

Phylogenetic placement of the enigmatic genus *Labullinyphia* van Helsdingen, 1985, with redescription of *Labullinyphia tersa* (Simon, 1894) from Sri Lanka (Araneae: Linyphiidae)

Autor(en): **Benjamin, Suresh P. / Hormiga, Gustavo**

Objektyp: **Article**

Zeitschrift: **Contributions to Natural History : Scientific Papers from the Natural History Museum Bern**

Band (Jahr): - **(2009)**

Heft 12/1

PDF erstellt am: **12.07.2024**

Persistenter Link: <https://doi.org/10.5169/seals-786966>

Nutzungsbedingungen

Die ETH-Bibliothek ist Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Inhalten der Zeitschriften. Die Rechte liegen in der Regel bei den Herausgebern.

Die auf der Plattform e-periodica veröffentlichten Dokumente stehen für nicht-kommerzielle Zwecke in Lehre und Forschung sowie für die private Nutzung frei zur Verfügung. Einzelne Dateien oder Ausdrucke aus diesem Angebot können zusammen mit diesen Nutzungsbedingungen und den korrekten Herkunftsbezeichnungen weitergegeben werden.

Das Veröffentlichen von Bildern in Print- und Online-Publikationen ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Die systematische Speicherung von Teilen des elektronischen Angebots auf anderen Servern bedarf ebenfalls des schriftlichen Einverständnisses der Rechteinhaber.

Haftungsausschluss

Alle Angaben erfolgen ohne Gewähr für Vollständigkeit oder Richtigkeit. Es wird keine Haftung übernommen für Schäden durch die Verwendung von Informationen aus diesem Online-Angebot oder durch das Fehlen von Informationen. Dies gilt auch für Inhalte Dritter, die über dieses Angebot zugänglich sind.

Phylogenetic placement of the enigmatic genus *Labullinyphia* VAN HELSDINGEN, 1985, with redescription of *Labullinyphia tersa* (SIMON, 1894) from Sri Lanka (Araneae: Linyphiidae)

Suresh P. Benjamin & Gustavo Hormiga

ABSTRACT

Contrib. Nat. Hist. 12: 161–181.

The endemic Sri Lankan spider genus *Labullinyphia* VAN HELSDINGEN, 1985 (Linyphiidae) is revised and the male of *Labullinyphia tersa* (SIMON, 1894) is described for the first time. We provide a detailed description of the genital and somatic morphology of both sexes of *L. tersa*. Based on a cladistic analysis of morphological data we hypothesize that *Labullinyphia* is a member of the subfamily Erigoninae. *L. tersa* is found in the highly fragmented rain forests of Sri Lanka's central highlands.

Introduction

Sri Lanka is considered to be part of the ancient Deccan Plate and is separated from the Indian mainland by a shallow ocean strip called the Palk Strait. Nevertheless, Sri Lanka possesses a diverse, highly endemic spider fauna, unusual for an island of its size (Benjamin 2000; Benjamin & Jocqué 2000; Benjamin 2001; Benjamin 2004; Huber & Benjamin 2005). Sri Lanka's endemic species are concentrated mostly in the small remnants of rain forest, in the southwest, and in the central highlands. Unfortunately, the lack of detailed faunistic and taxonomic studies hinders our understanding of these patterns of endemism. Here we provide a description of an endemic linyphiid species from Sri Lanka's central highlands. This study is part of an ongoing island-wide survey of spider diversity.

Labullinyphia VAN HELSDINGEN, 1985 is a spider genus of enigmatic phylogenetic position within Linyphiidae. *Labullinyphia tersa* (SIMON, 1894) was first described based on a small series of adult females. Simon (1894: 691) placed it within the genus *Linyphia*, perhaps influenced by its general somatic appearance, although he pointed out that the tibial spination pattern was like that of *Erigone* (it is very unlikely that Simon studied the remarkable internal

epigynal morphology of this species, although some of the copulatory duct coils can be seen through the cuticle). Van Helsdingen (1985) studied the syntype series of *L. tersa* (consisting of seven adult females and one subadult male) and concluded that the species was misplaced in *Linyphia*, erecting then the new genus *Labullinyphia* to accommodate this single species. Like Simon, van Helsdingen noted the presence of a single retrodorsal spine in tibia III and IV, a character typically found in many erigonine taxa, but argued against the placement of *Labullinyphia* in Erigoninae on the basis of its complex double-coiled epigynal morphology which, he pointed out, was reminiscent of the epigyna of *Labulla*, *Microlinyphia* and *Frontinellina*, and unknown in its complexity to him in any erigonine. To van Helsdingen (1985: 16), the epigynal morphology of *Labullinyphia tersa* suggested that the male of this species should have a "long and slender" embolus. He also predicted: "the availability of the male would greatly help to establish relationships".

We have been able to study several male and female specimens of *Labullinyphia tersa*, including some specimens recently collected by the first author. Detailed study of these specimens, particularly of the previously undescribed male, has helped to resolve the phylogenetic placement of this interesting species.

Material and Methods

Morphological methods are described in detail in Hormiga (2000; 2002). The taxonomic descriptions follow the format of Hormiga (2002). Specimens were examined and illustrated using a Leica MZ16A and a MZAPO stereoscopic microscope, with a camera lucida. Further details were studied using a Leica DMRM compound microscope with a drawing tube. Digital microscope images were recorded using a Nikon DXM1200F camera attached to a Leica MZ16A stereoscope and edited using the software package Auto-Montage®. A LEO 1430VP scanning electron microscope was also used to study and document morphological features. Left structures (palps, legs, etc.) are depicted unless otherwise stated. Most hairs and macrosetae are usually not depicted in the final palp and epigynum drawings. All morphological measurements are given in millimeters. Somatic morphology measurements were taken using a scale reticule in the dissecting microscope. Eye diameters are taken from the span of the lens. The cephalothorax length and height were measured in lateral view and its width was taken at the widest point. Similarly, the abdomen length was measured in lateral view and the width at the widest point as seen from a dorsal view. The measurements of the abdomen are

only approximations, because the abdomen size changes more easily in preserved specimens than do other more sclerotized parts (e.g. the chelicerae). The total length was measured in lateral view and is also an approximation, because it involves the size of the abdomen and its relative position. Approximate leg article lengths were measured in lateral view, without detaching the legs from the animal, by positioning the article being measured perpendicularly. The position of the metatarsal trichobothrium is expressed as in Denis (1949). Female genitalia were excised using surgical blades or sharpened needles. The specimen was then transferred to methyl salicylate (Holm 1979) for examination under the microscope, temporarily mounted as described in Grandjean (1949) and Coddington (1983). Male palps examined with the SEM were first excised and transferred to a vial with 70% ethanol and then cleaned ultrasonically for 1–3 min. The specimen was then transferred to absolute ethanol and left overnight. After critical point drying, the specimens were glued to rounded aluminum rivets using an acetone solution of polyvinyl resin (Paraloid B72) and then Au/Pd coated for examination in the SEM. For examination of the tracheal system the non-chitinous abdominal tissue was digested with SIGMA Pancreatin LP 1750 enzyme complex (Alvarez-Padilla & Hormiga, 2008), in a solution of sodium borate prepared following methods described in Dingerkus & Uhler (1977). The specimen was then stained using chlorazol black, immersed in distilled water and studied using transmitted light.

The following anatomical abbreviations are used in the text and figures; institutional abbreviations used in the text are given in the acknowledgements section.

Male palp:

CL	column
DSA	distal suprategular apophysis
E	embolus
MSA	marginal suprategular apophysis
P	paracymbium
PT	protegulum
R	radix
SPT	suprategulum
ST	subtegulum
T	tegulum

Epigynum:

CD	copulatory duct
----	-----------------

FD	fertilization duct
S	spermatheca
TP	turning point of copulatory duct

Cladistic analysis

Character Matrix

Taxa: We used a character-matrix cladistic approach to test the subfamilial placement of *Labullinyphia* within Linyphiidae. Van Helsdingen (1985) had hypothesized, at least implicitly, that *Labullinyphia* could be close to *Labulla*, *Microlinyphia* or *Frontinellina* (based in the shared similarities of the female genitalic morphology). A recent cladistic study on the phylogenetic placement of *Labulla* (Hormiga & Scharff 2005) provides a starting point for the search of the closest relative of *Labullinyphia*. Thus, we have used the character matrix of Hormiga & Scharff (2005) as it includes representative species of the genera *Labulla* and *Microlinyphia*, it also covers a sample of taxa of the most widely accepted linyphiid subfamilies (Stemonyphantinae, Mynogleninae, Erigoninae, Linyphiinae), as well as several araneoid outgroups. A cursory examination of the male palp of *Labullinyphia tersa* suggests that this species could very well be a member of the Erigoninae (e.g., it has a protegulum and a retrolateral tibial apophysis). Consequently, we have added *Leptorhoptrum robustum* (WESTRING, 1851) to the character matrix (for a total of three erigonine species) because of its basal cladistic placement within Erigonine (Miller & Hormiga 2004). Our character matrix includes 19 linyphiid species (in 16 genera), and attempts to represent morphological diversity at the subfamilial level. Outgroup taxa outside Linyphiidae include Pimoidae (represented by five species in two genera) and representatives of three araneoid families (Tetragnathidae, Theridiosomatidae and Theridiidae). The precise phylogenetic placement of *Labullinyphia* within Erigoninae (the largest subfamily within the Linyphiidae) or the relationships among the main linyphiid lineages are beyond the modest scope of this study.

