



Zoological Journal of the Linnean Society, 2011, **162**, 713–879. With 144 figures

# Morphological and phylogenetic atlas of the orb-weaving spider family Tetragnathidae (Araneae: Araneoidea)

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Received 23 October 2009; revised 29 July 2010; accepted for publication 6 August 2010

The present atlas documents the morphology of representative species of 22 tetragnathid genera, with emphasis on nontetragnathines. It includes approximately 960 scanning electron micrographs, morphological drawings and web photographs. The 213 characters used in the phylogenetic analyses are described and illustrated. We discuss the optimal cladograms obtained by the analysis of the morphological and behavioural data, and compare our results to a recent hypothesis of tetragnathid phylogenetic relationships that combined similar data with multigene DNA sequences. Based on the cladistic hypothesis that results from the total evidence analysis, we study the evolution of six morphological character systems within Tetragnathidae: spinneret spigots, respiratory structures, trichobothria, chelicerae, and male and female genitalia.

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doi: 10.1111/j.1096-3642.2011.00692.x

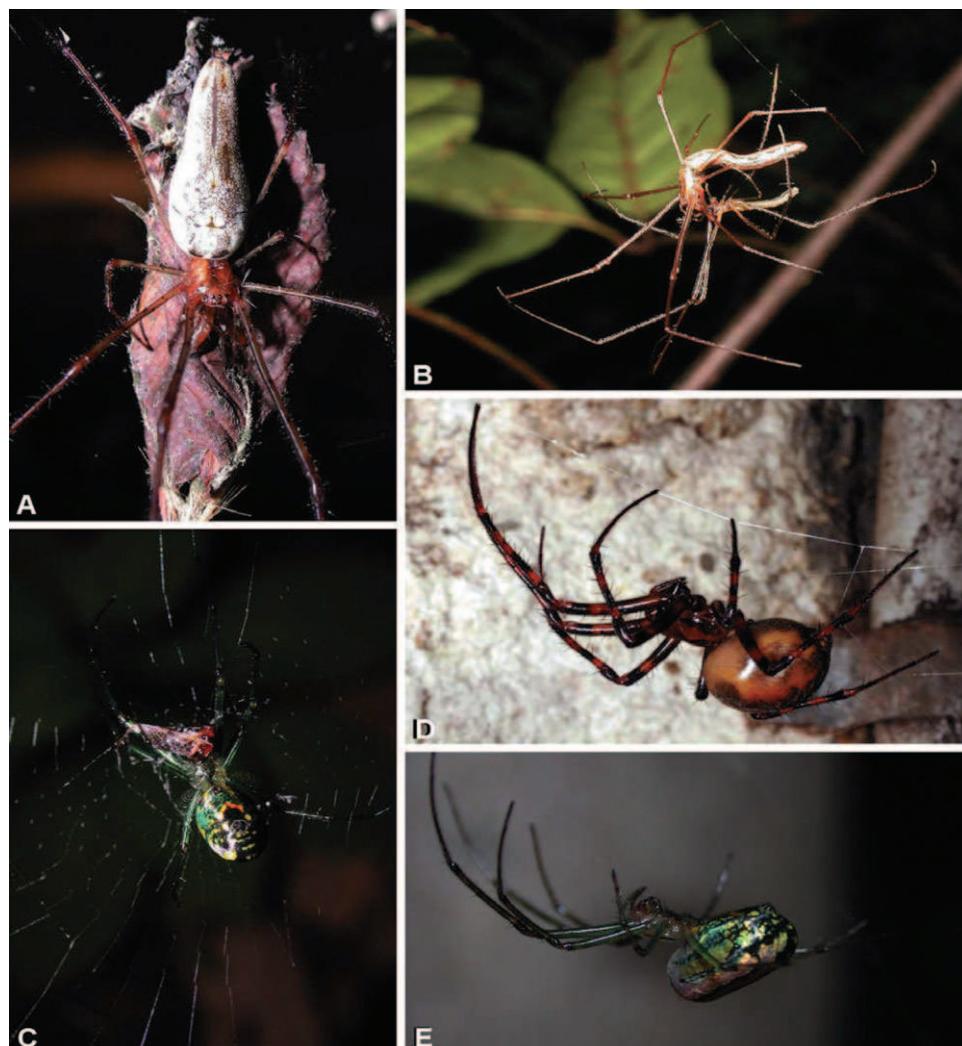
ADDITIONAL KEYWORDS: cladistics – classification – internal anatomy – Leucauginae – Metainae – Nanometinae – phylogenetic systematics – Tetragnathinae.

## INTRODUCTION

The orb-weaving spider family Tetragnathidae has a worldwide distribution and is particularly diverse in tropical and subtropical ecosystems. Nearly 1000 species of tetragnathids have been described so far, classified in 47 genera (Platnick, 2009). Probably only half or fewer of the species of Tetragnathidae have been described, as is the case in many other spider groups (Platnick, 1999); but a precise quantification of this task, if even possible, does not exist. We provide just a few examples simply to illustrate the dimensions of this problem. Levi (2005a, 2007) recently revised the American species of the orb weaver genus *Mangora* (Araneidae) and found that 81% of the

American *Mangora* were new (140 new species). In Platnick's (2000) revision of the Australian family Lamponidae 171 species were new (90%), out of a total of 190 described. Dimitrov & Hormiga (2009) monographed the Neotropical tetragnathid genus *Cyrtognatha* and found that of the 21 species that they treated 52% were undescribed, although their data suggest that more species remain to be described in that genus. Tetragnathids are at least 135 million years old, as evidenced by a fossil species from the lower Cretaceous limestone of north-east Spain, *Macryphantes cowdenei* (Selden, 1990; Penney, Wheater & Selden, 2003). There are 22 species of fossil tetragnathids classified in 12 genera, of which eight genera are extinct and four have extant representatives: *Azilia* Keyserling, 1881a; *Cyrtognatha* Keyserling, 1881a; *Homalometa* Simon, 1897, and

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**Figure 1.** Examples of tetragnathid spiders: A, *Tetragnatha versicolor* from Virginia, USA (voucher number DSCN7721, see Appendix 2 detailed locality data). B, *Tetragnatha* sp. from Daintree National Park, Australia (DSCN1180). C and E, *Leucauge venusta* from Virginia, USA (DSCN3055). D, *Meta menardi* from Zealand, Denmark (photograph by Nikolaj Scharff).

*Tetragnatha* Latreille, 1804. Most of these fossils have been found in Baltic and Dominican amber (Wunderlich, 1986, 2004; Dunlop, Penney & Jekel, 2009; Platnick, 2009).

Tetragnathids build typical orb webs formed by a radial frame that supports a spiral of viscous sticky silk specialized to retain prey (Figs 3–5). Webs similar to those of tetragnathids are built by other araneoid taxa such as nephilids, araneids, and some symphytognathoids (Figs 5, 6). Tetragnathids share with other araneoids several morphological and behavioural synapomorphies such as the presence of aggregate silk glands (which produce the viscous sticky silk) (Fig. 18E), the loss of the cribellum (Figs 56A, 119B), or the presence of a paracymbium (Fig. 16D; refer to Griswold *et al.*, 1998 and references therein for more

araneoid synapomorphies). Tetragnathids differ from other araneoids by their somewhat simpler male pedipalps with only one tegular apophysis and by having the conductor and embolus coiling together (Fig. 45A–C), by their spinneret spigot anatomy, which usually lacks aciniform spigots over the anterior surface of the posterior median spinnerets (Fig. 18F), and by their web building behaviours, such as the different legs used to place the sticky spiral on the web (in most tetragnathids this is done with the second legs whereas in nephilids it is done with the fourth; e.g. see Eberhard, 1982). Some of these characteristics, such as simpler genital organs in males and females, have been studied in some detail (e.g. Levi, 1980, 1986; Hormiga, Eberhard & Coddington, 1995; Griswold *et al.*, 1998).

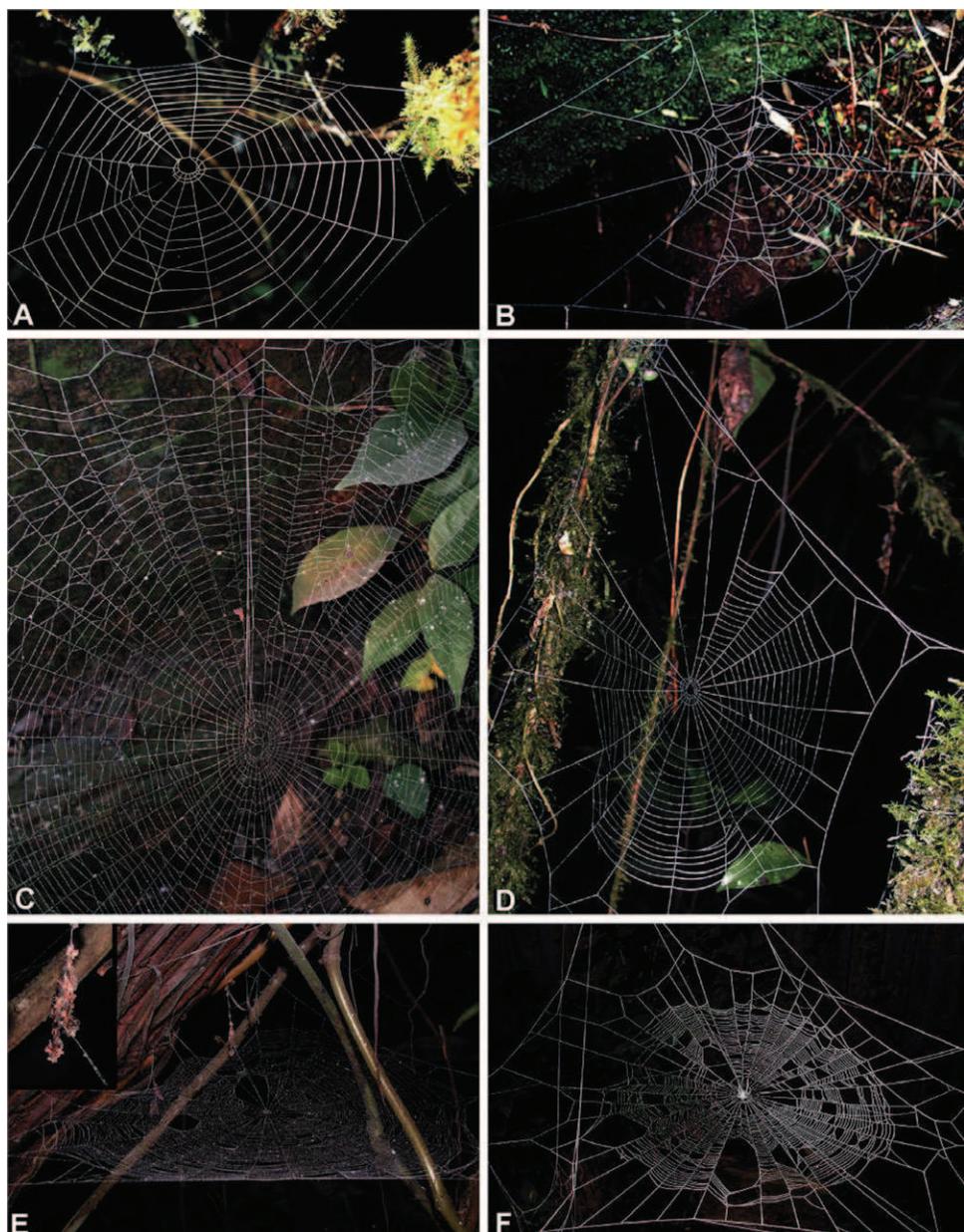


**Figure 2.** Examples of tetagnathid spiders: (A, B) and some outgroup taxa (C–F): A, *Cyrtognatha* sp. from Cachote Natural Reserve, Dominican Republic (DSCN7358). B, *Azilia* sp. from the same reserve (DSCN7469). C, *Herennia multipuncta* (Nephilidae) from Khao Sok National Park, Thailand (DSCN4400). D, *Phonognatha graeffei* (Araneidae) from Noosa National Park, Australia (Neph001). E, *Micrathena gracilis* (Araneidae) from Virginia, USA (DSCN3350). F, *Epeirotypus brevipes* (Theridiosomatidae) from Chiapas, Mexico (DSCN7740).

The intrafamilial phylogenetic relationships of tetagnathids and their placement within Araneoidea have been the subject of many studies (e.g. Levi, 1980; Coddington, 1990b; Hormiga *et al.*, 1995; Schütt, 2003; Pan *et al.*, 2004; Kuntner, Coddington & Hormiga, 2008; Álvarez-Padilla, 2007; Lopardo & Hormiga, 2008; Blackledge *et al.*, 2009). Currently some stability has been reached about tetagnathid relationships by combining molecular and morphological data (Álvarez-Padilla *et al.*, 2009; Dimitrov & Hormiga, 2011). These studies proposed two different hypotheses of internal relationships for Tetagnathidae. Tetagnathidae either has four subfamilies (Tetagnathinae, Leucauginae, Metainae, Diphinae) and the ‘*Nanometa* clade’ (Dimitrov & Hormiga, 2011); or it has three subfamilies and the ‘*Nanometa*

clade’ (Álvarez-Padilla *et al.*, 2009). Diphinae is only recovered as a tetagnathid lineage by Dimitrov & Hormiga’s (2011) study and the composition of Metainae varies. These two hypotheses placed Tetagnathidae as either sister to a clade that includes mimetids and *Arkys cornutus* (Dimitrov & Hormiga, 2011) or sister to a clade that includes representatives of linyphiids, theridiosomatids, and nesticids (Álvarez-Padilla *et al.*, 2009: fig. 3b). Nephilidae in the latter phylogenetic hypothesis is sister to Araneidae with a posterior probability of 99 (Álvarez-Padilla *et al.*, 2009; see also Blackledge *et al.*, 2009).

Information regarding the anatomy for these tetagnathid lineages is patchy; some taxa have been properly documented (e.g. some Tetagnathinae and Metainae: Hormiga *et al.*, 1995 and references



**Figure 3.** Webs of tetragnathids: A, *Cyrtognatha* sp. from Cachote Natural Reserve, Dominican Republic (35 cm horizontal). B, *Allende puyehuensis* from Puyehue National Park, Chile (25 cm horizontal). C, *Azilia* sp. detail of web centre (total web diameter is 42 cm horizontal) specimen from Chiapas, Mexico (DSCN3350). D, *Chrysometa* sp. from Scientific Reserve Valle Nuevo, Dominican Republic (22 cm vertical) (DSCN7336). E, *Dolichognatha* sp. from Chiapas, Mexico (18 cm horizontal) (DSCN7723). F, *Leucauge venusta* from Virginia, USA (50 cm horizontal) (DSCN3599). Photographs (A) and (B) by Gustavo Hormiga.

therein, Álvarez-Padilla, 2007, 2009), whereas the morphology for many other taxa has never been properly documented and studied (e.g. many Leucauginae genera such as *Opadometa* Archer, 1951). This study provides an atlas that illustrates the morphology of several species representing 22 extant tetragnathid genera. A total of 960 scanning electron microscope

(SEM) images, illustrations, and photographs are presented here. For each of these genera we have provided a diagnosis, description, and a synopsis of other studies on their biology and phylogenetics. This paper also provides character descriptions and illustrations for the 213 morphological and behavioural characters in the phylogenetic analysis of Álvarez-Padilla *et al.*



**Figure 4.** Webs of tetragnathids: A, *Mesida argentiopunctata* from Noosa National Park, Australia (37 cm horizontal) (Leuc004b). B, *Metabus ebanoverde* from Ébano Verde Natural Reserve, Dominican Republic (72 cm horizontal) (DSCN7567). C, *Meta menardi* from Zealand, Denmark (15 cm horizontal, photograph by Nikolaj Scharff). D, *Metleucauge eldorado* from California, USA (40 cm horizontal). E, *Mollemeta edwardsi* from Puyehue National Park, Chile (50 cm horizontal). F, *Nanometa* sp. from Lamington National Park, Australia (18 cm horizontal) (DSCN0492). Photographs (D) and (E) by Gustavo Hormiga.

(2009). The evolution of several morphological character complexes is discussed using the optimal total evidence cladogram of Álvarez-Padilla *et al.* (2009) (Fig. 144). Finally, Nanometinae is formally treated and diagnosed as a tetragnathid subfamily.

## MATERIAL AND METHODS

### SPECIMEN DATA

Specimen dissections and illustrations of spider external anatomy were made using a Leica MZ APO dissecting microscope with a camera lucida. Internal genitalic structures were cleared in methyl salicylate (Holm, 1979), mounted on a temporary slide (Grandjean, 1949; Coddington, 1983), examined with a Leica

DMRM compound microscope, and illustrated using a camera lucida. Spigots are named after their presumed silk glands, i.e. aciniform spigots = aciniform silk gland spigots. All measurements were taken with a reticule calibrated in millimetres on both microscopes. Illustrations were rendered on a drawing sketchbook and scanned for digital corrections. Scale bars for SEM photographs are presented on each image; scale bars for illustrations are 0.2 mm unless indicated on the figure text. Web diameter is presented in the figure legends. A LEO 1430 VP scanning electron microscope was used to study the ultrastructure of many morphological external and internal features. Internal tissues surrounding sclerotized organs and specimen mountings were digested



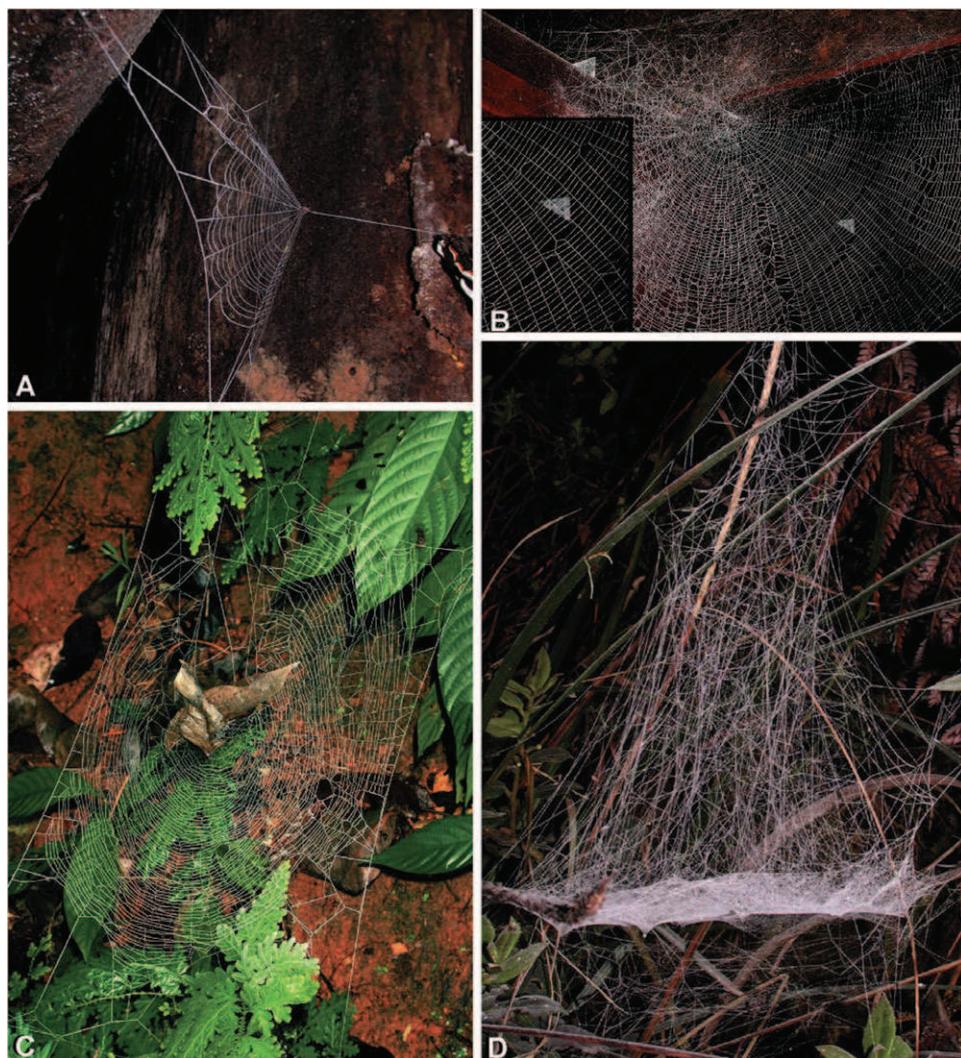
**Figure 5.** Webs of tetragnathids and outgroup taxa: A, *Opadometa* sp. from Chiang Mai, Thailand (65 cm horizontal) (DSCN3876). B, hub detail. C, *Orsinome* cf. *vethi* from Bang Lang National Park, Thailand (95 cm horizontal) (DSCN4297). D, *Tetragnatha versicolor* from Virginia, USA (65 cm horizontal) (DSCN3180). E, *Tylorida striata* from Khao Luang National Park, Thailand (35 cm horizontal) (DSCN4091). F, *Parasteatoda* sp. from Chiapas, Mexico (25 cm horizontal) (DSCN7996).

following the protocol of Álvarez-Padilla & Hormiga (2008). The tracheal system was studied using female specimens. Usually six preparations were carried out for each species, mounting separately the abdomen, cephalothorax, male pedipalp, epigynum, tracheal system, and leg IV. On average two females and one male specimen per species were dissected and mounted. All specimen preparations were subjected to critical point drying and coated with Au-Pd for SEM study. If study specimens of the type species were unavailable or too rare in museum collections, we then selected a species better represented in collections. In doing so we deemed that this latter species would be congeneric with the type species. For example, we chose an undescribed species of *Nanometa* from Queensland (see Appendix 2) because

we could not obtain specimens of *Nanometa gentilis* Simon, 1908, the type species, from Western Australia. Voucher data are given in Appendix 2.

#### PHYLOGENETIC ANALYSES OF THE MORPHOLOGY AND BEHAVIOUR DATA

Data analyses were performed using the parsimony criterion under equal weights and implied weights. All the analyses were carried out with the computer program TNT version 1.1 (Goloboff, Farris & Nixon, 2004). Character optimizations were visualized and optimized using WinClada version 1.00.08 (Nixon, 2002). The data set was edited with Nexus Data Editor version 0.5.0 (Page, 2001). This data set can be downloaded from <http://www.gwu.edu/~spiders/>



**Figure 6.** Webs of outgroups and other taxa: A, *Epeirotypus brevipes* (Theridiosomatidae) from Chiapas, Mexico (20 cm vertical) (DSCN7732). B, *Nephilengys malabarensis* (Nephilidae) from Queensland, Australia (95 cm horizontal complete web) (no photo voucher). C, *Fecenia* sp. (Psechridae) from Khao Sok National Park, Thailand (35 cm vertical) (DSCN4354). D, *Lomaita* sp. (Linyphiidae) from Scientific Reserve Valle Nuevo, Dominican Republic (15 cm sheet horizontal) (DSCN7476).

cladograms.htm with the image files used for character coding and description. The following tree search strategies were implemented: random seed 1, 5000 replicates of random stepwise addition of taxa, holding 100 trees per replicate and performing the tree bisection and reconnection (TBR) swapping algorithm. All collapsing rules were implemented to investigate differences in the strict consensus. Implied weights analyses (Goloboff, 1993) were executed using all concavities from 1 to 100. Jackknife support values (Farris *et al.*, 1995) were calculated performing 1000 iterations, each iteration with 100 random additions of taxa followed by TBR and saving 50 trees per random addition, random seed 1. For the analyses

with implied weights the support values were calculated using ‘Symmetric Resampling’ algorithms (Goloboff *et al.*, 2003). Absolute Bremer support values were calculated saving 50 000 trees (Bremer, 1988, 1995). The data matrix is presented in Appendix 1.

#### TAXON SELECTION

This phylogenetic analysis includes 47 taxa: 25 tetragnathids, 11 araneids, four nephilids, five terminals representing the ‘reduced piriform clade’ (RPC), *Uloborus glomosus* (Walckenaer, 1841) representing Deinopoidea, and *Oncodamus decipiens* Harvey, 1995



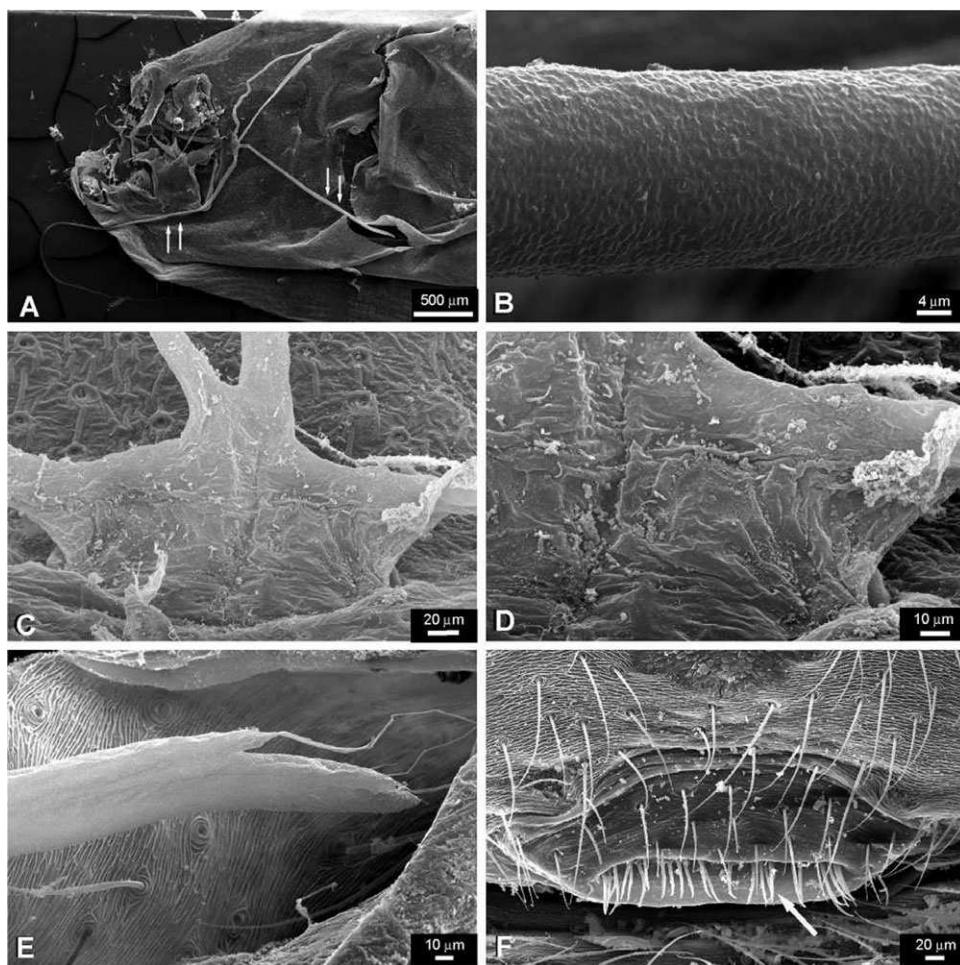
**Figure 7.** Webs of outgroup taxa: A, *Phonognatha graeffei* (Araneidae) from Noosa National Park, Australia (65 cm horizontal complete web) (Neph002). B, symphytognathid from Doi Inthanon National Park, Thailand (8 cm horizontal) (DSCN3937). C, *Ocrepeira* sp. from Ébano Verde Natural Reserve, Dominican Republic (orb 37 cm vertical) (DSCN7326). D, *Wagneriana* sp. from Chiapas, Mexico (13 cm horizontal) (DSCN8014).

(Nicodamidae) as the root. We used a nicodamid as the root following several studies that suggest the possibility that Nicodamidae is placed within Orbiculariae (Griswold *et al.*, 1998, 2005; Álvarez-Padilla *et al.*, 2009; Blackledge *et al.*, 2009). The species and families included in this taxonomic sample representing the RPC are: *Linyphia triangularis* (Clerck, 1757) (Linyphiidae); *Nesticus cellulanus* (Clerck, 1757) (Nesticidae); *Epeirotypus brevipes* O. P.-Cambridge, 1894 (Theridiosomatidae); *Parasteatoda tepidariorum* (Koch, 1841), and *Asagena americana* (Emerton, 1882) (Theridiidae). The taxonomic selection of nephilides includes five species representing the four genera currently included by Kuntner *et al.* (2008); *Nephila* is the only genus that is represented by two species. The taxonomic sample of all nontetragnathine tetragnathids was based on Hormiga *et al.* (1995) and Álvarez-Padilla (2007). Araneidae were

represented by 11 species selected based on the lineages recovered by the phylogenetic analyses of Scharff & Coddington (1997). The choice of araneoid outgroups was based on the hypotheses of Griswold *et al.* (1998) and Lopardo & Hormiga (2008). Polymorphic characters were coded if present within the species revised, not for the genus. Type species were chosen to represent the tetragnathid genera included in this analysis (Yeates, 1995; Prendini, 2000). If specimens conspecific with the type species were too rare in museum collections then a species sharing a similar diagnosis with the type was chosen.

#### CHARACTER DEFINITIONS

A character is defined here as a hypothesis of kinship between homologous morphological and behavioural features amongst different species. Morphological



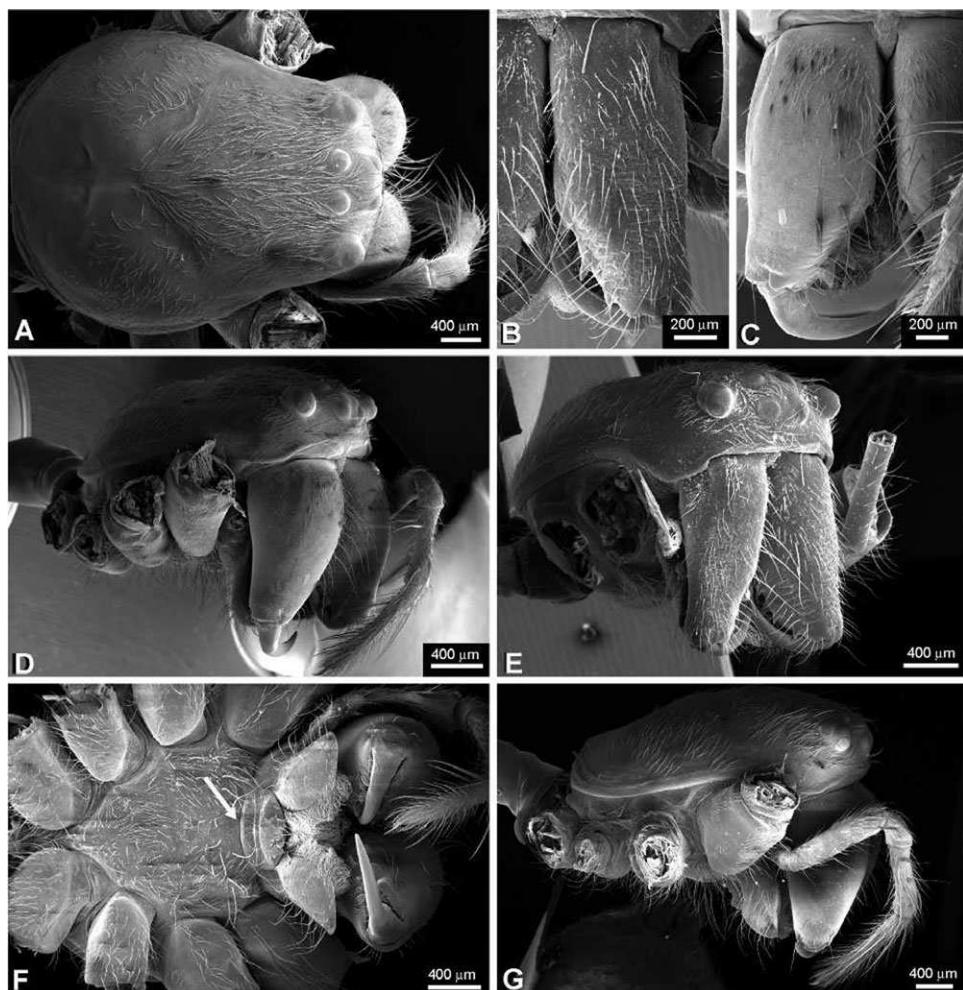
**Figure 8.** *Allende nigrohumeralis* abdomen: A, tracheal system dorsal view (arrows pointing upwards correspond to lateral trachea and downward pointing arrows median trachea; trachea follow the same arrangement on all images). B, lateral tracheal cuticle. C, tracheal spiracle posterior view. D, detail of tracheal spiracle. E, median trachea tip. F, epiandrous fusules (arrow). Images of tracheal system (SEMFAP058), epiandrous fusules (SEMFAP057).

features are proposed as homologous in the sense of primary homology (de Pinna, 1991), if they are either topologically equivalent or anatomically similar (Patterson, 1982; Hall, 1994; Rieppel, 1994; Scotland & Pennington, 2000; Kearney, 2002; Rieppel & Kearney, 2002). The presence of a character state is presumed to be homologous across the taxa that have it unless its homology is refuted by the incongruence with other character distributions. Similarity in developmental origin was not used here because of a lack of data; however, it has also been used to propose homology between morphological features (Fink, 1982; Kluge & Strauss, 1985; Roth, 1988; Mabee, 1989, 1996, 2000; Nelson, 1994; Laubichler, 2000). The characters used here are morphological features of the male and female somatic and genital anatomy, internal and external, and behavioural features. A total of 213 characters was coded for these taxa; 57

from the male pedipalp, 31 from the female reproductive system, 43 from the cephalothorax of both sexes, 28 from behaviour, 22 from the spinnerets, 15 from the abdomen and 17 from the legs, mainly the femora and tarsus IV because of the variation that is present within Tetragnathidae. The behavioural characters included here are those previously used in orbicularian and tetragnathid systematics (e.g. Eberhard, 1982; Hormiga *et al.*, 1995; Griswold *et al.*, 1998; Kuntner *et al.*, 2008). Data about some of these behaviours were obtained from web photographs taken during several field expeditions worldwide. Characters are cited in the text in parentheses as '(character number – state number)'.

#### CHARACTER CODING

We used a combination of binary coding with inapplicable entries and unordered multistate characters.



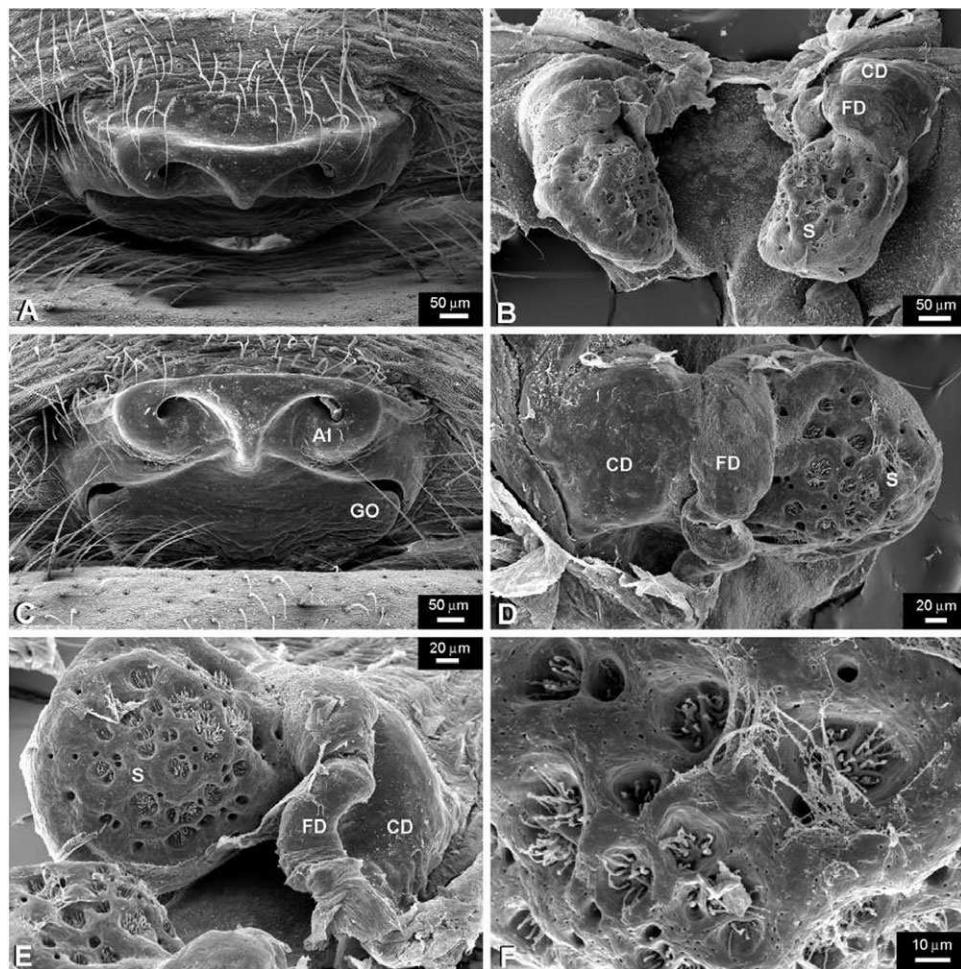
**Figure 9.** *Allende nigrohumeralis* cephalothorax: A, female dorsal view. B, male chelicerae. C, female chelicerae. D, female tangential view. E, male tangential view. F, female ventral view sternum and labium (arrow). G, female lateral view. Female and male images from SEMFAP057 and SEMFAP058, respectively.

These character combinations include first a character for the presence or absence of a feature followed by a character that describes the condition of that particular feature. Those taxa that lack the feature altogether were coded for the second character as ‘inapplicable’ (Platnick, Griswold & Coddington, 1991; Lipscomb, 1992; Strong & Lipscomb, 1999 and references therein). We agree with these authors in that there is no ‘perfect character coding method’. Inapplicable entries sometimes increase ambiguity in character optimization, collapsing supported nodes; and unordered multistate characters may fail to capture the information from the similarity between adjacent states on nonlinear progressions. All characters were treated as non-additive or unordered (Fitch, 1971). Inapplicable entries are represented in the matrix with dashes and missing or unknown information with question marks. For those characters in which

the primary homology hypotheses proposed here differ from those in the literature, a brief discussion of these differences is given under the character description section. Continuous characters are expressed as relative measurements between two features [e.g. the clypeal height is quantified relative to the anterior median eye (AME) diameter; character 89]. This ratio can be translated either to discrete states (e.g. less than one AME in height) or can be expressed as a continuous measurement (e.g. 1.2 AME diameters); the former option was followed in this paper (but see Goloboff, Mattoni & Quinteros, 2006 for a recent paper for the analysis of continuous characters).

#### ABBREVIATIONS USED IN TEXT AND FIGURES

AC, aciniform gland spigot(s); AG, aggregate gland spigot(s); AI, epigynum apical invaginations; ALE,



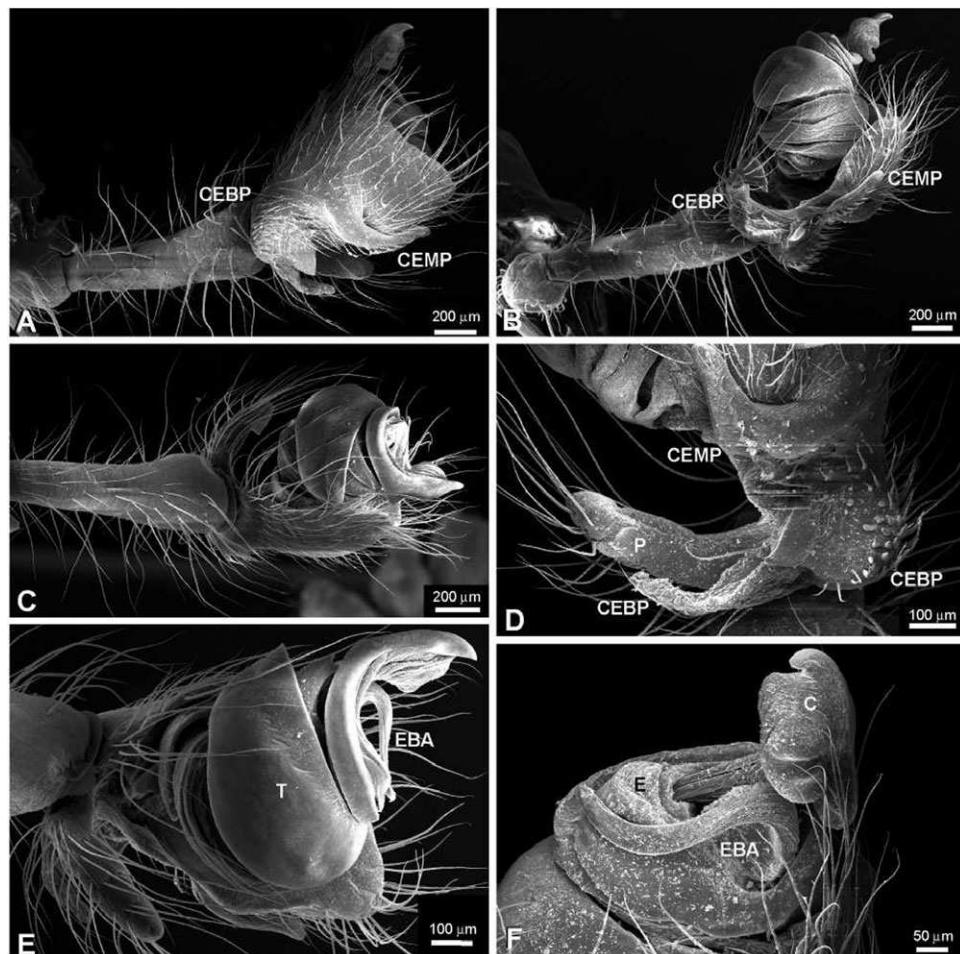
**Figure 10.** *Allende nigrohumeralis* epigynum: A, ventral view. B, dorsal view. C, posterior view. D, spermatheca lateral view. E, accessory glands. F, accessory glands detail. All images from SEMFAP057.

anterior lateral eye(s); ALS, anterior lateral spinnerets; AME, anterior median eye(s); BS, Bremer support value(s); C, conductor; CEBP, cymbial ectobasal process; CEMP, cymbial ectomedian process; CD, copulatory ducts; CDBP, cymbial dorsobasal process; CO, copulatory opening; CR, cribellum; CY, cylindrical gland spigot(s); E, embolus; EBA, embolic basal apophysis; F, fundus; FD, fertilization duct; FL, flagelliform gland spigot(s); JK, jackknife support value(s); MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; P, paracymbium; PF, pseudo-flagelliform spigot(s); PI, piriform gland spigot(s); PLE, posterior lateral eye(s); PLS, posterior lateral spinnerets; PME, posterior median eye(s); PMS, posterior median spinnerets; R, radix; S, spermatheca; SP, stipes; ST, subtegulum; STA, subterminal apophysis; T, tegulum; TA, terminal apophysis; TO, tarsal organ.

## RESULTS

### PHYLOGENETIC ANALYSES OF THE MORPHOLOGY AND BEHAVIOUR DATA

Analyses of the morphology and behaviour data set (see Appendix 1) resulted in five minimal length cladograms under equal weights [length ( $L$ ) = 1033, consistency index (CI) = 26, retention index (RI) = 58]. The same five cladograms were found with all the rules for collapsing unsupported nodes implemented by TNT (Coddington & Scharff, 1994). The strict consensus of these cladograms collapsed two nodes, one within Leucauginae and the other within the ‘reduced piriform clade’ (Fig. 143A). Implied weights analyses with concavities 1 to 100 produced six different cladograms. One of these cladograms was also found by the equal weights analyses obtained with concavities values greater than 19. The strict consen-



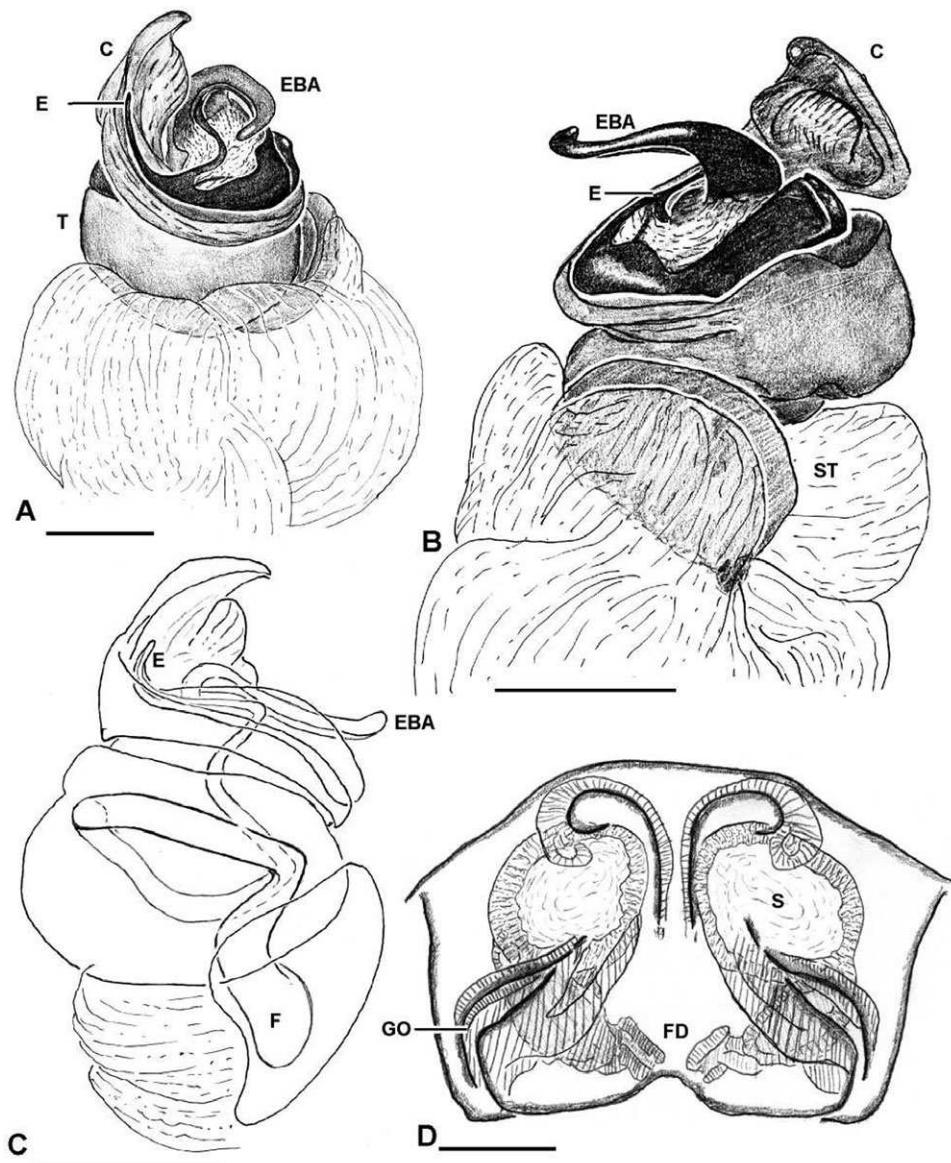
**Figure 11.** *Allende nigrohumeralis* male pedipalp: A, dorsal view. B, ectal view. C, mesal view. D, cymbial ectobasal process. E, ventral view. F, apical view. All images from SEMFAP058.

sus of all 11 cladograms obtained by the different weighting criteria collapsed 17 nodes: one inside the ‘reduced piriform clade’, three within Araneidae, and 13 within Tetragnathidae. The strict consensus of all concavity values shows which nodes are insensitive to weighting variations (Fig. 143B). When our morphology and behaviour data set (Appendix 1) was combined with the DNA sequences published by Álvarez-Padilla *et al.* (2009), and analysed using direct optimization methods, the optimal tree was the cladogram depicted in Figure 144. That cladogram (Fig. 144), which was also the preferred topology in Álvarez-Padilla *et al.* (2009: fig. 1a), represents our preferred phylogenetic hypotheses for tetragnathid interfamilial relationships, and was used to optimize the morphological and behavioural synapomorphies presented in Table 1.

## DISCUSSION

### TETRAGNATHID PHYLOGENETIC RELATIONSHIPS

Our working hypothesis for tetragnathid phylogenetic relationships (Fig. 144) was obtained by analysing under direct optimization (Wheeler *et al.*, 2006) the morphological and behavioural data set in Appendix 1 combined with c. 6300 nucleotide bases from six different genes (Fig. 144; Álvarez-Padilla *et al.*, 2009: fig. 1a). Álvarez-Padilla *et al.*’s direct optimization analysis produced a single most parsimonious tree of 54 536 weighted steps with indel and nucleotide substitution changes equal to four. Support values and synapomorphies for all nodes in this cladogram (Fig. 144) are presented in Table 1. We should note that *Allende* and *Mollemeta* were mislabelled in the cladogram of Álvarez-Padilla *et al.* (2009: fig. 1a). The



**Figure 12.** *Allende nigrohumeralis* genital anatomy illustrations: A, and B, male pedipalp expanded. C, male pedipalp bulb cleared with sperm duct depicted. D, cleared epigynum ventral view. Refer to Appendix 2 for information regarding specimens illustrated for these and all figures after.

correct placement of these two taxa is as depicted in Figure 144 ((*Allende* (*Mollemeta*, Tetragnathinae)). Some recently published analyses (Griswold *et al.*, 2005; Blackledge *et al.*, 2009) have suggested the possibility that nicodamids fall inside Orbiculariae. As mentioned earlier, we have rooted our optimal trees using the nicodamid representative (*Oncodamus decipiens*). Re-rooting those trees using the deinopoids of our taxon sample instead does not change the internal relationships of tetragnathids.

Álvarez-Padilla *et al.* (2009) found that Tetragnathidae is monophyletic and includes four clades:

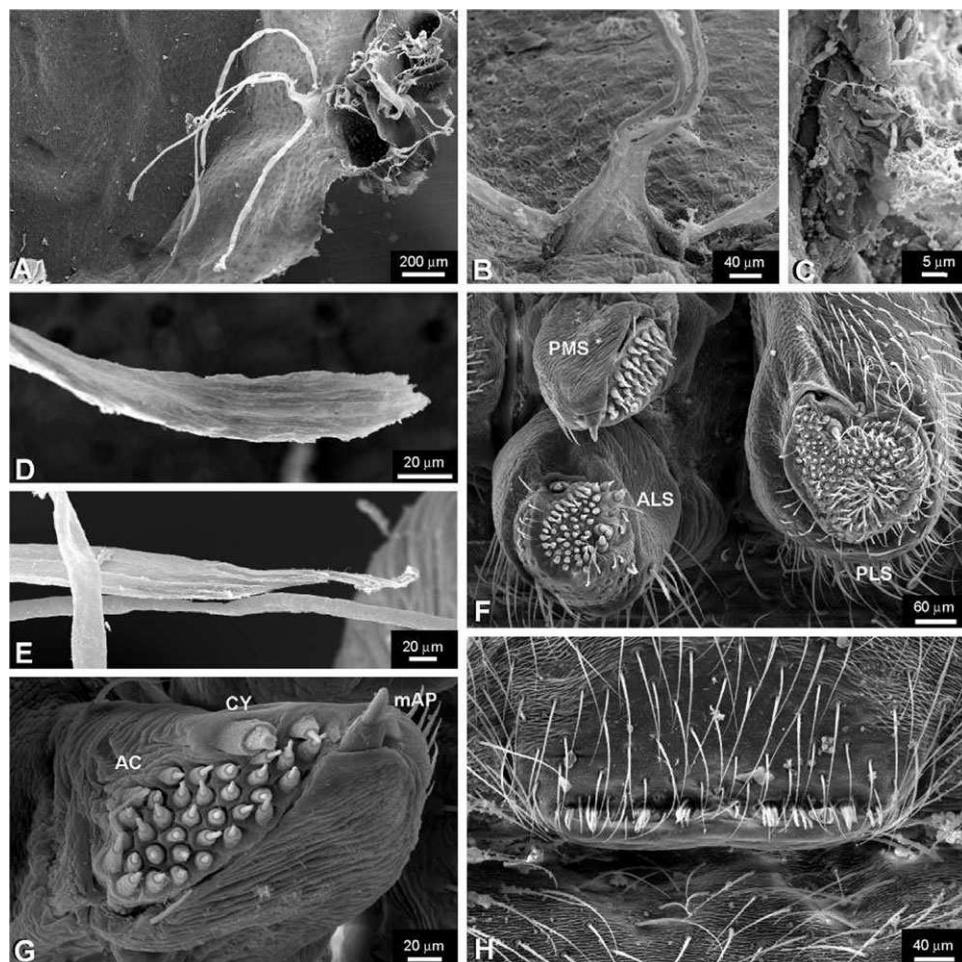
Tetragnathinae, Leucauginae, Metainae, and the 'Nanometa clade'. They also concluded that the placement of *Azilia*, *Allende*, *Chrysometa*, *Diphya*, and *Mollemeta* within tetragnathids was sensitive to data partitions and analytical methods; therefore, it received very low support values. Consequently, most of these genera were not formally included in any group as their phylogenetic placement is likely to change with the addition of data. Tetragnathidae was recovered sister to a clade that includes some of the 'reduced piriform clade' representatives (linyphiids, nesticids, and theridiosomatids). Araneidae is sister

**Table 1.** Morphological and behavioural synapomorphies for the cladogram in Figure 144 (see text and figure legend for additional details). Node numbers correspond to those presented in Figure 144

NODE	JN	1	2	3	4	5	6	7	8	9
1	–	Not applicable basal trichotomy								
Araneoidea	–	6:(1 > 0)	12:(0 > 1)	13:(0 > 1)	16:(1 > 0)	67:(0 > 2)	91:(2 > 0)	92:(0 > 1)	94:(0 > 1)	138:(0 > 1)
3	–	163:(0 > 1)	195:(0 > 1)	204:(0 > 1)						
Tetragnathidae	–	2:(0 > 1)	24:(0 > 1)	47:(1 > 0)	98:(0 > 1)	174:(0 > 1)	180:(0 > 1)	181:(0 > 1)		
5	–	1:(0 > 1)	7:(1 > 0)	80:(1 > 0)	87:(1 > 0)	124:(0 > 1)	164:(1 > 0)			
6	–	15:(1 > 0)	50:(0 > 1)	77:(0 > 1)	84:(0 > 1)	85:(0 > 1)	130:(0 > 2)			
7	51	26:(0 > 1)	28:(0 > 1)	91:(0 > 1)	182:(0 > 1)	194:(0 > 1)				
8	–	36:(1 > 0)	126:(0 > 1)	181:(1 > 2)						
9	–	58:(1 > 2)	68:(0 > 1)							
Tetragnathinae	–	15:(1 > 0)	25:(0 > 1)	26:(1 > 0)	28:(1 > 0)	35:(0 > 1)	55:(1 > 0)	76:(0 > 1)	82:(1 > 2)	111:(0 > 1)
		118:(1 > 2)	123:(1 > 0)	130:(0 > 2)	133:(0 > 1)	148:(0 > 1)	159:(0 > 1)	169:(0 > 1)		
11	–	57:(1 > 2)	92:(1 > 0)	116:(0 > 1)	170:(1 > 0)	172:(1 > 0)				
12	–	8:(0 > 1)	20:(1 > 0)	131:(1 > 0)	138:(1 > 0)	156:(0 > 1)	160:(4 > 5)	167:(0 > 1)	180:(1 > 0)	
13	–	83:(0 > 1)	209:(1 > 0)							
14	–	67:(2 > 0)	131:(1 > 0)	143:(2 > 1)	147:(0 > 1)					
Leucauginae	–	26:(1 > 0)	31:(0 > 1)	46:(0 > 1)	48:(0 > 1)	57:(1 > 2)	58:(1 > 2)	66:(0 > 1)	82:(1 > 2)	88:(1 > 0)
		98:(1 > 2)	137:(0 > 1)	141:(0 > 1)						
16	–	19:(0 > 1)	28:(1 > 0)	67:(0 > 1)	77:(0 > 1)	125:(0 > 1)	140:(1 > 0)	151:(0 > 1)	152:(0 > 1)	
17	–	83:(1 > 0)	98:(2 > 0)	112:(0 > 1)						
18	53	82:(2 > 1)	105:(1 > 0)	142:(0 > 1)	159:(0 > 1)					
19	64	103:(0 > 1)	108:(2 > 1)	192:(0 > 1)						
20	–	97:(1 > 0)	117:(1 > 0)							
21	53	41:(0 > 1)	91:(1 > 0)	142:(0 > 1)						
Nanometinae	–	29:(0 > 1)	55:(1 > 0)	69:(0 > 2)	84:(0 > 1)	144:(0 > 2)	145:(0 > 1)	168:(0 > 1)	180:(1 > 0)	185:(0 > 1)
23	–	36:(1 > 0)	97:(1 > 0)	98:(1 > 0)						

		47:(0 > 1)	64:(0 > 1)	78:(1 > 0)	130:(0 > 1)	138:(1 > 0)	159:(0 > 1)			
25	—	183:(1 > 0)								
26	—	15:(1 > 0)	91:(1 > 0)	118:(1 > 2)	163:(1 > 0)	207:(0 > 1)				
27	—	41:(0 > 1)	42:(0 > 1)	47:(1 > 0)	55:(1 > 0)	69:(0 > 2)	130:(1 > 0)	138:(0 > 1)	181:(1 > 0)	182:(1 > 0)
28	—	84:(0 > 1)	98:(0 > 2)	180:(0 > 1)						
Araneidae	—	44:(1 > 0)	107:(0 > 3)	193:(1 > 0)						
30	94	11:(0 > 1)	126:(0 > 1)	127:(0 > 1)	135:(0 > 1)					
31	62	5:(0 > 1)	9:(1 > 0)	107:(3 > 1)	118:(1 > 0)	128:(0 > 1)	159:(0 > 1)			
32	—	Supported only by nucleotide changes								
33	—	88:(1 > 0)	163:(0 > 1)							
34	52	83:(0 > 1)	91:(0 > 2)	97:(1 > 2)	127:(1 > 0)	139:(0 > 1)	146:(2 > 1)	158:(0 > 1)		
35	—	Supported only by nucleotide changes								
36	52	158:(0 > 1)								
37	75	90:(0 > 1)	120:(0 > 2)	121:(0 > 1)	131:(1 > 2)					
38	—	91:(0 > 1)								
39	75	14:(0 > 1)	15:(1 > 0)	112:(0 > 1)	117:(0 > 1)					
40	92	3:(1 > 0)	39:(0 > 1)	54:(1 > 0)	55:(1 > 0)	58:(0 > 2)	63:(0 > 1)	99:(0 > 1)	118:(1 > 2)	
		131:(1 > 0)	132:(0 > 1)	139:(0 > 1)	163:(0 > 1)	182:(0 > 1)	202:(0 > 1)			
Nephilidae	—	24:(0 > 1)	43:(0 > 1)	47:(1 > 0)	54:(1 > 0)	58:(0 > 3)	62:(1 > 0)	63:(0 > 1)	67:(2 > 1)	77:(0 > 1)
		81:(1 > 0)	82:(1 > 0)	91:(0 > 2)	106:(0 > 1)	121:(0 > 1)	159:(0 > 1)			
42	71	11:(0 > 1)	89:(0 > 1)	107:(0 > 2)	119:(0 > 1)	122:(0 > 1)	126:(0 > 1)	158:(0 > 1)	166:(0 > 1)	
43	—	56:(0 > 1)	131:(1 > 0)	136:(0 > 1)	198:(0 > 1)	212:(0 > 1)				
44	93	Supported only by nucleotide changes								
45	—	1:(0 > 1)	7:(1 > 0)	10:(0 > 1)	18:(0 > 1)	34:(0 > 1)	80:(1 > 0)	83:(0 > 1)	86:(0 > 1)	87:(1 > 0)
		97:(1 > 2)	125:(0 > 1)	178:(0 > 1)	187:(0 > 2)	192:(0 > 1)				
46	—	85:(0 > 1)	165:(1 > 0)							

JN, jackknife support values calculated using direct optimization methods, ‘—’, less than 50% of support. Synapomorphies are abbreviated as ‘Character number: (state transformation X > Y)’.



**Figure 13.** *Azilia affinis* abdomen: A, tracheal system dorsal view. B, tracheal spiracle posterior view. C, tracheal spiracle glands. D, and E, lateral tracheae tips. F, spinnerets. G, posterior median spinnerets. H, epiandrous fusules. All images from SEMFAP032.

