

Monophyly and phylogenetic placement of the spider genus *Labulla* Simon, 1884 (Araneae, Linyphiidae) and description of the new genus *Pecado*

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Received March 2004; accepted for publication July 2004

The genus *Labulla* Simon is circumscribed in phylogenetic terms to include the species *Labulla thoracica* (Wider), *L. flahaulti* Simon and *L. machadoi* sp. nov. The genital anatomy of the genus is described in detail and the taxonomy of the genus is reviewed. The monophyly of *Labulla* is supported by numerous morphological apomorphies of the male palp and female epigynum. Based on a cladistic analysis, a new genus, *Pecado* gen. nov., is erected to place *Labulla impudica* Denis, from Northern Africa. *Lepthyphantes insularis* Saito and '*Labulla*' *nepula* Tikader, both formerly included in *Labulla*, are not congeneric with the type species of *Labulla*. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 143, 359–404.

ADDITIONAL KEYWORDS: anatomy – cladistics – genitalia – morphology – phylogeny – systematics – taxonomy.

INTRODUCTION

The linyphiid genus *Labulla* includes one of the most common linyphiid species in central and northern Europe, *Labulla thoracica* (Wider, 1834). Although this species, originally described more than a century and a half ago, is relatively well known and has been described on numerous occasions (e.g. Lockett & Millidge, 1953; Wiehle, 1956; Roberts, 1987), the remaining species of this genus are poorly documented. The male and female genitalic anatomy of *Labulla* is both complex and rather unusual. Only one study (Merrett, 1963) has attempted to homologize the sclerites of the embolic division, studying *Labulla thoracica*. The circumscription of *Labulla* has never been discussed in phylogenetic terms and the genus as presently delimited is not monophyletic (Hormiga, 2003). In this paper we study in detail the genitalic anatomy of *Labulla* species to re-circumscribe the genus in phylogenetic terms. We also describe a new species from Portugal (*Labulla machadoi* sp. nov.) and redescribe the poorly known southern European

species *Labulla flahaulti* Simon, 1914. By means of a cladistic analysis we show that *Labulla impudica* Denis, 1945 is incorrectly classified in the genus *Labulla* and that no current generic circumscription is available properly to accommodate this species from northern Africa. We describe a new genus, *Pecado* gen. nov., to place *Labulla impudica*.

Eugène Simon (1884) erected the linyphiid genus *Labulla* to accommodate the European species *Linyphia thoracica* Wider, 1834 and his newly described species *Labulla rupicola* Simon, 1884 [the latter was subsequently transferred to the family Pimoidae; see Hormiga (1994a) for references]. For this generic concept Simon used a rather obscure name (although he did not document the etymology): *Labulla* is an invented Latin proper name for an adulteress in the salacious comic epigrams of the Roman poet Martial (1st century AD; Martial Book 4 epigram 9 and Book 12 epigram 93), an author who Simon would easily have known as he was in the habit of gleaning such proper names from antiquity at random (H. Don Cameron, pers. comm.). Since then, a diverse array of linyphiid and pimoid species has been included in *Labulla*, many of them not closely related

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to the type species (*L. thoracica*). As a result, there have been numerous generic transfers, the most recent of which have been the two 'Labulla' species described by Simon (1900) from Hawaii, currently placed in the linyphiid genus *Orsonwelles* Hormiga (Hormiga, 2002; Hormiga, Arnedo & Gillespie, 2003) and the Japanese species of *Labulla*, now placed in the pimoid genus *Weintrauboa* Hormiga, 2003. From a modern perspective, the genus *Labulla* had been used as a dumping ground for morphologically deviant linyphioids.

As presently delimited the genus *Labulla* is polyphyletic (Hormiga, 1994b, 2002, 2003). *Labulla nepula* Tikader, 1970 from India is not congeneric with the type species. Of the currently described species only *L. flahaulti* Simon, 1914 (from France and Spain) seems to be congeneric with *L. thoracica* (see Hormiga, 2002). Despite the many transfers of species from *Labulla* to other genera and families no modern study has explicitly tackled the circumscription of this genus. During the course of our study we have found specimens of an undescribed species collected in Portugal by the late António de Barros Machado (1912–2002), which is formally described here. We have also included information on the web architecture of *Labulla thoracica*, as the webs of most linyphiid species remain undocumented and few studies have addressed web architecture in Linyphiidae (but see Hormiga, 2002).

MATERIAL AND METHODS

Morphological methods are described in detail in Hormiga (2000, 2002). Taxonomic descriptions follow the format of Hormiga (2002). Specimens were examined and illustrated using a Leica MZAPO stereoscopic microscope, with a camera lucida. Further details were studied using a Leica DMRXE 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 JEOL JSM840 scanning electron microscope was also used to study and photograph 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 millimetres. 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 as the widest point as seen from a dorsal view. The measurements of the abdomen are only approxi-

mations, 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) and Locket & Millidge (1953). 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 aluminium rivets using an acetone solution of polyvinyl resin (Paraloid B72) and then Au/Pd coated for examination in the SEM. Webs were photographed as described in Hormiga (2002). We have colour coded the embolic division sclerites (see Fig. 4) to facilitate comparison of homologous structures. In the figure captions, the direction of the arrows (left, right, etc.) refers to the pointing direction of the arrowhead.

The following anatomical abbreviations are used in the text and figures

Male palp:

BH	basal haematodocha
CB	cymbium
CL	column
DSA	distal suprategular apophysis
E	embolus
LC	lamella characteristic
m	membrane (or membranous)
MSA	marginal suprategular apophysis
P	paracymbium
R	radix
SF	suprategular foramen
SPT	suprategulum
ST	subtegulum
T	tegulum
TA	terminal apophysis
TM	ectal tegular flap

Epigynum:

CD	copulatory duct
CO	copulatory opening
FD	fertilization duct
S	spermatheca
TP	turning point of copulatory duct

Somatic morphology:

AC	aciniform gland spigot(s)
AG	aggregate gland spigot(s)
ALS	anterior lateral spinneret
AME	anterior median eye(s)
CY	cylindrical gland spigot(s)
FL	flagelliform gland spigot(s)
MAP	major ampullate gland spigot(s)
mAP	minor ampullate gland spigot(s)
PI	piriform gland spigot(s)
PLE	posterior lateral eye(s)
PLS	posterior lateral spinneret
PME	posterior median eye(s)
PMS	posterior median spinneret

Institutional abbreviations used in the text are given in the Acknowledgements.

CLADISTIC ANALYSIS

TAXA

The taxonomic sample used in the cladistic analysis was designed to test the conjecture that, based on the available evidence, *Labulla impudica* is not congeneric with the type species of *Labulla*, *L. thoracica*. The analysis also tests the monophyly of the genus *Labulla*. We have included the following four *Labulla* species: *L. thoracica*, *L. flahaulti*, *L. machadoi* sp. nov. and '*L. impudica*'. We also included in the character matrix (see Appendix 2) 13 linyphiid species (in 12 genera), in a modest attempt to represent morphological diversity at the subfamilial level, but it is not the goal of this study to investigate the phylogenetic relationships of the main linyphiid lineages. Our taxonomic sample follows that of Hormiga (2000, 2002) with the exception of the Erigoninae, which are represented here by two species.

Outgroup selection follows the taxonomic sample of Hormiga (2003). Pimoidae, the sister group of Linyphiidae, is represented by five species in two genera. Representatives of three araneoid families (Tetragnathidae, Theridiosomatidae and Theridiidae) were used to root the 'linyphioids'.

CHARACTERS

A total of 78 characters were scored (see Appendix 1): 46 male and 11 female genitalic characters, 18 somatic morphological characters and three behavioural characters. These characters were selected with the main goal of investigating the placement of '*Labulla impudica*'.

A total of four characters in Appendix 2 are parsimony uninformative in this taxonomic context, but were kept in the analysis because they are potentially useful to reconstruct 'linyphioid' relationships.

ANALYSES

The parsimony analyses were performed using the computer programs NONA version 2.0 (Goloboff, 1993a), PAUP* 4.0 (Swofford, 2001) and Pee-Wee version 3.0 (Goloboff, 1993b). WinClada version 1.00.08 (Nixon, 1999), MacClade 4 (Maddison & Maddison, 2001) and Nexus Data Editor 0.4.9 (Page, 2001) were used to study character optimizations on the cladograms and to build and edit the character matrix, respectively. Ambiguous character optimizations were usually resolved so as to favour reversal or secondary loss over convergence (Farris optimization or ACC-TRAN); if not, the optimization scheme is discussed in the text. The 15 multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch, 1971). NONA (Goloboff, 1993a) was used to calculate Bremer support indices ('decay indices') (Bremer, 1988, 1995; Donoghue *et al.* 1992) using the following commands: hold2000; sub1; find*; hold4000; sub3; find*; hold8000; sub5; find*; bsupport.

RESULTS

CLADISTIC ANALYSIS

Heuristic searches in NONA under equal weights and 'amb-' using hold10000; hold/500; and 1000 replicates of mult (mult*1000; using 'tree bisection-reconnection') resulted in four minimal length trees of 170 steps (the strict consensus cladogram is presented in Fig. 24), with CI and RI of 0.58 and 0.76, respectively. None of these four trees is fully resolved. Using the command 'amb=' in NONA to interpret clade support (thus considering ambiguous change as support) produces 72 topologies of minimal length, summarized by the same strict consensus cladogram that results from the analysis under 'amb-' (Fig. 24). The same 72 trees are found by PAUP with heuristic methods, equal weights and random addition sequence (1000 replications). When the 72 tree solution set was filtered for compatible but polytomous topologies (using the 'Do not retain a nonbinary tree if a more highly resolved but compatible tree exists' in the 'Filter Trees/New Filter' menu of PAUP), 48 trees resulted (all of which are fully resolved).

Implied weighting in Pee-Wee, which weights the characters according to a concave function of homoplasy (Goloboff, 1993c), using 'k' values of 3 and 6 (and same search parameters as given for NONA), produces the same 72 trees (Fit = 613,6; Length 170) found by NONA and PAUP. Using a 'k' value of 1 (thus maximizing the weights against homoplastic characters) produces 30 trees (Fit = 531,9; Length 173) with a strict consensus topology similar to Figure 24, except for the placement of *Pityohyphantes* and *Microlinyphia*. *Pityohyphantes* moves down the tree

and becomes sister to a clade (a 5-tomy) including *Pecado*, *Orsonuelles* (*Linyphia*, *Neriene*) (*Micronetini*, *Labulla*) and *Microlinyphia*.

Successive character weighting in PAUP, which by default weights characters by their rescaled consistency index, produces 36 trees of minimal length (170 steps long under equal weights). When filtered for compatible but polytomous topologies, 16 fully resolved trees remained. The strict consensus of these 16 trees is the same as in Figure 24, except that the *Labulla* clade is fully resolved. As the dataset did not include a full set of characters to analyse internal relationships within the genus *Labulla*, we do not consider the proposed phylogeny of the three *Labulla* species reliable and therefore prefer to refer to the strict consensus cladogram of the equally weighted data (Fig. 24). One of the 16 fully resolved minimal length trees has been selected as the preferred topology for character optimization (Fig. 25). Bremer support values for the individual nodes are given in Figure 24.

COMPARATIVE GENITALIC ANATOMY OF *LABULLA* SPECIES

Male palp

In *L. thoracica* (Fig. 1A) and *L. machadoi* sp. nov. (Fig. 1E) the size of the male palps, relative to body size, is distinctively large; in *L. flahaulti* (Fig. 1C) they are considerably smaller. Palpal patella unmodified. Tibia with a dorsal apophysis whose morphology varies across the species (Figs 5A, 8A, 11A). Cymbium, as seen in dorsal view (Figs 5C, 8C, 11C), sinuous and with a thin membranous ectal margin that overhangs the subtegulum and the basal part of the tegulum (e.g. Fig. 5C). Tarsal organ ectoapical. Paracymbium connected to the cymbium-tibia membrane at the base of the cymbium (Fig. 5C) via a membrane at the apex of the proximal paracymbial branch. Paracymbium with a caudally projecting apophysis in its median curvature whose morphology is species specific (Figs 5A, 8A, 9A, 11A–C, 16B, 21F). Subtegulum circular. Tegulum elongated, provided with a membranous and transparent flap (termed here ‘tegular membrane’) running along its ectal margin, most easily seen in an ectal view, and present in all species but particularly conspicuous in *L. thoracica* (Figs 5A, 6A, 17A – arrow left). In ventral view, the tegulum appears ectally projected (especially in *L. thoracica* and *L. machadoi* sp. nov.), with an anteriorly directed lobe on its apical region (Figs 6A, 9A, 12A). Spermduct running along the external margin of the tegulum, with a loop in the anterior lobe (Figs 6A, 9A, 12A). Spermduct diameter decreases as it enters the suprattegulum; in *L. machadoi* sp. nov. the trajectory also shows a kink (Fig. 12A).

Suprattegulum large and conspicuous (e.g. Fig. 4A, D – blue) with a pointed distal apophysis that reaches the cymbial apex (in ectal view). Suprattegulum heavily sclerotized, except for a small region, anterior to the suprattegular foramen, that is only slightly sclerotized and shows a clear posterior margin (Figs 6A, 9A, 12A). All species provided with a small pointed apophysis adjacent to the column, mesal to the suprattegular foramen (marginal suprattegular apophysis; Figs 6A, 9A, 12A, D – arrow, 17A). On its ectal margin, also adjacent to the column, all species have a distinctive and morphologically similar bifid suprattegular apophysis (Fig. 17F). No embolic membrane can be discerned as such (but see Discussion). Radix large and with a highly sclerotized core surrounded by membranes connecting it to other embolic division sclerites. All species have a sclerotized radical process that projects mesally (Figs 6C, 9D, 11B, 12C, 16D, H, 21D, 22B). Embolus length and morphology highly variable across species, but always turning anticlockwise (left palp, ventral) in a plane parallel to the cymbium. In *L. thoracica* the embolus makes about two and a quarter turns (Fig. 5B), in *L. machadoi* sp. nov. about one complete turn (Fig. 11B) and in *L. flahaulti* (Fig. 9D) less than half a turn; in the first two species the embolus is filiform and has an internal membranous margin. A minute filiform membrane projects from the membranous region of the base of the embolus in *L. thoracica* (Fig. 17B, D) and *L. machadoi* sp. nov. (Figs 11B, 22A, C). In the latter species this filiform process can be easily discerned with a dissecting stereoscope; in the former this is barely possible and SEM is required. A homologous structure was not found in *L. flahaulti*.

Lamella characteristic large and conspicuous, of semi-membranous and partially transparent appearance (Figs 5A, 6B–D, 8A, 9B, 11A, 12B, C, 16H). The ectal margin of the lamella is folded ventrally and in the unexpanded palp it contains along its length the distal part of the embolus (Fig. 21H). The apical end of the embolus is housed in the apical end of the lamella; the internal surface of the latter is covered with pili-form papillae, densely distributed in *L. thoracica* (Fig. 17G) and *L. machadoi* sp. nov. (Fig. 22D) and sparsely in *L. flahaulti* (Fig. 21H). The external surface of the apical region of the lamella is covered with small denticles (Fig. 17G). The membranous connection between the lamella and the radix is in the anterior radical region (Figs 6C, 9B, 16C). The morphology of the terminal apophysis is highly variable across species (Figs 17C, 21G, 22C), but it always connects to the radix in its dorsal anterior region. The terminal apophysis consists of an arm that runs along the longitudinal axis (dorsally) of the palp and that has a distinctive process at its apical end. It also has a

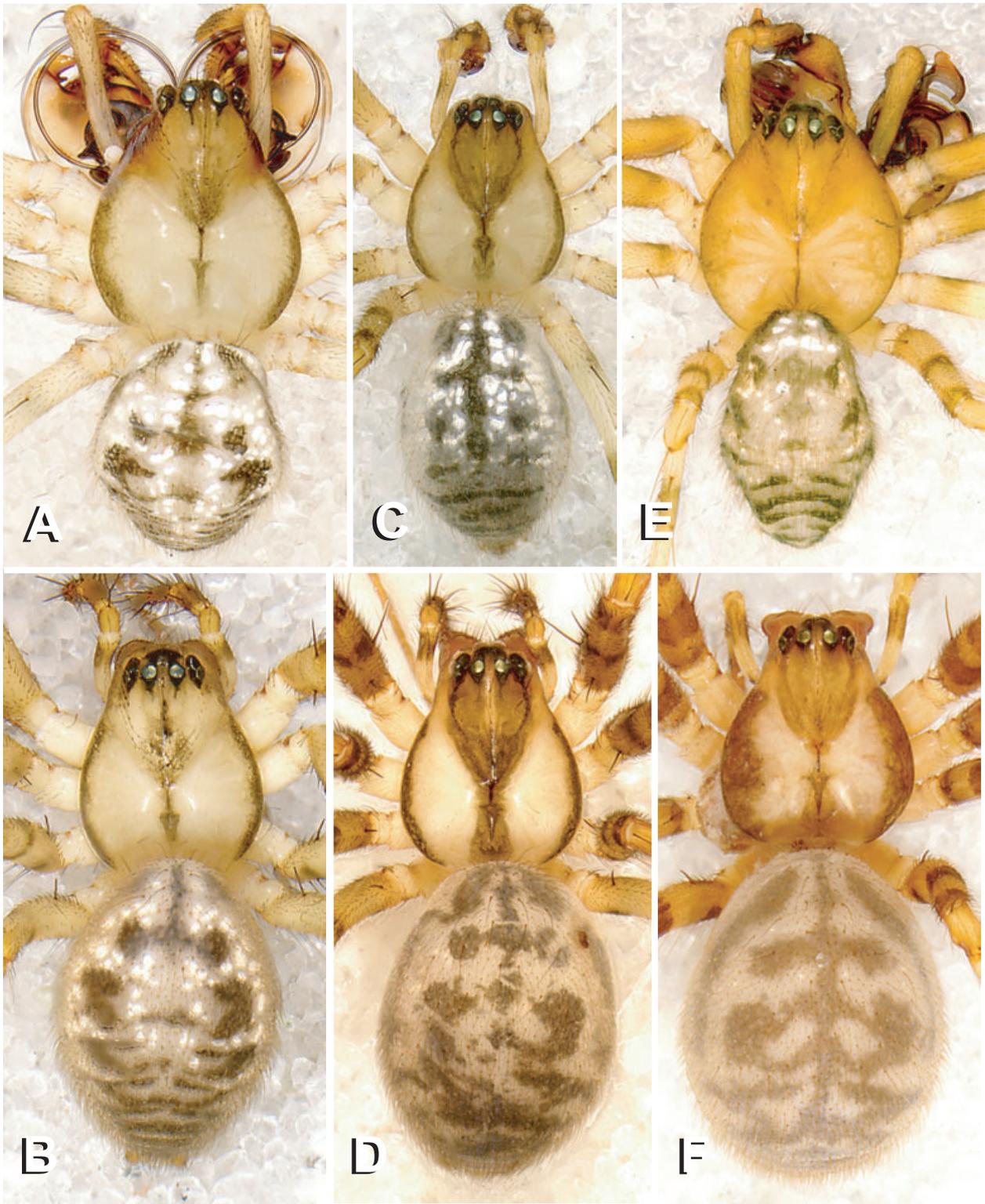


Figure 1. *Labulla thoracica* (Wider) (A, B), *L. flahaulti* Simon (C, D), *L. machadoi* sp. nov. (E, F). Male (A) and female (B) from Hestehaven, Jutland, Denmark; male (C) and female (D) from Gipuzkoa, Spain; male (E) and female (F) from Porto, Portugal.

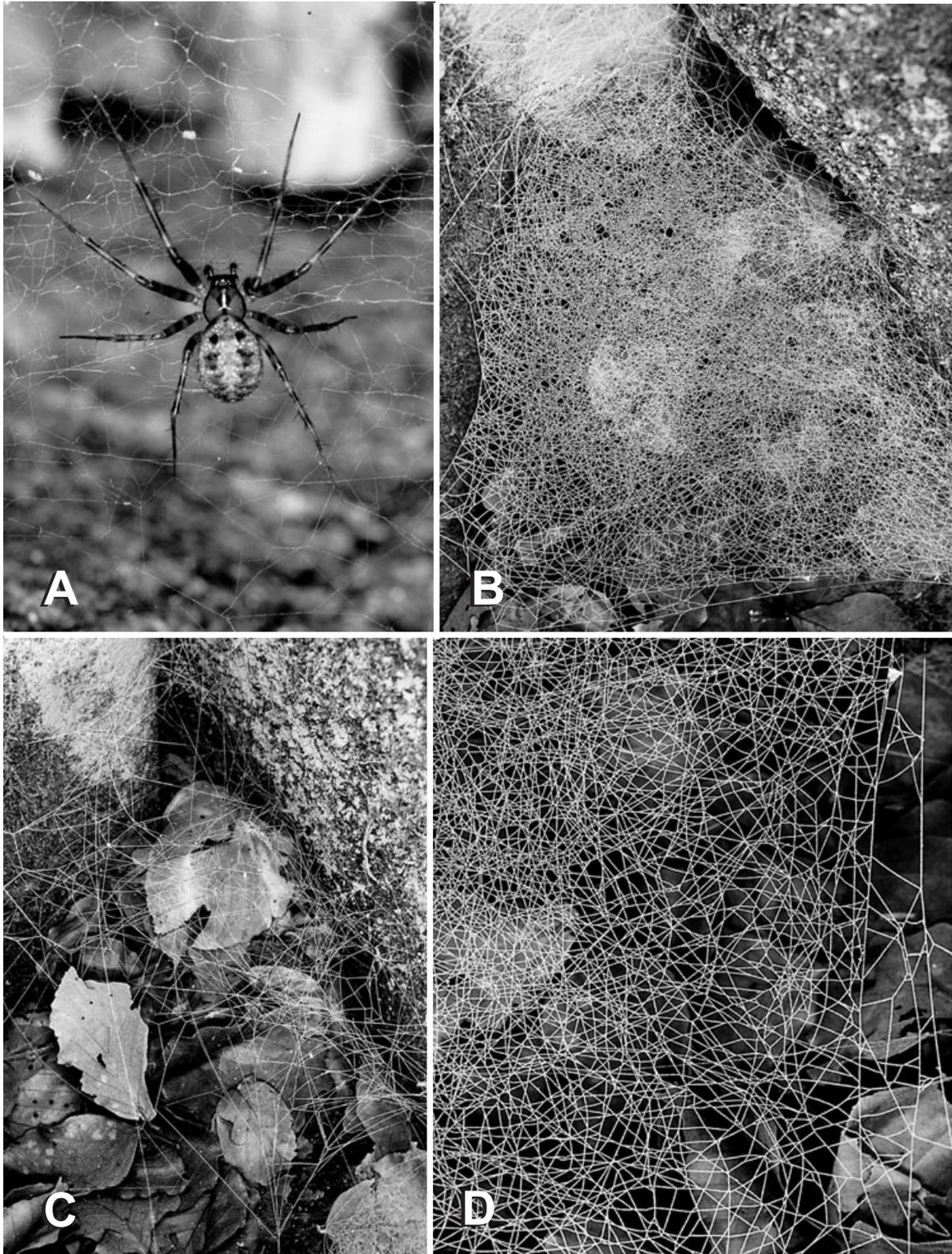


Figure 2. *Labulla thoracica* (Wider), from Hestehaven, Jutland, Denmark. A, female; B, adult female web, woven at the base of a tree, c. 28 cm long and 60 cm wide; C, same web, detail of the mesh below the main sheet (removed); D, same web, detail of the mesh of the main sheet.