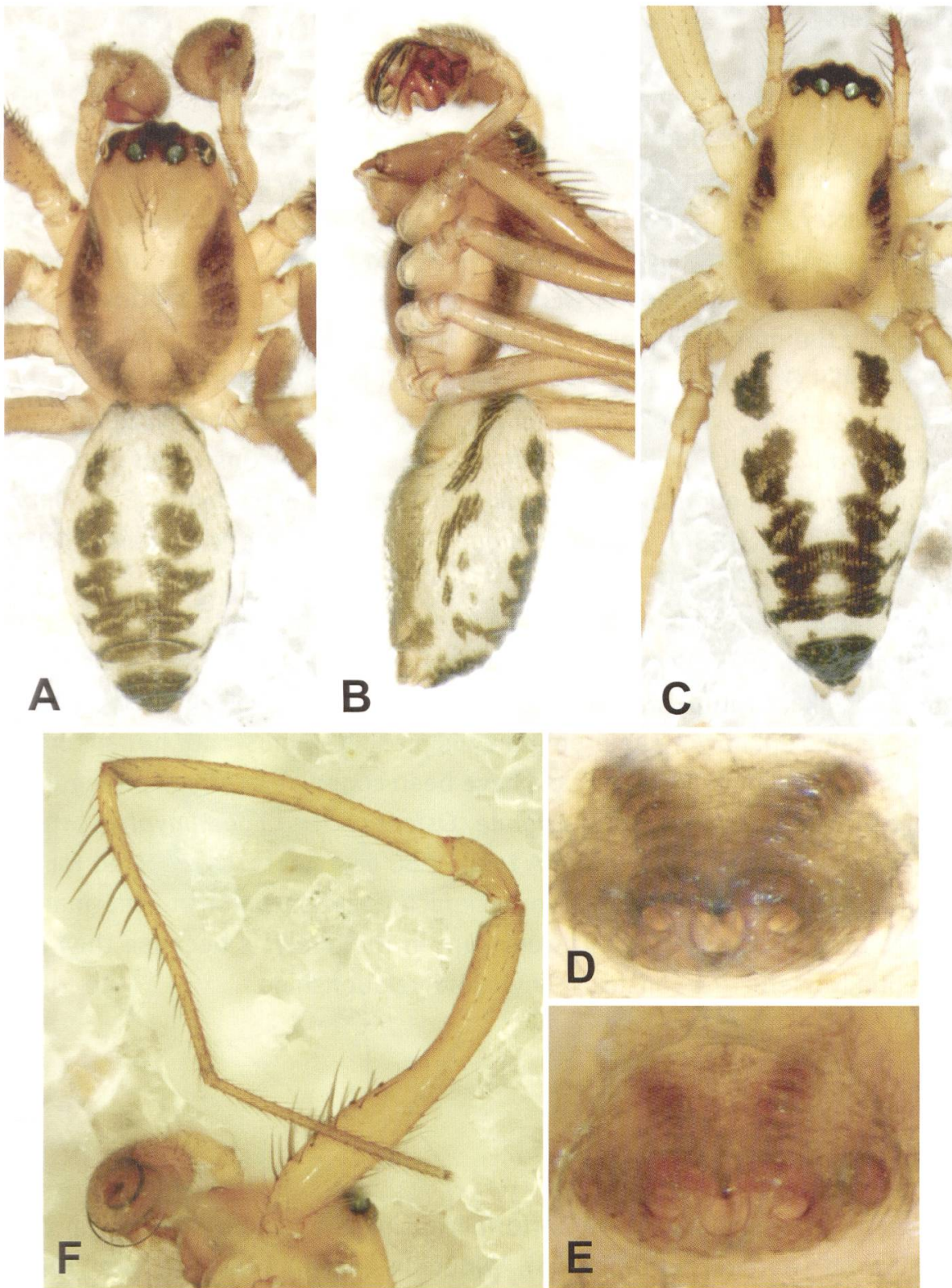


Fig. 1. *Labullinyphia tersa* from Agrabopath (A–D, F) and Hakgala (E). – A: male, dorsal; – B: same, lateral; – C: female, dorsal; – D, E: epigynum, ventral; – F: male leg I, lateral.

Characters

We have used the 78 characters of the matrix of Hormiga & Scharff (2005). To those we have added two (characters 79 and 80) because they have been shown to be important for erigonine systematics.

Character 79 describes the presence (state 1) of epiandrous fusules. Most adult araneoid males have these fusules (which they use to spin their sperm web), but they are absent in the Erigoninae. The loss of the epiandrous fusules supports the monophyly of Erigoninae (Hormiga 2003; Hormiga & Scharff 2005; Miller & Hormiga 2004). In our matrix all taxa are scored as having the fusules (state 1), with exception of *Erigone*, *Ostearius*, *Leptorhoptrum* and *Labullinyphia*, which lack them. This character remains unstudied in the following species in our character matrix (which have been coded as '?'): *Pimoa rupicola* (SIMON, 1884), *Pimoa lihengae* GRISWOLD, LONG & HORMIGA, 1999 and *Pecado impudicus* (DENIS, 1945).

Character 80 describes the presence (state 1) of the protegulum. The protegulum (Holm 1979; Hormiga 2002; Miller & Hormiga 2004) is a membranous, often sac-like, protuberance of the ectoapical part of the tegulum. Its function remains unknown. The protegulum is present in most, but not all, erigonine spiders. In our sample all taxa have been coded as lacking a protegulum (state 0) with the exception of *Erigone*, *Ostearius*, and *Labullinyphia* (which have been coded as '1'; Fig. 5E). A total of 80 characters were scored for 28 taxa (see Appendix 1). A total of four characters are parsimony uninformative in this taxonomic context, but were kept in the analysis because they are potentially useful to reconstruct 'linyphioid' relationships.

Analysis

The parsimony analyses were performed using the computer program TNT version 1.1 (Goloboff et al., 2003). WinClada version 1.00.08 (Nixon 1999) and Mesquite version 1.12 (Maddison & Maddison 2006) were used to study character optimizations on the cladograms and to build and edit the character matrix, respectively. Ambiguous character optimizations were resolved so as to favor reversal or secondary loss over convergence (Farris optimization or ACCTRAN). The 15 multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; (Fitch 1971)). TNT was used to calculate Bremer support indices (Bremer 1988; Bremer 1994) holding 50,000 trees to search for suboptimal trees up to five steps longer. Successive char-

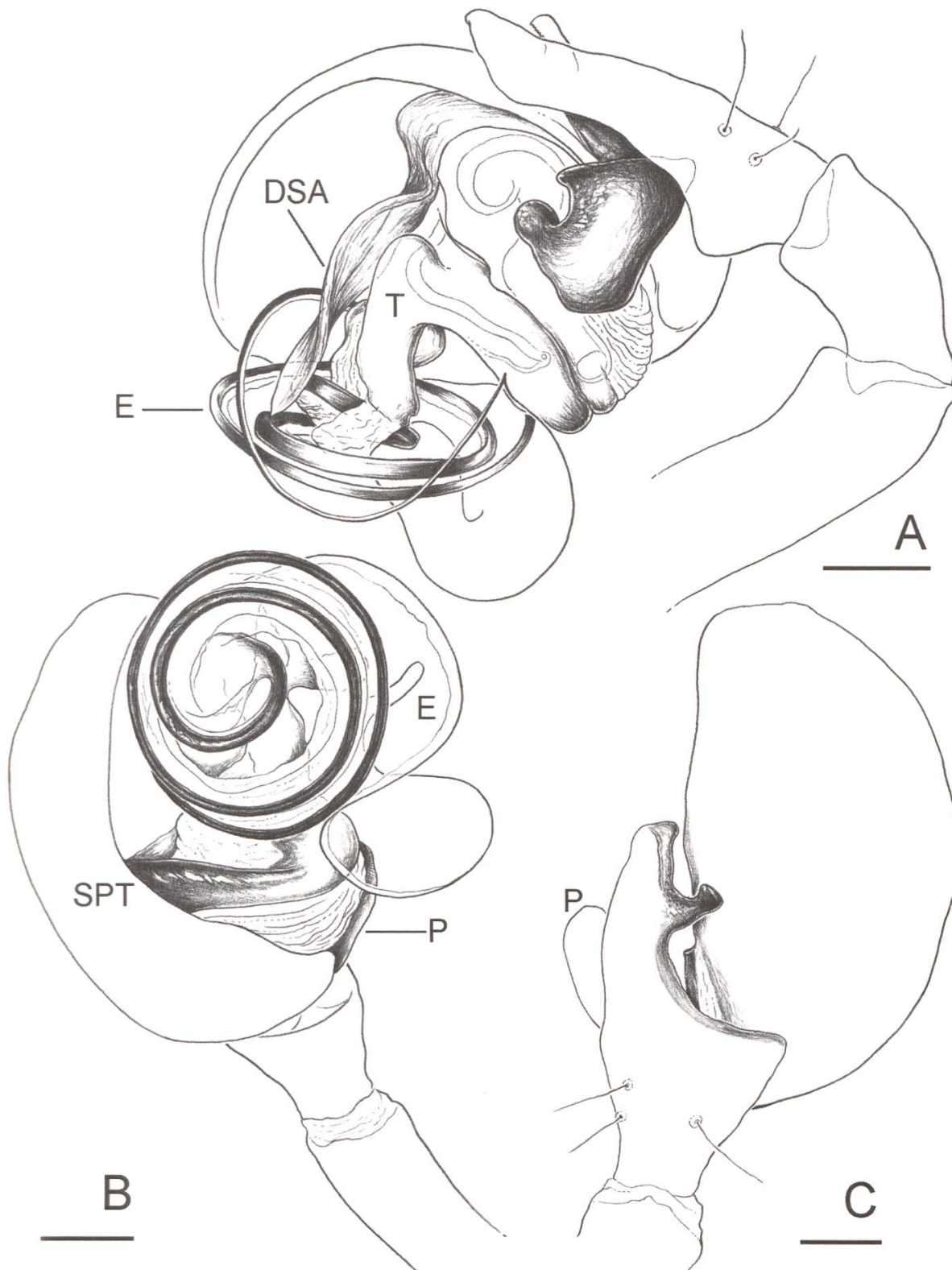


Fig. 2. *Labullinyphia tersa* from Agrabopath, male palp. – A: ectal; – B: mesoventral; – C: tibial apophysis, dorsal. Scale bars = 0.1 mm.

acter weighting was implemented in NONA version 2.0 (Goloboff 1993) with the macro 'swt.run' (which uses the consistency index as a weighting function).