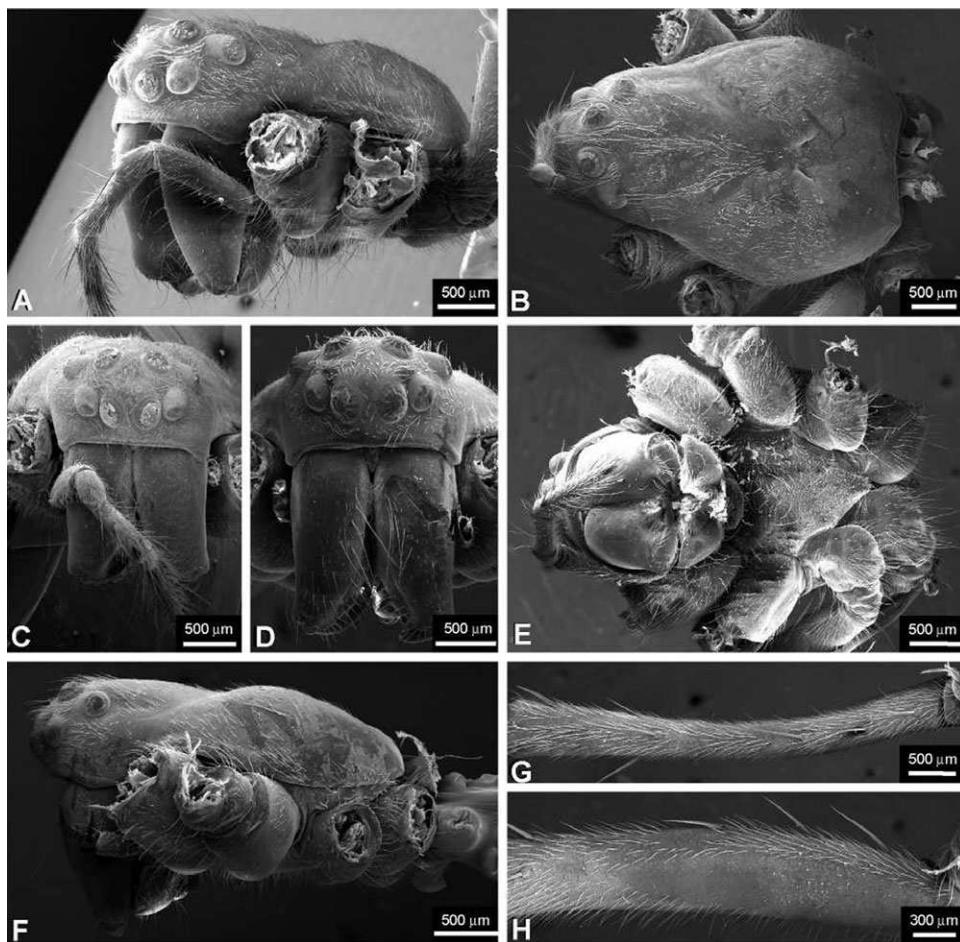
to Nephilidae and this is clade sister to theridiids (Fig. 144).

#### CLADOGRAM COMPARISON OF THE TOTAL EVIDENCE DATA SET AND THE MORPHOLOGY AND BEHAVIOUR SUBSET

In this section we contrast and discuss the phylogenetic signal of the two data set partitions (i.e. the total evidence data of Álvarez-Padilla *et al.*, 2009 and the subset presented in Appendix 1). The optimal cladograms of both data sets recovered Tetragnathidae, Tetragnathinae, Leucauginae, and the ‘*Nanometa* clade’ (hereafter referred as the subfamily Nanometinae) as monophyletic. The taxonomic composition of Metainae remains variable. This latter clade included three genera with the morphology and

behaviour partition, whereas the total evidence analyses recovered two more genera (Figs 143, 144).

The taxonomic composition of Tetragnathinae, Leucauginae, and Nanometinae are the same in both cladograms, although their generic internal phylogenetic relationships vary. Within Leucauginae: *Mesida*, *Opadometa*, *Metleucauge*, and *Leucauge* are the only nodes that do not change between cladograms. *Azilia* is either sister to Leucauginae with the morphology and behaviour data, or sister to all other tetragnathids with all data combined. Inside Tetragnathinae only *Cyrtognatha* changes placement as either sister to *Tetragnatha* or sister to all other tetragnathines. In Nanometinae the phylogenetic placement of *Nanometa* changes as either sister to ‘*Orsinome*’ *sarasini* with all data, to sister to an undescribed nanometine from Australia with the morphology and behaviour data (Figs 143, 144).



**Figure 14.** *Azilia affinis* cephalothorax: A, female tangential view. B, female dorsal view. C, female chelicerae. D, male chelicerae. E, female cephalothorax ventral view and sternum. F, female lateral view. G, femur IV dorsal view. H, femur IV mesal view. All images from SEMFAP032.

The phylogenetic relationships amongst these three subfamilies and Nanometinae change depending on the weighting functions used. With the morphology and behaviour data all tetagnathid genera include two large clades, Leucauginae and the ‘metaine tetagnathine complex’. The molecular partition has four major clades and *Azilia* sister to a clade that includes all four lineages (Fig. 144). The clade that includes Tetagnathinae also includes *Allende* and *Mollemeta*, but these taxa were not included within Tetagnathinae because of their instability (Fig. 144).

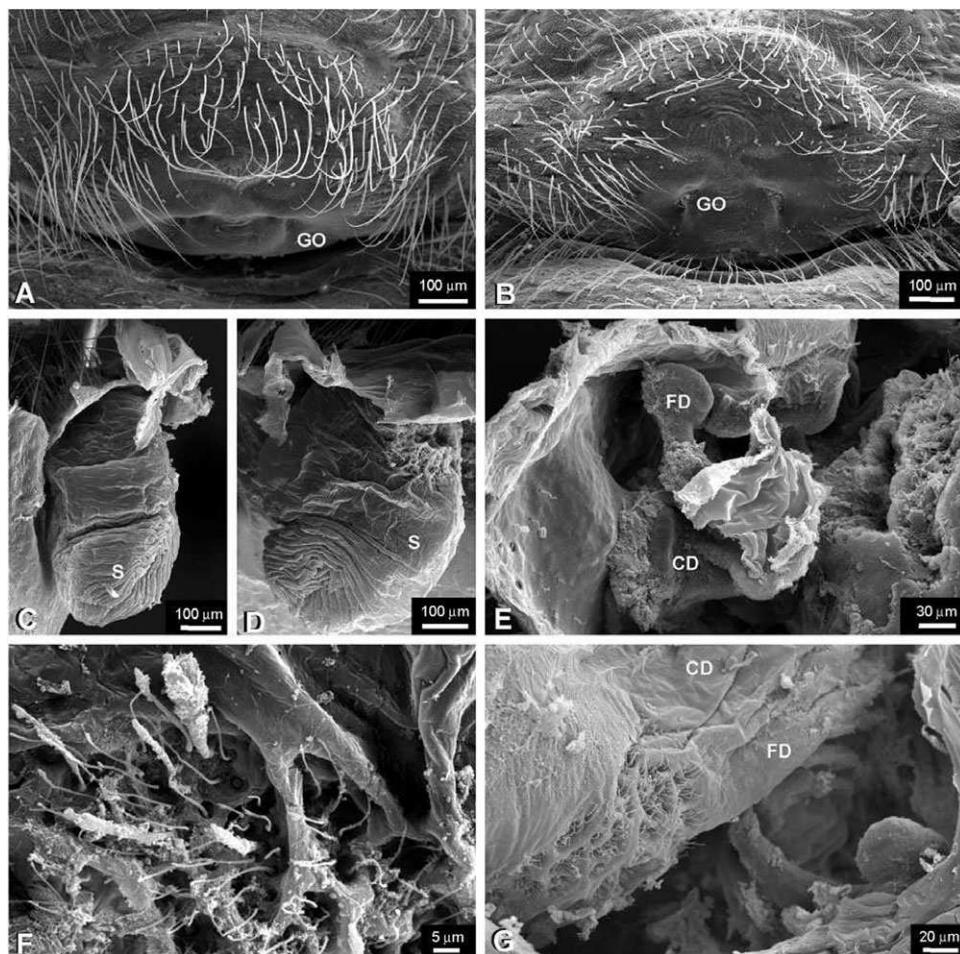
The phylogenetic placement of Tetagnathidae in Araneoidea varies depending on the partitions. The morphology and behaviour data recovered Tetagnathidae and Nephilidae as sister taxa (Fig. 143A); when these data are combined with DNA sequences, Tetagnathidae is sister to clade that included *Linyphia*, *Nesticus*, and *Epeirotypus* (Fig. 144). Furthermore, the clade that includes *Phonognatha* and *Deliochus* is not sister to Nephilidae, but to *Zygiella*.

and this last clade nested within Araneidae. The ‘reduced piriform clade’ is polyphyletic (Fig. 144).

#### EVOLUTION OF TETRAGNATHID SOMATIC MORPHOLOGY

##### *Spinnerets*

Spinnerets are associated with silk glands that lie within the abdomen and constitute the organs where the silk is finally expelled and manipulated. Abdominal spinnerets are autapomorphic for spiders and are homologous to either abdominal appendages as suggested by the expression of the *Distal-less Cs-dll* gene (Schoppmeier & Damen, 2001), or homologous to booklungs as the coexpression of the genes *pdm/nub* and *apterous* during development suggests (Damen, Saridaki & Averof, 2002). Female araneoids produce seven different types of silk associated with different types of spigots. Tetagnathid spinnerets are similar to those of other araneoidean spiders; they have two



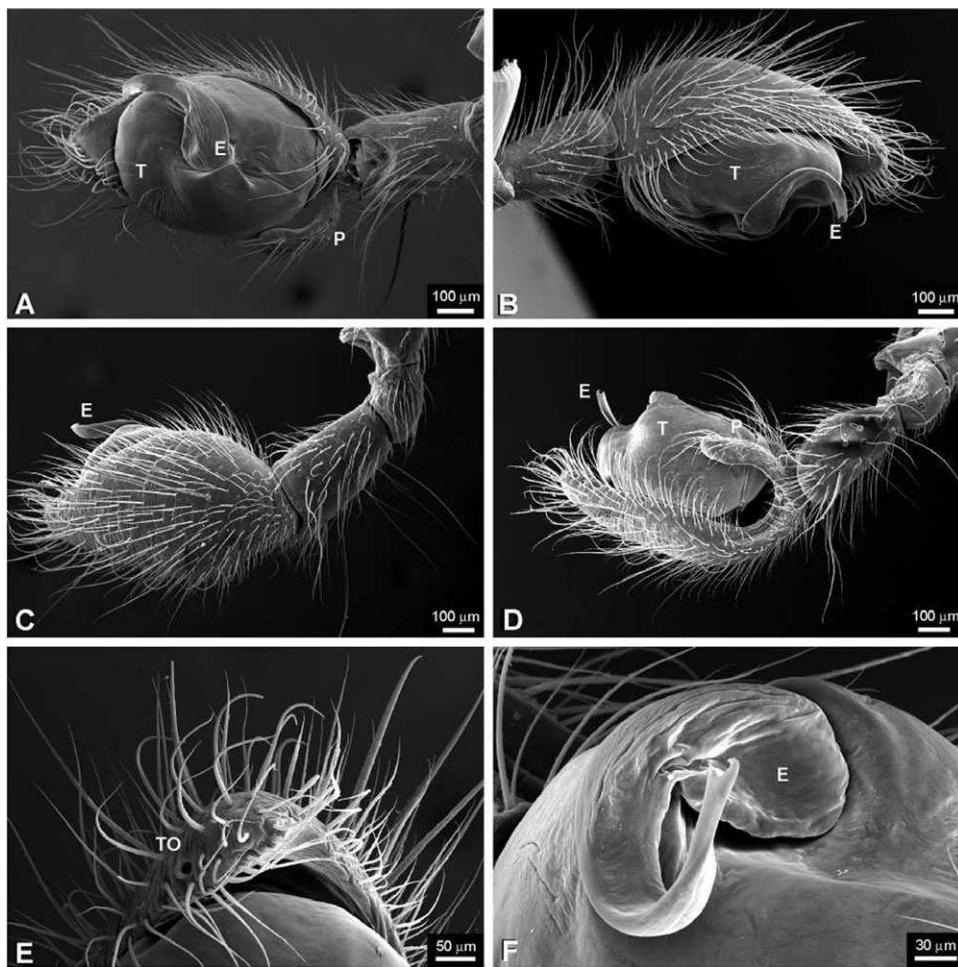
**Figure 15.** *Azilia affinis* epigynum: A, ventral view. B, posterior view. C, spermatheca lateral view. D, spermatheca dorsal view. E, copulatory and fertilization ducts. F, accessory glands detail. G, accessory glands position. All images from SEMFAP032.

aggregate (character 12, state 1 abbreviated thereafter as 12-1) plus one flagelliform spigot forming the ‘triplet’ on the PLS (13-1). In addition tetragnathids, have a squamose cuticle on the spinnerets (16-0) and one cylindrical spigot on the PMS (6-0). The first two features are unique to araneoids amongst spiders, the only exception within Tetragnathidae is *Pachygnatha* that lacks aggregate and flagelliform spigots as an adult (Fig. 105E). Many other lineages within Araneoidea also have also independently lost the ‘triplet’ as adults (Griswold *et al.*, 1998, 2005 and references therein).

Piriform bases can either be tightly wrapped around the column base or separated from the column leaving a torus (2-1: fig. 26F insert box). Separated piriform bases are synapomorphic for Tetragnathidae (RI = 55). The evolution for the ALS piriform bases within Araneoidea is very homoplastic (CI = 11), this character is optimized as having independently evolved in *Clita-*

*etra*, *Epeirotypus*, and four times within Araneidae. Within Tetragnathidae piriform bases that wrap the column base have two independent reversals within *Meta* and *Mollemeta*. The ALS piriform spigots cover evenly all the surface of the apical segment in all taxa revised (119 C-F) except in *Phonognatha* and *Deliochus* that have a smooth area without spigots near the ectal margin (3-0, Fig. 135C, D arrows).

The PMS spinnerets of most tetragnathids lack a brush of aciniform spigots (4-1) (Figs 87H, 114E); only *Meta menardi* and *Azilia affinis* have this brush (Figs 13F, 56C). The PMS aciniform spigot brush is also present in Nephilidae and Araneidae (Fig. 120; Hormiga *et al.*, 1995: fig. 16C), but absent in *Parasteatoda* Archer, 1946, *Asagena* Sundevall, 1833, *Linyphia*, *Nesticus*, and *Epeirotypus* (Fig. 120B) making the optimization of this character ambiguous. Addition of more taxa, particularly more symphytognathoids and other *Azilia* species may resolve the

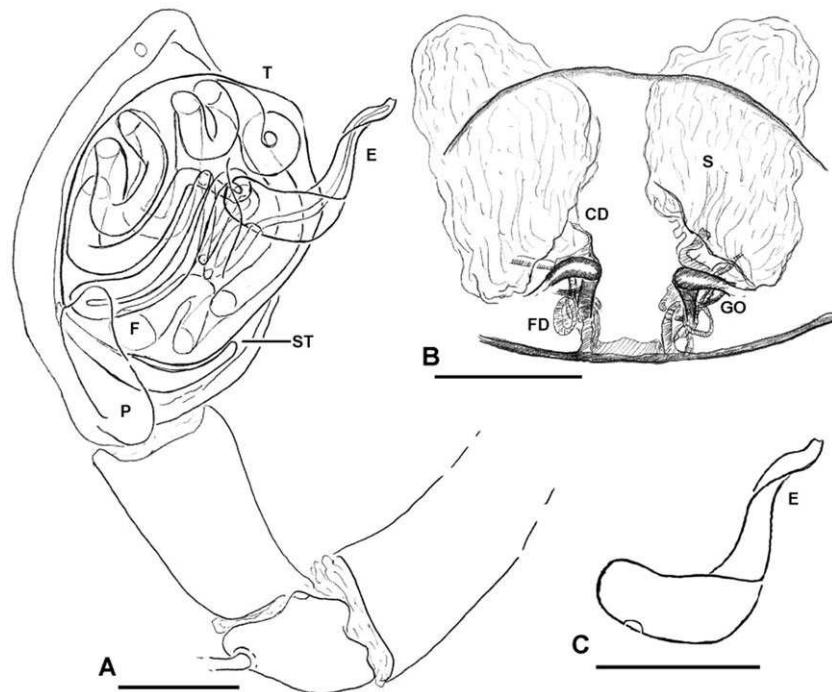


**Figure 16.** *Azilia affinis* male pedipalp. A, ventral view. B, mesal view. C, dorsal view. D, ectal view. E, tarsal organ. F, embolus. All images from SEMFAP032.

evolution of the PMS aciniform brush. Furthermore, our observations under a dissecting microscope of *Azilia histrio* Simon 1895, *Azilia marmorata* Mello-Leitão, 1948, and *Azilia guatemalensis* O. P.-Cambridge 1889; found that *A. affinis* is the only species of that genus that presents this PMS aciniform spigot brush.

Most araneoids have two cylindrical spigots on the PLS (6–0). In some taxa, the basal spigot is considerably larger than the distal. Spigot size differences are optimized as synapomorphic for *Glenognatha* and *Pachygnatha*, and homoplastic in *Linyphia* (8–1). Most linyphiids and pimoids have the basal cylindrical spigot base larger; this character has been proposed as synapomorphic for the clade that includes Linyphiidae and Pimoidae (Hormiga, 1994a: figs 22D, 25D; Griswold *et al.*, 1998; Hormiga & Tu, 2008). The PLSs of tetragnathids and some araneoids have a median area of aciniform spigots that originates between the cylindrical spigots and ends on one side

of the aggregate spigots (Figs 46F, 77E). In some nephilids and araneids these spigots extend well beyond the triplet (Figs 121C, D, 122A). This extended aciniform field (11–1) is synapomorphic for *Nephila*, *Herennia*, *Nephilengys*, and for a clade that includes all araneids (Figs 121C–F, 122A) except *Zygiella*, *Deliochus*, and *Phonognatha* (Fig. 122D). The flagelliform spigot is usually located between the aggregate spigots and far apart from the cylindrical spigots, except in *Zygiella*, *Deliochus*, and *Phonognatha* where the flagelliform spigot is closer to one of the cylindrical spigots (14–1) (Figs 114G, 121E, F, 122D, 135E, F). The association of the flagelliform and aggregate spigots varies through tetragnathid evolution. The flagelliform spigot distal edge can be either separated from the aggregate spigots (Fig. 109F), or covered by them (Fig. 51E). Flagelliform spigots not covered by the aggregate spigots are optimized as synapomorphic for Tetragnathinae (Arnedo, Hormiga & Scharff, 2009), a clade that



**Figure 17.** *Azilia affinis* genital anatomy illustrations: A, male pedipalp bulb cleared. B, cleared epigynum ventral view. C, embolus.

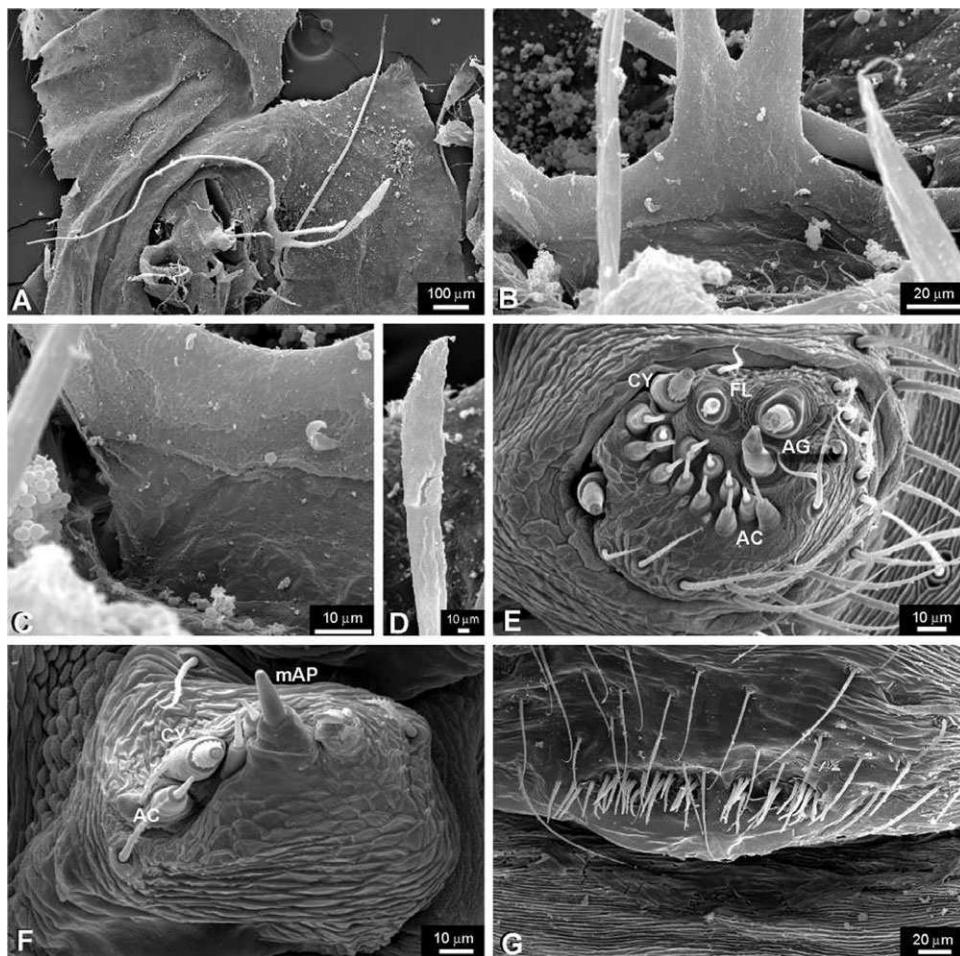
includes *Dolichognatha*, *Chrysometa*, and *Diphyia*, and is homoplastic in *Azilia* plus ‘*Orsinome sarasini*’ (15-0).

#### Respiratory system

Booklungs are homologous amongst arachnids and spider booklungs resemble those of amblypygids and uropygids in their internal anatomy and ultrastructure (Scholtz & Kamenz, 2006). The respiratory system in spiders has been the subject of many studies (Lamy, 1902; Purcell, 1910; de Machado, 1951; Levi, 1967; Brignoli, 1979; Forster, 1970, 1980; Ramírez, 2000; Schmitz & Perry, 2000, 2001; Griswold *et al.*, 2005). The posterior tracheal trunks in all Araneomorphae are derived from the posterior booklungs (lateral tracheae) and from the two entapophyses of the same segment associated with the ventral longitudinal muscles (median tracheae); these changes have been attributed to selective pressures in metabolic rates and water loss through respiration (Purcell, 1910; Forster, 1970, 1980; Ramírez, 2000). Forster (1980) studied the transformation series for the posterior book tracheae in araneomorph spiders based on a direct comparison of several taxa, and postulated 11 posterior tracheal variations and several paths to derive them from the four booklungs and entapophyses of *Hypochilus* (Forster, 1980: fig. 11). The study of Ramírez (2000) concluded that enlarged entapophyses are homologous across

Araneomorphae, absent in most Haplodynae, and that well-developed tracheae from the entapophyses were apomorphic for Entelegynae although median tracheae have also independently evolved within Haplodynae. These results were obtained by combining in a phylogenetic analysis new characters from the respiratory system, the observations by Purcell (1910) and Forster (1980), and other morphological features (Ramírez, 2000).

The anatomy of the median tracheae in all Entelegynae spiders also varies significantly (Forster, 1970; Griswold *et al.*, 2005). The tracheal spiracle of most orbicularians consists of a single opening, but in the Cyatholipidae there are two spiracles (see Griswold, 2001: fig. 8A and references therein). Median tracheae can extend into the prosoma, even inside its appendages, or remain confined to the abdomen, and may form two single trunks or be ramified abundantly, with rounded tips or leaf-shaped ends, amongst other features (Lamy, 1902; Forster, 1980; Opell, 1987; Hormiga, 1994a; Brescovit & Lopardo, 2008). Within our taxonomic sample representing Orbiculariae ramified median tracheae evolved independently at least three times: in *Uloborus*, in *Glenognatha*, and in the clade that includes *Nanometa* and the undescribed Nanometinae from Australia (161-1). A potential synapomorphy for *Pachygnatha* plus *Glenognatha* could be the branching of their median tracheae, and although *Pachygnatha autumn-*



**Figure 18.** *Chrysometa alajuela* abdomen: A, tracheal system dorsal view. B, tracheal spiracle posterior view. C, tracheal spiracle glands. D, lateral trachea tip. E, posterior lateral spinnerets. F, posterior median spinnerets. G, epiandrous fusules. All images from SEMFAP046.

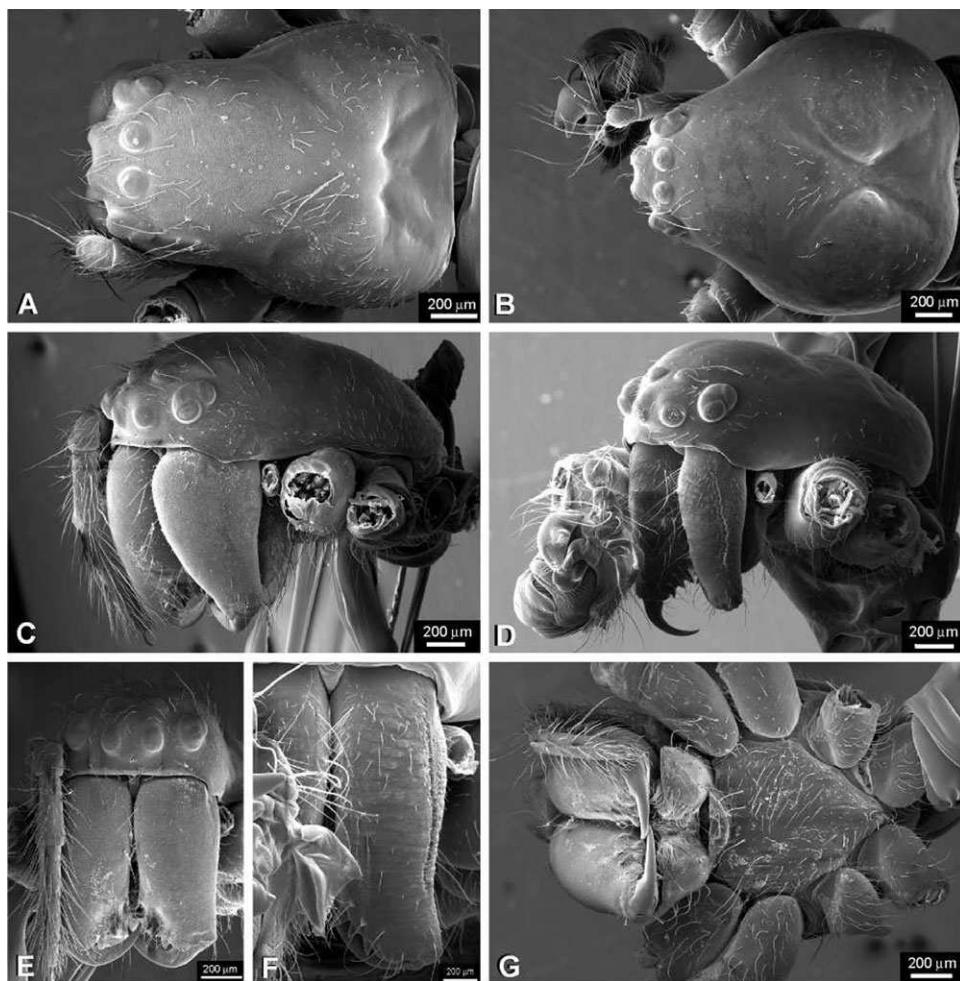
*nalis* has entire tracheae, other *Pachygnatha* species have bifurcated tracheae. Furthermore, other tetragnathid genera such as *Dyschiriognatha* have ramified tracheae (Bosmans & Bosselaers, 1994: figs 50, 51, 147). Twenty steps are necessary to account for the different origins of median tracheae and tip shapes (either round or a leaf-shaped lamella; 162-2) (Figs 41D, 124C-F). Finally, the internal surface of the tracheal spiracle presents pits presumably associated with glands (Fig. 125C, D). The presence of these pores is optimized as plesiomorphic for Araneoidea with six independent losses in *Nanometa* within Tetragnathidae, *Parasteatoda*, *Nephilengys*, *Cyclosa*, *Mecynogea*, and a clade that includes *Linyphia*, *Epeirotypus*, and *Nesticus* (164-1).

#### Trichobothria

Trichobothria are long seta-shaped mechanoreceptors with a very flexible attachment point to a cuticular

fold or depression (Foelix, 1996). In many spiders this fold can form two overlapping plates or be a projected cylinder (Fig. 42F; Griswold *et al.*, 2005: figs 154–156). Within spiders most of the studied trichobothria have been those of the wandering spider *Cupiennius salei* (Keyserling, 1877) (Ctenidae). These studies have addressed aspects such as neurone excitability at different wind speeds, sound frequencies (between 40 to 600 Hz), and their integration as a sensory organ (Hergenröder & Barth, 1983; Barth & Höller, 1999; Bathellier *et al.*, 2005).

Most orbicularian spiders lack femoral trichobothria although they can be found in some uloborids (Opell, 1979), some linyphiids (Hormiga, 2000), and in some groups of tetragnathids (169-1). In Tetragnathidae the cuticular folds of the trichobothrial bases are fused into a cylinder that surrounds the shaft (Figs 93E, 110E). These trichobothria are usually present on the dorsal surface of all femora,



**Figure 19.** *Chrysometa alajuela* cephalothorax: A, female dorsal view. B, male dorsal view. C, female tangential view. D, male tangential view. E, female chelicerae. F, male chelicerae. G, female cephalothorax ventral view and sternum. All images from SEMFAP046.

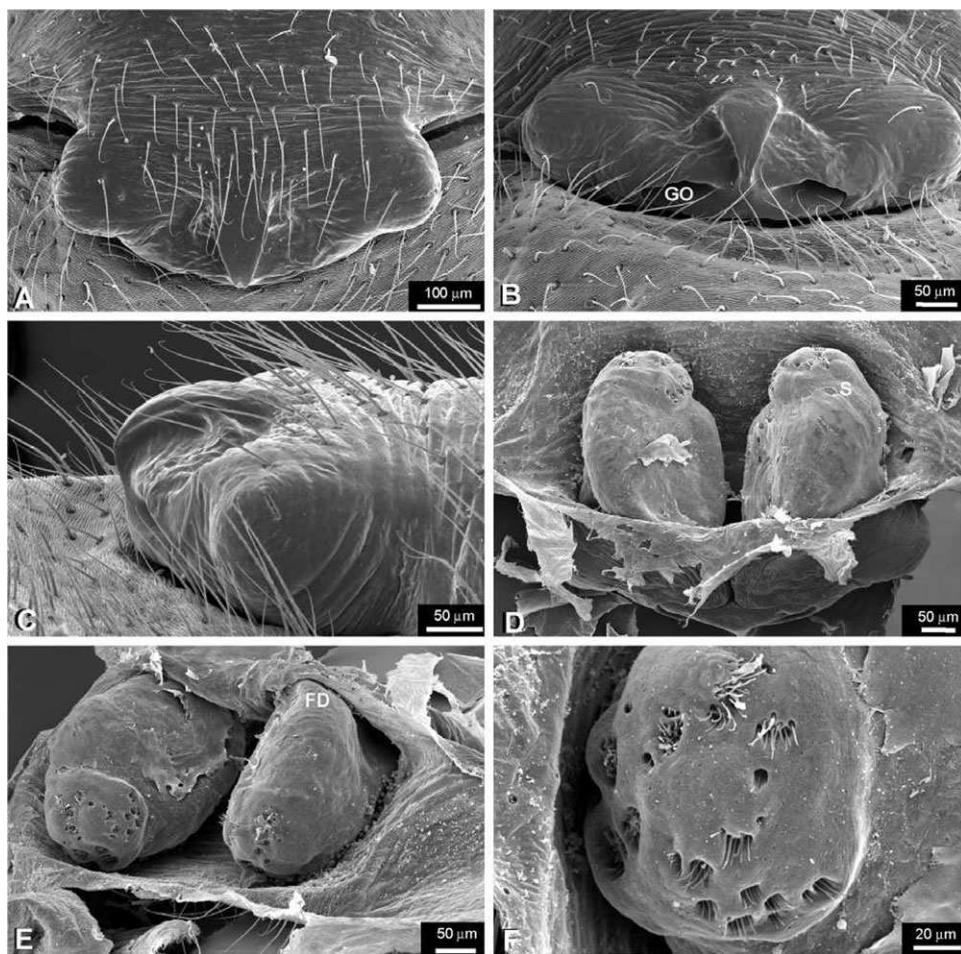
but the ones on the fourth leg are abundant and more conspicuous. Femur IV trichobothria length varies from 0.2 to 0.4 mm in tetragnathid spiders; the longest trichobothria that we have observed are those of *Opadometa* (Fig. 97E, F), the shortest were found in *Tetragnatha* (Fig. 110E). Femoral trichobothria have independently evolved twice within Tetragnathidae: in Tetragnathinae and in one or two clades of Leucauginae (depending on the hypothesis of character optimization; 169-1). The absence of trichobothria in *Metleucauge* and *Metabus* makes the optimization of this character ambiguous (Figs 62C, 78E).

Tetragnathine trichobothria are located on the dorsal surface of femur IV (170-0), are organized in one irregular line (171-0), and their flagella are smooth (173-0), except in *Cyrtognatha*, which has branched flagella and the trichobothria line displaced laterally (Figs 24C, 106F, 110E). Leucaugine tricho-

bothria are branched (173-1), are organized in two lines (171-1) displaced towards the prolateral surface (170-1) and covering up to one third of the femur IV length (172-1) (Figs 47F, 52G, 93C). These trichobothria are characteristic of most leucaugines, except *Tylorida* and *Orsinome*. In the latter two genera the trichobothria resemble more those of *Tetragnatha*, both in distribution and in morphology (Figs 101G, 115F).

#### Chelicerae

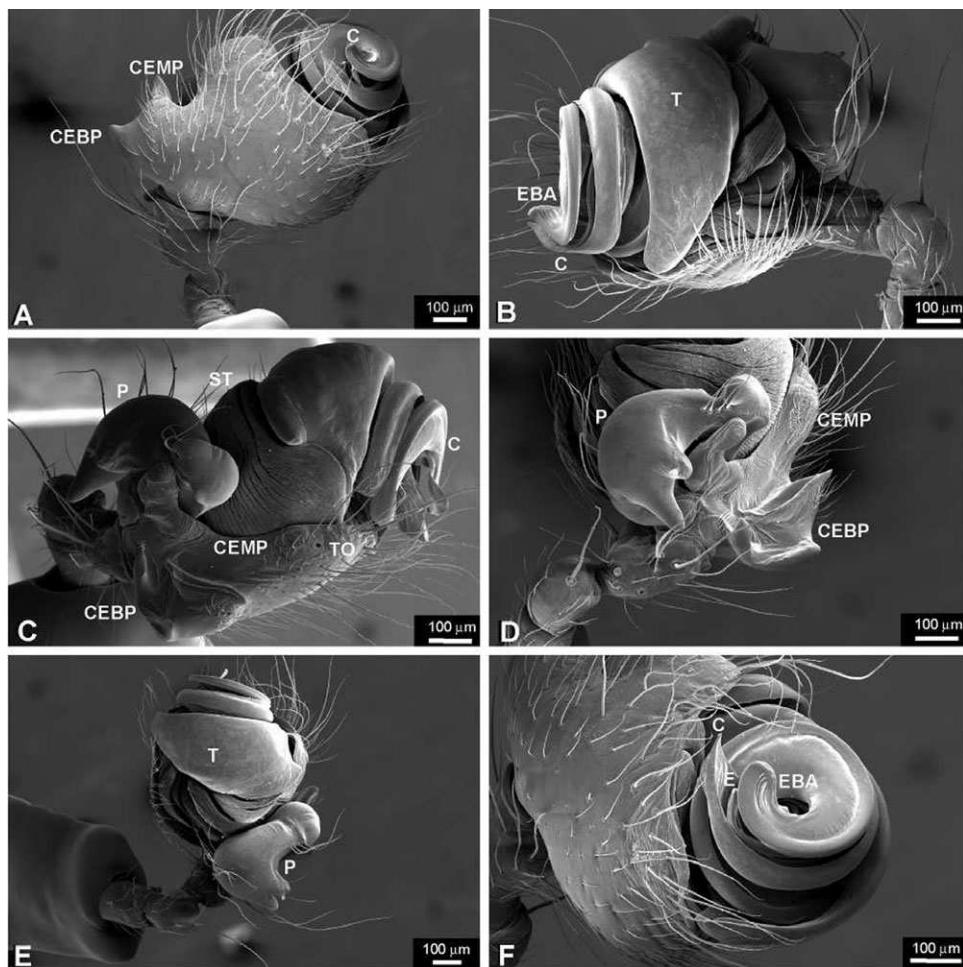
The venom gland and the muscles responsible for the fang and cheliceral movements fill most of the internal cavity of the paturon. The cheliceral musculature is relatively uniform amongst spiders (Palmgren, 1978b) and amongst tetragnathids it has been studied in some *Meta*, *Tetragnatha*, and *Pachygnatha* species (Palmgren, 1978b: figs 24, 25). The chelicerae of many tetragnathids can be remarkably long (82-2), for



**Figure 20.** *Chrysometa alajuela* epigynum: A, ventral view. B, posterior view. C, lateral view. D, dorsal view. E, fertilization ducts origin. F, accessory glands. All images from SEMFAP046.

example, in some tetragnathines and in *Dolichognatha* species they can be longer than the cephalothorax (Figs 32F, G, 110A, B; Simon, 1894; Smith, 2008: figs 38, 54, 46; Brescovit & de Cunha, 2001: figs 2, 22, 27). In Tetragnathinae male chelicerae are usually the longest (118-1), are distally divergent (111-1), and bear apical apophyses (118-2, 115-2). Within Leucauginae the only taxon found with divergent chelicerae is *Orsinome* cf. *vethi* (111-1) (Figs 101F, H). In some *Tetragnatha* species the male and female interlock their chelicerae during copulation (213-1) (Fig. 1B, e.g. Levi, 1981: pl. 4; Eberhard & Huber, 1998a; Danielson-François & Bukowski, 2005). This behaviour is probably linked to the development of cheliceral apophyses, although some *Leucauge* species also interlock the chelicerae during mating but lack apophyses (Eberhard & Huber, 1998a). Male leucaugines have modified macrosetae on the chelicerae and this shared derived trait provides support for a clade that includes *Mesida*, *Opadometa*, and *Leucauge argyra* (112-1) (Figs 47C, D, 95D).

Sexual dimorphism in the cheliceral length in Tetragnathidae (118-1) is represented by the male chelicera being longer than those of the female. This dimorphism has evolved at least five times within tetragnathids: as synapomorphic for Tetragnathinae, at least twice within Leucauginae, once inside Nanometinae, and in a clade that includes *Dolichognatha*, *Diphya*, and *Chrysometa*. Male chelicera smaller than those in the female are common within Araneidae, *Uloborus*, and *Epeyrotypus*. The male chelicerae cuticle can be either similar to that of the clypeus or rugose. This latter cuticular texture has evolved at least five times within Tetragnathidae: in *Metleucauge*, *Chrysometa*, *Cyrtognatha*, *Allende*, and Nanometinae (113-1). The optimization of the origin of cheliceral cuticle sexual dimorphism is ambiguous: either as synapomorphic for a clade that includes all tetragnathids except *Azilia*, or as independently evolving five times within the family (117-1). Male and female tetragnathids have a cheliceral boss with few exceptions in *Glenognatha*,



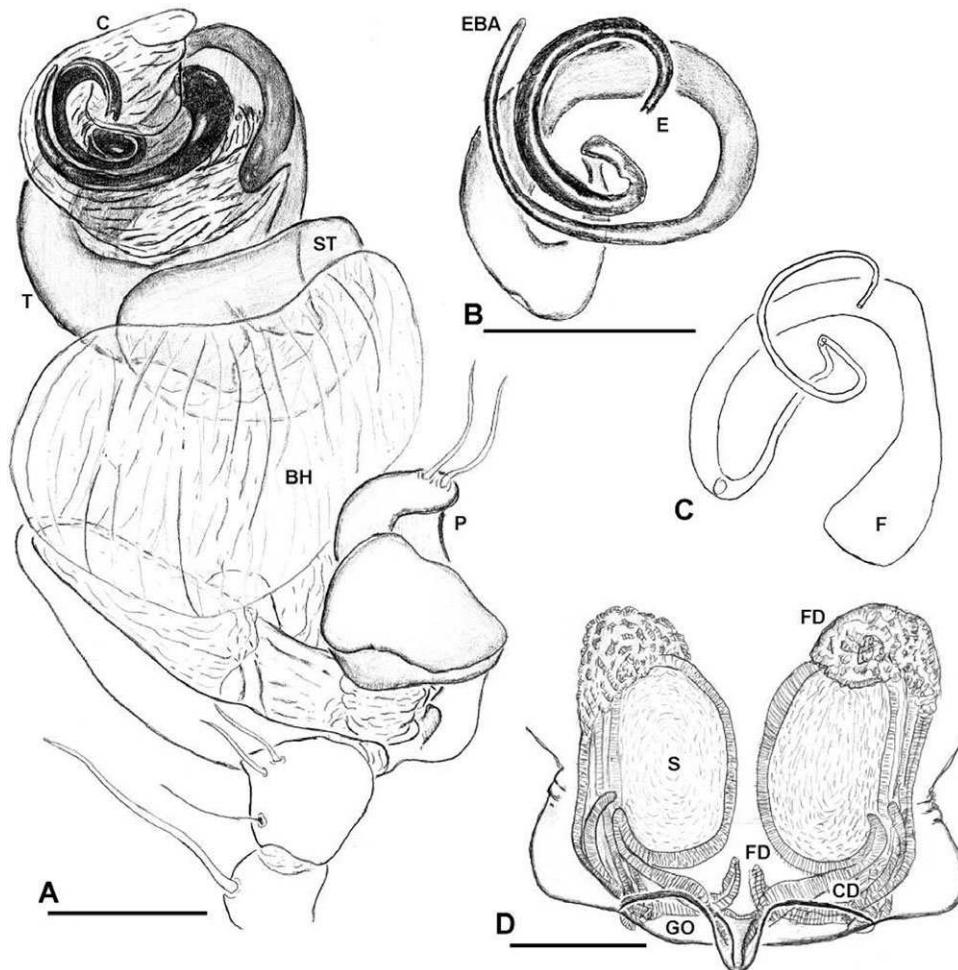
**Figure 21.** *Chrysometa alajuela* male pedipalp: A, dorsal view. B, mesal view. C, ectal view. D, cymbial ectobasal process. E, ventral view. F, apical view. All images from SEMFAP046.

*Tylorida*, and *Leucauge* (80-1, 110-0). Finally, the presence of denticles between the cheliceral margins, very common and synapomorphic for Nephilidae and Araneidae has evolved independently within Tetragnathidae as synapomorphic for Nanometinae (84-1).

#### Evolution of female genitalia

Spiders retain the sperm mass in an invagination of the uterus externus, or in a derived structure such as spermathecae, until the eggs are ready for fertilization. Female spiders nurture the sperm mass with secretory glands that open through pores, until the sperm is expulsed by hydraulic pressure probably also produced by these glands (Forster, 1980; Austad, 1984; Eberhard, Guzman-Gomez & Catley, 1993; Uhl, 2002). The development of the female reproductive system during ontogeny has been the subject of a few studies; however, so far most of the evidence supports

the idea that spermathecae develop from the uterus externus anterior wall (Sierwald, 1989 and references therein). Forster (1980) hypothesized three different levels of organization of female genital systems in spiders. Secretory genitalia are those in which the pores of the secreting glands open directly to the anterior wall of the uterus externus, found in liphistiids and some dysderoids. Haplogyne genitalia are those in which the pores open into a spermatheca that connects to the uterus externus through a copulatory duct (Fig. 38B, C). Entelegynae genitalia are those in which the copulatory duct has been displaced far from the uterus externus and a new duct is created to fertilize the eggs (Fig. 58D–F). Simon (1894) was the first to mention some of the differences between the haplogyne and entelegyne spider genital systems. Haplogyne spiders were those associated with a spiracle-shaped female copulatory opening and ‘simple’ male pedipalps in contrast with entelegyne

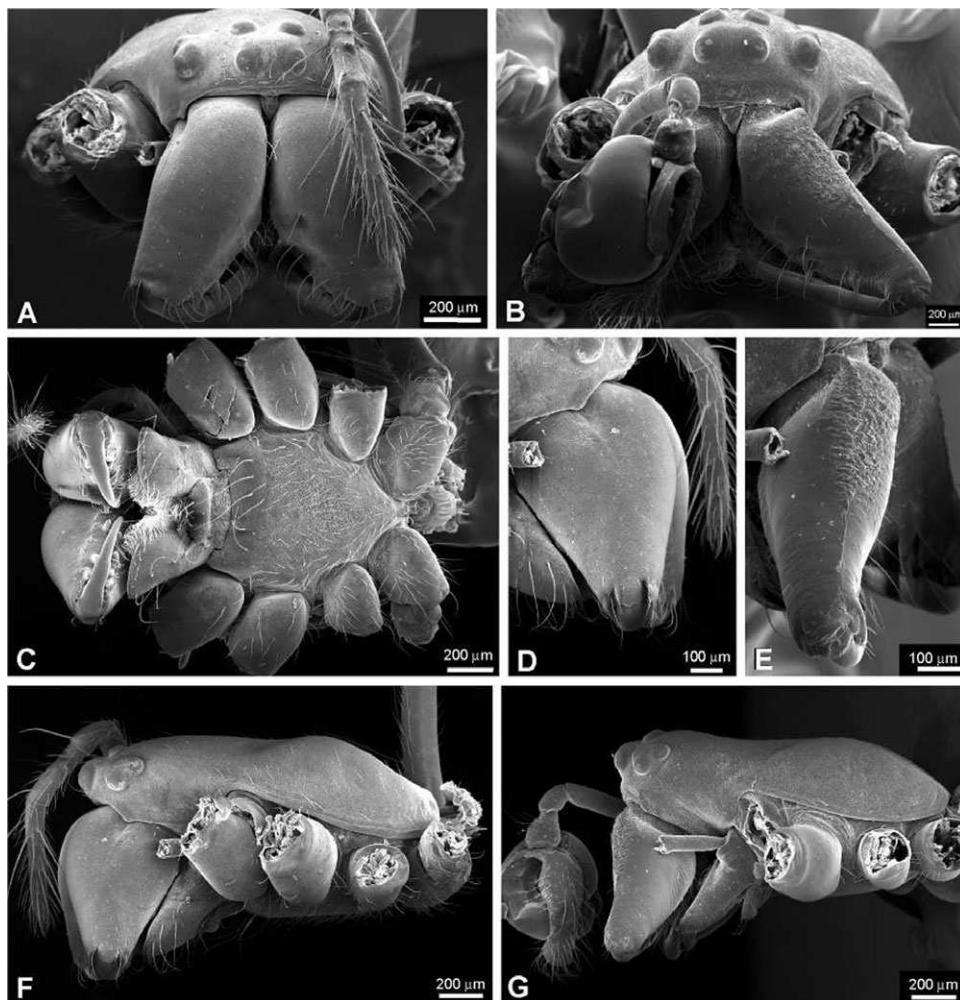


**Figure 22.** *Chrysometa alajuela* genital anatomy illustrations: A, male pedipalp expanded. B, embolus. C, sperm duct. D, cleared epigynum ventral view.

spiders, which have copulatory openings associated with a sclerotized plate (epigynum) and complicated male pedipalps armed with apophyses.

The female reproductive system in Tetragnathidae presents a diverse array of modifications across lineages. Members of the subfamily Tetragnathinae have evolved haplogyne genitalia (i.e. they have spermathecae that open into only one set of ducts, which function both as copulatory and fertilization ducts) from entelegyne ancestors (148-1). The female reproductive system in tetragnathines consists of one or many central membranous sacs and one spermatheca on each side (Figs 24D, 38C, D, 111C). The spermathecae can be functional as in the case of some *Tetragnatha* species or vestigial as in the case of *Cyrtognatha* (Fig. 24F, G). The spermathecae found in most tetragnathines are homologous to those found in all other araneoid spiders; however these spiders independently developed a median membranous sac to store sperm (Dimitrov, Álvarez-Padilla & Hormiga,

2007). The spermathecae of all Leucauginae and of *Azilia* are weakly sclerotized and resemble two membranous sacs (137-1). Spermathecae in Nanometinae are reduced to a sclerotized sphere near the fertilization duct and the copulatory ducts are modified as sacs (145-1) (Fig. 91C, D). Metainae, *Allende*, and *Mollemeta* have a more conventional araneoid entelegyne system with well-sclerotized spermathecae and both copulatory and fertilization ducts (Figs 70D, 136A-F). The cuticle of the copulatory ducts in most tetragnathids is rigid and well sclerotized, in contrast to the flexible and weakly sclerotized cuticle of Nanometinae and most leucaugines. Exceptions (reversals) can be found in the well-sclerotized copulatory ducts of *L. argyra* and *Orsinome cf. vethi*. Membranous copulatory ducts are also found in *Azilia*, *Epeirotypus*, *Uloborus*, and *Deliochus* (147-1). The length and trajectory of the fertilization duct are also variable: most tetragnathids have short and slightly curved fertilization ducts, but leucaugines



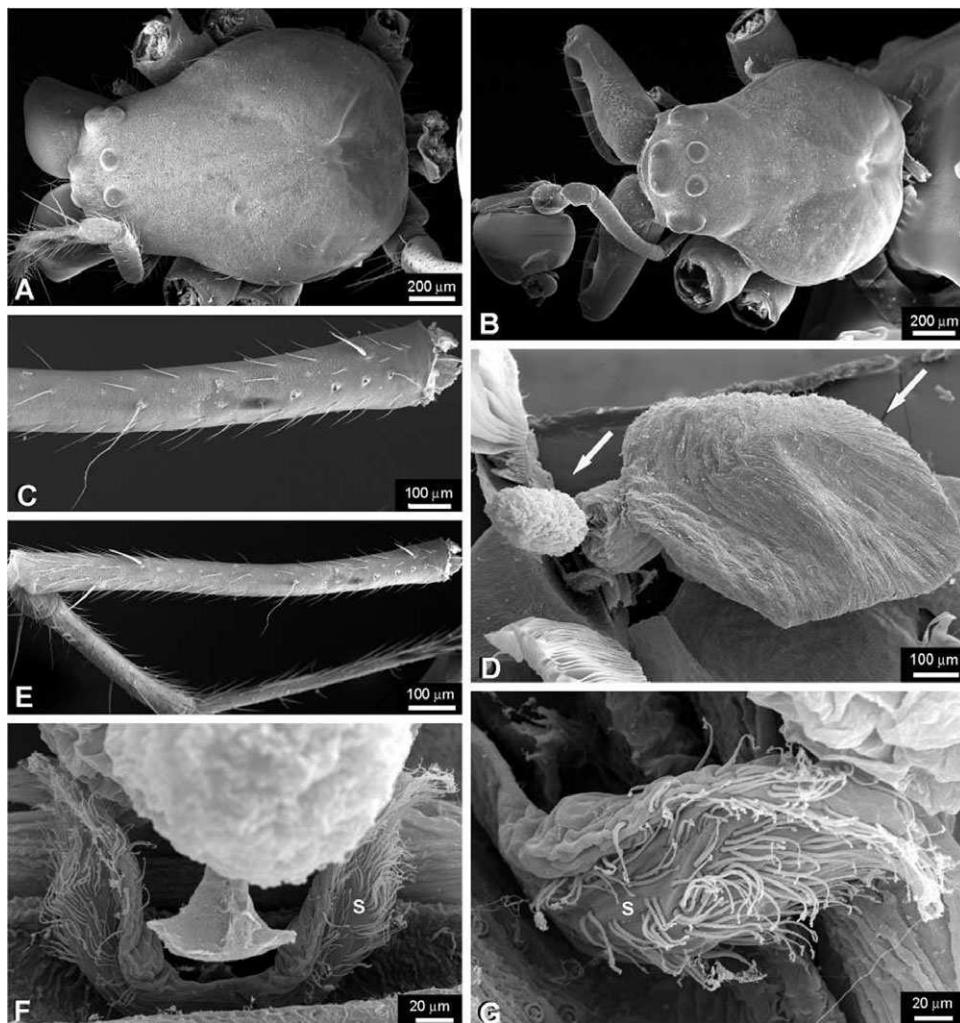
**Figure 23.** *Cyrtognatha espaniola* cephalothorax: A, female anterior view. B, male anterior view. C, female cephalothorax ventral view and sternum. D, female chelicerae. E, male chelicerae. F, female lateral view. G, male lateral view. All images from SEMFAP031.

have long and coiled fertilization ducts, with homoplastic occurrences in *Azilia*, *Allende*, and *Metella* (151-1).

#### Evolution of tetragnathid male genitalia

The male pedipalp of tetragnathids has only one tegular apophysis which is hypothesized to be homologous with the araneoid conductor (Levi, 1980, 1981; Coddington, 1990a; Hormiga *et al.*, 1995; Griswold *et al.*, 1998). The only tetragnathids that lack a conductor are the species of the genus *Azilia*. The conductor attachment to the tegulum can be either sclerotized or membranous (59-1). The conductors of *Nanometra* sp., the undescribed nanometinae sp., *Orsinome sarasini*, and *Mollemetra edwardsi* (a Chilean endemic) have a membranous appearance although their conductor edges are sclerotized and fused to the tegulum. The conductor of these Austra-

lian taxa expands when submerged in and transferred between KOH and distilled water (Figs 76A–C, 91A, B). Sclerotized conductor-tegulum attachments are found in several tetragnathids such as *Allende nigrohumeralis*, *Opadometa* sp., *Metellina segmentata*, and *Dolichognatha pentagona* (Figs 12B, 35A, 70B), as well as in some other araneoids. Membranous attachments are common amongst nephilids (Hormiga *et al.*, 1995: figs 9, 10) and leucaugines (Figs 45A, 55A, B). The shape of the embolus varies across tetragnathid lineages: it can be tubular (e.g. Nanometinae and most tetragnathines, except *Cyrtognatha*; Figs 39D, 108A, 113A), filiform (e.g. leucaugines, except *Metleucauge*; Figs 44D, 55A, 81A, B), a lamelliform sclerite that can bear an apophysis [e.g. most Metainae, *Allende*, and most *Cyrtognatha* species (67-2); Figs 12B, 60B, 70B]. The embolus connection to the tegulum is membranous in all tetrag-

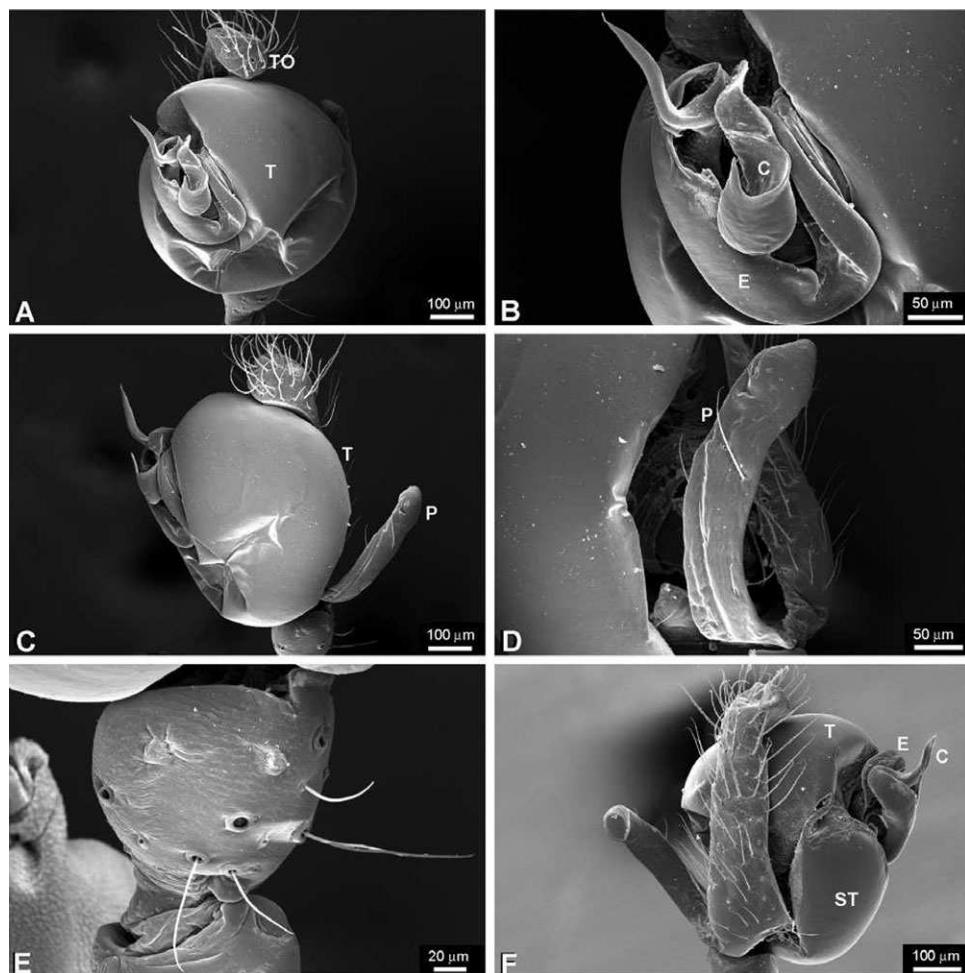


**Figure 24.** *Cyrtognatha espaniola* cephalothorax and female genitalia: A, female cephalothorax dorsal view. B, male cephalothorax dorsal view. C, and E, female femur IV trichobothria. D, female genitalia dorsal view; arrows indicate the specialized membranous sacs to store sperm. F, female genitalia anterior view. G, reduced spermathecae with accessory glands. All images from SEMFAP031.

nathids; however, this character is optimized as ambiguous at the family node because of the presence of a membranous connection in *Linyphia* (63-1) (such membrane, connecting the tegular and embolic division of linyphiids, is known as the ‘column’, Merrett, 1963; Millidge, 1977; Hormiga, 1994a, 2000; Hormiga *et al.*, 1995).

The cymbium of tetragnathids often bears one or more processes. The presence of an ectobasal process (26-1) and an ectomedian process (28-1) are optimized as synapomorphic for a clade that includes all tetragnathids except *A. affinis*, although other *Azilia* species (not coded in our character matrix) also have cymbial processes (Figs 11A, 21D, 99D). Usually both processes are present, but *Dolichognatha*, *Diphya*, and *Metellina* only have the ectobasal process

(Figs 29D, 34A, 69C). Ectal cymbial processes are absent in all tetragnathines and leucaugines although most of the species studied in the latter clade have a dorsobasal process in the cymbium (except *Leucauge venusta* (Walckenaer, 1841), 31-1). This latter process is usually small and spine-shaped (Figs 49C, 64C, D, 117F), in contrast to the massive ectobasal process found in most Metainae. Another cymbial modification unique to tetragnathines is a median constriction of the cymbium, synapomorphic for the subfamily (25-1) (Figs 25F, 39F, 108C, 112B). The sperm reservoir inside the pedipalp also varies in shape amongst tetragnathids. In most leucaugines and *Azilia* the sperm reservoir is extremely coiled resembling a tangled piece of rope (78-1) (Figs 17A, 104B, 118A, B), in *Meta* and *Dolichognatha* these



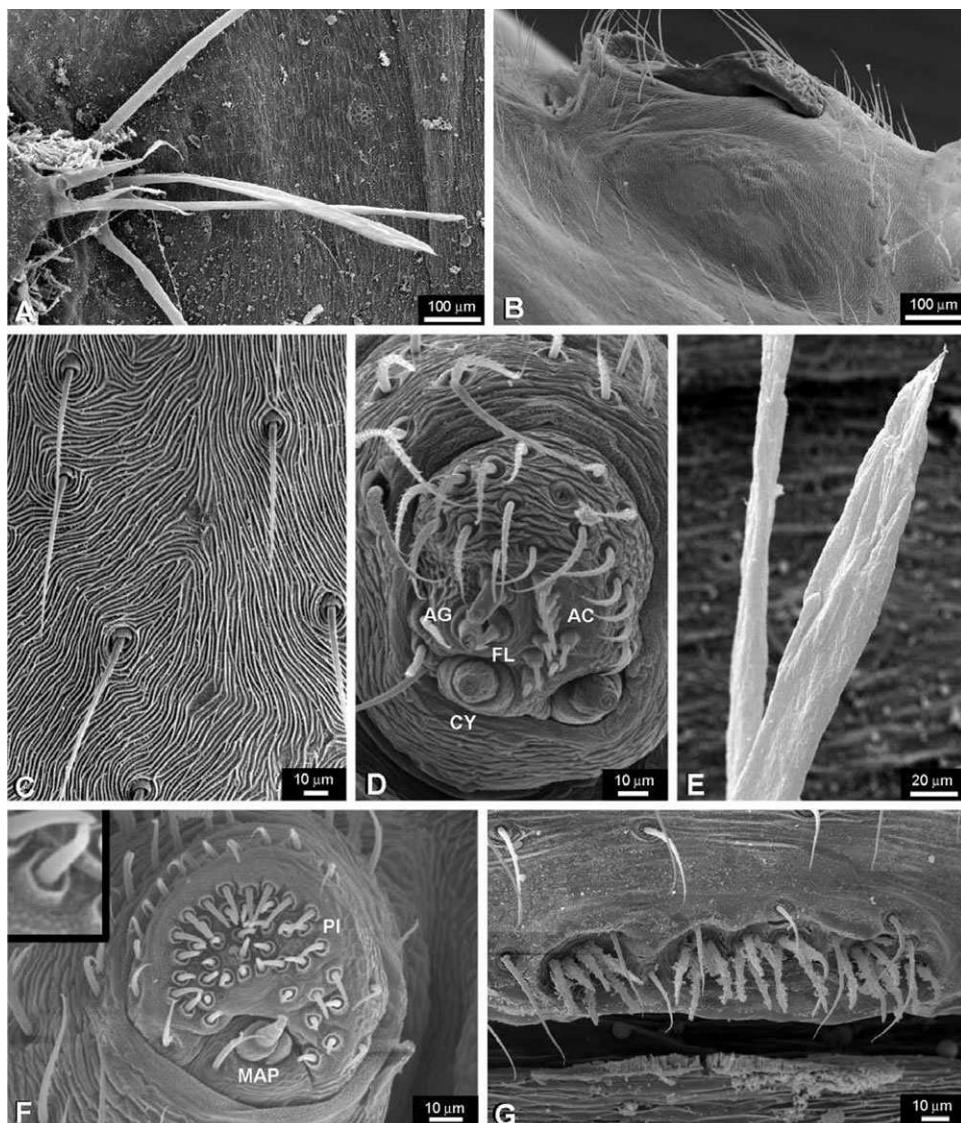
**Figure 25.** *Cyrtognatha espaniola* male pedipalp: A, apical view. B, embolus and conductor. C, ventral view. D, paracymbium. E, palpal tibia. F, dorsal view. All images from SEMFAP031.

coils are simpler and have a single switch-back (77-1) (Figs 35C, 60D). The sperm reservoir of other tetragnathids is spiral, being medially enlarged in all Tetragnathines (76-1) (Figs 40A, 113C). Finally, contralateral pedipalp insertion (right male pedipalp inseminates the left spermatheca) has been observed in species of *Leucauge*, *Tetragnatha*, and *Pachygnatha*; contrary to the apparently more widespread ipsilateral pedipalp insertion (right pedipalp inseminates right spermatheca) but more studies are required to document this behaviour in other tetragnathids (Huber & Senglet, 1997). Future studies on the subject may resolve whether contralateral palp insertion is apomorphic for Tetragnathidae.