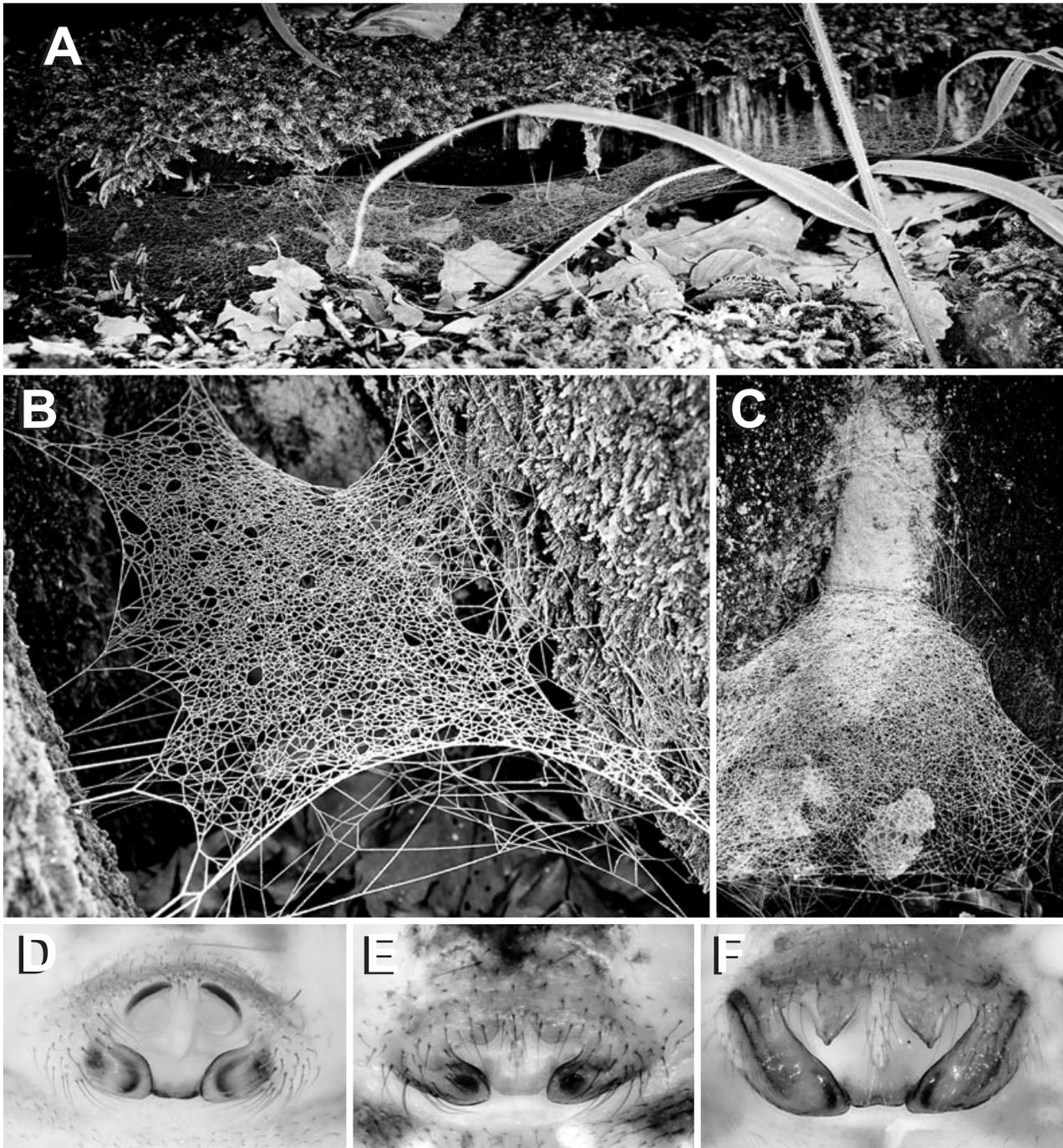


Figure 3. *Labulla thoracica* (Wider) webs from Hestehaven, Jutland, Denmark (A–C) and ventral views of the epigyna of *Labulla* species (D–F). A, adult female web, woven under a moss mat; B, adult male web at the base of a tree; C, adult female web, woven at the base of a tree; D, *Labulla thoracica* (Wider) from Hestehaven, Jutland, Denmark; E, *L. flahaulti* Simon, from Gipuzkoa, Spain; F, *L. machadoi* sp. nov. from Porto, Portugal.

membranous connection to the radix at the proximal end. In *L. thoracica* (Fig. 6C) and *L. machadoi* sp. nov. (Fig. 12C) the distal process is larger than in *L. flahaulti* (Fig. 9C) but in all three species the distal

process has a membranous or blade-like posterior part. In addition, the latter two species have a plumose process in the terminal apophysis (Figs 21G, 22C).

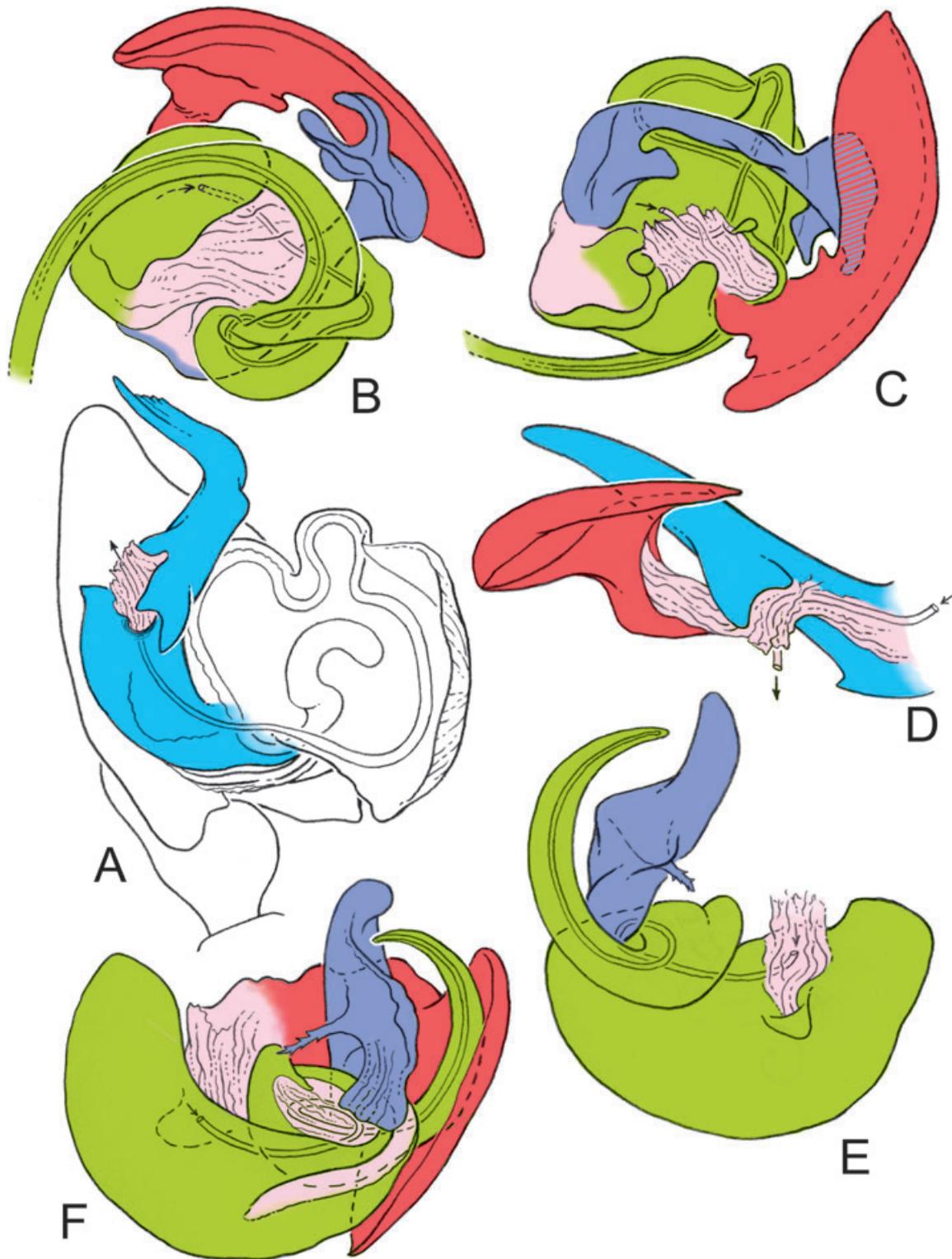


Figure 4. Schematic representation of the palp morphology of *Labulla thoracica* (Wider) (A–C) and *L. flahaulti* Simon (D–F). The sclerites have been colour-coded as follows: lamella characteristic (red), supratregulum (blue), radix and embolus (green), terminal apophysis (violet), column and membranes (pink). A, ventral palp with embolic division excised; B, embolic division, ventral; C, embolic division, dorsal; D, supratregulum with lamella characteristic, ventral; E, embolic division (lamella removed), dorsal; F, embolic division, ventral.

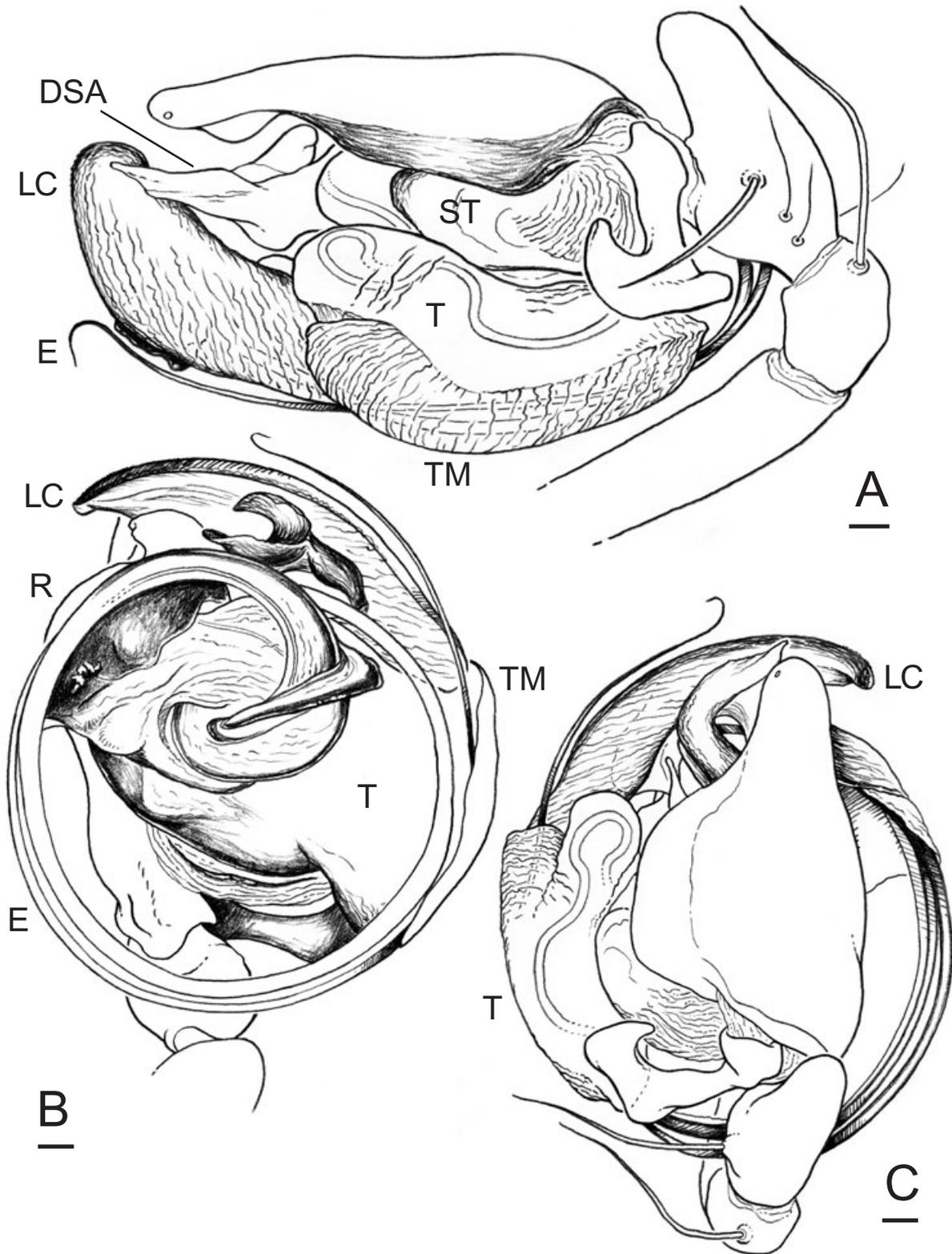


Figure 5. *Labulla thoracica* (Wider), male palp, from Hestehaven, Jutland, Denmark. A, ectal; B, ventral; C, dorsal. Scale bars = 0.1 mm.

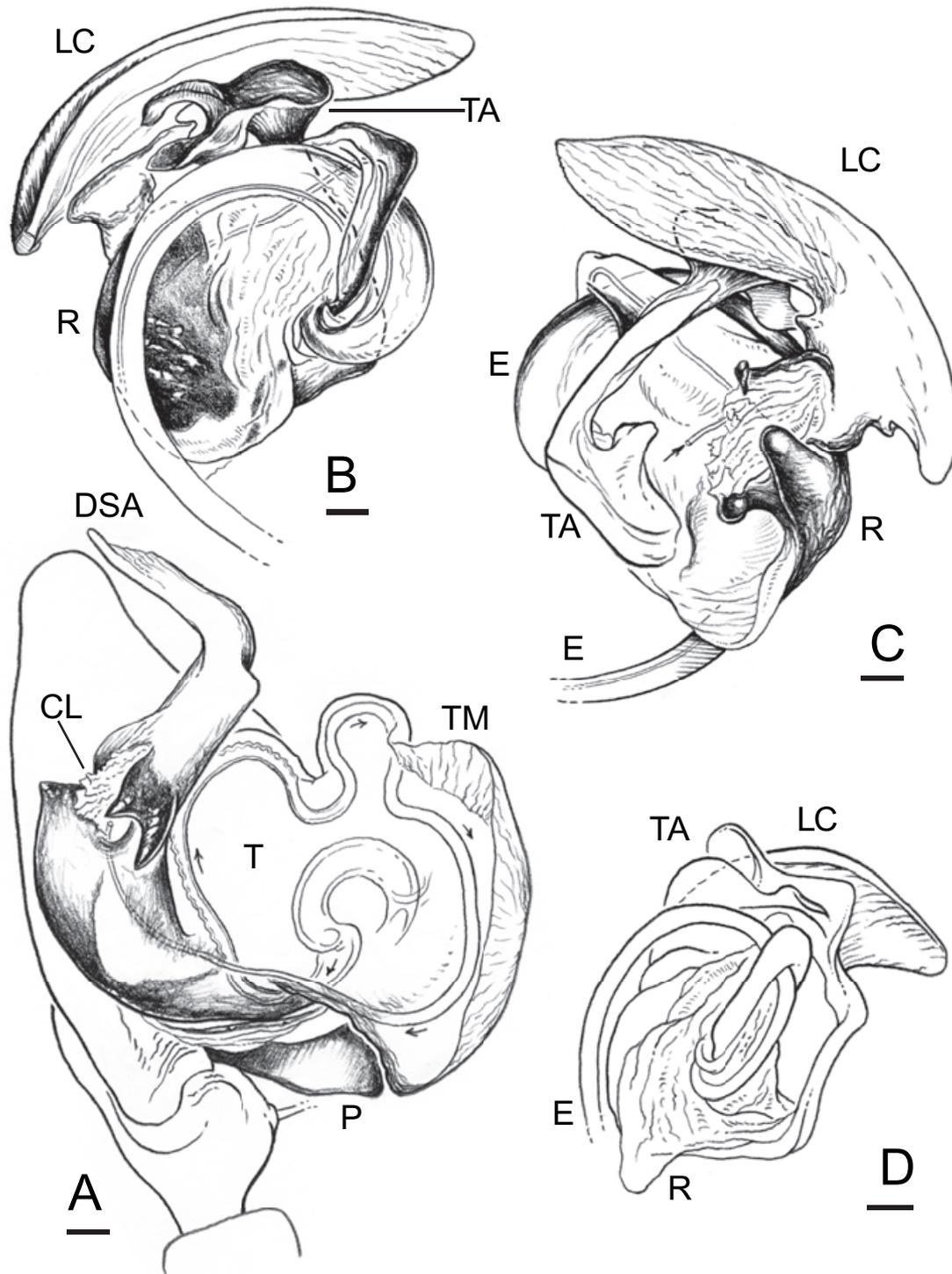


Figure 6. *Labulla thoracica* (Wider), male palp, from Hestehaven, Jutland, Denmark. A, ventral palp with embolic division excised; B, embolic division, ventral; C, embolic division, dorsal; D, embolic division, caudomesal. Scale bars =0.1 mm.

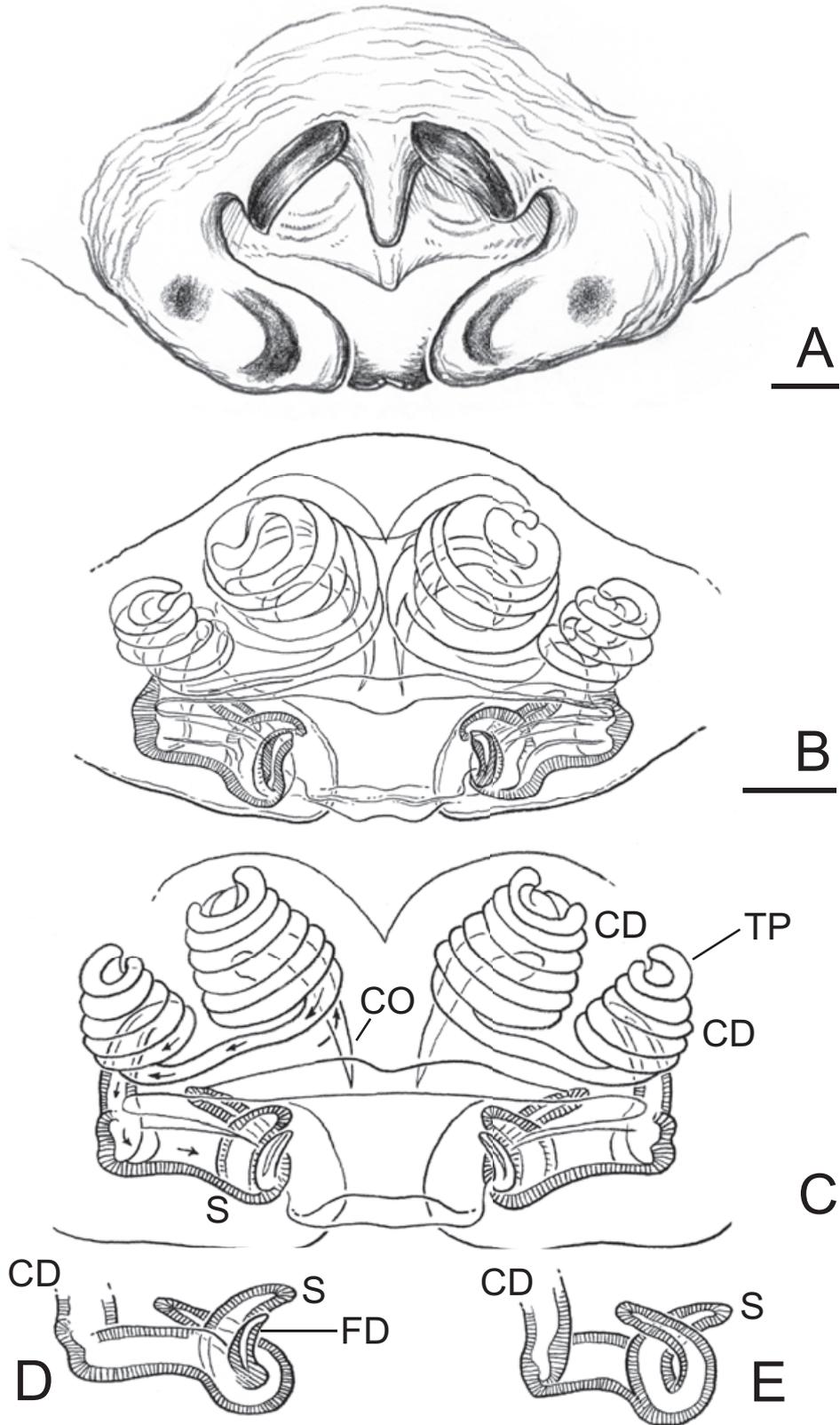


Figure 7. *Labulla thoracica* (Wider), epigynum, from Hestehaven, Jutland, Denmark. A, ventral; B, dorsal (cleared); C, dorsal (schematic); D, spermatheca, dorsal (schematic); E, spermatheca, ventral (schematic). Scale bars = 0.1 mm.