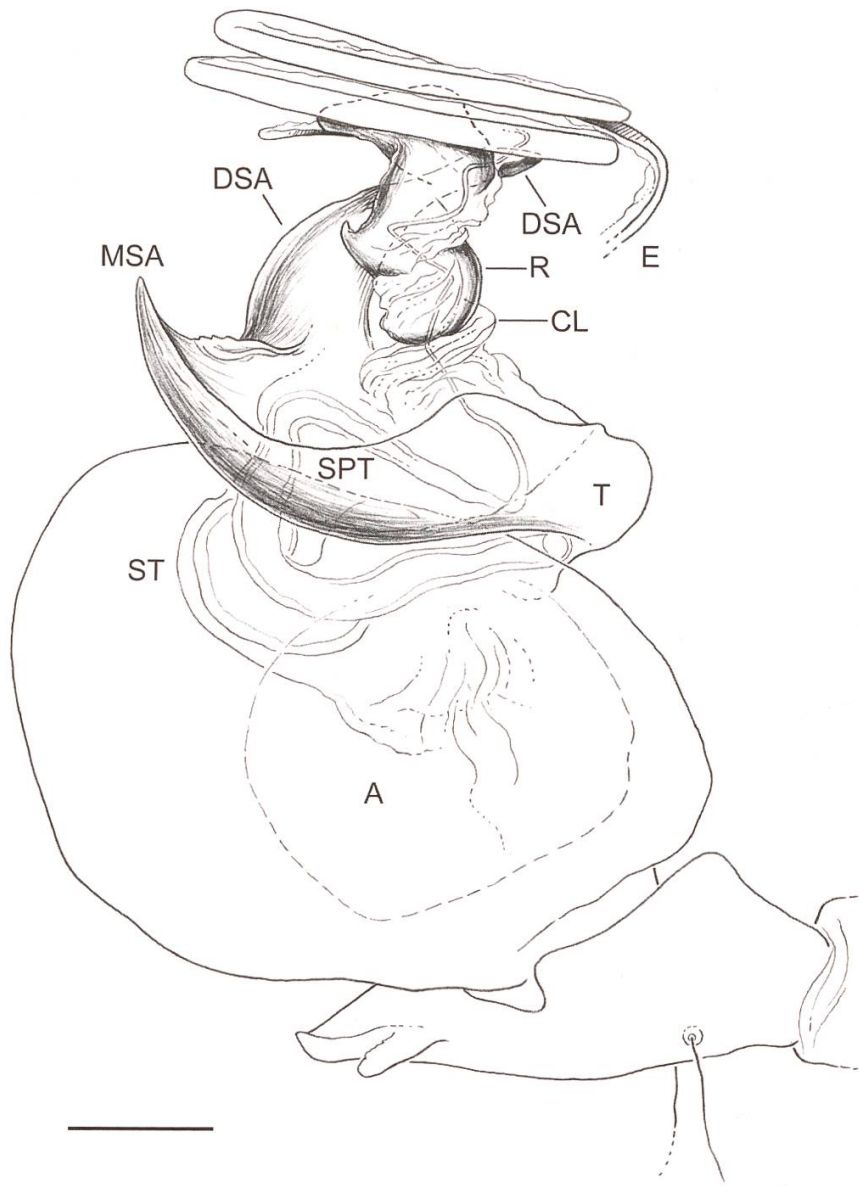


Fig. 3. *Labullinyphia tersa* from Agrabopath, male palp partially expanded (distal part of embolus not rendered). Scale bar = 0.1 mm.

Results

Systematics

Linyphiidae Blackwall, 1895

Labullinyphia VAN HELSDINGEN, 1985

Type species: *Linyphia tersa* SIMON, 1894 (by monotypy)

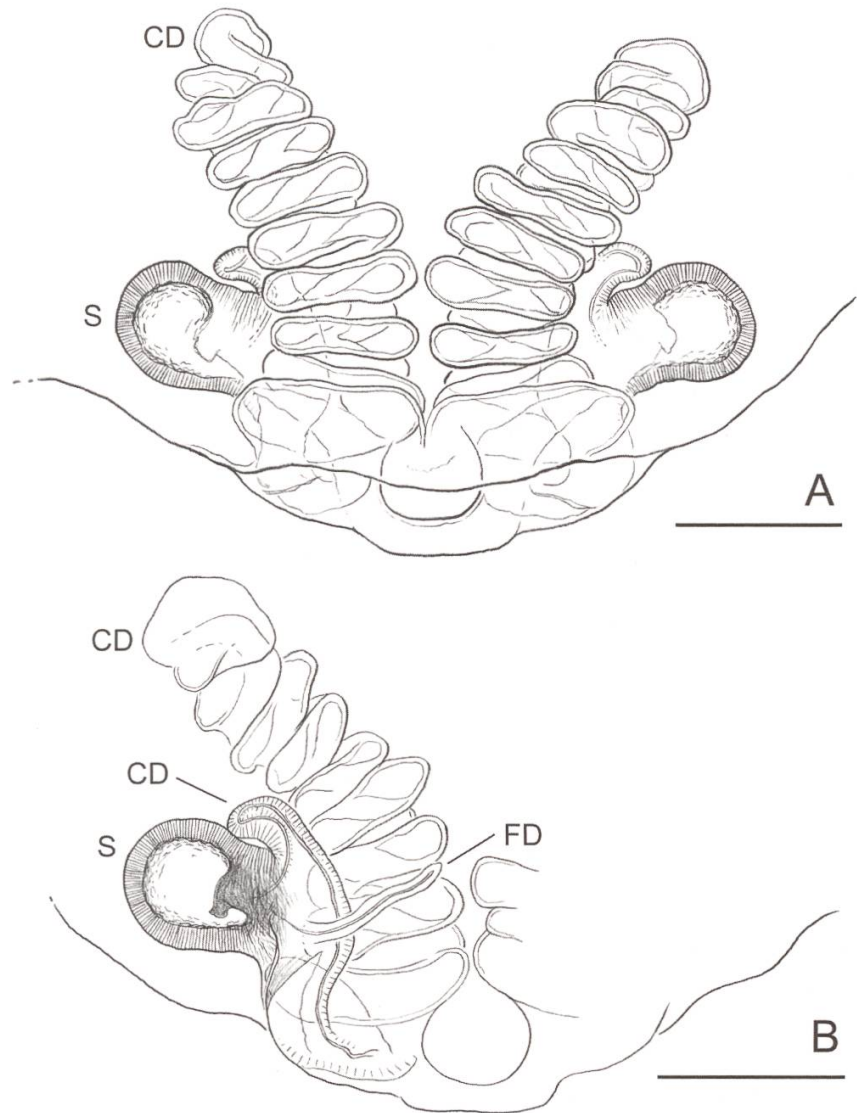
Diagnosis: See species section below.

Description: See species section below.

Composition: One species, *Labullinyphia tersa* (SIMON, 1894).

Distribution: Sri Lanka.

Fig. 4. *Labullinyphia tersa* from Agrabopath, cleared epigynum.
 – A: ventral;
 – B: dorsal (right side not depicted).
 Scale bars = 0.1 mm.



***Labullinyphia tersa* (SIMON, 1894)** (Figs. 1–9)

Linyphia tersa; Simon (1894): 691. Type: one female lectotype and 11 other females from the type-series, all from Sri Lanka (deposited at MNHN; examined).

Labullinyphia tersa; van Helsdingen (1985): 16. Millidge (1993): 146.