#### TETRAGNATHID MORPHOLOGICAL ATLAS

Our taxon sample attempts to represent the diversity of tetragnathids, but ultimately the taxon selection was influenced partly by the availability of study

specimens in museum collections. The species chosen to represent each genus and to provide a diagnosis and a description varied as a function of the information available; we have given preference to those species more intensively studied. Specimens of the type species of each genus, or a similar species, were selected to study the characters presented in this atlas. These data were compared to either specimens of congeneric species or to previous studies, such as taxonomic revisions or species descriptions. For many genera the information on their biology and anatomy is very fragmentary, e.g. the web architecture may have been documented for a different species to the one whose anatomy has been studied in detail. The species studied in each genus are indicated within the corresponding section. Each genus section is organized with the following subsections: type species and museum depository of the type material, number of described species (as reported in Platnick, 2009), geo-



**Figure 26.** *Diphya spinifera* abdomen: A, tracheal system dorsal view. B, booklung external cuticle. C, cuticle of the abdomen, close up of median lateral section. D, posterior lateral spinnerets. E, lateral tracheae tips. F, anterior lateral spinnerets. G, epiandrous fusules. Images (A) and (E) from SEMFAP051, the rest from SEMFAP053.

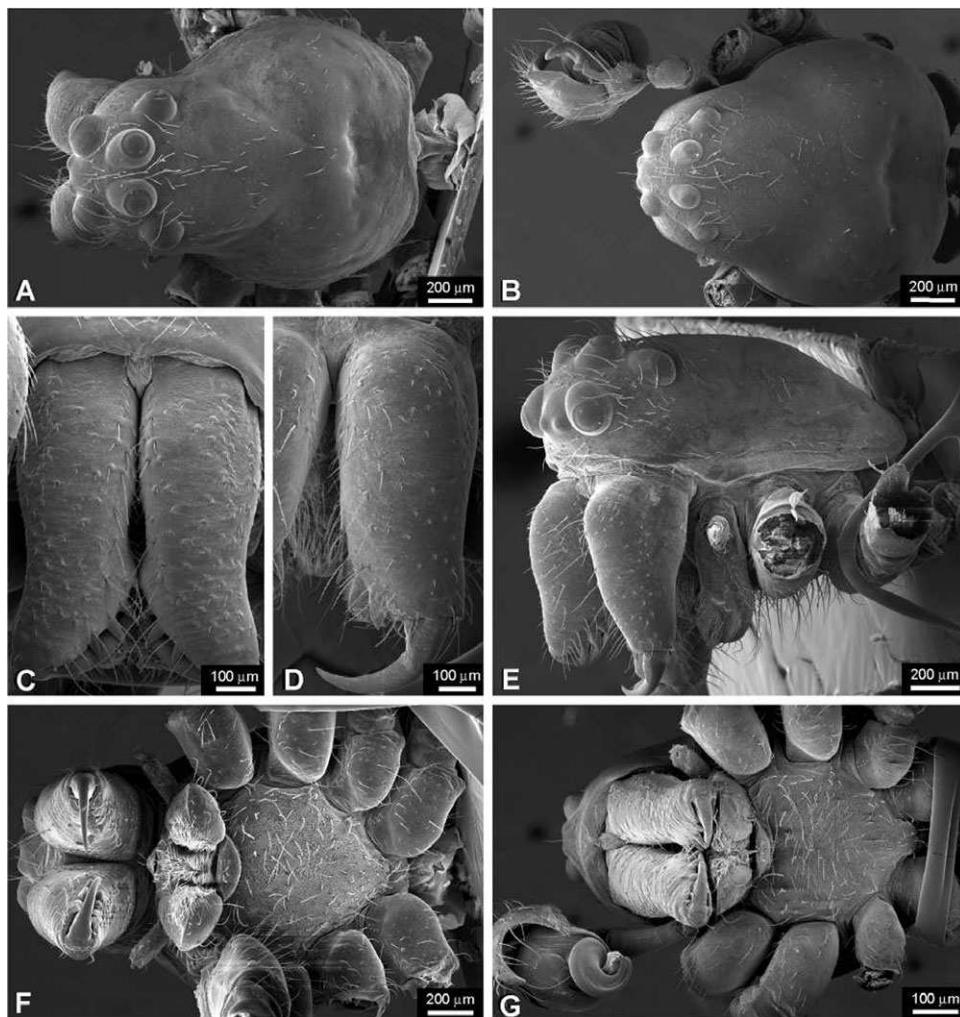
graphical distribution, description of the web and habitat (when available), generic diagnosis, description of the somatic and genital anatomy for females and males, comments on the taxonomic status, phylogenetic relationships, and a summary of studies regarding its biology. This atlas includes information about 20 tetragnathid genera, representing 42% of the genera described in the family. Interactive identification keys for all the tetragnathid genera are available online at <http://www.gwu.edu/~spiders/interactiveKeys.htm> (accessed February 2011). An identification key is not provided in this paper because, as mentioned earlier, our study only

addresses and illustrates a fraction of the genera in Tetragnathidae.

#### TETRAGNATHIDAE MENGE, 1866

*Type genus: Tetragnatha* Latreille, 1804.

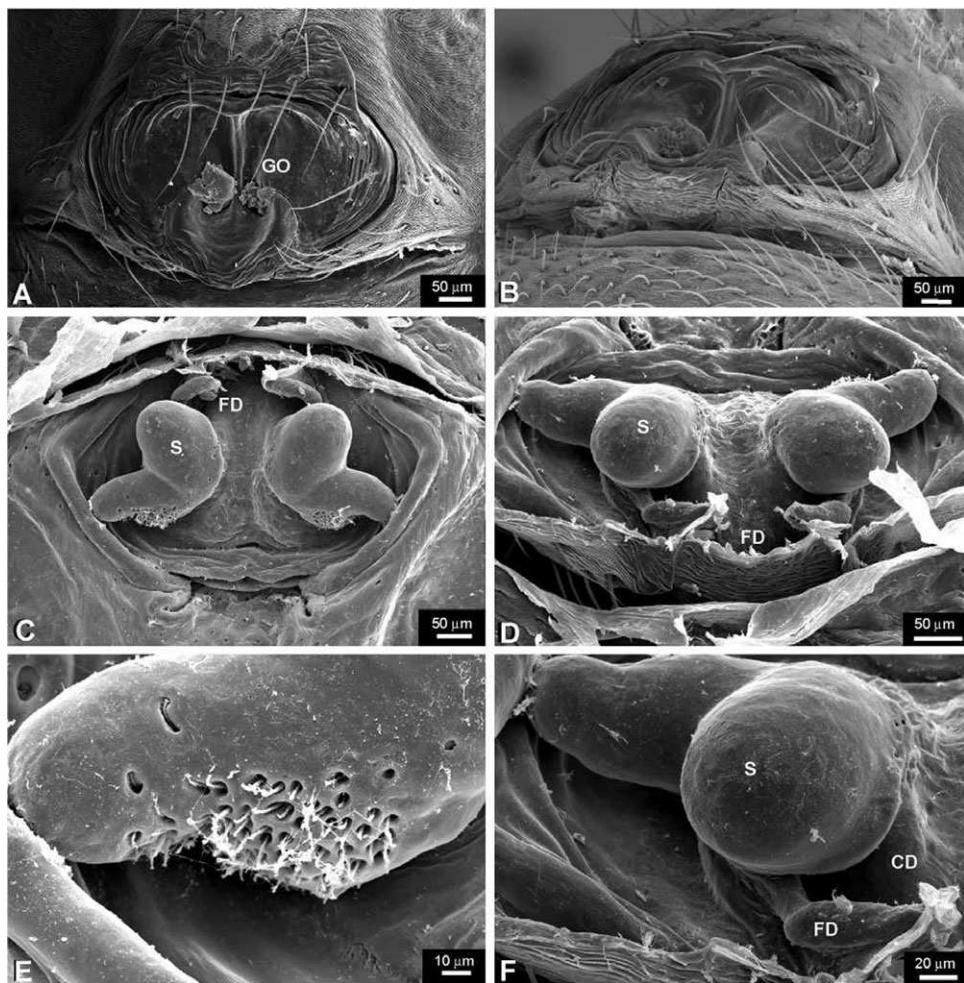
*Diagnosis:* Tetragnathid females can be differentiated from other araneoids by the following combination of features: cheliceral boss present with its cuticle either smooth or similar to the rest of the anterior surface of chelicerae (Figs 9C, 23D, E, 57D, 101D); clypeus more than one AME diameter high; labium trapezoidal and



**Figure 27.** *Diphya spinifera* cephalothorax: A, female dorsal view. B, male dorsal view. C, male chelicerae. D, female chelicerae. E, female tangential view. F, female cephalothorax ventral view and sternum. G, male ventral view. All images from SEMFAP053.

rebordered (Figs 19G, 23C, 47G); a flat epigynum, when present (124-0 Figs 79A, 81D, 89A); ALS piriform spigot bases separated from the spigot shaft by a torus (Fig. 66B arrow in insert box points to the torus area wrapping the piriform spigot shaft), absent in *Meta* and *Mollemeta* (Figs 56B, 82E); absence of aciniform spigots on the PMS, present in *Azilia* and *Meta* (4-0: Figs 13G, 56C, 71A, 109D); and cylindrical spigots on the PLS peripheral in position (Figs 26D, 77E). Males of Tetragnathidae are distinguished from other araneoids by their large cymbial tarsal organ, larger than the surrounding macrosetal bases; absence of tegular apophyses, except for the conductor (*contra* Archer, 1951: 4–5); conductor and embolus coiled together; apical position of the embolic division; and by having the embolus connected to the tegulum by a membrane. Tetragnathids differ from nephilids

by the absence of cheliceral denticles (Fig. 93D), except in Nanometinae (Figs 73C, 88D) and by their cylindrical paracymbium (Fig. 112D). The paracymbium of nephilids is more rectangular (Fig. 138D). The webs of nephilids have secondary and tertiary radii (Figs 6B, 7A), whereas the radii of most tetragnathid webs are undivided (Figs 4C, F, 5D), and usually have open hubs, few radii, and few spirals of sticky silk (fewer than 20), although exceptions exist, such as the webs of *Azilia* and *Dolichognatha* species, which are denser and can have secondary radii (Fig. 3C, E). Secondary radii can also be found in some *Glenognatha* species (G. Hormiga, unpubl. data). Tetragnathid phylogenetic relationships are discussed in the previous sections. The monophyly of Tetragnathidae is supported by seven morphological synapomorphies: piriform spigot base edges separated



**Figure 28.** *Diphya spinifera* epigynum: A, ventral view. B, posterior view. C, dorsal view. D, anterior view. E, accessory glands. F, copulatory and fertilization ducts. All images from SEMFAP053.

from the spigot shaft (2-1: Fig. 66B), cymbium tarsal organ diameter larger than the contiguous macrosetae bases (24-1: Fig. 112C), oval to spherical tegulum (47-0: Fig. 112A), carapace moderately hirsute (98-1: Fig. 62A), femora IV mesal surface without basal macrosetae (174-1: Fig. 14H); male palpal patella with one macroseta (180-1: Fig. 29F); and male palpal tibia length approximately two times the widest point of the tibia (181-1: Fig. 69C).

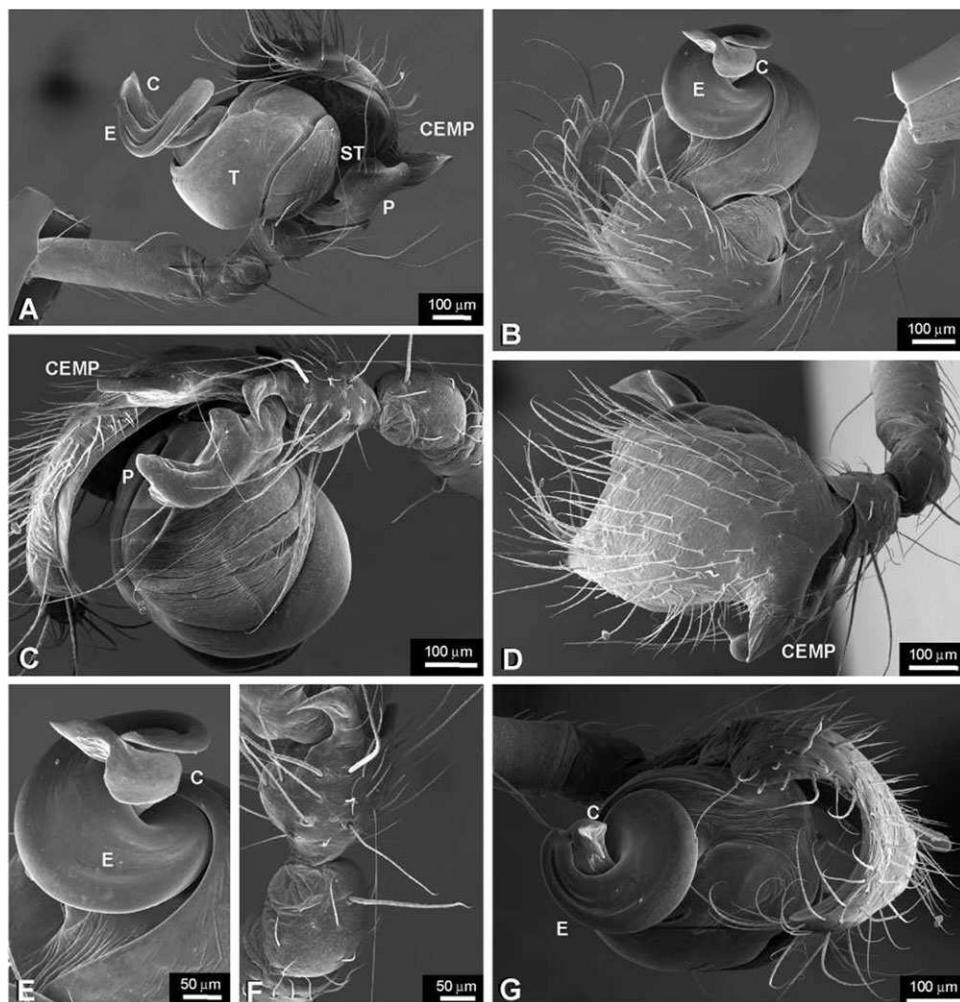
ALLENDE ÁLVAREZ-PADILLA, 2007 (FIGS 3B, 8–12)

**Type species:** *Allende puyehuensis* Álvarez-Padilla, 2007. The holotype of this species is a female specimen from Osorno (Chile) deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (examined).

**Diagnosis:** *Allende* species can be distinguished from all other tetragnathid genera by the following combination of characters: epigynum projected and with

two apical invaginations (Fig. 10C); cymbial base covered with small denticles (Fig. 11D); cymbial ectomedian process with short and thick macrosetae (Fig. 11B).

**Description: Female:** body length from 7.6 to 13.33 mm. Carapace thoracic region slightly elevated and with a shallow semi-circular fovea (Fig. 9A). Ocular area higher than cephalothorax lateral margins (Fig. 9D, G). Sternum triangular, projecting between coxae IV (Fig. 9F). Secondary eyes with canoe-shaped tapetum. Eyes subequal in size, lateral eyes slightly larger. Lateral eyes juxtaposed and on a tubercle. Clypeus height is 1.5 AME diameter. Anterior surface of chelicerae smooth (Fig. 9C). Cheliceral boss present (Fig. 9C, D). Labium trapezoidal and rebordered. Endites rebordered, longer than wide (Fig. 9F). Femora without trichobothria. Booklung covers smooth. Tracheal spiracle located near the ALS. Median tracheae undivided, with leaf-shaped apex,

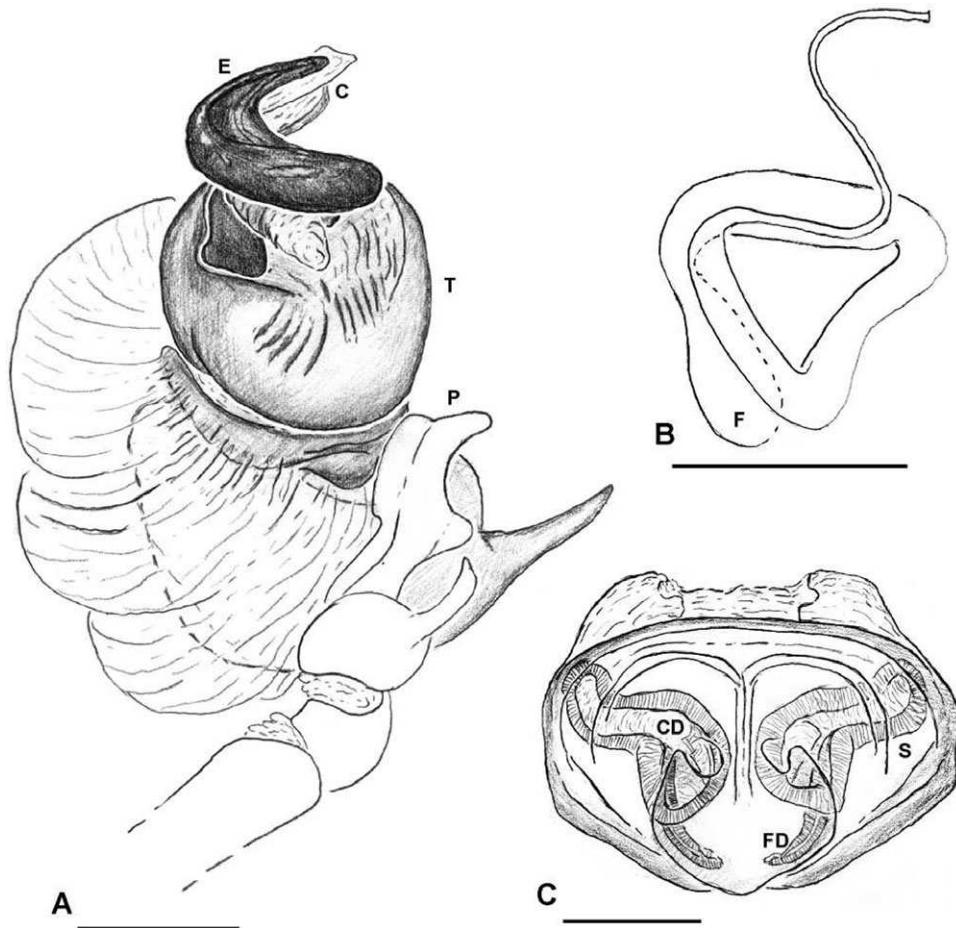


**Figure 29.** *Diphya spinifera* male pedipalp: A, ventral view. B, mesal view. C, ectal view. D, dorsal view. E, conductor and embolus. F, palpal patella and tibia. G, apical view. All images from SEMFAP053.

longer than half the lateral tracheae length, tracheal spiracle with several glands (more than four on each side) (Fig. 8A–E). ALS with c. 60 piriform spigots. PMS with three aciniform spigots between the cylindrical and the minor ampullate spigots; minor ampullate spigot nubbin present. PLS with 13 aciniform spigots arranged roughly in two lines; cylindrical spigots peripheral; aggregate spigots embracing the flagelliform (Álvarez-Padilla, 2007: fig. 9f–h). Epigynum protruding and well sclerotized, copulatory openings groove-shaped and located at the sides of the base of median plate (Fig. 10C). Copulatory ducts short and well sclerotized. Fertilization ducts short, arising behind the copulatory duct insertion area and crossing over the spermathecae (Figs 10D, E, 12D). Spermathecae surface rugose, covered with small pits and accessory gland openings arranged in groups (Fig. 10F).

*Male:* body length from 5.4 to 8.9 mm. Legs relatively longer than those in the females, without modi-

fications. Ocular area as in female (Fig. 9E). Anterior surface of chelicerae rugose (Fig. 9B). Epiandrous fusules arranged in clusters inside a depression on the epiandrous plate (Fig. 8F). PLS triplet reduced to nubbins, cylindrical spigots absent (Álvarez-Padilla, 2007: fig. 9i). Pedipalp patella with a single macroseta (Fig. 11A, B). Palpal tibia 3.5 times longer than wide, and with dorsal trichobothria at its base. Paracymbium cylindrical, longer than wide, with a distal sclerotized outgrowth, covered with macrosetae and attached to the cymbium by means of a membrane. Tegulum wider than long, cup-shaped, and with the subtegulum located at its base (Figs 11E, 12C). Embolus enlarged basally and with a single apophysis, which is attached to the embolus by an S-shaped sclerotized ridge that inserts into its median section, the rest of the attachment is membranous (Fig. 12A). Conductor well sclerotized, arising dorsally from the tegulum, following its margin and gradually wrap-



**Figure 30.** *Diphya spinifera* genital anatomy illustrations: A, male pedipalp expanded. B, sperm duct. C, cleared epigynum ventral view.

ping the embolus, attachment to the tegulum sclerotized (Fig. 12B). Sperm reservoir spiralled (Fig. 12C).

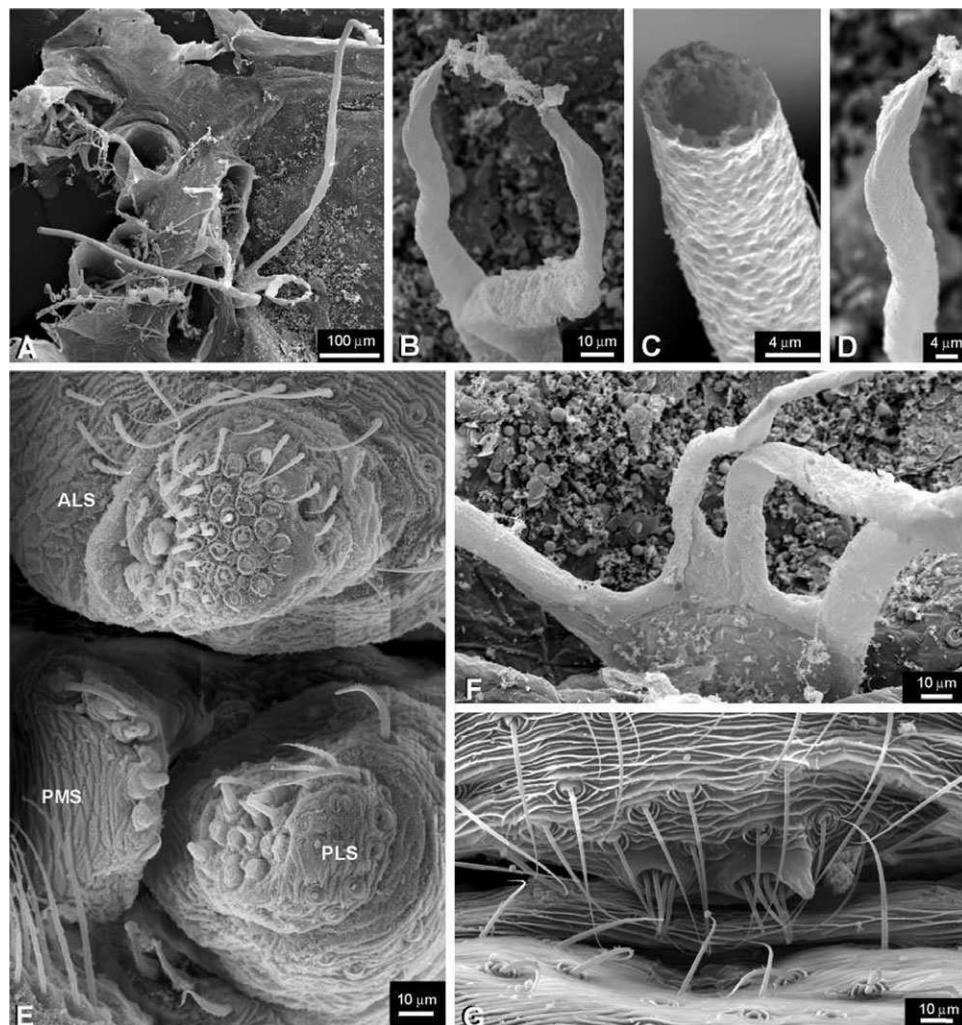
**Natural history:** This genus includes four species endemic to the western slopes of the Chilean Andes. They live in temperate cloud forests amongst low vegetation or near rivers. Only the web of *Allende puyehuensis* has been documented (Fig. 3B): it builds horizontal webs with c. 11 radii, c. ten spirals, an open sector, and open hubs.

**Taxonomy:** The monophyly of this genus is well supported with BS and JK values of 4 and 97, respectively, in the morphology plus behaviour analyses (Fig. 143A, B). Six morphological synapomorphies support the monophyly of *Allende*: PLS aggregate spigots distal parts embracing the flagelliform spigot, cymbial ectobasal process covered with denticles (Fig. 11D), cymbial ectomedian process longer than half the cymbium width, and covered with macrosetae thicker than those of the cymbium (Fig. 11A, D);

conductor with a distal hook with several lobes at the tip (Fig. 11F), and the protruding epigynum plate (Fig. 10A). A previous phylogenetic analysis proposed *Allende* as sister to *Chrysometa* (Álvarez-Padilla, 2007; Fig. 142B). The analysis of the morphological and behavioural data set recovered *Allende* as sister to a large clade of tetragnathids that includes *Chrysometa*, *Nanometinae*, *Diphya spinifera*, and *Tetragnathinae* (Fig. 143A). The total evidence analysis recovered *Allende* as sister to *Tetragnathinae* (Fig. 144). Our genus diagnosis and description takes into account all described species of *Allende* (Álvarez-Padilla, 2007). We coded specimens of *A. nigrohumeralis* (F. O. P. Cambridge, 1889) for the phylogenetic analysis.

#### AZILIA KEYSERLING, 1881 (FIGS 2B, 3C, 13–17)

**Type species:** *Azilia formosa* Keyserling, 1881a. According to Levi (1980) the type specimens of *A. formosa* are from Peru and were deposited at the



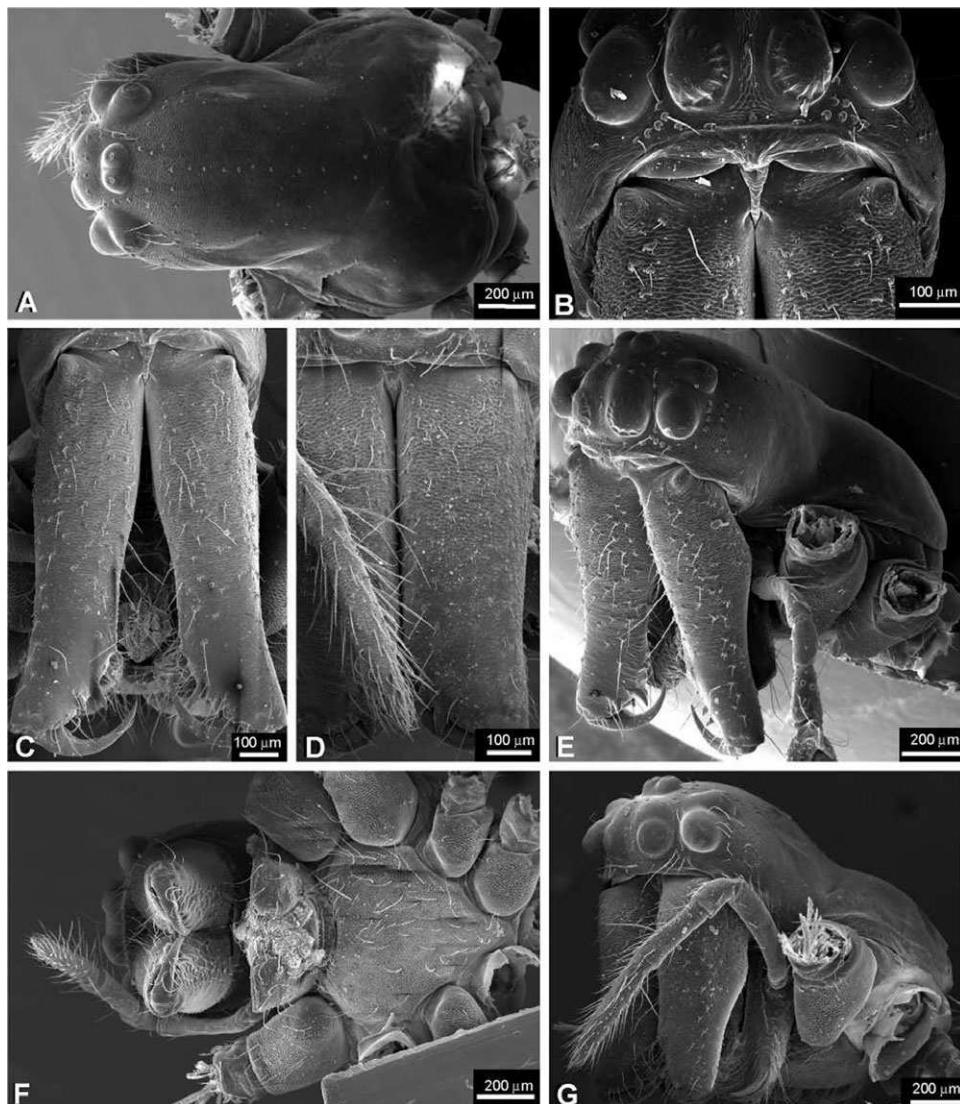
**Figure 31.** *Dolichognatha pentagona* abdomen: A, tracheal system dorsal view. B, median tracheae tips. C, lateral tracheae transversal cut. D, median trachea tip. E, spinnerets. F, tracheal spiracle posterior view. G, epiandrous fusules. All images from SEMFAP045.

Polish Academy of Sciences, but are presumed to be lost. There are no indications in either Keyserling or Levi's studies of the number of syntypes.

**Diagnosis:** *Azilia* species can be distinguished from all other tetragnathid genera by the following combination of characters: all eyes without tapeta, the rhabdome arranged in rows that form loops (Levi, 1980: figs 299, 300); lateral eyes of both sexes separated (i.e. not juxtaposed), more than one PLE diameter apart (Figs 2B, 14A, B); male pedipalp without conductor (Fig. 16A–F); epigynum flat (Fig. 15A, B); spermathecae walls weakly sclerotized (Figs 15C, D, 17B); and absence of femoral trichobothria (Fig. 14G, H).

**Description: Female:** body length from 6.9 to 9.9 mm. Carapace thoracic and cephalic regions at the same height, cephalothorax ocular area slightly lower than

the carapace lateral margins and cephalic fovea formed by two longitudinal pits (Fig. 14A, B). Clypeus height less than one AME diameter. Anterior surface of chelicerae smooth (Fig. 14C). Cheliceral boss present. Sternum longer than wide. Labium trapezoidal and rebordered. Endites rebordered, longer than wide (Fig. 14E). Abdomen oval, sometimes with a hump above the spinnerets (Levi, 1980: fig. 297). Booklung covers smooth. Median tracheae undivided and longer than half the lateral tracheae length (Fig. 13A), leaf-shaped apically (Fig. 13D). Tracheal spiracle near the spinnerets, with more than four accessory glands on each side (Fig. 13B, C). ALS with more than 60 piriform spigots. PMS anterior surface with c. 32 aciniform spigots. PLS cylindrical spigots near spinneret margins, with c. 40 aciniform spigots and aggregate spigots on the distal margin separated from the flagelliform spigot apex (Fig. 13F, G). Epigy-



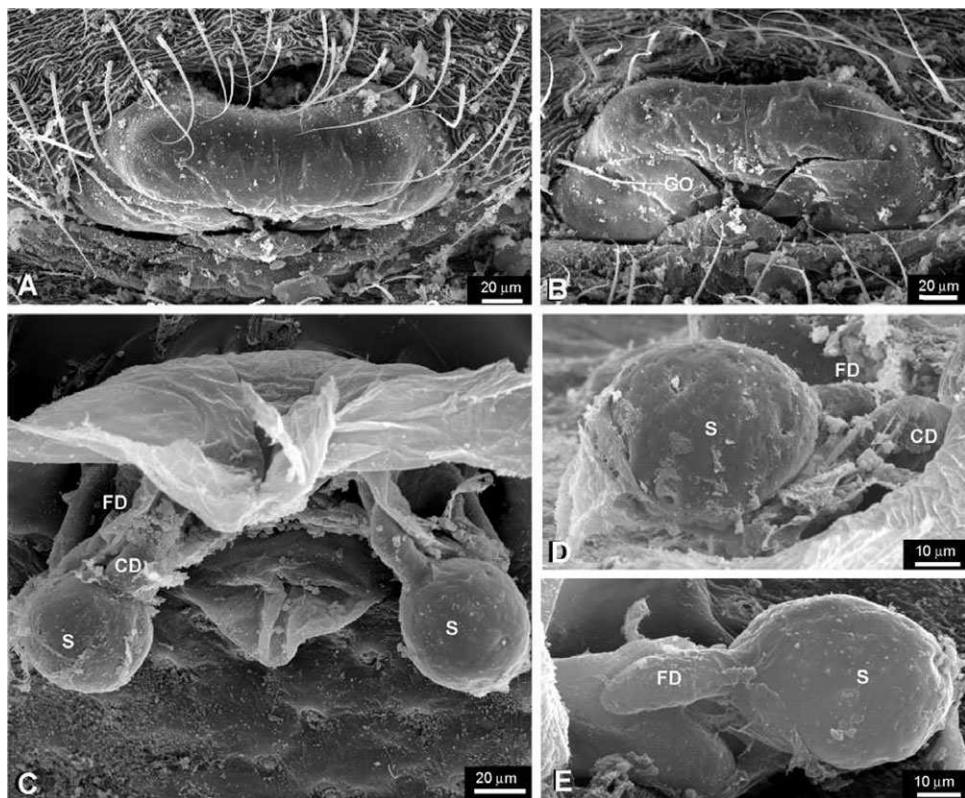
**Figure 32.** *Dolichognatha pentagona* cephalothorax: A, female dorsal view. B, male clypeus. C, male chelicerae. D, female chelicerae. E, male tangential view. F, female cephalothorax ventral view and sternum. G, female tangential view. All images from SEMFAP045.

num flat, copulatory openings as two pits posteriorly orientated (Fig. 15A, B). Spermathecal walls weakly sclerotized, accessory gland openings arranged in groups (Figs 15F, G, 17B). Fertilization and copulatory ducts shorter than half the spermathecae length, coiled (Figs 15E, 17B).

**Male:** body length from 5.2 to 6.9 mm. Somatic morphology as in female. PLS triplet reduced to nubbins. Epiandrous fusules immersed in pits, arranged in a transversal line of many clusters and over a flat sclerotized plate (Fig. 13H). Male palpal patella with one macroseta, tibia from two to more than four times longer than wide (*A. marmorata*; Mello-Leitão, 1948: fig. 7); tibial ectal surface with

trichobothria (Fig. 16D). Paracymbium shorter than half the cymbium length, covered with macrosetae, and its attachment to the cymbium well sclerotized (Fig. 16D). Conductor absent. Sperm duct coiled (Fig. 17A). Embolus lamelliform, curving less than one turn (Figs 16F, 17C).

**Natural history:** *Azilia* includes ten species found mainly in the Neotropical region (Bryant, 1940; di Caporiacco, 1954; Keyserling, 1881a; Mello-Leitão, 1940, 1948; O. P. Cambridge, 1889, 1893). The only species with a geographical range extending to the north temperate regions is *A. affinis* O. P. Cambridge, 1893 (Levi, 1980). These spiders build horizontal



**Figure 33.** *Dolichognatha pentagona* epigynum: A, ventral view. B, posterior view. C, dorsal view. D and E, spermathecae lateral views. All images from SEMFAP045.

webs with numerous radii and spirals – more than 30 each, a closed hub and secondary radii (Fig. 3C). Their webs are usually found between tree buttresses and similar cavities; at night time the spider is often found at the centre of the web.

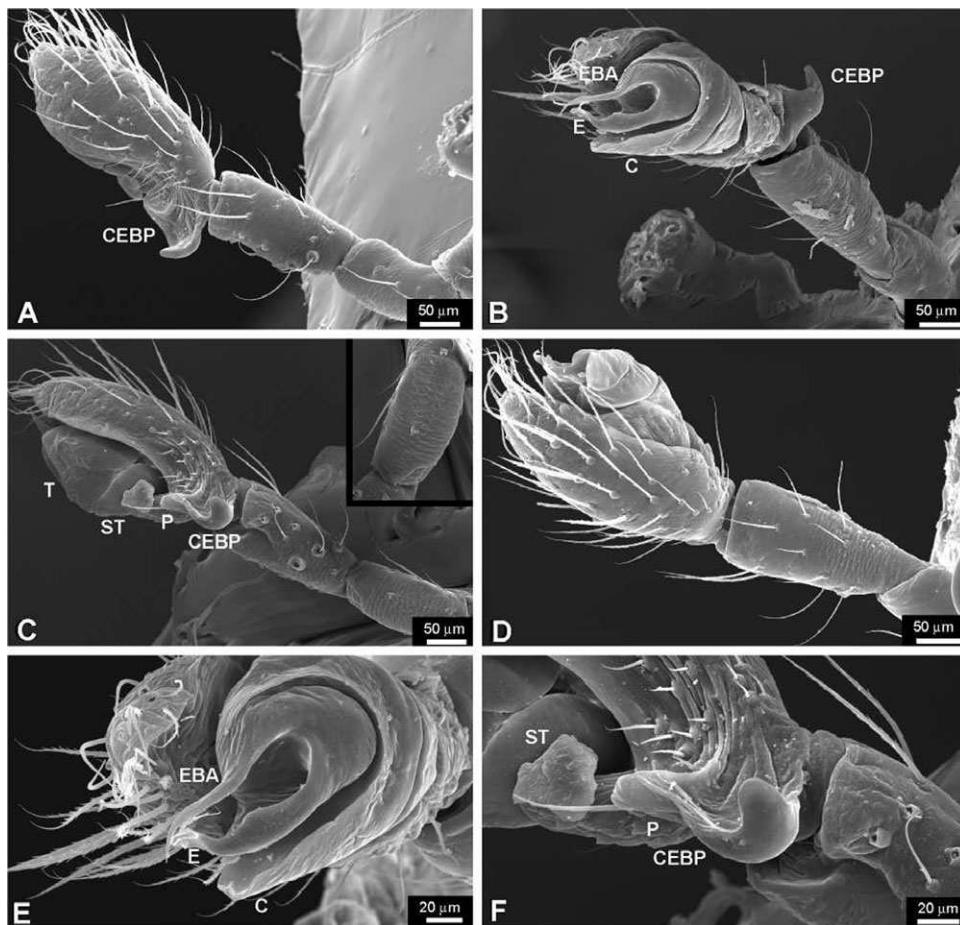
**Taxonomy:** There are no taxonomic revisions or phylogenetic analyses that test the monophyly of this genus. Only the taxonomy of *A. affinis* has been revised for the USA (Levi, 1980). Both sexes are known only in three of the described species: *A. affinis*, *A. marmorata*, and *A. guatemalensis* O. P.-Cambridge, 1889. The male pedipalpal femur and tibia of *A. marmorata* (Mello-Leitão, 1948) are extremely long, resembling those of *Metleucauge eldorado* Levi, 1980 (Fig. 78F). *Azilia marmorata* and other species have embolic apophyses. The other seven species are known only from female specimens except *Azilia vachoni* (di Caporiacco, 1954) which was described from an immature specimen. Some aspects of the behaviour of *Azilia* species have been studied, for example, the extended position of legs I and II while the spider is resting, how these spiders initiate airborne lines, and to some extent, their web building behaviour (Eberhard, 1982, 1984, 1987).

The diagnosis and description are based on *A. affinis*, *A. histrio*, *A. marmorata* from the Dominican Republic, and *A. guatemalensis* from Mexico. As the anatomy of *A. affinis* has been studied in more detail, many characters in the description refer to this species. The phylogenetic placement of *Azilia* is far from clear. Previous to this study two hypotheses existed about the sister taxon of *Azilia*: either as sister to *Dolichognatha* (Hormiga *et al.*, 1995: fig. 141A), or as sister to all other leucaugines (Álvarez-Padilla, 2007: fig. 142B). We coded specimens of *A. affinis* for the morphology in the phylogenetic analysis.

#### CHYSOMETA SIMON, 1894 (FIGS 3D, 18–21)

**Type species:** *Chrysometa tenuipes* (Keyserling, 1864). Levi (1986) designated a female lectotype and five female paralectotypes from Bogota (Colombia), which are deposited at The Natural History Museum, London.

**Diagnosis:** *Chrysometa* species can be distinguished from all other tetragnathid genera by the following

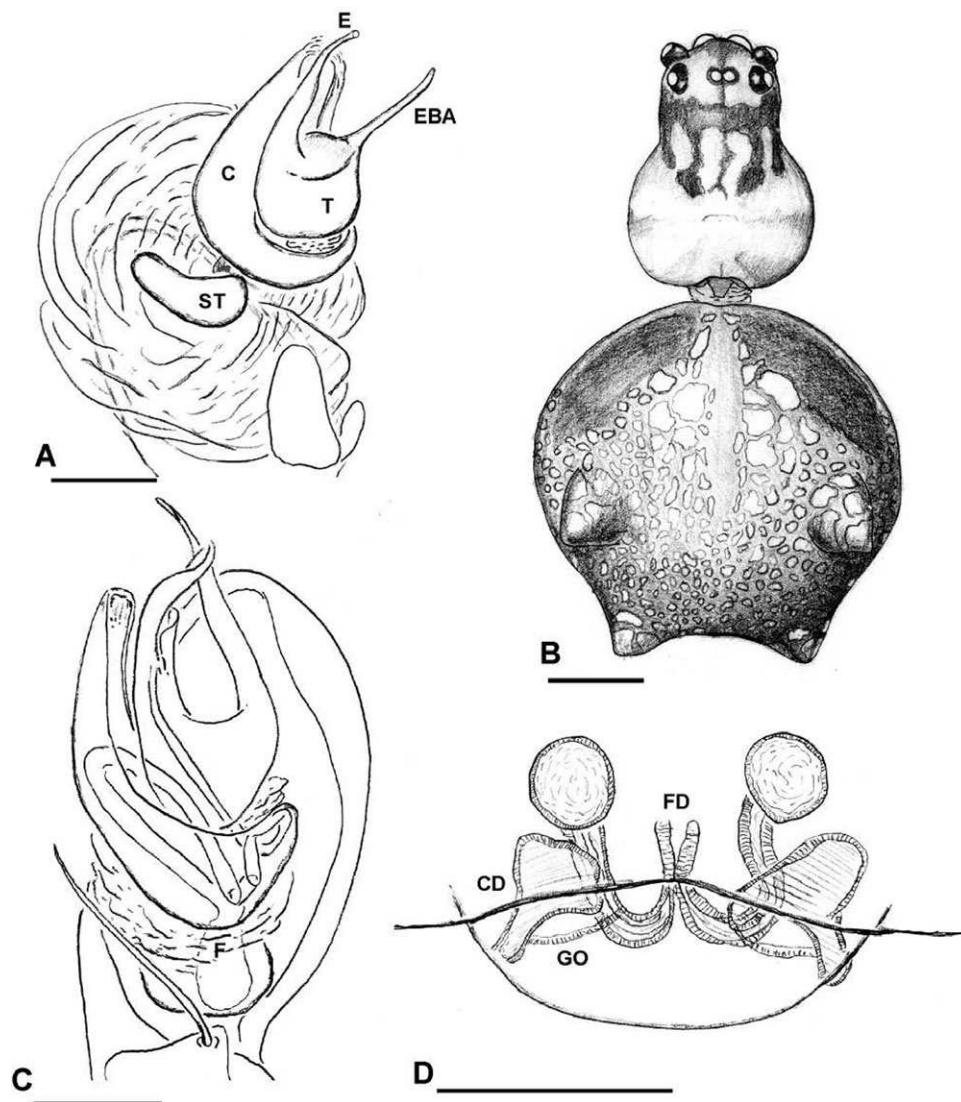


**Figure 34.** *Dolichognatha pentagona* male pedipalp: A, dorsal view. B, ventral view. C, ectal view. D, mesal view. E, conductor and embolus. F, cymbial ectobasal process. All images from SEMFAP045.

combination of characters: femora without trichobothria; abdomen covered with silver guanine patches (Levi, 1986: fig. 651); epigynum flat (Fig. 20A, B); fertilization ducts originating anteriorly and crossing over the spermathecae (Figs 20E, 22D); male palpal tibial length approximately as long as its widest point; paracymbium articulated and bearing several apophyses located at both extremes (Fig. 21C, D); male cephalic region narrower than in the female, relative to the thoracic region (Fig. 19A, B); and cymbial ectobasal process and cymbial ectomedian process present (Fig. 21A, C).

**Description: Female:** body length c. 10.0 mm. Carapace with a deep transverse m-shaped groove, cephalic region more than 70% of thoracic region width (Fig. 19A). Ocular area higher than the carapace lateral margins (Fig. 19C). Sternum as wide as long, labium trapezoidal and rebordered (Fig. 19G). Anterior surface of chelicerae smooth (Fig. 19E). Cheliceral boss present (Fig. 19E, F). Secondary eyes with

canoe-shaped tapetum. Eyes subequal in size, lateral eyes slightly smaller, juxtaposed and on a tubercle. Clypeus higher than one AME diameter. Median tracheae not ramified, with the tips leaf-shaped (Fig. 18D) and less than half the lateral tracheae length (Fig. 18A). Tracheal spiracle near the spinnerets, with fewer than four accessory glands on each junction with the tracheal trunks (Fig. 18B, C). ALS with several piriform spigots (Hormiga *et al.*, 1995; fig. 16A–D). PMS anterior surface without aciniform spigots (Fig. 18F; Hormiga *et al.*, 1995; Fig. 20C). PLS with c. ten aciniform spigots roughly arranged in two parallel lines; aggregate spigots apex not embracing the flagelliform spigot tip (Fig. 18E; Hormiga *et al.*, 1995; Fig. 20D). Epigynal plate well sclerotized, slightly protruded ventrally and copulatory openings posteriorly orientated (Fig. 20A–C). Spermathecae well sclerotized; fertilization ducts crossing over the spermatheca and originating anteriorly; accessory glands concentrated at the fertilization duct-spermatheca junction and arranged in groups



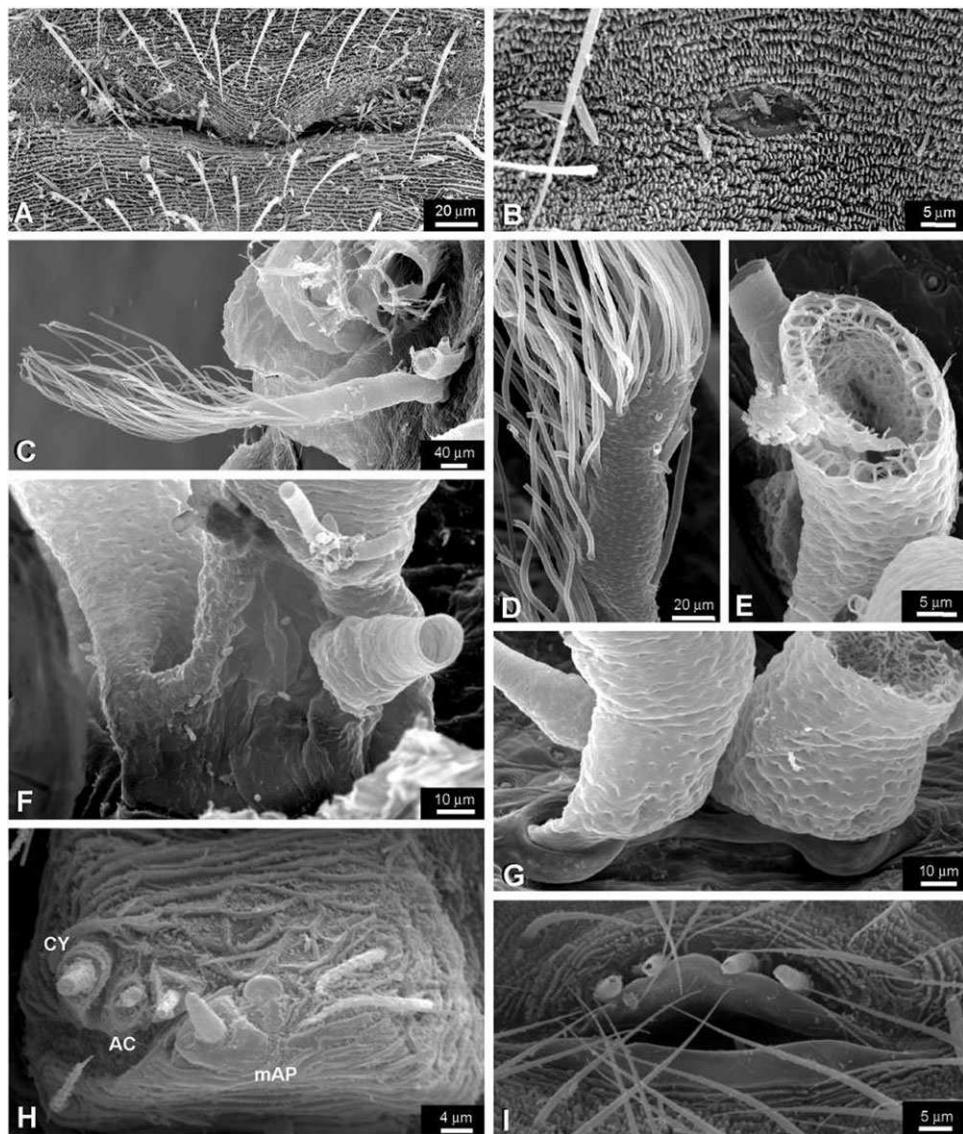
**Figure 35.** *Dolichognatha pentagona* genital anatomy and habitus illustrations: A, male pedipalp expanded. B, female habitus, abdomen showing tubercles. C, pedipalp bulb cleared ventral view. D, cleared epigynum ventral view.

(Figs 20E, 22D). Copulatory duct walls well sclerotized and slightly longer than half the spermatheca length and fertilization ducts also well sclerotized (Fig. 22D).

*Male:* body length c. 8.0 mm. Cephalic area less than 70% of thoracic region width, cephalic fovea deep, elongated x-shaped (Fig. 19B). Ocular area is higher than the carapace lateral margins (Fig. 19C, D). Cheliceral anterior-ectal margin rugose (Fig. 19F). PLS aggregate and flagelliform spigots reduced to nubbins. Epiandrous fusules arranged in a transversal line, formed by several spigot clusters that are immersed in pits (Fig. 18G). Male palpal patella with one macroseta (Fig. 21D). Paracymbium with several basal and distal apophyses, with few macrosetae, and attached to the cymbium by a membrane

(Figs 21C–E, 22A). Tegulum cup-shaped, with elevated apical margin (Figs 21B, 22A). Conductor membranous and originating behind a tegular ectal margin projection (Fig. 22A). Embolus lamelliform and coiled. Embolic metine apophysis present ('terminal apophysis' in Levi, 1986), coiled with the embolus and firmly attached to its base (Fig. 22B). Sperm duct spiralled without switchbacks (Fig. 22C).

*Natural history:* *Chrysometa* is the third most diverse genus of tetragnathids, with 130 species described so far (Platnick, 2009). These species inhabit the tropical and south temperate regions of the Americas, being more diverse in the tropical areas (Levi, 1986). These spiders build vertical webs amongst the forest vegetation. Their webs usually have few radii, few spirals

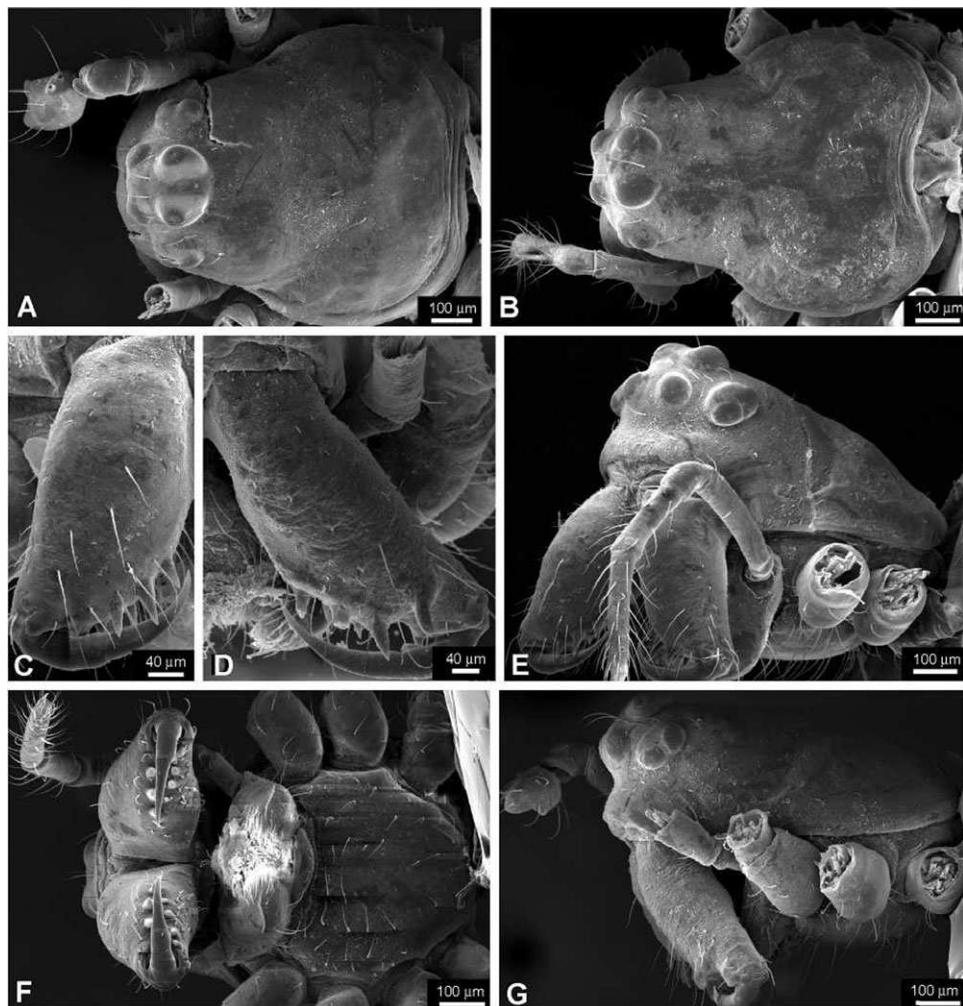


**Figure 36.** *Glenognatha foxi* abdomen: A, tracheal spiracle. B, cuticle of the abdomen, close up of median lateral section. C, median tracheae. D, median trachea ramifications. E, median tracheae transversal cut. F, tracheal spiracle lateral view. G, tracheal spiracle posterior view. H, posterior median spinnerets. I, epiandrous fusules. All images from SEMFAP029.

(fewer than 30), an open hub, and an open sector at the top of the web (Fig. 3D; Levi, 1980: plates 1–2). This open sector, when present, has a ‘telegraph’ silk line that connects the centre of the web with the spider retreat (outside the web). These spiders are usually found hiding in their retreat holding the end of this line.

**Taxonomy:** *Chrysometa* was revised by Levi (1986) who illustrated all 127 species. It seems very likely that many new species of *Chrysometa* remain to be discovered. Some aspects of the behaviour of *Chrysometa* have been studied, such as the sequence of leg

movements used during web construction (Eberhard, 1982, 1984, 1987). The diagnosis and description of this genus is based on Levi (1986) plus additional observations of specimens from the following species: *Chrysometa nuboso*, *Chrysometa saladito*, *Chrysometa acinosa*, *Chrysometa flava*, and other specimens of *Chrysometa* spp. from Colombia. Some characters in the genus description refer only to *Chrysometa alajuela* Levi, 1986 (from Costa Rica) because they have only been studied in this species so far. The monophyly of *Chrysometa* remains to be tested with a large taxonomic sample. The only phylogenetic analysis to date included only six species, and was designed



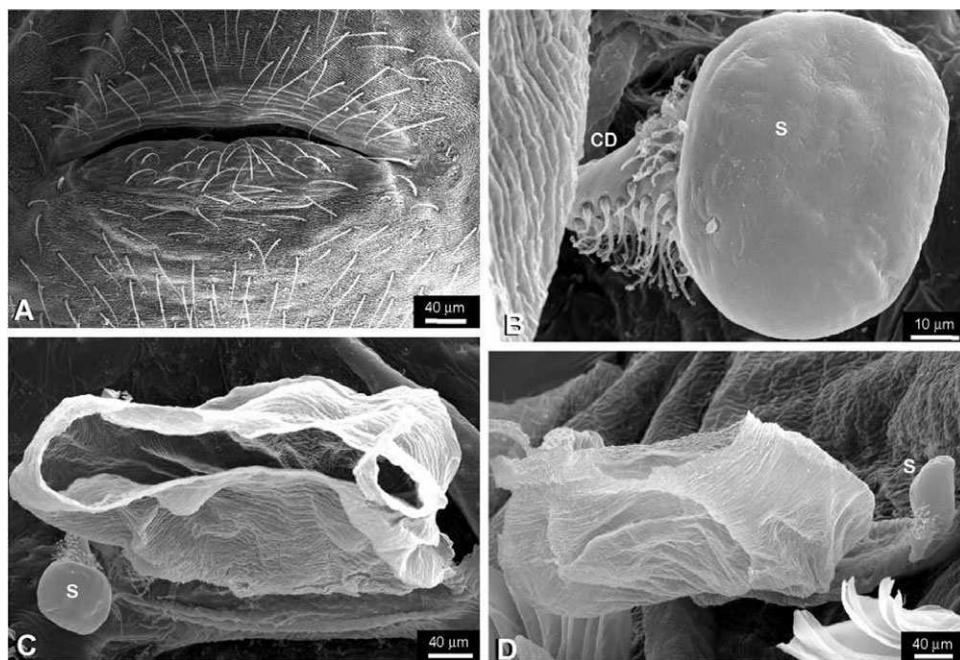
**Figure 37.** *Glenognatha foxi* cephalothorax: A, male dorsal view. B, female dorsal view. C, female chelicera. D, male chelicera. E, female tangential view. F, female cephalothorax ventral view and sternum. G, female lateral view. All images from SEMFAP029.

to test whether the two described Chilean *Chrysometa* species belonged to this genus (Álvarez-Padilla, 2007). The synapomorphies proposed for *Chrysometa* in that study must be taken as tentative because of the relatively small taxonomic sample used. *Chrysometa* has been proposed as sister to *Metellina* (Hormiga *et al.*, 1995) or *Allende* (Álvarez-Padilla, 2007). The present phylogenetic analysis based on morphology and behaviour recovered *Chrysometa* as sister to a large clade of tetragnathids that includes: the Nanometinae, *D. spinifera*, and Tetragnathinae (Fig. 143A). When these data are combined with the nucleotide sequences *Chrysometa* is recovered as sister to *Diphya* and this clade is nested within Metinae (Fig. 144). We coded specimens of *c. alajuela* for the phylogenetic analysis.

#### CYRTOGNATHA KEYSERLING, 1881 (FIGS 2A, 3A, 23–25)

*Type species:* *Cyrtognatha nigrovittata* Keyserling, 1881a. The holotype of *c. nigrovittata* is a male specimen from Pumamarca (Peru) deposited at the Polish Academy of Sciences (Dimitrov & Hormiga, 2009).