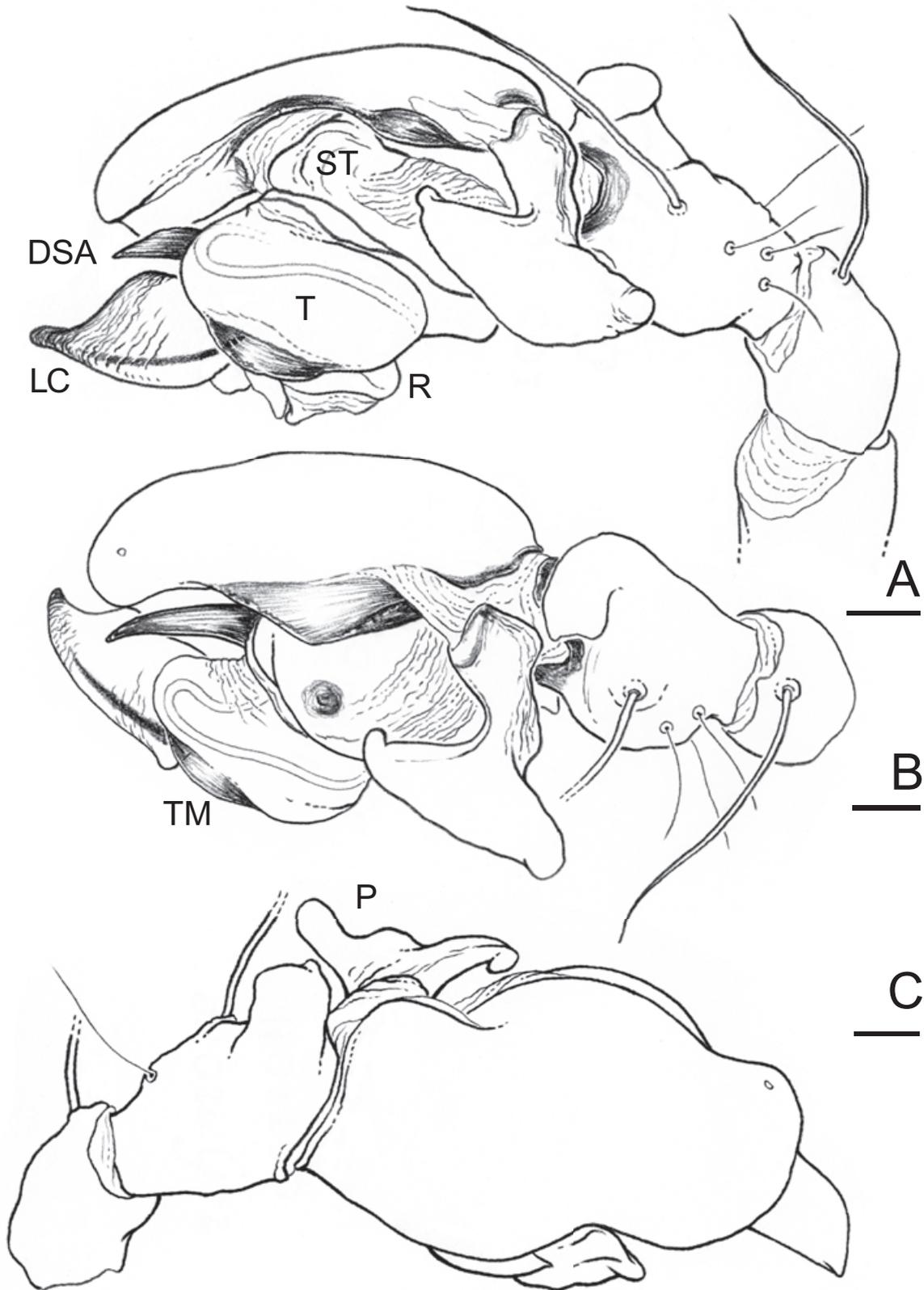


Figure 8. *Labulla flahaulti* Simon, male palp, from Gipuzkoa, Spain. A, ectal; B, dorsoectal; C, dorsal. Scale bars = 0.1 mm.

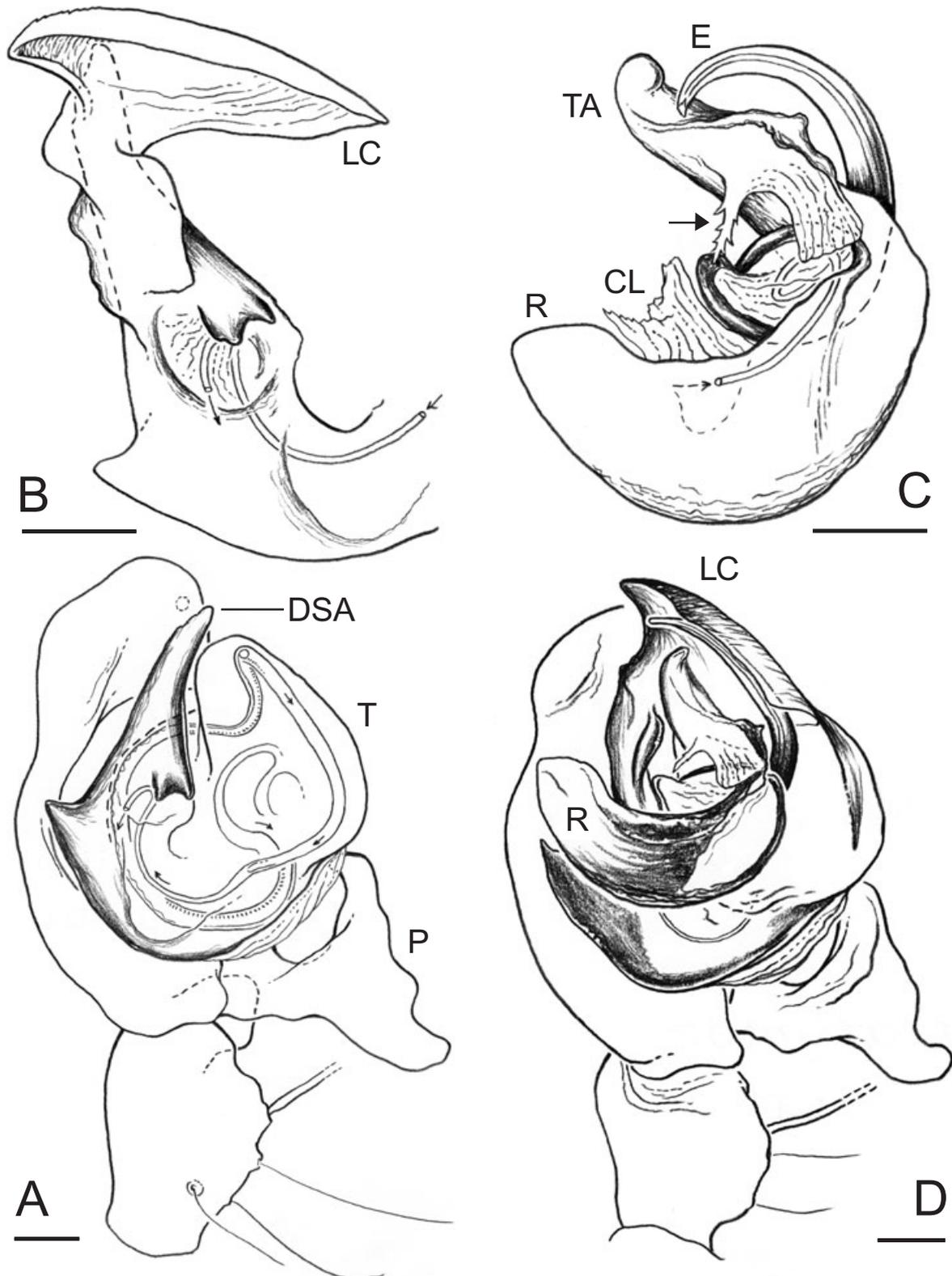


Figure 9. *Labulla flahaulti* Simon, male palp, from Gipuzkoa, Spain. A, ventral palp with embolic division excised; B, supratégulum with lamella characteristica, ventral; C, embolic division (lamella removed), ventral (arrow, plumose process of terminal apophysis); D, palp, ventral. Scale bars = 0.1 mm.

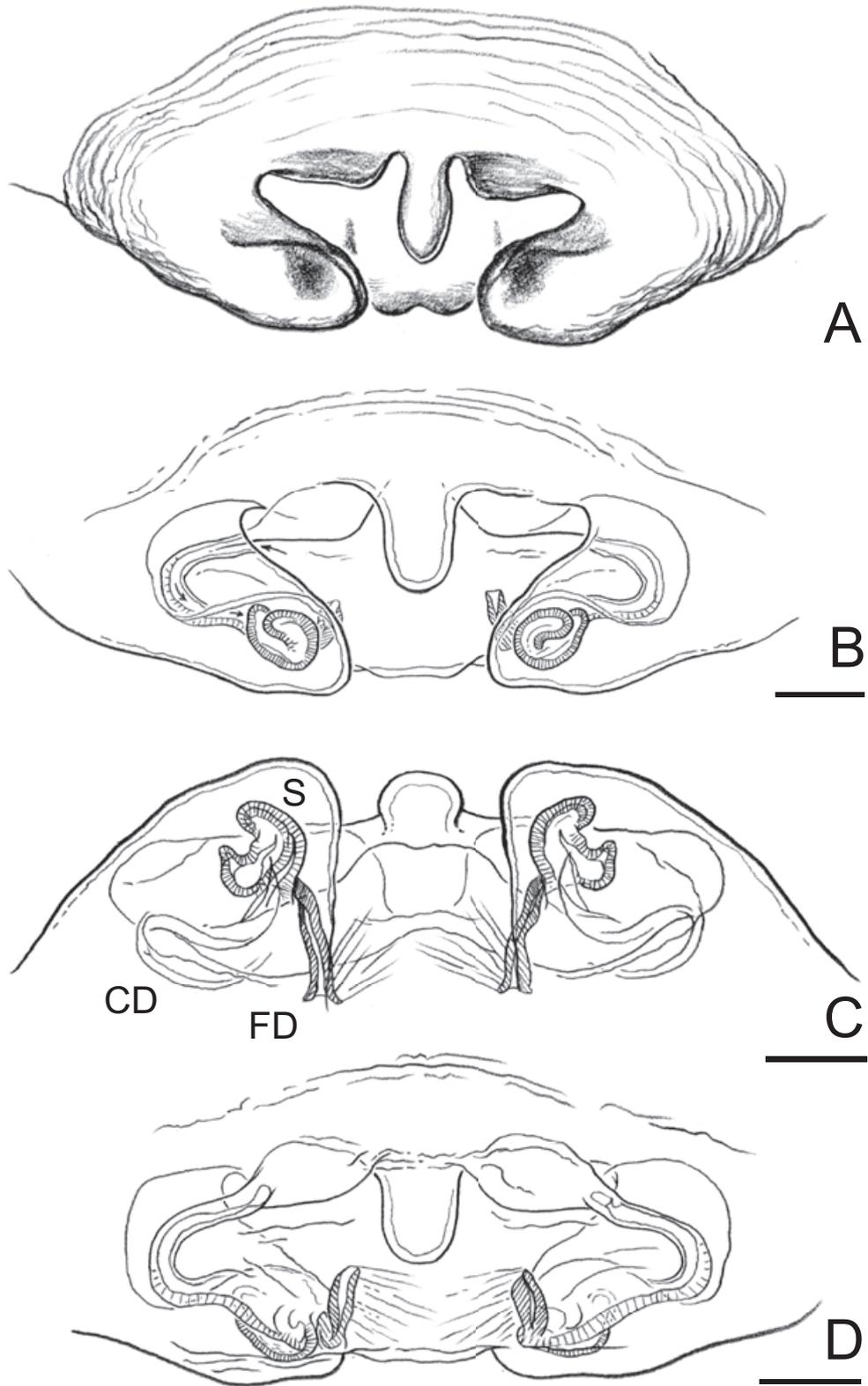


Figure 10. *Labulla flahaulti* Simon, epigynum, from Gipuzkoa, Spain. A, ventral; B, ventral (cleared); C, caudal (cleared); D, dorsal (cleared). Scale bars = 0.1 mm.

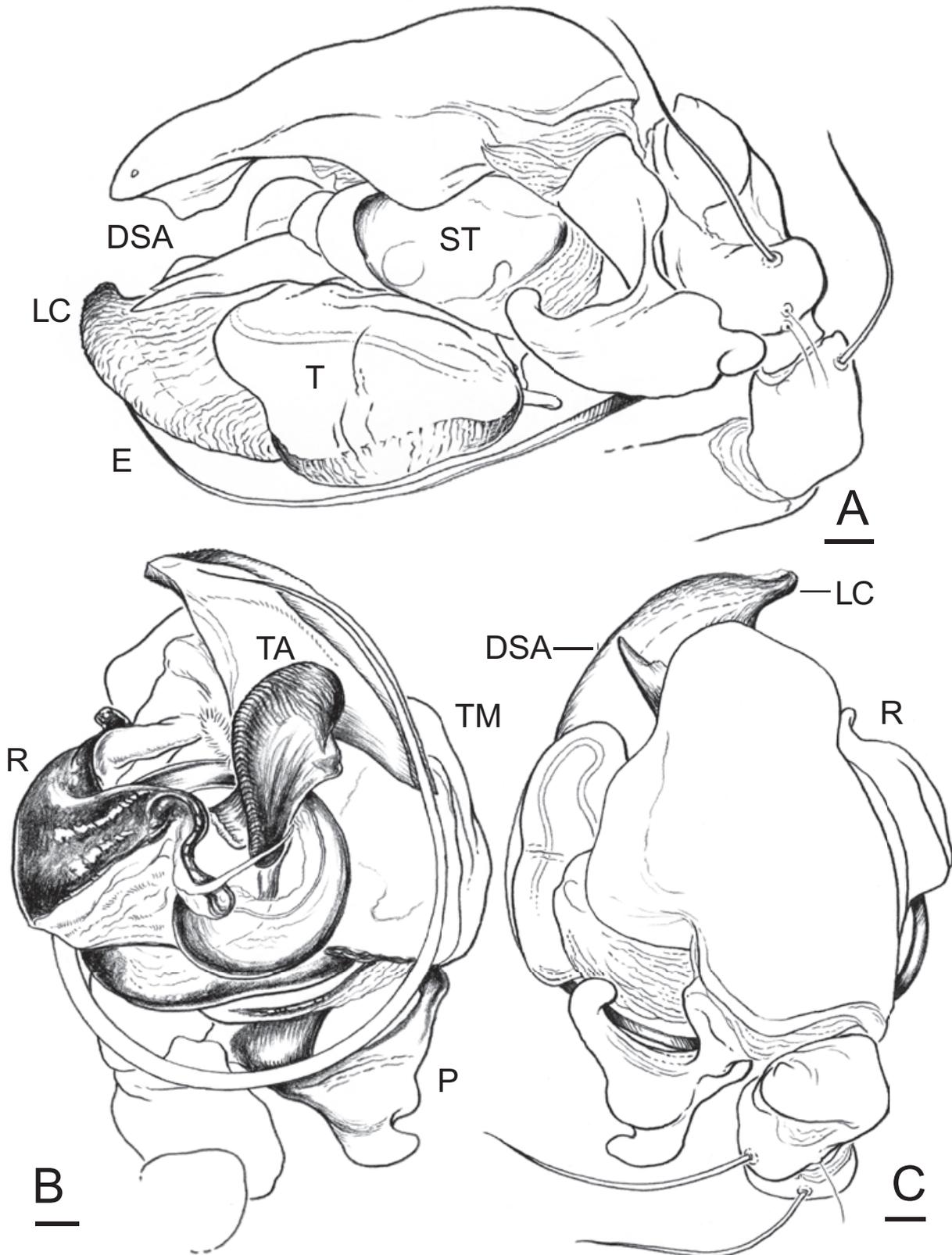


Figure 11. *Labulla machadoi* sp. nov., male palp, from Porto, Portugal. A, ectal; B, ventral; C, dorsal. Scale bars = 0.1 mm.

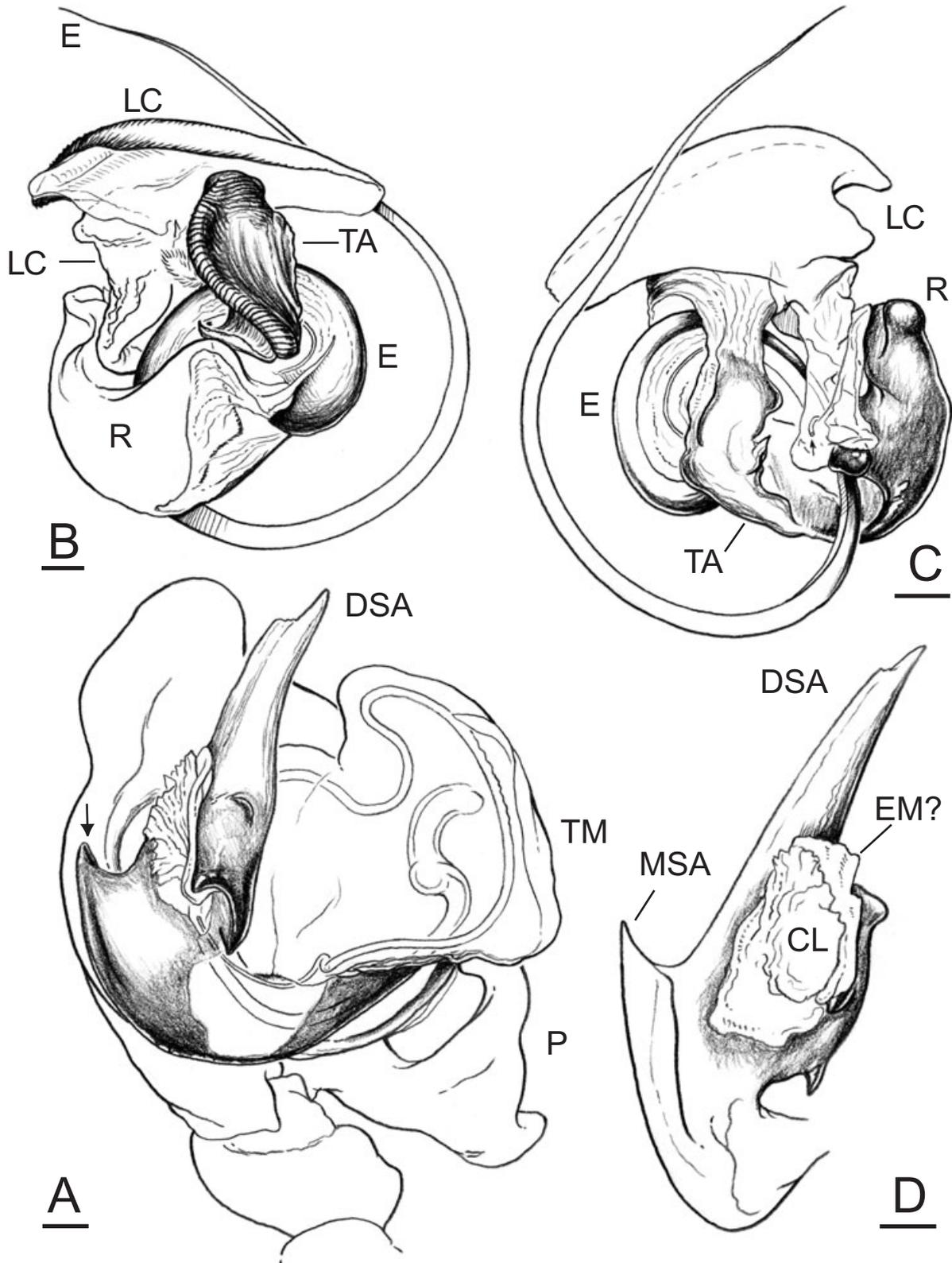


Figure 12. *Labulla machadoi* sp. nov., male palp, from Porto, Portugal. A, ventral palp with embolic division excised (arrow, mesal suprategular apophysis); B, embolic division, ventral; C, embolic division, dorsal; D, suprategulum, ventral. Scale bars = 0.1 mm.

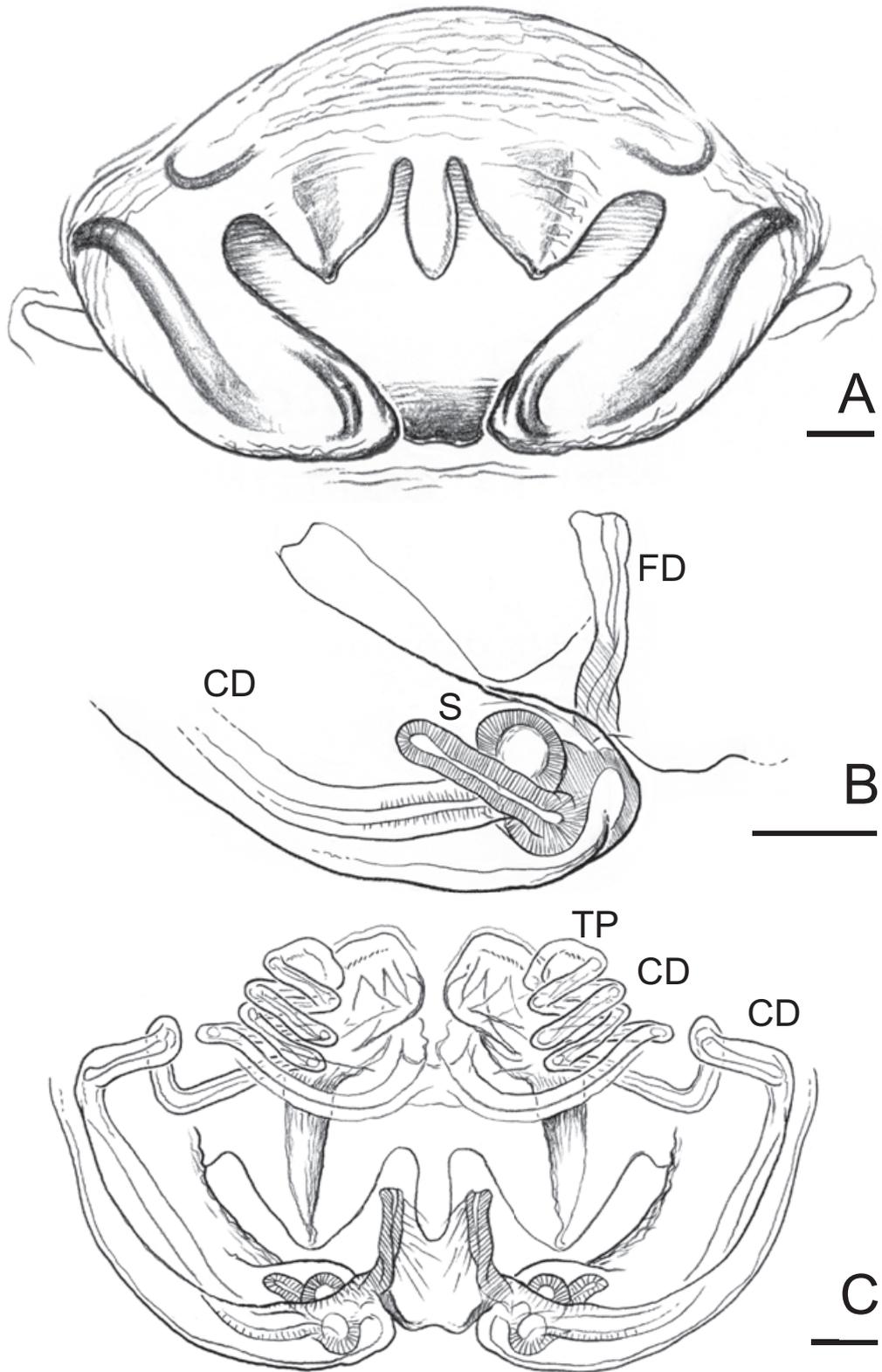


Figure 13. *Labulla machadoi* sp. nov., epigynum, from Porto, Portugal. A, ventral; B, detail of spermatheca and fertilization duct, ventral; C, dorsal (cleared). Scale bars = 0.1 mm.

