

ON THE MONOPHYLY OF THE SPIDER SUBORDER MESOTHELAЕ (ARACHNIDA: ARANEAE)

NORMAN I. PLATNICK AND PABLO A. GOLOBOFF

Department of Entomology, American Museum of Natural History,
Central Park West at 79th Street, New York, New York 10024 and
Museo Argentino de Ciencias Naturales "Bernardino Rivadavia,"
Av. Angel Gallardo 470, 1405 Buenos Aires, Argentina

Abstract.—A newly observed character, apparently unique to liphistiid spiders, supports a hypothesis of their monophyly. Flattened spurs situated distally on the prolateral and retrolateral sides of tibiae I–III can contact slightly raised, oval, unsclerotized areas situated proximally on the sides of metatarsi I–III. The character is found in juvenile and adult females and in juvenile males, and may function as a proprioceptor of lateral leg deflection.

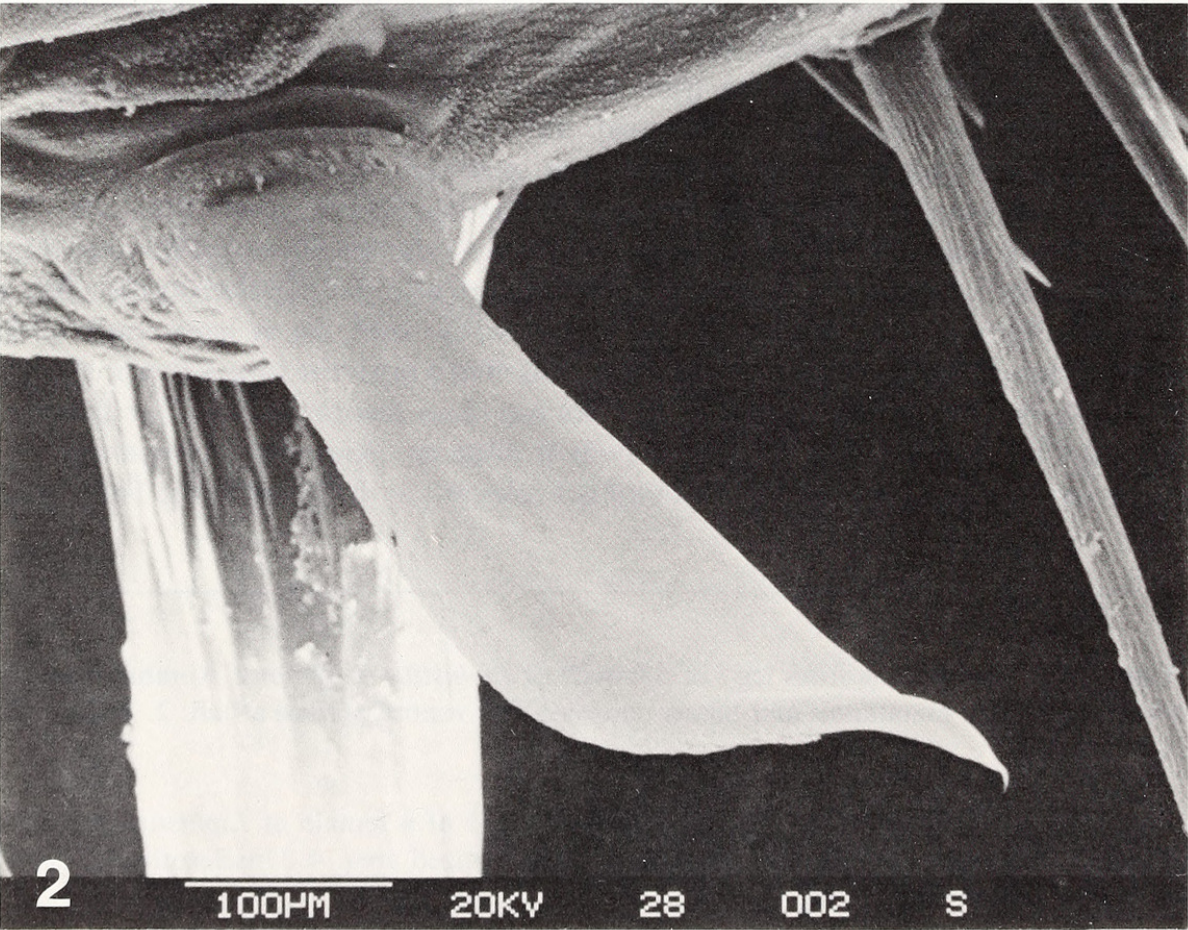
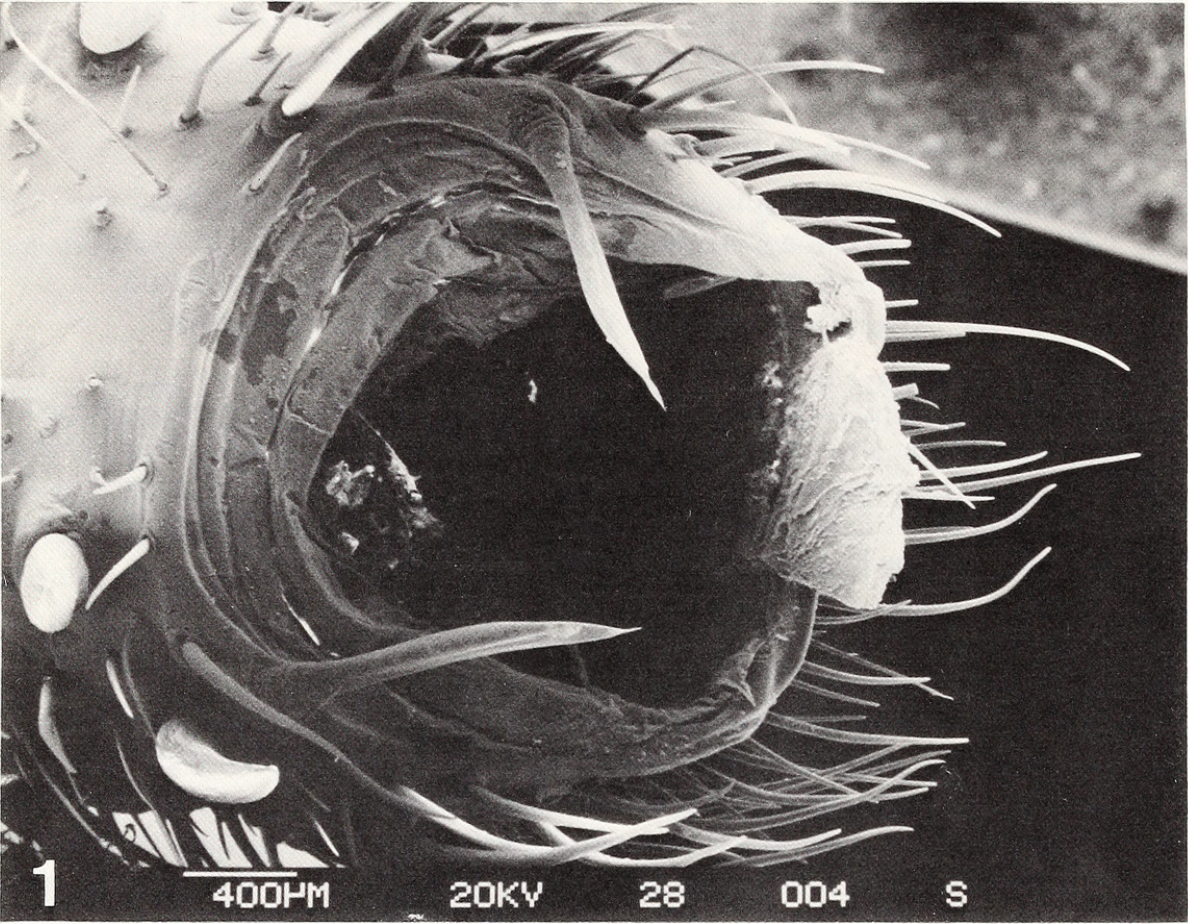
Liphistiids have long been regarded as the most primitive of living spiders, primarily because of their retention of such obviously plesiomorphic features as a full complement of abdominal tergites and two pairs of booklungs. As indicated by Haupt (1983), hypotheses of monophyly are particularly crucial for groups that (like the Mesothelae) were classically recognized largely or entirely on the basis of plesiomorphies. Platnick and Gertsch (1976) examined the Mesothelae and concluded, on the basis of four putative synapomorphies, that the group is indeed monophyletic. Haupt (1983, fig. 15) accepted this conclusion and used those four synapomorphies at the base of a cladogram of the three genera he recognized within the group.