*Diagnosis:* *Cyrtognatha* species can be distinguished from all other tetragnathid genera by the following combination of characters: the presence of feathered trichobothria on femur IV (Fig. 24C, E); PLS ectal surface with a straight line of long and robust macrosetae with enlarged bases (Dimitrov & Hormiga, 2009: fig. 35E, F); spermathecae reduced, the sperm being stored in a specialized membranous sac



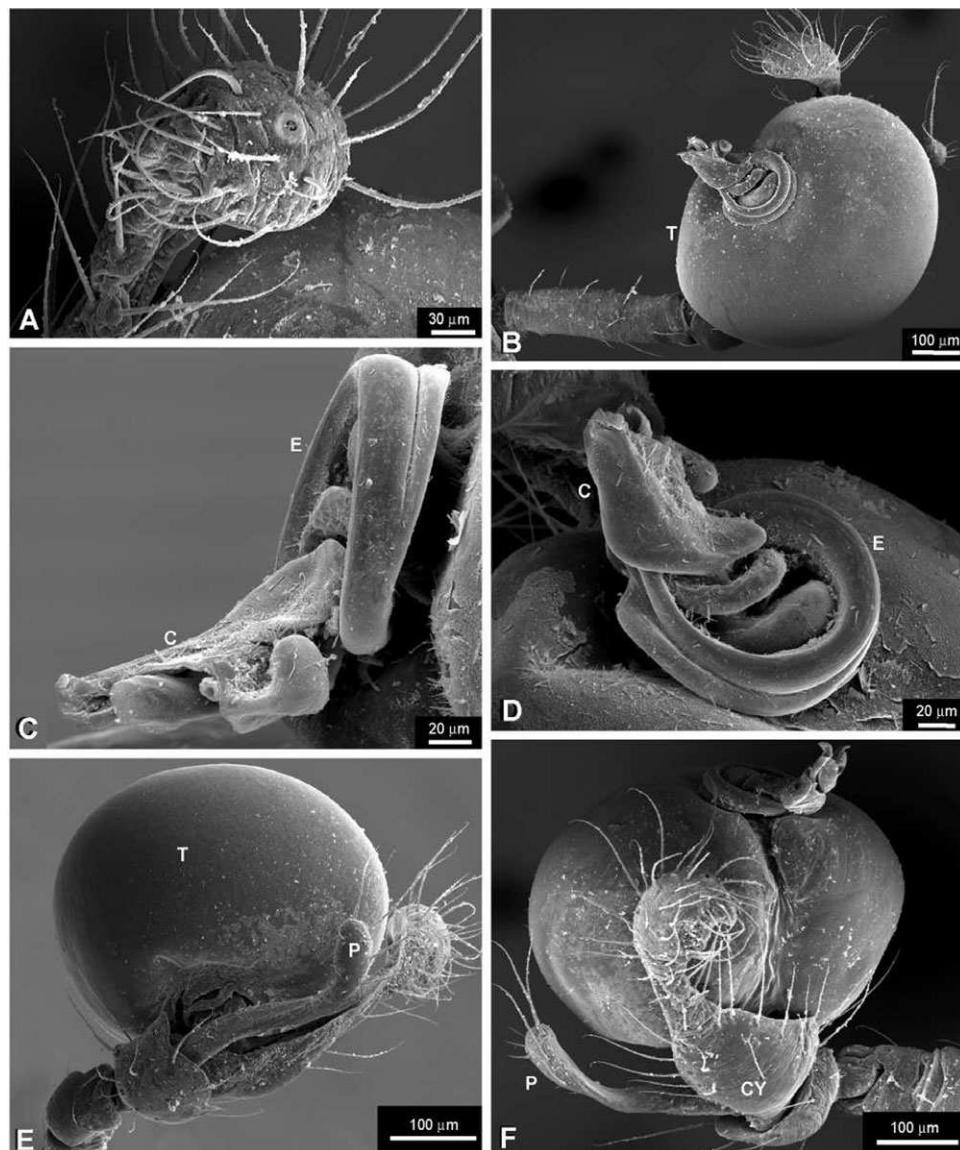
**Figure 38.** *Glenognatha foxi* female genitalia: A, genital spiracle. B, spermathecae. C, dorsal view. D, lateral view. All images from SEMFAP029.

(Fig. 24D–G; Dimitrov, Álvarez-Padilla & Hormiga, 2007: fig. 3A–F); male chelicerae not projected, wider distally and conspicuously divergent in its distal two thirds (Fig. 23A, B); embolus enlarged and bearing a basal apophysis that can be subdivided (Dimitrov & Hormiga, 2009: fig. 6A, E); sclerotized paracymbium and cymbium joint (Dimitrov & Hormiga, 2009: fig. 41D–F); and conductor with several apophyses (Fig. 25A, B; Dimitrov & Hormiga, 2009: fig. 6C).

**Description: Female:** body length variable, c. 4.5 to 6.0 mm (Dimitrov & Hormiga, 2009). Cephalothorax fovea transverse (Fig. 24A). Femora IV with both branched and smooth trichobothria (Fig. 24C–E; Dimitrov & Hormiga, 2009: figs 12H, 29F, *Cyrtognatha quichua* and *Cyrtognatha pachygnathoides*, respectively). Ocular area lower than carapace lateral margins (Fig. 23F). Labium trapezoidal, wider than long and rebordered. Sternum longer than wide (Fig. 23C). Chelicerae not divergent, anterior surface smooth and cheliceral boss present (Fig. 23A, D). Clypeus less than one AME diameter. Abdomen cylindrical with silver guanine patches and with anterior and caudal tubercles. Booklung cuticle smooth (Dimitrov & Hormiga, 2009: fig. 36F). Tracheal spiracle located near the spinnerets. ALS have an extensive field of piriform spigots (Dimitrov & Hormiga, 2009: fig. 35G). PMS anterior surface are without aciniform spigots (Dimitrov & Hormiga, 2009: fig. 36A). PLS with c. 15 aciniform spigots arranged in two parallel

lines, distal end of the aggregate spigots separated from the distal end of the flagelliform spigot (Dimitrov & Hormiga, 2009: fig. 35E, F). Epigynal plate absent, copulatory opening as a transverse spiracle (Dimitrov & Hormiga, 2009: fig. 36E). Spermathecae vestigial, presumably not functional (Fig. 24F, G; Dimitrov *et al.*, 2007: fig. 3A–F). Copulatory ducts weakly sclerotized, not membranous, covered with accessory glands. Fertilization ducts absent. Two types of accessory glands are present, long-stem gland ductiles over the copulatory ducts and short-stem gland ductiles over the posterior sac (Fig. 24D, F, G, respectively, and Dimitrov *et al.*, 2007: fig. 3B). Accessory glands immersed in individual pits (Fig. 24G).

**Male:** body length from 3.0 to 4.3 mm (Dimitrov & Hormiga, 2009). Somatic morphology similar to that of the female, except that the chelicerae are considerably larger, divergent, with the ectal surface rugose and with distal apophyses (Fig. 23A, B). Abdomen without caudal tubercle (Dimitrov & Hormiga, 2009: fig. 28A–D). PLS triplet reduced to nubbins. Epandrous fusules area as the surrounding abdominal cuticle; fusules arranged in one transverse line with enlarged bases. Palpal patella with one macroseta. Palpal femur more than four times its width, tibia approximately as long as the widest point of the tibia (Figs 24B, 25E). Paracymbium cylindrical, longer than half the cymbium length, with few macroseta and without a basal apophysis (Fig. 25D, F). Paracymbium and cymbium attachment with a sclerotized

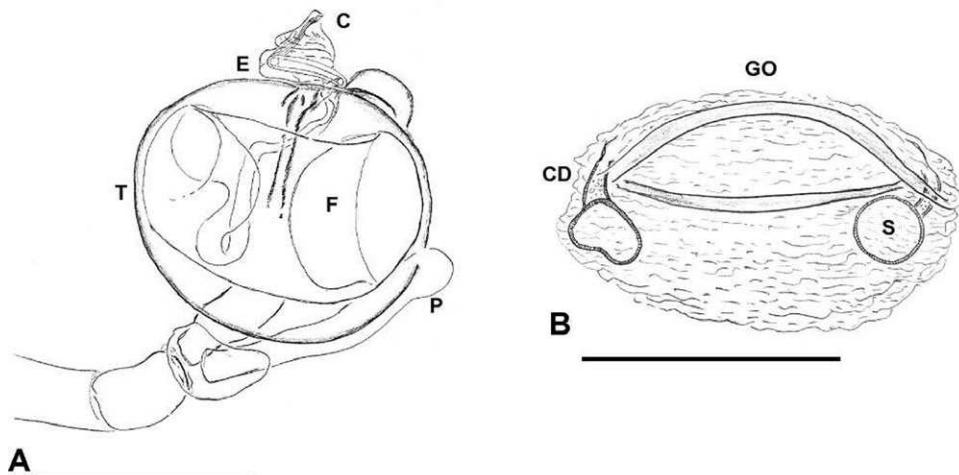


**Figure 39.** *Glenognatha foxi* male pedipalp: A, tarsal organ. B, ventral view. C and D, conductor and embolus lateral view and apical view, respectively. E, ectal view. F, dorsal view. All images from SEMFAP029.

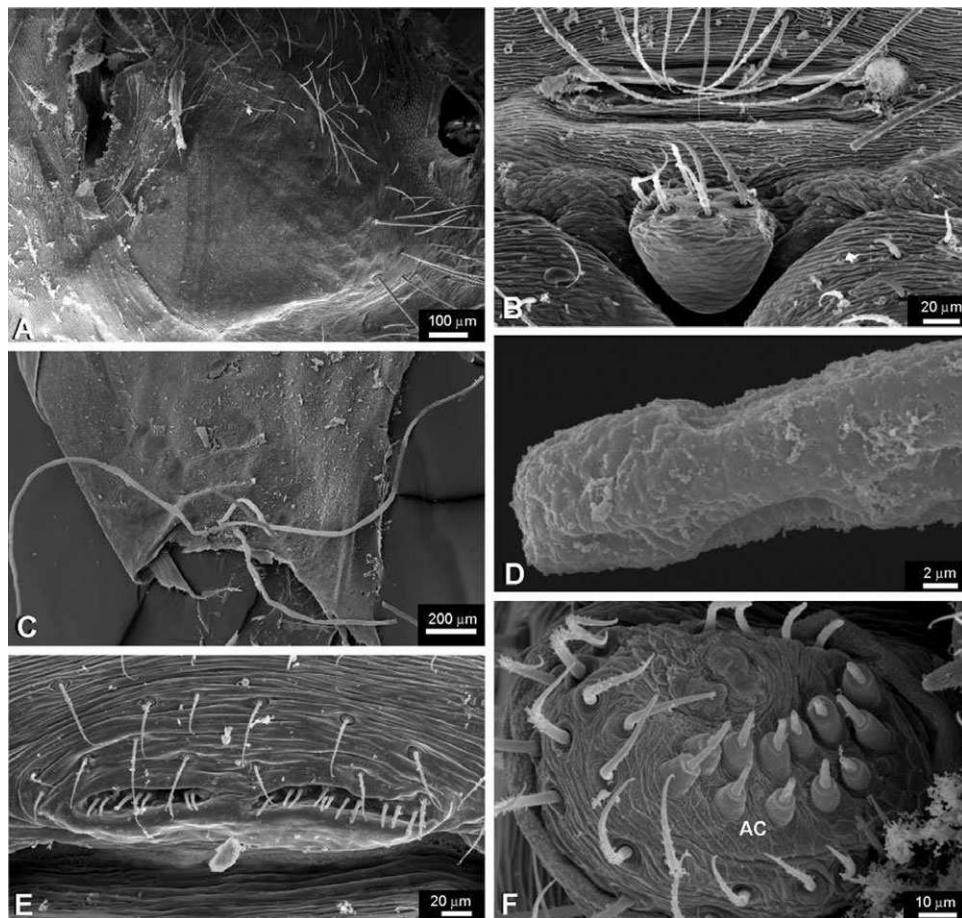
continuous margin. Tegulum spherical (Fig. 25C). Conductor-tegulum attachment membranous, located on the centre of the tegulum (Fig. 25A). Embolus lamelliform, coiled and without basal apophyses (Fig. 25E). Most *Cyrtognatha* species have basal apophyses on the embolus (Dimitrov & Hormiga, 2009: fig. 6A, B, D, E). Sperm duct spiralled and considerably enlarged in its middle section (Dimitrov & Hormiga, 2009: fig. 6A, E).

**Natural history:** There are 21 *Cyrtognatha* species described, but most of them are known from only a few museum specimens (Dimitrov & Hormiga, 2009). *Cyrtognatha* species live in cloud and rain forests in

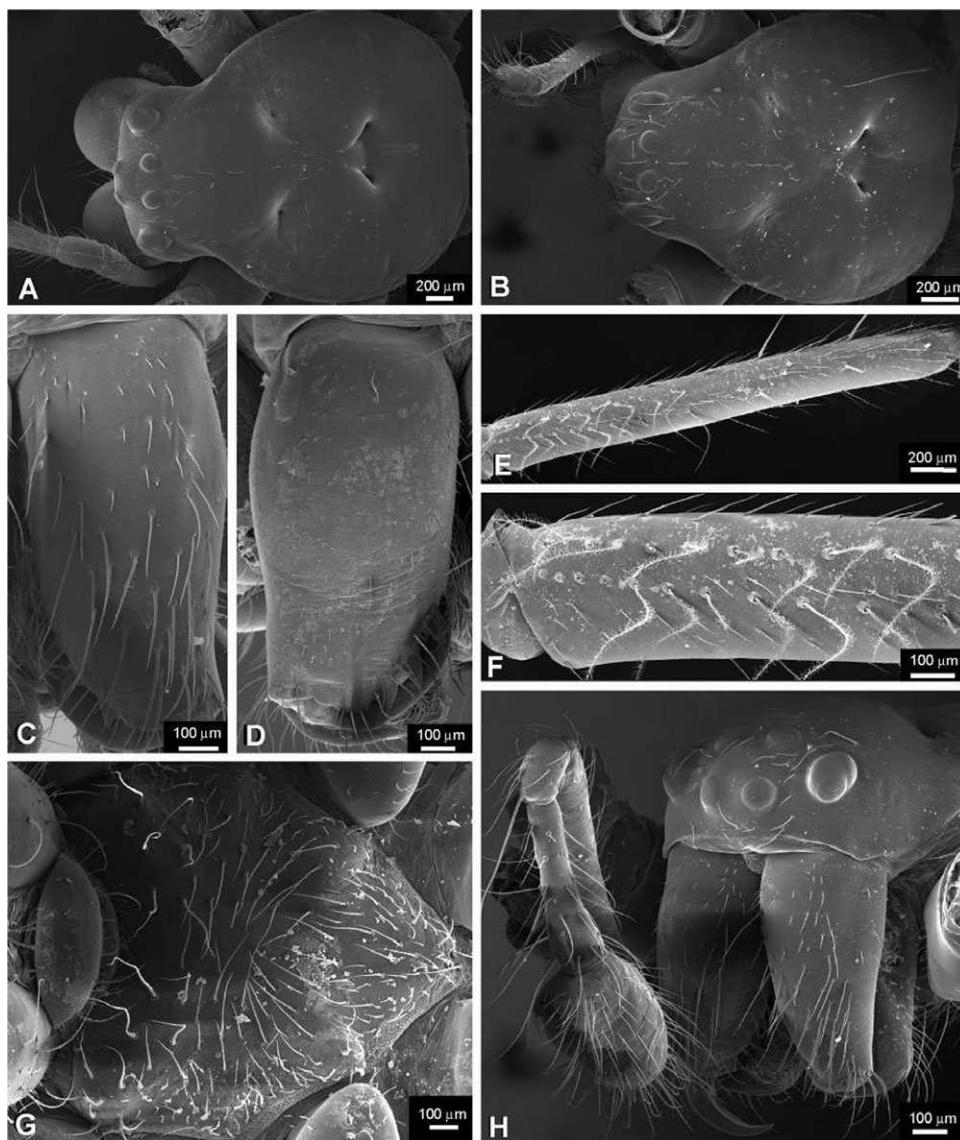
the Americas, from Mexico to Argentina, the West Indies, and are more diverse in the tropical areas. The wide geographical distribution of the genus and its poor representation in collections suggests that many species of *Cyrtognatha* remain to be discovered. *Cyrtognatha* species are found resting on the centre of the web with legs I and II extended, legs I always in contact with radii (Fig. 2A). They usually build horizontal orb webs with open hub and the number of radii and spirals vary considerably amongst species (Fig. 3A; Dimitrov & Hormiga, 2009: fig. 2C, E). The web building behaviours of a *Cyrtognatha* species were described by Eberhard (1982). The information in the diagnosis and description is based on Dimitrov



**Figure 40.** *Glenognatha foxi* genital anatomy illustrations: A, pedipalp cleared ventral view. B, cleared female genitalia.



**Figure 41.** *Leucauge venusta* abdomen: A, booklung external cuticle. B, tracheal spiracle and colulus. C, tracheal system dorsal view. D, lateral trachea tip. E, epiandrous fusules. F, male posterior lateral spinnerets, note the absence of flagelliform and aggregate spigots. All images from SEMFAP033.



**Figure 42.** *Leucauge venusta* cephalothorax: A, female dorsal view. B, male dorsal view. C, male chelicera. D, female chelicera. E and F, female femur IV trichobothria. G, female cephalothorax ventral view and sternum. H, male tangential view. All images from SEMFAP033.

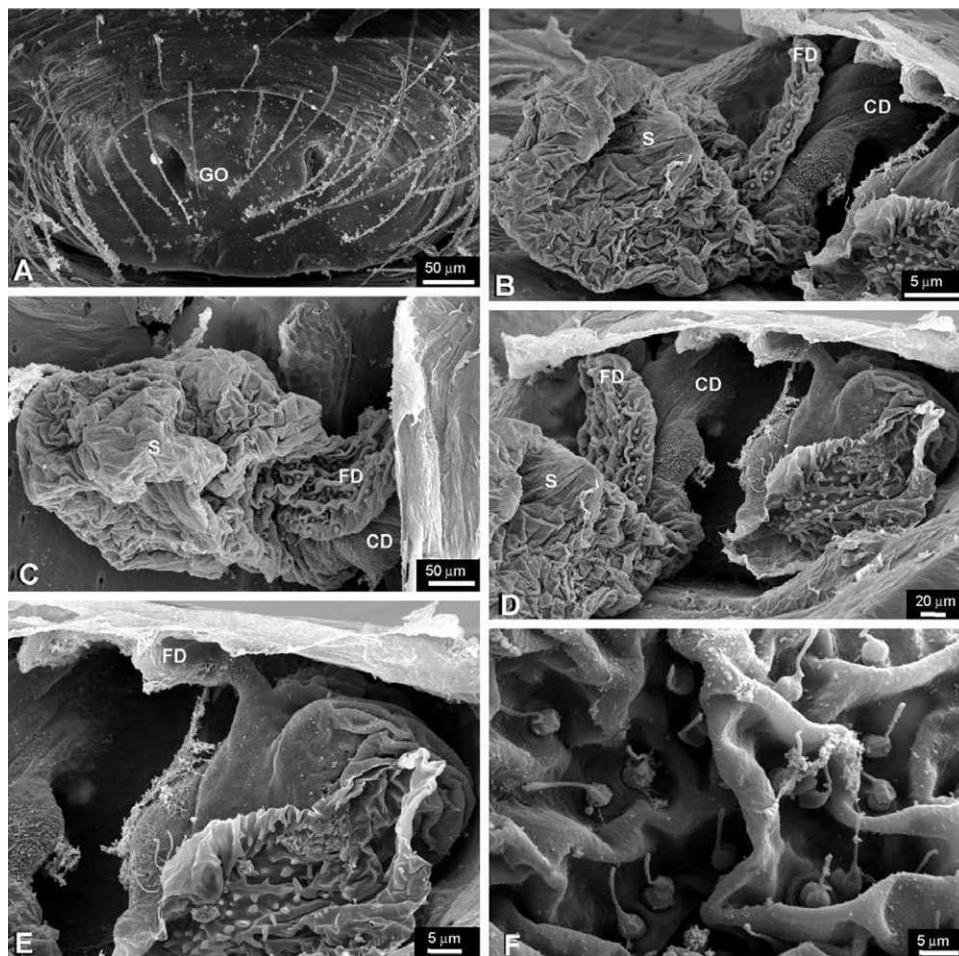
& Hormiga's (2009) monograph. We coded specimens of *Cyrtognatha espanola* (Bryant, 1945) in this phylogenetic analysis.

**Taxonomy:** This genus has been recently revised, its monophyly tested, and its phylogenetic relationships studied (Dimitrov & Hormiga, 2009). The monophyly of *Cyrtognatha* is well supported with BS values of 13 and JK values of 99. These authors concluded that the sister group of *Cyrtognatha* is *Tetragnatha*. The present phylogenetic analysis with morphology and behaviour also recovered *Cyrtognatha* and *Tetrag-*

*natha* as sister taxa (Fig. 143A); however, when these data were combined with the DNA partition *Cyrtognatha* was recovered as sister to a clade that including *Tetragnatha*, *Pachygnatha*, and *Glenognatha* (Fig. 144).

#### DIPHYA NICOLET, 1849 (FIGS 26–30)

**Type species:** *Diphya macrophthalma* Nicolet, 1849. The holotype of *D. macrophthalma* is a female specimen from Valdivia (Chile), deposited at the Museum National d'Histoire Naturelle, Paris (examined).

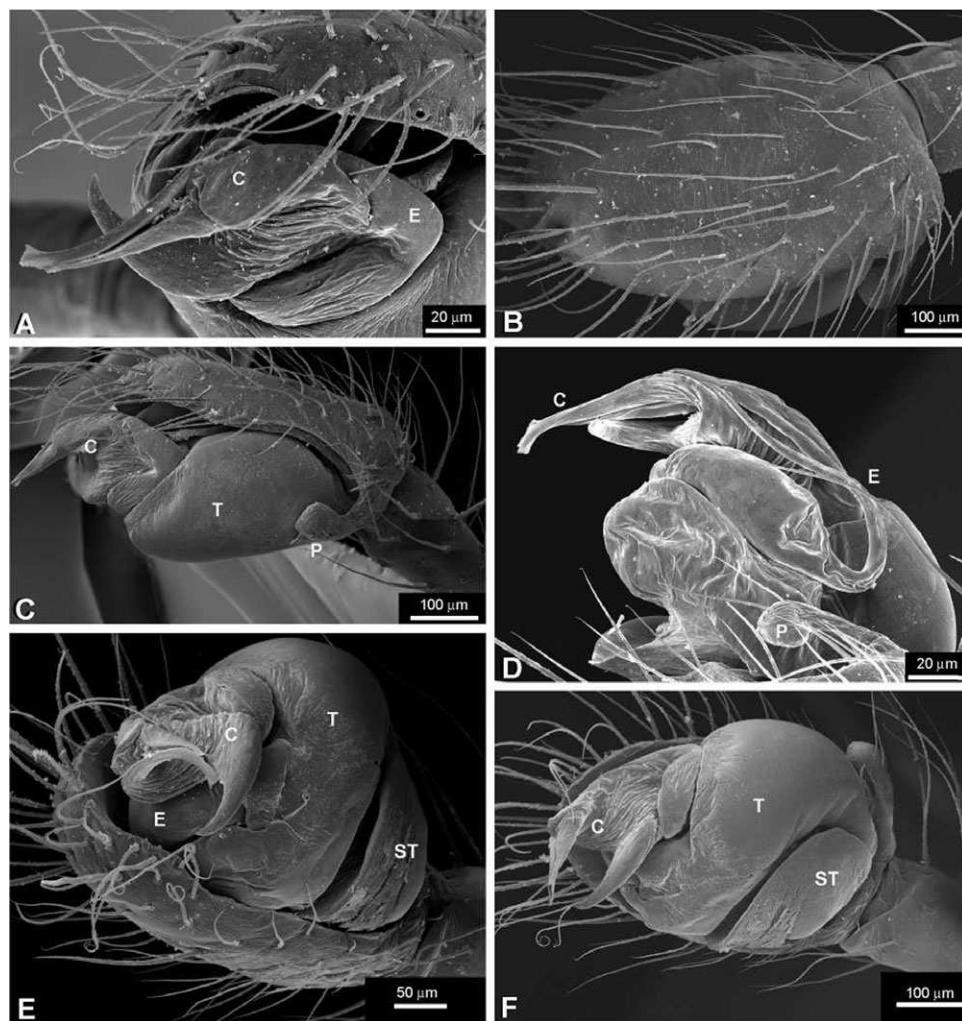


**Figure 43.** *Leucauge venusta* epigynum: A, ventral view. B, spermatheca lateral view. C, spermatheca dorsal view. D and E, copulatory and fertilization ducts. F, accessory glands. All images from SEMFAP033.

**Diagnosis:** *Diphya* species can be distinguished from all other tetragnathid genera by the following combination of characters: AME considerably smaller and PLE on separate tubercles (Fig. 27E); secondary eyes without reflective tapetum; legs I and II armed with a mesal row of macrosetae; epigynum a flat sclerotized plate with the copulatory openings ventrally orientated (Fig. 28A, B); spermathecae well sclerotized (Figs 28C, 30C); palpal tibia with a distal apophysis (Fig. 29F); cymbium only with the cymbial ectomedian process (Fig. 29D); paracymbium with an anterior apophysis, distally swollen (Fig. 29C); spherical tegulum (Fig. 29A). Conductor of membranous appearance but with the margins well sclerotized, coiled and firmly attached to the tegulum centre (Fig. 29G). Embolus lamelliform and coiled, opposite to conductor (Fig. 29E).

**Description: Female:** body length c. 0.5 mm. Transverse and shallow cephalothorax thoracic fovea

(Fig. 27A). Ocular area higher than carapace lateral margins (Fig. 27E). Sternum as wide as long, with sculpted cuticle (Fig. 27F). Cheliceral boss present, anterior cheliceral cuticle smooth (Fig. 27D). Labium trapezoidal, wider than long and rebordered (Fig. 27F). Anterior cheliceral cuticle as in clypeal area. Clypeus height less than one PLE diameter, AME considerably reduced. Abdomen oval lacking tubercles and silver guanine patches. Median tracheae not ramified, leaf-shaped apically (Fig. 26A, E). ALS with c. 40 piriform spigots (Fig. 26F). PMS anterior surface without aciniform spigots. PLS with fewer than 20 aciniform spigots arranged roughly in one line, aggregate spigots tips not embracing the flagelliform spigot apex (Fig. 26D). Copulatory and fertilization ducts also well sclerotized and considerably shorter than half the spermatheca length (Figs 28C, 30C). Accessory gland openings immersed in individual pits, located away from the copulatory and fertilization ducts (Fig. 28C, E).



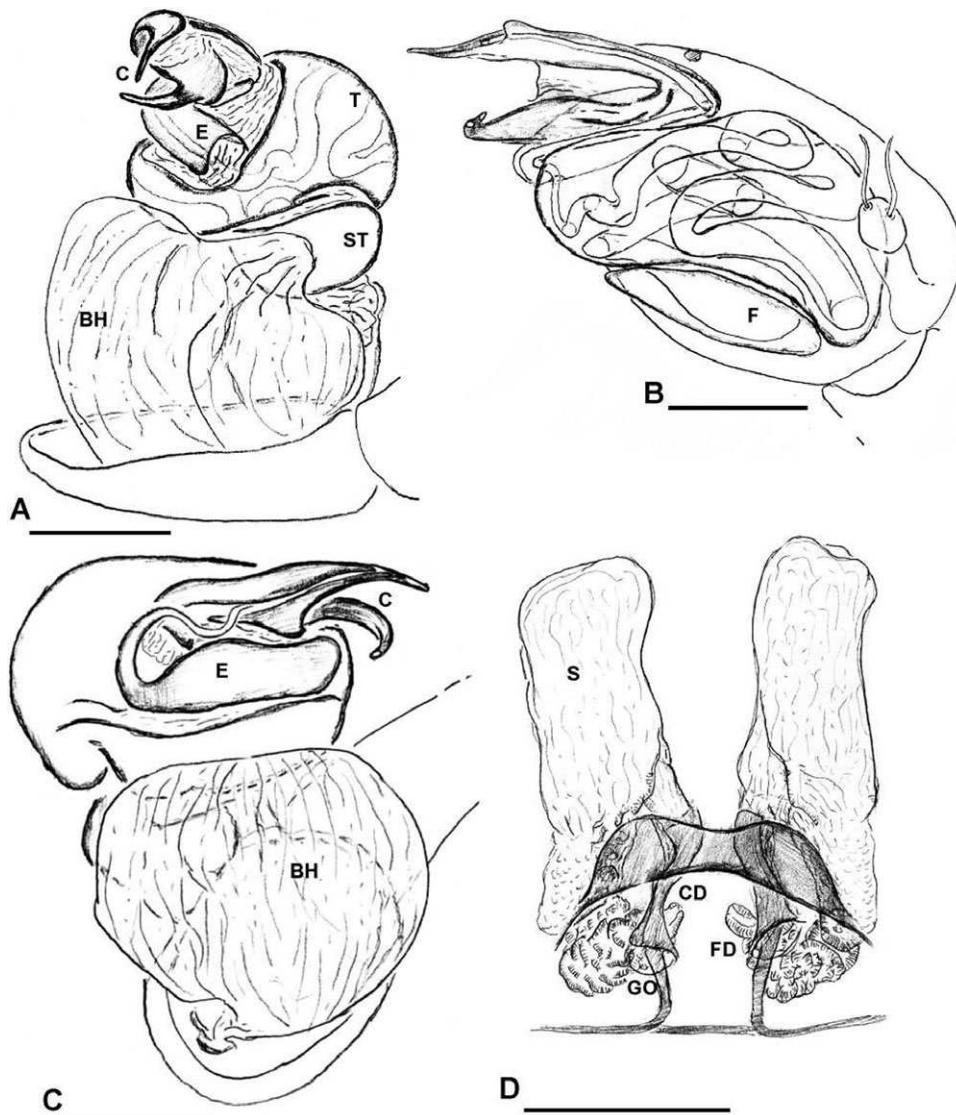
**Figure 44.** *Leucauge venusta* male pedipalp: A, apical view. B, dorsal view. C, ectal view. D, conductor and embolus. E, mesal view. F, ventral view. All images from SEMFAP033.

**Male:** body length c. 2.8 mm. Somatic morphology as in female, except that the chelicerae are longer, with rugose cuticle on the anterior surface (Fig. 27C). Epiandrous fusules concentrated in clusters, arranged in one transverse line (Fig. 26G), with bases not immersed in pits. PLS triplet reduced to nubbins. Male palpal tibia as wide as long, with a hook-shaped apophysis on the ectodistal margin (Fig. 29F). Palpal patella with one macroseta. Conductor membranous, with sclerotized edges at the base and apex, originating at the centre of the tegulum (Fig. 30A). Sperm duct spiralled (Fig. 30B).

**Natural history:** *Diphya* includes 11 species with a widespread geographical distribution that includes Argentina, Brazil, Chile, China, Japan, Korea, Madagascar, South Africa, and Taiwan. The type species is from Chile (Nicolet, 1849; Simon, 1894; Tanikawa,

1995; Vellard, 1926; Zhu, Song & Zhang, 2003). Nothing is known about their biology and whether they build orb webs or not remains undocumented (Namkung, 2003).

**Taxonomy:** *Diphya* has been revised by Tanikawa (1995), who described the first species from China, Japan, Korea, and Taiwan. Tanikawa (1995) revised and illustrated all known species except *Diphya bicolor* Vellard, 1926 (from Brazil) and *Diphya simoni* Kauri, 1950 (from South Africa). Our diagnosis and genus description is based on these studies plus additional specimens of an unnamed *Diphya* from Tanzania. The anatomy of *D. spinifera* has been studied in more detail than that of the other species; therefore, some characters in the description refer only to this species. Although the monophyly of *Diphya* remains untested by quantitative cladistic methods, similarity



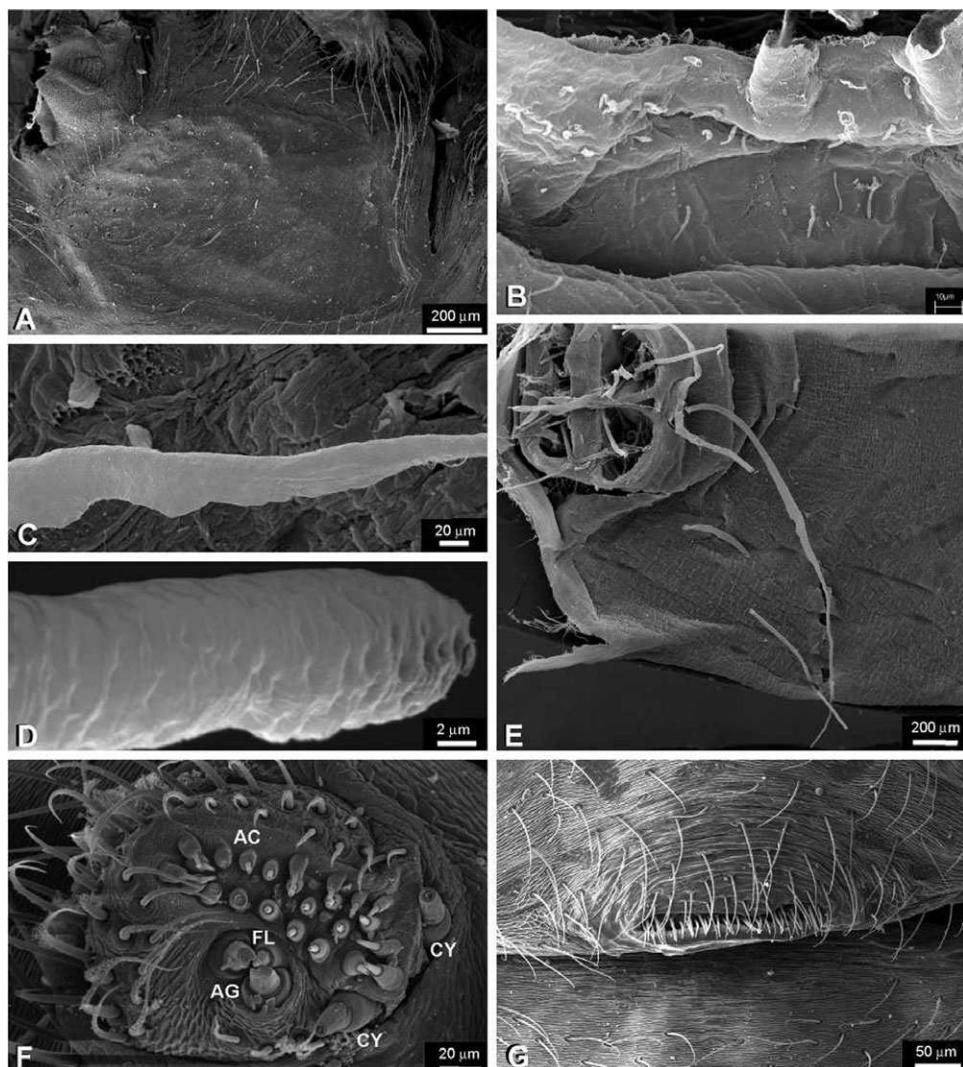
**Figure 45.** *Leucauge venusta* genital anatomy illustrations: A, male pedipalp expanded. B, pedipalp bulb cleared ventral view. C, male pedipalp expanded. D, cleared epigynum ventral view.

in the anatomy of all the species described and illustrated by Tanikawa (1995) suggests the monophyly of these taxa, except for the Malagasy species (unpubl. data). The present morphological and behavioural analysis proposed *Diphya* as sister to Tetragnathinae (Fig. 143A); however, when molecular data are combined, *Diphya* and *Chrysometa* are recovered as sister taxa. In this last analysis there were no sequences for *Diphya*; therefore its position as sister to *Chrysometa* is a result of the indirect optimization of morphological characters imposed by the congruence with the total evidence topology. We coded specimens of *D. spinifera* Tullgren, 1902 in the phylogenetic analysis.

#### DOLICHOGNATHA O. P.-CAMBRIDGE 1869 (FIGS 3E, 31–35)

*Type species:* *Dolichognatha nietneri* O. P.-Cambridge 1869. The holotype of *D. nietneri* is a male specimen from Sri Lanka deposited in The Natural History Museum, London (O. P.-Cambridge, 1869; Levi, 1981).

*Diagnosis:* *Dolichognatha* species can be distinguished from all other tetragnathids by the following combination of characters: PME close together, when present, and smaller than the PLE (Fig. 32A); clypeus height less than one AME diameter; chelicerae longer than the cymbial width, male chelicera longer, in some species longer than the carapace (Fig. 32C, D);

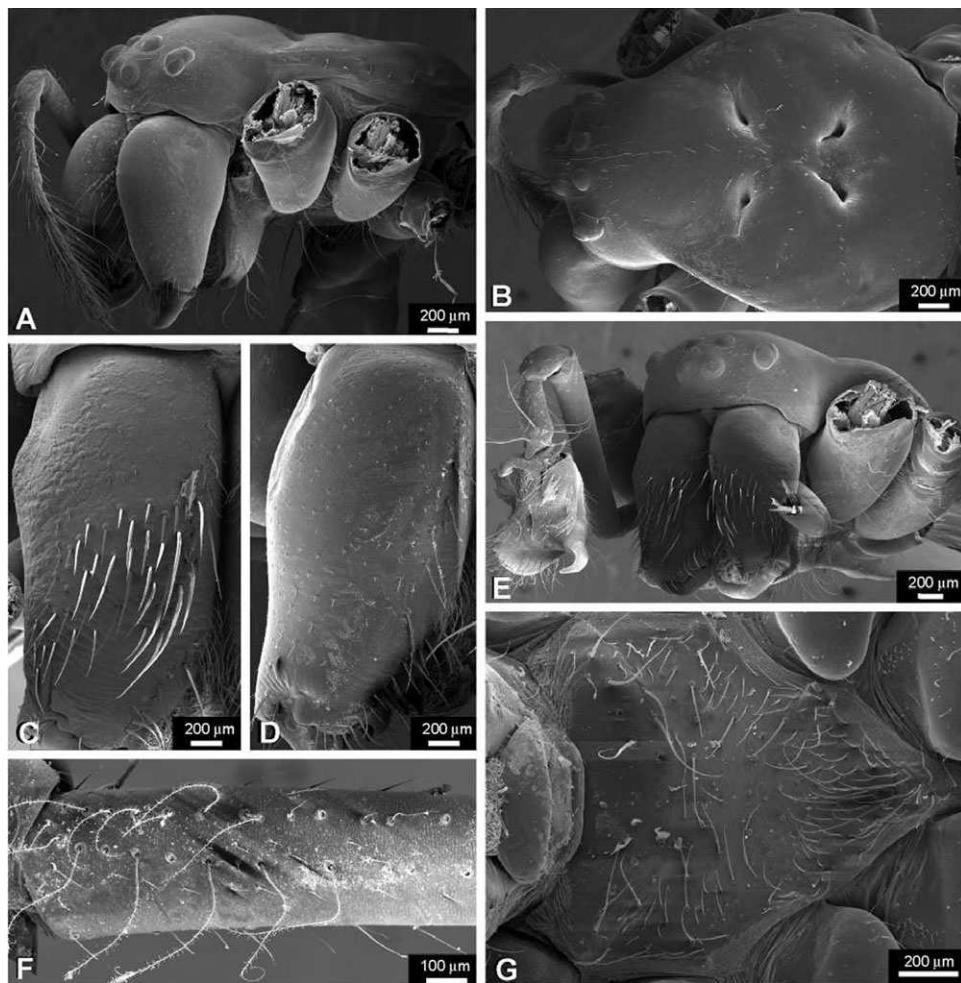


**Figure 46.** *Leucauge argyra* abdomen: A, booklung external cuticle. B, tracheal spiracle posterior view. C, median trachea tip. D, lateral trachea tip. E, tracheal system dorsal view. F, posterior lateral spinnerets. G, epiandrous fusules. Images (A–F) from SEMFAP054, (G) from SEMFAP034.

abdomen wider than long, with tubercles (Fig. 35B); male palpal patella macroseta absent (Fig. 32E); cymbial ectobasal process present (Fig. 34A, B); metaine embolic apophysis present (Figs 34E, 35A).

**Description: Female:** body length from 2.6 to 4.0 mm. Transverse and shallow thoracic fovea, cephalic region considerably longer than the thoracic region (Figs 32A, 35B). Female sternum sculpted and longer than wide (Fig. 32F). Labium trapezoidal, wider than long and rebordered. Ocular area higher than the carapace lateral margins (Fig. 32E, G); lateral eyes on separated tubercles (Fig. 32E, G). Cheliceral boss present, cuticle of anterior cheliceral surface rugose

(Fig. 32B–D). Abdomen with four pairs of caudal tubercles (Fig. 35B), without silver guanine patches. Median tracheae considerably shorter than the lateral tracheal trunks, not ramified and with rounded tips (Fig. 31A–D). Tracheal spiracle near the spinnerets, with fewer than four accessory glands on each side (Fig. 31F). ALS with many piriform spigots. PMS anterior surface without aciniform spigots. PLS aggregate distal end apart from the flagelliform spigot (Fig. 31E; Hormiga *et al.*, 1995: fig. 24A–D). Epigynum well sclerotized, membranous in the middle, and slightly swollen. Copulatory openings as grooves orientated posteriorly (Figs 33A, B, 35D). Spermathecae spherical, well sclerotized, with one to two accessory glands (Fig. 33C–E). Copulatory and



**Figure 47.** *Leucauge argyra* cephalothorax: A, female tangential view. B, female dorsal view. C, male chelicera. D, female chelicera. E, male tangential view. F, female femur IV trichobothria. G, female cephalothorax ventral view and sternum. Images of male specimens from SEMFAP034 and female specimens SEMFAP054.

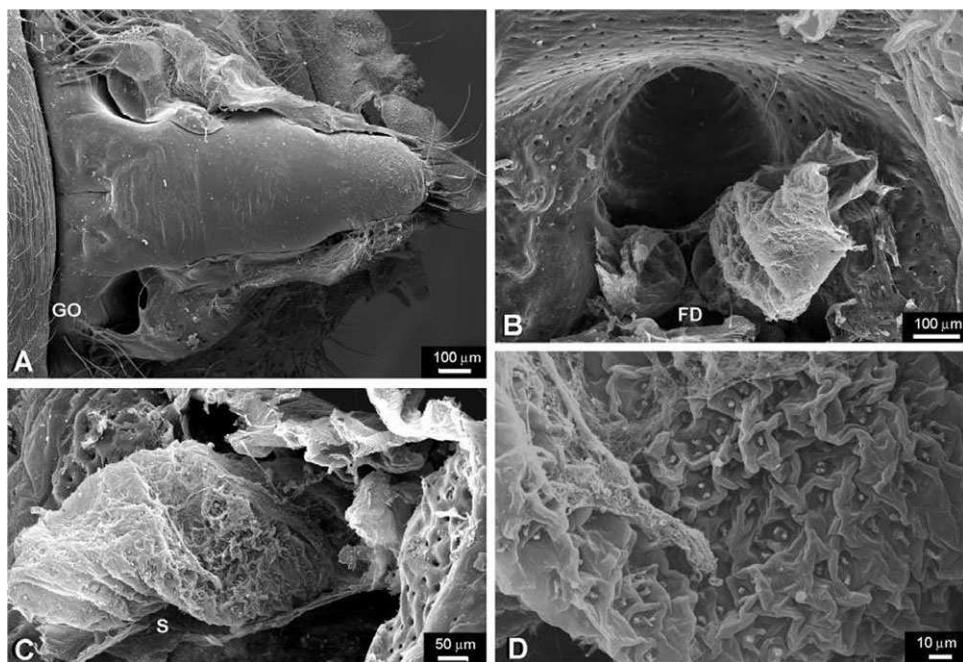
fertilization ducts well sclerotized, running in parallel before entering the spermathecae (Fig. 33D).

**Male:** body length from 2.6 to 3.2 mm. Somatic morphology as in female, except chelicerae, which are considerably longer (Fig. 32E; Lise, 1993: figs 1–8). PLS triplet reduced to nubbins. Epiandrous fusules concentrated in two clusters, immersed in individual pits (Fig. 31G). Male palpal tibia length approximately twice as long as wide. Conductor well sclerotized, fused to the tegulum, with a membranous apex. Tegulum larger than the subtegulum, cup-shaped (Fig. 35A). Embolic metaine apophysis present, fused to embolus base, and longer than wide. Embolus short and tubular, similar in shape to the basal apophyses (Figs 34E, 35A, C). Sperm duct with two switchbacks (Fig. 35C).

**Natural history:** *Dolichognatha* includes 27 species with a geographical distribution that includes the Old

and New World tropics (O. P. Cambridge, 1869; Keyserling, 1883; Simon, 1895; Lessert, 1938; Marples, 1955; Tanikawa, 1991; Lise, 1993; Brescovit & de Cunha, 2001; Smith, 2008). The best documented species by far is *Dolichognatha pentagona* (Hentz, 1850), with a geographical distribution that extends from Venezuela to the southern USA (Levi, 1981). *Dolichognatha pentagona* builds horizontal webs with more than 30 spirals and radii, sometimes with secondary radii and a closed hub. These webs are usually found between tree buttresses and roots or near the ground (Fig. 3E). The web building behaviour of *D. pentagona* has been described by Eberhard (1982).

**Taxonomy:** *Dolichognatha* has never been revised and its monophyly has never been tested with a global taxon sample. A recent study included four *Dolichognatha* species from South-East Asia and Australia, and recovered this genus as monophyletic, supported



**Figure 48.** *Leucauge argyra* epigynum: A, posterior view. B, dorsal view, note how the projection of the epigynal plate is hollow. C, spermatheca lateral view. D, accessory glands. All images from SEMFAP054.

by four synapomorphies: male versus female cheliceral size larger, palpal patellar macroseta absent, paracymbium secondary process procurved and metine embolic apophysis present (Smith, 2008). We coded specimens of *D. pentagona* in the character matrix. Information available in the descriptions also includes the following species: *Dolichognatha matucana* Lise, 1993 and the species included in Brescovit & de Cunha (2001) and Smith (2008). Two hypotheses have been proposed regarding the sister taxon of *Dolichognatha*: as either sister to *Azilia* (Hormiga *et al.*, 1995) or *Metellina* (Álvarez-Padilla, 2007). This latter sister group relationship is recovered in this study with the morphology and behavioural data set under all weighting criteria (Fig. 143B). With the addition of DNA sequence data *Dolichognatha* was proposed as sister to a clade formed by *Chrysometa* and *Diphya* (Fig. 144).

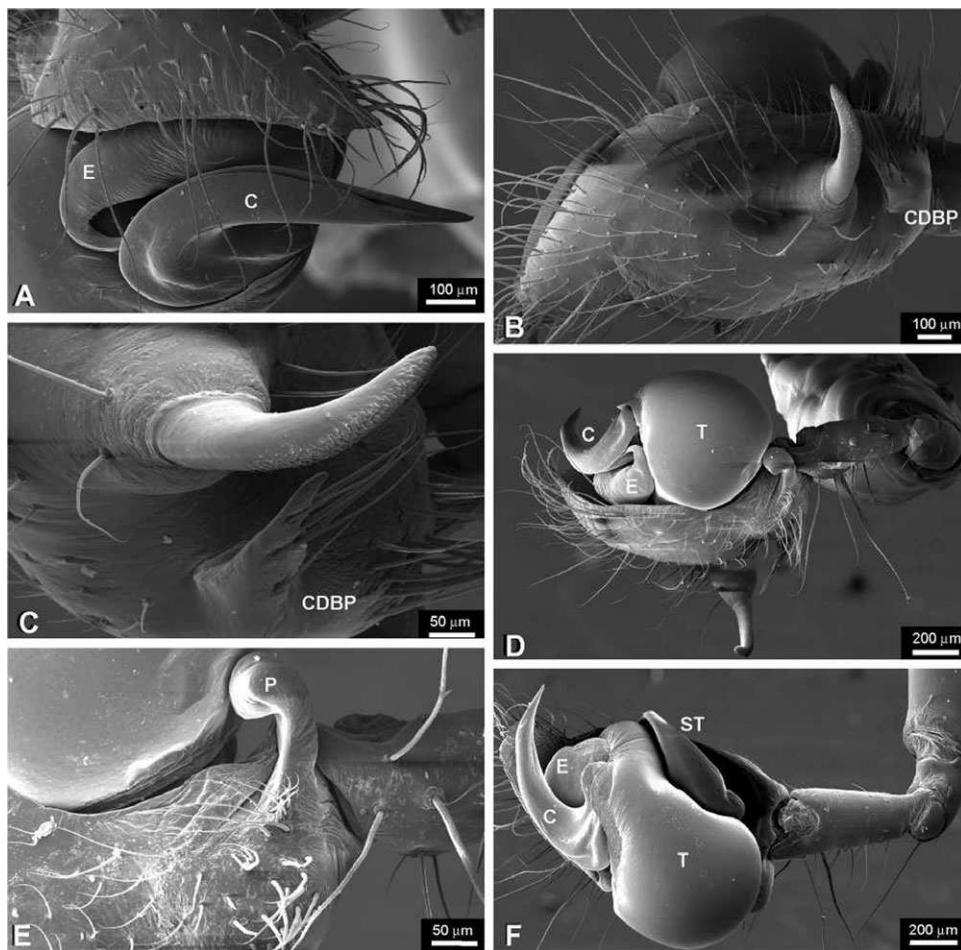
#### GLENOGNATHA SIMON, 1887 (FIGS 36–40)

*Type species:* *Glenognatha emertoni* Simon, 1887. The holotype of *G. emertoni* is a male specimen from Arizona (USA), deposited at the Museum National d'Histoire Naturelle, Paris (Levi, 1980).

*Diagnosis:* *Glenognatha* species can be distinguished from all other tetragnathid genera by the following combination of characters: body under 5 mm in length; abdomen oval to spherical, length less than

one and a half times its width (Levi, 1980; Hormiga & Döbel, 1990: figs 3, 12, 25); posterior tracheal spiracle anteriorly displaced and located in the middle of the abdomen venter (Fig. 36A); median tracheal trunks divided into numerous small tracheoles (Fig. 36C–G); spermathecae present but lacking epigynum and fertilization ducts (Fig. 38A, B, see also Dimitrov *et al.*, 2007); and tegulum spherical and considerably larger than the conductor and embolus (Fig. 39B).

*Description: Female:* thoracic fovea absent (Fig. 37B). Ocular area higher than the carapace lateral margins (Fig. 37E). Sternum as wide as long (Fig. 37F). Labium trapezoidal, wider than long, and rebordered. Chelicerae slightly divergent, anterior cuticle smooth as in clypeal area (Fig. 37C). Cheliceral boss present. Clypeus higher than two AME diameters (Fig. 37E). Eyes subequal in size; lateral eyes slightly smaller. PME without canoe-shaped tapetum, with rhabdoms arranged in loops; PLE with canoe-shaped tapetum (Levi, 1980: figs 261, 262). Median tracheal trunks considerably wider than lateral tracheae and branching into several tracheoles at the tip and on the sides, some of these tracheoles extend to the prosoma; the lateral tracheae present fewer branches (Levi, 1980: figs 260, 275). Tracheal spiracle wider than long and with fewer than four accessory glands on each side (Fig. 36F, G). ALS with c. 12 piriform spigots (Hormiga *et al.*, 1995: fig. 25B). PMS with two aciniform spigots between the cylindrical and minor



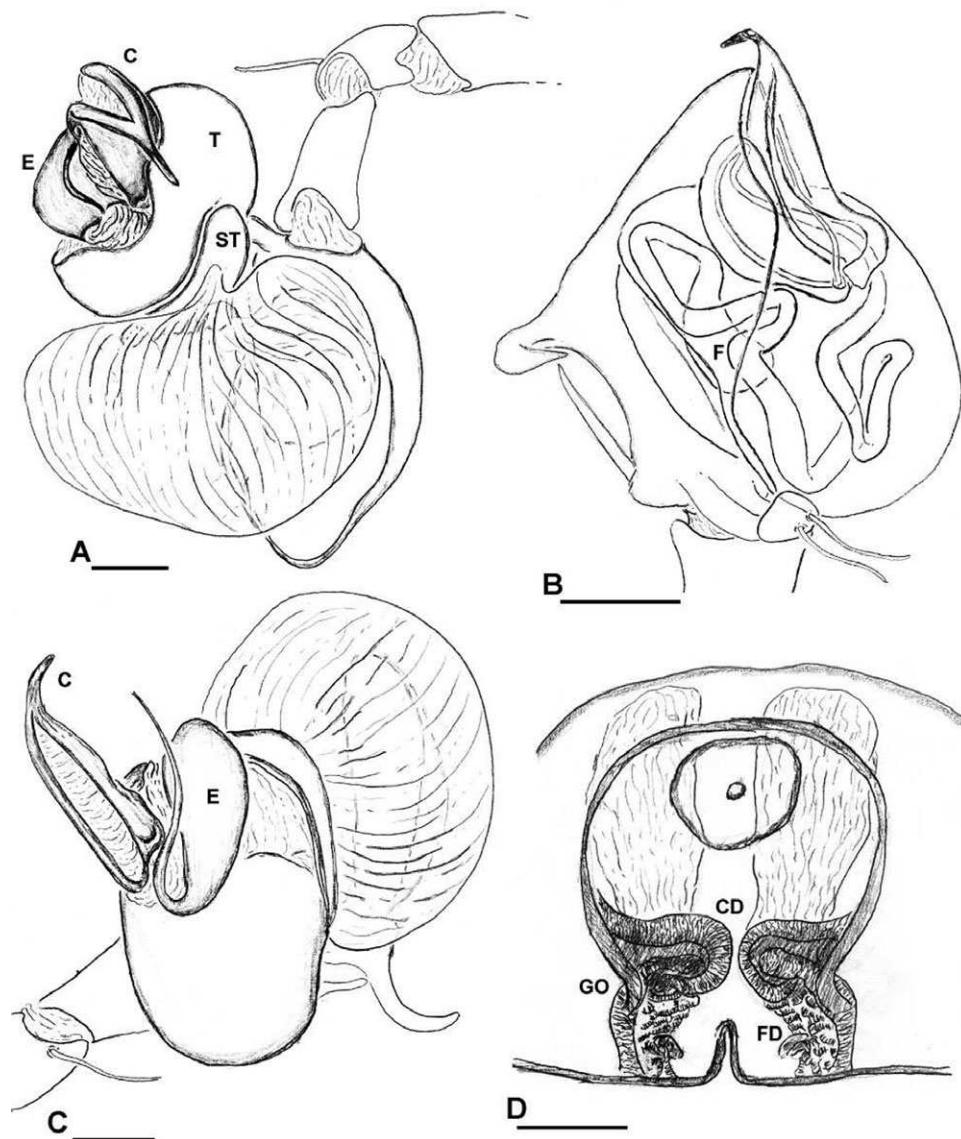
**Figure 49.** *Leucauge argyra* male pedipalp: A, apical view. B, dorsal view. C, cymbial dorsobasal process. D, pedipalp ectal view. E, paracymbium. F, pedipalp ventral view. All images from SEMFAP034.

ampullate silk gland spigots but without any aciniform spigots over the anterior surface (Fig. 36H; Hormiga *et al.*, 1995: fig. 25C). Femora IV without trichobothria. Epigynum absent, copulatory opening spiracle-shaped with both margins slightly sclerotized. Spermathecae well sclerotized and connected to a membranous sac, probably homologous to an enlargement of the uterus externus (Figs 38C, D, 40B). Accessory glands openings located on separate pits, concentrated on the copulatory ducts, and with their bases enlarged (Fig. 38B, C, see also Dimitrov *et al.*, 2007).

**Male:** size and somatic morphology similar to the female, but with more divergent chelicerae, without cheliceral boss and bearing distal apophyses (Fig. 37A, D, G). PLS triplet is present in the adult. Epiandrous fusules immersed in a transverse depression, arranged linearly. Lower margin of epiandrous plate enlarged (Fig. 36I). Palpal patella without macrosetae; palpal tibia as wide as long (Fig. 39E).

Paracymbium almost as long as cymbium (Fig. 39E). Conductor-tegulum attachment well sclerotized, located on the centre of the tegulum (Fig. 39B). Embolus tubular, without basal apophyses (Levi, 1980: figs 280, 289). Sperm duct spiralled, its diameter considerably wider on its middle section (Fig. 40A).

**Natural history:** This genus includes 20 species with a worldwide geographical distribution; most described species inhabit the north temperate regions (Levi, 1980; Hormiga & Döbel, 1990; Bosmans & Bosselaers, 1994 and references therein). The webs of *Glenognathia heleios* Hormiga & Döbel, 1990 are horizontal with c. 15 radii, more than 30 spirals and open hubs. Some species have split radii (G. Hormiga, unpubl. data). Their webs are usually found near the ground of marshes, waterlands, or near meadows, but also in forests and agricultural fields (Levi, 1980; Hormiga & Döbel, 1990: fig. 2). The phenology of some North



**Figure 50.** *Leucauge argyra* genital anatomy illustrations: A, male pedipalp expanded. B, pedipalp cleared ventral view. C, male pedipalp expanded. D, cleared epigynum ventral view.

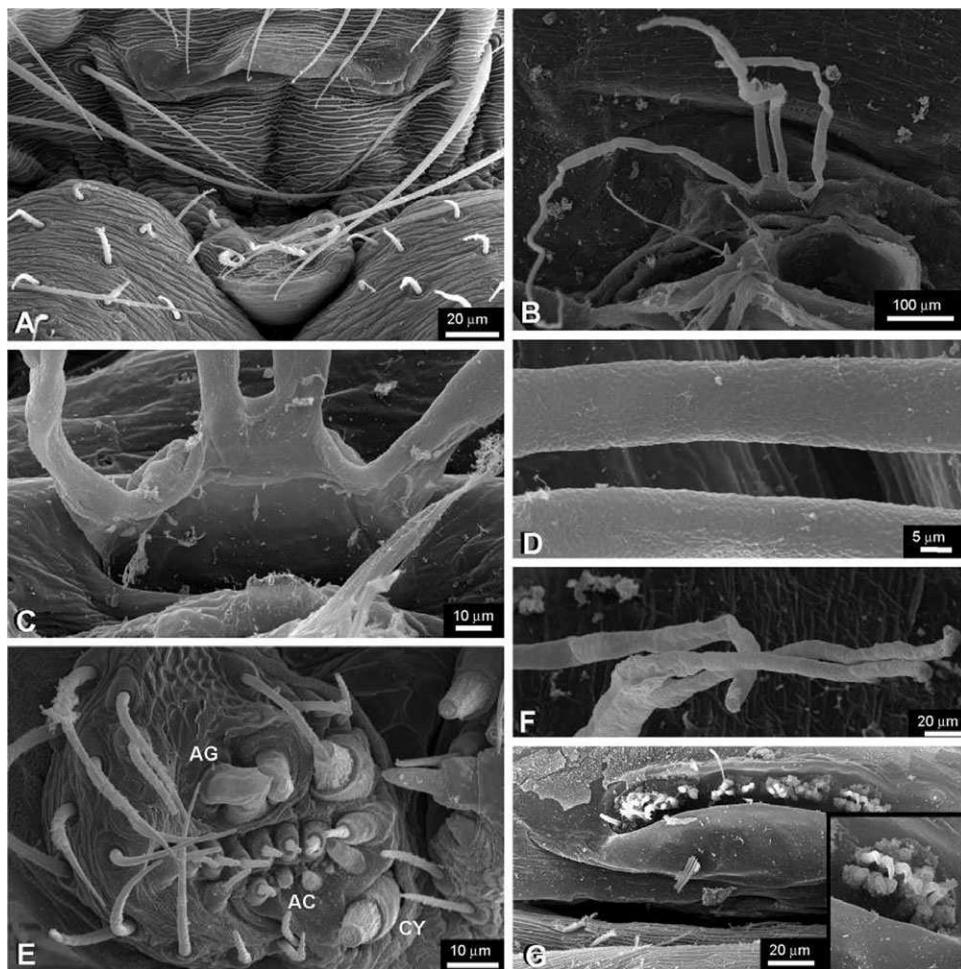
American *Glenognatha* species have been studied (Hormiga & Döbel, 1990). In addition, the mating behaviour and natural history have been studied recently for *G. emertoni* Simon, 1887 (Danielson-François, 2006). The web building behaviour of an undescribed *Glenognatha* species was documented by Eberhard (1982).

**Taxonomy:** *Glenognatha* has never been revised, with the exception of the North American species (Levi, 1980; Hormiga & Döbel, 1990), and its monophyly has never been tested. The diagnosis and description for *Glenognatha* was based on *Glenognatha foxi*, species

coded for the phylogenetic analysis, plus the information for the species included in Levi (1980) and Hormiga & Döbel (1990). All recent phylogenetic analyses have recovered *Glenognatha* as sister to *Pachygnatha* with morphology alone and molecules combined (Hormiga *et al.*, 1995; Álvarez-Padilla, 2007; Dimitrov & Hormiga, 2009).