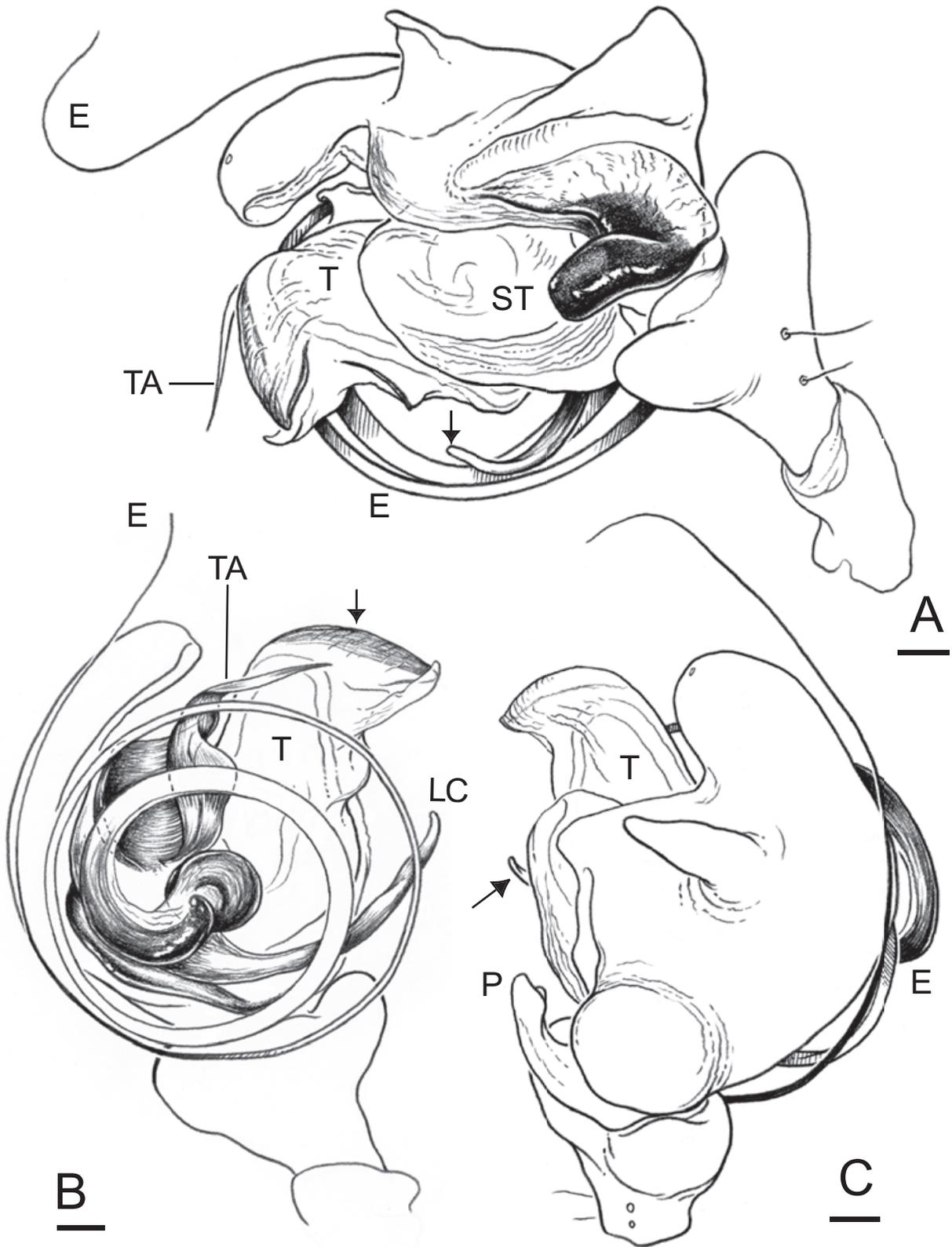


Figure 14. *Pecado impudicus* (Denis), male palp (holotype). A, ectal; B, ventral; C, dorsoectal (arrows in A and C, posterior process of lamella, in B, distal tegular flap). Scale bars = 0.1 mm.

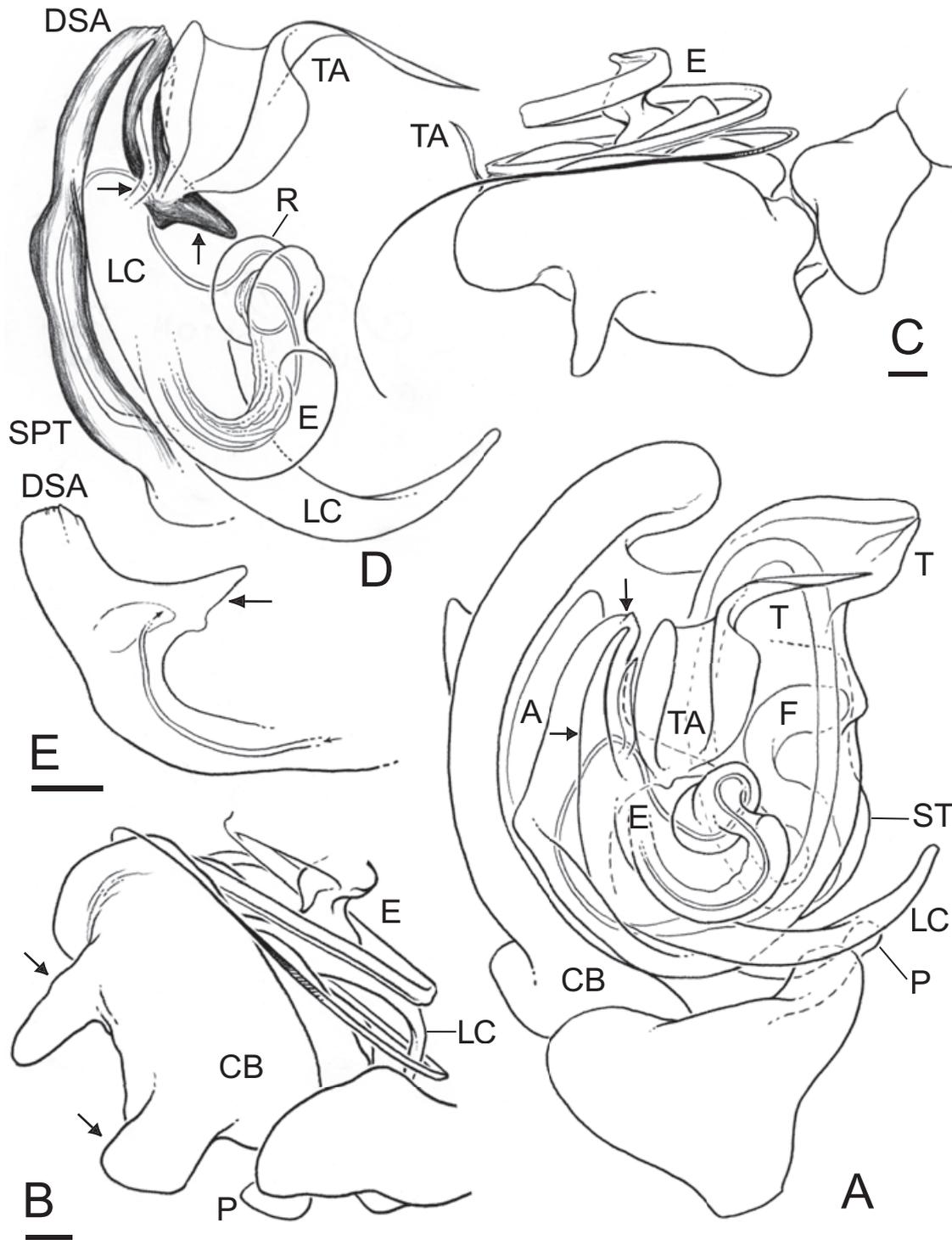


Figure 15. *Pecado impudicus* (Denis), male palp (holotype). A, meso ventral, schematic view of cleared palp with embolus rendered only in its basal region (down arrow, distal suprategular apophysis; right arrow, anterior process of lamella); B, posteromesal (arrows, cymbial processes); C, dorsomesal; D, embolic division and suprategulum, schematic view of cleared palp with embolus rendered only in its basal region (column and intersclerite membranes not rendered; right arrow, embolic membrane; up arrow, marginal suprategular apophysis); E, suprategulum (arrow, ectal suprategular apophysis). Scale bars = 0.1 mm.

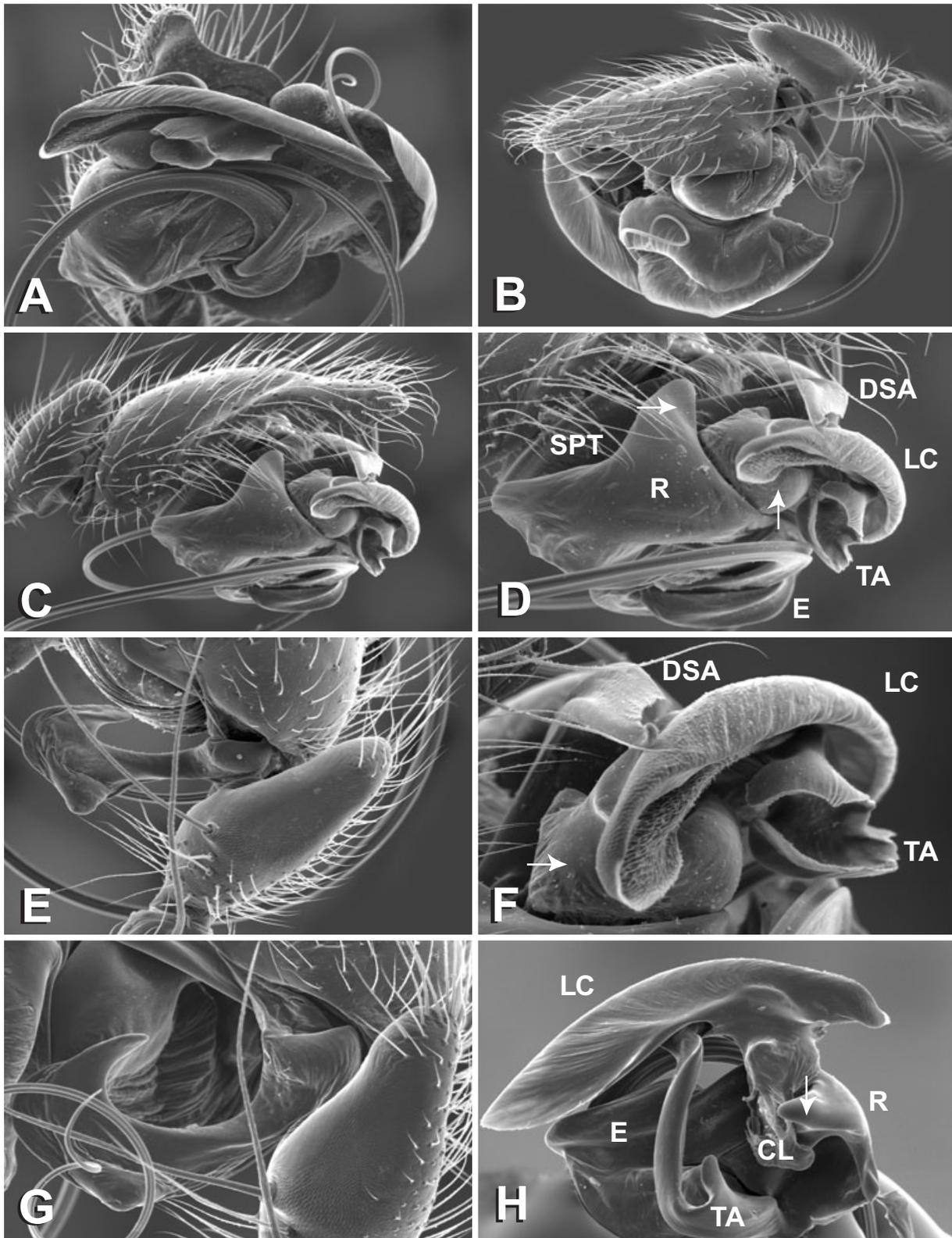


Figure 16. *Labulla thoracica* (Wider), male palp. A, apicoventral; B, ectal; C, mesal; D, embolic division, mesal (arrow right, radical process; arrow up, base of lamella); E, paracymbium and tibial apophysis, ectal; F, embolic division, mesoapical (arrow, base of lamella); G, paracymbium, ectal; H, embolic division (excised), dorsal (arrow, radical process).

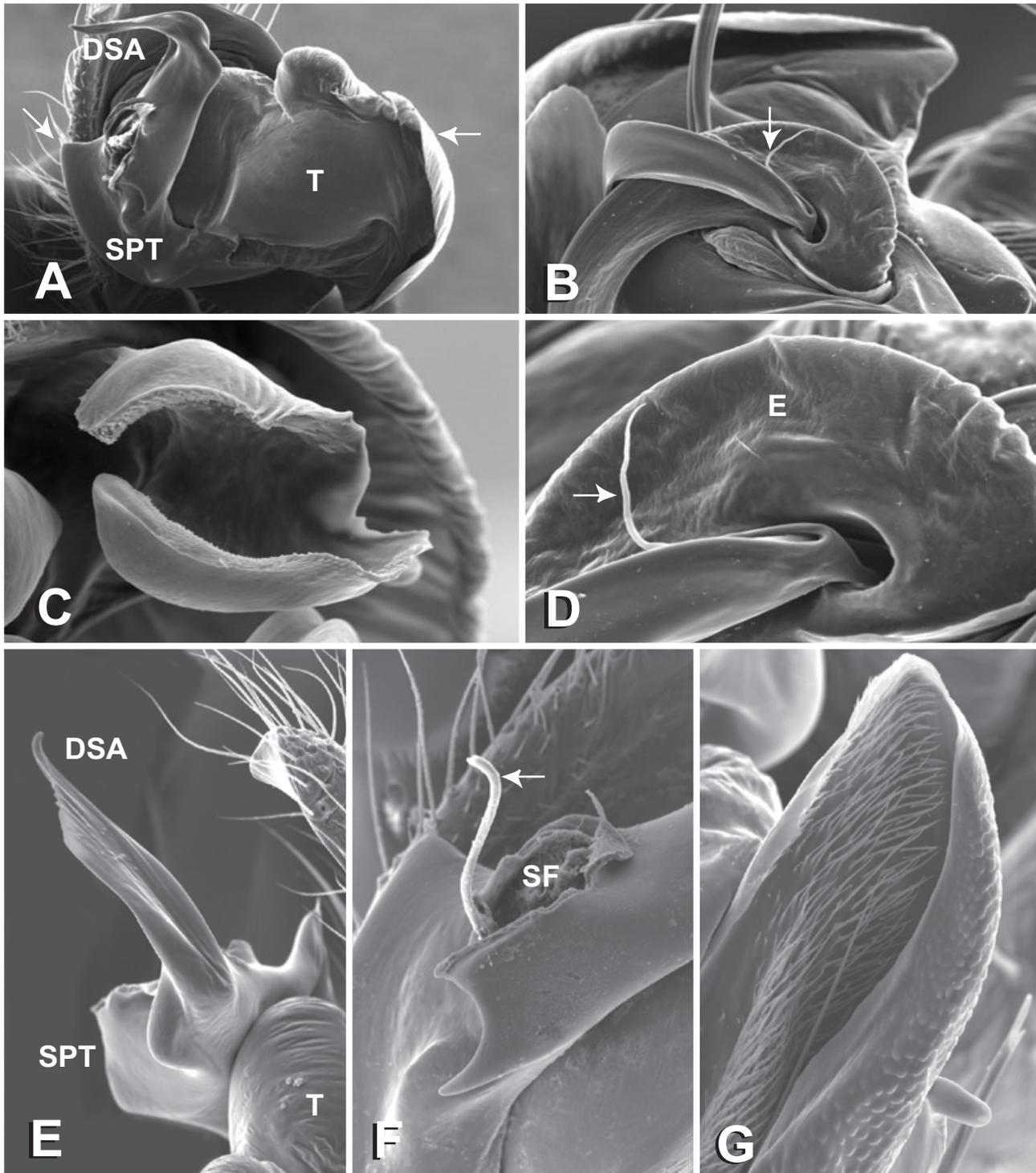


Figure 17. *Labulla thoracica* (Wider), male palp. A, tegular division with embolic division removed (arrow, tegular membrane), ventral; B, embolus base, ventral (arrow, filiform membrane); C, terminal apophysis, distal region; D, embolus base, detail of filiform membrane, ventral (arrow); E, distal suprategular apophysis, apical; F, bifid suprategular apophysis, ectoventral (arrow, sperm duct); G, internal surface of apical region lamella characteristic.

Epigynum

The external morphology of the epigynum is more uniform across species than is the palp morphology (Figs 3D–F, 20A–F). In ventral view, all species have a ventral plate-like scape with a flap (the modified anterior edge of the epigynal cavity) on each side and conspicuous posterior lateral lobes on both sides of the caudal edge of the dorsal plate. The scape lacks a socket. The morphology of the anterior flaps is the most variable interspecific external epigynal feature. The flaps are most conspicuous in *L. machadoi* sp. nov. (Figs 3F, 20E, F), where they are large and V-shaped. In *L. thoracica* (Figs 3D, 20A, B), the flaps are thin, blade-like and sclerotized. In *L. flahaulti* (Figs 3E, 20C, D), the flaps are rather inconspicuous and slightly more sclerotized than the rest of the epigynum. A septum lies beneath the scape, most conspicuously in *L. thoracica* (Fig. 20A), dividing the epigynal cavity (atrium) into a left and a right chamber. In a caudal view of the epigynum of *L. thoracica* (Fig. 20B) and *L. machadoi* sp. nov. (Fig. 20F), the spiralled coils of the copulatory duct can be seen in the deep anterior end of the epigynal cavity.

The copulatory openings are located on both sides of the septum. The internal epigynal morphology is much more variable across species than externally (Figs 7, 10, 13), mainly due to the copulatory duct. In *L. flahaulti* (Fig. 10B–D), the copulatory ducts curve from the copulatory openings directly into the spermathecae and are considerably shorter than the ducts of the other two species studied. In *L. thoracica* (Figs 3D, 7B–E, 18A–F), the copulatory ducts are extremely long and are arranged as two sets of coils, a median pair and a lateral pair (Fig. 18A, B). The median pair is longer than the lateral, and its diameter is also wider, although the diameter of the duct itself remains more or less uniform. Both sets of coils have a turning point (where the duct begins turning in the opposite direction) at the apex of its anterior region. The axis of the coiling sets is filled by a mesh (Fig. 18C) whose function is probably to prevent collapse of the coils. The wall of the last coil of the lateral set, just before joining the spermathecae (Figs 7B, 18E), is different from the rest of coils, being wider in diameter and very similar to the wall of the spermathecae (probably glandular in nature). In *L. machadoi* sp. nov., the morphology of the copulatory duct is similar to that of *L. thoracica* except that the former species lacks the lateral set of coils and the median set is smaller, consisting of two coils running anteriorly, a turning point and two sets of coils running posteriorly (Fig. 13C). The region of the duct prior to the spermathecae can be seen by transparency in the ectal side of the lateral lobes of the epigynum (Fig. 13A). The overall morphology of the spermathecae is rather uniform across species (Figs 7, 10, 13, 18E, F), being U-

shaped, with the open end of the U facing anteriorly. The spermathecae can be partially seen by transparency in the median region of the lateral lobes of the untreated epigynum (Figs 7, 10, 13). Fertilization ducts connecting to the posterior region of the spermathecae are orientated anteriorly (Figs 7B–E, 10C, 13B).

DISCUSSION

Any discussion of hypotheses of homology is, by definition, inextricably linked to discussion of the phylogenetic relationships of the taxa. For this reason we shall briefly review the various placements of *Labulla* in evolutionary classifications as well as in our cladistic analysis before discussing the problems of homologizing the palpal sclerites. Linyphiid classifications and phylogenetic work since 1963 have been summarized in Hormiga (2000). In his study of the palp morphology of linyphiids, Merrett (1963: 456) concluded that *Labulla thoracica* was closely related to *Linyphia*, and classified *Labulla* in his 'Group B', along with the genera *Linyphia* (whose generic circumscription then included the genera *Nerienne* and *Microlinyphia*), *Porrhomma*, *Bathyphantes*, *Diplostyla* and *Allomengea*, and perhaps also *Taranucnus* and *Sintula*. Merrett's 'Group B' was very similar in composition to Wiehle's (1956) Linyphieae plus *Porrhomma*.

Millidge's (1977) work on the conformation of linyphiid palps could not place *Labulla*, although he suggested that its basic palp conformation was closer to the '*Lepthyphantes* area' than to the '*Linyphia* area'. Millidge did not illustrate the palp of *Labulla*, so we do not know how he interpreted the homologies of the embolic division sclerites. Based on the study of the tracheal and epigynal anatomy, Millidge (1984) classified *Labulla* in the subfamily Linyphiinae, although he noted that the internal duct structure of the epigynum was 'more complex than usual for the Linyphiinae' and that the male palp morphology was also 'aberrant'. From these observations, Millidge (1984: 244) concluded that *Labulla* (along with *Australolinyphia* and *Diplostyla*) were primitive branches of the Linyphiinae and possibly sister to remaining members of his newly re-circumscribed subfamily. Further work on epigynal morphology by Millidge (1993) resulted in a new circumscription of Linyphiinae (based on the presence of coiled copulatory ducts posterior to the spermathecae, as in *Linyphia*) and the removal of *Labulla*, *Australolinyphia* and *Wiehlea* from this newly defined subfamily. In his revised classification (Millidge, 1993) *Labulla* could not be assigned to any of the main six branches of Linyphiidae that he proposed. Although Millidge's classification work intended to be phylogenetic, it lacked

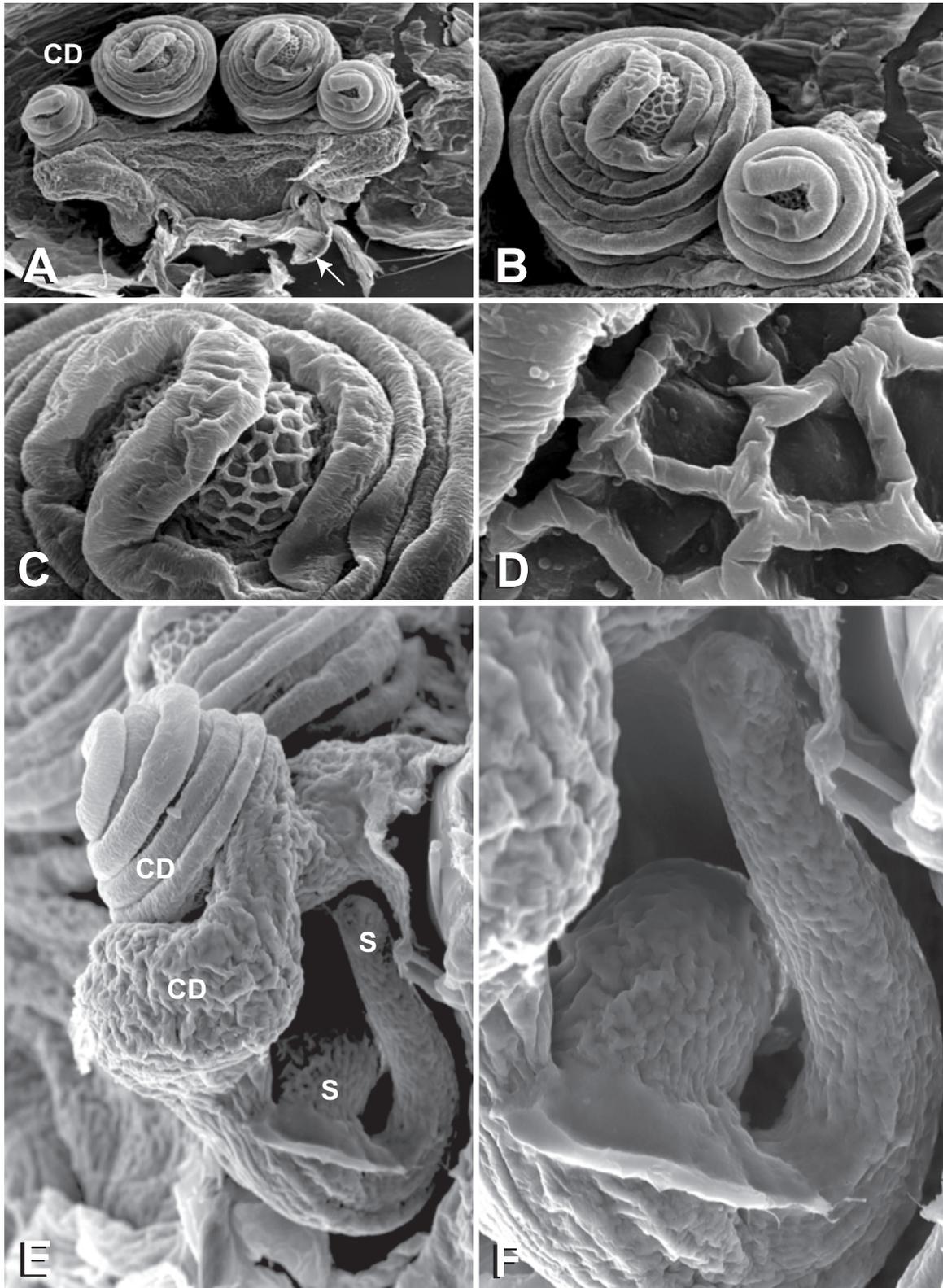


Figure 18. *Labulla thoracica* (Wider), internal morphology of epigynum (KOH digested). A, dorsal (arrow, fertilization duct); B, right copulatory duct coils, dorsal; C, apical core of median copulatory coil; D, apical core of median copulatory coil, detail; E, left lateral copulatory duct coil and spermatheca, caudoectal; F, left spermatheca, caudoectal.