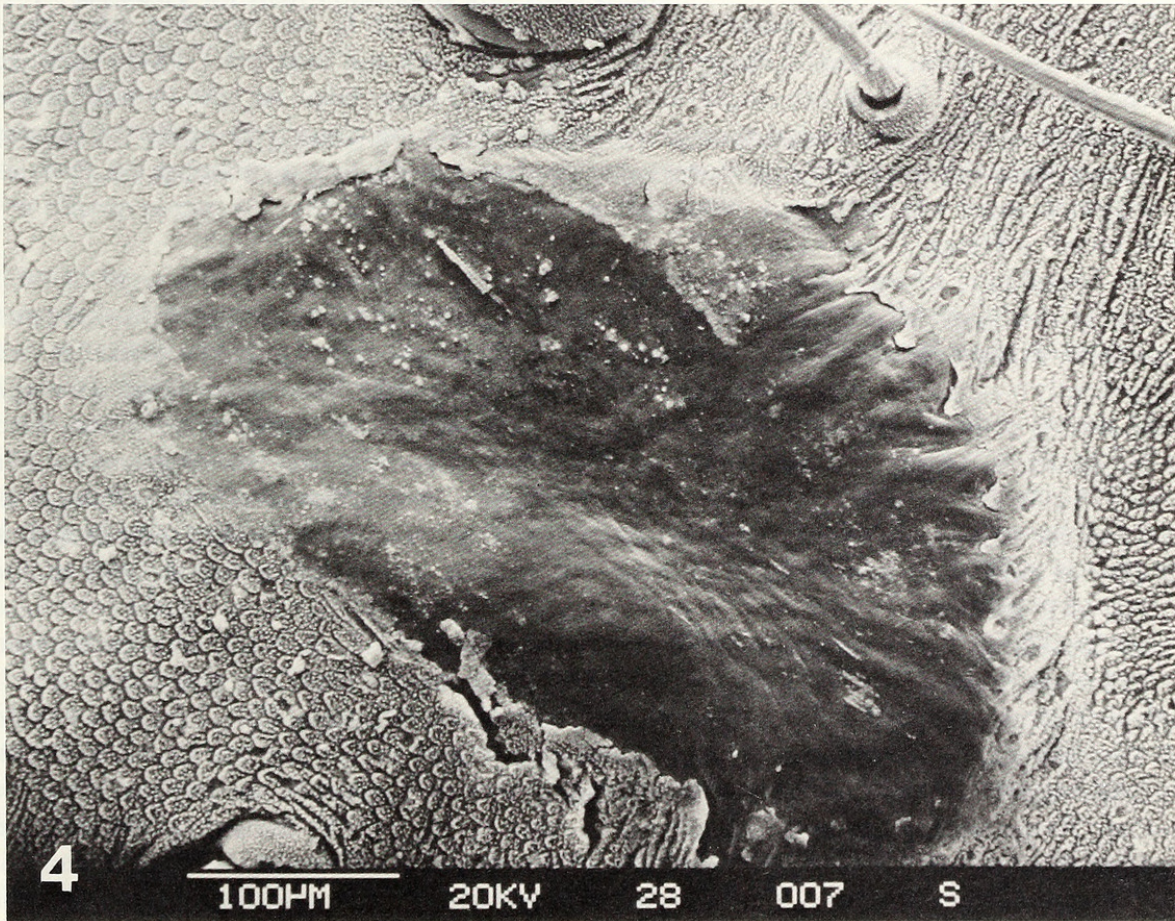
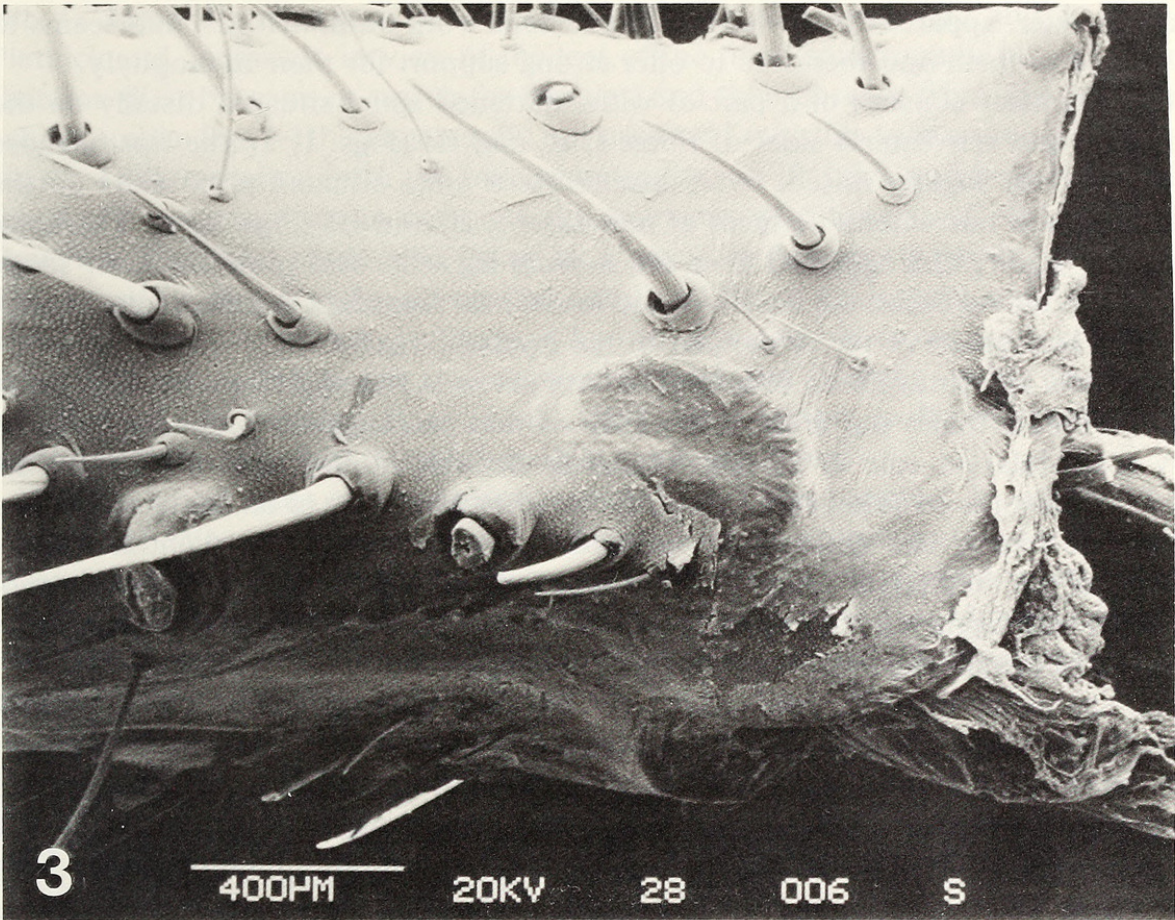
Haupt (1983, p. 289) also put forward, however, a list of conceivable objections to those four putative synapomorphies. For example, with regard to Platnick and Gertsch's first character (invaginated fourth coxae), Haupt conjectured that those invaginations might be functionally correlated with the (plesiomorphic) retention of the first opisthosomal sternite, and hence might also be plesiomorphic. But the relevant outgroup (the Amblypygi) belies that conjecture, for at least some amblypygids do retain the first abdominal sternite (often in a bipartite form), but nonetheless lack invaginations on the fourth coxae. Rather than respond in similar fashion to Haupt's other conceivable objections (which even he ultimately disregarded in his cladogram), we present instead new evidence relevant to the hypothesis. This consists