#### LEUCAUGE WHITE, 1841 (FIGS 1C, E, 41–50)

**Type species:** *Epeira venusta* Walckenaer, 1841 (see Dimitrov & Hormiga, 2010). *Linyphia* (*Leucauge*) *argyrobapta* White, 1841, is a junior synonym of *Epeira venusta* Walckenaer, 1841. The type of *Epeira*



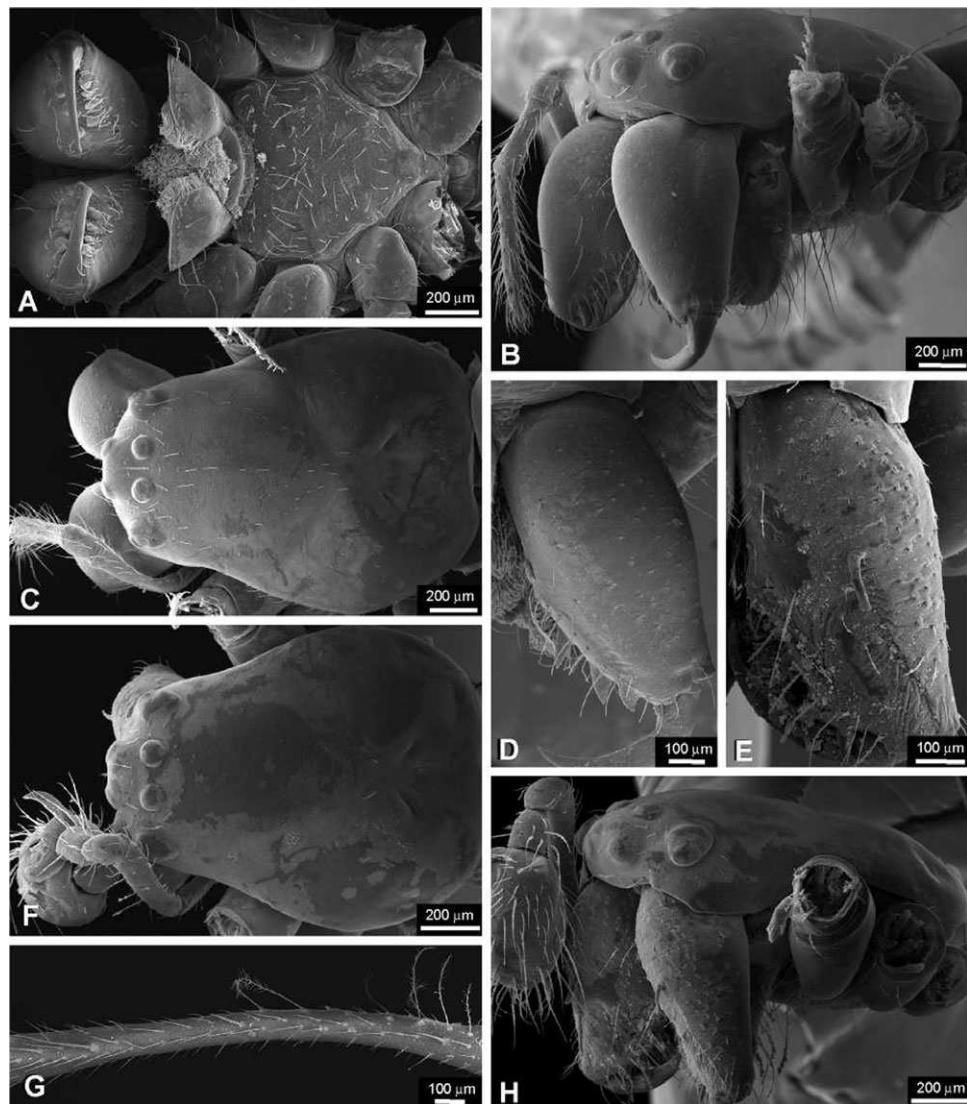
**Figure 51.** *Mesida argentiopunctata* abdomen: A, tracheal spiracle and colulus. B, tracheal system dorsal view. C, tracheal spiracle posterior view. D, lateral tracheae cuticle. E, posterior lateral spinnerets. F, median tracheae. G, epiandrous fusules; insert, detail of fusules. Images (A–E) from SEMFAP061, (G) from SEMFAP037.

*venusta* is an illustration by John Abbot (1792) from his unpublished manuscript on the spiders of Georgia (USA). Abbot's original illustration is in the library of The Natural History Museum in London. Walckenaer (1841) used Abbot's manuscript (p. 13, fig. 113) to describe *Epeira venusta*. A photocopy of Abbot's illustration, in the Museum of Comparative Zoology, was examined by Levi (1980) for his redescription of *Leucauge venusta*. The name *venusta* was published in 1841, before White's *argyrobapta*, as can be seen from White's (1841: 473) footnote about Walckenaer's work.

**Diagnosis:** *Leucauge* species can be distinguished from all other tetragnathid genera by the following combination of characters: two parallel rows of feathered trichobothria on the IV femoral ectal surface (Figs 1C, 42E, F, 47F); spermathecae walls

translucent and weakly sclerotized (Figs 43C, 48C); fertilization ducts coiled around the copulatory ducts (Figs 45D, 50D); flagelliform embolus with an elongated base (Figs 44D, 50C); conductor apically projected (Fig. 49F); and sperm duct with more than four switchbacks (Figs 45B, 50B).

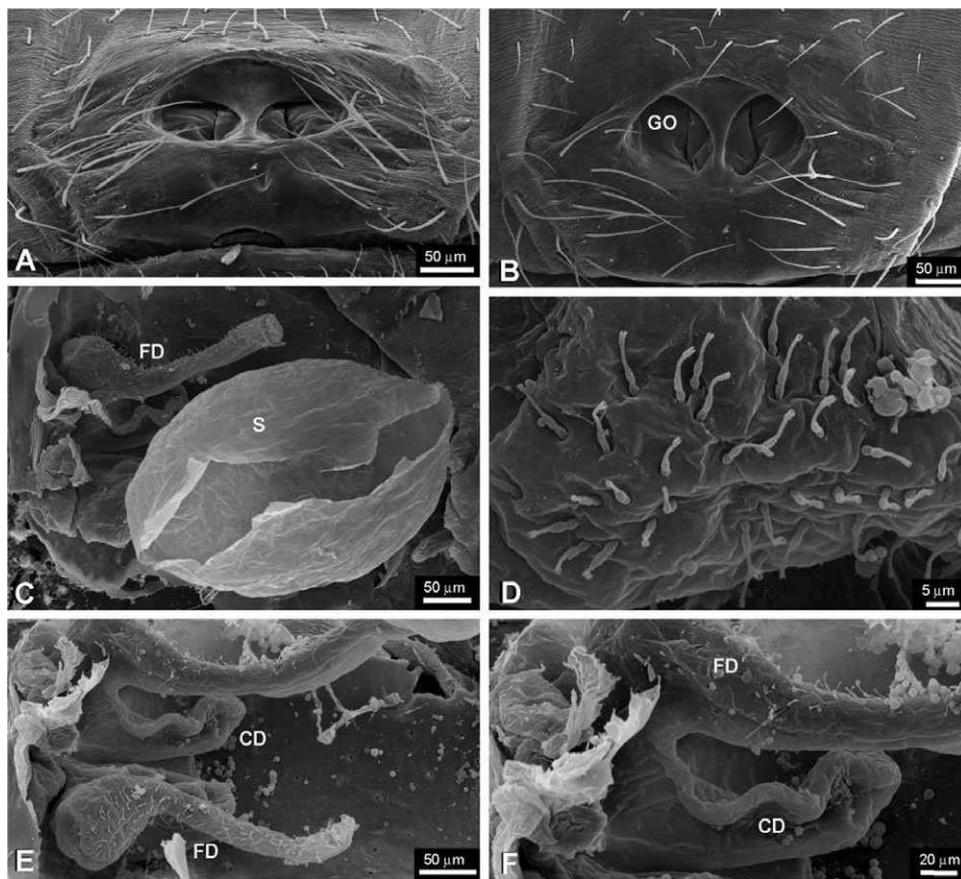
**Description: Female:** body length from 3.2 to 10.3 mm. Cephalothorax fovea formed by two deep longitudinal pits (Figs 42A, 47B). Sternum as wide as long (Figs 42H, 47G). Labium trapezoidal, wider than long, and rebordered. Ocular area lower than carapace lateral margins (Fig. 47A). Anterior surface of chelicerae smooth, boss present (Figs 42D, 47D). Secondary eyes with canoe-shaped tapetum (Levi, 1980: figs 48, 49, 65, 66). Eyes subequal in size, lateral eyes slightly smaller, juxtaposed and on a tubercle. Clypeus one AME diameter high. Abdomen longer



**Figure 52.** *Mesida argentiopunctata* cephalothorax: A, female cephalothorax ventral view and sternum. B, female tangential view. C, female dorsal view. D, female chelicera. E, male chelicera. F, male cephalothorax dorsal view. G, female femur IV trichobothria. H, male tangential view. Images of female specimens from SEMFAP061, male images from SEMFAP037.

than wide, covered with silver guanine patches (Fig. 1E). Booklung cuticle smooth (Figs 41A, 46A). Tracheal spiracle near the spinnerets (Fig. 41B), internally covered with more than eight accessory glands (Fig. 46B). Median tracheae not ramified, with rounded tips (Figs 41C, D, 46C–E). ALS with c. 65 piriform spigots. PMS with three to four aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface. PLS with c. 20 aciniform spigots roughly arranged in two parallel lines; distal end of the aggregate spigots embracing the distal end of the flagelliform spigot. Epigynal

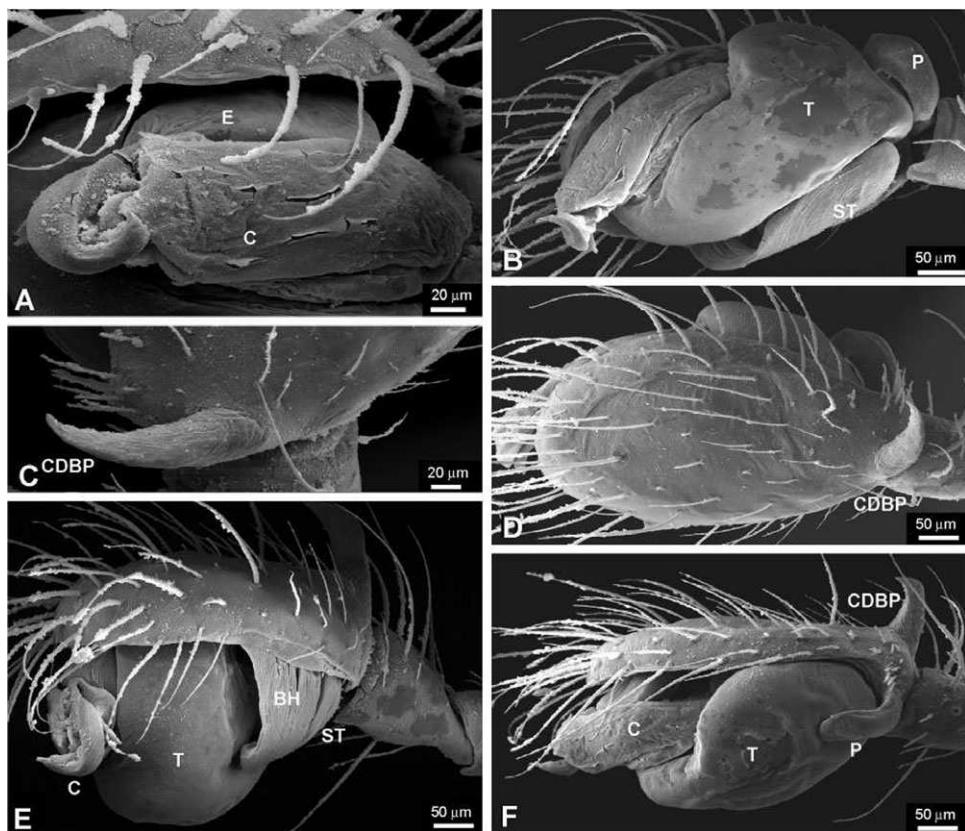
plate well sclerotized and flat in most species, ventrally projected in *L. argyra* (Figs 43A, 48A, B). Copulatory openings ventrally orientated, laterally displaced in *L. argyra* (Fig. 50D). Copulatory ducts more than half the spermathecae length but less than its total length, cuticle sclerotization variable (Figs 45D, 50D). Fertilization duct sclerotization variable, distal section usually well sclerotized (Fig. 43B–E). Accessory glands concentrated between the spermathecae and fertilization duct junction (Fig. 43B–D). Accessory gland bases considerably enlarged giving them an inverted acorn form (Figs 43F, 48D).



**Figure 53.** *Mesida argentiopunctata* epigynum: A, posterior view. B, ventral view. C, dorsal view. D, accessory glands. E and F, copulatory and fertilization ducts. All images from SEMFAP061.

**Male:** slightly smaller than females; no significant sexual size dimorphism has been reported for *Leucauge* species. Male somatic morphology as in female except for having the cheliceral anterior surface macrosetae thicker and lacking the cheliceral boss (Figs 42C, H, 47C). Epiandrous plate well sclerotized, fusules immersed in a transverse groove. This groove can be continuous or subdivided (Figs 41E, 46G). Epiandrous fusules not immersed in pits and with their bases wider than the fusule shaft. PLS triplet reduced to nubbins (Figs 41F, 46F). Male palpal patella with one long macroseta, palpal tibia more than twice as long as wide (Figs 42H, 49F). Cymbium dorsal surface can be either smooth (Fig. 44B) or with processes and modified macrosetae; the cymbium of *L. argyra* has an enormous modified macroseta and a cymbial dorsobasal process (Fig. 49C). Paracymbium hook-shaped, without apophyses, and considerably shorter than the cymbium length (Figs 44C, 49E). Tegulum roughly oval, with a mesal depression produced by the displaced subtegulum (Figs 44F, 49F). Conductor

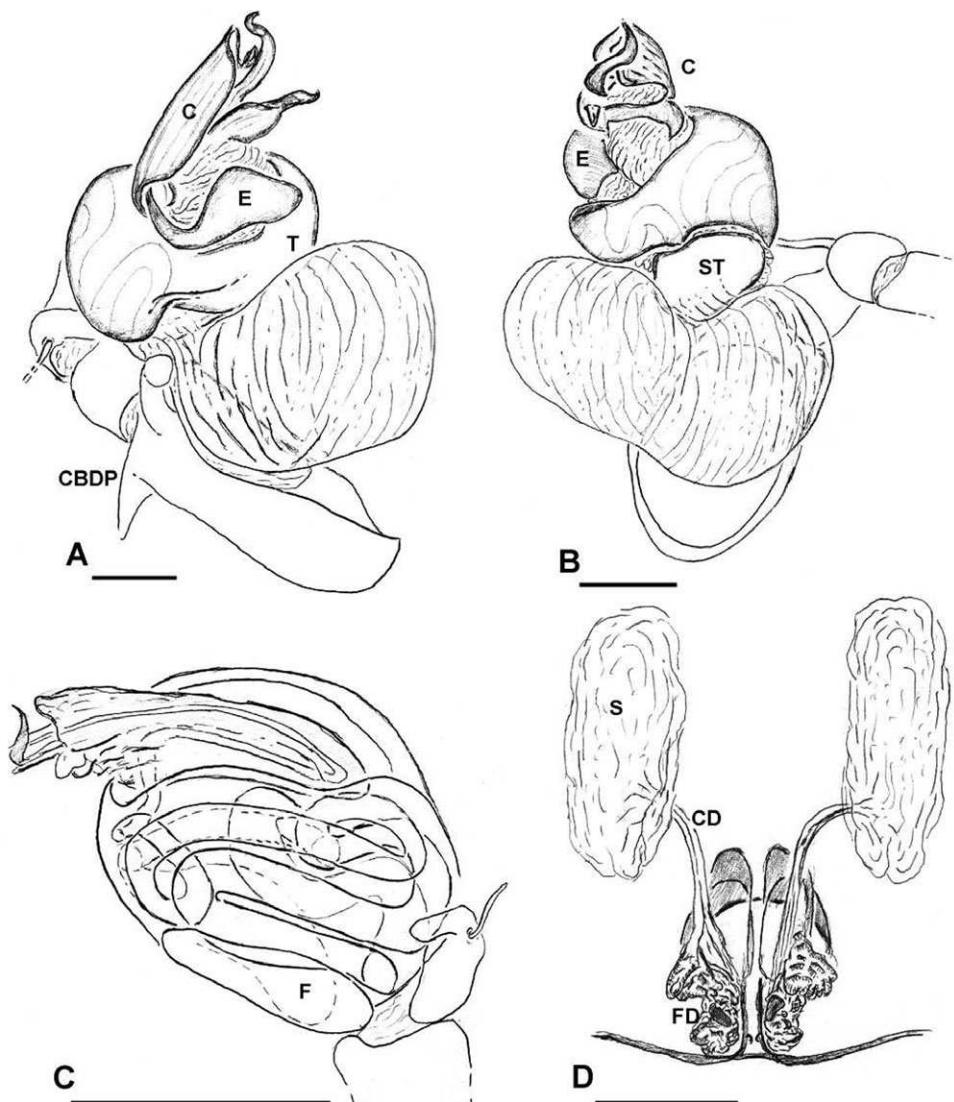
rigid, although some parts are weakly sclerotized, its attachment to the tegulum membranous and originating at the ventral edge of the tegulum. The part of the tegulum where the embolus and conductor arise is membranous in *L. venusta* and other leucaugine genera, in the former species the embolus and tegulum attachment are close together. Usually the conductor's base apex and margins are more sclerotized and can bear distal apophyses (Figs 44A, E, F, 45A, 49D, F, 50A). Embolus base rectangular, longer than wide. Embolus flagelliform, considerably narrower than its base (Figs 44D, 45C, 50C), flexible and weakly sclerotized. Sperm duct path convoluted with several coils (Figs 45B, 50B). Although Archer (1951: fig. 7) mentioned that *L. argyra* has a median apophysis we have not found any tegular apophyses, other than the conductor, in any of the tetragnathid species that we have studied, including *L. argyra*. This species has a huge macroseta on the dorsal surface of the cymbium (Fig. 49B, C) not homologous to the cymbial dorsobasal process by the conjunction test (Patterson, 1982).



**Figure 54.** *Mesida argentiopunctata* male pedipalp: A, apical view. B, ventral view. C, cymbial dorsobasal process. D, pedipalp dorsal view. E, mesal view. F, ectal view. All images from SEMFAP037.

**Natural history:** This genus includes 170 species and eight subspecies with a worldwide geographical distribution, except western Europe (Platnick, 2009). Many *Leucauge* species build horizontal webs with more than 30 radii and spirals, an open hub, and a barrier web below the orb (Fig. 3F; Levi, 1980: plates 4–5; Eberhard, 1982, 1987, 1988a, 2001). Their webs are usually found on low vegetation in a diversity of habitats and are often built in open sunny spots, such as patches of secondary growth along roads and forest gaps, and in gardens and orchards. Some species prefer habitats along the shores of fresh water bodies whereas other species are found in pristine primary forests. Many studies have been published on a diversity of aspects of the biology of a few *Leucauge* species, to the extent that these spiders can be referred as to model organisms for spider biology. For example, studies of *Leucauge mariana* (Taczanowski, in Keyserling, 1881b) include those of the early and late stages of web building behaviours (Eberhard, 1982, 1988a, b, 1990a; Zschokke, 2002), internal anatomy (Palmgren, 1979), effects of gravity on web architecture, the behaviour involved in dispersal by

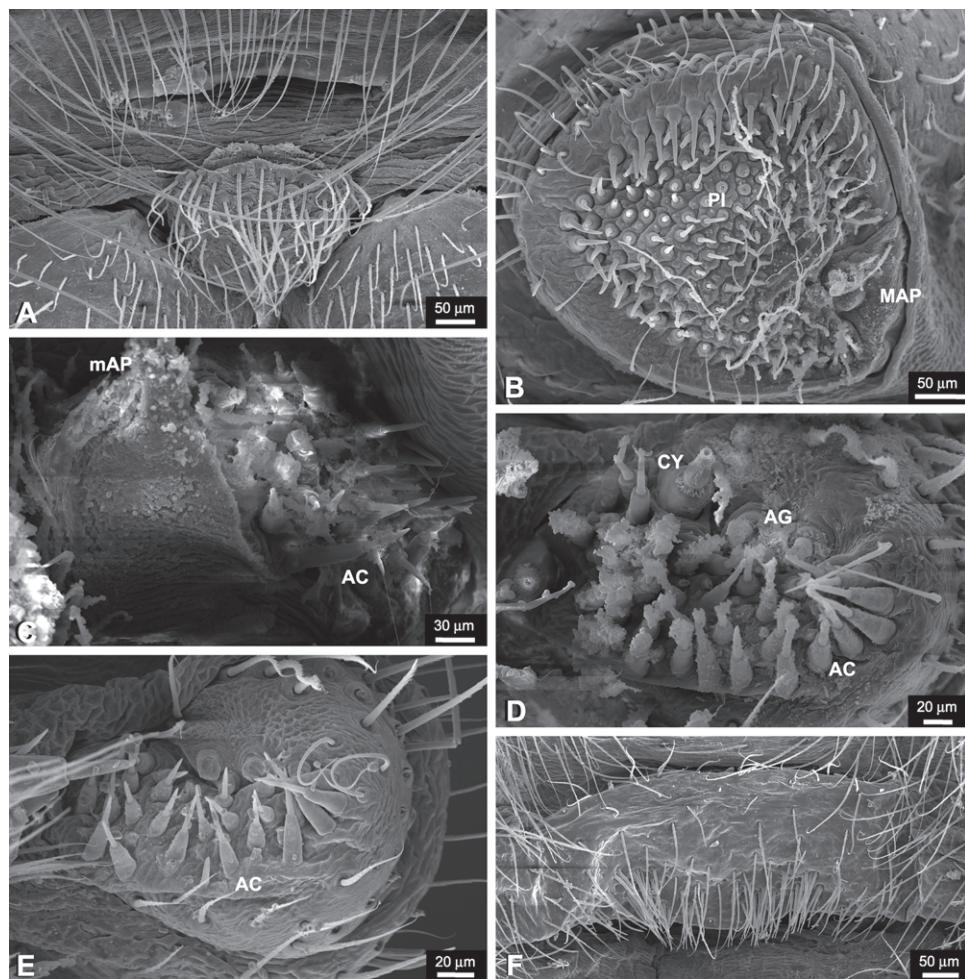
airborne silk lines (Eberhard, 1987), mating behaviour and sexual selection in relation to genitalic development (Eberhard & Huber, 1998a, b), kleptoparasitic associations, and predation rates and preferences (Hénaut, 2000). *Leucauge venusta* has been studied for capture silk stickiness (Opell, 1997), variations in web construction (Hénaut, García-Ballinas & Alauzet, 2006), web architecture variations either in solitary or aggregations (Buskirk, 1986), kleptoparasitic interactions (Hénaut *et al.*, 2005), community structure (Peck, 1966; Post & Riechert, 1977), variations in the material properties of dragline silk across many spiders including *L. venusta* (Swanson *et al.*, 2006), amongst many others. Other works on American species include the study of the effects of parasitoid toxins in the web building behaviour of *L. argyra* (Eberhard, 2001). In addition, a considerable number of studies has been conducted with some Palaeotropical *Leucauge* species such as the predatory behaviour of *Leucauge magnifica* (Yoshida, 2000) or web architecture in relation to predation in *Leucauge decorata* (Blackwall, 1864; Li & Lee, 2004), amongst others.



**Figure 55.** *Mesida argentiopunctata* genital anatomy illustrations: A and B, male pedipalp expanded. C, pedipalp bulb cleared ventral view. D, cleared epigynum dorsal view.

**Taxonomy:** *Leucauge* has never been revised except for treatments of some North American (Levi, 1980) and Asian species (Yaginuma, 1954; Kim, Kim & Lee, 1999; Song, Zhu & Chen, 1999; Hu, 2001; Namkung, 2003; Zhu *et al.*, 2003). The specimens that we have studied for the description and diagnosis of this genus belong to *L. venusta* (Walckenaer, 1841) and *L. argyra* (Walckenaer, 1841), two of the species that have been most intensively studied. The current number of described species of *Leucauge* in the Neotropics represents a small fraction of the total number of species found in museum collections. A phylogenetic analysis that included four *Leucauge* species recovered this genus as monophyletic and sister to a clade that includes *Okileucauge*, *Tylorida*, and *Mesida* (Tanikawa, 2001; Fig. 141B). In Tanikawa's analysis

*Leucauge* monophyly was supported by a single synapomorphy, the presence of parallel trichobothria rows with more than ten pairs on femur IV. It is likely that the genus *Leucauge* as currently delimited is either polyphyletic or paraphyletic. *Leucauge argyra*, which has been previously recognized as belonging to a different genus (*Plesiometra* F. O. P. Cambridge, 1903; e.g. see Eberhard, 2001 and Levi, 2005b), was recovered in our analysis as sister to *L. venusta*. The genera *Alcimosphenus* Simon, 1895 and *Opas* O. P. Cambridge, 1896, previously included in *Leucauge*, have been recently recognized as different genera (Levi, 2005c, 2008). The analyses of both data sets (morphology plus behaviour and morphology plus behaviour plus DNA sequences) recover *L. venusta* and *L. argyra* as sister taxa (Figs 143A, B, 144). In



**Figure 56.** *Meta menardi* abdomen: A, tracheal spiracle and colulus. B, anterior lateral spinnerets. C, posterior median spinnerets. D, female posterior lateral spinnerets. E, male posterior lateral spinnerets. F, epiandrous fusules. Images (A–D) from SEMFAP042, (E–F) from SEMFAP076.

order to test whether *L. argyra* could belong to a separate genus (and whether the remaining species in *Leucauge* form a clade), a larger sample of *Leucauge* species and representatives from closely genera would be required. Both data sets suggest that *Leucauge* is sister to the Palaeotropical genus *Opadometa*.

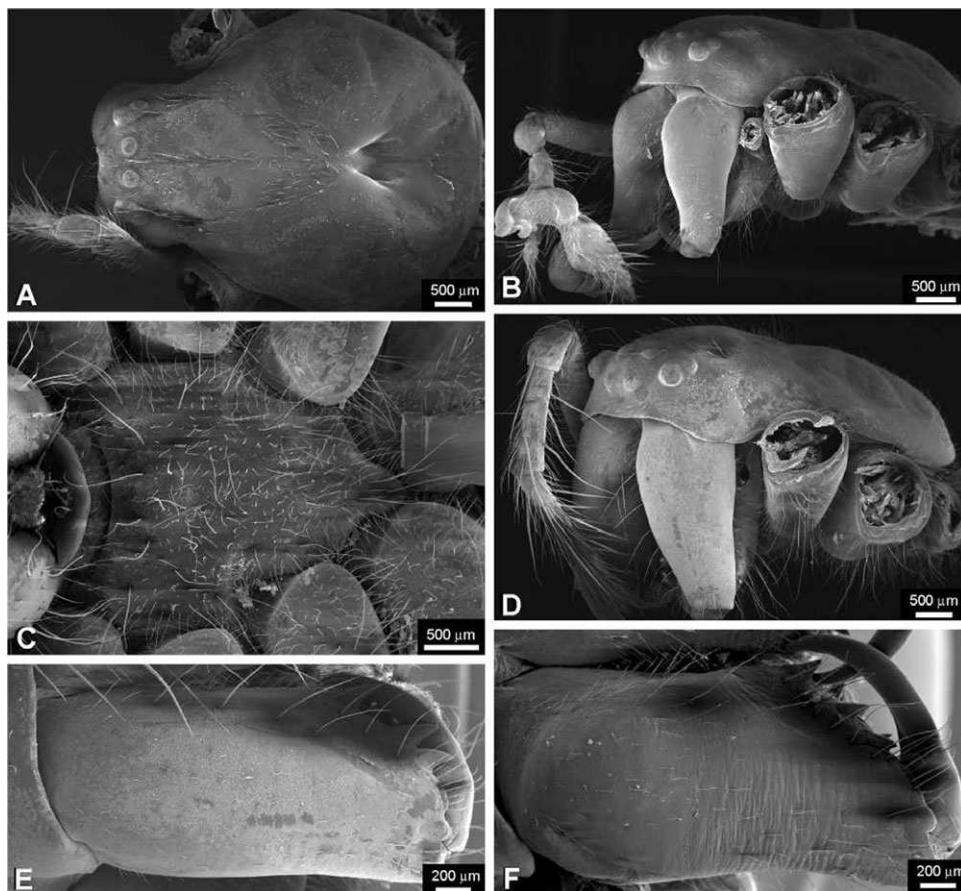
#### MESIDA KULCZYŃSKI, 1911 (FIGS 4A, 51–55)

**Type species:** *Mesida humilis* Kulczyński, 1911. Type specimen a female from Papua New Guinea, depository unknown.

**Diagnosis:** *Mesida* species are very similar to those of *Leucauge* but can be distinguished from the latter and from all other tetragnathids by the following combination of characters: two parallel rows of feathered trichobothria on the femora IV ectal surface (Fig. 61H); copulatory and fertilization ducts running

parallel before entering the spermathecae (Figs 43E, 55D); flat epigynal plate with a round atrium (Fig. 53A, B; Chrysanthus, 1975: fig. 6); male cheliceral anterior surface with a median spur (Fig. 52E; Chrysanthus, 1975: fig. 7); and the presence of a cymbial dorsobasal process (Fig. 54C, D).

**Description: Female:** body length c. 7.0 mm. Cephalothorax fovea formed by two short longitudinal pits, carapace cephalic area almost as wide as thoracic area (Fig. 52C). Ocular area lower than carapace lateral margins (Fig. 52B). Labium trapezoidal, wider than long and rebordered. Sternum as wide as long (Fig. 52A). Anterior surface of chelicerae smooth; boss present (Fig. 52D, E). Secondary eyes with canoe-shaped tapetum. Eyes subequal in size, lateral eyes slightly smaller, juxtaposed, and on a tubercle. Clypeus less than one AME diameter. Abdomen longer than wide, covered with silver guanine

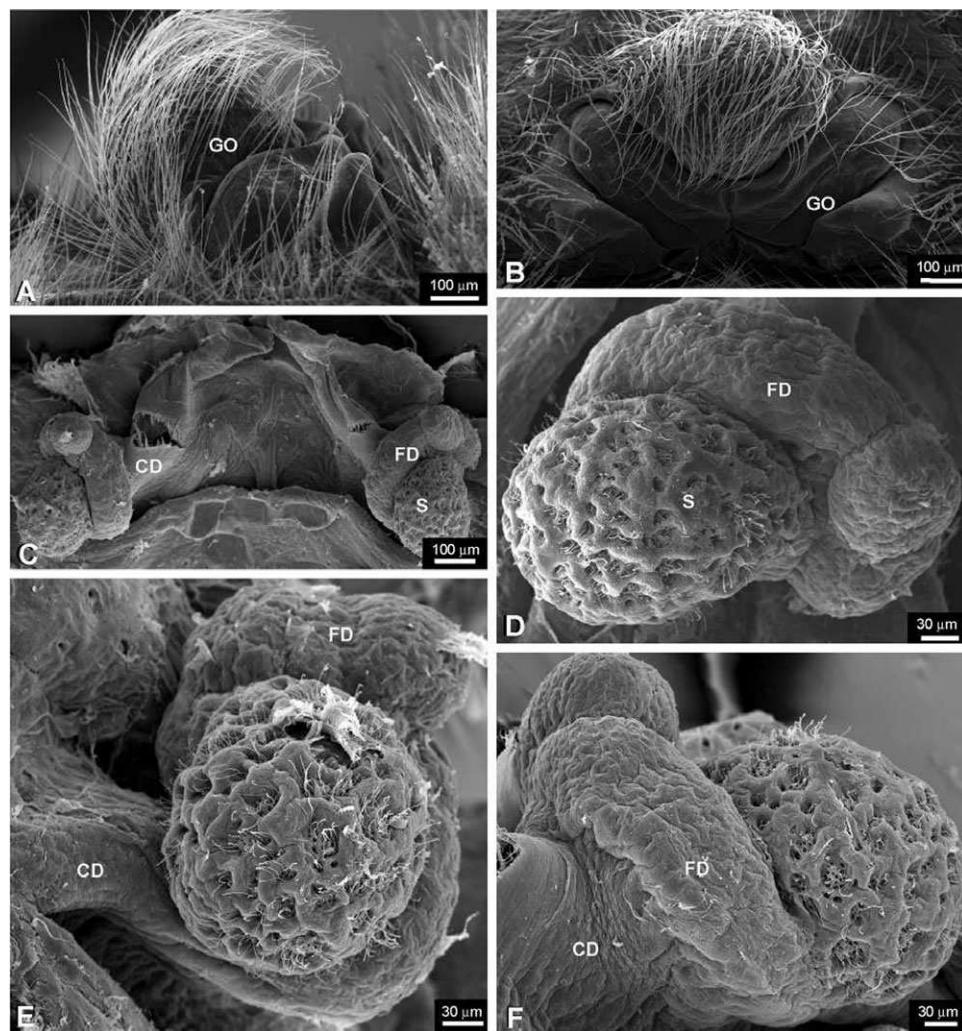


**Figure 57.** *Meta menardi* cephalothorax: A, female dorsal view. B, male tangential view. C, female sternum. D, female tangential view. E, female chelicera. F, male chelicera. Images from female specimens SEMFAP042, from male SEMFAP076.

patches, some species such as *Mesida argentiopunctata* have a caudal abdominal tubercle. Booklung cuticle smooth. Tracheal spiracle near the spinnerets, with few accessory glands (Fig. 51C). Median tracheae not ramified, with rounded tips (Fig. 51B, D, F). ALS with c. 60 piriform spigots. PMS with three aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface. PLS with c. 20 aciniform spigots roughly arranged in two parallel lines, distal end of the aggregate spigots embracing the distal end of the flagelliform spigot (Fig. 51E). Epigynal plate flat, copulatory openings ventrally orientated and in the shape of longitudinal grooves (Fig. 53A, B). Spermathecae walls weakly sclerotized (Fig. 53C). Copulatory ducts more than half the spermathecae length but less than its total length, cuticle weakly sclerotized (Fig. 53C). Fertilization ducts coiled and sclerotized at their distal end (Fig. 55D). Accessory glands concentrated over the

ducts, with their bases slightly wider than the duct (Fig. 53D–F).

**Male:** size and somatic morphology similar to that of the female, except that the cheliceral anterior surface cuticle is rugose, with a dorsal apophysis (Fig. 52E). Epiandrous plate well sclerotized, posterior margin thicker than the anterior margin (Fig. 51G); fusules immersed in a transverse groove, their bases wider than the fusule shaft. PLS triplet reduced to nubbins. Male palpal patella with one macroseta. Paracymbium hook-shaped, without apophyses and considerably shorter than the cymbium length (Fig. 54F). Tegulum roughly oval, with an ectal depression produced by the displaced subtegulum (Fig. 54B). Conductor rigid, with sclerotized edges although some parts are weakly sclerotized. Conductor-tegulum attachment membranous, originating at the ventral edge of the tegulum (Figs 54B, 55B). Embolus base rectangular, longer than wide (Fig. 55A). Embolus flexible and weakly sclerotized.

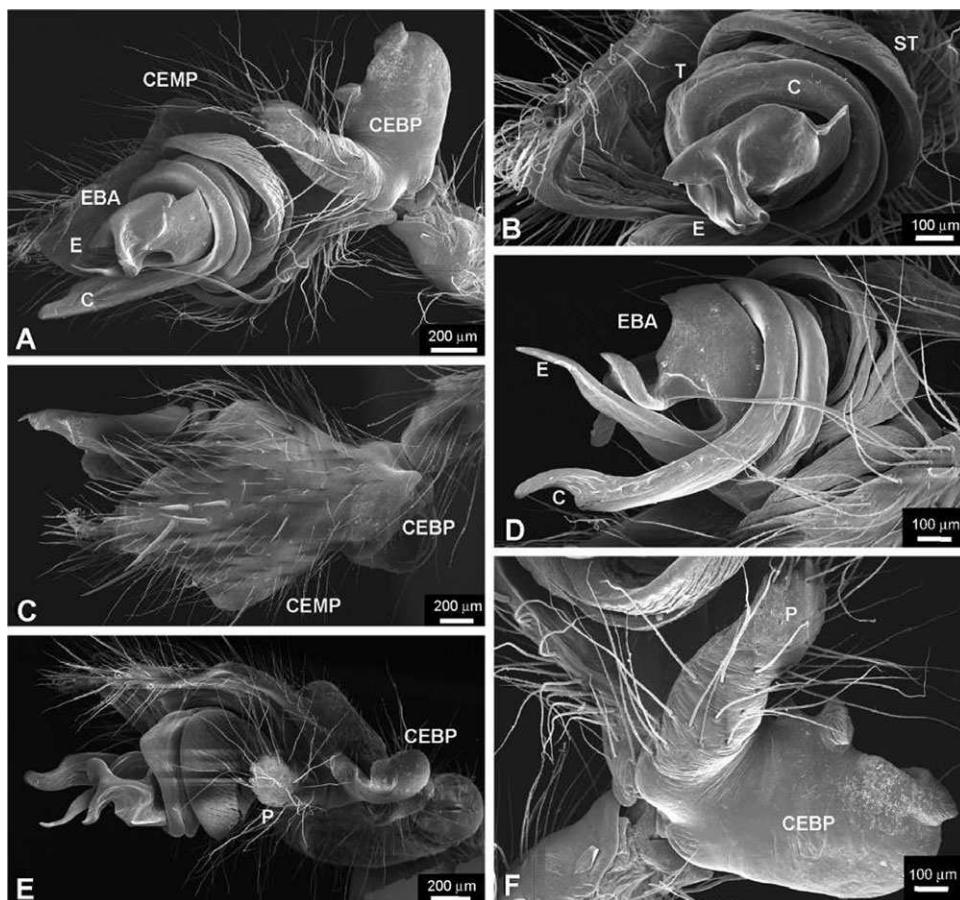


**Figure 58.** *Meta menardi* epigynum: A, lateral view. B, posterior view. C, dorsal view. D–F, spermatheca and ducts view. All images from SEMFAP042.

Sperm duct path convoluted with several coils (Fig. 55C).

**Natural history:** This genus includes 12 species and one subspecies, all with an Australasian distribution (Chrysanthus, 1975; Davies, 1988; Barrion & Litsinger, 1995; Zhu *et al.*, 2003). *Mesida argentiopunctata* builds vertical webs with c. 20 radii, fewer than c. 20 spirals and open hubs (Fig. 4A). These webs are usually found on the forest lower vegetation. The biology of *Mesida* remains largely unknown. A recent study comparing the spider communities between habitats with different levels of disturbance found that *Mesida gemmea* (Hasselt, 1882) and *Leucauge argentina* (Hasselt, 1882) were the most abundant species in primary forest on the Orchid Island, south of Taiwan (Chen & Tso, 2004).

**Taxonomy:** *Mesida* has never been revised. Our description and diagnosis is based on specimens of *M. argentiopunctata* and the species descriptions and illustrations of *M. humilis* by Chrysanthus (1975). The best documented species of this genus is *M. argentiopunctata*, which we have coded in our character matrix. It is possible that *Mesida* is a clade within *Leucauge* or paraphyletic in relation to this latter genus (although *Leucauge*'s monophyly has not been tested in sufficient depth). Several Asian species of *Leucauge* share many diagnostic characters with *Mesida*, such as the long and perpendicular cymbial dorsobasal process (Song *et al.*, 1999: fig. 122A–N). Tanikawa (2001) proposed that *Mesida* and *Tylorida* were sister taxa based on one synapomorphy, the presence of a spur on the male chelicera (Fig. 52H). In Tanikawa's analysis *Mesida* was represented by two species: *M. argentiopunctata* plus one unidentified



**Figure 59.** *Meta menardi* male pedipalp: A, ventral view. B, apical view. C, dorsal view. D, embolic division. E, ectal view. F, cymbial ectobasal process and paracymbium. All images from SEMFAP076.

species (Tanikawa, 2001: fig. 141B). The cladistic analysis of Álvarez-Padilla (2007: fig. 142B) recovered *Mesida* and *Opadometa* as sister taxa based on one synapomorphy, the male chelicerae proportionally larger than the female chelicerae. The analyses of both our data sets (morphology plus behaviour and morphology plus behaviour plus DNA sequences) recovered *Mesida* as sister to a clade that includes *Opadometa* plus *Leucauge* (Figs 143A, 144).

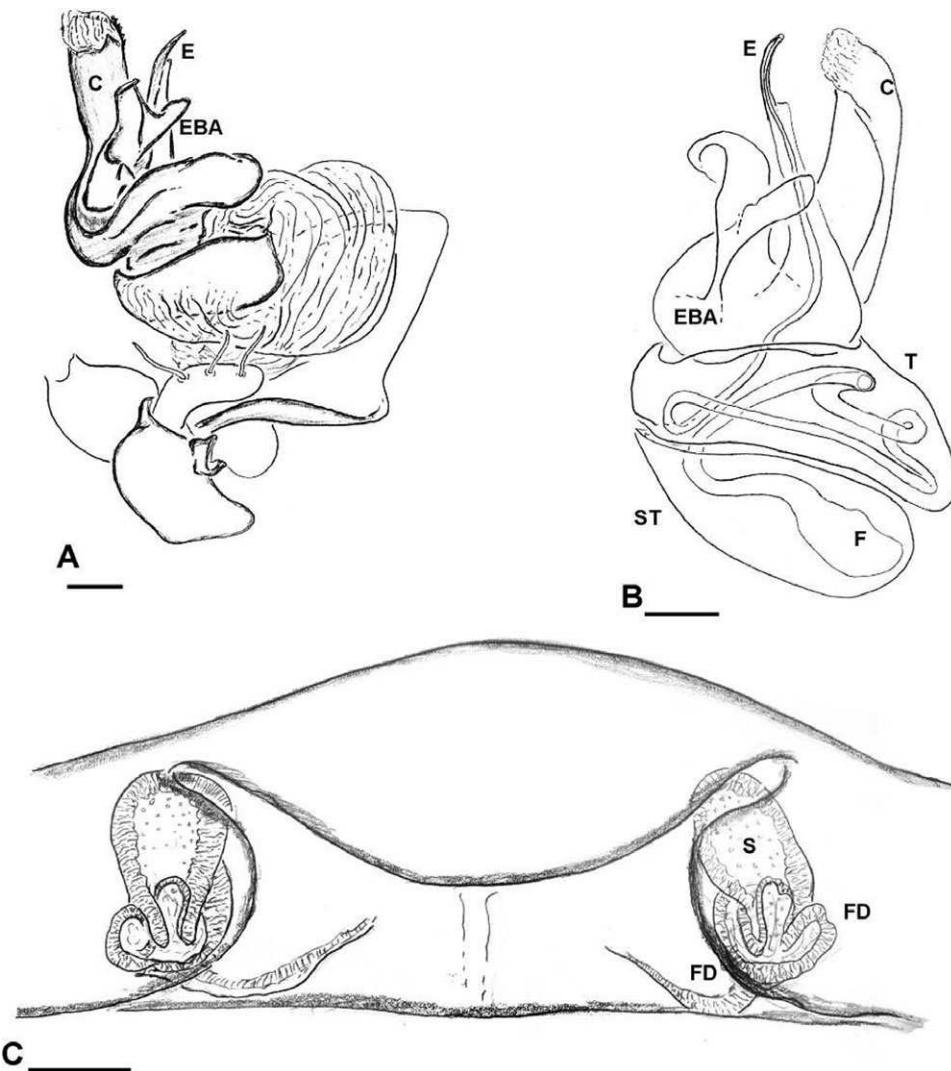
#### META C. L. KOCH, 1836 (FIGS 1D, 4C, 56–60)

*Type species:* *Meta menardi* Latreille, 1804. The type specimens of *Aranea menardi* are lost (Levi, 1980).

*Diagnosis:* *Meta* species can be distinguished from all other tetragnathid genera by the following combination of characters: abdomen as high as long (Fig. 1D; Levi, 1980: figs 113–115); PMS anterior surface with more than 20 aciniform spigots (Fig. 56C); epigynum ventrally projected with the copulatory openings posteriorly orientated (Fig. 58A, B); fertilization ducts crossing over the spermathecae (Figs 58C–F, 60C);

cymbial ectobasal process and cymbial ectomedian process present (Fig. 59A); cymbial ectobasal process formed by a massive cuticular fold and cymbial ectomedian process shorter than half the cymbial width without macrosetae (Fig. 59A–F); and by having the metaine embolic apophysis, when present, fused to the embolus base (Fig. 60A, B).

*Description: Female:* body length c. 14.0 mm. Cephalic fovea formed by two deep longitudinal pits (Fig. 57A). Ocular area lower than the carapace lateral margins (Fig. 57B, D). Labium trapezoidal, wider than long and rebordered. Sternum as wide as long (Fig. 57C). Anterior surface of chelicerae smooth, boss present (Fig. 57B, D). Secondary eyes with canoe-shaped tapetum (Levi, 1980: figs 122, 123). Eyes roughly subequal in size, lateral eyes slightly smaller and juxtaposed and on a tubercle (Fig. 57A, B, D). Clypeus c. 1.5 times the AME diameter. Booklung cuticle grooved. Tracheal spiracle near the spinnerets (Fig. 56A). ALS piriform spigots base rounded (Fig. 56B). PLS with more than 20 aciniform spigots;

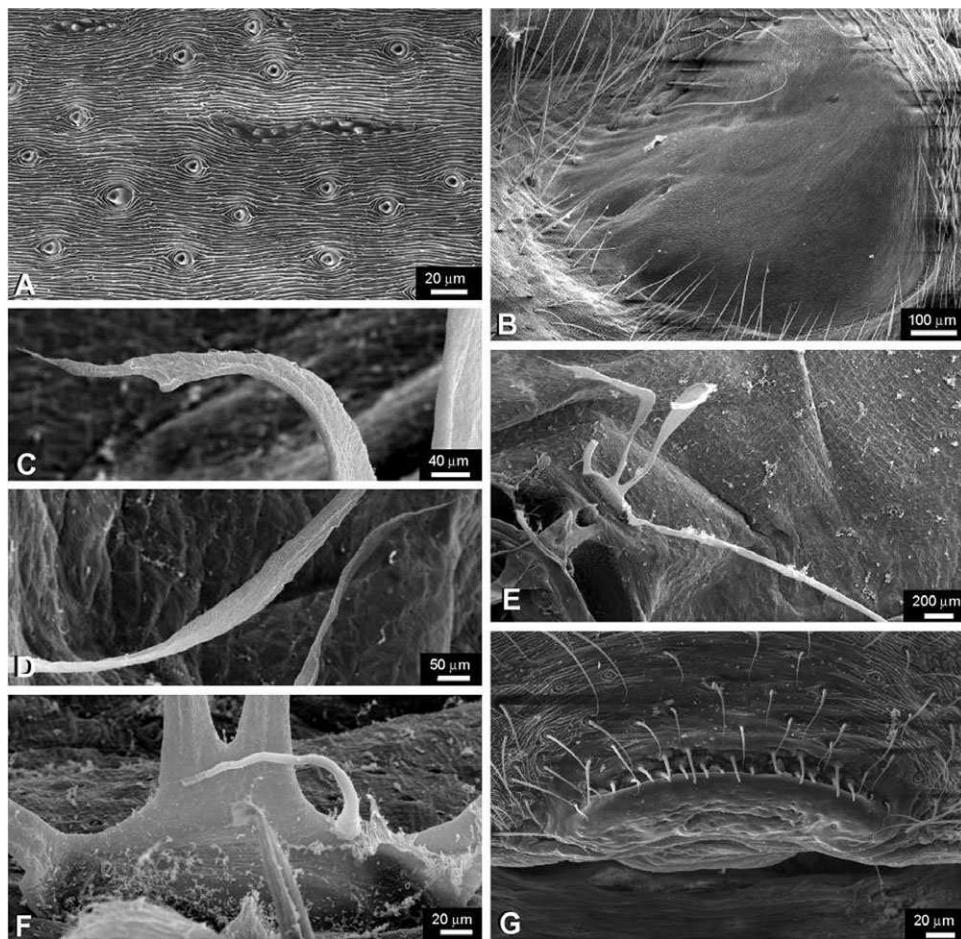


**Figure 60.** *Meta menardi* genital anatomy illustrations: A, male pedipalp expanded. B, pedipalp bulb cleared ventral view. C, cleared epigynum dorsal view.

distal end of the aggregate spigots embracing the tip of the flagelliform spigot (Fig. 56D; Hormiga *et al.*, 1995: fig. 19A–D). Epigynal plate protruded, copulatory openings posteriorly orientated and in the shape of longitudinal grooves (Fig. 58A, B). Spermathecae walls well sclerotized (Fig. 58C–F). Cuticle of copulatory ducts well sclerotized and shorter than half the spermathecae (Figs 58F, 60C). Wiegle (1967) proposed that *M. menardi* had a semi-entelegyne reproductive system, lacking fertilization ducts and, as in haplogyne reproductive systems, that the sperm must pass through the copulatory ducts to fertilize the eggs. Levi (1980: 40) mentioned that he could not verify that *M. menardi* lacked fertilization ducts, but did not state that this species had them. We found by means of SEM that *M. menardi* indeed has fertilization ducts; furthermore, these ducts cross over

the spermathecae and copulatory duct junction (Fig. 58D–F). Owing to this particular configuration it is difficult to differentiate both ducts in cleared epigyna (Fig. 60C). Accessory glands distributed over the spermathecae, with gland openings arranged in groups (Fig. 58E).

**Male:** body length c. 10.0 mm. Cephalothorax morphology as in females, except that the anterior cheliceral cuticle is rugose (Fig. 57B, F). Abdomen cylindrical. PLS triplet reduced to nubbins (Fig. 56E). Epiandrous fusules dispersed over a flat plate and immersed in pits (Fig. 56F). Palpal patella with one macroseta; palpal tibia slightly longer than wide. Tegulum wider than long and slightly larger than the subtegulum (Fig. 60B). Conductor well sclerotized and fused to the tegulum (Fig. 60A). Embolic apophysis bearing several processes. Embolus short and well



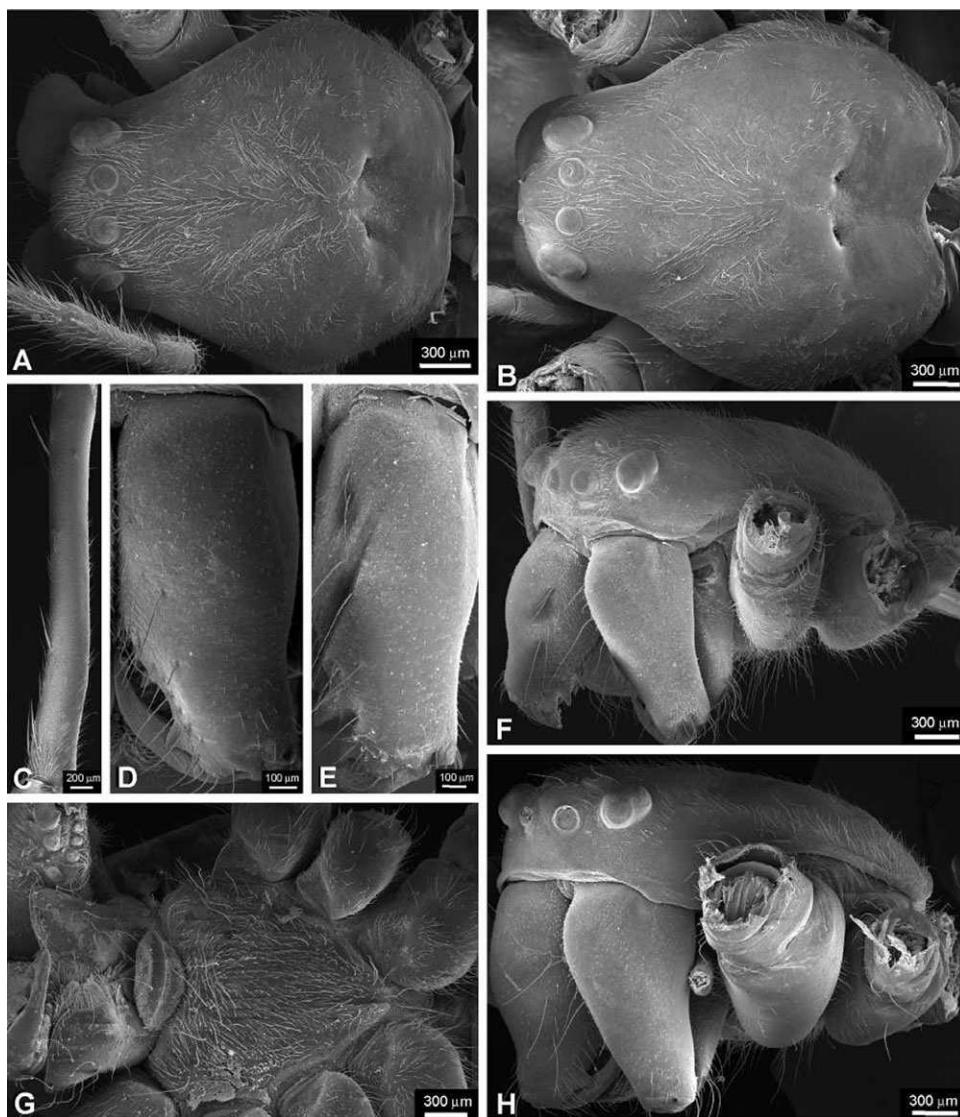
**Figure 61.** *Metabus ocellatus* abdomen: A, cuticle of the abdomen, close up of median lateral section. B, booklung external cuticle. C and D, median tracheae tip. E, tracheal system dorsal view. F, tracheal spiracle posterior view. G, epiandrous fusules. All images from SEMFAP036.

sclerotized (Figs 59B, 60A, B). Sperm duct with fewer than two switchbacks (Fig. 60B).

**Natural history:** *Meta* includes 37 species with a Holarctic distribution (Platnick, 2009). *Meta menardi* builds vertical webs with open hubs, few radii, and few spirals (fewer than 15) (Fig. 4C). These spiders are usually found inside caves, near the entrance or deep inside, and in humid dark places such as tunnels, mines, and wells (Levi, 1980). The egg-sac is white, large, drop-shaped, and hangs from a thread near the web (Comstock, 1948; Levi, 1980). *Meta menardi* is the only species in which the biology is relatively well documented (Ecker & Moritz, 1992). The web building behaviour of *M. menardi* was described by Eberhard (1982). Some studies of this species have covered aspects of its diet and predatory behaviour (Yoshida & Shinkai, 1993; Smithers, 1996, 2005a), its distribution within its habitat (Smithers,

1995), and observations on its dispersal biology and early life stages (Smithers, 2005b; Smithers & Smith, 1998).

**Taxonomy:** North American *Meta* and some European and Japanese species have been revised (Levi, 1980; Marusik, 1986; Yaginuma, 1986; Marusik & Koponen, 1992). Our description and diagnosis are based on the species included in Levi (1980), Marusik & Koponen (1992), and the illustrations of Roberts (1985) of the European species. We coded *M. menardi* for the phylogenetic analysis, by far the species that has been most intensively studied. We propose that *Meta* and *Metellina* are different genera, as suggested by previous authors (Palmgren, 1978a; Levi, 1980; Coddington, 1990a; Marusik & Koponen, 1992). However, this hypothesis has not been cladistically tested with a sufficiently large taxonomic sample of both genera. The phylogenetic analysis that has included more



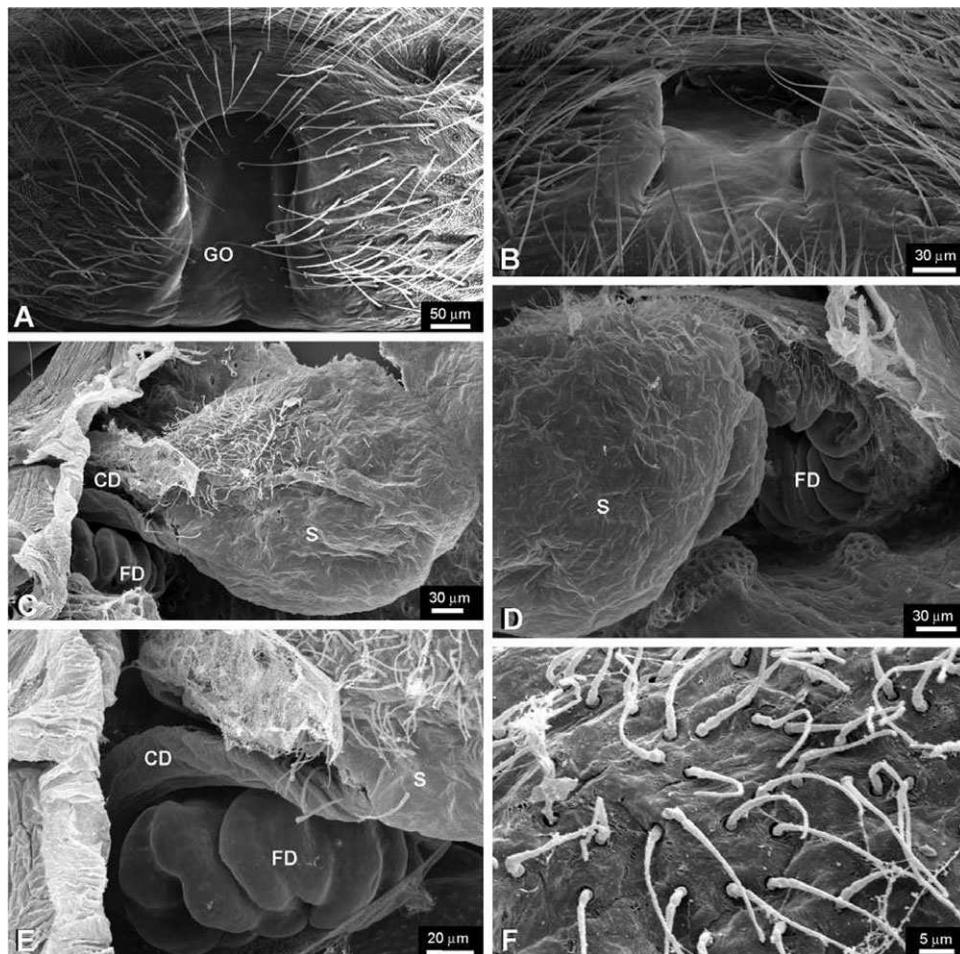
**Figure 62.** *Metabus ocellatus* cephalothorax: A, female dorsal view. B, male dorsal view. C, female femur IV ectal view. D, male chelicera. E, female chelicera. F, female tangential view. G, female cephalothorax ventral view and sternum. H, male tangential view. All images from SEMFAP036.

*Meta* species to date included only *Meta nigridorsalis* Tanikawa, 1994 and *M. reticuloides* Yaginuma, 1958 (Tanikawa, 2001: fig. 141B). This latter author proposed five synapomorphies for the genus *Meta*: male chelicerae larger than female chelicerae; large teeth on the chelicera fang furrow; sperm duct with switch backs; paracymbium large and modified; and epigynum weakly sclerotized (Tanikawa, 2001). Other phylogenetic analyses have found *Meta* as sister either to a clade comprised by *Metellina* and *Chrysometa* (Hormiga *et al.*, 1995) or to a clade including *Dolichognatha* and *Metellina* (Álvarez-Padilla, 2007). The morphology plus behaviour data set recovered *Meta*

as sister to a clade that includes *Metellina* and *Dolichognatha*; when these data were combined with DNA sequences *Meta* came out as sister to a clade that includes the previous taxa plus *Chrysometa* and *Diphya* (Fig. 144).

#### *METABUS* O. P.-CAMBRIDGE 1899 (FIGS 4B, 61–65)

*Type species:* *Metabus ocellatus* (Keyserling, 1864). The syntype series of *Tetragnatha ocellata* consists of two males and seven females from Bogota (Colombia), deposited at the Natural History Museum, London (examined).

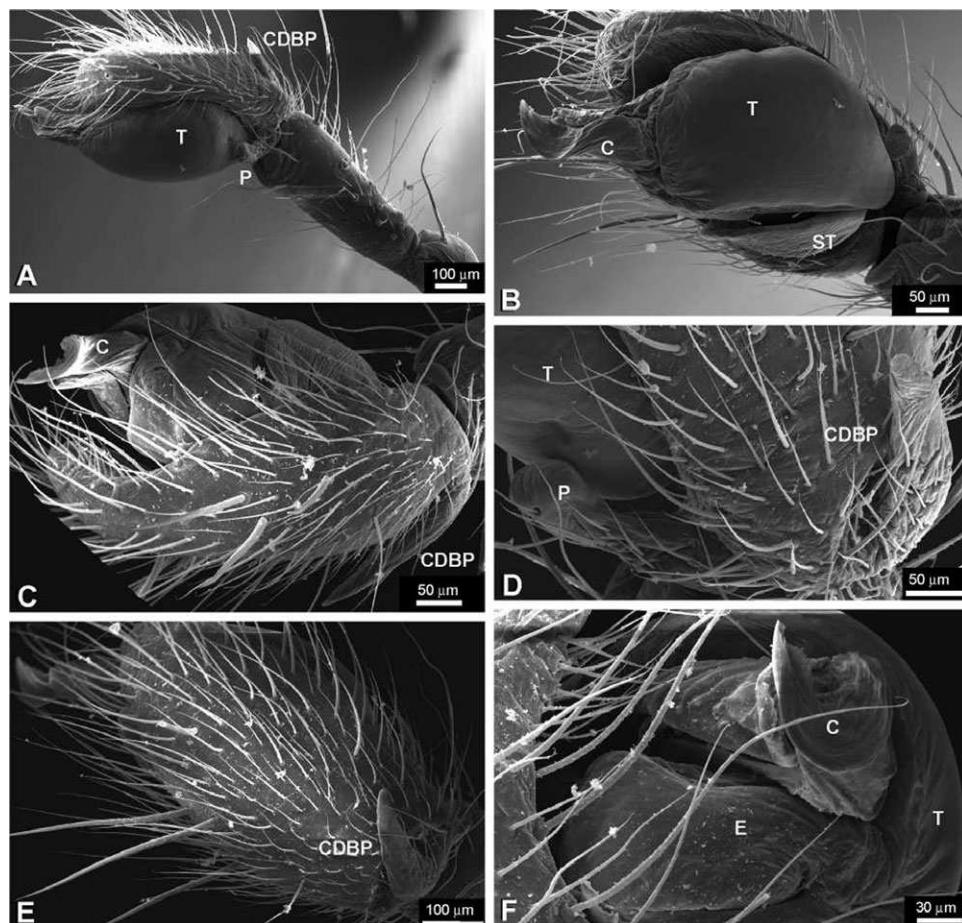


**Figure 63.** *Metabus ocellatus* epigynum: A, ventral view. B, posterior view. C, spermatheca dorsal view. D, spermatheca lateral view. E, copulatory and fertilization ducts. F, accessory glands. All images from SEMFAP036.