Diagnosis: Males can be distinguished from other erigonine species by the following combination of characters: protegulum consisting of a long sclerotized stalk with a distal membranous region (Figs. 2A, 5E); absence of embolic membrane; embolus very long and filiform, coiling about two and a half times into concentric spiral turns in the apical region of the palp before continuing to curve out of plane (Figs. 2A–B, 5D–E); femur I with a thickened basal region provided with large macrosetae (Figs. 1F, 7F); and metatarsus I sinuous, with a dorsal row of large macrosetae of diminishing length (Fig. 1F). Females can be distinguished from other erigonine species by the long spirally

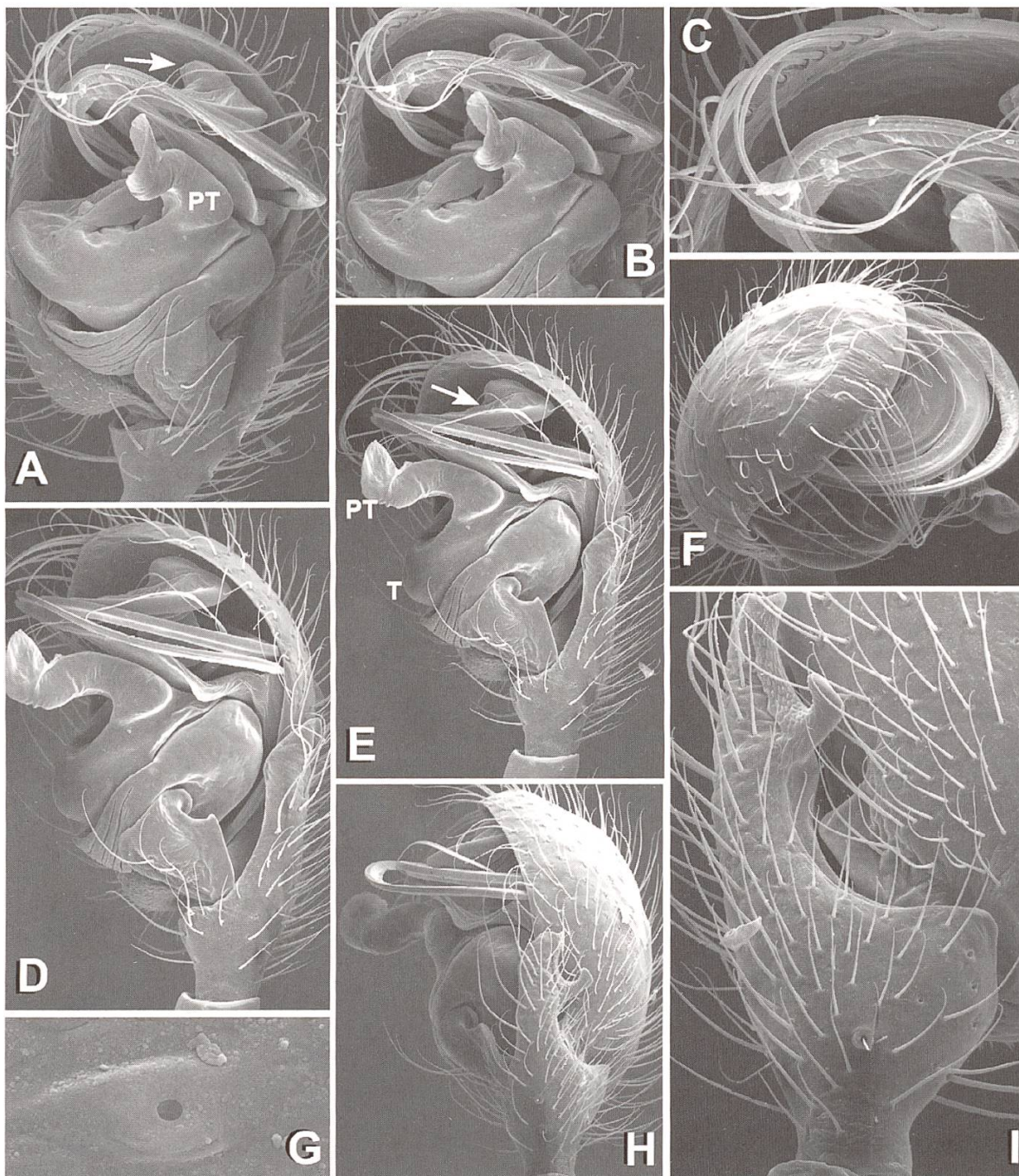


Fig. 5. *Labullinyphia tersa*, palp of male from Agrabopath. – A, B, C: ventral; – D, E: ectal, view; – F: apical; – G: tarsal organ, apical; – H: dorsoectal; – I: tibial apophysis, dorsal. Arrow in A and E, radix.

coiled copulatory ducts with an anterior turning point and the lateral globular spermathecae (Fig. 4). Both sexes lack cheliceral stridulatory striae (however, note the fine scaling; Fig. 7D, E, I).

Male (from Hakgala Botanical Gardens): Total length, 2.48. Cephalothorax 1.24 long, 0.93 wide. Sternum 0.65 long, 0.45 wide. Abdomen 1.24 long, 0.93 wide. Cephalothorax and chelicerae pale yellowish brown, with dark markings as in Figs. 1A–B. The dark markings extend from cephalic area to posterior rim of cephalothorax. Black pigmentation around all eyes. Sternum dark greyish

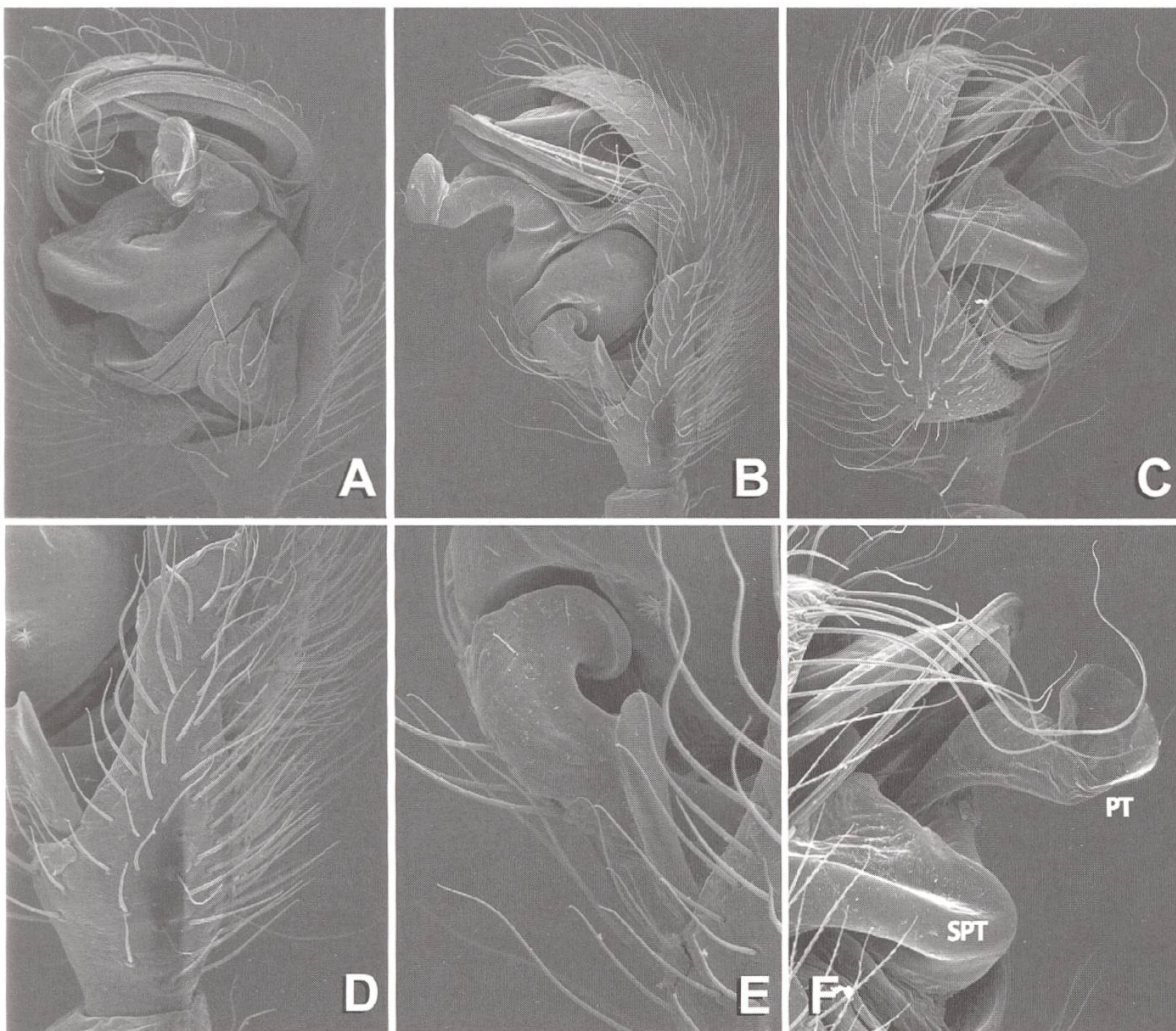


Fig. 6. *Labullinyphia tersa*, palp of male from Hakgala. – A: ventral; – B: ectal; – C: mesal; – D: tibial apophysis, ectal; – E: paracymbium, ectal; – F: protegulum, mesal.

brown. Legs yellowish brown, legs I and II darker than the rest. Abdomen light grey, anteriorly with three pairs of dorsal spots and posteriorly with black chevron-like pattern (Fig. 1A). Cephalothorax pear-shaped. AME diameter 0.07. Cephalic region raised posterior of the PMEs, with a row of macrosetae. Carapace fovea absent. Clypeus height two times one AME diameter. Chelicerae with five large equally spaced promarginal teeth and four smaller retromarginal teeth; stridulatory striae absent. Femur I 1.56 long, 1.26 times the length of cephalothorax, with a thickened basal region provided with large macrosetae, particularly on the ventral part. Metatarsus I sinuous, with a dorsal row of large macrosetae of diminishing length. Trichobothrium in metatarsus I absent in male.