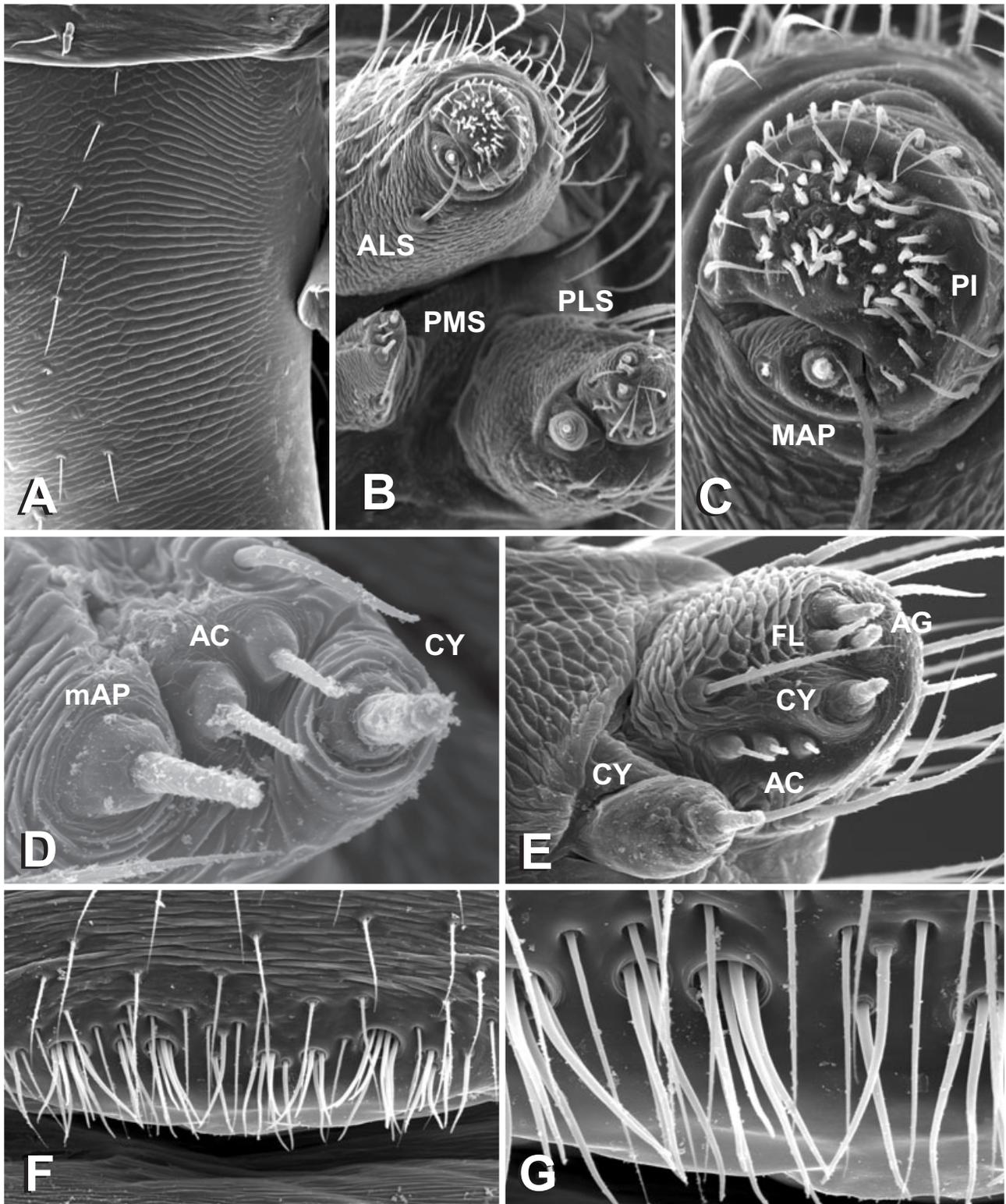


Figure 19. *Labulla thoracica* (Wider), female (A–E) and male (F,G). A, cheliceral stridulatory striae; B, left spinnerets; C, ALS; D, PMS; E, PLS; F, epiandrous region with fusules; G, detail of epiandrous fusules.

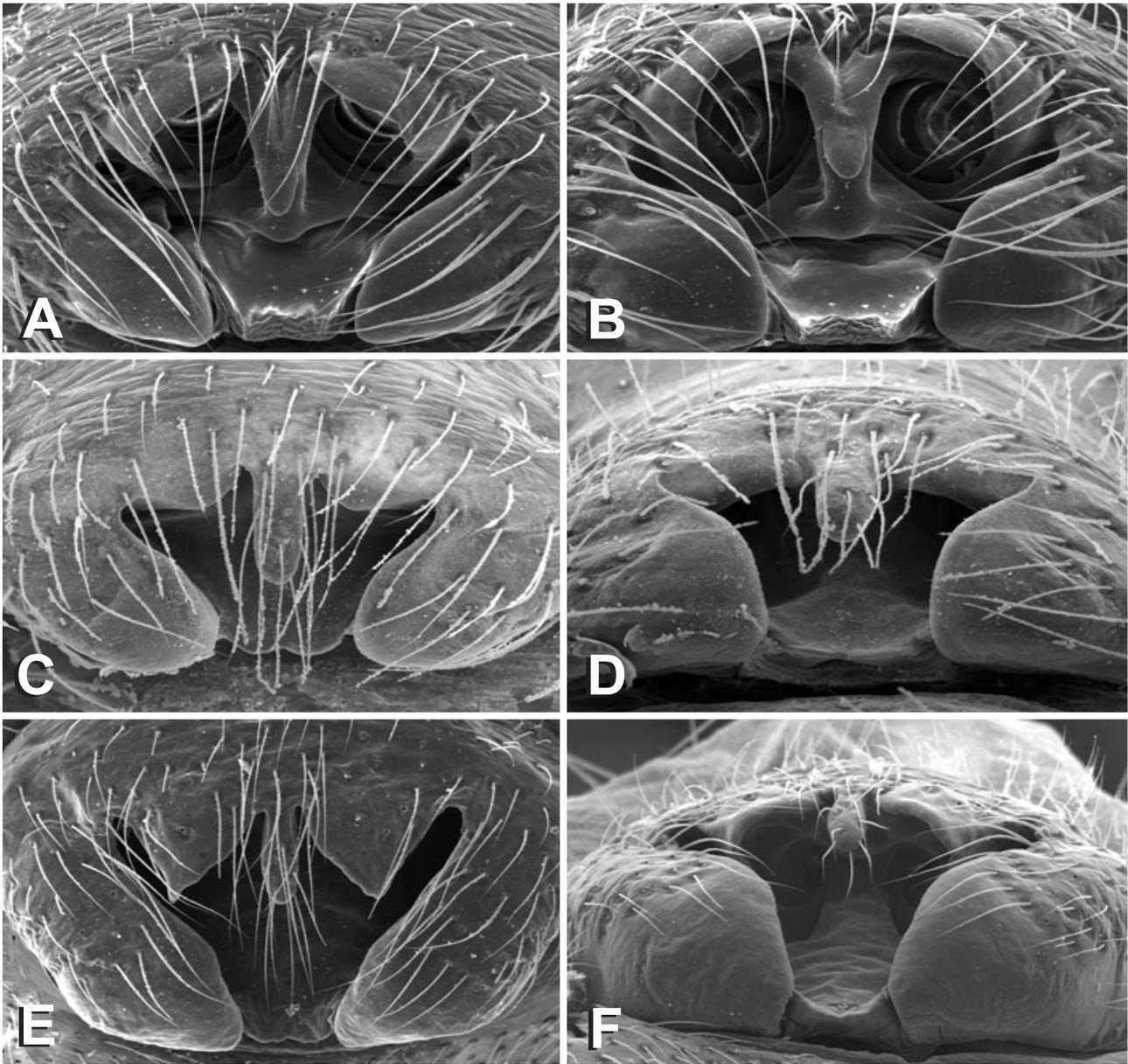


Figure 20. *Labulla thoracica* (Wider) (A,B), *L. flahaulti* Simon (C,D) and *L. machadoi* sp. nov. (E,F), epigyna. A, C, E, ventral; B, D, F, caudal.

explicit methods and criteria to group taxa and to assess incongruence among character systems.

The only phylogenetic analyses that have used an explicit methodology and that have included the genus *Labulla* (represented by *L. thoracica*, the type species) are those of Hormiga *et al.* (2003) and Hormiga (2002, 2003). The first two of these three analyses were explicitly designed to test the monophyly of the genus *Orsonwelles* and the conjecture that *Labulla* was only distantly related to *Orsonwelles* (two species of the latter genus had been originally classi-

fied in *Labulla* by Simon). The character matrix of the third study was designed to test the monophyly of two pimoid genera (*Pimosa* and *Weintrauboa*). That of Hormiga (2002) is based on morphological evidence; Hormiga *et al.* (2003) combined morphological characters and sequence data from five genes. Both analyses recovered the monophyly of Linyphiini (*sensu* Hormiga, 2000), which was represented by *Labulla thoracica*, *Pityohyphantes costatus* (Hentz, 1850), *Microlinyphia dana* (Chamberlin & Ivie, 1943), *Linyphia triangularis* (Clerck, 1757), *Neriene*

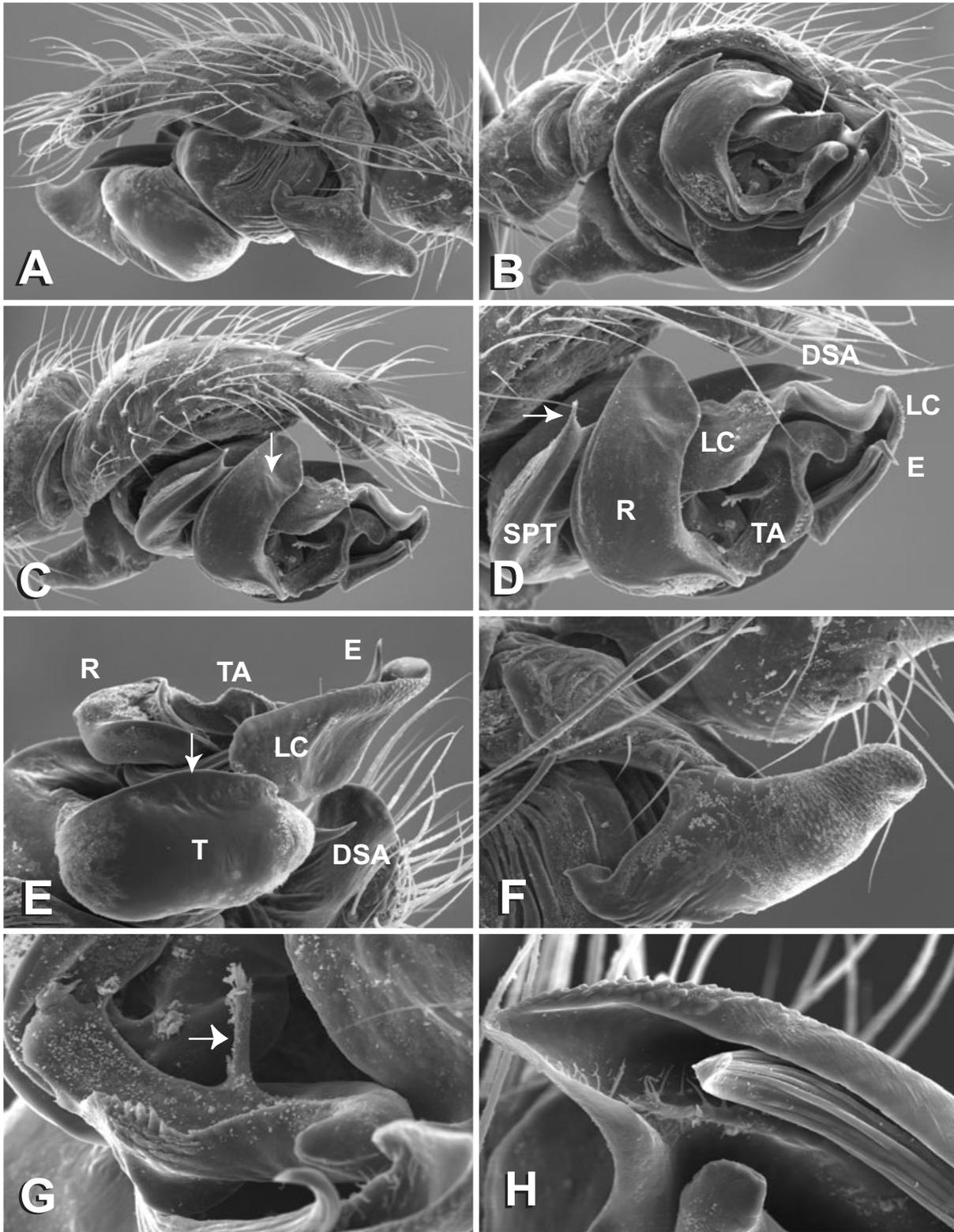


Figure 21. *Labulla flahaulti* Simon, male palp. A, ectal; B, ventral; C, mesal (arrow, radical process); D, embolic division, mesal (arrow, suprategular apophysis); E, tegulum and embolic division, ectoapical (arrow, tegular membrane); F, paracymbium, ectal; G, terminal apophysis (arrow, plumose process); H, internal surface of apical region lamella characteristic (embolus housed inside fold).

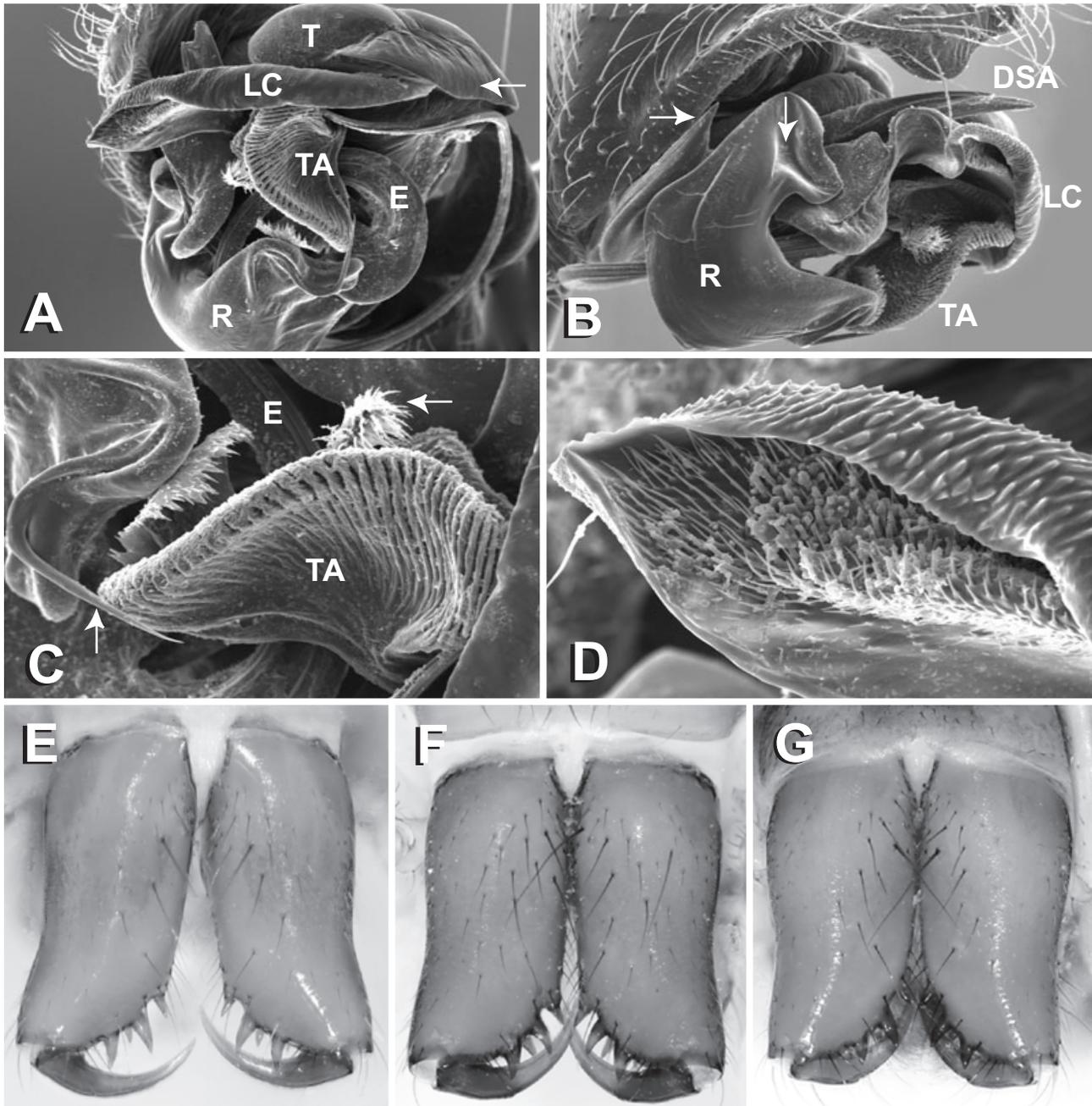


Figure 22. *Labulla machadoi* sp. nov. (A–D, G), *L. thoracica* (Wider) (E), and *L. flahaulti* Simon (F). A, male palp, api-coventral (arrow, tegular membrane); B, male palp, mesal (arrow right, suprategular apophysis; arrow down, radical process); C, terminal apophysis (arrow up, filiform membrane; arrow left, plumose process); D, internal surface of apical region lamella characteristic; E–G, female chelicerae, anterior.

radiata (Walckenaer, 1842), *N. variabilis* (Banks, 1892), *Orsonwelles malus* Hormiga, 2002 and *O. polites* Hormiga, 2002 (Hormiga, 2002, included two additional species of *Orsonwelles*, namely *O. calx* Hormiga, 2002 and *O. arcanus* Hormiga, 2002). Two micronetine species were used as outgroups in these

two studies: *Tenuiphantes tenuis* (Blackwall, 1852) and *Bolyphantes luteolus* (Blackwall, 1833) in Hormiga (2002) and *Lepthyphantes minutus* (Blackwall, 1833) and *Bolyphantes alticeps* (Sundevall, 1833) in Hormiga *et al.* (2003). In the most parsimonious trees resulting from both studies, rooted with the

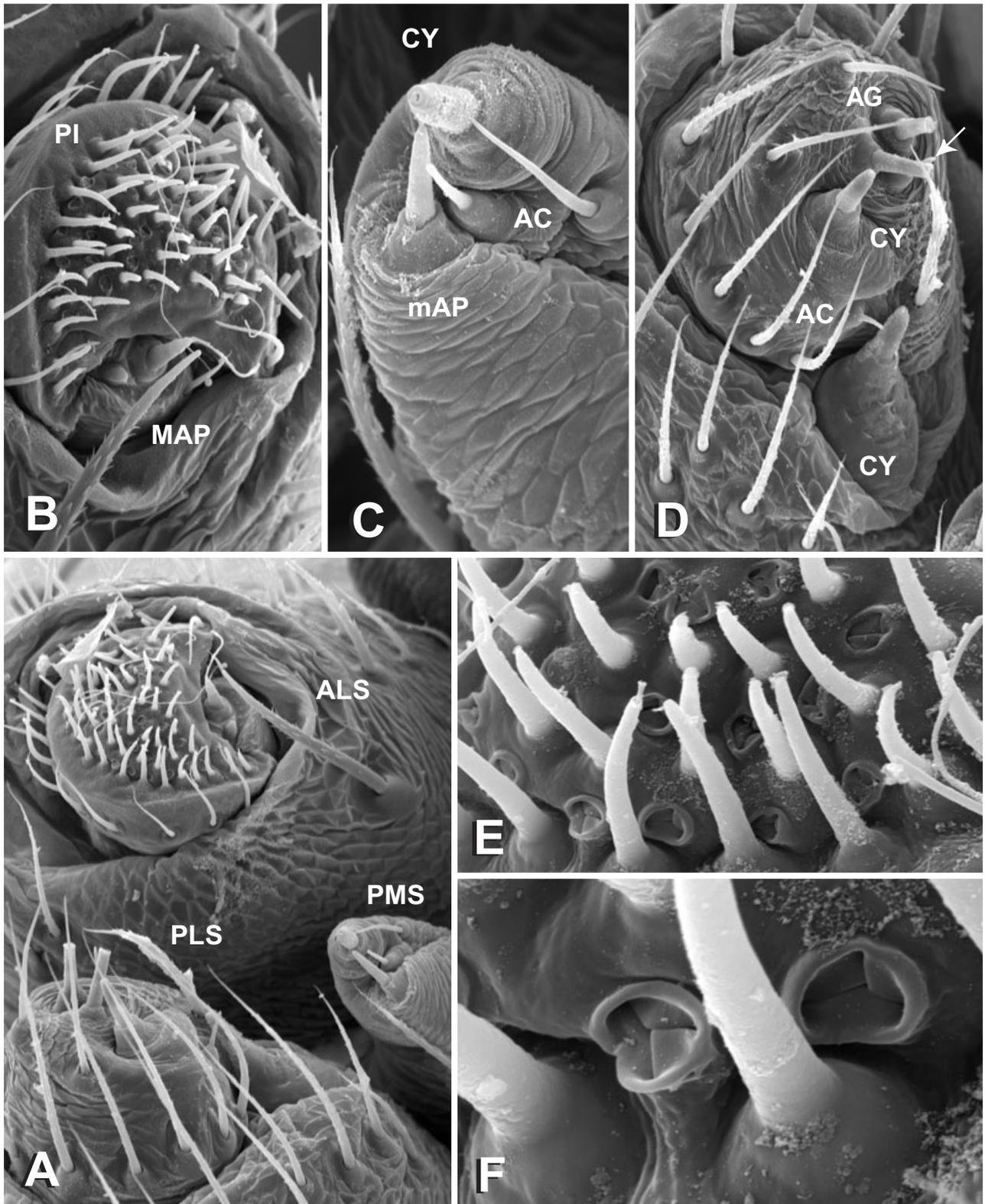


Figure 23. *Labulla machadoi* sp. nov. A, right spinnerets; B, ALS; C, PMS; D, PLS (arrow, flagelliform gland spigot); E, piriform spigots; F, detail of piriform spigots and tartipores.

micronetines, *Labulla* is the sister group to the remaining Linyphiini species.