**Diagnosis:** *Metabus* species can be distinguished from all other tetragnathid genera by the following combination of characters: leg I more than four times the body length; femur IV without trichobothria (Fig. 62C); epigynum flat, well sclerotized and with a rectangular atrium (Fig. 63A, B); spermathecae weakly sclerotized (Figs 63C, 65C); fertilization ducts coiled over the copulatory ducts (Fig. 63B); CEDP longer than half the cymbial width and parallel to the cymbium longitudinal axis; conductor longer than wide and apically projected (Fig. 64B).

**Description: Female:** body length c. 14.0 mm. Cephalothorax fovea formed by two short transverse grooves (Fig. 62A). Ocular area lower than carapace lateral margins (Fig. 62F). Labium trapezoidal, wider than long and rebordered. Sternum longer than wide (Fig. 62G). Anterior surface of chelicerae smooth; boss present (Fig. 62E). Secondary eyes with canoe-shaped tapetum. Eyes subequal in size,

lateral eyes slightly smaller, juxtaposed, and on a tubercle. Clypeus more than one AME diameter high. Abdomen covered with silver guanine patches. Booklung cuticle smooth (Fig. 61B). Tracheal spiracle near the spinnerets, almost without accessory glands (Fig. 61F). Median tracheae not ramified, with leaf-shaped tips and shorter than half the lateral tracheae length (Fig. 61C–E). ALS with c. 70 piriform spigots. PMS with three aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface. PLS with c. 20 aciniform spigots roughly arranged in two parallel lines; distal end of the aggregate spigots embracing the distal end of the flagelliform spigot (Álvarez-Padilla, 2007: fig. 9A–C). Epigynal plate flat (Fig. 63A, B). Copulatory openings ventrally orientated with the shape of longitudinal grooves located under the atrial edges (Fig. 65C). Spermathecae walls weakly sclerotized. Copulatory ducts more than half the spermathecae



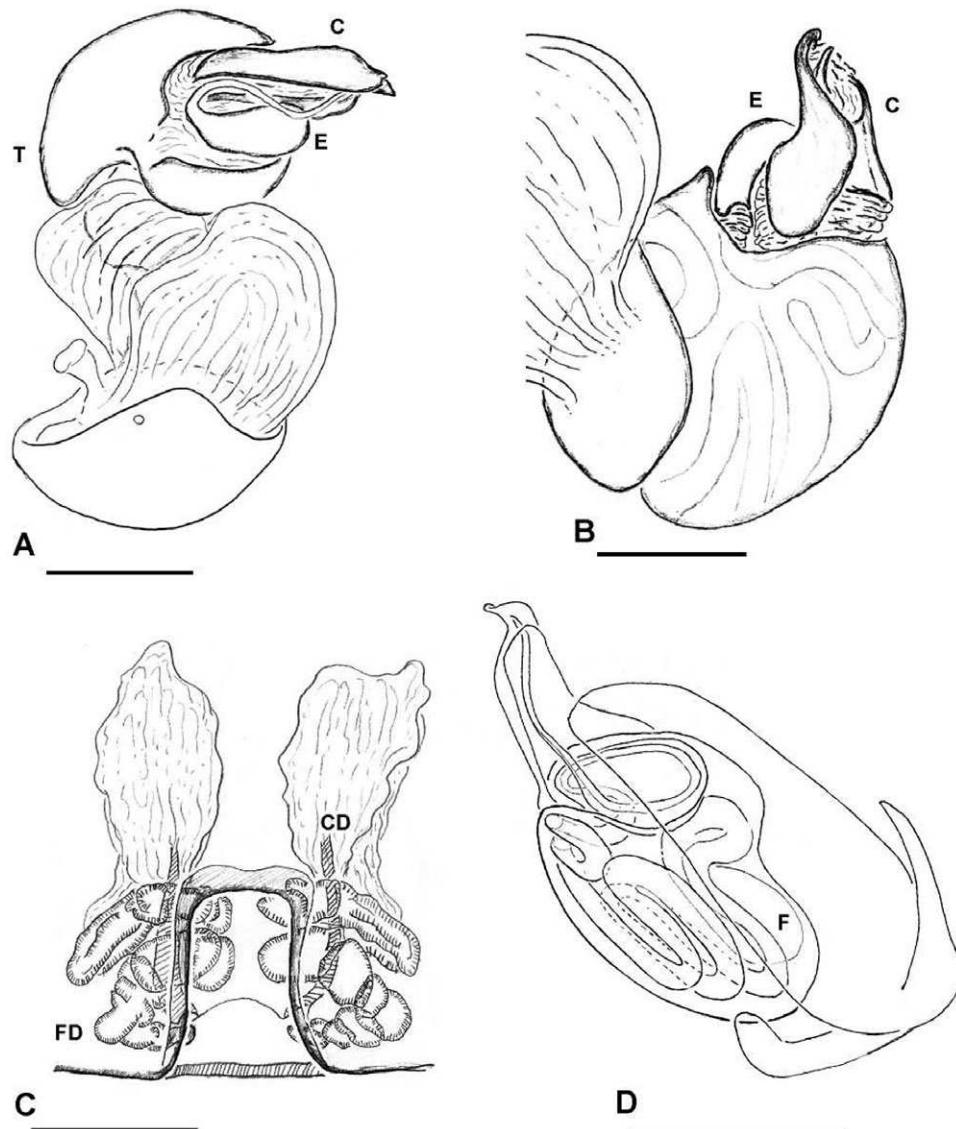
**Figure 64.** *Metabus ocellatus* male pedipalp: A, mesal view. B, ventral view. C, dorsal view. D, cymbial dorsobasal process. E, pedipalp dorsal view. F, embolus and conductor. All images from SEMFAP036.

length but less than its total length, cuticle weakly sclerotized. Fertilization ducts well sclerotized, coiled around copulatory ducts (Figs 63C–E and 65C). Accessory glands ducts in individual pits, concentrated over spermatheca-fertilization duct junction (Fig. 63C, F).

**Male:** size and somatic morphology similar to that of the female, except that legs I and II are considerably longer. Epiandrous plate well sclerotized, fusules immersed in a transverse groove with bases wider than fusule shaft. Posterior margin of the epiandrous plate thicker than the anterior margin (Fig. 61G). PLS triplet reduced to nubbins (Álvarez-Padilla, 2007: fig. 9D). Male palpal patella with one macroseta. Paracymbium hook-shaped, without apophyses and considerably shorter than cymbium length (Fig. 64A). Tegulum roughly ovoid, with an ectal depression produced by the displaced subtegulum (Fig. 64B). Conductor rigid, with sclerotized edges, although some parts are weakly sclerotized. Conductor-tegulum attachment membranous, origi-

nating at the ventral edge of the tegulum (Fig. 65A, B). Embolus base rectangular, longer than wide (Fig. 65A). Embolus flexible and weakly sclerotized. Sperm duct path convoluted, with several coils (Fig. 65D).

**Natural history:** This genus includes four species with a Neotropical distribution. *Metabus ebanoverde* Álvarez-Padilla, 2007, builds horizontal webs with open hubs, fewer than ten radii, and fewer than 20 spirals (Fig. 4B), but other *Metabus* species seem to have denser webs (Lopardo *et al.*, 2004: fig. 16). *Metabus ocellatus* (Keyserling, 1864) builds communal orb webs over ponds and shares a communal retreat during the night (Buskirk, 1975a: fig. 1, 1986; Uetz & Craig, 1997). This communal behaviour has not been reported for any other species in the family. The web building behaviour of *M. ocellatus* was described by Eberhard (1982). The communal behaviour of *M. ocellatus* has been described and discussed by Buskirk (1975b).



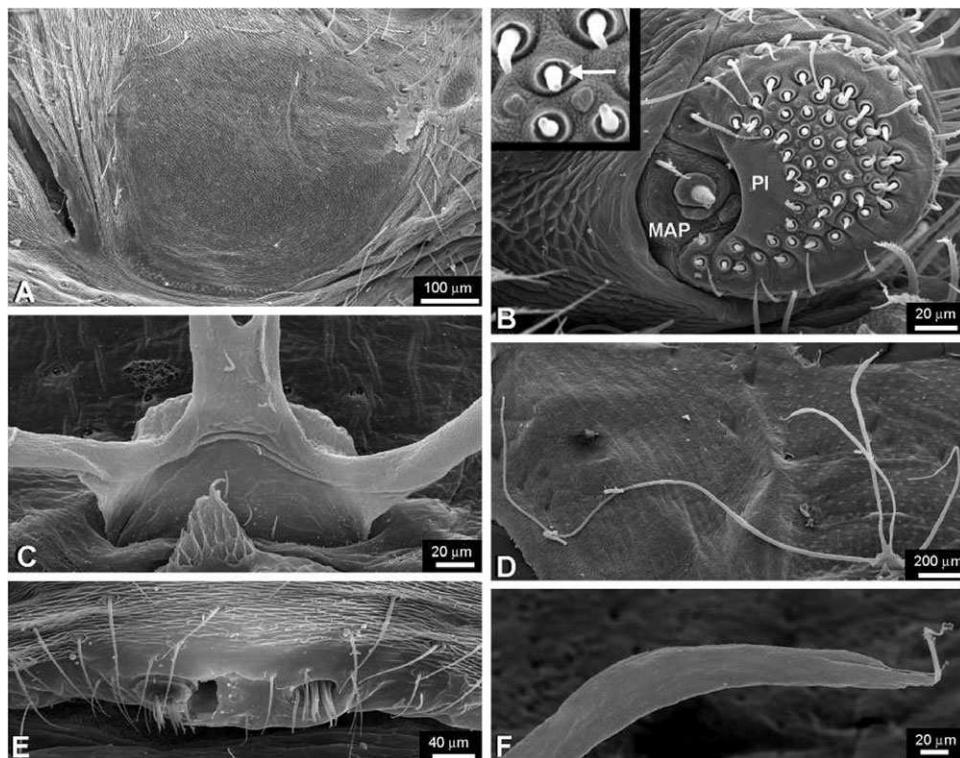
**Figure 65.** *Metabus ocellatus* genital anatomy illustrations: A, and B, male pedipalp expanded. C, cleared epigynum dorsal view. D, pedipalp bulb cleared ventral view.

**Taxonomy:** *Metabus* has recently been revised and its monophyly tested (Álvarez-Padilla, 2007). Synapomorphies for *Metabus* include the conductor apex curved apically and the absence of trichobothria on the fourth femora. In that study *Metabus* was sister to a clade that included *L. venusta* and *L. argyra* (Álvarez-Padilla, 2007: fig. 9B). *Okileuauge* Tanikawa, 2001 species are very similar to *Metabus* in their genital anatomy and somatic morphology, i.e. both genera lack femoral trichobothria. However, a previous phylogenetic analysis proposed that *Metabus* and *Okileuauge* were not sister taxa; instead *Metabus* was hypothesized to be sister to a clade that included *Leucauge*, *Okileuauge*, *Tylorida*, and

*Mesida* (Tanikawa, 2001; Fig. 8B). The morphology plus behaviour data set did not resolve *Metabus* sister taxa relationships with either *Tylorida* or *Orsinome* (Fig. 143A). When these data are combined with DNA sequences *Metabus* come out as sister to a clade that includes *Orsinome* and *Tylorida* (Fig. 144).

#### METELLINA CHAMBERLIN & IVIE, 1941 (FIGS 66–70)

**Type species:** *Metellina curtisi* (McCook, 1894). The syntypes of *Pachygnatha curtisi* are fragments of three male specimens from California (USA), deposited at the Academy of Natural Sciences, Philadelphia (Levi, 1980).



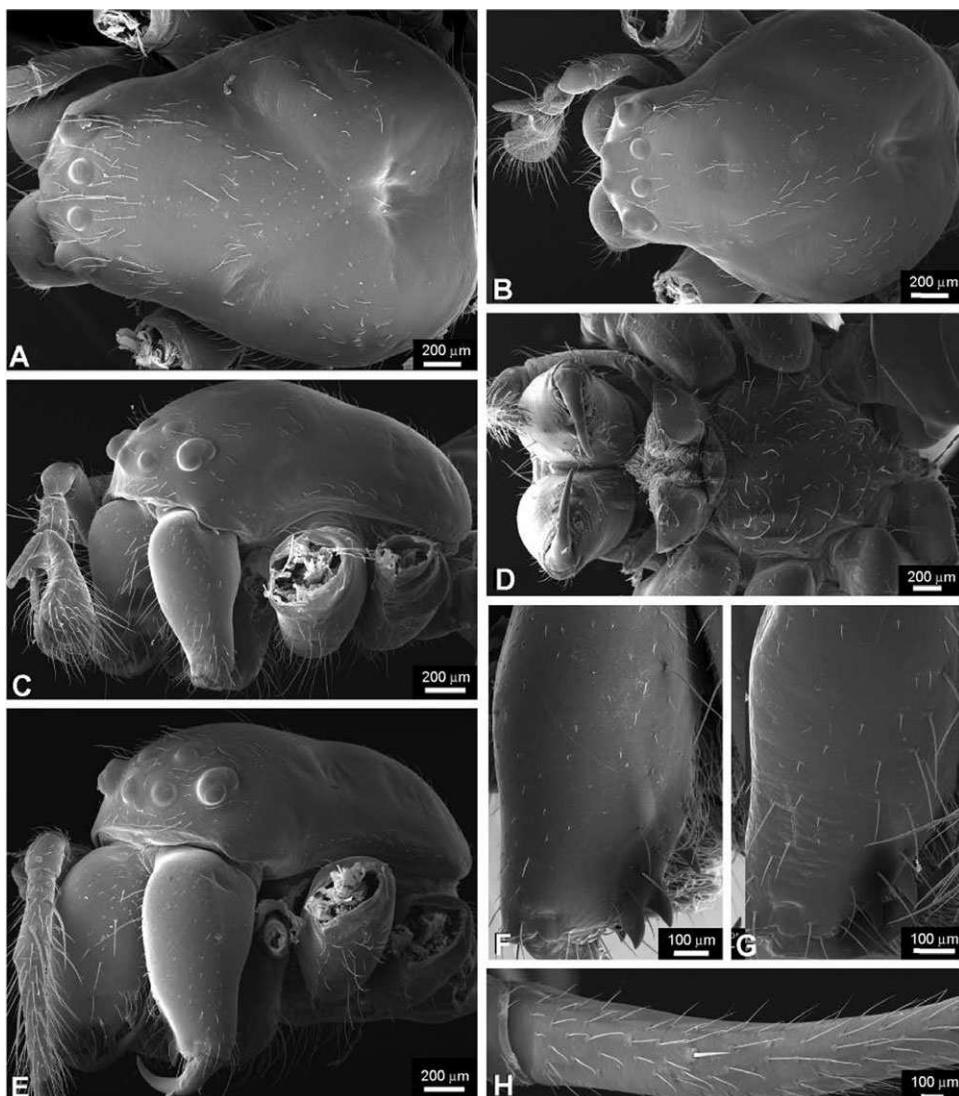
**Figure 66.** *Metellina segmentata* abdomen: A, booklung external cuticle. B, anterior lateral spinnerets; arrow in insert indicates the space between the piriform spigot bases and the spigot shaft. C, tracheal spiracle posterior view. D, tracheal system dorsal view. E, epiandrous fusules. F, median trachea tip. All images from SEMFAP044.

**Diagnosis:** *Metellina* species can be distinguished from all other tetragnathid genera by the following combination of characters: abdomen oval, longer than wide; secondary eyes with canoe-shaped tapetum (Levi, 1980: figs 95, 96); PLE on a single tubercle (Fig. 67C, E); epigynal plate flat (Fig. 68A, B); copulatory openings posteriorly orientated (Fig. 68D); fertilization ducts originating on the anterior surface of the spermathecae (Figs 68C, 70D); accessory glands concentrated near the copulatory ducts (Fig. 68F); cymbial ectobasal process formed by a massive cuticular fold (Fig. 69C, D); cymbial ectomedian process absent (Fig. 69D); paracymbium slightly longer than half the cymbium length; and sperm duct without switch backs (Fig. 70C).

**Description: Female:** body length c. 8.0 mm. Cephalic fovea formed by a transverse, deep, M-shaped groove (Fig. 67A). Ocular area higher than carapace lateral margins (Fig. 67C, E). Labium trapezoidal, wider than long and rebordered. Sternum slightly longer than wide (Fig. 67D). Anterior surface of chelicerae smooth; boss present (Fig. 67C, E). Eyes subequal in size, lateral eyes slightly smaller, juxtaposed, and on a tubercle. Clypeus c. 1.5 times the AME diameter. Booklung cuticle smooth (Fig. 66A). Tracheal spiracle

near the spinnerets. Median tracheae not ramified, longer than half the lateral tracheae length (Fig. 66D). Tracheal spiracle without accessory glands, median tracheae tips leaf-shaped (Fig. 66C, F). ALS with c. 60 piriform spigots (Fig. 66B). PMS with two aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface. PLS with more than 20 aciniform spigots, distal end of the aggregate spigots embracing the tip of flagelliform spigot. Epigynal plate flat, copulatory openings posteriorly orientated and in the shape of longitudinal grooves (Fig. 68A, B, D). Spermathecae walls well sclerotized (Fig. 68C–F). Copulatory and fertilization ducts cuticle well sclerotized. Copulatory ducts shorter than half the spermathecae length, fertilization ducts longer than the spermatheca width (Figs 68F, 70D). Accessory glands distributed on one side of the spermathecae, accessory gland openings arranged in groups (Fig. 68E, F).

**Male:** size and somatic morphology similar to that of the female, except the chelicerae are slightly larger and divergent (Fig. 67B, C, F). PLS triplet reduced to nubbins. Epiandrous plate flat, fusules arranged in two groups and immersed in pits (Fig. 66E). Palpal patella with one macroseta, palpal tibia slightly



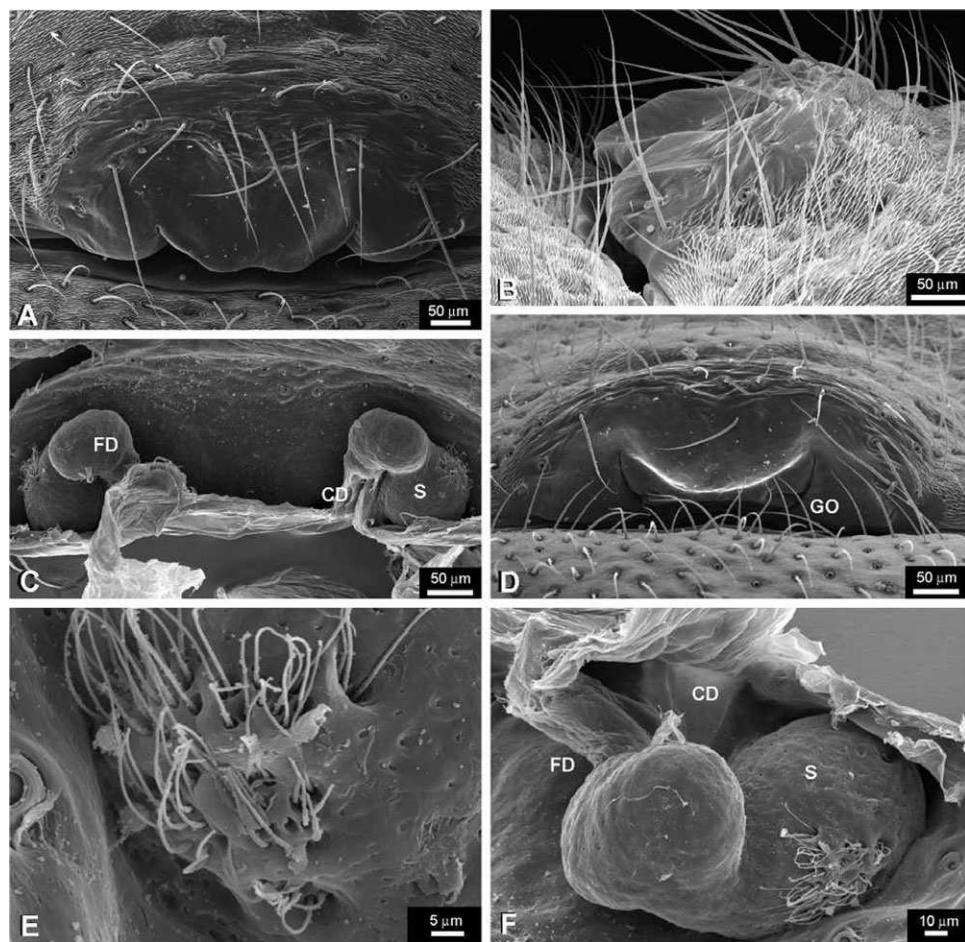
**Figure 67.** *Metellina segmentata* cephalothorax: A, female dorsal view. B, male dorsal view. C, male tangential view. D, female cephalothorax ventral view and sternum. E, female tangential view. F, female chelicera. G, male chelicera. H, female femur IV dorsal. All images from SEMFAP044.

longer than wide. Tegulum wider than long and larger than the subtegulum. Conductor well sclerotized and fused to the tegulum (Fig. 70B, C). Embolic apophysis massive and square in ectal view; embolus short and well sclerotized (Figs 69B, 70B). Sperm duct spiralled (Fig. 70C).

**Natural history:** The Holarctic genus *Metellina* includes seven species and one subspecies (Levi, 1980; Marusik, 1986). *Metellina* builds vertical webs with c. 25 radii, more than 30 spirals, and an open hub (Levi, 1980: pl. 6). These spiders are found either in dark and humid places or amongst the forest low vegetation. A few aspects of the biology of *M. segmentata* have been studied, such as the reproductive biology

(Rubenstein, 1987; Prenter, Montgomery & Elwood, 1995; Hack, Thompson & Fernandez, 1997; Malakov, Bilde & Lubin, 2004), the phenology and life cycle, including that of *Metellina mengei* (Blackwall, 1869; Toft, 1983), and the sperm ultrastructure and development (Michalik, Sacher & Alberti, 2005).

**Taxonomy:** *Metellina* has never been revised, except for the North American species (Levi, 1980). Our diagnosis and description includes the species revised by Levi (1980). We coded *M. segmentata* for the phylogenetic analysis. The monophyly of *Metellina* has never been tested. Two hypotheses exist regarding the sister group of *Metellina*, either sister to *Chrysometa* (supported by the chelicerae of



**Figure 68.** *Metellina segmentata* epigynum: A, ventral view. B, lateral view. C, dorsal view. D, posterior view. E, accessory glands. F, spermatheca, fertilization and copulatory ducts. All images from SEMFAP044.

the male larger than those of the female and by having the sperm duct without switch backs; Hormiga *et al.*, 1995); or sister to *Dolichognatha* (Álvarez-Padilla, 2007). The morphology plus behaviour data set recovered *Metellina* as sister to *Dolichognatha* (Fig. 143A, B); when these data are combined with DNA sequences, *Metellina* comes out as sister to a clade that includes *Dolichognatha*, *Chrysometa*, and *Diphya* (Fig. 144).

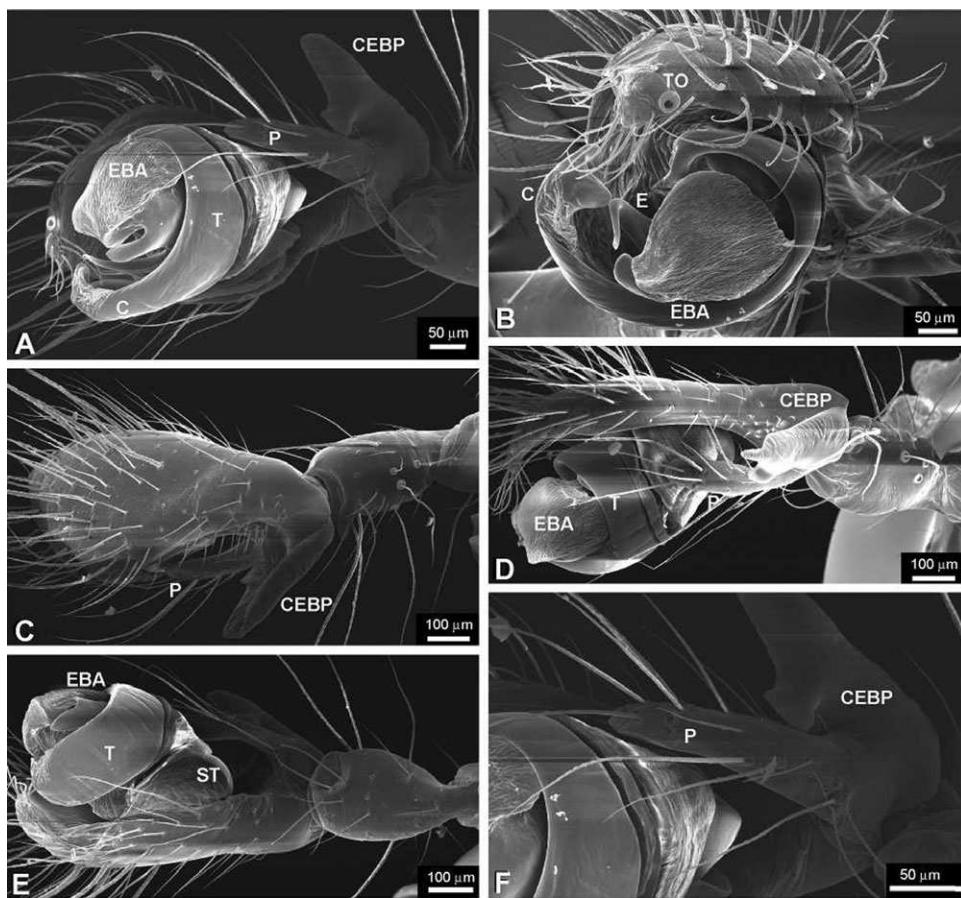
#### METLEUCAUGE LEVI 1980 (FIGS 4D, 77–81)

**Type species:** *Metleuauge eldorado* Levi 1980. The holotype of *M. eldorado* is a female specimen from California (USA), deposited at the Museum of Comparative Zoology, Harvard University (not examined).

**Diagnosis:** *Metleuauge* species can be distinguished from all other tetragnathid genera by the following combination of characters: cephalic fovea of both sexes resembling two deep pits (Fig. 78A); femora

without trichobothria (Fig. 78E); epigynum flat with two deep atria (Fig. 79A, B); spermathecae weakly sclerotized (Figs 79C, D, 81D); (Fig. 78G, H); male palpal trochanter with a large distal apophysis, palpal femora and tibia longer than four times its width, almost half the carapace length (Fig. 78F); cymbial dorsobasal process and cymbial ectomedian process present (Fig. 80B, E); and conductor subdivided (Fig. 81A, B).

**Description: Female:** body length c. 11.0 mm. Ocular area lower than carapace lateral margins (Fig. 78C). Labium trapezoidal, wider than long and rebordered. Sternum longer than wide (Fig. 78B). Anterior surface of chelicerae smooth; boss present (Fig. 78C, G). Secondary eyes with canoe-shaped tapetum (Levi, 1980: figs 139, 140). Eyes subequal in size, lateral eyes slightly smaller, juxtaposed and on a tubercle. Clypeus c. 1.5 times the AME diameter. Booklung cuticle smooth (Fig. 77A). Tracheal spiracle near the spinnerets, without accessory glands (Fig. 77D).



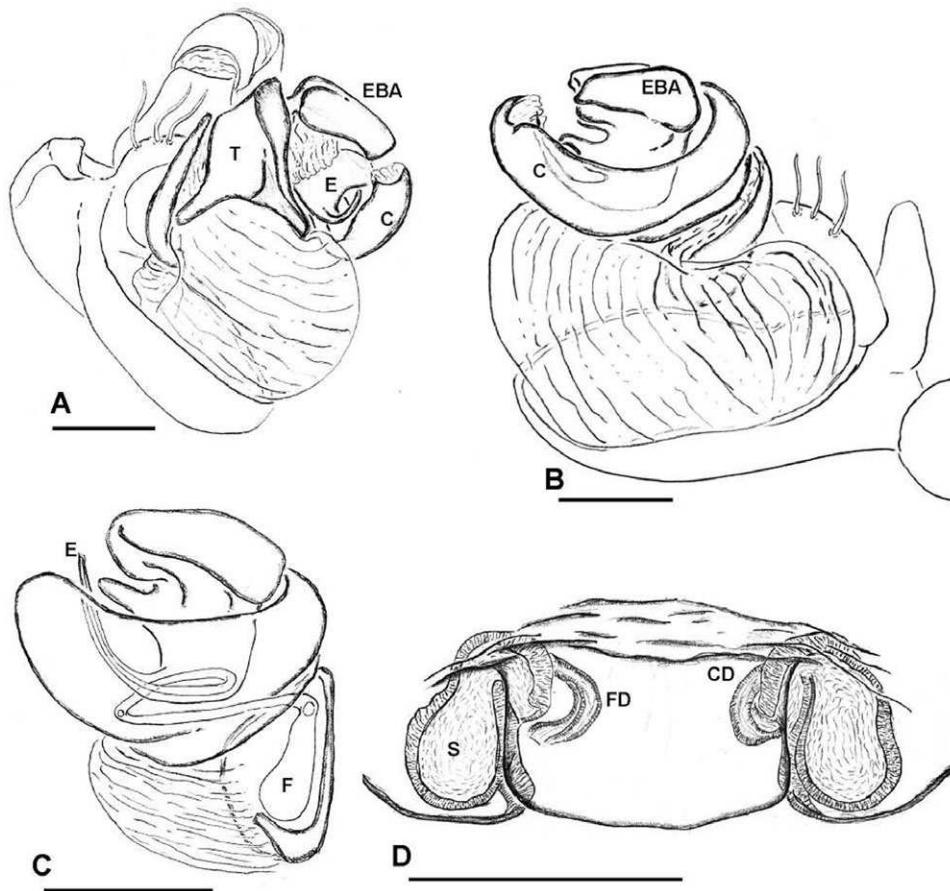
**Figure 69.** *Metellina segmentata* male pedipalp: A, ventral view. B, apical view. C, dorsal view. D, ectal view. E, mesal view. F, paracymbium and cymbial ectobasal process. All images from SEMFAP044.

Median tracheae not ramified, tips leaf-shaped (Fig. 77C, F). ALS with an extensive field of piriform spigots (Fig. 77B). PMS with five aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface (Fig. 77G). PLS with c. 25 aciniform spigots arranged in roughly parallel lines; distal end of aggregate spigots embracing tip of flagelliform spigot (Fig. 77E). Epigynal plate flat, copulatory openings ventrally orientated. Spermathecae walls weakly sclerotized (Fig. 79A–D). Copulatory and fertilization ducts shorter than the spermatheca length and cuticle well sclerotized. Fertilization ducts curved, but not coiling around the copulatory ducts. Accessory glands evenly distributed over the spermathecae, with gland openings arranged in groups (Fig. 79C, D).

**Male:** size and somatic morphology similar to that of the female, except the chelicerae are longer and their anterior cuticle is rugose (Fig. 78D, H, F). PLS triplet reduced to nubbins. Epiandrous plate flat, fusules arranged in an irregular line of clusters,

fusules not immersed in pits (Fig. 77F). Palpal patella with one macroseta (Fig. 78D). Paracymbium rectangular, with a basal apophysis, and considerably shorter than the cymbium length (Fig. 80B). Tegulum roughly oval, with an ectal depression produced by the displaced subtegulum (Fig. 80A). Both conductor parts are well sclerotized; one presents a translucent membranous process (Fig. 81A, B). Conductor attachment to tegulum and between its two parts membranous. Embolus base rectangular, longer than wide; embolus roughly the same length as its base, well sclerotized (Fig. 81C). Sperm duct path with fewer than three coils (Fig. 81C).

**Natural history:** There are seven described species of *Metleucauge*, with a geographical distribution on both sides of the Pacific (Levi, 1980; Tanikawa, 1992; Zhu *et al.*, 2003). These spiders build horizontal webs with open hubs, fewer than ten radii and spirals (Fig. 4D). Their webs are spun between rocks or near streams (Levi, 1980; G. Hormiga, pers. observ.). Little is known about the biology of *Metleucauge* species, but a



**Figure 70.** *Metellina segmentata* genital anatomy illustrations: A and B, male pedipalp expanded. C, pedipalp bulb cleared ventral view. D, cleared epigynum dorsal view.

pioneering study by Yoshida (1989) documented and compared the feeding behaviours and prey composition for three Japanese species.

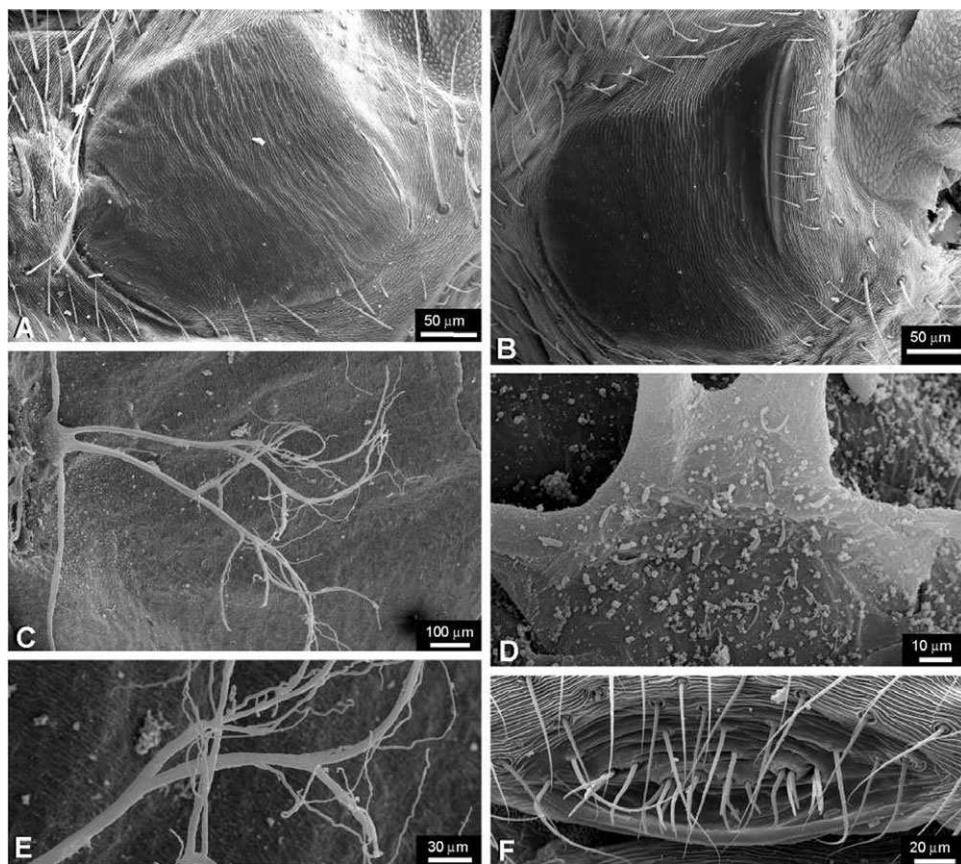
**Taxonomy:** Both the Asian and North American species of *Metleucauge* have been studied relatively recently (Levi, 1980; Tanikawa, 1992; Tanikawa & Chang, 1997); however the monophyly of this genus remains untested. Our diagnosis and description are based on *M. eldorado* specimens and the illustrations of the species described by Tanikawa (1992). The specimens that we coded for the phylogenetic analysis belong to *M. eldorado*. Tanikawa's (2001) phylogenetic analysis proposed *Metleucauge chikunii* Tanikawa, 1992 as sister to a clade formed by a large sample of leucaugines. Support for Tanikawa's hypothesis was provided by three synapomorphies: presence of cymbial processes other than the paracymbium, seminal receptacles of the female not sclerotized, and a deep thoracic groove (Tanikawa, 2001; Fig. 8B). Both our data sets recovered *Metleucauge*

as sister to a clade that includes *Metabus*, *Orsinome*, *Tylorida*, *Mesida*, *Opadometa*, and *Leucauge* (Figs 143A, B, 144).

#### MOLLEMETA ÁLVAREZ-PADILLA, 2007 (FIGS 4E, 82–86)

**Type species:** *Mollemeta edwardsi* (Simon, 1904). The holotype of *Landana edwardsi* is a female from Chile deposited at the Museum National d'Histoire Naturelle, Paris (examined).

**Diagnosis:** *Mollemeta* can be distinguished from other tetragnathids by the following combination of characters: epigynum with a small spherical scape; copulatory openings located in deep curved grooves (Fig. 84A–C); cymbial ectobasal process and cymbial ectomedian process present (Fig. 85C); male palpal femora and tibia longer than four times its width, approximately half the carapace length (Fig. 83E); paracymbium cone-shaped, much shorter than the cymbial ectobasal process (Fig. 85C); tegulum reduced



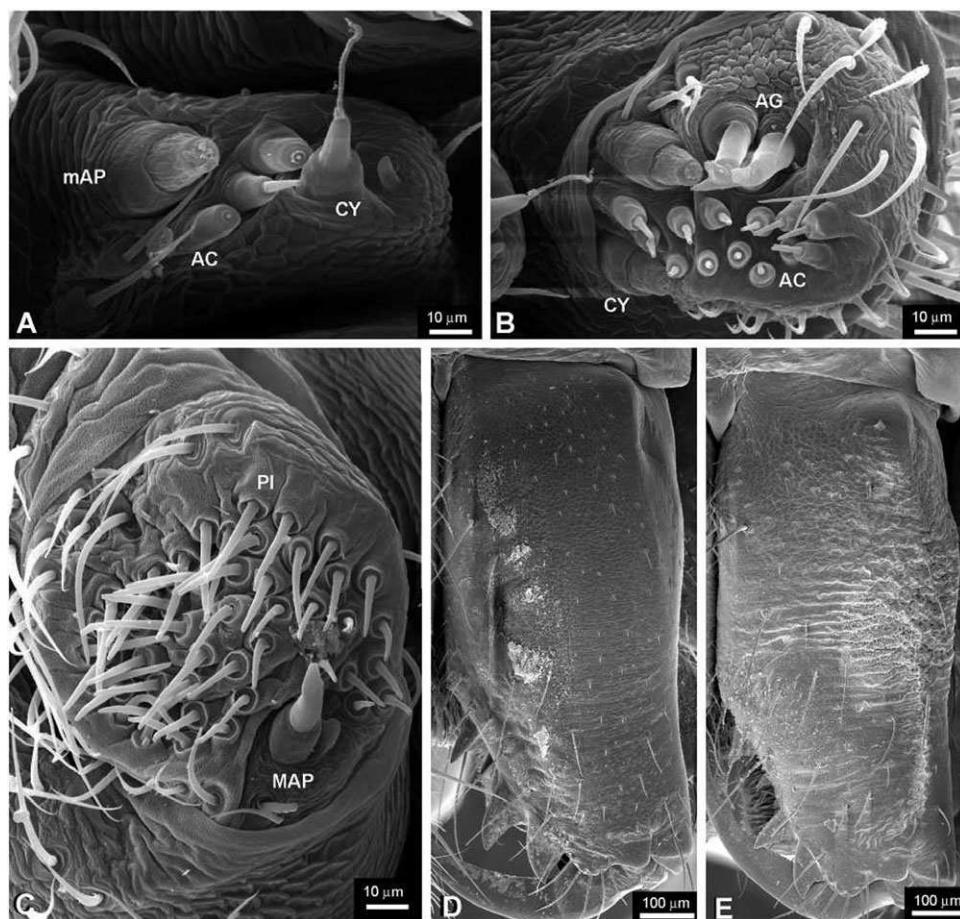
**Figure 71.** *Nanometinae* sp. abdomen: A, female booklung cuticle. B, male booklung cuticle. C, tracheal system dorsal view. D, tracheal spiracle posterior view. E, median tracheae ramifications. F, epiandrous fusules. All images from SEMFAP049.

to a narrow ring (Fig. 86A–C); membranous conductor (Fig. 86C); and embolus without basal apophyses (Fig. 85F).

**Description: Female:** body length c. 10.0 mm. Thoracic fovea transverse and deep (Fig. 83A). Ocular area higher than carapace lateral margins (Fig. 83G). Labium trapezoidal, wider than long and rebordered. Sternum longer than wide (Fig. 83F). Anterior surface of chelicerae smooth; boss present (Fig. 83C). Secondary eyes with canoe-shaped tapetum. Eyes subequal in size, lateral eyes slightly smaller, juxtaposed, and on a tubercle. Clypeus c. 1.5 times the AME diameter. Booklung cuticle grooved (Fig. 82B). Tracheal spiracle near the spinnerets, with accessory glands (Fig. 82C). Median tracheae not ramified, tips leaf-shaped (Fig. 82D, F). ALS piriform spigots bases rounded (Fig. 82E). PMS with three aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface. PLS with c. 25 aciniform spigots arranged in roughly parallel lines; distal end of aggregate spigots

embracing tip of flagelliform spigot (Álvarez-Padilla, 2007: fig. 9L, M). Epigynal plate flat (Fig. 84A, B), copulatory openings posteriorly orientated (Fig. 86D). Spermathecae walls well sclerotized. Copulatory ducts coiled, longer than the spermatheca diameter (Fig. 84C). Fertilization ducts path straight, slightly longer than spermatheca, with well-sclerotized cuticle (Fig. 84F). Accessory glands concentrated over the anterior surface of spermathecae, gland openings arranged in groups (Fig. 84C–E).

**Male:** size and somatic morphology similar to that of the female (Fig. 83B, D, E). PLS triplet reduced to nubbins (Álvarez-Padilla, 2007: fig. 9N). Epiandrous plate flat, fusules arranged in an irregular line of fusules clusters, fusules not immersed in pits (Fig. 82G). Palpal patella with one macroseta. Conductor membranous, with rigid edges. Conductor-tegulum attachment membranous (Fig. 86A, C). Embolus base rectangular and slightly longer than wide; embolus almost as long as the cymbium, well sclerotized (Figs 85D–F, 86A). Sperm duct path with one loop before reaching fundus (Fig. 86B).



**Figure 72.** *Nanometinae* sp. abdomen and chelicerae: A, posterior median spinnerets. B, posterior lateral spinnerets. C, anterior lateral spinnerets. D, female chelicera. E, male chelicera. All images from SEMFAP049.

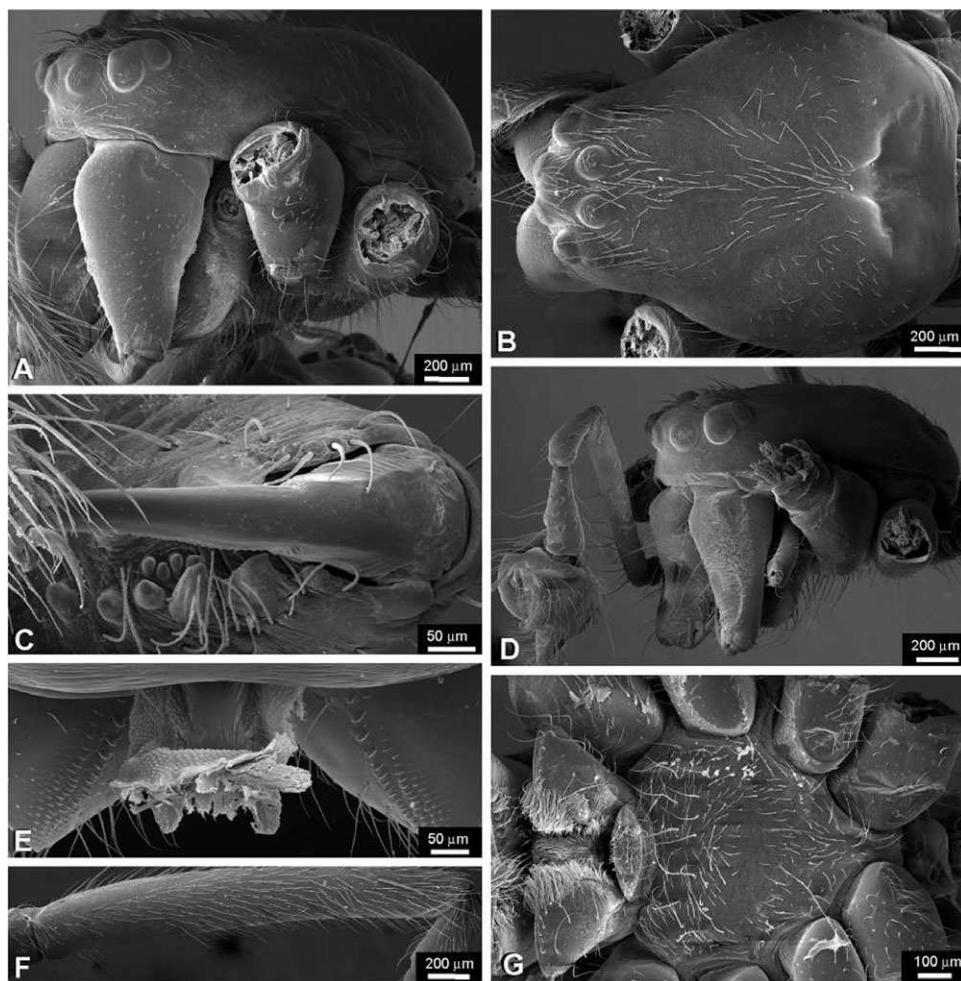
**Natural history:** *Mollemeta* is a monotypic genus endemic to Chile. These spiders build vertical webs, longer than wide, with a closed hub, with more than 30 spiral turns and radii. The webs of *Mollemeta* are spun over tree trunks (Fig. 4E).

**Taxonomy:** The monotypy of this genus was based on the results of a previous cladistic analysis that recovered *M. edwardsi* as sister to a clade that contains the genera *Meta*, *Metellina*, *Dolichognatha*, *Allende*, and *Chrysometa* (Álvarez-Padilla, 2007). This sister group relationship was supported by a single synapomorphy, the paracymbium on the base of the cymbial ectobasal process. The morphological + behavioural data set recovered *Mollemeta* as sister to a clade that includes *Metainae*, *Nanometinae*, *Tetragnathinae*, *Chrysometa*, and *Allende* (Fig. 143A); when these data were combined with DNA sequences, *Mollemeta* was placed as sister to a clade that includes *Allende* plus *Tetragnathinae* (Fig. 144).

#### NANOMETA SIMON, 1908 (FIGS 4F, 87–91)

**Type species:** *Nanometa gentilis* Simon, 1908. The type specimen of *N. gentilis* is a female from Western Australia deposited at the Museum National d'Histoire Naturelle, Paris (examined).

**Diagnosis:** *Nanometa* can be distinguished from other tetragnathids by the following combination of characters: small size (body length c. 3–4 mm); abdomen covered with silver guanine patches; ramified median tracheal trunks (Fig. 87B–D); absence of femoral trichobothria; denticles between the cheliceral fang furrows (Fig. 87D); flat epigynum (Fig. 89A); copulatory ducts modified as sacs and separated from the spermathecae (Figs 89B, D, 91C); male book lung with a stridulatory file (Fig. 87A); male coxa IV mesal surface with cusps (Fig. 88F); cheliceral ectal margin rugose and dimorphic (the female cheliceral surface is smooth, Fig. 88A, E); and cymbial ectobasal process and cymbial ectomedian process present (Fig. 90A, C).

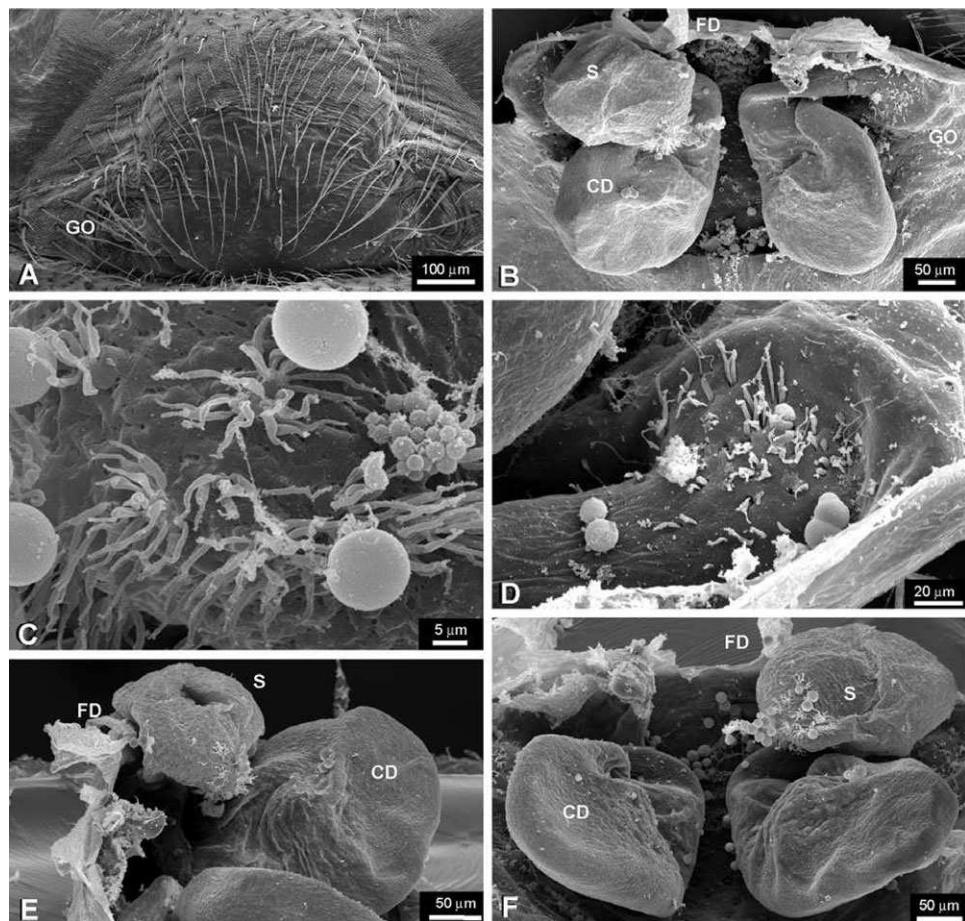


**Figure 73.** *Nanometinae* sp. cephalothorax and chelicerae: A, female tangential view. B, female dorsal view. C, cheliceral denticles. D, male tangential view. E, coxa dorsal surface. F, femur IV ectal view. G, female cephalothorax ventral view and sternum. All images from SEMFAP049.

**Description: Female:** cephalic fovea absent (Fig. 88B). Ocular area higher than carapace lateral margins (Fig. 88A). Labium trapezoidal, wider than long and rebordered; sternum longer than wide (Fig. 88C). Anterior surface of chelicerae smooth; cheliceral boss present (Fig. 88A). Eyes subequal in size, juxtaposed, and on a tubercle (Fig. 88A). Secondary eyes with canoe-shaped tapetum. Clypeus height approximately one AME diameter. Booklung cuticle smooth. Tracheal spiracle located near the spinnerets, without accessory glands (Fig. 87C). ALS with c. 30 piriform spigots. PLS and PMS with c. eight aciniform spigots. PLS distal end of aggregate spigots embracing tip of flagelliform spigot (Fig. 87H). Epigynal plate flat, copulatory openings ventrally orientated and in the shape of pits (Fig. 89A). Spermathecae walls well sclerotized, fertilization ducts short and slightly curved (Figs 89B, 91C). Accessory gland openings

grouped on a common pit near the spermatheca ducts junction (Fig. 89B–D).

**Male:** body length and cephalothorax morphology as in the female, except that the anterior cheliceral cuticle is rugose and the booklung covers have an stridulatory organ (Figs 87A, 88E). PLS triplet reduced to nubbins (Fig. 87G). Epiandrous fusules concentrated in two groups and immersed in pits (Fig. 87E). Palpal patella without macrosetae, palpal tibia slightly longer than wide (Fig. 90A, D). Paracymbium very small, smaller than the cymbial ectobasal process (Fig. 90E). Tegulum wider than long, spherical to oval (Fig. 91A). Conductor edges well sclerotized and fused to the tegulum; centre of conductor membranous (it expands when repeatedly transferred between KOH 10% and distilled water; Fig. 91A). Embolic apophysis without processes; embolus and its base continuous and well



**Figure 74.** *Nanometinae* sp. epigynum: A, ventral view. D, dorsal view. C and D, accessory glands. E, lateral view. F, anterior view. All images from SEMFAP049.

sclerotized (Fig. 91A). Sperm duct spiralled without switchbacks.

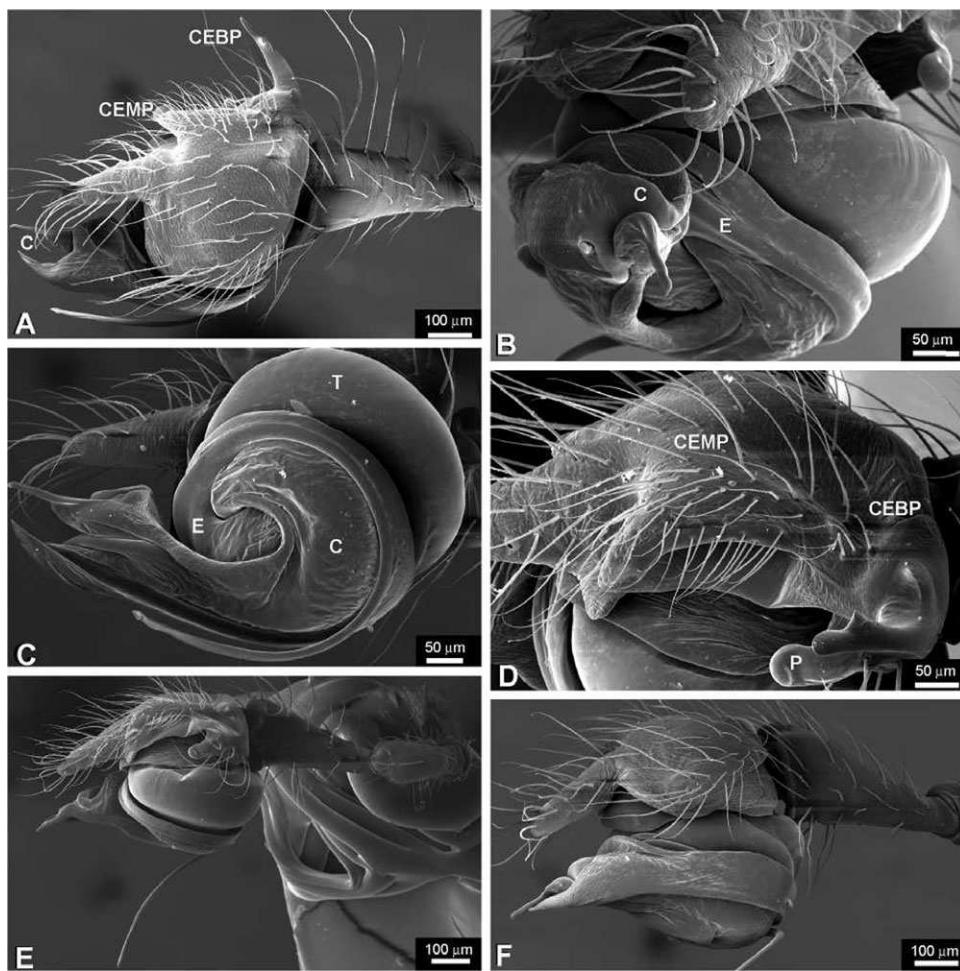
**Natural history:** *Nanometa* is a monotypic genus endemic to Australia (Platnick, 2009); however, at least 20 more species from Australia (including Tasmania) remain to be described (Ray Forster, unpubl. data). These spiders build horizontal webs with c. 16 spirals, c. 16 radii, and open hubs (Fig. 4F). They are found in forests building their webs in the low vegetation.

**Taxonomy:** *Nanometa* has never been revised, and new species wait to be described (Forster & Forster, 1999). The specimens studied for the diagnosis and description belong to an undescribed species morphologically similar to *N. gentilis*, which we have also coded in the phylogenetic analysis. Davies (1988: fig. 17) illustrated another undescribed *Nanometa* species similar to the one that we examined. The anatomy of *Nanometa* is similar to that of the

specimens referred in the text as ‘*Nanometinae* sp.’; however, this latter undescribed species differs considerably in size (7.0 mm body length, in comparison with *Nanometa*, which is 4.0 mm). This ‘*Nanometinae* sp.’ is similar in size to that illustrated by Davies (1988), also from Queensland, and referred there as ‘*Metine* sp.’ (Davies, 1988: fig. 17), and the same species as ‘metaine from Australia’ in Álvarez-Padilla *et al.* (2009). We decided to leave this species unnamed until its phylogenetic placement is resolved using a larger taxonomic sample of *Nanometinae*. The morphology plus behaviour data set recovered *Nanometa* as sister to ‘*Orsinome*’ *sarasini* (Fig. 144); when these data are combined with the DNA sequences, *Nanometa* is placed as sister to ‘*Nanometinae* sp.’ (Fig. 143A, B).

#### *OPADOMETA* ARCHER, 1951 (FIGS 5A, B, 92–95)

**Type species:** *Opadometa grata* (Guérin, 1838). The type specimen depository of *Epeira grata* is unknown.

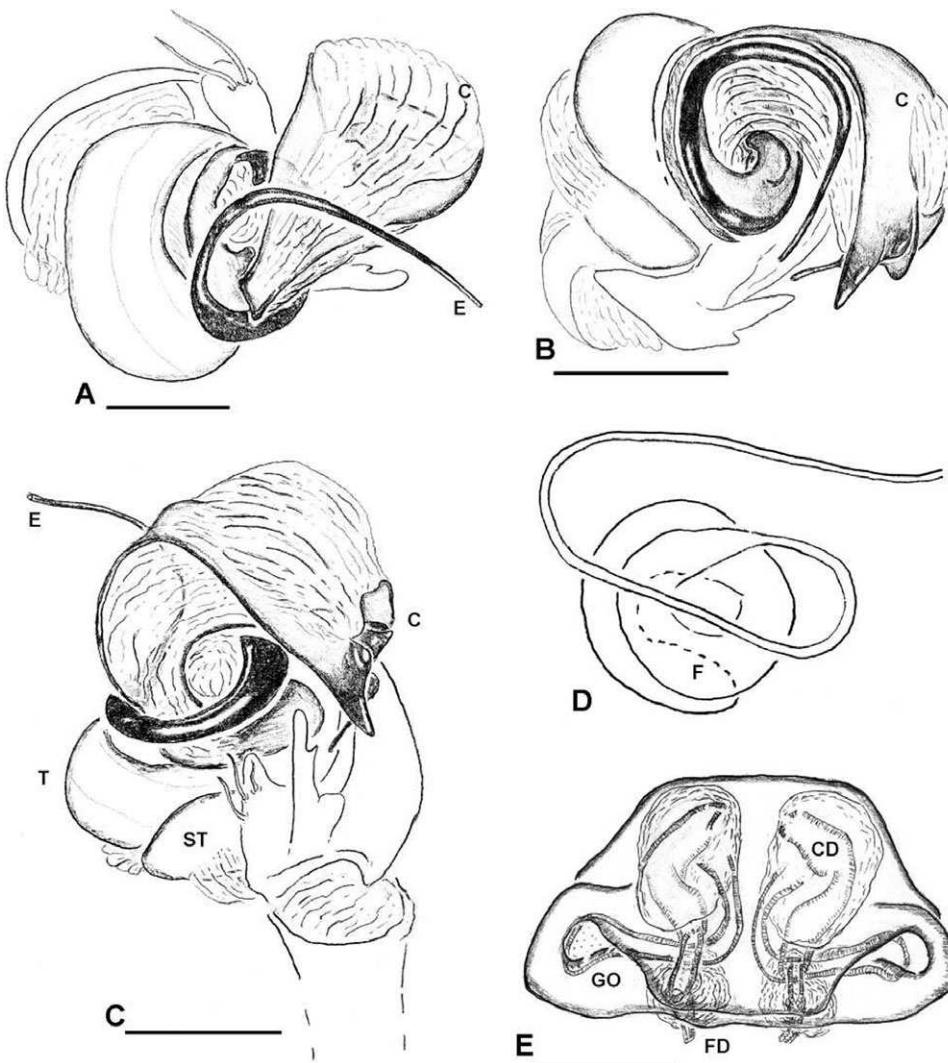


**Figure 75.** *Nanometinae* sp. male pedipalp: A, dorsal view. B, apical. C, ventral view. D and E, ectal view. F, mesal view. All images from SEMFAP049.