Pedipalp as in Figures 2–3. Pedipalpal tibia with a retrolateral apophysis with a small mesal process curved anteriorly; one prolateral and two retrolateral trichobothria. Paracymbium with a broad distal arm, knob-shaped apically. Protegulum anteriorly directed, consisting of a long sclerotized stalk with a distal membranous region. Suprategulum with a pointed marginal

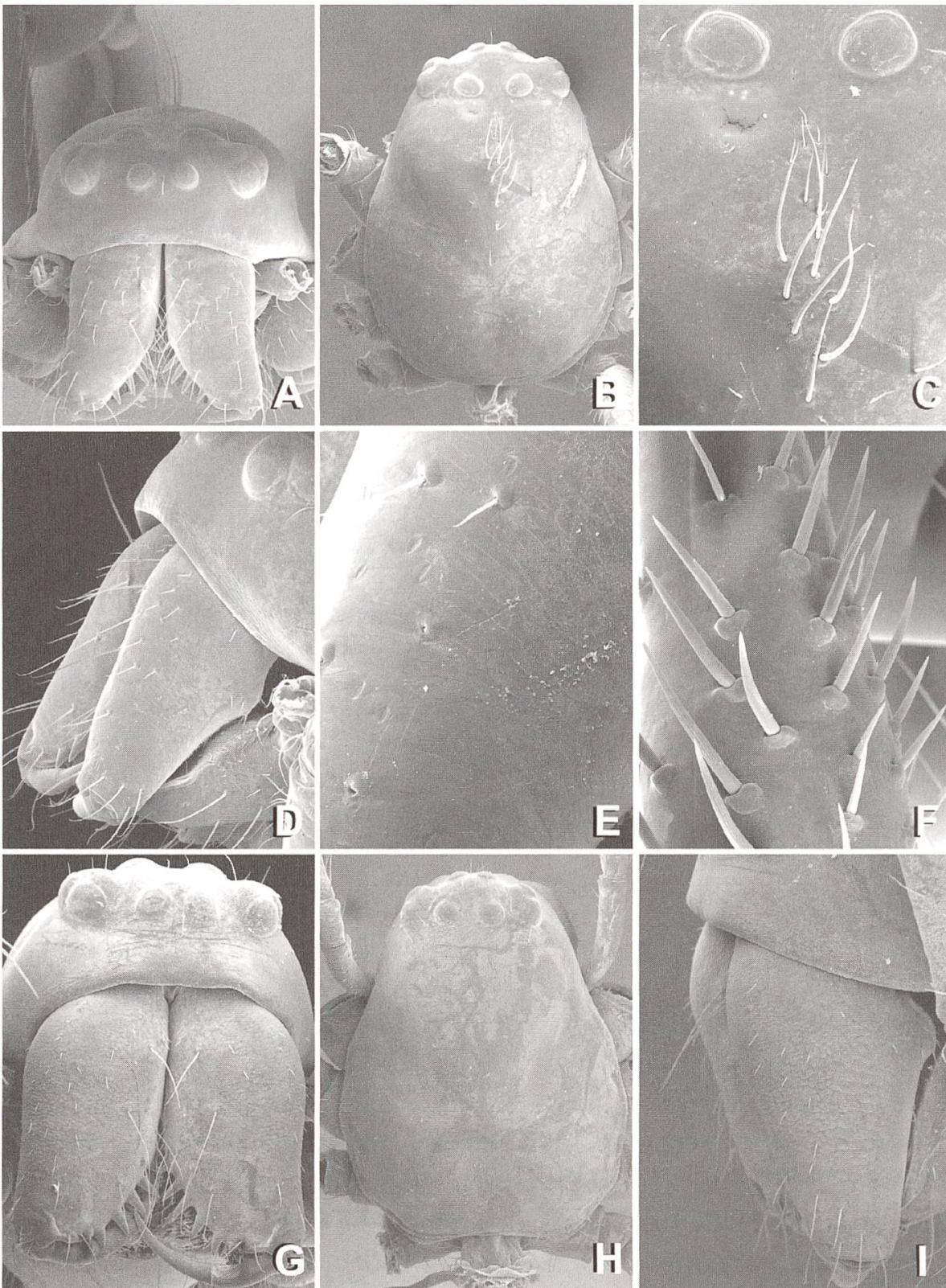


Fig. 7. Male (A–F) and female (G–I) *Labullinyphia tersa* from Agrabopath. – A: prosoma, anterior; – B: same, dorsal; – C: PME and carapace macrosetae, dorsal; – D, E: chelicerae, lateral; – F: femur of left leg I, ventral; – G: prosoma, anterior; – H: same, dorsal; – I: chelicerae, lateral.

suprategular apophysis and a large membranous distal apophysis. Column without embolic membrane. Radix small and spirally shaped, with a very long and filiform embolus that coils about two and a half times into concentric spiral turns in the apical region of the palp before continuing to curve out of

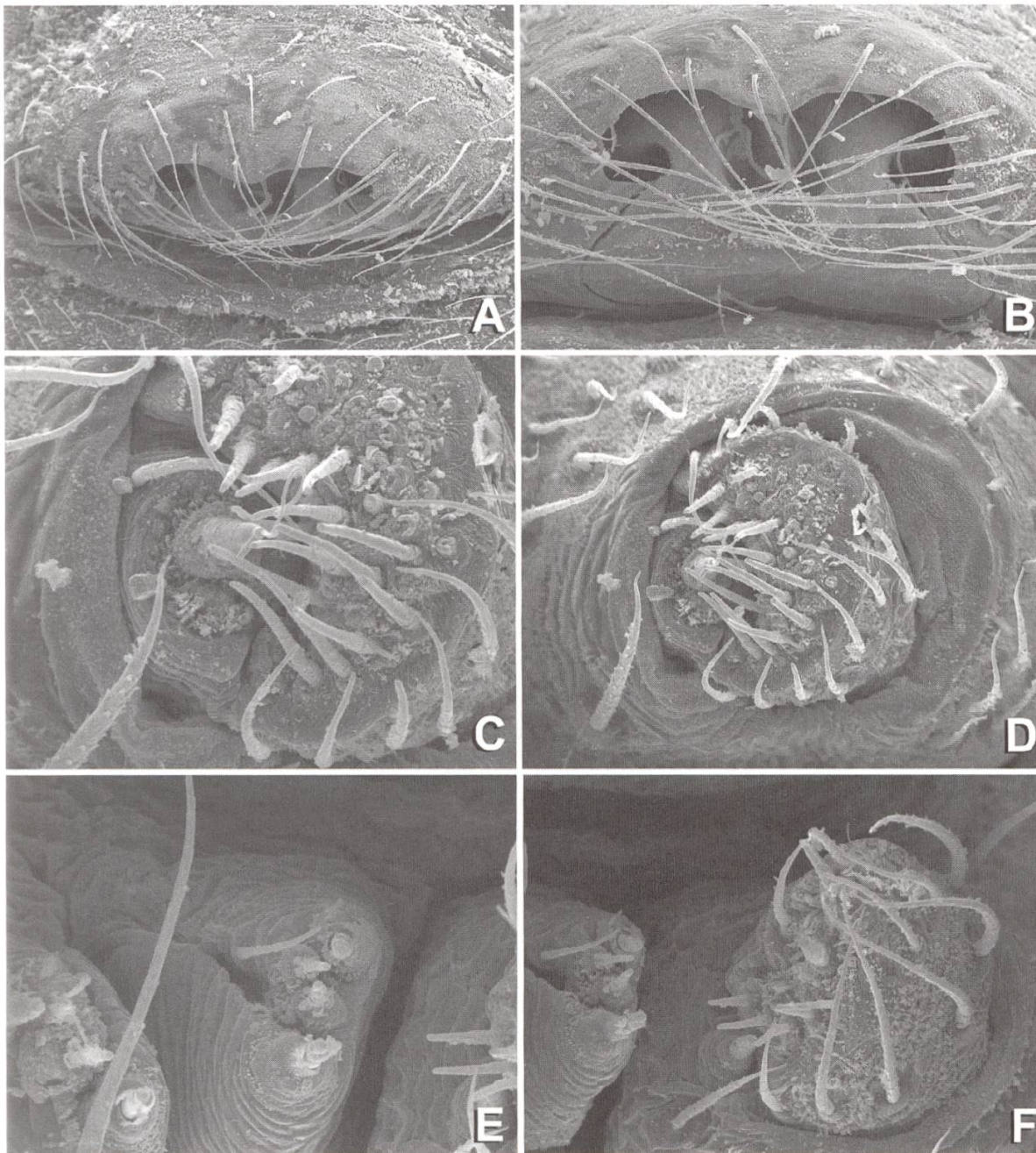


Fig. 8. *Labullinyphia tersa*, female from Agrabopath. – A: epigynum, ventral; – B, same, caudal; – C, D: ALS; – E: PMS; – F: PLS.

plane. Embolus provided with a membranous margin along its full length that includes the sperm duct. Apical region of the cymbium with about 8–10 very long setae, arranged in a row along the margin, whose distal ends converge on the apical region of the embolic division (Fig. 5A, F). Spinnerets as in Figs. 9B–E; PLS with two aggregate and one flagelliform gland spigot. Epiandrous fusules absent (Fig.9A).