The analysis of Hormiga (2003: fig. 11), with a denser linyphiid and pimoid sample, places *Labulla* as sister to the micronetine lineage (*Bolyphantes* and *Tenuiphantes*). The parsimony analysis of the character matrix presented in Appendix 2 supports the monophyly of the three *Labulla* species included (Fig. 24). All minimal length topologies (Fig. 24) agree on a sistergroup relationship between *Labulla* and the micronetine clade (*Tenuiphantes* plus *Bolyphantes*), which is supported by at least the following synapomorphies: presence of paracymbial apophyses, ventral position of the ectal suprategular apophysis, the bifid shape of this apophysis and the presence of a ventral plate epigynal scape. Differences in the placement of *Labulla* between this and some of the previous analyses (Hormiga, 2002; Hormiga *et al.*, 2003) are largely due to the taxonomic sample. The current character matrix (Appendix 2) has a denser representation of outgroups than those of Hormiga (2002) and Hormiga *et al.* (2003). Analysis of a reduced version of the matrix given in Appendix 2 (to include only *Labulla*, *Pecado* and the other five Linyphiini taxa) and rooting the minimal length cladograms with the micronetines recovers a monophyletic *Labulla* as the sister group of a clade with the remaining Linyphiini species as well as with *Pecado* and *Orsonwelles*.

The genus *Labulla* is monophyletic based on the following unambiguous synapomorphies (Fig. 25): marginal suprategular apophysis, ectal tegular flap, absence of embolic membrane, ectal position of the terminal apophysis (of ambiguous optimization in some of the optimal trees), lamella sheath-like with a longitudinal fold housing the embolus, anterior epigynal flaps and large posterior lateral epigynal lobes. Additional synapomorphies (albeit of ambiguous optimization) are the paracymbial apophysis as a posterior outgrowth of the medial branch and the dorsal tibial apophysis (a synapomorphy in only some of the most parsimonious trees). As to the placement of *impudicus*, the available data provide three most parsimonious alternatives, none of which indicates sistergroup relationship or membership in *Labulla*: sister to a clade containing all linyphiines, sister to *Orsonwelles* or sister to *Labulla* plus Micronetini. *Pecado impudicus* is known after a single male specimen, and thus it can be only partially scored in the matrix (27 characters are scored as '?' for this species), which undoubtedly contributes to the topological instability of this taxon. No unambiguous character change exists in the minimal length trees to support the sistergroup relationship between *Orsonwelles* (a genus endemic to Hawaii) and *Pecado* (from Algeria). Although both taxa share a mesal orientation of the terminal apophysis (character 35), it is difficult to imagine that this

sistergroup relationship would survive the addition of data. Therefore, no credible morphological evidence exists to include *impudicus* in the genus *Orsonwelles*. Inclusion of *impudicus* in *Labulla* would render the latter genus either polyphyletic or paraphyletic. Under these circumstances a new genus is required for *impudicus*.

GENITALIC ANATOMY

In general terms, the male palp of *Labulla* species conforms to the morphology of 'linyphiines' but it is unique in many details. The resolution of the homologies of some of the sclerites of the embolic division is far from straightforward owing to their unusual morphology.

There are several possible ways of interpreting the homologies of the embolic division without invoking novel sclerites. Merrett (1963: fig. 33) is the only author who has labelled the sclerites of the embolic division in *Labulla*. In Table 1 we compare Merrett's hypothesis to our preferred hypothesis (Fig. 4) plus three alternative hypotheses. We discuss these hypotheses by evaluating the potential homologies of the various sclerites. The embolic division sclerite that we have labelled as lamella characteristica is large and sheath-like in all *Labulla* species, carrying the embolus along its longitudinal fold (Fig. 4B, F – red). A large flat lamella is typical of Linyphiini (e.g. *Neriene*, *Linyphia*, *Microlinyphia*), but the ecto-apical position of this sclerite in *Labulla* is unusual, as most Linyphiini have this in a mesoventral position, clearly seen in the mesal view of the palp (e.g. van Helsdingen, 1969: fig. 322 for *Neriene radiata*). Merrett (1963: fig. 33) homologized this sclerite in *L. thoracica* with a process of the 'median apophysis' (currently termed 'suprategulum'); for him the lamella characteristica's homologue was what we have labelled as the terminal apophysis (in Merrett's illustrations no sclerite of *L. thoracica* receives the label 'terminal apophysis').

There are several lines of evidence that support our conjecture about the homology of the lamella (and thus help us to discard as less logical Hypotheses 1, 2 and 3). The lamella characteristica of *Labulla* species shares with other linyphiini lamella its overall appearance, namely being a large, more or less flat plate. Although the lamella is topologically located in the ecto-apical region, its origin (i.e. connection to the radix) is mesoapical (Figs 5B, 11B, 16D, 21C). The surface microstructure of the apical end is consistent with the function of linyphiini lamella, as described in van Helsdingen's (1969) work on copulatory functional morphology, e.g. in *Neriene hammeni* (van Helsdingen, 1963) the distal margin of the lamella is pressed against the ventral surface of the epigynum (van Helsdingen, 1969: 16, figs 4, 6, 7). The presence of

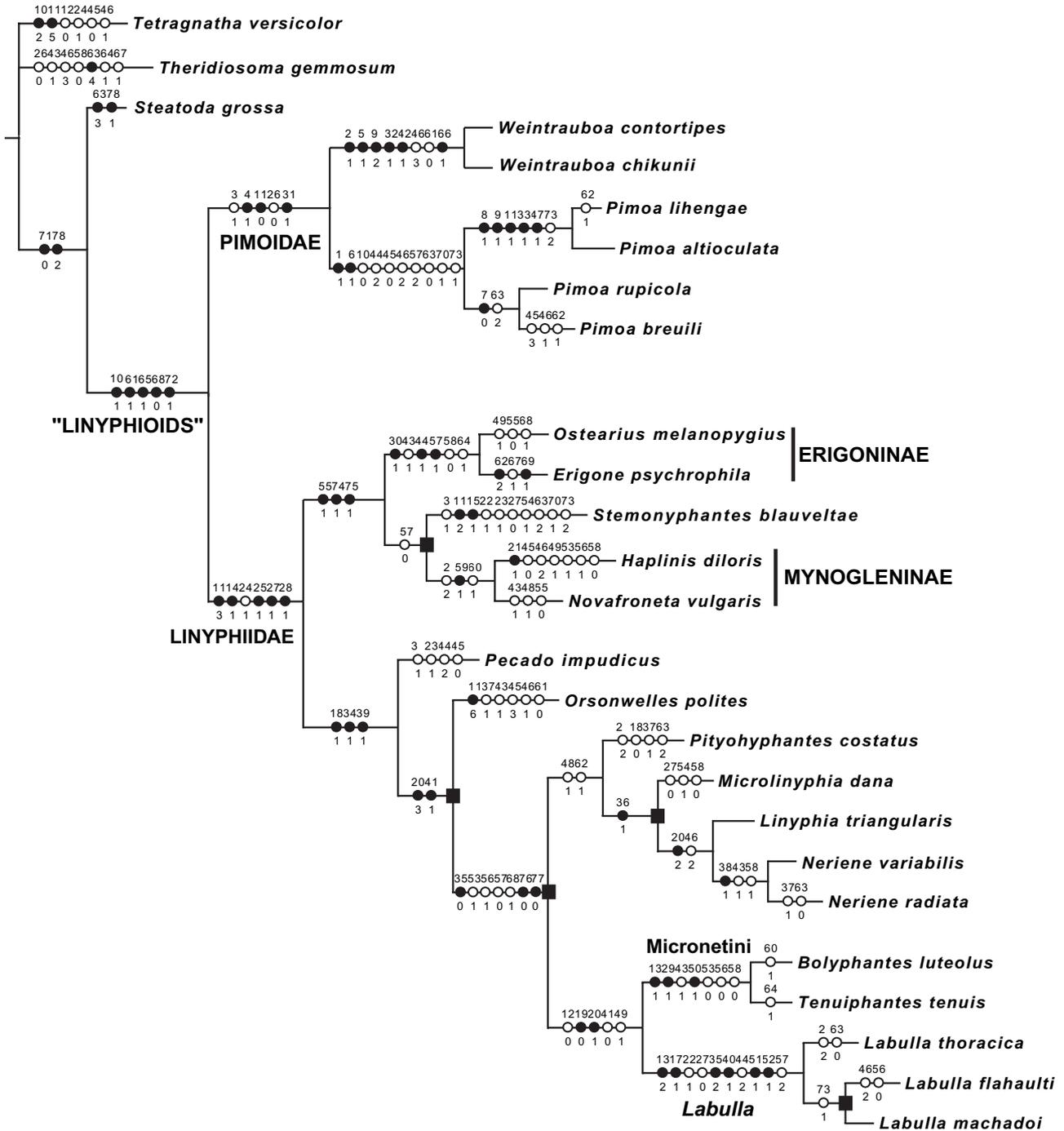


Figure 25. One of the 16 minimal length trees of 170 steps that result from the analysis of the data matrix presented in Appendix 1 (CI = 0.53, RI = 0.73) (see text for details). Most of the ambiguous character changes are resolved under 'ACCT-RAN optimization'. Closed circles represent non-homoplasious character changes. The nodes that collapse in the strict consensus cladogram of the 72 most parsimonious cladograms are marked with a closed square.

rugosities on the cuticular surface of the distal margin of the lamella of all *Labulla* species studied (Figs 17G, 21H, 22D) is therefore consistent with the function of a structure that is pressed against another.

If, nonetheless, this structure were to be homologous to a sclerite other than the lamella, the most parsimonious alternatives would be to postulate homology either to the embolic membrane

Table 1. Alternative hypothesis for the homologies of the embolic division sclerites of *Labulla* species. Merrett's (1963, fig. 33) is based on *Labulla thoracica*. The preferred explanation ('Hypothesis 0') hypothesis has been followed in the accompanying figures (and colour coded in Fig. 4). See text for explanation

Merrett (1963: fig. 33)	Hypothesis 0 (Preferred, see Fig. 4)	Hypothesis 1	Hypothesis 2	Hypothesis 3
Radix	Radix	Radix	Radix	Radix
Embolus	Embolus	Embolus	Embolus	Embolus
Suprateregular apophysis (process of 'median apophysis') (ma)	Lamella characteristica	Embolic membrane	Embolic membrane	Terminal apophysis
Lamella (TA absent) (l)	Terminal apophysis	Lamella characteristica (TA absent)	Terminal apophysis (LC absent)	Lamella characteristica
Membrane (m)	Embolic membrane absent (?)	–	–	Embolic membrane absent

(Hypotheses 1 and 2) or to the terminal apophysis (Hypothesis 3). The first alternatives (Hypotheses 1 and 2) fail to meet the criteria of topological correspondence and special similarity, as the alleged embolic membrane (our lamella) would be an outgrowth of the radix, rather than of the column, as is the case in most linyphiids (Hormiga, 1994b, 2000). Furthermore, this structure does not have the general appearance of an embolic membrane (in *Labulla* this sclerite is too large and too sclerotized relative to the embolic membrane found in most Linyphiini). So, the only similarity of the lamella to an embolic membrane is functional, namely the fact that it covers the tip of the embolus. In addition, these two hypotheses require the loss of the terminal apophysis (Hypothesis 1) or the loss of the lamella (Hypothesis 3). The remaining alternative (Hypothesis 3), that what we have labelled as the lamella is a terminal apophysis, is also less convincing than Hypothesis 0. First, it requires assigning the homology to the lamella to a sclerite that does not have the general morphology of the linyphiini lamella, when in fact a sclerite more of the typical appearance of a lamella is already available. Second, it has been experimentally shown in several species of linyphiini (in the genera *Linyphia* and *Neriene*) that during copulation the terminal apophysis is inserted into the epigynal atrium, and that there is good morphological correspondence between the shape of the terminal apophysis and the atrium (van Helsdingen, 1969). Because the sclerite that we have homologized with the terminal apophysis (Fig. 4) is of similar size to the epigynal atrium, it seems logical to predict that this sclerite is inserted into the atrium during copulation and that its shape would fit the spiral grooves of the epigynum (Fig. 20B). It seems inconceivable that the lamella would fit the epigynal atrium (a likely, but not necessary, functional requirement of being homologous to the terminal apophysis in Hypotheses 1 and 3),

even if the atrium stretched during copulation, as occurs in *Linyphia triangularis* (see van Helsdingen, 1969). Further evidence in favour of Hypothesis 0 is the fact that morphological variation in the terminal apophysis among *Labulla* species is higher than the variation in the lamella, as is usually the case [e.g. compare the terminal apophysis and lamella illustrations of the species of *Neriene* and *Orsonwelles* in the taxonomic monographs of van Helsdingen (1969) and Hormiga (2002)].

We cannot find a structure that could easily be homologized to the embolic membrane found in most linyphiids, which usually consists of a membranous outgrowth of the column. Merrett (1963: fig. 33A, C) depicts a membranous lobe, adjacent to the base of the embolus of *Labulla thoracica*, that he labelled as an embolic membrane ('m'). This structure is located in a region of the radix that is membranous (where the various radical sclerites connect to the radix), but away from the column. We cannot find such a membranous lobe of the radix in any of the specimens of the three species we have examined and therefore have to conclude that a typical column membrane is absent in *Labulla*. Nonetheless we have identified a small membranous outgrowth of the column of *L. machadoi* sp. nov. (Fig. 12A, D) that could be the homologue of the embolic membrane. Observation of this structure requires dissection of the column, and thus it is very difficult to assess whether this small outgrowth is a small embolic membrane or merely an artefact of the excision of the column (lack of specimens prevented further dissections of *L. machadoi*). We could not find a similar column outgrowth in either *L. thoracica* (Fig. 6A) or *L. flahaulti* (Fig. 9A–C).

Labulla thoracica (Fig. 17B, D) and *L. machadoi* (Figs 11B, 12B, 22C) have a very small filiform appendage that arises from the membranous connection of the embolus base to the radix. This filiform

appendage could be a homologue of the embolic membrane that has shifted its position from the column to the radix.

In summary, we consider that the most logical and consistent assignment of homologies to the palp sclerites is that of Hypothesis 0 (see Table 1) and therefore have adopted it as our working hypothesis [this scheme was also followed in the coding of *Labulla thoracica* in the matrices of Hormiga (2002, 2003) and Hormiga *et al.* (2003)].

Determining the homologies of the epigynal structures in *Labulla* species is not problematic. Although the external epigynal morphology is quite uniform across the three species (Fig. 20A–F), the length and arrangement of the copulatory duct varies considerably from one species to another (Figs 7B–E, 10B–D, 13B, C). The length of the copulatory duct correlates with the embolus length. As mentioned above, there seems to be correspondence between the size of the epigynal atrium and the size of the terminal apophysis, suggesting that, as in other linyphiini, the latter is inserted into the atrium during copulation.

In his redescription of *Taranucnus ornithes* (Barrows, 1940), van Helsdingen (1973: 52) suggested that this genus clearly fits 'in the tribe Linyphieae and seems very close to *Labulla*'. We have studied van Helsdingen's (1973) excellent illustrations of *T. ornithes* and specimens of both sexes of the type species, *T. setosus* (O.-P. Cambridge, 1863), which is morphologically very similar to the former. The male palp of *T. setosus* is illustrated in Merrett (1963), who shows the highly unusual details of the palp morphology (contra Millidge, 1984: 237). We cannot find any special similarity between *Taranucnus* and *Labulla*, other than the presence of a long embolus, an otherwise common feature in many linyphiids. Embolus length is a poor predictor of phylogenetic relationships [e.g. this character has a consistency index of 0.09 in Hormiga's (2000) matrix]. In fact, in most genitalic details these two genera are rather different. For example, both *T. ornithes* and *T. setosus* lack the lamella and the terminal apophysis (present in *Labulla*), and have a very large embolic membrane (absent in *Labulla*). Both Merrett (1963) and Millidge (1977) have stated that the embolic division of *Taranucnus* is very similar to that of the subfamily Erigoninae. The suprategula in *Taranucnus* and *Labulla* are also very different (compare van Helsdingen's figs 5 and 6 with Fig. 6A). The epigyna of these two genera are also quite different, except for the presence of anteriorly directed fertilization ducts and subtle lateral epigynal lobes in *T. setosus* (the latter are absent in *T. ornithes*, and the direction of the fertilization ducts in the former is unknown). Although both genera have long coiled copulatory ducts (most likely correlated with the long embolus), they are very different

when examined in detail [compare Millidge's (1984) fig. 33 with Figs 7B, 10D, 13C]. In summary, detailed examination of the morphological features of *Labulla* and *Taranucnus* does not support a close phylogenetic relationship between these two genera.

SYSTEMATICS

LINYPHIIDAE BLACKWALL, 1859

LABULLA SIMON, 1884

Labulla Simon (1884: 261). Type species: *Linyphia thoracica* Wider, 1834: 254, pl. 17, f. 180. Although Simon described the genus in 1884, the type species was designated in Simon (1894: 707).

Diagnosis

Male *Labulla* differ from other linyphiids by the following combination of characters: palpal tibia with dorsal process; paracymbium with a caudad apophysis in the medial branch, presence of an ectal tegular flap (membranous and running along longitudinal axis), presence of a bifid suprategular apophysis adjacent to the column; absence of embolic membrane and sheath-like lamella characteristic with a longitudinal fold housing distal region of the embolus. Females differ from other female linyphiids by the following combination of characters: presence in the epigynum of anterior flaps on both sides of a ventral plate, scape (without socket) and conspicuous posterior lateral lobes and U-shaped spermathecae with anteriorly orientated fertilization ducts. Males and females of all species have a patch of white spots ventrally on the abdomen, just in front of the spinnerets. This can be difficult or impossible to see in old preserved material.

Description

Medium to large linyphiid spiders, total length 4.00–5.20 in males and 3.36–6.32 in females. Carapace longer than wide, piriform, 1.90–2.40 in males and 1.60–2.41 in females. Cephalothorax and chelicerae pale yellowish brown, carapace with greyish brown borders, with darker yellowish brown cephalic area (except male of *L. machadoi* sp. nov., Fig. 1). Black rings around all eyes (Fig. 1). Thoracic furrow deep, running longitudinally from the posterior end of the cephalon to the posterior edge of the carapace. Sternum dark greyish brown. Legs yellowish brown, with dark annulations. Abdomen light grey, with dark grey pattern and white spots (Fig. 1A). Ventrums with white dots, in variable pattern, between the book lungs and spinnerets (this can be difficult or impossible to see in old preserved material). Chelicerae with stridulatory striae. Clypeus height 5.75–2.23 times one AME diam-

eter in males and 1.91–2.50 times one AME diameter in females. Chelicerae with three large widely spaced prolateral teeth and three to four small closely spaced retrolateral, proximal teeth (Fig. 22E–G). Femur I 1.64–1.96 (males) and 1.27–1.76 (females) times the length of cephalothorax. Legs covered with numerous spines. Femur I–IV with one dorsal spine; femur I with additional prolateral spine. Tibia I–IV with two dorsal spines; all tibiae with additional ventral, pro- and retrolateral spines. Metatarsi I–IV with two dorsal spines; all metatarsi with additional pro- and retrolateral spines, but no ventral spines. Metatarsus I trichobothrium 0.2–0.3 (sometimes absent in male *L. thoracica*). Metatarsus IV trichobothrium absent. Female palp with tarsal claw. Leg autospasy at the patella–tibia junction. Colulus large and fleshy, covered with short setae and two long setae (longer than the colulus itself) on each side. Spinnerets typical of a linyphiine (Hormiga, 1994b, 2002) (Fig. 23A–E). ALS have a small piriform field with tartipores (Townley & Tillinghast, 2003; Fig. 23B, E, F). PMS have between one and two aciniform spigots between the cylindrical and the minor ampullate spigot (Fig. 19D). PLS have between one and three aciniform spigots (Fig. 19E); base of the peripheral cylindrical spigot at least twice the diameter of the base of the distal one (Fig. 19E). The flagelliform and aggregate gland spigots (araneoid ‘triplet’) are well developed (Fig. 19E). Triplet absent in the adult male (studied in *L. thoracica*). Epiandrous fusules (studied in *L. thoracica*, Fig. 19F, G) arranged linearly in sockets containing from nine to two fusules; also a few individual fusules (without socket; Fig. 19F, G). Tracheal system haplotracheate [studied in *L. thoracica* (see Blest, 1976)].

Male palpal tibia with dorsal process, one prolateral and two retrolateral trichobothria. Paracymbium with a caudad apophysis in the medial branch. Tegulum with an ectal tegular flap, membranous and running along its longitudinal axis. Suprategulum with a bifid suprategular apophysis adjacent to the column, a pointed apophysis, mesal to the suprategular foramen and a distal suprategular apophysis that is more or less flat in section. Typical embolic membrane absent. Lamella characteristic sheath-like, with a longitudinal fold housing the distal region of the embolus. Terminal apophysis morphology diverse. Embolus filiform, of varying length, coiling anticlockwise (left palp, ventral). Epigynum provided with anterior flaps on both sides of a ventral plate scape (without socket) and conspicuous posterior lateral lobes. Spermathecae U-shaped with anteriorly orientated fertilization ducts.

Composition

Three species: *Labulla thoracica*, *L. flahaulti* and *L. machadoi* sp. nov.

Phylogenetics

The monophyly of *Labulla* is supported by the following putative synapomorphies: marginal suprategular apophysis, ectal tegular flap, absence of embolic membrane, ectal position of the terminal apophysis, lamella sheath-like with a longitudinal fold housing the embolus, anterior epigynal flaps, and large posterior lateral epigynal lobes (see Discussion).

Natural history

Most of what we know about *Labulla* is based on the central European species *Labulla thoracica*. Information about the natural history of this species is given under the species description.

Distribution

Europe.

Misplaced species

The following three species do not belong in the genus *Labulla*:

‘Labulla’ impudica Denis, 1945. See comments and description under *Pecado* gen. nov.