**Diagnosis:** *Opadometa* can be distinguished from other tetragnathids by the following combination of characters: female tibia IV with a brush of macroseta on the distal third (Simon, 1894: fig. 817); fourth femora with two parallel rows of trichobothria with branched shafts (Fig. 93E, F); epigynum flat with a triangular atrium and soft spermathecae (Figs 94A, 95E); male cheliceral anterior surface armed with many macrosetae (Fig. 95D); conductor fused to the tegulum (Fig. 95C); and by having the adult male size less than half the size of the females.

**Description: Female:** body length is c. 12.0 mm. Cephalothorax fovea formed by two short transverse grooves (Fig. 93A). Ocular area lower carapace lateral margins (Fig. 93B, C). Labium trapezoidal, wider than long, and rebordered. Sternum as wide as long (Fig. 93D). Anterior surface of chelicerae smooth; boss present. Secondary eyes with canoe-shaped tapetum. Eyes subequal in size, lateral eyes slightly smaller,

juxtaposed, and on a tubercle. Clypeus less than one AME diameter. Abdomen longer than wide, covered with silver guanine patches, and anteriorly projected. Booklung cuticle smooth (Fig. 92A). Tracheal spiracle near the spinnerets, almost without accessory glands (Fig. 92C, E). ALS with c. 50 piriform spigots (Fig. 92A). PMS with three aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface (Fig. 92D). PLS with c. 20 aciniform spigots roughly arranged in two parallel lines; distal end of aggregate spigots embracing tip of flagelliform spigot (Fig. 92F). Epigynal plate flat and triangular in shape (Fig. 93A); copulatory openings ventrally orientated, located at the middle base of the atria and in the shape of short longitudinal grooves (Figs 94A, 95E). Spermathecae walls weakly sclerotized (Fig. 94B, D). Copulatory ducts are more than half the spermathecae length but less than its total length, cuticle weakly sclerotized. Fertilization ducts



**Figure 76.** Nanometinae sp. genital anatomy illustrations: A–C male pedipalp expanded. D, sperm duct. E, cleared epigynum ventral view.

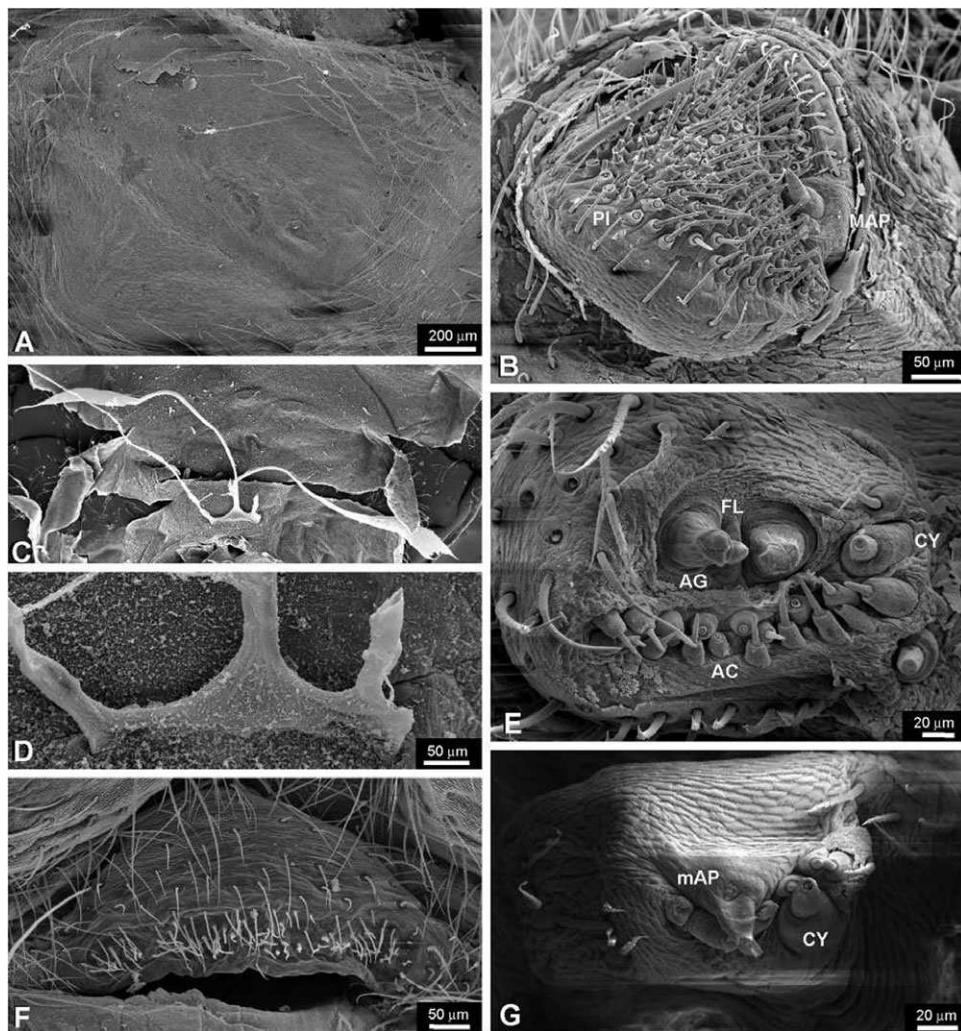
coiled and sclerotized at their terminal part (Fig. 95E). Accessory glands concentrated over the ducts, with their bases slightly wider than the duct (Fig. 94E, F).

*Male:* considerably smaller than the female, 7.0 mm body length, somatic morphology similar to a male of *L. venusta* except that the chelicerae are proportionally longer and the macrosetae on the anterior surface are larger (Fig. 95D). Male palpal patella without macrosetae. Cymbial dorsobasal process present, longer than more than half the cymbial width and perpendicular to the cymbium longitudinal axis (Fig. 95A). Paracymbium hook-shaped, without apophyses and considerably shorter than the cymbium length (Fig. 95C). Tegulum roughly oval with an ectally displaced subtegulum (Fig. 95C). Conductor rigid, with sclerotized edges, bearing a basal apophy-

sis. Conductor-tegulum attachment well sclerotized (Fig. 95C). Embolus base rectangular, longer than wide; embolus flexible and weakly sclerotized. Sperm duct path convoluted with five coils (Fig. 95B).

*Natural history:* *Opadometa* has two described species (and eight subspecies), distributed in the South-East Asian tropics (Simon, 1894; Chrysanthus, 1963, 1975). These spiders build vertical webs ( $> 45^\circ$ ), with c. 30 radii, c. 30 spiral turns, and open hubs (Fig. 5A, B). They are found along rivers, roads, or in the low vegetation of open spaces.

*Taxonomy:* The monophyly of *Opadometa* has never been tested or its taxonomy revised. The males of *Opadometa* species are extremely rare in collections and in overall morphology resemble a small *Leucauge*



**Figure 77.** *Metleucauge eldorado* abdomen: A, female booklung cuticle. B, anterior lateral spinnerets. C, tracheal system dorsal view. D, tracheal spiracle posterior view. E, posterior lateral spinnerets. F, epiandrous fusules. G, posterior median spinnerets. All images from SEMFAP041, except (G) from SEMFAP075.

species. In contrast, female specimens are very abundant. Our diagnosis and description of this genus are based in specimens of a species similar to *Opadometa grata* (Chrysanthus, 1963, 1975). Data on *Opadometa fastigata* were taken from Simon (1894). Both our data sets (morphology plus behaviour and these data combined with DNA sequences) suggest that *Opadometa* is sister to *Leucauge*.

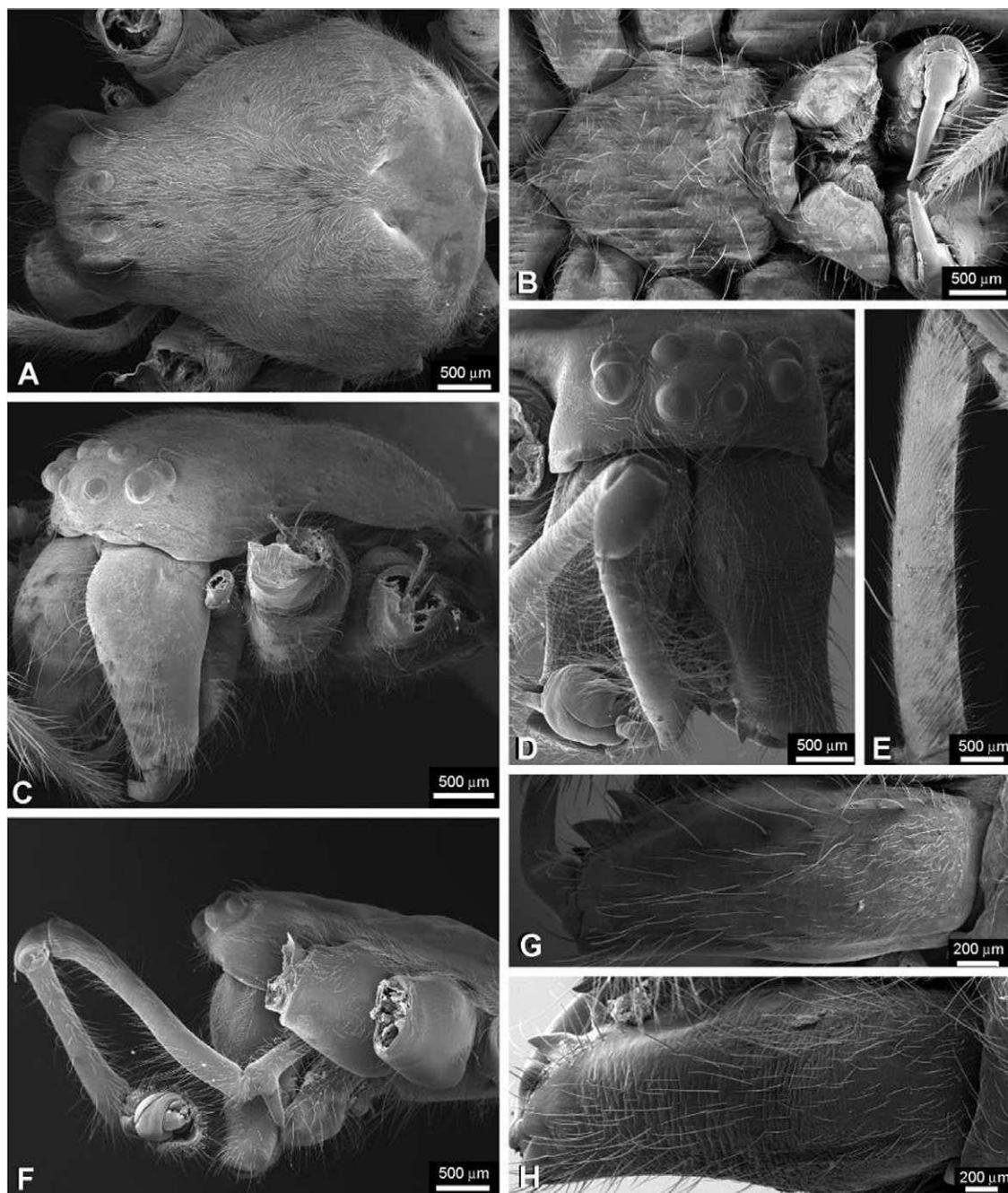
*ORSINOME* THORELL, 1890  
(FIGS 5A, B, 91B, D, 96–104)

*Type species:* *Orsinome vethii* (Hasselt, 1882). The type specimen depository of *Pachygnatha vethii* is unknown to us.

*Diagnosis:* *Orsinome* species can be distinguished from other tetragnathids by the following combination of characters: femora IV with trichobothria

(Fig. 101G); female chilum present; copulatory ducts well sclerotized and coiled; copulatory openings inside a common chamber on the centre of the epigynal plate (Figs 102A–D, 104E); male cephalothorax ocular area higher than lateral margins (Fig. 101B, D); embolus base resting on the subtegulum (Fig. 104A); and having the dorsobasal process of the cymbium made of a cuticular fold that extends to the middle of the cymbium (Fig. 103C).

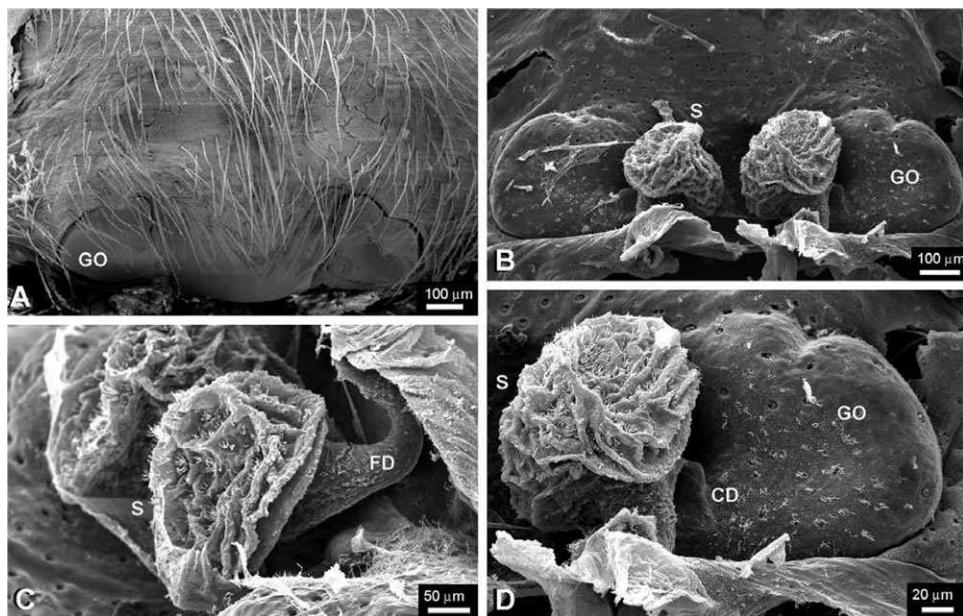
*Description: Female:* body length c. 14.0 mm. Femora IV trichobothrial shaft not branched (Fig. 101G). Ocular area lower than carapace lateral margins (Fig. 101B). Labium trapezoidal, wider than long and rebordered. Sternum longer than wide (Fig. 101C). Anterior surface of chelicerae smooth; boss present (Fig. 101F). Secondary eyes with canoe-shaped



**Figure 78.** *Metelucauge eldorado* cephalothorax: A, female dorsal view. B, female cephalothorax ventral view and sternum. C, female tangential view. D, male anterior view. E, female femora IV ectal view. F, male cephalothorax lateral view. G, female chelicera. H, male chelicera. Female images from SEMFAP041, male images from SEMFAP075.

tapetum. Eyes subequal in size, lateral eyes slightly smaller, juxtaposed, and on a tubercle. Clypeus almost twice one AME diameter. Abdomen cylindrical, covered with silver guanine patches (Murphy & Murphy, 2000: fig. 10). Booklung cuticle smooth (Fig. 100A). Tracheal spiracle near the spinnerets. Median tracheae not ramified, longer than half the lateral tracheae length,

with leaf-shaped tips (Fig. 100A, C). ALS with an extensive field of piriform spigots (Fig. 100B). PMS with three aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface (Fig. 100G). PLS with c. 22 aciniform spigots arranged in roughly parallel lines, distal end of the aggregate



**Figure 79.** *Metleucauge eldorado* epigynum: A, ventral view. B, dorsal view. C and D, spermatheca and ducts. All images from SEMFAP041.

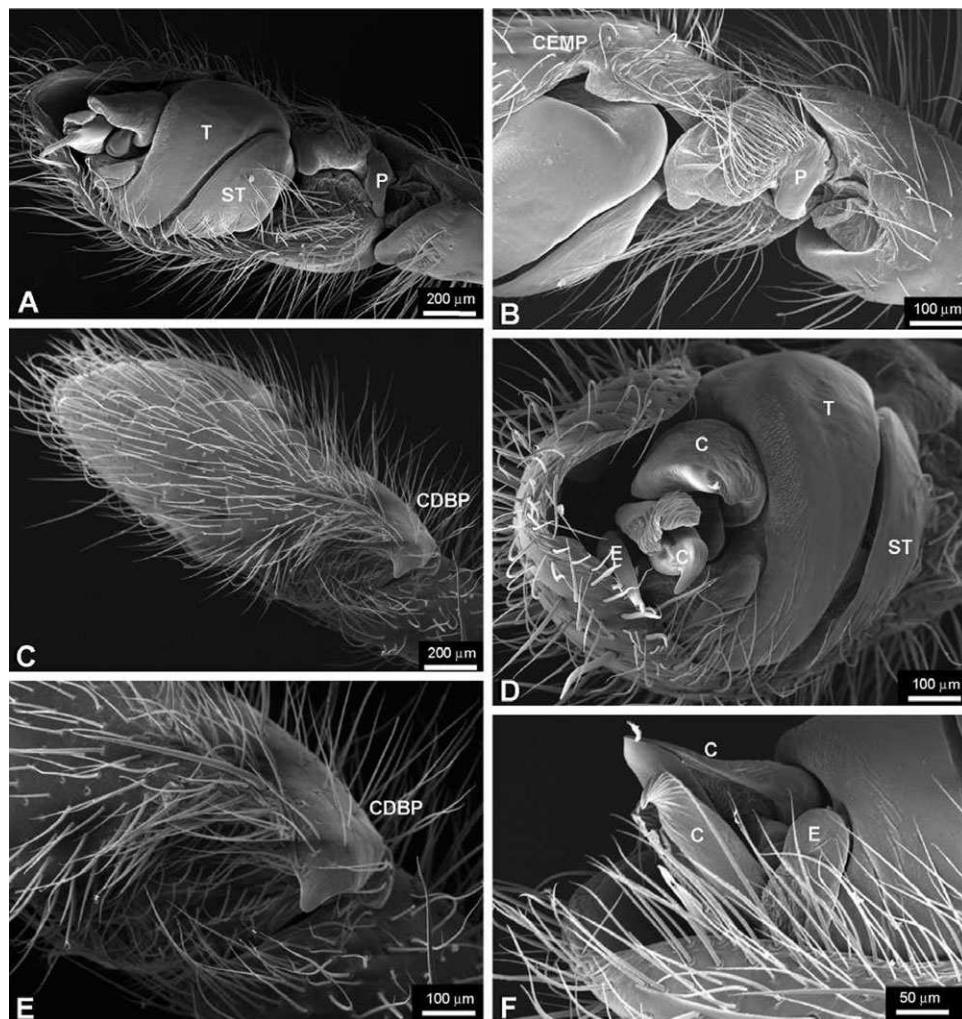
spigots embracing the tip of the flagelliform spigot (Fig. 100D). Epigynal plate flat, copulatory openings ventrally orientated. Spermathecae walls weakly sclerotized (Figs 100B, 104E). Copulatory and fertilization ducts coiled, longer than the spermatheca length with well-sclerotized cuticle. Accessory concentrated near the duct junction, accessory glands acorn-shaped and in individual pits (Fig. 104B–F).

**Male:** size and somatic morphology similar to that of the female, except the chelicerae are considerably larger, with a massive median apophysis on the internal margins (Fig. 101H). PLS triplet reduced to nubbins. Epiandrous plate well sclerotized, fusules immersed in a transverse groove with their bases wider than the fusule shaft (Fig. 100F). Palpal patella without macrosetae. Palpal femora very long, more than four times its width. Tibia length twice its width. Paracymbium shorter than half the cymbium length, curved, with swollen distal margin (Fig. 103F). Cymbial dorsobasal process fused to the cymbium more than two thirds of its length (Fig. 103C, D). Tegulum roughly oval, with an ectal depression produced by the displaced subtegulum (Fig. 104A, B). Conductor parts well sclerotized, attachment to tegulum membranous (Fig. 104C, D). Embolus base rectangular and longer than wide, located between tegulum and cymbium. Embolus displaced between the tegulum and cymbium with its distal part resting on the subtegulum (Fig. 104A). Embolus approximately as

long as the cymbium, thin and well sclerotized (Fig. 104C). Sperm duct with more than five coils (Fig. 104B).

**Natural history:** *Orsinome* includes 17 described species distributed in the South-East Asian tropics and Madagascar (Thorell, 1890; Chrysanthus, 1971; Zhu *et al.*, 2003). They build horizontal webs, with c. 20 spirals, c. 13 radii, and open hubs (Fig. 5C). Their webs are found over the water between the rocks, and over vegetation along rivers.

**Taxonomy:** Two species are included in this analysis, *Orsinome* cf. *vethi* and '*Orsinome*' *sarasini* Berland, 1924, but the results of our analysis suggest that they are not congeneric. The first species belongs to the leucaugines, whereas '*Orsinome*' *sarasini* belongs to Nanometinae (Fig. 144). The taxonomic status of '*O.*' *sarasini* should be revised when a larger taxonomic sample of these Australasian lineages is studied in more depth. A new genus name is required for this lineage of species from New Caledonia, South-eastern Australia, and Tasmania (Urquhart, 1891; Berland, 1924). '*Orsinome*' *sarasini* differs from the taxa in Nanometinae by the following characteristics: distal end of aggregate spigots embracing the distal end of flagelliform spigot (Fig. 96C); paracymbium cylindrical, longer than half the cymbium length and with a basal apophysis (Fig. 97E); and median tracheae not ramified (Fig. 97F). All other studied morphological



**Figure 80.** *Metleucauge eldorado* male pedipalp: A, ventral view. B, paracymbium and cymbial ectobasal process. C, dorsal view. D, apical view. E, cymbial dorsobasal process. F, conductor and embolus. All images from SEMFAP075.

features are similar to *Nanometa* sp. and ‘*Nanometinae* sp.’ (Figs 91B, D, 96–99). The relationships of *Orsinome* to other Leucauginae genera are unresolved by the data set of morphology plus behaviour (Fig. 143A, B); however when these data are combined with DNA sequences *O. cf. vethi* is placed as sister to *Tylorida* (Fig. 144).

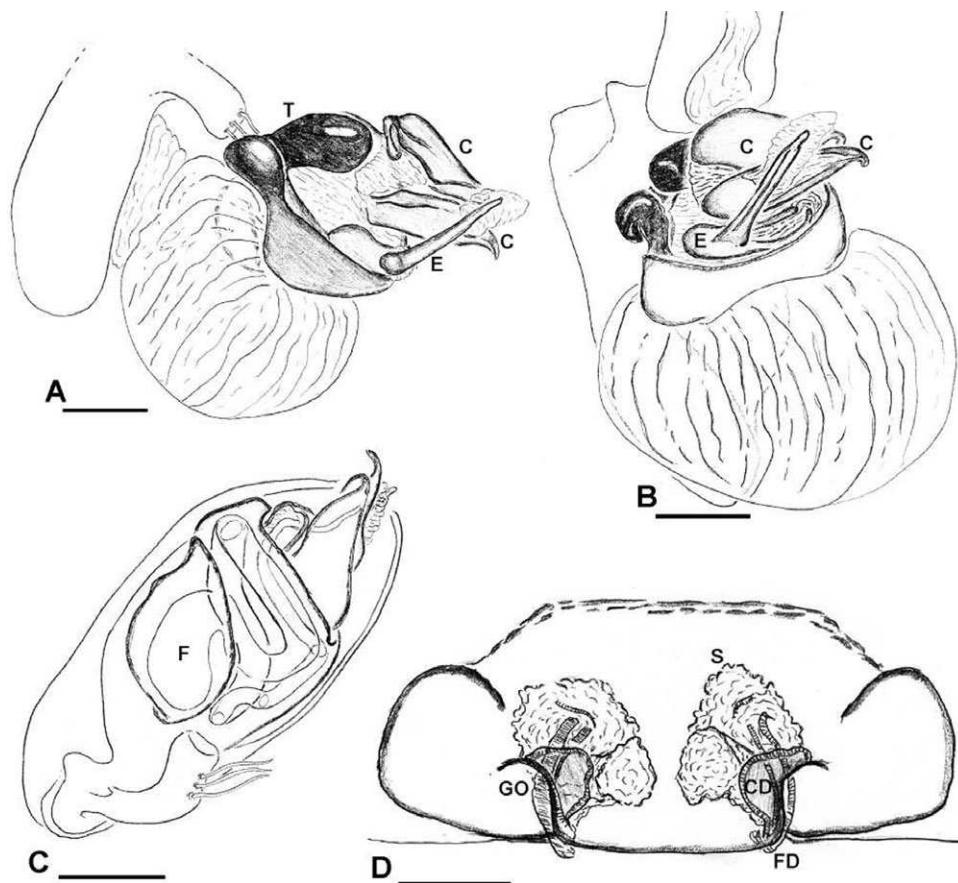
#### PACHYGNATHA SUNDEVALL, 1823 (FIGS 105–108)

*Type species:* *Pachygnatha clercki* Sundevall, 1823. The type specimens of *P. clercki* are deposited at the Natural History Museum of Geneva (Levi, 1980).

*Diagnosis:* *Pachygnatha* species can be distinguished from other tetragnathids by the following combination of characters: lack of aggregate and flagelliform silk gland spigots and the PMS spigot

nubbin (Fig. 105C, E); sternum projecting between the coxae (Fig. 106B); carapace covered with thin and short macrosetae immersed in pits (Fig. 106A); femora IV with a single trichobothrium (Fig. 106F); thick and cylindrical median and lateral tracheal trunks (Fig. 105B); haplogyne system (Fig. 107B–D); copulatory opening as a spiracle, more sclerotized than the surrounding cuticle (Fig. 107A), displaced to the centre of the abdomen.

*Description: Female:* body length c. 5.0 mm. Ocular area higher than carapace lateral margins (Fig. 106C). Sternum longer than wide projecting between the coxae; labium trapezoidal, wider than long, and rebordered (Fig. 106B). Chelicerae divergent, anterior cuticle smooth as in the clypeal area (Fig. 106C–E); boss present. Clypeus higher than two AME diameters. Eyes subequal in size; PME without



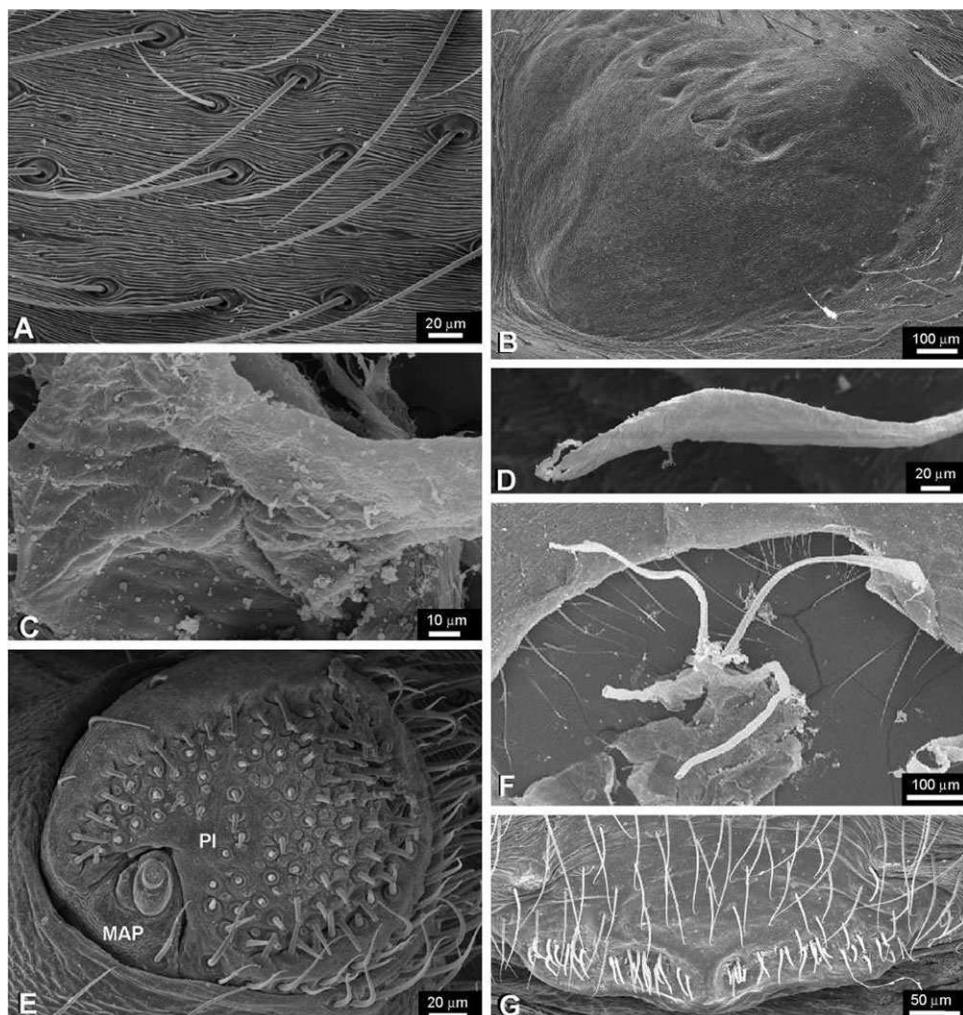
**Figure 81.** *Metleucauge eldorado* illustrations: A and B, male pedipalp expanded. C, pedipalp bulb cleared ventral view. D, cleared epigynum dorsal view.

canoe-shaped tapetum, with rhabdoms arranged in loops. PLE with canoe-shaped tapetum (Levi, 1980: figs 156–161). Abdominal cuticle formed by small cylinders arranged in lines (Fig. 105A, F). Tracheal spiracle located near the spinnerets, wider than long, with fewer than four accessory glands on each side (Fig. 105B, D). ALS with c. 35 piriform spigots. PMS with two aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface (Fig. 105C). Femora IV with a single trichobothrium (Fig. 106F). Epigynum absent, copulatory opening spiracle-shaped, with both margins slightly sclerotized. Spermathecae well sclerotized and connected to a membranous sac that leads to the only copulatory opening (Fig. 116B; Levi, 1980: figs 206, 207). Accessory gland openings in separate pits, concentrated near the copulatory ducts (Fig. 107C, D).

**Male:** size and somatic morphology similar to the female. Epiandrous fusules immersed in a transverse depression and arranged in a single line. Lower margin of the epiandrous plate swollen (Fig. 105F). Palpal patella without macrosetae; palpal tibia as

wide as long (Fig. 108B). Palpal femur length more than four times its width. Cymbium constricted in the middle (Fig. 108C). Paracymbium-cymbium attachment membranous. Paracymbium longer than half the cymbium length, with distal apophyses (Fig. 108D). Conductor-tegulum attachment well sclerotized, located at the centre of the tegulum (Fig. 108A). Embolus tubular, without basal apophyses. Sperm duct spiralled, considerably enlarged on its middle section (Levi, 1980: fig. 177).

**Natural history:** *Pachygnatha* has 40 described species and two subspecies described. Most species have a Holarctic distribution with some exceptions in South-East Asia, central and southern Africa (Platnick, 2009). Adults of *Pachygnatha* do not build capture webs but juveniles construct a small orb web (4 to 6 cm in diameter), with 13 to 17 radii and open hubs although the web has never been photographed (Levi, 1980: 50). Adults are found wandering in moist places on the ground, lack aggregate and flagelliform silk gland spigots, and the tarsal accessory claw is reduced. Juveniles have these gland spigots and their



**Figure 82.** *Mollemeta edwardsi* abdomen: A, cuticle of the abdomen, close up of median lateral section. B, female booklung cuticle. C, tracheal spiracle. D, median trachea tip. E, anterior lateral spinnerets. F, tracheal system dorsal view. G, epiandrous fusules. Images (C), (D), and (F), from SEMFAP060; images (A), (B), (E), and (G), from SEMFAP043.

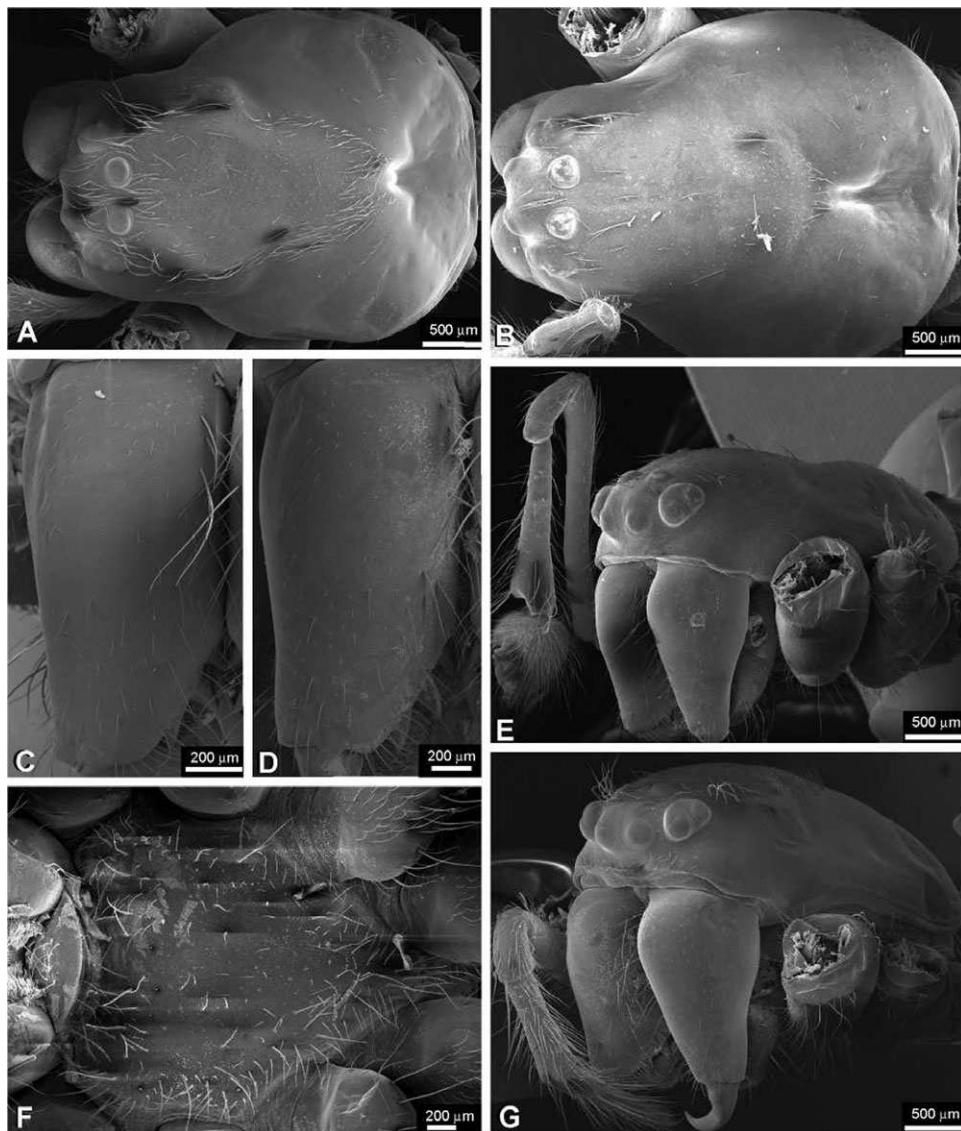
accessory claws are well developed (Levi, 1980). Some aspects of the biology of *Pachygnatha* have been studied, such as a comparison and description of the life cycles of *Pachygnatha degeeri* Sundevall, 1830 and *Pachygnatha clercki* Sundevall, 1823 (Alderweireldt & de Keer, 1990); the role of *P. degeeri* as an aphid predator (Harwood, Sunderland & Symondson, 2005); and the sperm ultrastructure of *Pachygnatha listeri* Sundevall, 1830 (Michalik *et al.*, 2005). The female genital anatomy of *P. autumnalis* was described by Dimitrov *et al.* (2007).

**Taxonomy:** The monophyly of *Pachygnatha* has never been tested. The taxonomy of the North American (Levi, 1980), European and the Afrotropical species (Bosmans & Bosselaers, 1994) has been revised. We have coded *P. autumnalis* Marx, in Key-

serling, 1884 in the character matrix. Our diagnosis and description were based on this latter species and on the *Pachygnatha* species descriptions of Levi (1980) and Bosmans & Bosselaers (1994). Previous phylogenetic analyses have recovered *Pachygnatha* as sister to *Glenognatha* (Hormiga *et al.*, 1995; Álvarez-Padilla, 2007; Dimitrov & Hormiga, 2009). Both the morphology plus behaviour and the total evidence data sets recover this latter sister group relationship (Figs 143, 144).

**TETRAGNATHA LATREILLE, 1804**  
(FIGS 1A, B, 5D, 109–113)

**Type species:** *Tetragnatha extensa* (Linnaeus, 1758). The type specimens of *Aranea extensa* are lost (Levi, 1981).

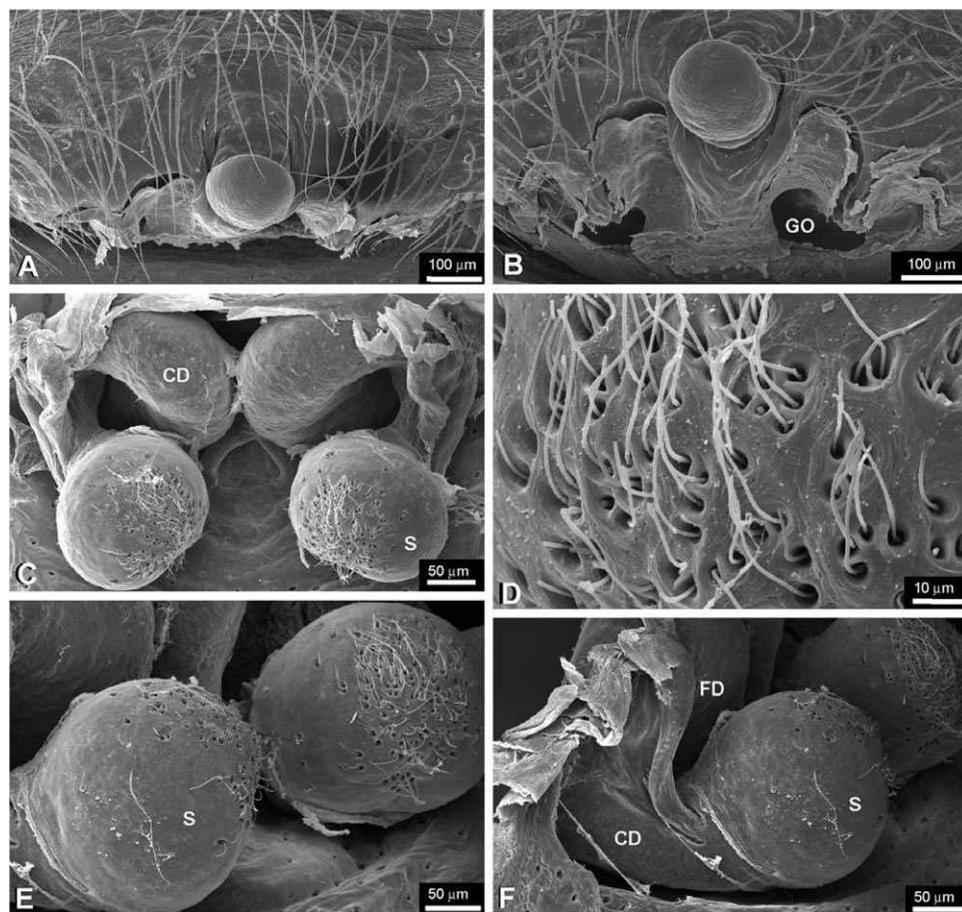


**Figure 83.** *Mollemeta edwardsi* cephalothorax: A, female dorsal view. B, male dorsal view. C, male chelicera. D, female chelicera. E, male tangential view. F, female ventral view. G, female tangential view. All images from SEMFAP043.

**Diagnosis:** The genus *Tetragnatha* is diagnosed by the following features: PLE tapetum absent but PLE canoe-shaped tapetum present (Levi, 1981: figs 20, 21); female lateral eyes on separate tubercles; cephalic fovea deep, divided in two pits (Fig. 110D); smooth femoral trichobothrial shaft, arranged in an irregular line; and haplogyne genitalia (Fig. 113D). In many species mature females have the copulatory opening displaced posteriorly relative to the epigastric furrow (Fig. 111A, B).

**Description: Female:** body length variable 5.4 to 13.3 mm (Levi, 1981). Femora IV trichobothrial shaft not branched (Fig. 110E). Ocular area lower than carapace lateral margins (Fig. 110B). Labium trap-

ezoidal, wider than long, and rebordered (Fig. 110F). Sternum longer than wide. Chelicerae divergent, anterior surface smooth and cheliceral boss present (Fig. 110B). Clypeus slightly higher than one AME diameter. Abdomen cylindrical, covered with silver guanine patches. Booklung cuticle smooth. Tracheal spiracle located near the spinnerets. ALS with extensive field of piriform spigots (Fig. 109B). PMS with three aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface (Fig. 109D). PLS with c. 20 aciniform spigots arranged in roughly parallel lines, distal end of the aggregate spigots separated from the tip of the flagelliform spigot (Fig. 109F). Epigynal plate absent, copu-



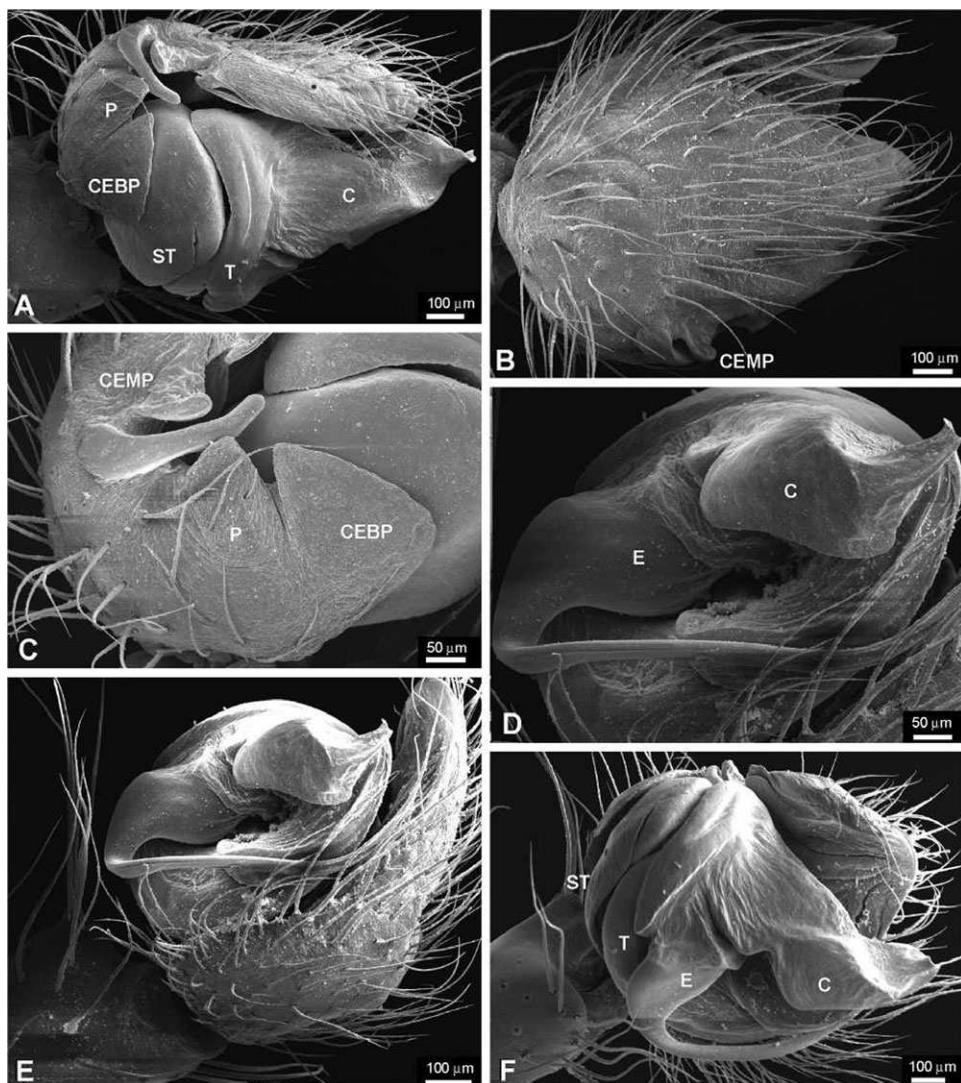
**Figure 84.** *Mollemeta edwardsi* epigynum: A, ventral view. B, posterior view. C, dorsal view. D, accessory glands. E, spermatheca. F, copulatory and fertilization ducts. Images (A) and (B), from SEMFAP043, all other from SEMFAP060.

latory opening as a transverse spiracle (Fig. 111A, B). Spermathecae with two chambers, walls well sclerotized (Figs 111C–F, 113D). Copulatory ducts short, well sclerotized and attached to a membranous sac (Fig. 113D). Fertilization ducts absent. Spermathecae accessory gland ductiles evenly distributed over the spermatheca, but more concentrated in the chamber near the copulatory duct. Accessory glands immersed in individual pits (Fig. 111E, F).

**Male:** body length 4.3 to 9.2 mm (Levi, 1981); somatic morphology similar to that of the female, except chelicerae considerably larger and with distal apophyses (Fig. 110A, C). PLS triplet reduced to nubbins (Fig. 109E). Epiandrous plate well sclerotized, fusules distributed in two groups, individual fusules not immersed in pits (Fig. 109C). Palpal patella with one macroseta. Palpal femora and tibia very long, more than four times its width (Fig. 110A). Paracymbium cylindrical, longer than half the cymbium length, evenly covered with macrosetae, and with a basal apophysis. Paracymbium-cymbium attachment membranous (Fig. 113A, D). Tegulum

spherical (Fig. 112A). Conductor-tegulum attachment well sclerotized, located on the centre of the tegulum (Fig. 113A). Embolus tubular, without basal apophyses. Sperm duct spiralled and considerably enlarged in its middle section (Fig. 113B, C).

**Natural history:** *Tetragnatha* is the most diverse genus in the family, with 325 described species and 15 subspecies that are distributed worldwide (Platnick, 2009). These spiders usually build webs over the vegetation inside forests or along ponds and rivers. The orb architecture is very variable (Fig. 5D; Levi, 1981: pl. 3) and some species do not build webs (Okuma, 1990; Gillespie, 1991b). The biology of *Tetragnatha* species has received more attention than that of any other tetragnathid genus. The web building behaviours of several *Tetragnatha* species were described by Eberhard (1982). Some studies on the biology of *Tetragnatha* include those of habitat selection in several Nearctic *Tetragnatha* species (Gillespie, 1987; Aiken & Coyle, 2000); the evolution, taxonomy, and biogeography of radiations of *Tetragnatha* species on the

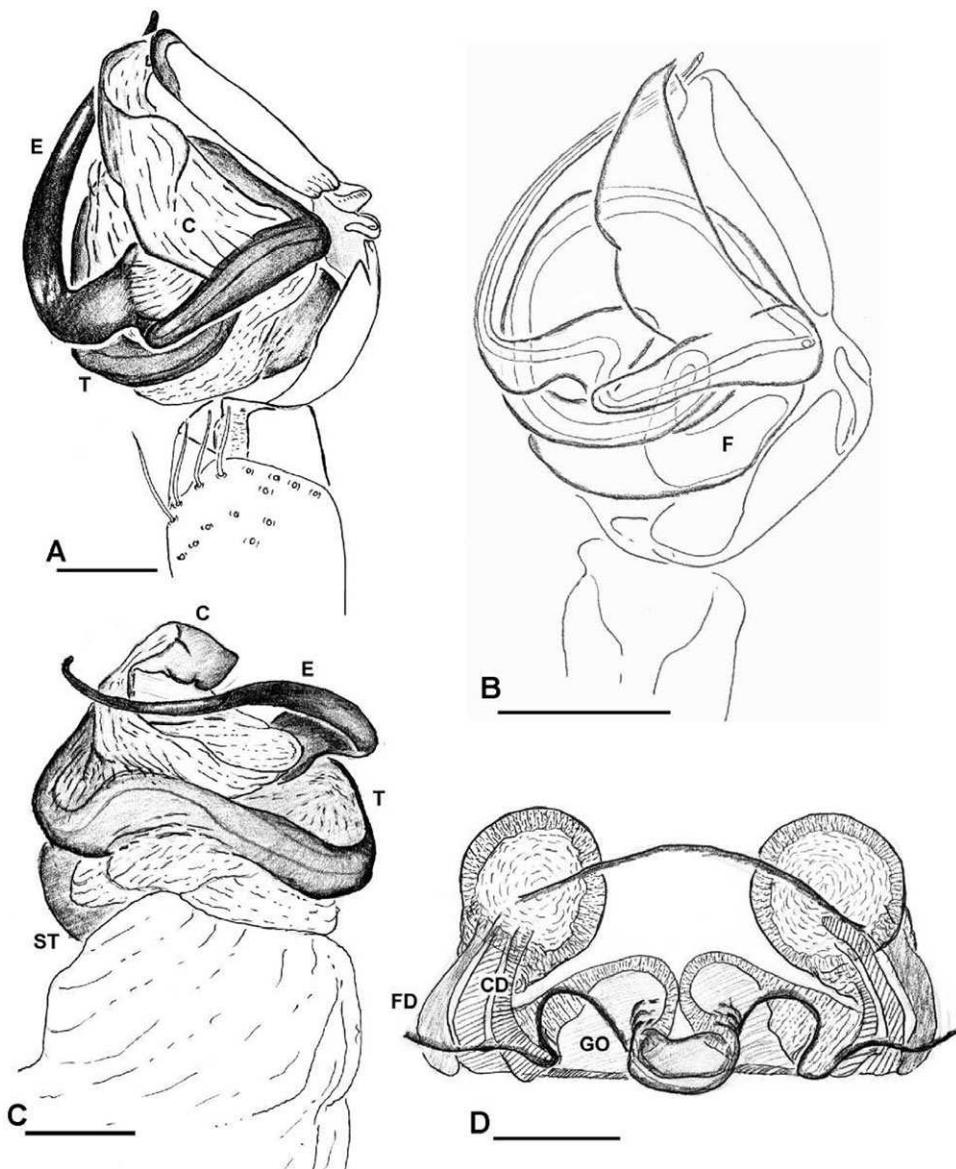


**Figure 85.** *Mollemeta edwardsi* male pedipalp: A, ectal view. B, dorsal view. C, cymbial ectobasal process and cymbial ectomedian process. D, conductor and embolus. E, apical view. F, ventral view. All images from SEMFAP056.

Hawaiian archipelago and Society Islands (Blackledge & Gillespie, 2004; Gillespie, 1991a, 1997, 1999, 2002; Pons & Gillespie, 2003; Vandergast, Gillespie & Roderick, 2004); venom composition (Binford, 2001); the relationship of the ‘haploxyne’ type of genital anatomy and sperm priority in *Tetragnatha extensa* (Austad, 1984; West & Toft, 1999); and sexual selection based on mating histories and body condition (Danielson-François & Bukowski, 2005).

**Taxonomy:** The taxonomy of *Tetragnatha* has received considerable attention and although a global taxonomic revision has never been attempted, several regional taxonomic revisions are available. The North American *Tetragnatha* species were revised by Seeley (1928), Chickering (1959), and Levi (1981). The species

from Mexico, Central America, Jamaica, and Panama were revised by Chickering (1957a, 1957b, 1957c, 1962). The Hawaiian fauna has been studied by Gillespie (2003a, b, c). Some *Tetragnatha* species from the Far East of Russia were revised by Kurenshchikov (1994). The Australasian and Japanese *Tetragnatha* were revised by (Okuma 1979, 1987, 1988a, b); this latter author also revised some of the African *Tetragnatha* (Okuma, 1985). Several of the *Tetragnatha* species from China have been illustrated (Song *et al.*, 1999). Finally the *Tetragnatha* species from paddy fields in Thailand and China have also been studied (Vungsilabutr, 1988; Barrion & Litsinger, 1995; Zhu, Wu & Song, 2002). We coded *Tetragnatha versicolor* in the character matrix. Our diagnosis and description were based on this latter species plus the species



**Figure 86.** *Mollemeta edwardsi* genital anatomy illustrations: A, male pedipalp ventral view. B, cleared pedipalp bulb ventral view. C, expanded pedipalp. D, cleared epigynum ventral view.

descriptions in Levi (1981). The morphology plus behaviour data set recovered *Tetragnatha* and *Cyrtognatha* as sister taxa (Fig. 143A, B); however, when these data are combined with DNA sequences, *Tetragnatha* is sister to a clade that includes *Glenognatha* and *Pachygnatha* (Fig. 144).

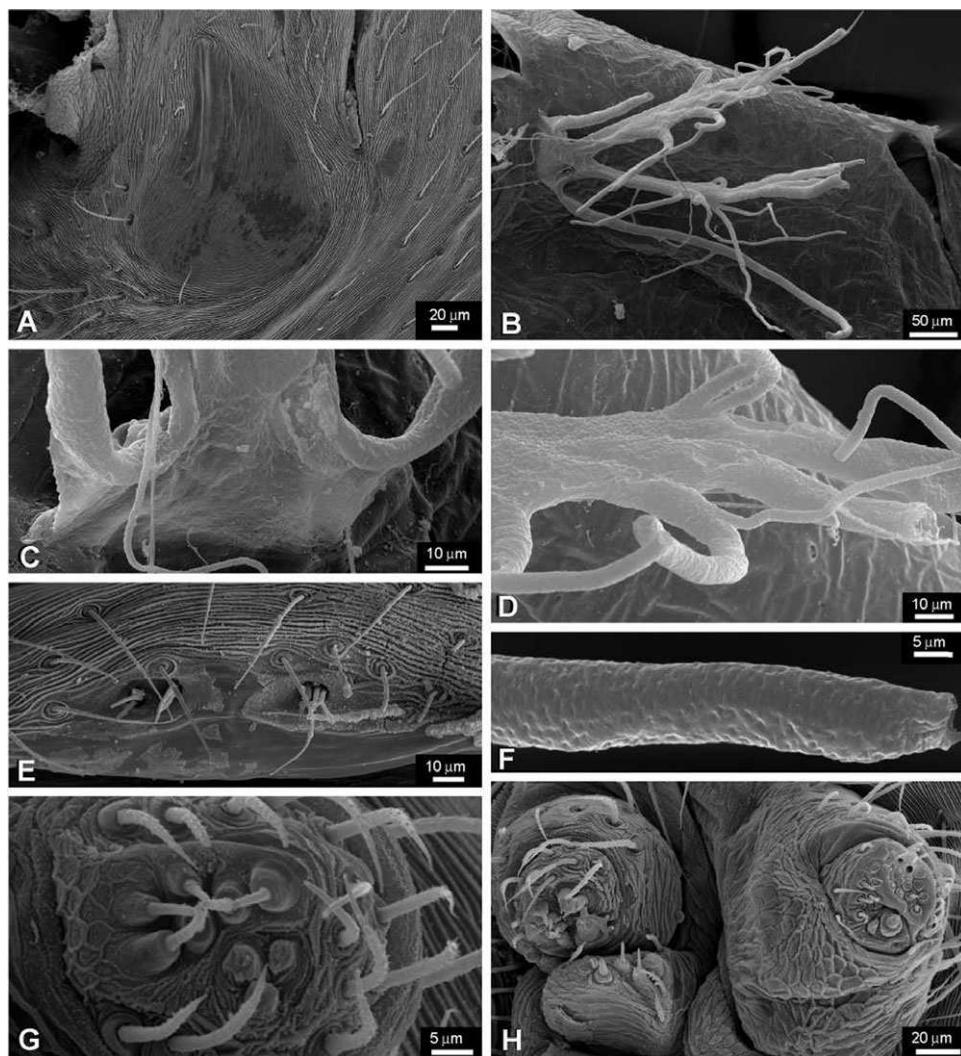
#### TYLORIDA SIMON, 1894 (FIGS 5E, 114–118)

*Type species:* *Tylorida striata* (Thorell, 1877). Type specimen and depository museum unknown.

*Diagnosis:* *Tylorida* species differ from other tetragnathids in the following combination of characters: femora IV with smooth trichobothrial shaft

(Fig. 115F); copulatory and fertilization ducts running parallel before entering the spermathecae (Fig. 116C); tegulum ventrally swollen (Fig. 117B); cymbial dorso-basal process shorter than half the cymbial width and perpendicular to the cymbium longitudinal axis (Fig. 117A, F). The following description is based on our study of *Tylorida striata*.

*Description: Female:* body length c. 10.0 mm. Femora IV trichobothrial shaft not branched, shorter than half the femur length (Fig. 115F). Ocular area lower than carapace lateral margins (Fig. 115B, D). Labium trapezoidal, wider than long, and rebordered. Sternum longer than wide (Fig. 115E). Anterior

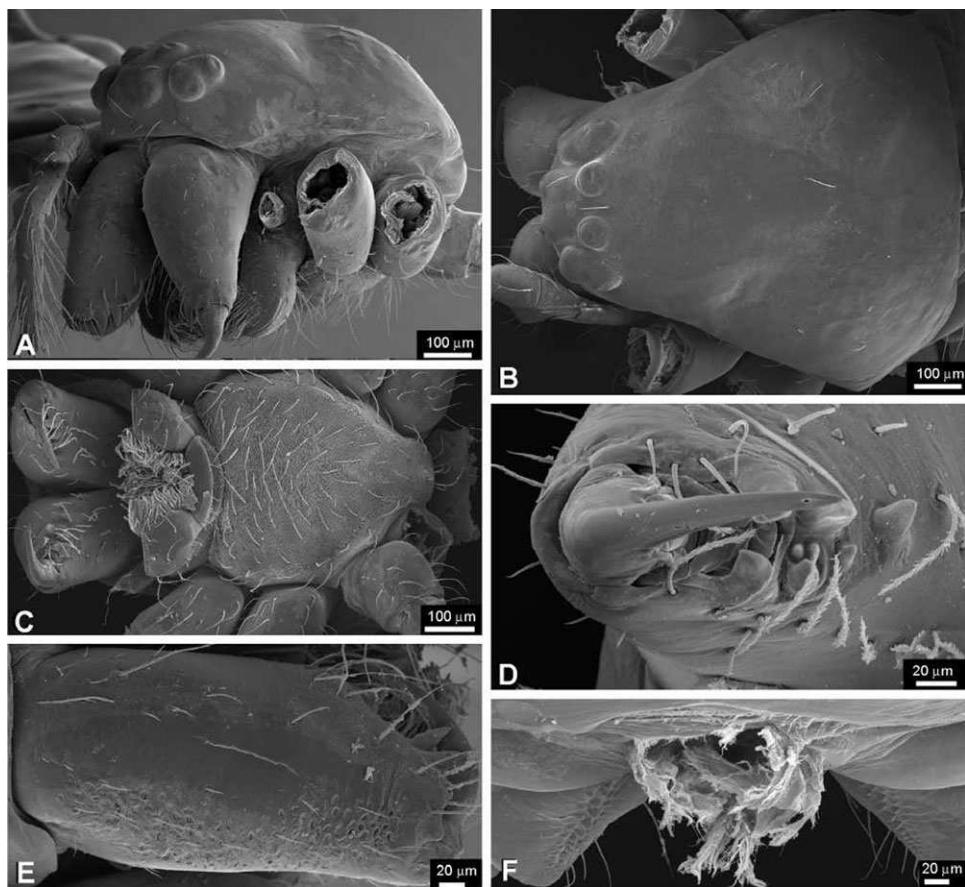


**Figure 87.** *Nanometa* sp. abdomen: A, male book cuticle. B, abdomen tracheal system dorsal view. C, tracheal spiracle posterior view. D, median tracheae ramifications. E, epiandrous fusules. F, lateral trachea tip. G, male posterior lateral spinnerets. H, female spinnerets. All images from SEMFAP048.

surface of chelicerae smooth; boss present (Fig. 115B). Secondary eyes with canoe-shaped tapetum. Eyes subequal in size, lateral eyes juxtaposed, and on a tubercle. Clypeus almost 1.5 times the AME diameter. Abdomen anteriorly projected and covered with silver guanine patches that form longitudinal lines (Tani-kawa, 2005: figs 1, 2). Booklung cuticle smooth. Tracheal spiracle near the spinnerets. Median tracheae not ramified, longer than half the lateral tracheae length (Fig. 114A, C, D). ALS with an extensive field of piriform spigots (Fig. 114B). PMS with three aciniform spigots between the cylindrical and minor ampullate silk gland spigots but without any aciniform spigots over the anterior surface (Fig. 114E). PLS with c. 20 aciniform spigots arranged in roughly parallel lines; distal end of aggregate spigots sepa-

rated from tip of the flagelliform spigot (Fig. 114G). Epigynal plate flat, copulatory openings ventrally orientated (Fig. 116A). Spermathecae walls weakly sclerotized. Copulatory and fertilization ducts coiled, longer than the spermatheca length and cuticle well sclerotized (Figs 116F, 118D). Accessory gland ductiles concentrated near the duct junction, accessory glands acorn-shaped and in individual pits (Fig. 116B, E).