Female (same locality and date as male): Total length 2.54. Cephalothorax 1.25 long, 0.5 wide. Sternum as long as wide (0.62). Abdomen 1.75 long, 0.53 wide. Cephalothorax and chelicerae pale yellowish brown, with dark markings

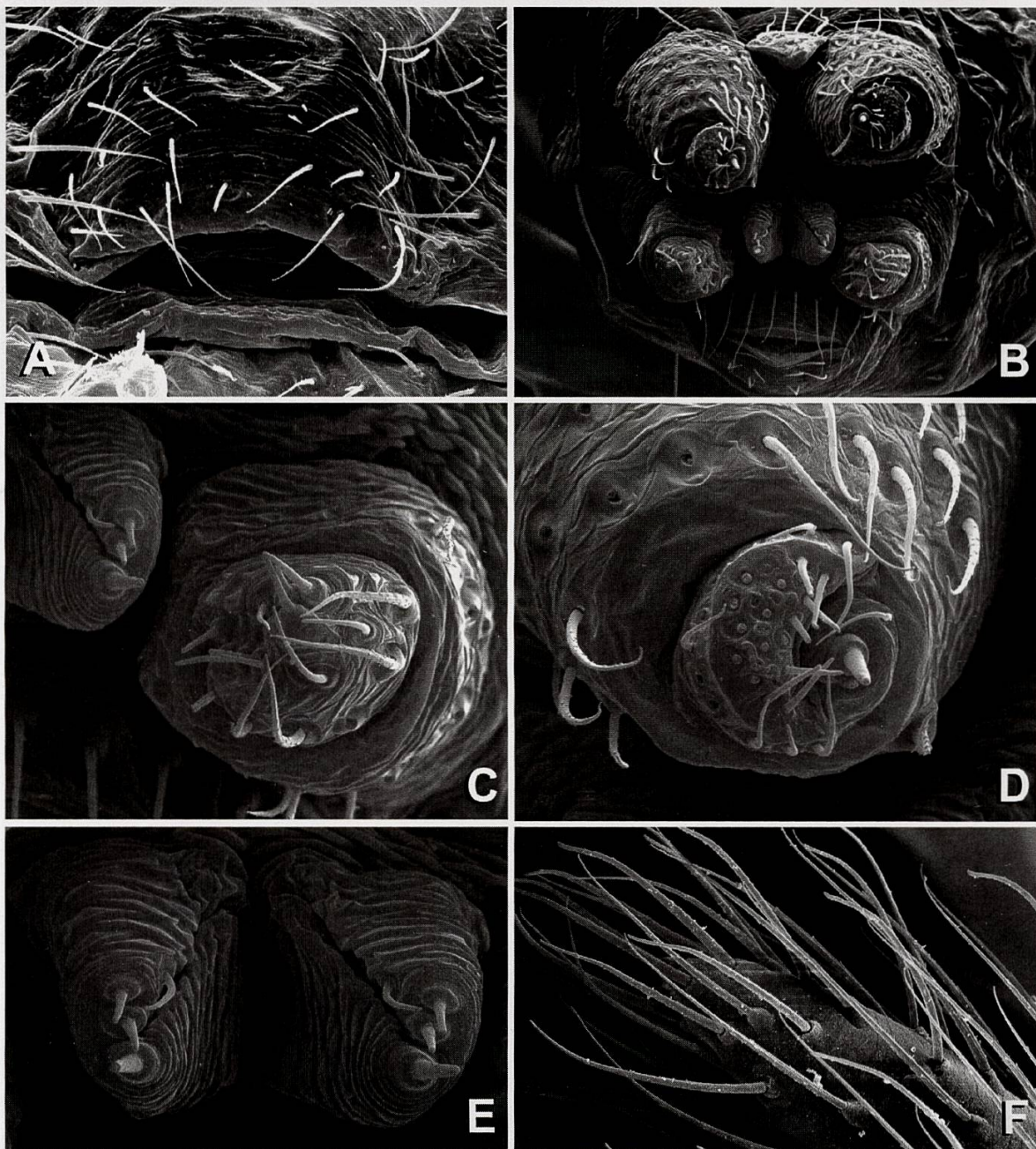


Fig. 9. Male (A–E) and female (F) *Labullinyphia tersa*, male from Agrabopath. – A: epiandrium, ventral; – B: spinnerets, caudal; – C: PLS; – D: ALS; – E: PMS; – F: left palpal tarsus.

as in Fig. 1C. Dark coloration extending from cephalic area to posterior rim of carapace. Black rings around all eyes. Sternum dark greyish brown. Legs yellowish brown, with dark rings (annulations). Abdomen light yellow, with a pattern like that of the male (Fig. 1C). Cephalothorax pear-shaped. AME diameter 0.04. Carapace fovea absent. Clypeus height 3.75 times one AME diameter. Chelicerae with five large, equally spaced, promarginal teeth and four/five smaller retromarginal teeth. Cheliceral stridulatory striae absent. Femur I 1.7 long, 0.73 times the length of cephalothorax. Trichobothrium in metatarsus I 0.5. Pedipalp tarsal claw absent (Fig. 9F). Epigynum and vulva as in Figs. 1 D–E, 4 A–B, 8 A–B. Posteroventral epigynal plate with a central socket,

with long spirally coiled copulatory ducts with an anterior turning point and lateral globular spermathecae. Fertilization ducts mesally oriented and converging towards the mid point. Spinnerets as in Figs. 8C–F. Tracheal system (one female dissected): Desmitracheate, with an atrium served by two unbranched lateral trunks, restricted to the abdomen, and a pair of wider median trunks that about half way towards the pedicel branch into numerous tracheoles (without taenidia) that go into the prosoma, reaching into all the appendages and the eyes.

Variation: Male cephalothorax ranges in length from 1.2 to 1.3 (n=4). Female cephalothorax ranges in length from 1.4 to 1.6 (n=3). Male total length ranges from 2.5 to 2.9 (n=4). Female total length ranges from 3.1 to 3.7 (n=3).

Natural history: Most of the specimens were collected by beating forest vegetation up to a height of about 2 m.

Distribution: Endemic to the central highlands of Sri Lanka.

Additional material examined: Sri Lanka, Central province: Agrapathana, Agrapath forest reserve, 07.–08. III. 2000, leg. S. Nanayakara, beating vegetation; 2 ♂ (MHNG); June 2003, leg. Suresh P. Benjamin, beating vegetation; 4 ♀, 2 ♂ (MHNG). Horton Plains National Park, 2100 m, 9. III. 2000, leg. Suresh P. Benjamin, 1 ♀ (MHNG). Hakgala, Hakgala Forest Reserve, 27. VII. 1996, leg. Suresh P. Benjamin; 1 ♂ (MHNG). Hakgala, Hakgala Botanical Gardens, 250 ft, 6.–8. X. 1976, leg. G. F. Hevel, R. F. Dietz IV, S. Karunaratne, D. W. Balasooriya; 1 ♂, 1 ♀ (USNM).

Cladistic analysis

TNT, using the collapsing rule 'min. length = 0,' found four most parsimonious cladograms of 184 steps (CI = 0.55, 0.54 after exclusion of uninformative characters; RI = 0.75). The strict consensus cladogram (Fig. 10), as calculated in TNT, is like that of Hormiga & Scharff (2005: fig. 24) except for the erigonine clade, which now includes *Leptorhoptrum* as sister to a clade with the other two erigonines in the analysis plus *Labullinyphia*. In all four most parsimonious cladograms the erigonines are monophyletic and include *Labullinyphia* as sister to *Erigone*. The successive character weighting analysis stabilizes at the second iteration, resulting in two most parsimonious cladograms (184 steps long under equal weights) whose strict consensus is like that of the four optimal cladograms under equal weights except for collapsing the position of *Pityohyphantes* (as in Hormiga & Scharff (2005: fig. 24) and fully