‘Lepthyphantes’ insularis Saito, 1935. This species was described based on a single female specimen from Sakhalin Island (located between the Sea of Japan and the Sea of Okhotsk). Tanasevitch & Eskov (1987: 194) remarked that *Lepthyphantes insularis* did not belong in *Lepthyphantes*, based on Saito’s (1935, fig. 1b) epigynum illustration. Tanasevitch & Eskov did not provide any new illustrations or redescription of *insularis*, nor did they examine the type. In their view, *Lepthyphantes insularis* should probably be transferred to *Labulla*, and it could be a (junior) synonym of *L. thoracica*, although they did not formalize any transfer or new synonymy. Marusik *et al.* (1993: 75) synonymized *L. insularis* with *Labulla chikunii* Oi, 1979 [now *Weintrauboa chikunii* (Oi), in the family Pimoidae], but this unjustified synonymy was rejected by Hormiga (2003: 276). Unfortunately, Tanasevitch & Eskov’s (1987) casual and perfunctory remarks on the affinities of *L. insularis* with *Labulla thoracica* have been formalized in Platnick’s (2004) catalogue, where *insularis* appears as a valid species of *Labulla*. We formally reject here the placement of *Lepthyphantes insularis* in the genus *Labulla*, based on the absence of the two synapomorphies that we can assess in the external epigynum morphology of Saito’s illustration (Saito, 1935, fig. 1b): *insularis* lacks both the anterior epigynal flaps and posterior epigynal lateral lobes that characterize *Labulla* as defined in the present work. Additional support for this conjecture is provided by the lack of pigmentation around the PMEs (compare

Saito's fig. 1a with our Fig. 1) and the almost uniform dark brown coloration of the prosoma of *insularis* (unlike any *Labulla* species). But as Tanasevitch & Eskov (1987: 194) have also remarked (and with which we agree), *insularis* is not congeneric with the type species of *Lepthyphantes* [*L. minutus* (Blackwall, 1833)]. This is hardly surprising if we examine Saito's (1935: 59) argument for placing *insularis* in the genus *Lepthyphantes*: 'The spider apparently resembles the European species, *L. minutus* in general appearance and coloration, but it is distinct in having an epigynum which has only a tongue-like scape and lacks the parmula, while *L. minutus* has both well defined.' Saito's type material, formerly at the University of Hokkaido, is presumably lost (H. Ono, in litt.). Because the species description is inadequate and insufficient to place *insularis* within another generic circumscription, we suggest that this species is cataloged as *incertae sedis*.

'*Labulla*' *nepula* Tikader, 1970. This species, described from Sikkim (located in India, between Nepal and Bhutan), was placed in *Labulla* because it 'resembles *Labulla thoracica* (Wider)' (Tikader, 1970: 21). How *nepula* resembles *thoracica*, as opposed to many other linyphiids, is a mystery that Tikader does not explain in his publication. The type material (holotype female, and one male and one female paratypes) is presumably deposited in the National Zoological Collections, Zoological Survey of India (Calcutta), but we have not been able to borrow these specimens. Tikader's description provides no information on genitalic morphology, other than his single illustrations of the palp and the epigynum. The palp (fig. 13d, presumably the left one) is illustrated in an unconventional view (at least for the single illustration of a new species), as it seems to be a dorsomesal view (e.g. no paracymbium can be discerned and in the embolic division, only the distal region of the embolus can be seen in some detail). None of the male *Labulla* synapomorphies can be found on this figure. The epigynum (a ventral view, fig. 13c) does not reveal any of the generic synapomorphies either. Consequently, we reject the placement of *nepula* in the genus *Labulla*. Because the species description is inadequate and insufficient to place *nepula* within another generic circumscription, we suggest that this species is cataloged as *incertae sedis*.

LABULLA THORACICA (WIDER, 1834)

(FIGS 1A, B, 2, 3A–D, 4A–C, 5–7, 16–19, 20A, B, 22E)

Linyphia thoracica Wider, 1834: 254, pl. 17, f. 180.

Linyphia cauta Blackwall, 1841: 655. – Blackwall, 1864: 220, pl. 15, fig. 145.

Bathypantes thoracicus Förster & Bertkau, 1883: 253.

Labulla thoracica (Wider, 1834): Simon, 1884: 262. – Chyzer & Kulczynski, 1894: 61, pl. 2, fig. 30. – Becker, 1896: 35, pl. 5, fig. 2. – Bösenberg, 1901: 92, pl. 8, fig. 111. – Simon, 1929: 625, 741, figs 942, 943. – Wiehle, 1952: 231, figs 9, 10. – Lockett & Millidge, 1953: 375, fig. 224D,E. – Wiehle, 1956: 293, figs 481–485. – Merrett, 1963: 377, fig. 33A–E. – Miller, 1971: 222, pl. XLIII, fig. 4. – Palmgren, 1975: 77, figs 7.28–32. – Roberts, 1987: 142, figs 73b, 74a. – Heimer & Nentwig, 1991: 176, fig. 471. – Millidge, 1993: 146, fig. 1. – Roberts, 1995: 352. – Roberts, 1998: 364.

Diagnosis

Males of *L. thoracica* can most easily be distinguished from other *Labulla* species by the presence of a long tegular flap (Fig. 5A, longer than in *machadoi* sp. nov.), long embolus (more than two complete turns, Fig. 5B), the shape of the terminal apophysis and the absence on it of a plumose process (Fig. 5B), and the shape of the dorsal tibial apophysis (vertical and inclined over the cymbium, Fig. 5A). Females are diagnosed externally by the blade-like epigynal flaps (Figs 3D, 7A) and internally by the presence of two pairs of copulatory duct coils (Fig. 7B).

Description

Male (from Denmark: Hestehaven, Rønne, 22 km north-east of Århus, 56°17.46'N, 10°28.50'E, 31.viii.1994, Bjørn, Christensen, Coddington, Griswold, Hormiga, Krat, Langemark, Scharff & Sørensen leg.; cat. no. ZMUC00004683). Total length 5.20. Cephalothorax 2.24 long, 2.00 wide. Sternum 1.12 long, 1.25 wide. Abdomen 3.04 long, 1.92 wide. Cephalothorax and chelicerae pale yellowish brown, with greyish brown borders and darker yellowish brown cephalic area (Fig. 1A). The dark coloration extends from cephalic area to posterior rim of cephalothorax (midline). Black rings around all eyes (Fig. 1A). Sternum dark greyish brown. Legs yellowish brown, with dark annulations. Abdomen light grey, with dark grey pattern and white spots (Fig. 1A). Ventrums with three white dots in front of spinnerets. Cephalothorax pear-shaped. Cheliceral stridulatory striae present, but faint. AME diameter 0.12. Clypeus height 5.75 times one AME diameter (raised cephalon). Chelicerae with three large widely spaced prolateral teeth and three small retrolateral (four in other specimen) more closely spaced proximal teeth. Femur I 4.40 long, 1.96 times the length of cephalothorax. Metatarsus I trichobothrium absent (see comments under 'Variation'). Pedipalp as in Figures 4–6, 16, 17. Pedipalpal tibia with three trichobothria (one prolateral and two retrolateral) and a strong retrolateral spine. Epiandrous

fusules (studied in two specimens) arranged more or less linearly in sockets, which contain from nine to two fusules. A few individual fusules, not in sockets, can also be found (Fig. 19F, G).

Female (from same locality, and with same data as male). Total length 5.98. Cephalothorax 2.41 long, 1.89 wide. Sternum as long as wide (1.16). Abdomen 4.03 long, 2.60 wide. Same coloration as male, but with more pronounced annuli on all legs and pedipalps (Figs 1B, 2A). Cephalothorax pear-shaped. Cheliceral stridulatory striae present (Fig. 19A). AME diameter 0.18. Clypeus height 2.04 times one AME diameter. Chelicerae (Fig. 22E) with three large widely spaced prolateral teeth and three to four small retrolateral closely spaced proximal teeth (three on one chelicera and four on the other). Femur I 3.20 long, 1.33 times the length of cephalothorax. Metatarsus I trichobothrium 0.21. Epigynum as in Figures 3D, 7, 18, 20A, B. Spinnerets (Fig. 19B–E) typical for the family, with two aciniform spigots on PMS (Fig. 19D) and three on PLS (Fig. 19E).

Variation

Male total length ranges from 4.00 to 5.20 ($N = 5$; average 4.64). Female total length ranges from 4.32 to 6.20 ($N = 6$; average 5.14). Male cephalothorax ranges in length from 2.00 to 2.32 ($N = 5$; average 2.18). Female cephalothorax ranges in length from 1.84 to 2.41 ($N = 6$; average 2.17). Male femur I ranges in length from 3.60 to 4.40 ($N = 5$; average 4.06). Female femur I ranges in length from 2.93 to 3.52 ($N = 6$; average 3.10). Trichobothrium metatarsus I varies between 0.21–0.30 and is occasionally absent in males (Roberts, 1987).

Distribution

Labulla thoracica appears in faunal listings of most Central and Northern European countries, including the British Isles and Ireland, France, Italy, Belgium, the Netherlands, Liechtenstein, Switzerland, Austria, Germany, Poland, Czech Republic, Croatia, Slovenia, Slovakia, Yugoslavia, Romania, Denmark, Sweden, Norway, Finland, Ukraine and Russia. It has never been recorded from Spain or Portugal.

Natural history

Numerous works on European spiders provide general information about the natural history of this species (e.g. Simon, 1884; Nielsen, 1928; Locket & Millidge, 1953; Wiehle, 1956; Bristowe, 1958; Roberts, 1987; Harvey, Nellist & Telfer, 2002). According to these accounts *Labulla thoracica* is relatively common in

the British Isles and Central Europe, spinning sheet webs, mainly at ground level, in wooded areas. The webs are usually found at the base of trees between the buttresses, in overhanging banks, under logs and in a variety of shady habitats, including man-made structures such as cellars and outhouses. In the British Isles adults of both sexes are found mainly between August and October, but females and occasionally males can be found in most months (Harvey *et al.*, 2002). In Hestehaven (Denmark), adults were found from May to December (Scharff *et al.*, 2003). Eggsacs are concealed under loose objects (bark, moss, etc.) on the ground some distance from the web (Nielsen, 1928; Bristowe, 1958: fig. 423). Egg sacs are slightly domed, covered with white curled silk and approximately 1 cm in diameter. Eggs are light yellow (Nielsen, 1928).

We have collected this species throughout Denmark (e.g. Scharff *et al.*, 2003), where it is abundant and common in wooded areas. We have photographed seven different webs (two male and five female adult webs), and four of them are depicted in Figures 2B–D, 3A–C to illustrate the general architecture of this species. During the daytime the spiders hide in a retreat in the less exposed area of the web and they are rarely seen; at night they are found, upside-down (as in all linyphiids), in the centre of the web. Adult males are often found together with females, suggesting that when males move into female webs they occupy their webs for some time after copulation.

Webs consist of a main platform or sheet, with the perimeter often delimited by relatively long silk lines in the same plane (e.g. Figs 2B, 3B) as is generally the case in non-erigonine linyphiids. The mesh of the main platform shows the usual pattern of linyphiid mesh (Fig. 2D), with silk lines that can be 'traced' for quite some length. The upper scaffolding is most often absent, except perhaps for a few vertical lines, but some webs do show some upper mesh (Fig. 3A). Presence or absence of any upper scaffolding is most likely determined in part by the availability of attachment points, but this architectural feature, although variable, is generally absent. By contrast, a three-dimensional mesh of silk lines is usually found under the main platform (Fig. 2C), although in some webs this under-mesh is lacking altogether. We have found a rather different pattern in the main platform silk mesh of male (Fig. 3B) and female webs (Figs 2B, D, 3C), as well as in the dimensions of the platform (adult male webs seem smaller); but we lack sufficient information to report whether these differences are consistent. It is also unknown for how long males remain in their webs after reaching maturity (the PLS triplet is reduced to nubbins in the adult male). As is generally the case for large linyphiid webs, they are maintained for long periods of time and often show signs of repair

and senescence. Nielsen (1928) suggests that the web of *Labulla* traps small flying insects (such as fungus gnats) that seek shelter in the dark cavities of tree buttresses. Clouds of small flies emerge from these cavities, when one tries to catch *Labulla thoracica* on the webs in between the tree buttresses (Nielsen, 1928; our own observations).

When disturbed these animals often 'drop dead' to the ground, as is commonly seen in other linyphiids (e.g. in *Orsonwelles* species, Hormiga, 2002: fig. 4F).

Mating is in type 2 position, as is typical of Linyphiidae [see Foelix (1996) for definitions and additional references]. Gerhardt (1921, 1923, 1925, 1928) studied the mating behaviour of this species [see Huber (1998) for a summary of Gerhardt's observations].

Material examined

Germany: Rothiemurchus Forest, 12.ix.1965, J.A.L.C., 1 male (AMNH); Denmark: Zealand, Vesterlyng, south-west of Havnsø, 55°44.6'N, 11°17.5'E, 16.viii.2003, 1 female, G. Hormiga & N. Scharff leg. (ZMUC); Zealand, Dragerup Forest near Tjebberup, 55°42.8'N, 11°47.5'E, 15.viii.2003, 1 male & 1 female, G. Hormiga & N. Scharff leg. (ZMUC); same locality and data, 2 males & 1 female, G. Hormiga & N. Scharff leg. (ZMUC); Jutland, Hestehaven, Rønde, 22 km north-east of Århus, 56°17.46'N, 10°28.50'E, 30.viii.1994, 2 males & 2 females, Bjørn, Christiansen, Coddington, Griswold, Hormiga, Krat, Langemark, Scharff & Sørensen leg. (ZMUC00004682); same locality and same data, 12 females & 10 males (ZMUC00004687); same locality, same data, 3 females & 4 males (ZMUC); Zealand, Roden and Frejlev Forest, 7–13.ix.1883, 1 female, Løvendal leg. (ZMUC00004691); Jutland, Lille Vildmose, Høstemark Forest, 56°56'N, 10°13'E, 20–24.viii.1999, 9 males & 6 females, N. Scharff leg. (ZMUC00007706).

LABULLA FLAHAULTI SIMON, 1914

(FIGS 1C, D, 3E, 4D–F, 8–10, 20C, D, 22F)

Labulla flahaulti Simon, 1914: 478 (syntype material in MNHN, examined); Simon, 1929: 626 and 741, figs 944, 945; Fage, 1935: 179, fig. 2D.

Diagnosis

Males of *L. flahaulti* can most easily be distinguished from other *Labulla* species by the smaller size of the palps (Fig. 1C), the short length of the embolus (less than half a coil, Fig. 9C), the large size of the paracymbial process (Fig. 8A, B), the shape of the terminal apophysis, with a small plumose process on it (Fig. 9C – arrow) and the shape of the dorsal tibial apophysis (blunt, orientated ectally, Fig. 8A). Females are diag-

nosed externally by the subtle epigynal flaps (Figs 3E, 10A) and internally by the absence of any copulatory duct coils (Fig. 10B).

Description

Male (from Spain: Gipuzkoa, San Sebastián, Igara, 50 m, 7.ix.2002, A. de Castro & A. Casis leg., AZE). Total length 4.45. Cephalothorax 2.10 long, 1.55 wide. Sternum as long as wide (1.11). Abdomen 2.73 long, 1.56 wide. Cephalothorax and chelicerae pale greyish white, with greyish brown borders and cephalic area (Fig. 1C). The dark coloration extends from cephalic area to posterior rim of cephalothorax. Black rings around all eyes. Sternum dark greyish brown. Legs yellowish brown, with dark annulations. First two pairs of legs darker than the rest. Abdomen light grey, with dark grey pattern (Fig. 1C). Ventrums with one to three patches of white dots. Two posterior to the book-lungs, just behind the epigastric furrow, and one patch just in front of the spinnerets. Patch in front of spinnerets may include two to five smaller white dots. Cephalothorax pear-shaped. Cheliceral stridulatory striae present, but faint. AME diameter 0.14. Clypeus height 2.23 times one AME diameter. Chelicerae with three large widely spaced prolateral teeth and three small retrolateral (four in other specimen) more closely spaced proximal teeth. Femur I 4.00 long, 1.91 times the length of cephalothorax. Trichobothrium metatarsus I 0.24. Pedipalp as in Figures 8, 9, 21. Pedipalpal tibia with one prolateral and two retrolateral trichobothria.

Female (from same locality, and with same data as male). Total length 5.40. Cephalothorax 2.30 long, 1.88 wide. Sternum as long as wide (1.20). Abdomen 5.07 long, 2.54 wide. Cephalothorax and chelicerae pale yellowish brown, with greyish brown borders and cephalic area (Fig. 1D). The dark coloration extends from cephalic area to posterior rim of cephalothorax. Black rings around all eyes. Sternum dark greyish brown. Legs yellowish brown, with dark rings (annulations). Abdomen light grey, with dark grey pattern (Fig. 1D). Cephalothorax pear-shaped. Cheliceral stridulatory striae present. AME diameter 0.17. Clypeus height 1.91 times one AME diameter. Chelicerae (Fig. 22F) with three large widely spaced prolateral teeth and four small retrolateral closely spaced proximal teeth. Femur I 4.05 long, 1.76 times the length of cephalothorax. Trichobothrium metatarsus I 0.20. Epigynum as in Figures 3E, 10, 20C, D.

Variation

Male total length ranges from 4.40 to 4.45 ($N = 2$; average 4.43). Female total length ranges from 4.80 to

6.00 ($N = 5$; average 5.59). Male cephalothorax ranges in length from 1.90 to 2.10 ($N = 2$; average 2.00). Female cephalothorax ranges in length from 2.25 to 2.60 ($N = 5$; average 2.40). Male femur I ranges in length from 3.90 to 4.00 ($N = 2$; average 3.95). Female femur I ranges in length from 3.12 to 4.05 ($N = 6$; average 3.44). The length of the epigynal scape is variable.

Distribution

Southern France and northern Spain (Simon, 1914, 1929; Bosmans & Keer, 1985; Ribera & Hormiga, 1985; Bosmans, Maelfait & Kimpe, 1986; Ledoux, Emerit & Pinault, 1996; Castro, 2004).

Natural history

Simon (1914, 1929) reported that in France *L. flahaulti* lives in fir and beech forests and that their large webs, similar to those of *L. thoracica*, are often found in overhanging banks. Ribera & Hormiga (1985: 186) have reported this species in conifer and beech forests in northern Spain (c. 960–1415 m), with small numbers of adults collected in pitfall traps between July and September. Ledoux *et al.* (1996) have reported this species from Nohèdes (Pyrénées Orientales). Bosmans *et al.* (1986: 75) reported it from St. Lary (Midi Pyrénées) in July at 1500–1700 m (montane zone), in fir forest (*Picea abies*). Castro (2004) provides the most detailed account available on the natural history of *Labulla flahaulti*, based on his ecological work on the Cantabrian oak forests of the Basque country. In this region *flahaulti* is mainly found in forested areas, where their webs can be seen on tree trunks. Males are adult in September, females between September and November and juveniles are found between spring and autumn. This suggests that mating takes place at the end of the summer or early in autumn and that the species over winters in the eggsac. Although Castro (2004) collected this species in almost all forest strata, *flahaulti* seems to prefer the higher parts (tree trunks, branches, etc.).

Material examined

Spain: Gipuzkoa, San Sebastián, Igara, 50 m, 7.ix.2002, 8 females & 2 males (incl. those described above), A. de Castro & A. Casis leg. (AZE); Huesca, San Juan de la Peña, C. Pedrocchi, 1 male, Pinar medio, 29.viii.1977; Abetal Alto, 1 male, 16.viii.1977 (UB). France: Fôret de la Massane de Valmanya du Canigou, 3 males, 8 females, 1 juv., 22873 (syntype series, in part; MNHN).

LABULLA MACHADOI SP. NOV.

(FIGS 1E, F, 3F, 11–13, 20E, F, 22A–D, G, 23)

Type. Male holotype and female paratype from Hto. Dias Ferreira, Porto, Portugal; March 1937, A.B. Machado leg. (cat. no. 267; deposited in MB).

Etymology

Named after the collector, António de Barros Machado.

Diagnosis

Males of *L. machadoi* sp. nov. can most easily be distinguished from other *Labulla* species by the presence of a long tegular flap (Fig. 11A, shorter than in *thoracica*), long embolus (only one complete turn, Fig. 11B), the hooked paracymbial process (Fig. 11A–C), the shape of the terminal apophysis, with a plumose process on it (Fig. 11B), and the shape of the dorsal tibial apophysis (pointed, orientated ectally, Fig. 11A, C). Females are diagnosed externally by the V-shaped epigynal flaps (Figs 3F, 13A) and internally by the presence of one pair of copulatory duct coils (Fig. 13C).

Description

Male holotype: Total length 4.20. Cephalothorax 2.10 long, 1.70 wide. Sternum 1.20 long, 1.12 wide. Abdomen 2.40 long, 1.60 wide. Cephalothorax and chelicerae yellowish brown, darker in cephalic area. Black rings around all eyes (Fig. 1E). Sternum greyish brown. Legs same colour as cephalothorax, but with dark annulations. Abdomen light grey, with dark grey pattern (Fig. 1E). Shape of cephalothorax more oval than in *L. thoracica* and *L. flahaulti* (Fig. 1A, C, E). Cheliceral stridulatory striae present. AME diameter 0.16. Clypeus height 2.52 times one AME diameter. Chelicerae with three large widely spaced prolateral teeth and four small retrolateral closely spaced proximal teeth. Femur I 3.44 long, 1.64 times the length of cephalothorax. Trichobothrium metatarsus I 0.22. Pedipalp as in Figures 11, 12, 22A–D. Pedipalpal tibia with one prolateral and two retrolateral trichobothria.

Female paratype (together with male holotype): Total length 5.60. Cephalothorax 2.20 long, 1.90 wide. Sternum as long as wide (1.15). Abdomen 3.90 long, 2.60 wide. Same colour pattern as male, but brown instead of yellowish brown (Fig. 1F). Cephalothorax pear-shaped. Cheliceral stridulatory striae absent. AME diameter 0.14. Clypeus height 2.50 times one AME diameter. Cheliceral dentation as in male. Femur I 2.80 long, 1.27 times the length of cephalothorax.

Trichobothrium metatarsus I 0.22. Epigynum as in Figures 3F, 13, 20E, F. Spinnerets as in Figure 23. PMS and PLS with only one aciniform spigot.

Variation

Male total length ranges from 4.20 to 4.80 ($N = 4$; average 4.42). Female total length ranges from 3.36 to 5.60 ($N = 7$; average 4.28). Male cephalothorax ranges in length from 2.10 to 2.40 ($N = 4$; average 2.26). Female cephalothorax ranges in length from 1.60 to 2.20 ($N = 7$; average 1.90). Male femur I ranges in length from 3.44 to 4.16 ($N = 4$; average 3.85). Female femur I ranges in length from 2.12 to 3.12 ($N = 7$; average 2.59). The shape of the epigynal flaps and the length of the scape is variable.

Distribution

Only known from Portugal.

Natural history

Specimens have been taken under moss in a 'Horto' (garden/orchard) in Porto. Adult males present in October and December, and adult females in March, August and October.