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Figs. 1, 2. Tibial spurs from leg I of a female of *Liphistius malayanus* Abraham. 1. Distal view of tibia, with metatarsus and tarsus removed and ventral surface at left. 2. Inner surface of a tibial spur.

Figs. 3, 4. Metatarsal unsclerotized area from leg I of a female of *Liphistius malayanus* Abraham. 3. Metatarsus, showing location of unsclerotized area. 4. Unsclerotized area; note lack of denticulate sculpturing.





of a character, apparently overlooked in previous work on liphistiids, that seems to be unique to them and therefore to offer strong support for their monophyly.

The character consists of a pair of wide, flattened spurs situated distally on the prolateral and retrolateral sides of tibiae I, II, and III (Figs. 1, 2); the tips of those spurs override slightly raised, oval, unsclerotized areas situated proximally on the prolateral and retrolateral surfaces of metatarsi I, II, and III (Figs. 3, 4). The tibial spurs are readily distinguished from the normal leg setae and spines by their shape and unarticulated bases; the unsclerotized metatarsal areas lack the denticulate sculpturing characteristic of the remainder of the liphistiid leg cuticle.

The tibial spurs have been observed in both juvenile and adult females; they occur in penultimate males but are lost in adults of that sex, suggesting that they do not play a stridulatory role in mating (scanning electron micrographs also reveal no rasping structures on either the inner surface of the tibial spurs or on the unsclerotized metatarsal areas). The spurs are so situated, however, that even a slight lateral deflection of the metatarsus relative to the longitudinal axis of the tibia presses one or the other spur against a metatarsal area. It seems likely, therefore, that the structures function as proprioceptors of lateral leg deflection.

The character was first observed (by the second author) in a female of *Liphistius malayanus* Abraham, and we have subsequently been able to confirm its presence in *L. birmanicus* Thorell, *L. lordae* Platnick and Sedgwick, *L. bristowei* Platnick and Sedgwick,¹ *L. yangae* Platnick and Sedgwick, *L. langkawi* Platnick and Sedgwick, *L. murphyorum* Platnick and Sedgwick,¹ *L. desultor* Schiödte, *L. sumatranus* Tho-

¹ Unfortunately, two specific names, *Liphistius bristowei* and *L. murphyorum*, have been validated twice in recent papers by Haupt (1983) and by Platnick and Sedgwick (1984). Although the issue (December 1983) of the journal including Haupt's paper bears no specific publication date, his usage of those names apparently has priority, for that issue was received by the Library of the American Museum of Natural History on February 4, 1984, four days before the Platnick and Sedgwick paper was published. Nonetheless, the authorship of the two names should not be attributed to Haupt.