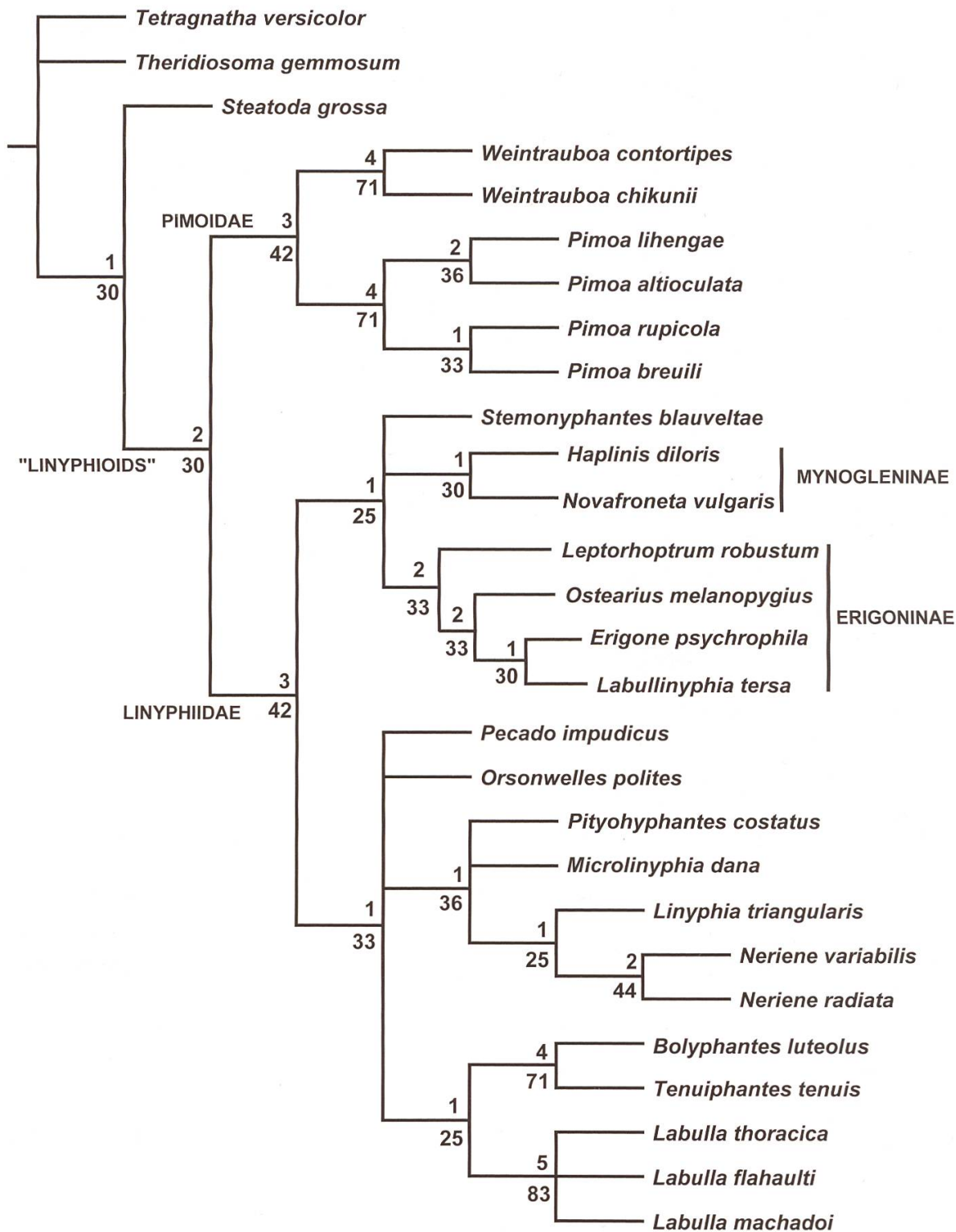


Fig. 10. Strict consensus cladogram (L= 187, CI=0.54, RI=0.74) of the four most parsimonious trees found by TNT when analyzing the data matrix presented in Appendix 1. Numbers above and below branches denote Bremer and Relative Bremer Support values (see text for details).

resolving the relationships of the three species of *Labulla* (with *L. thoracica* sister to *L. flahaulti* plus *L. machadoi*). One of the four most parsimonious cladograms resulting from equal weights was arbitrarily chosen to map character transformations (Fig. 11).

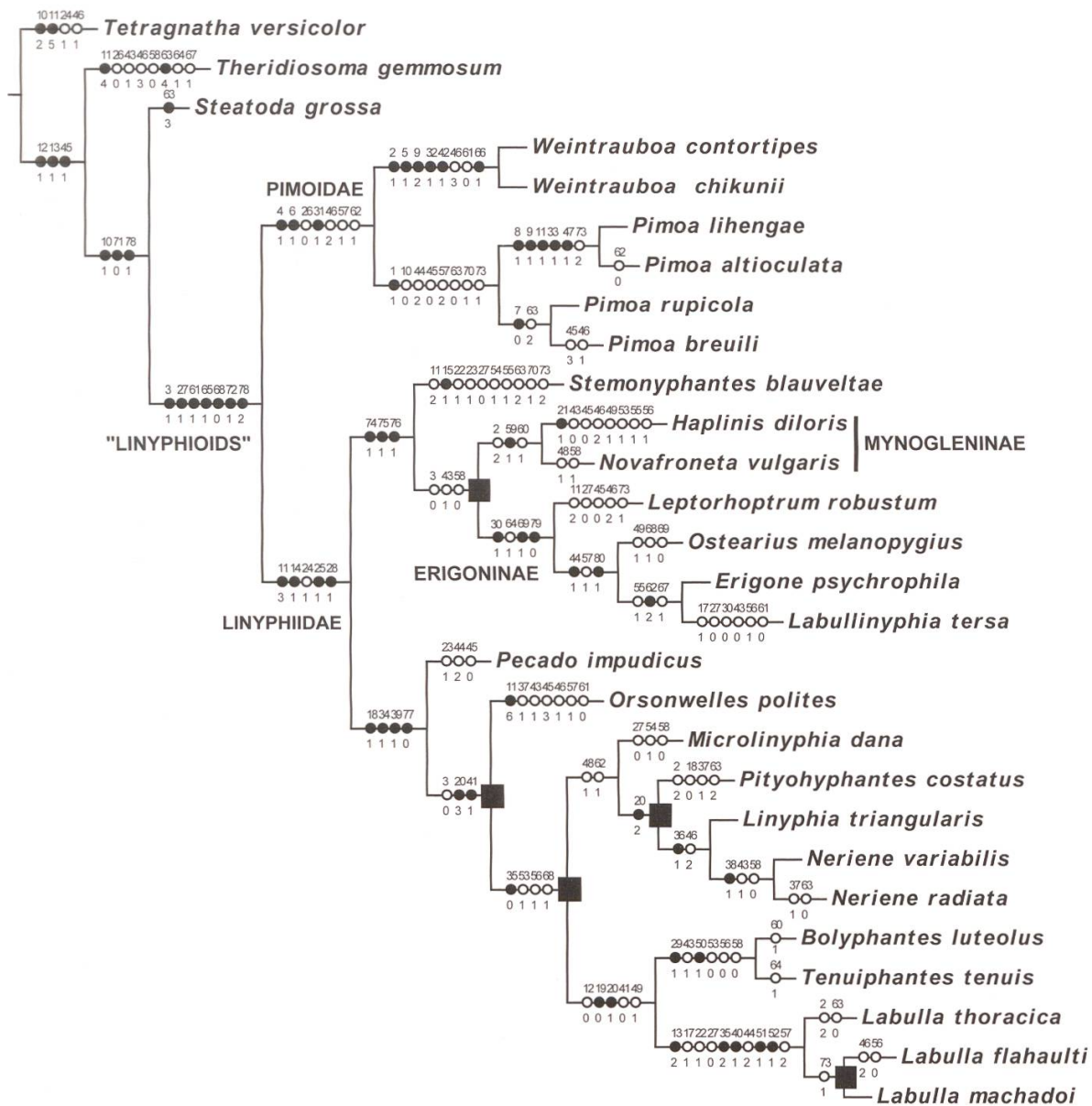


Fig. 11. One of the four minimal length trees of 184 steps that result from the analysis of the data matrix presented in Appendix 1 (CI = 0.55, RI = 0.75) (see text for details). Ambiguous character changes are resolved under "ACCTRAN optimization." Closed circles represent non-homoplasious character changes. The nodes that collapse in the strict consensus cladogram of the four most parsimonious cladograms (Fig. 10) are marked with a closed square.

Discussion

The morphology of *Labullinyphia tersa* provides robust support for its placement within the subfamily Erigoninae. Some of these characters include: absence of epiandrous fusules, retention of araneoid PLS triplet in the adult male, absence of the female pedipalpal claw, tibia III and IV with a single dorsal spine, desmitracheate system, and the retrolateral tibial apophysis and the protegulum of the male palp. Modifications of the first leg in males is a very rare trait in the Linyphiidae, although it is found in some species of

pimoids (Hormiga 1994; Hormiga 2003). While searching for the closest relatives of *Labullinyphia* is beyond the scope of this paper, we should point out that there are a number of similarities in the details of both the male and female genitalic morphology of *L. tersa* and *Emenista bisinuosa* SIMON, 1894. The latter erigonine species was redescribed by van Helsdingen (1985) based on the original material from Kodaikanal, India (Tamil Nadu state) studied by Simon. The internal morphology of the epigynum of *E. bisinuosa* (van Helsdingen 1985: figs. 26–27) is remarkably similar to that of *L. tersa*: a socket in the posterior epigynal plate, spirally-coiled copulatory ducts with a turning point (however, with fewer turns), a final loop into spherical and laterally placed spermathecae, and fertilization ducts converging towards the mid point. The male has a retrolateral tibial apophysis similar to that of *L. tersa* (Figs. 2C, 5I), including a small sclerotized mesal process (van Helsdingen 1985: figs. 28–29). The embolus of *E. bisinuosa* is also filiform and coiled and the protegulum has a long basal stalk. The nature of the long sheath-like membrane is unclear but it could possibly be the homolog of the distal suprategular apophysis, which is also membranous in *L. tersa* (Fig. 2A).

Acknowledgements

This paper is dedicated to Prof. Konrad Thaler (1940–2005) who introduced one of us (SPB) to the wonderful world of spiders; he was a great mentor, guide and friend. His rigorous and careful work and his many contributions to linyphiid taxonomy have always been a source of inspiration to both authors. Thanks to Mr. A.H. Sumanasena (Department of Wild Life Conservation, Colombo) for providing a research permit to collect in Sri Lanka. Comparative material was provided by Jonathan Coddington and Dana De Roche (National Museum of Natural History, Smithsonian Institution, Washington, D.C., USNM) and Christine Rollard and Elise-Anne Leguin (Muséum National d'Histoire Naturelle, Paris, MNHN). Funding for this research has been provided by grants from the U.S. National Science Foundation (DEB-0328644) to G. Hormiga and G. Giribet and EAR-0228699 to W. Wheeler, J. Coddington, G. Hormiga, L. Prendini and P. Sierwald) and by a REF grant from The George Washington University (to GH). Field work in Sri Lanka was funded by SPB's personal funds.

