy and relationships: The presence of a subtegular apophysis on the pedipalpal organ of *Liphistius* males is quite rare. Such an indistinct apophysis is present in *L. lordae* PLATNICK & SEDGWICK, 1984 (Myanmar) in the *birmanicus*-species group. A distinct subtegular apophysis is found in *L. bristowei* PLATNICK & SEDGWICK, 1984, *L. yamasakii* ONO, 1988 and *L. lannaianus* SCHWENDINGER, 1990 (all three from northern Thailand) in the *bristowei*-group, and in *L. tenuis* SCHWENDINGER, 1996 (from northeastern Thailand), *L. thaleri* sp. nov., two undescribed *Liphistius* species (all from southern Thailand), *L. langkawi* and *L. murphyorum* (both from West Malaysia) in the *trang*-group. *Liphistius tenuis* occurs about 650 km northeast of Ko Libong (the type locality of *L. thaleri* sp. nov.), occupies an isolated systematic position in the *trang*-group, and is probably closely related to congeners of superspecies B (according to Schwendinger 1996: 139–140 and 1998: 28, table 2) in central and eastern Thailand. *Liphistius langkawi*, *L. murphyorum* and *L. thaleri* sp. nov. occur in geographical proximity to each other on islands off the western coast of the Thai-Malaysian peninsula, and their females possess similar poreplates with paired protuberances on the ventral rim. These three species thus obviously belong to a distinct phylogenetic lineage, which is here called "superspecies D" (see Schwendinger 1998: table 2 for species in Thailand). Two undescribed species from other islands in southern Thailand belong here too. Within this lineage *L. murphyorum* is the least derived species, possessing a normal-sized paracymbium, a relatively short subtegular apophysis (Fig. 20) and an unmodified para-embolic plate in males (Fig. 21), as well as a relatively simple poreplate with only four small ventral protuberances in an anterior position on the poreplate rim in females (see Platnick & Sedgwick 1984: figs. 43–44). *Liphistius langkawi* and *L. thaleri* sp. nov. are most closely related to each other. Both have a strongly inflated paracymbium (Platnick &

Sedgwick 1984: figs. 38–39 and Figs. 2–3) and a strongly elongated subtegular apophysis on the pedipalpal organ of males (Fig. 13 and Figs. 2–4, 6–7), as well as more complicated poreplates with five to six distinctly elevated marginal protuberances in females (Figs. 16–19 and Figs. 8–12). *Liphistius langkawi* is clearly the most derived of these three species. It possesses a peculiar para-embolic plate, which is divided into a low, widely triangular or rounded part and a slightly curved, spatulate part (Figs. 14–15). A similar modification in *L. phuketensis* (not closely related) is less distinctly developed (see Schwendinger 1998: fig. 5c,d and Schwendinger 1999: fig. 5c,d). The anterior pair of ventral protuberances on the poreplate of females, still separated in *L. murphyorum* (Platnick & Sedgwick 1984: fig. 44) and *L. thaleri* sp. nov. (Figs. 8–12), has become more or less distinctly fused in *L. langkawi* (Platnick & Sedgwick 1984: fig. 37 and Figs. 16–19).

It is interesting to note that Ko Tarutao, which lies only about 8 km north of Pulau Langkawi (*L. langkawi*) and about 60 km south of Ko Libong (*L. thaleri* sp. nov.), houses an undescribed species that is not closely related to *L. langkawi* but belongs to a different lineage.

Biogeography*:* The islands off the coast of Thailand and peninsular Malaysia are rich in *Liphistius* species, many of them probably endemic to individual islands. The following described species are known from these islands: 1. *L. nesioticus* SCHWENDINGER, 1996 (Ko Chang), *L. phileion* SCHWENDINGER, 1998 (Ko Samet), *L. phuketensis* (Ko Phuket), *L. thaleri* sp. nov. (Ko Libong), *L. langkawi* (Pulau Langkawi), *L. murphyorum* (Pulau Penang), *L. desultor* SCHIÖDTE, 1849 (Pulau Penang), *L. tioman* PLATNICK & SEDGWICK, 1984 (Pulau Tioman). Several more, still undescribed *Liphistius* species occur on other islands in the region. Only *L. nesioticus* and *L. desultor* are also known from the mainland (Schwendinger 1996, Platnick & al. 1997); the same is probably also the case in *L. phuketensis*. Interestingly, *Liphistius* has never been reported from the well-investigated island of Singapore, and I also have not found these spiders there or on Indonesian islands south of Singapore (i. e. Pulau Bintan, Pulau Mapur, Pulau Lingga, Pulau Singkep and Pulau Belitung), nor did I find any mesothelids on Phu Quoc, an island off the southwestern coast of Vietnam. On the other hand, *Liphistius* occurs on Sumatra (but not on other islands in the Malay Archipelago), being represented there by the widely distributed *L. sumatranus* THORELL, 1890 – though not so widely as indicated by Haupt (2003: fig. 57). The northern locality on Haupt's distribution map shows Sibolga (possibly a confusion with Silago, which lies east of Padang, Western Sumatra Province), but no *Liphistius* records from there are known to me, nor have I found any traces of these spider near Sibolga or anywhere else in Northern Sumatra Province. *Liphistius sumatranus* possesses strongly autapomorphic structures in its genitalia, but appears more closely related to congeneric species of the *trang*-group in the western part of the Thai-Malaysian Peninsula and offshore island, than to *L. malayanus* ABRAHAM, 1923 and its close relatives in central and eastern peninsular Malaysia. For the occurrence of island-dwelling species of other mesothelid genera in southern Japan, see Haupt 2003: figs. 59–60.