Material examined

Portugal: Porto, Hto Dias Ferreira, 31.x.1937, 4 females and 1 male together with holotype and paratype, A.B. Machado leg. (cat. no. 267; MB); same locality, iii.1937, 5 females, A.B. Machado leg. (cat. no. 3; MB); Amarante, iii.1937, 1 female, A.B. Machado leg. (cat. no. 276; MB); Joane, 3.x.1941, 2 females and 3 juveniles, A.B. Machado leg. (cat. no. 983; MB); Joane, 10.x.1937, 1 female, A.B. Machado leg. (cat. no. 248; MB); Joane, Baltar, 7.x.1937, 5 females, A.B. Machado (cat. no. 225; MB); Paredes de Coura, Mantelcus (Mate), 12.x.1940, 2 females, A.B. Machado leg. (cat. no. 677; MB); Paredes de Coura, Ramalhosa de Vascões, 25.viii.1940, 1 female, A.B. Machado leg. (cat. no. 662; MB); Joane, Ciridade, 4.x.1937, 1 male, A.B. Machado (cat. no. 224; MB); Porto, 5.xii.1937, 1 male, A.B. Machado leg. (cat. no. 297; MB).

PECADO GEN. NOV.

Type species: Labulla impudica Denis, 1945

Etymology

Derived from the Spanish word 'pecado' (sin) in reference to widespread practice of erecting monotypic genera, especially in the Linyphiidae, in absence of a

phylogenetic justification. The noun is masculine in gender.

Diagnosis

Males of *Pecado* can be distinguished from other linyphiid species by the presence of two cymbial processes (Figs 14A, B, 15B – arrow; Denis, 1945; p. 13 and figs 26–28), one at the base of and the second in the dorsal median region of the cymbium, the blade-like projection of the proximal branch of the paracymbium (Fig. 14A) and the unusual coiling direction of the embolus. In *Pecado impudicus* the embolus coils anticlockwise (left palp, ventral view) for about one turn and then clockwise for almost its remaining length (Fig. 14B).

Description

Since the genus is monotypic, the description is given under *Pecado impudicus*.

Phylogenetics

See comments about its phylogenetic placement under the Discussion section.

Natural history

Unknown.

Composition

One species, *Pecado impudicus* (Denis, 1945).

Distribution

Algeria.

PECADO IMPUDICUS (DENIS, 1945) (FIGS 14, 15)

Labulla impudica Denis, 1945: 52, figures 26–28

Type: Male holotype, label reads '1898.8.16. 34–50 (part) *Labulla impudica* J. Denis, Cape Verde, St. Vincent, Porto Grande. F. Cambridge' (in BMNH, examined; the specimen is in poor condition and the right palp is missing). The type locality information, given on the label inside the vial with the holotype (handwritten by Denis), does not agree with the type locality data published by Denis (1945: 13): 'Algérie, Alger, 1 male (C. Hirst, 1911)'. Denis (1945: 1) states at the beginning of his paper on North African spiders that 'during the course of a study of the spiders of the Canary Islands and the Cape Verde Islands (Denis,

1941) I was able to examine part of a collection from the British Museum consisting of an assembly of specimens collected by a diversity of naturalists in very diverse regions of northern Africa'. Given the absence of additional specimens, it is impossible at this point to know with certainty the origin of the holotype of *Labulla impudica*. Nevertheless, it seems conceivable that during his study of the British Museum Canary and Cape Verde Islands specimens Denis mislabelled a specimen from Algeria, also from the British Museum, as coming from the Cape Verde. It seems logical to argue that if *L. impudica* had been collected in the Cape Verde Islands Denis would have published his description in his 1941 paper, where all other Cape Verde spiders were dealt with.

Diagnosis

See above, under genus description.

Description

Male (holotype): Most legs broken off, and cephalothorax and abdomen separated. Cephalothorax 1.98 long, 1.47 wide. Sternum 1.13 long, 0.93 wide. Abdomen 2.26 long, 1.04 wide. Cephalothorax and chelicerae brown, darker in cephalic area. Black rings around all eyes. Sternum brown. Legs same colour as cephalothorax, but with dark rings (annulations). Abdomen light grey, with dark grey pattern. Cheliceral stridulatory striae absent. AME diameter 0.14. Clypeus height 1.93 times one AME diameter. Chelicerae with four widely spaced prolateral teeth of variable size and two retrolateral teeth of variable size. Legs broken off, with several segments missing. It is therefore not possible to provide measurements of Femur I length and Tm I. Pedipalp as in Figures 14, 15. Pedipalpal tibia with two prolateral and two retrolateral trichobothria, a dorsal process (with numerous macrosetae) and an ectoventral process (Fig. 14A). Cymbium with two processes (Figs 14A, C, 15B), one at the base (with a pointed apex) and the second on the dorsomedian region (with a rounded apex, Fig. 15B – arrow). Paracymbium U-shaped, with a blade-like projection or crest running along dorsal region from the proximal branch through the median region (Fig. 14A). Paracymbium with ventral margin of proximal branch sclerotized and continuous with ectal cymbial margin but connected to cymbium by means of a membrane. Tegulum with a crest or sclerotized membrane on its apical region (Fig. 14A). Suprattegulum with a blunt and very short distal apophysis hidden behind the terminal apophysis (Fig. 15D, E) and a pointed ectal apophysis (Fig. 15E). Radix a small enlargement of the embolus base (Fig. 15D). Terminal apophysis in mesal

position, with a long and thin process (Figs 14B, 15D). Lamella characteristic with two long falciform processes, one anteriorly directed and the other posteriorly orientated but curving ectally in its distal portion (Figs 14A, B, 15A). Embolic membrane small, anteriorly directed, and located between the anterior process of the lamella and the terminal apophysis (Fig. 15D). Embolus filiform and extremely long (Figs 14B, 15C), coiling anticlockwise (left palp, ventral view) for about one turn and then clockwise almost its remaining length.

Female: Unknown.

Distribution

Only known from the type locality in Algeria (see comments under 'Type').

Natural history

Unknown.

Material examined

Only the holotype.

ACKNOWLEDGEMENTS

We would like to thank the following individuals and institutions for making specimens available for study (collection abbreviations used in text are given in parentheses): Carlos Almaça (Museu Bocage, Lisboa, Portugal; MB), Janet Beccaloni (The Natural History Museum, London, UK; BMNH), Alberto de Castro (Aranzadi Zientzi Elkarteak (Sociedad de Ciencias Aranzadi), Donostia, Spain; AZE), Jonathan Coddington (Smithsonian Institution, Washington, DC), Norman Platnick (American Museum of Natural History, New York; AMNH), Carles Ribera (Departament de Biologia Animal, Universitat de Barcelona; UB), Christine Rollard (Muséum National d'Histoire Naturelle, Paris; MNHN). All material of *Labulla thoracica* from Denmark is deposited in the Zoological Museum, University of Copenhagen (ZMUC). Anthony Russell-Smith made available specimens of *Taranucnus setosus* for study. Pedro Cardoso (University of Lisbon, Portugal) helped with locality data from Portugal and made us aware of the existence of *Labulla* specimens in the Barros Machado collection of the Museu Bocage. Howard Don Cameron (University of Michigan, Ann Arbor) provided expert etymological advice and deciphered the mysterious origin of Simon's name *Labulla*. Miquel Arnedo (University of Barcelona) shared with us his knowledge on Denis' Northern Africa localities and specimen labels. Alberto de Castro

(Aranzadi Zientzi Elkarteak (Sociedad de Ciencias), Donostia, Spain), Anthony Russell-Smith (Kent, UK), Peter van Helsdingen (European Invertebrate Survey, Leiden, The Netherlands), and three anonymous referees provided us with valuable comments to an earlier draft of the manuscript. Birgitte Rubæk coloured our palpal homologies plate and gave advice on computer illustrations. Funding for this research has been provided by grants from the US National Science Foundation (G.H.: DEB-0328644 and EAR-0228699), a VELUX Visiting Professorship from the Villum Kann Rasmussen Fond (to support G.H. at the University of Copenhagen), and a grant from the Danish Natural Science Research Council (N.S.: 21020502).

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APPENDIX 1

Most of the characters presented here are discussed in detail and illustrated in Hormiga (1994a, b, 2000, 2002, 2003). References to those characters are abbreviated as H94a, H94b, H00, H02 and H03, respectively. The abbreviation is followed by the character number in the cited reference. For example, H02-16 refers to Character 16 in the matrix of Hormiga (2002). Only those characters that are new or that have been recoded are discussed in this section (they are indicated with an asterisk after the character number). In general, when the same character has been used in several matrices we only cite the most recent usage as an example of its definition. Citation does not necessarily imply authorship of the homology concept. For example, the number of retro-lateral cheliceral teeth (character 63 in this matrix) has been traditionally used in spider taxonomy from the 19th century. Consequently, this character often appears in spider cladistic matrices, including all those cited above. We refer to it as H03-57, but Hormiga (2003) is not the author of this character. The scoring of these characters for the study taxa is presented in Appendix 2. All multistate characters were treated as non-additive.

MALE PALP

1. Alveolar sclerite: (0) absent; (1) present (H03-1).
2. Distal end of cymbium: (0) rounded; (1) elongated; (2) conical (H03-9).
3. Cymbium morphology (ectal region): (0) smooth (no process); (1) with ectal cymbial process (H03-2).
4. Cymbial cuspules: (0) absent; (1) present (H03-3).
5. Cymbial cuspules location: (0) on cymbial process itself; (1) on dorsal surface of cymbium (not on process) (H03-4).
6. Pimoid cymbial sclerite: (0) absent; (1) present (H03-5).
7. Pimoid cymbial sclerite flap: (0) with membranous flap; (1) without membranous flap (H03-6).
8. Pimoid cymbial sclerite relative to paracymbium: (0) attached/fused to paracymbium; (1) separate from paracymbium (H03-7).
9. Pimoid cymbial sclerite – cymbium connection: (0) sclerotized and rigid; (1) membranous; (2) intermediate (H03-8).
10. Paracymbium attachment: (0) integral; (1) inter-segmental; (2) articulated (H03-10).
11. Paracymbium morphology: (0) linguiform; (1) triangular; (2) *Stemonyphantes* type; (3) U or J shaped; (4) hook; (5) straight and narrow; (6) knob (*Orsonwelles* type) (H03-11).
12. Paracymbium apophyses: (0) present; (1) absent (H03-12).
- 13*. Paracymbial apophysis: (0) anterobasal (Hormiga, Eberhard & Coddington, 1995: fig. 7C); (1) distal branch (Hormiga, 1994b: fig. 13A; Hormiga 2000, pl. 6B); (2) posteromedial outgrowth (Figs 5A, 16B).
14. Suprategulum: (0) absent; (1) present (H00-11).
15. Suprategulum's connection to tegulum: (0) continuous with tegulum; (1) articulated (H00-12; see also (H94b).
16. Distal Suprategular Apophysis (DSA): (0) absent; (1) present (H00-13). For the present taxonomic sample this character is uninformative, as it consists of only occurrences of state 1 or inapplicable (for the taxa lacking a suprategulum). It may be argued that *Pecado impudicus* lacks a distal suprategular apophysis (or if it has one, it is so small that should be coded with a different state; see Fig. 15D, E). If we recode *Pecado* as having state 0 (lacking this apophysis) or a unique state the character change becomes an autapomorphy and therefore it has no topological consequences for the analysis. Therefore, we have retained this character in the matrix as a potential autapomorphy of *Pecado*.
17. Marginal Suprategular Apophysis (MSA): (0) absent; (1) present (H00-14; Fig. 12D).
- 18*. Ectal suprategular apophysis: (0) absent (Hormiga, 2000; fig. 22C, pl. 52D); (1) present (Figs 6A, 15E). This apophysis is usually located at the base of the suprategulum, on the ectal margin, close to the suprategular foramen; its exact position and shape is rather variable (see characters 19 and 20).
- 19*. Ectal suprategular apophysis position: (0) ventral (Fig. 6A); (1) marginal (Fig. 15E).
- 20*. Ectal suprategular apophysis shape: (0) single point (Fig. 15E); (1) bifid points (Fig. 6A); (2) flat with depression (van Helsdingen, 1969; fig. 164); (3) flat without depression (Hormiga, 2002; figs 25E, 29D).

21. Mynoglenine tegular process: (0) absent; (1) present (H00-7). Mynoglenines have been coded as having a suprategulum and an additional tegular process (the latter is absent in *Novafroneta*).
- 22*. Ectal tegular flap (Tegular Membrane): (0) absent; (1) present (Fig. 5A, labelled as 'TM'). *Labulla* species have a thin, rigid and sclerotized flap of membranous appearance, of varying length, on the ectal side of the tegulum. In the same region of the tegulum of *Stemonyphantes* [at least in *S. blauveltae* Gertsch, 1951 and *S. lineatus* (Linnaeus, 1758)] there is a similar flap, ectal to the tegular pocket (van Helsdingen, 1968, fig. 1; Hormiga, 1994b, fig. 2A).
- 23*. Distal tegular flap: (0) absent; (1) present (Fig. 14B). *Pecado impudicus* has a thin and sclerotized flap in the tegular apex (Figs 14A–C, 15D). A similar flap in the same tegular region is found in *Stemonyphantes*, distal to the tegular pocket (at least in *S. blauveltae* and *S. lineatus*; van Helsdingen, 1968, fig. 1; Hormiga, 1994b, fig. 2A). As *Stemonyphantes* has both the ectal and distal tegular flaps, conjunction refutes the hypothesis of homology between these two types of tegular modifications. Consequently we have coded them as two separate characters.
24. Median apophysis: (0) present; (1) absent (H03-21; see Griswold *et al.* (1998) for a discussion of this character in Araneoidea).
25. Conductor: (0) present; (1) absent (H03-22; see Griswold *et al.* (1998) for a discussion of this character in Araneoidea).
26. Column: (0) absent; (1) present (H00-24).
27. Embolic membrane: (0) absent; (1) present (H00-18).
28. Radix: (0) absent; (1) present (H00-20).
29. Fickert's gland: (0) absent; (1) present (H00-25).
30. Radical tail piece: (0) absent; (1) present (H00-21).
31. Pimoid embolic process: (0) absent; (1) present (H03-26).
32. Pimoid embolic process shape: (0) elongated; (1) compact (H03-27).
33. Shape of elongated pimoid embolic process: (0) bifurcated; (1) simple (H03-28).
34. Terminal apophysis: (0) absent; (1) present (H00-26). We have coded pimoids and other outgroups as lacking a terminal apophysis and a lamella. It could be argued that these two characters are 'inapplicable' to them, as they lack a radix. Recoding them as '-' makes no topological difference in the results of the cladistic analysis.
35. Terminal apophysis position: (0) apical-ectovertral; (1) mesal; (2) ectal (H02-16).
36. Terminal apophysis coiling: (0) not coiled; (1) spirally coiled (H02-19).
37. Terminal sclerite: (0) absent; (1) present (H02-21).
38. Transversal sclerite: (0) absent; (1) present (H02-22).
39. Lamella characteristica: (0) absent; (1) present (H00-27). See comments for character 34.
- 40*. Lamella characteristica shape: (0) compact (without a groove or fold), not housing embolus (Hormiga, 2002, fig. 23A, C, E, F); (1) sheath-like with longitudinal fold housing the embolus, at least in part (Fig. 5B).
41. Mesal tooth of lamella characteristica: (0) absent; (1) present (H02-26).
42. Embolic flap: (0) absent; (1) present (H03-25).
- 43*. Embolus apical half: (0) filiform (Fig. 5B); (1) broad or not threadlike (Hormiga, 1994b, fig. 13B).
44. Male pedipalp tibial apophysis: (0) absent; (1) retrolateral; (2) dorsal (H00-28).
- 45*. Prolateral trichobothria in male pedipalpal tibia: (0) two; (1) one; (2) zero; (3) three (modified from H00-30 to add state 3).
46. Retrolateral trichobothria in male pedipalpal tibia: (0) two; (1) four; (2) three; (3) one (H00-31).

EPIGYNUM

47. Epigynum form: (0) protruding less than its width; (1) protruding more than its width (H03-40).
48. Dorsal plate scape: (0) absent; (1) present (H00-32).
49. Ventral plate scape: (0) absent; (1) present (H00-33).
50. Ventral plate scape shape: (0) straight; (1) sigmoid (H00-34).
- 51*. Anterior epigynal flaps: (0) absent; (1) present (Fig. 7A). The presence of anterior epigynal flaps (Figs 7A, 10A, 13A) is a synapomorphy of *Labulla*.
- 52*. Posterior lateral epigynal lobes: (0) absent or inconspicuous (Hormiga, 2000, pl. 4F, 6D); (1) present, large (Fig. 7A). The presence of large and conspicuous lateral lobes (Figs 7A, 10A, 13A) is a synapomorphy of *Labulla*.
53. Atrium: (0) absent; (1) present (H00-36).
54. Copulatory duct: (0) separate from fertilization duct; (1) spirals fertilization duct (at least one complete turn of CD around FD) (H00-37).
55. Copulatory duct encapsulation: (0) absent; (1) present (H00-38). *Stemonyphantes* has been recoded as having an encapsulated copulatory duct (e.g. van Helsdingen, 1968, fig. 14).

- 56*. Copulatory duct turning point: (0) absent; (1) present (Figs 7C, 13C). The turning point (van Helsdingen, 1969) is the region of the copulatory duct where the duct trajectory reverses its direction before connecting to the spermathecae.
57. Fertilization duct orientation: (0) posterior; (1) mesal; (2) anterior (H03-48).

SOMATIC MORPHOLOGY

- 58*. Thoracic furrow (from J. Miller & G. Hormiga, unpubl. data): (0) nearly smooth, often recognizable only from pigment, not invagination (Hormiga, 2000; pl. 26C); (1) thoracic furrow a distinct invagination (*Pimoa*, Hormiga, 1994a, fig. 356).
59. Subocular clypeal sulci: (0) absent; (1) present (H00-47).
60. Male cephalothorax cuticular pores: (0) absent or rare; (1) present (H00-50).
61. Male chelicerae: (0) smooth; (1) stridulatory striae (H00-55).
62. Cheliceral stridulatory striae: (0) ridged; (1) scaly; (2) imbricated (H00-56).
- 63*. Retrolateral teeth female chelicera: (0) three; (1) four or more; (2) two; (3) zero; (4) one (modified from H00-58).
64. Female pedipalpal tarsus: (0) with claw; (1) without claw (H00-59).
65. Patella-tibia leg autospasy: (0) absent; (1) present (H00-60).
- 66*. Male Metatarsus I proximal apophysis: (0) absent; (1) present (modified from H03-60).
67. Dorsal spines tibia IV: (0) two or more; (1) one (H00-64).
68. Trichobothrium metatarsus IV: (0) present; (1) absent (H00-65).
69. Tracheal system: (0) haplotracheate; (1) desmitracheate (H00-51).
70. Aciniform spigots in female PMS: (0) 1 or more; (1) absent (H00-66).
71. PMS mAP nubbins: (0) absent; (1) one (H00-67).
72. PLS mesal CY base: (0) same size as other CY; (1) enlarged (H00-68).
73. Aciniform spigots in female PLS: (0) two or more; (1) one; (2) absent (H00-69).
74. PLS aggregate in male: (0) absent or nubbin; (1) present (H00-70).
75. PLS flagelliform in male: (0) absent; (1) present (H00-71).

BEHAVIOUR

76. Male position during construction of sperm web: (0) above sperm web; (1) below sperm web (H94b-46).
77. Male position during ejaculation: (0) above sperm web; (1) below sperm web (H94b-47; see also Huber, 1998, for a review of Gerhardt's behavioural observations).
78. Web architecture: (0) orb; (1) tangle; (2) sheet. See comments in Griswold *et al.* (1998) for difficulties in coding this behavioural suite (note that in fig. 5D of Griswold *et al.* (1998) the web of *Bathypantes pallidus* was incorrectly labelled as '*Frontinella pyramitela*').

APPENDIX 2
CHARACTER STATE MATRIX

<i>Tetragnatha versicolor</i>	0000-0---25000-----000101000-0--0---0--000010-----10?0-1000010010000?10
<i>Theridiosoma gemmosum</i>	0000-0---041-0-----000000-00-0--0---0--01013000-000000000?0-4100110010000??0
<i>Steatoda grossa</i>	0000-0-----0-----000001000-0-0---0--00010000-000000010?0-3000010000000?11
<i>Pimoa rupicola</i>	101101000001-0-----000000-00-1000---0--00202000-00000021001?2010000101100???
<i>Pimoa breuili</i>	101101000001-0-----000000-00-1000---0--00231000-000000210011?010000?01100???
<i>Pimoa lihengae</i>	101101111011-0-----000000-00-1010---0--00202100-000000210?11001000?1012???
<i>Pimoa altiocolata</i>	101101111011-0-----000000-00-1010---0--00202100-000000210010?010000101200???
<i>Weintrauboa contortipes</i>	011111102101-0-----000000-00-11-0---0--10013000-000000110?0-101100?001000???
<i>Weintrauboa chikunii</i>	011111102101-0-----000000-00-11-0---0--100130??-???????10?0-??110???????????
<i>Stemonyphantes blauveltae</i>	0010-0---121-11100--01111101000-0-0---000--00010000-0001100100102010000101211???
<i>Haplinis diloris</i>	0200-0---131-10100--10011111000-0-0---000--000020010001011001110101000000101111?
<i>Novafroneta vulgaris</i>	0200-0---131-10100--00011111000-0-0---000--01010010-0000000111101010000001011???
<i>Ostearius melanopygius</i>	0000-0---131-10100--00011111010-0-0---000--0111000100000001000101110010001011112
<i>Erigone psychrophila</i>	0000-0---131-10100--00011111010-0-0---000--01110000-0000101000121110101001011112
<i>Labulla thoracica</i>	0200-0---1302101110101011101000--12000110002100010111001210?100010010001000002
<i>Labulla flahaulti</i>	0000-0---1302101110101011101000--12000110002120010111000210?1?101001?0011?????
<i>Labulla machadoi</i>	0000-0---1302101110101011101000--12000110002100010111001210?1?101001?0011?????
<i>Pecado impudicus</i>	0010-0---131-1010110001111110000--1100010000200??????????10?1???10???????????
<i>Orsonwelles polites</i>	0000-0---161-1010113000111111000--1101010101031000-00000011000-1010000001000???
<i>Pityohyphantes costatus</i>	0200-0---131-10100--00011111000--1001010100010010-001001010?11201001?0010?????
<i>Microlinyphia dana</i>	0000-0---131-101011300011101000--1--0010100010010-0011010000111010010001000002
<i>Linyphia triangularis</i>	0000-0---131-1010112000111111000--1010010100012010-0010010100111010010001000002
<i>Neriere variabilis</i>	0000-0---131-1010112000111111000--1010110101012010-001001000?11101001???10?0002
<i>Neriere radiata</i>	0000-0---131-1010112000111111000--1011110101012010-001001000?11001001?0?10?0002
<i>Bolyphantes luteolus</i>	0000-0---1301101010100011111100--100001000101000110000000001101010010001000???
<i>Tenuiphantes tenuis</i>	0000-0---1301101010100011111100--100001000101000110000000000101110010001000002