References

- Álvarez–Padilla, F. & Hormiga, G. (2008): A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. — *Journal of Arachnology* 35: 538–542.
- Benjamin, S.P. (2000): *Epidius parvati* sp. n., a new species of the genus *Epidius* from Sri Lanka (Araneae: Thomisidae). — *Bulletin of the British Arachnological Society* 11: 284–288.
- Benjamin, S.P. (2001): The genus *Oxytate* L. Koch, 1878 from Sri Lanka, with description of *Oxytate taprobana* sp. n. (Araneae: Thomisidae). — *Journal of South Asian Natural History* 5: 153–158.
- Benjamin, S.P. (2004): Taxonomic revision and a phylogenetic hypothesis for the jumping spider subfamily Ballinae (Araneae, Salticidae). — *Zoological Journal of the Linnean Society* 142: 1–82.
- Benjamin, S.P. & Jocqué, R. (2000): Two new species of the genus *Suffasia* from Sri Lanka (Araneae: Zodariidae). — *Revue suisse de Zoologie* 107: 97–106.
- Bremer, K. (1988): The limits of amino acid sequence data in angiosperm phylogenetics reconstruction. — *Evolution* 42: 795–803.
- Bremer, K. (1994): Branch support and tree stability. — *Cladistics* 10: 295–304.
- Coddington, J.A. (1983): A temporary slide-mount allowing precise manipulation of small structures. — *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)* 26: 291–292.
- Denis, J. (1949): Notes sur les étrigonides. XVI. Essai sur la détermination des femelles d'étrigonides. — *Bulletin de la Société d'Histoire Naturelle de Toulouse* 83: 129–158.
- Dingerkus, G. & Uhler, L.D. (1977): Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. — *Stain Technology* 52: 229–232.
- Fitch, W.M. (1971): Towards defining the course of evolution: Minimal change for a specific tree topology. — *Systematic Zoology* 20: 406–416.
- Goloboff, P.A. (1993): NONA, Version 2. Program available at <http://www.cladistics.com>
- Goloboff, P.A., Farris, J. & Nixon, K. (2003): TNT, version 1.1. Program available at <http://www.cladistics.com>
- Grandjean, F. (1949): Observation et conservation des très petits arthropodes. — *Bulletin du Muséum National d'Histoire naturelle* 21: 363–370.
- Helsdingen, P.J. van (1985): Araneae: Linyphiidae of Sri Lanka, with a note on Erigonidae. — *Entomologica Scandinavica Supplements* 30: 13–30.
- Holm, A. (1979): A taxonomic study of European and East African species of the genera *Pelecopsis* and *Trichopterna* (Araneae, Linyphiidae), with descriptions of a new genus and two new species of *Pelecopsis* from Kenya. — *Zoologica Scripta* 8: 255–278.
- Hormiga, G. (1994): A revision and cladistic analysis of the spider family Pimoidae (Aranoi-dea: Araneae). — *Smithsonian Contributions to Zoology* 549: 1–104.
- Hormiga, G. (2000): Higher level phylogenetics of erigonine spiders (Araneae, Linyphiidae, Erigoninae). — *Smithsonian Contributions to Zoology* 609: 1–160.
- Hormiga, G. (2002): *Orsonwelles*, a new genus of giant linyphiids spiders (Araneae) from the Hawaiian island. — *Invertebrate Systematics* 16: 369–448.

Hormiga, G. (2003): *Weintrauboa*, a new genus of pimoid spiders from Japan and adjacent islands, with comments on the monophyly and diagnosis of the family Pimoidae and the genus *Pimoa* (Araneoidea, Araneae). — Zoological Journal of the Linnean Society 139: 261–281.

Hormiga, G. & Scharff, N. (2005): Monophyly and phylogenetic placement of the spider genus *Labulla* SIMON, 1884 (Araneae: Linyphiidae) and description of the new genus *Pecado*. — Zoological Journal of the Linnean Society 143: 359–404.

Huber, B.A. & Benjamin, S.P. (2005): The pholcid spiders from Sri Lanka: redescription of *Pholcus ceylonicus* and description of a new genus (Araneae: Pholcidae). — Journal of Natural History 39: 3305–3319.

Maddison, W.P. & Maddison, D.R. (2006) Mesquite: a modular system for evolutionary analysis. Version 1.12. Program available at <http://mesquiteproject.org>

Miller, J.A. & Hormiga, G. (2004): Clade stability and the addition of data: A case study from erigonine spiders (Araneae: Linyphiidae, Erigoninae). — Cladistics 20: 385–442.

Millidge, A.F. (1993): Further remarks on the taxonomy and relationships of the Linyphiidae, based on the epigynal duct confirmations and other characters (Araneae). — Bulletin of the British Arachnological Society 9: 145–156.

Nixon, K. (1999): Winclada, Version 1.00.08. Program available at <http://www.cladistics.com>

Simon, E. (1894): Histoire naturelle des Araignées, Tome 1 (3). — pp. 489–760. Roret, Paris.

Addresses of the authors:

Suresh P. Benjamin^{1,2} & Gustavo Hormiga¹

¹ Department of Biological Sciences
The George Washington University
2023 G Street. NW
Washington, D.C. 20052, USA

² Institute of Fundamental Studies
Hantana Road
Kandy, Sri Lanka

E-mail: suresh.benjamin@gmail.com
hormiga@gwu.edu

Appendix 1

Character state matrix

<i>Tetragnatha versicolor</i>	0000-0-25000-----000101000-0-0-0-0-000010-----10?0-10000100100000?1010
<i>Theridiosoma gemmosum</i>	0000-0-0-041-0-----000000-0-0-0-0-01013000-000000000?0-41001100100000?010
<i>Steatoda grossa</i>	0000-0-0-0-0-----000001000-0-0-0-0-00010000-000000010?0-30000100000000?1110
<i>Pimoida rupicola</i>	101101000001-0-----000000-0-0-1000-0-0-00202000-00000021001?20100001011000??0?
<i>Pimoida brevilii</i>	101101000001-0-----000000-0-0-1000-0-0-00231000-000000210011?010000?011000??0?
<i>Pimoida lihengae</i>	10110111011-0-----000000-0-0-1010-0-0-00202100-000000210?11001000?1012??0?2?0
<i>Pimoida altioculata</i>	10110111011-0-----000000-0-0-1010-0-0-00202100-000000210010?010000101200?2?10
<i>Weintrauboa contortipes</i>	011111102101-0-----000000-0-0-11-0-0-0-10013000-0000000110?0-101100?0010000?2?10
<i>Weintrauboa chikunii</i>	011111102101-0-----000000-0-0-11-0-0-0-100130??-??0??0?10?0-?110??0??0??0?10
<i>Stemonyphantes blauveltiae</i>	0010-0-121-11100-01111101000-0-0-000-00010000-0001100100102010000101211??0?10
<i>Haplisis diloris</i>	0200-0-131-10100-10011111000-0-0-000-0000200100001011001110101000000101111?10
<i>Novafroneta vulgaris</i>	0200-0-131-10100-00011111000-0-0-000-01010010-0000000111101010000001011??0?10
<i>Ostearius melanopygius</i>	0000-0-131-10100-00011111010-0-0-000-011100010000000100010111001000101111201
<i>Erigone psychrophila</i>	0000-0-131-10100-00011111010-0-0-000-011110000-0000101000012111010100101111201
<i>Labulla thoracica</i>	0200-0-130210111010101101000-12000110002100010111001210?100010010001000000210
<i>Labulla flahaulti</i>	0000-0-1302101110101011010000-12000110002120010111000210?1?101001?0011??0?210
<i>Labulla machadoi</i>	0000-0-1302101110101011010000-12000110002100010111001210?1?101001?0011??0??0?
<i>Pecado impudicus</i>	0010-0-131-101011000111110000-1100010000200??0??0??0?10?1??10??0??0??0??0?
<i>Orsonwelles polites</i>	0000-0-161-101011300011111000-11010101031000-000000011000-10100000010000?210
<i>Pityohyphantes costatus</i>	0200-0-131-10100-00011111000-1001010100010010-001001010?11201001?0010??0?210
<i>Microlinyphia dana</i>	0000-0-131-101011300011101000-1-0010100010010-00110100000111010010001000000210
<i>Linyphia triangularis</i>	0000-0-131-101011200011111000-1010010100012010-00100101000111010010001000000210
<i>Nerene variabilis</i>	0000-0-131-101011200011111000-1010110101012010-001001000?11101001??10?000210
<i>Nerene radiata</i>	0000-0-131-101011200011111000-10111101012010-001001000?11001001?0?10?000210
<i>Bolyphantes luteolus</i>	0000-0-13011010100011111100-1000010001010001100000000011010100100010000??0?10
<i>Tenuiphantes tenuis</i>	0000-0-13011010100011111100-100001000101000110000000000101110010001000000210
<i>Labullinyphia tersa</i>	0000-0-131-10110-00011101000-0-0-000-00110000-00001110000-1110101001011??0?1
<i>Leptorhoptrum robustum</i>	0000-0-121-10100-00011101010-0-0-000-01002000-000000000001011100010011111??0?00