Palaeobiogeography: The fossil record for mesothelid spiders is extremely poor. There is only one fossil that can be clearly attributed to this group: The Upper Carboniferous *Palaeothele montceauensis* (SELDEN, 1996) from France. Other spider fossils with a segmented opisthosoma from Carboniferous deposits in North America and Europe (Dunlop 1993, Selden 1996, Shear & Kukalová-Peck 1990, Dunlop & al. 2008) may or may not represent mesothelids (J. A. Dunlop personal communication). There is thus only fossil evidence for the presence of Mesothelae from the Palaeozoic of what then were tropical and subtropical regions of Euramerica (= "Old Red Continent"). The recently established arachnid order Uraraneida SELDEN & SHEAR, 2008, currently comprising *Attercopus fimbriungis* (SHEAR, SELDEN & ROLFE, 1987) from the Devonian Gilboa formation near New York (Selden & al. 1991) and *Permarachne novokshonovi* ESKOV & SELDEN, 2005 from a Russian "Lagerstätte" west of the Ural Mountains (Selden 1996, Eskov & Selden 2005), from within which the Araneae probably evolved, also lived in Euramerica. Therefore there is good reason to believe that the Mesothelae (and with them the entire Araneae) originated on this minor supercontinent. Euramerica was situated on the equator throughout the Devonian and Carboniferous. It collided with Gondwana in the late Carboniferous and became the northwestern part of Pangea.

Extant mesothelid spiders, on the other hand, occur only in East and Southeast Asia, from where no Palaeozoic arachnids are known. How did these spiders get from Europe to East and Southeast Asia? According to currently available palaeogeographical and palaeoclimatological data (Cox & Moore 2005, Rogers & Santosh 2004, Scotese 2002, Torsvik & Cocks 2004) there are two possibilities: (1) Through a southern route along the northern margin of Gondwana, or (2) through a northern route along the southern margin of plates that successively accreted to Euramerica as Laurasia formed. The southern route is quite unlikely as it was open only between the accretion of Euramerica to Gondwana in the late Carboniferous and the rift of the Sibumasu terrane (eastern Myanmar, western Thailand, northwestern peninsular Malaysia and a part of Sumatra; Golonka & al. 2006) from the northeastern margin of Gondwana in the Permian. During that period much of northeastern Gondwana was situated in high southern latitudes and was largely covered by epicontinental seas and glaciers. Other areas that harbour mesothelid spiders today, Annamia (eastern peninsular Malaysia, eastern Thailand, part of eastern China and Indochina) and South China, then were isolated terranes in the Palaeotethys, situated near the equator. South China, Annamia and Sibumasu accreted to southeastern Laurasia in the late Triassic (Scotese 2002; mid to late Mesozoic according to Rogers & Santosh 2004). It is quite likely that not long after this geological event mesothelid spiders arrived through the northern route in this warm and humid region, where they persist until today.

All islands known to harbour extant mesothelid spiders lie quite close to mainland Southeast Asia and were connected to it by land bridges exposed by lowered sea levels during cryogenous periods in the Pleistocene. Considering also the morphological similarities between these island species and those of the mainland, I believe that their ancestors have dispersed from mainland Southeast Asia to nearby islands during glacial periods. *Liphistius phileion* (and also other congeners) lives in dry, exposed coastal habitats just above the high tide line (see Schwendinger 1998: 25) and is thus pre-adapted to colonize dry-fallen land once vegetation has sprung up. This would explain why *Liphistius* has never been found on any of the main islands in the Malayan Archipelago apart from Sumatra. The other islands are simply too far away from the mainland to be reached by these slowly dispersing spiders during the relatively short periods of lowered sea levels. The occurrence of mesothelid spiders on the islands of southern Japan, on the other hand, is probably not the result of immigration via landbridges that formed in the mid- to late Pleistocene, but more likely predates the separation of the Japanese island arc from mainland Asia in the Tertiary (Rogers & Santosh 2004).

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Address of the author:

Dr. Peter J. Schwendinger
Département des arthropodes et d'entomologie I
Muséum d'histoire naturelle de la Ville de Genève
Case postale 6434
CH–1211 Genève 6, Switzerland