Upon completion of their *Liphistius* revision, Platnick and Sedgwick sent a copy of their manuscript to Haupt, for they proposed a relimitation of the genus vis-à-vis *Heptathela* and Haupt had worked extensively with that genus (as it happened, those authors and Haupt had independently reached the same conclusion regarding the generic limits). Haupt was kind enough to send several helpful comments on the manuscript, perhaps the most useful of which indicated that the Zoologisk Museum, Copenhagen, housed a male *Liphistius* from the type locality of a species Platnick and Sedgwick were describing as new on the basis of females only (*L. bristowei*). Thanks to the prompt assistance of Dr. H. Enghoff of that institution, Platnick and Sedgwick were able to borrow the male specimen in time to include it in their published paper as the holotype of *L. bristowei*.

From the Platnick and Sedgwick manuscript, Haupt determined that he had misidentified two specimens in his paper, then already in proofs. One was the male just mentioned, which Haupt had erroneously placed as the male of *L. birmanicus* Thorell. The other was a male from Penang Island, Malaysia, belonging to *L. murphyorum*; like Murphy and Platnick (1981), Haupt had misidentified a male of this small species as that of the much larger *L. desultor* Schiödte. Haupt sent Platnick and Sedgwick a copy of his proofs, indicating that he was correcting these two misidentifications and listing the specimens as merely "n. sp. A" and "n. sp. B." In the published version, both headings include descriptions and references to illustra-

rell, *L. batuensis* Abraham, *L. panching* Platnick and Sedgwick, and *L. tioman* Platnick and Sedgwick. In view of the loss of the tibial spurs in adult males (which abandon their burrows to search for females) and their absence from the fourth legs (which, unlike legs I–III, are generally not used by *Liphistius* to monitor the “fishing lines” of silk radiating from the burrow entrance; see Platnick and Sedgwick, 1984, figs. 4, 5), it is tempting to associate the character with the use of “fishing lines.” However, the tibial spurs also occur in *Heptathela kimurai* Kishida, *H. sinensis* Bishop and Crosby, *H. schensiensis* (Schenkel), *H. bristowei* Gertsch, and “*Ryuthela*” *nishihirai* (Haupt),² which (so far as is known) construct burrows without “fishing lines.” Moreover, the fourth metatarsi of females and juvenile males, and all the metatarsi of adult males, occasionally show what appear to be remnants of the unsclerotized areas, even though the tibial spurs are absent.

Both the tibial spurs and metatarsal unsclerotized areas seem to be unique to the Mesothelae. We are unaware of similar structures in any other group of spiders, and a search for possible homologs in amblypygids and in the more plesiomorphic families of mygalomorphs (Atypidae, Antrodiaetidae, Mecicobothriidae, Microstigmatidae, and Hexathelidae) has been unsuccessful. We therefore regard the structures as a fifth synapomorphy of the suborder.

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tions that would be sufficient to validate names had any been given there; “n. sp. A” is given only a “Locus typicus” but under “n. sp. B” a holotype is designated (although, of course, only a specific name can actually have a holotype).

No nomenclatorial difficulties arise from this portion of Haupt’s treatment. However, Haupt had indicated that he also planned to add a final note to his proofs saying that “n. sp. A” and “n. sp. B” would be described as *L. murphyorum* and *L. bristowei*, respectively, in the Platnick and Sedgwick revision. Those authors immediately (September 20, 1983) requested that he *not* add such a note, and repeated that request in another letter of December 2, 1983. Despite their informing Haupt on both occasions that the addition of such a note, in conjunction with his brief treatments of “n. sp. A” and “n. sp. B,” would be sufficient to validate the names, the published version of Haupt’s paper does include the final note (p. 293). That note makes it clear, however, that Platnick and Sedgwick are alone responsible for the names, and Haupt has informed us that he intends to request the International Commission of Zoological Nomenclature to suppress his usage of the two names. Accordingly, we here attribute the names to their legitimate authors.

² Raven (in press) rejects Haupt’s proposal of a separate genus for this species and hence also Haupt’s proposal of a separate family Heptathelidae.

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