**Male:** size and somatic morphology similar to that of the female (Fig. 115C, D). PLS triplet reduced to nubbins. Epiandrous plate well sclerotized, fusules immersed in a transverse groove with their bases wider than fusule shaft (Fig. 114F). Palpal patella without macrosetae. Palpal femora very long, more than four times its width. Tibia length slightly more



**Figure 88.** *Nanometa* sp. cephalothorax: A, female tangential view. B, female dorsal view. C, female ventral view. D, female cheliceral denticles. E, male chelicera. F, male IV coxae dorsal view. All images from SEMFAP048.

than one times its width (Fig. 117D). Paracymbium shorter than half the cymbium length, curved and with the distal margin swollen (Fig. 117F). Subtegulum ectally displaced (Fig. 117C). Conductor edges well sclerotized, median sections rigid but weakly sclerotized. Conductor-tegulum attachment membranous (Figs 117E, 118C). Embolus base rectangular, longer than wide (Fig. 118C). Embolus flexible and weakly sclerotized. Sperm duct with more than five coils (Fig. 118A, B).

**Natural history:** There are nine described species of *Tylorida*, all from the Australasian region, with some species extending to western South Africa and Cameroon (Chrysanthus, 1975; Davies, 1988; Zhu *et al.*, 2003). *Tylorida striata* builds horizontal webs with c. 20 spiral switchbacks, c. 15 radii, an open hub, and an open sector (Fig. 5E). The reproductive behaviour of *Tylorida ventralis* (Thorell, 1877) has been recently documented (Preston-Mafham & Cahill, 2000). The web building behaviour of *T. striata* was described by Eberhard (1982).

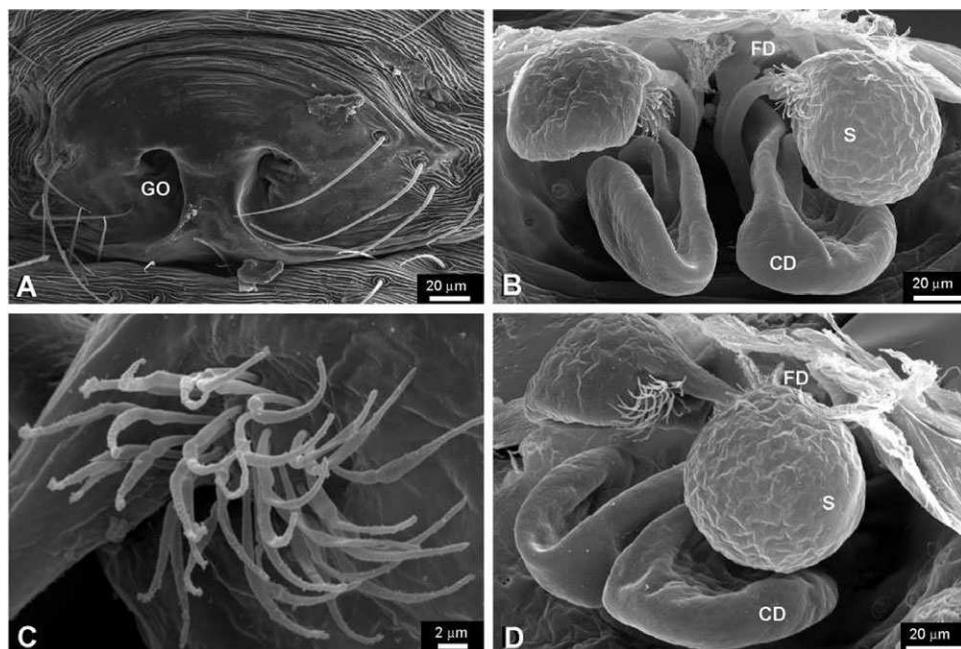
**Taxonomy:** The monophyly of *Tylorida* remains to be tested. The Chinese *Tylorida* species were recently treated by Zhu *et al.* (2002) and the Japanese species by Tanikawa (2005). A previous phylogenetic analysis proposed *T. striata* as sister to *Mesida* (Fig. 141B; Tanikawa, 2001). The sister taxa relationships of *Tylorida* with other Leucauginae genera are unresolved by the data set of morphology plus behaviour (Fig. 143A, B). In the total evidence analysis *Tylorida* is sister to *Orsinome* (Fig. 144).

#### TAXONOMIC SUPPLEMENT

##### NANOMETINAE FORSTER & FORSTER, 1999 NEW RANK (FIGS 4F, 71–76, 87–91, 96–99)

**Type genus:** *Nanometa* Simon, 1908. This family name was first proposed by Forster & Forster (1999: 166) at the family rank, but it has never been formally diagnosed.

**Diagnosis:** Nanometines can be differentiated from other tetragnathids by the following combination of characters: female cheliceral denticles present (84-1;



**Figure 89.** *Nanometa* sp. epigynum: A, ventral view. B, dorsal view. C, accessory glands. D, spermatheca and copulatory ducts. All images from SEMFAP048.

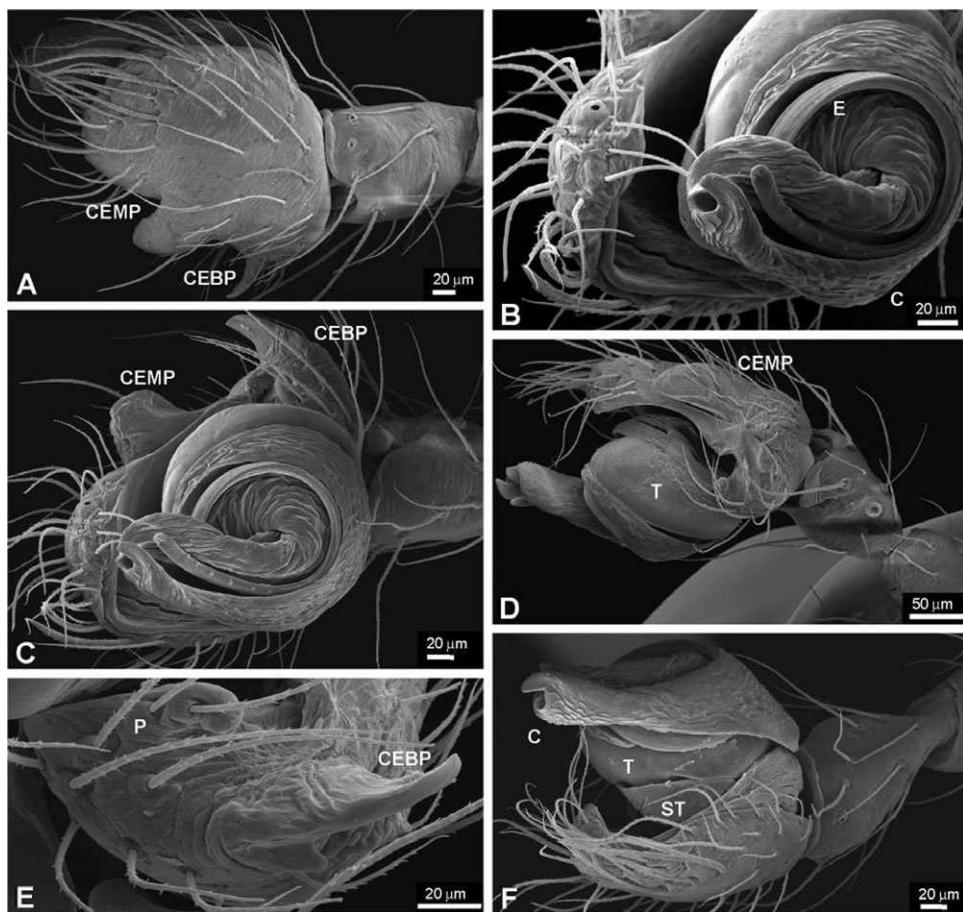
Figs 73C, 88D), absence of trichobothria on femur IV (Fig. 73F) and the remaining femora, female genital openings often plugged with amorphous material (132-3: Figs 74A, 98B), male palpal patella without macrosetae (180-0: Figs 73D, 97H), conductor originating on the centre of the tegulum (55-0), solid, uniform degree of sclerotization between tegulum and conductor (59-0); and tubular embolus shape (67-0) (Figs 75E, 76A-C, 90C, 91A). These six characters also represent the morphological synapomorphies supporting this lineage obtained by the total evidence analysis of Dimitrov & Hormiga (2011), in which they are labelled as ‘*Nanometa* clade’ (see also Álvarez-Padilla *et al.*, 2009). Additional diagnostic characters of nanometines are the female copulatory ducts longer than the spermathecae length (146-2; Figs 74B, 89D, 98D), shorter in *Pinkfloydia* Dimitrov & Hormiga, 2011: figs 8G, H, 15F); the presence of a cymbium ectobasal process (26-1); and having the cymbium ectomedian process more than half the cymbial width (30-1: Figs 75A, 90A, C, 99D). The characteristic branched tracheal system of many nanometines (such as *Nanometa* and ‘*Orsinome*’ *sarasini*; see Forster & Forster, 1999: 166) is not found in *Pinkfloydia*, which has its median tracheal trunks confined to the abdomen and not branched (Dimitrov & Hormiga, 2011).

**Taxonomic and natural history:** Forster & Forster (1999) were the first to recognize this group endemic

to Australasia as ‘*Nanometidae*’ and discussed some interesting aspects of nanometine anatomy such as the presence of an stridulatory organ on the booklung covers of males opposite to a row of denticles on the IV coxa (Figs 71A, B, 73E). They also included in their ‘*Nanometidae*’ the monotypic genus *Eryciniolia* Strand, 1912 and *Orsinome lagenifera* (Urquhart, 1888). There are many species to be described in Nanometinae, some which are new (e.g. Dimitrov & Hormiga, 2011) but others are misplaced, such as the case of ‘*Orsinome*’ *sarasini* (Figs 143A, B, 144), which is not congeneric with the type species of *Orsinome* and belongs in the Nanometinae. At the present time Nanometinae includes the genera *Nanometa* and *Pinkfloydia*. The monophyly of Nanometinae has been tested in recent phylogenetic analyses that also included molecular data and the group is relatively well supported (Álvarez-Padilla *et al.*, 2009; Dimitrov & Hormiga, 2011).

#### CHARACTER DESCRIPTIONS

The following section provides descriptions and illustrations for the 213 morphological and behavioural characters, with their respective character states, that we have coded in the data matrix. These characters were scored for 47 terminals, 23 of them tetragnathids and outgroup taxa (described in the previous section). The resulting data matrix has 8506 data entries, 1505 are either inapplicable or still unknown for this data

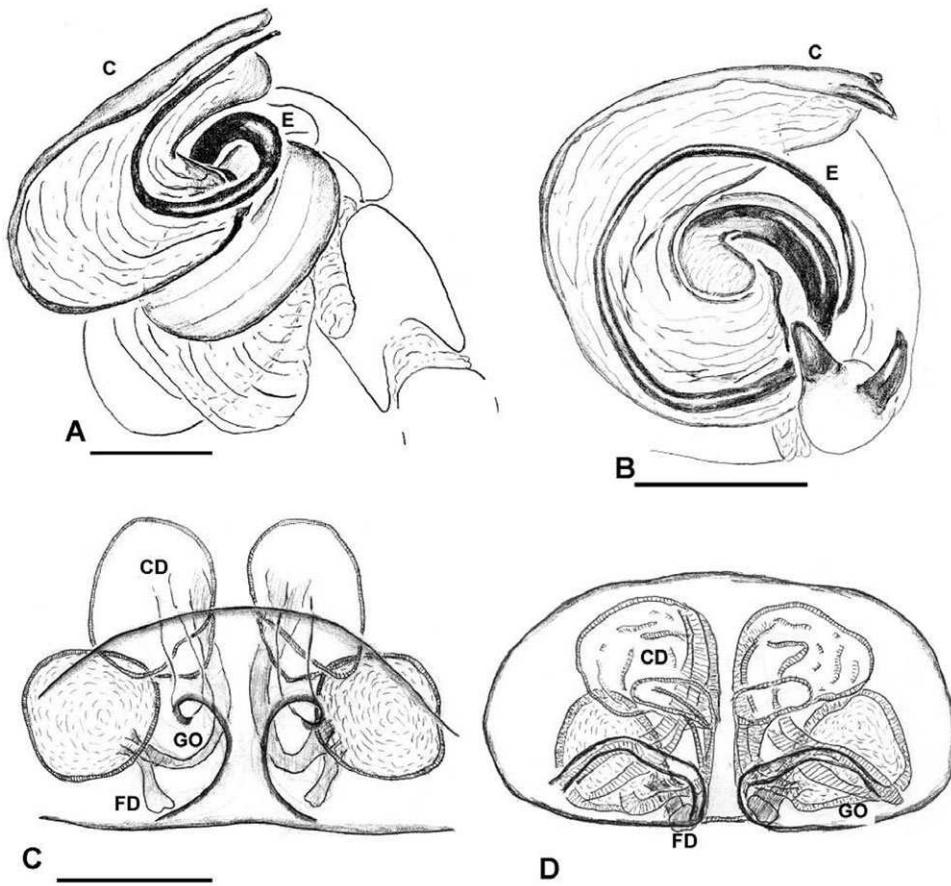


**Figure 90.** *Nanometa* sp. male pedipalp: A, dorsal view. B, apical view. C, ventral view. D, ectal view. E, cymbial ectobasal process. F, mesal view. All images from SEMFAP048.

set (Appendix 1). Spinneret spigot and epiandrous fusule morphology is coded from characters 1 to 22. Features for the male pedipalp are coded from characters 23 to 79. Male and female cephalothoracic morphology is covered from characters 80 to 122. Epigynum anatomy is coded from characters 123 to 153. Characters 154 to 168 code the tracheal system and other abdominal features. Features of the fourth leg and other appendages are coded from characters 169 to 185. Finally, a compilation of behavioural characters from previous studies is presented in characters 186 to 213. This data set can be downloaded from <http://www.gwu.edu/~spiders/cladograms.htm>. Many of these characters had been used in previous phylogenetic studies; in that case, a code at the end of each character indicates these references. The following codes are used: Levi, 1980 = L80; Coddington, 1990a = C90; Hormiga, 1994a, b = H94; Hormiga *et al.*, 1995 = H95; Scharff & Coddington, 1997 = S97; Griswold *et al.*, 1998 = G98; Tanikawa, 2001 = T01; Agnarsson, 2004 = A04; Griswold *et al.*, 2005 = G05; Kuntner 2005, 2006; Kuntner *et al.*, 2008 = K08;

Álvarez-Padilla, 2007 = A07, and Dimitrov & Hormiga, 2009 = DIP. Citation does not necessarily mean character authorship – for example, many of these characters have been described and used in spider systematics since the nineteenth century.

1. *ALS piriform spigot base height*: (0) tall (*Tetragnatha versicolor*, Fig. 109B); (1) low (*Epeirotypus brevipes*, Fig. 119D). Tall piriform spigot bases are those higher than 1/4 of the spigot shaft; low piriform spigot bases are shorter. These spigots serve piriform silk glands that produce the cement used to attach drag lines. Spigots are formed by a shaft and a base, both made of cuticle. Low piriform spigot bases are a synapomorphy of the clade that includes linyphioids, theridiidoids, and symphytognathoids (the ‘reduced piriform clade’ of Griswold *et al.*, 1998) (H95, S97, G98, A04, G05, K08, A07, DIP).
2. *ALS piriform spigot base distal edge*: (0) tightly wrapping column base (*Araneus marmoreus*, Fig. 119C insert box); (1) separated from the

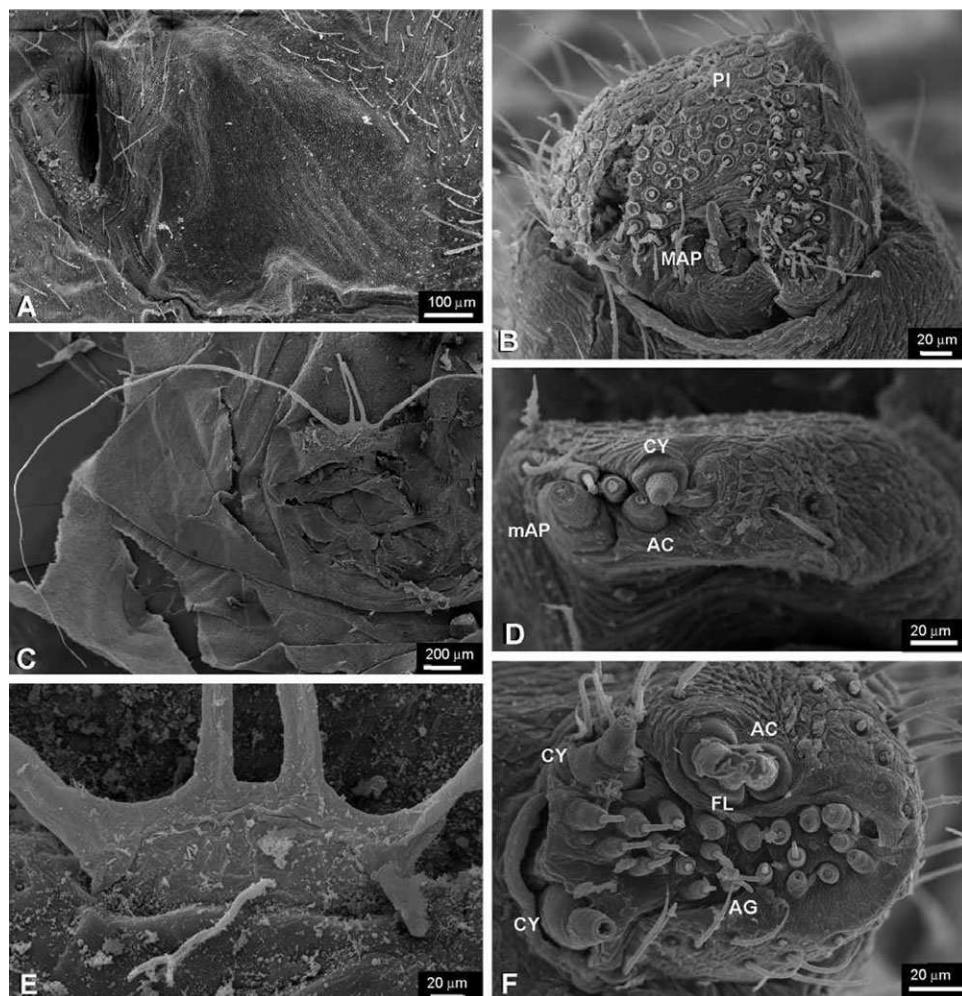


**Figure 91.** *Nanometa* sp. and ‘*Orsinome*’ *sarasini* genital anatomy illustrations: A, *Nanometa* sp. palp expanded. B, ‘*Orsinome*’ *sarasini*, pedipalp expanded. C, *Nanometa* sp. cleared epigynum ventral view. D, ‘*Orsinome*’ *sarasini* cleared epigynum ventral view.

column base leaving a torus (*Metellina segmentata*, Fig. 66B, arrow in insert box points to the torus area wrapping the piriform spigot shaft). Separated piriform base margins are common amongst tetragnathids except in *Meta menardi* and *Mollemeta edwardsi* (Figs 56B, 82E). The cyrtophorine *Mecynogea lemniscata* (Araneidae) has both types of piriform margin bases and is coded as polymorphic (Fig. 119E) (G05).

- 3. *ALS* piriform field perimeter: (0) notched (*Phonognatha graeffei*, Fig. 135C, arrow); (1) uniform (*Zygiella x-notata*, Fig. 119F). *Deliochus* sp. (Fig. 135D, arrow) and *Phonognatha graeffei* have a cuticular area opposite to the MAP delimited by a notch of the piriform field perimeter. The cuticle in this area is different from both the nearby spinneret cuticle and the cuticular surface between the piriform spigots. The piriform field of *Mecynogea lemniscata* is also notched, but the cuticle of this notch is similar to that between the piriform spigots (Fig. 119E).

- 4. *PMS* anterior surface: (0) without aciniform spigots (*Tetragnatha versicolor*, Fig. 109D); (1) with aciniform spigots (*Cyclosa conica*, Fig. 120A). The PMS anterior surface is the area between the cylindrical gland spigot and the anterior base of the spinneret. All tetragnathids lack aciniform spigots in this area, except *Azilia affinis* and *Meta menardi* (Fig. 13G; Hormiga *et al.*, 1995: fig. 19B, C). The PMS anterior surface is considered with aciniform spigots if there is at least one spigot separated from the cylindrical spigot base (*Micrathena gracilis*, Fig. 120E) (H94, H95, S97, G98, A04, G05, K08, A07, DIP).
- 5. *PMS* aciniform anterior spigots: (0) 20 or fewer AC spigots (*Gasteracantha cancriformis*, Fig. 120C); (1) more than 20 spigots (*Mangora gibberosa*, Fig. 120D) (H94, H95, S97, G98, A04, G05, K08, A07, DIP).
- 6. *PMS* cylindrical spigot number: (0) one (*Glenognatha foxi*, Fig. 36H); (1) two (*Uloborus glomosus*,



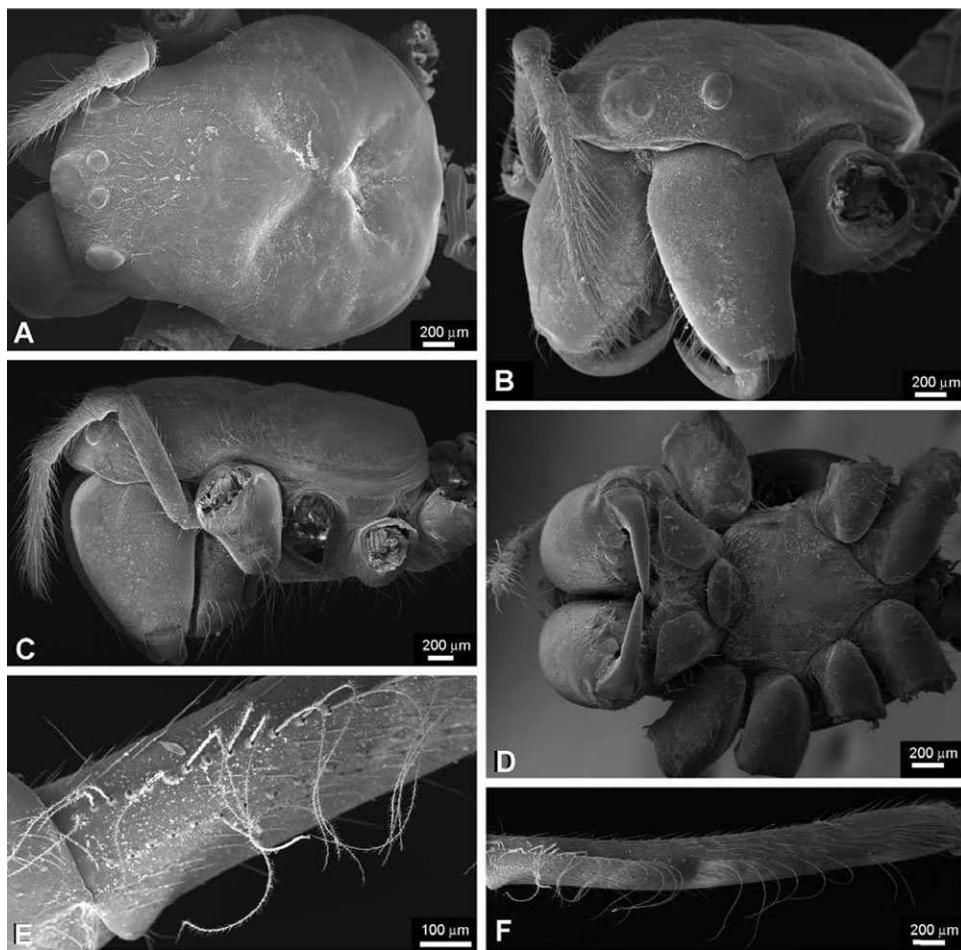
**Figure 92.** *Opadometa* sp. abdomen: A, female booklung cuticle. B, anterior lateral spinnerets. C, tracheal system dorsal view. D, posterior median spinnerets. E, tracheal spiracle posterior view. F, posterior lateral spinnerets. All images from SEMFAP038.

Fig. 121A). The presence of only one cylindrical spigot on the PMS is synapomorphic for araneoids (Griswold *et al.*, 1998, 2005); *Uloborus* and *Oncodamus decipiens* have many (Fig. 120F) (G98, G07).

7. *PMS nubbin*: (0) absent (*Epeirotypus brevipes*, Fig. 120B); (1) present (*Tylorida striata*, Fig. 114E). Spigot nubbins and tartipores can be confused, nubbins are projected whereas tartipores are flat (Griswold *et al.*, 2005: 58–59 and references therein); *Epeirotypus brevipes* has a tartipore that can be confused with a spigot nubbin (Fig. 120B arrow). The lack of the mAP spigot nubbin is synapomorphic for the ‘reduced piriform clade’ (*Linyphia triangularis* Hormiga, 1994a: fig. 21A, C), but some symphytognathoids have it (e.g. *Anapis* sp. in Griswold *et al.*, 1998: fig. 31C; see also Lopardo & Hormiga,

2008). All tetragnathids observed have the mAP spigot nubbin except *Pachygnatha autumnalis* (Fig. 105C) (H95, S97, G98, A04, G05, K08, A07, DIP).

8. *PLS cylindrical spigot bases*: (0) same size (*Diphya spinifera*, Fig. 26D); (1) mesal larger than the more distal spigot base (*Pachygnatha autumnalis*, Fig. 105E). PLS cylindrical spigot bases are the same size in almost all araneoids. Linyphiids, pimoids, anapids, symphytognathoids, and some tetragnathids have the mesal cylindrical spigot base larger on the PLS (Hormiga, 1994a, 2000; Griswold *et al.*, 1998) (H94, H95, G98, A04, A07, DIP).
9. *PLS cylindrical spigot position*: (0) central (*Mangora gibberosa*, Fig. 121F); (1) peripheral (*Tylorida striata*, Fig. 114G). The PLS cylindrical spigot’s position can be either central, immersed



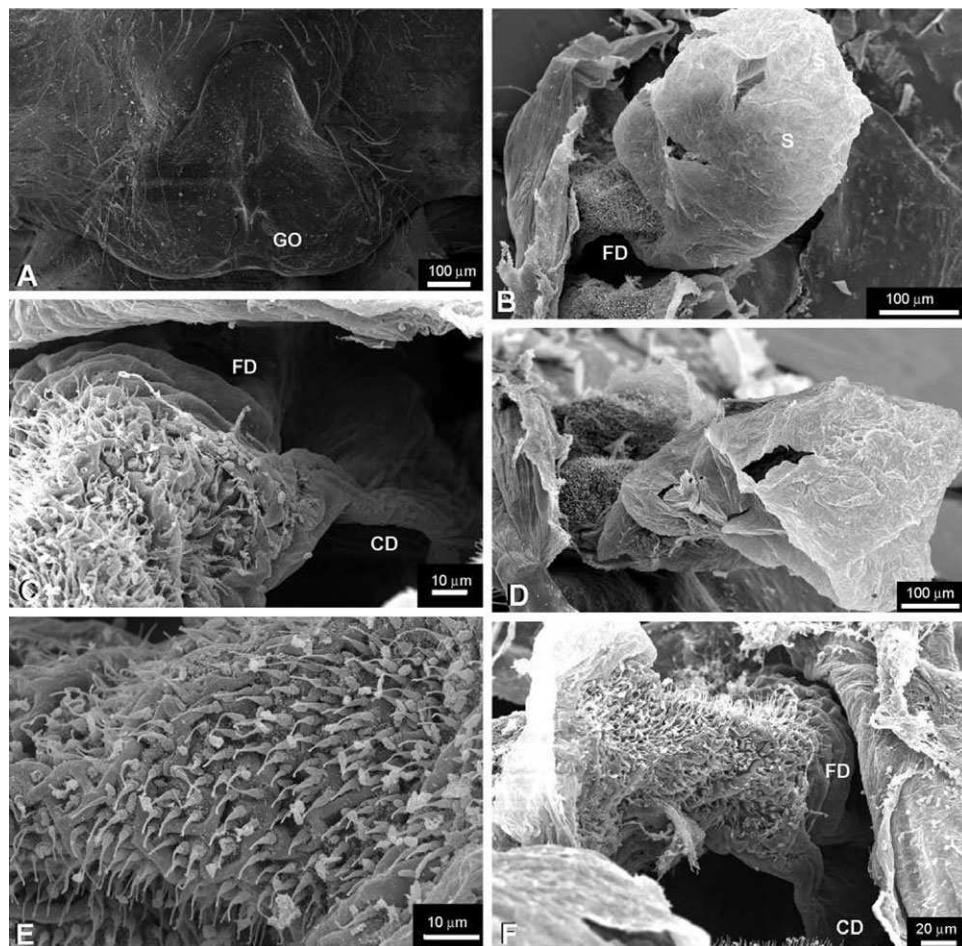
**Figure 93.** *Opadometa* sp. cephalothorax: A, female dorsal view. B, female tangential view. C, female lateral view. D, female ventral view. E and F, female femora IV trichobothria. All images from SEMFAP038.

in a brush of 20 aciniform spigots; or displaced toward the anterior edge. Peripheral cylindrical spigots are plesiomorphic for Orbiculariae with two independent origins of the central position, within araneids and in *Uloborus glomosus* (H95, G98, G05, K08, A07, DIP).

10. *PLS aggregate gland spigots*: (0) approximately the same size as the distal cylindrical spigot (*Leucauge argyra*, Fig. 46F); (1) enlarged (*Asagena americana*, Fig. 121B). Enlarged aggregate gland spigots (i.e. at least twice the size of the cylindrical spigot) are synapomorphic for nesticids and theridiids (Coddington, 1989; Griswold *et al.*, 1998) (H95, G98, A04, K08, A07, DIP).
11. *PLS distal aciniform spigots*: (0) not extending beyond the triplet area (*Chrysometa alajuela*, Fig. 18E); (1) extending beyond the triplet area (*Nephilengys malabarensis*, Fig. 122A). The PLS distal area is located between the aggregate spigot base and the spinneret edge. As defined here, state 0 applies when there are nine or fewer

aciniform spigots on this area beyond the triplet. State 1 applies when there are ten or more spigots. *Pachygnatha autumnalis* lacks the triplet and the aciniform field (Fig. 105E). *Oncodamus* and *Uloborus* are coded as having an extensive aciniform brush despite the absence of the triplet (Fig. 122B, C).

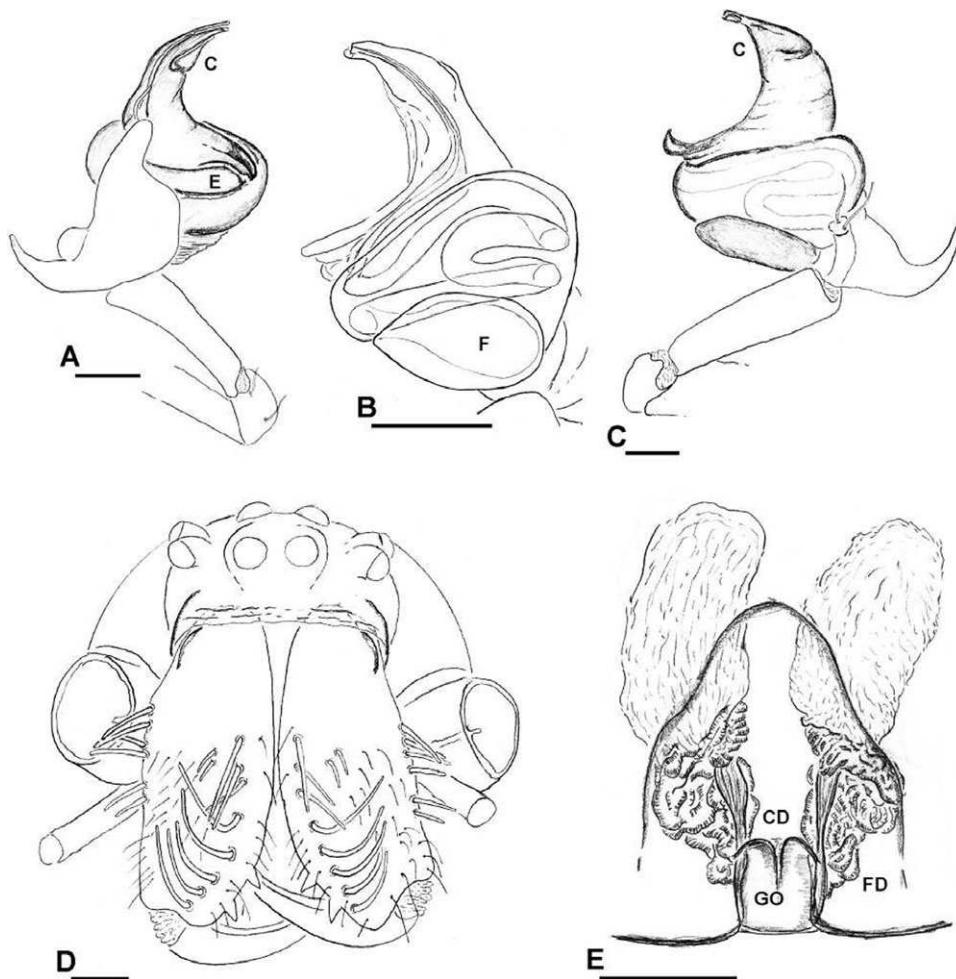
12. *Aggregate spigots*: (0) absent (*Uloborus glomosus*, Fig. 122C); (1) present (*Araneus marmoreus*, Fig. 121C). These spigots are associated with the aggregate glands that produce the liquid viscous silk unique to araneoid spiders. Araneoids use this viscous silk to capture or retain their prey. Other orbicularians lack aggregate glands and produce their sticky silk with the cibellum. Aggregate spigots are synapomorphic for Araneoidea with secondary losses in several araneoid taxa (Griswold *et al.*, 1998, 2005) (H95, G98, G05, A07, DIP).
13. *Flagelliform spigots*: (0) absent (*Oncodamus decipiens*, Fig. 122B); (1) present (*Cyclosa conica*,



**Figure 94.** *Opadometa* sp. epigynum: A, ventral view. B, spermatheca dorsal view. C, copulatory and fertilization ducts. D, spermatheca lateral view. E and F, accessory glands. All images from SEMFAP038.

- Fig. 121E). Flagelliform glands produce the axial fibres onto which the viscid silk is deposited; aggregate glands coat the flagelliform fibre with sticky glue as it is spun. The presence of flagelliform spigots is synapomorphic for Araneoidea (Sekiguchi, 1952; Griswold *et al.*, 1998). These spigots are homologous to the pseudoflagelliform spigots found in deinopoids (Fig. 121A; Coddington, 1989: fig. 5) and absent outside Orbiculariae. Flagelliform spigots are also absent in *Pachygnatha autumnalis* (Fig. 105E) (G98, A04, G05).
14. *Flagelliform spigot position:* (0) near the aggregate spigots (*Argiope argentata*, Fig. 121D); (1) apart (*Zygiella x-notata*, Fig. 122D). In most araneoid taxa the aggregate spigots flank the flagelliform spigot. The flagelliform spigot is also separated towards the anterior spinneret edge at least one aggregate spigot diameter apart in *Deliochus* sp. (Fig. 135E), *Phonognatha graeffei* (Fig. 135E), and *Zygiella x-notata*.

15. *AG-flagelliform triad:* (0) aggregate spigot distal ends apart from flagelliform spigot (*Tetragnatha versicolor*, Fig. 109F); (1) distal ends of the aggregate spigots embracing the distal end of the flagelliform spigot (*Mesida argentiopunctata*, Fig. 51E). The flagelliform spigot distal edges can be either separated from the aggregate spigots, or surrounded by them (H95, K08, A07, DIP).
16. *Spinneret cuticle:* (0) squamose (*Chrysometa alajuela*, Fig. 18F); (1) rugose (*Oncodamus decipiens*, Fig. 122B). The spinneret cuticle of araneoid spiders is scaly. Such squamose spinneret cuticle is synapomorphic for Araneoidea (Griswold *et al.*, 1998). The spinneret cuticle of *Uloborus* and *Oncodamus* has a ‘fingerprint’ pattern (Lehtinen, 1975) (G98, G05).
17. *Sclerotized ring around spinnerets:* (0) absent (*Uloborus glomosus*, Fig. 119B); (1) present (*Gasteracantha cancriformis*, Fig. 119A). The area surrounding the spinnerets can be either like the rest of the abdomen, or surrounded by



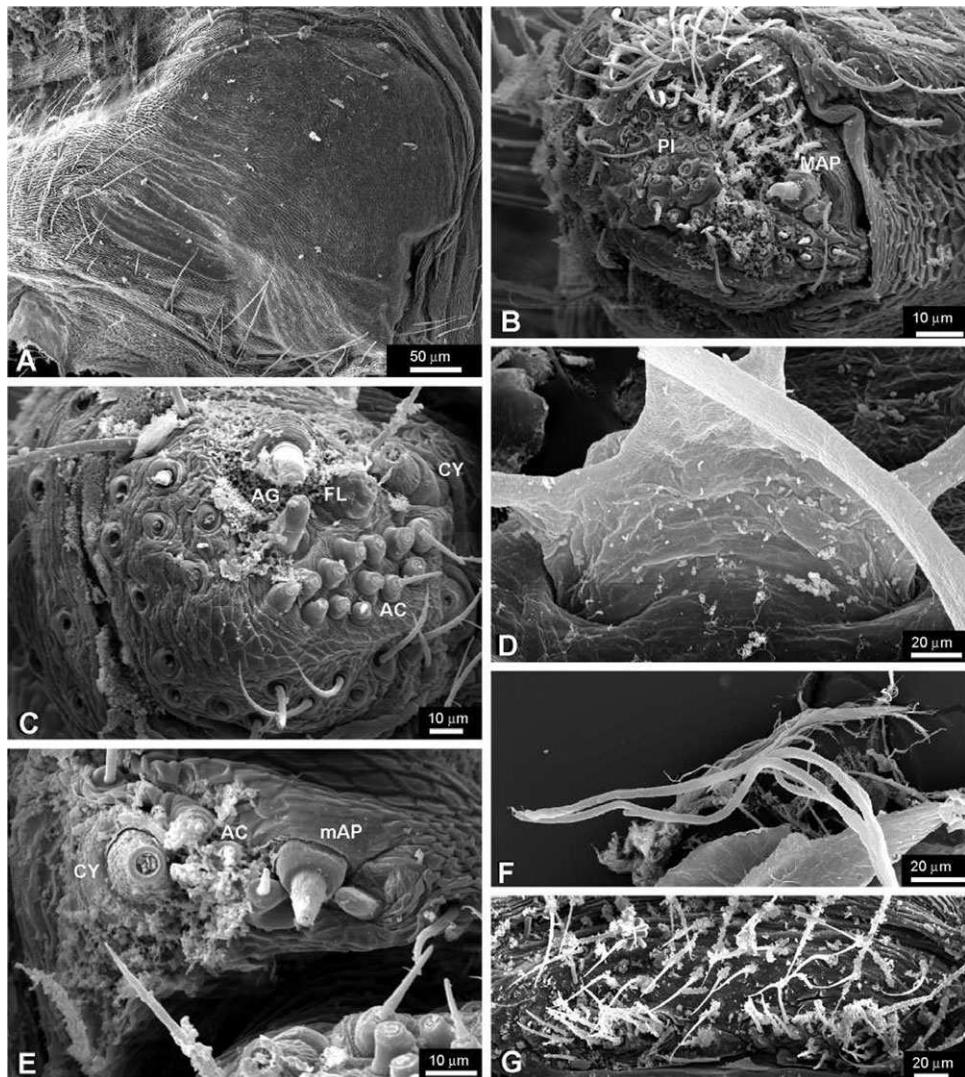
**Figure 95.** *Opadometa* sp. genital anatomy and male cephalothorax illustrations: A, male pedipalp dorsal view. B, male pedipalp cleared ventral view. C, male pedipalp ectal view. D, male carapace anterior view. E, epigynum cleared ventral view.

a thick sclerotized ring (Scharff & Coddington, 1997: figs 23, 45, 46). This sclerotized ring is optimized as synapomorphic for *Gasteracantha* and *Micrathena* (S97, G98, A04, G05, A07, DIP).

18. *Epiandrous fusules arrangement:* (0) one transverse line (*Orsinome* nr. *vethi*, Fig. 100F); (1) two main clusters (*Dolichognatha pentagona*, Fig. 31G). The epiandrous fusules are found exclusively in males and are used to spin the sperm web and have been hypothesized as serial homologues of the median spinnerets (de Machado, 1951; Fage & de Machado, 1951; Marples, 1967) (A04, G05).
19. *Epiandrous fusule line:* (0) level with the surrounding cuticle (*Tetragnatha versicolor*, Fig. 109C); (1) within a groove (*Leucauge argyra*, Fig. 46G). The epiandrous fusule bases can be either level with the surrounding cuticle,

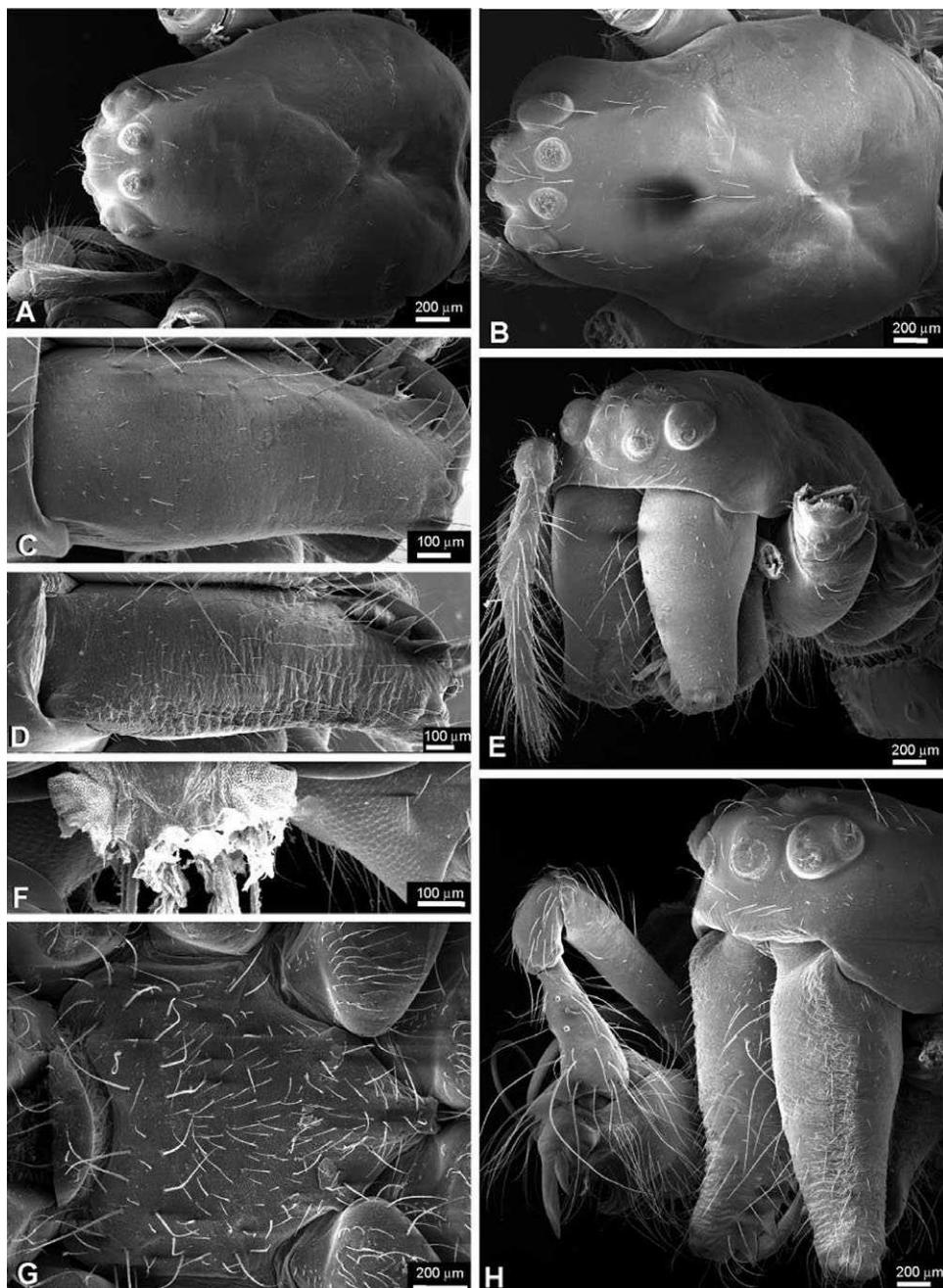
or inside a groove. An epiandrous groove is defined here as a longitudinal depression that results from a cuticular fold along the posterior margin of the epiandrous region. When a groove is present, both longitudinal edges of the fold are higher than half of the epiandrous fusule shaft height.

20. *Epiandrous fusule pits:* (0) absent (*Metamenardi*, Fig. 56F); (1) present (*Larinoides cornutus*, Fig. 122F). The bases of the epiandrous fusules can be levelled with the surrounding cuticle, or immersed in pits. The number of spigots per pit can vary in the same specimen from one to several.
21. *Epiandrous fusule base distal margin:* (0) sharp edge (*Epeirotypus brevipes*, Fig. 122E); (1) round edge (*Mesida argentiopunctata*, Fig. 51G). The apical edge of the base of the fusules can be either sharp or round.



**Figure 96.** ‘*Orsinome*’ *sarasini* abdomen: A, male booklung cuticle. B, anterior lateral spinnerets. C, posterior lateral spinnerets. D, tracheal spiracle posterior view. E, posterior median spinnerets. F, median tracheae tips. G, epiandrous fusules. All images from SEMFAP050.

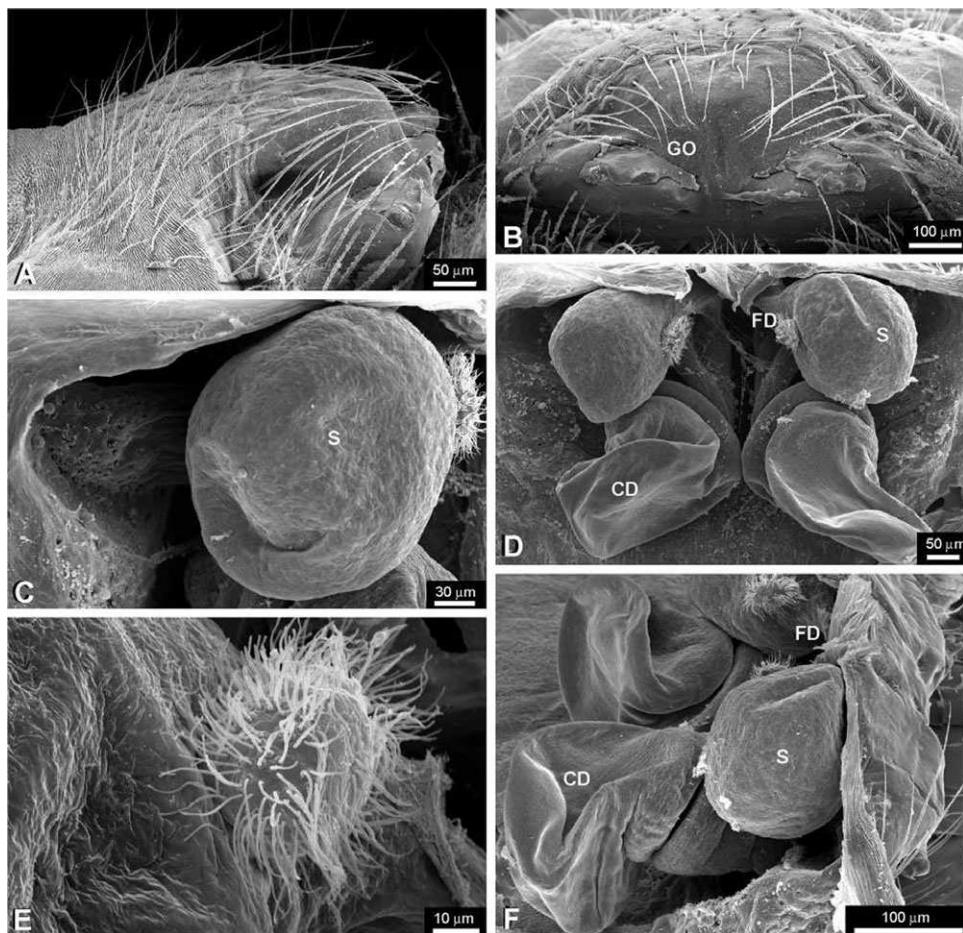
- 22. *Epiandrous plate posterior edge*: (0) as the upper edge (*Diphya spinifera*, Fig. 26G); (1) swollen (*Metabus ocellatus*, Fig. 61G). The posterior margin of the epiandrous region can be either undifferentiated from the surrounding cuticle or distinctively swollen.
- 23. *Cymbium orientation*: (0) dorsal (*Meta menardi*, Fig. 59A); (1) mesal (*Cyclosa conica*, Fig. 140B). The orientation of the cymbium to the bulb of the male palp is displaced, and in dorsal view the cymbium is mesal to the bulb and the sclerites face laterally (Scharff & Coddington, 1997) (H95, S97, G98, K08, A07, DIP).
- 24. *Cymbial tarsal organ diameter*: (0) as the surrounding macrosetal base diameter (*Argiope argentata*, Fig. 137C); (1) larger (*Tetragnatha versicolor*, Fig. 112C) (A04).
- 25. *Cymbium median width*: (0) entire, not constricted (*Leucauge venusta*, Fig. 44B); (1) constricted (*Glenognatha foxi*, Fig. 39F). In entire cymbia the median section has the same width as its base and apex, giving them a spoon-like appearance. In constricted cymbia the median part is considerably narrower.
- 26. *Cymbial ectobasal process*: (0) absent (*Leucauge venusta*, Fig. 44B); (1) present (*Dolichognatha pentagona*, Fig. 34A, C). In most araneoids the ectobasal cymbial margin has only one process known as the paracymbium. In some tetragnathids the cymbial base bears another process close to the paracymbium called the cymbial



**Figure 97.** '*Orsinome*' *sarasini* cephalothorax: A, male dorsal view. B, female dorsal view. C, female chelicera. D, male chelicera. E, female tangential view. F, male coxa IV dorsal view. G, female sternum. H, male tangential view. All images from SEMFAP050).

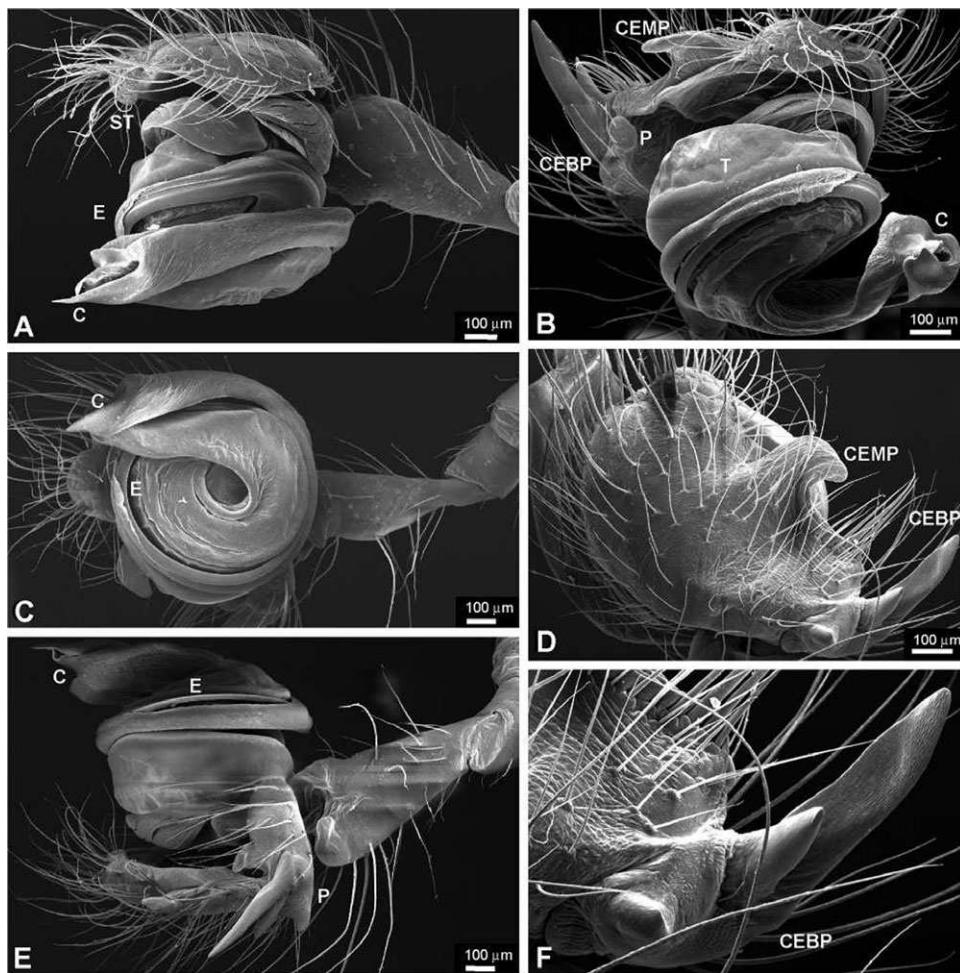
ectobasal process (Kuntner & Alvarez-Padilla, 2006). Cymbia with similar but not homologous processes are found in Pimoidae (Hormiga, 1994b: figs 301–304, 310, 311) and in some linyphiids. In tetragnathids this process has been considered as part of the paracymbium in other studies (Levi, 1980: fig. 124; Hormiga *et al.*, 1995: fig. 6C) (L80, H95, A07, DIP).

27. *Cymbial ectobasal process shape:* (0) longer than wide (*Chrysometa alajuela*, Fig. 21D); (1) cuticular fold (*Meta menardi*, Fig. 59A, F). Variation in cymbial ectobasal process shape can be summarized in two main patterns: longer than wide and a broad cuticular fold thicker than the paracymbium (Figs 34F, 69D, 75D, 85C, 90E, 99D). The cymbial ectobasal process of *Allende nigro-*



**Figure 98.** ‘*Orsinome*’ *sarasini* epigynum: A, lateral view. B, ventral view. C, spermatheca. D, dorsal view. E, accessory glands. F, lateral view. All images from SEMFAP050.

- humeralis* is covered with denticle-shaped setae (cuspules, see Fig. 11D) but not all *Allende* species have these modifications (Álvarez-Padilla, 2007) (A07, DIP).
28. *Cymbial ectomedian process*: (0) absent (*Metellina segmentata*, Fig. 69D); (1) present (*Allende nigrohumeralis*, Fig. 11A). In addition to the cymbial ectobasal process and the paracymbium, the ectal edge of the cymbium has another process located at the middle region called the cymbial ectomedian process. All taxa with a cymbial ectobasal process have a cymbial ectomedian process except *Dolichognatha pentagona*, *Metellina segmentata*, and *Diphya spinifera*. *Diphya spinifera* represents an interesting case because its cymbial ectomedian process could be interpreted either as such or as homologous to the cymbial ectobasal process. None of these alternative codings produced topological changes in the most parsimonious trees (A07, DIP).
29. *Cymbial ectomedian process macrosetae*: (0) absent (*Meteluage eldorado*, Fig. 80B); (1) as in the cymbium (*‘Orsinome’ sarasini*, Fig. 99D); (2) thicker (*Allende nigrohumeralis*, Fig. 11D). The cymbial ectomedian process surface can be glabrous, covered with macrosetae of the same size as the ones on the cymbium, or covered with thicker macrosetae (A07, DIP).
30. *Cymbial ectomedian process length*: (0) less than half the cymbial width (*Diphya spinifera*, Fig. 29D); (1) more than half the cymbial width (*Allende nigrohumeralis*, Fig. 11A) (A07, DIP).
31. *Cymbial dorsobasal process*: (0) absent (*Azilia affinis*, Fig. 16C); (1) present (*Tylorida striata*, Fig. 117A). The dorsobasal surface of the cymbium in most araneoids lacks any processes or apophyses. Some tetragnathids have a spine-shaped process at the dorsobasal surface of the cymbium. We suggest that, based on the conjunction test, the cymbial dorsobasal process is not homologous to the cymbial ectal processes,



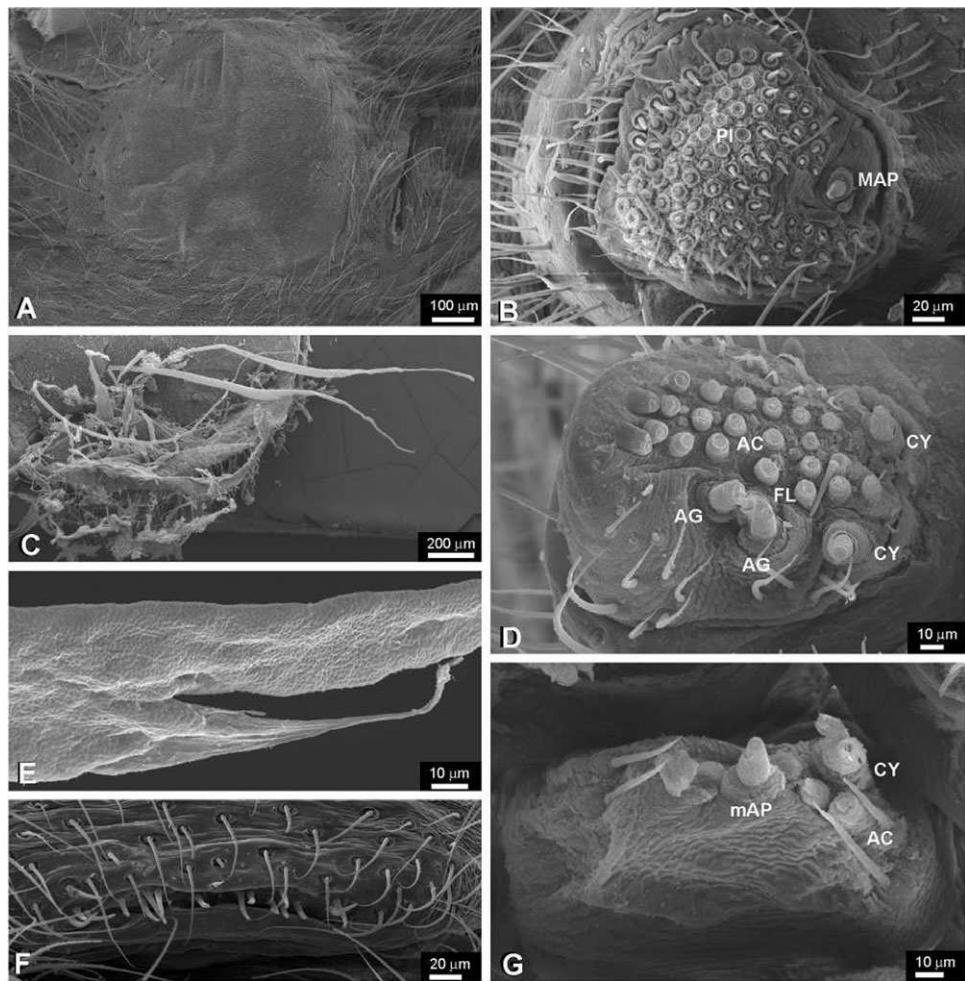
**Figure 99.** ‘*Orsinome*’ *sarasini* male pedipalp: A, mesal view. B, apical view. C, ventral view. D, dorsal view. E, ectal view. F, cymbial ectobasal process. All images from SEMFAP050.

because *Metleucauge eldorado* has both cymbial ectomedian process and CEDP (Fig. 80B, E). The cymbial ectobasal process and the CEDP were hypothesized to be homologous in previous studies, and an extra character added to account for their topological differences (Álvarez-Padilla, 2007); these alternative hypotheses produced no changes in the topology of the optimal trees (A07, DIP).

- 32. *Cymbial dorsobasal process length:* (0) shorter than the cymbial width (*Metleucauge eldorado*, Fig. 80C); (1) longer than the cymbial width (*Metabus ocellatus*, Fig. 65D) (A07, DIP).
- 33. *Cymbial dorsobasal process orientation:* (0) perpendicular in relation to the cymbial longitudinal axis (*Mesida argentiopunctata*, Fig. 54C); (1) parallel (*Leucauge argyra*, Fig. 49B, C) (A07, DIP).
- 34. *Cymbium-bulb lock mechanism:* (0) absent (*Nesticus cellularis*, Agnarsson, 2004: fig. 2A,

B); (1) present (*Anelosimus* sp., Agnarsson, 2004: fig. 28F). The cymbium internal ectal margin has an apophysis, previously thought to be homologous with the paracymbium, which interacts with the median apophysis locking the bulb in theridiids (Agnarsson, 2004: fig. 31F, and references therein). This locking mechanism is synapomorphic for Theridiidae (G98, A04, A07, DIP).

- 35. *Cymbium length:* (0) shorter than twice its width (*Argiope argentata*, Fig. 137A); (1) longer (*Orsinome* cf. *vethi* Fig. 103C) (K08, A07, DIP).
- 36. *Cymbium ectal margin sclerotization:* (0) sclerotized as the rest of the cymbium; (1) less sclerotized, transparent. The ectal cymbial margin can be either sclerotized as the rest of the cymbium, or modified as a translucent cuticular flap. The flap of *Phonognatha graeffei* is interpreted here as a paracymbium (see Hormiga *et al.*, 1995 for justification) and therefore *Phonognatha* is coded



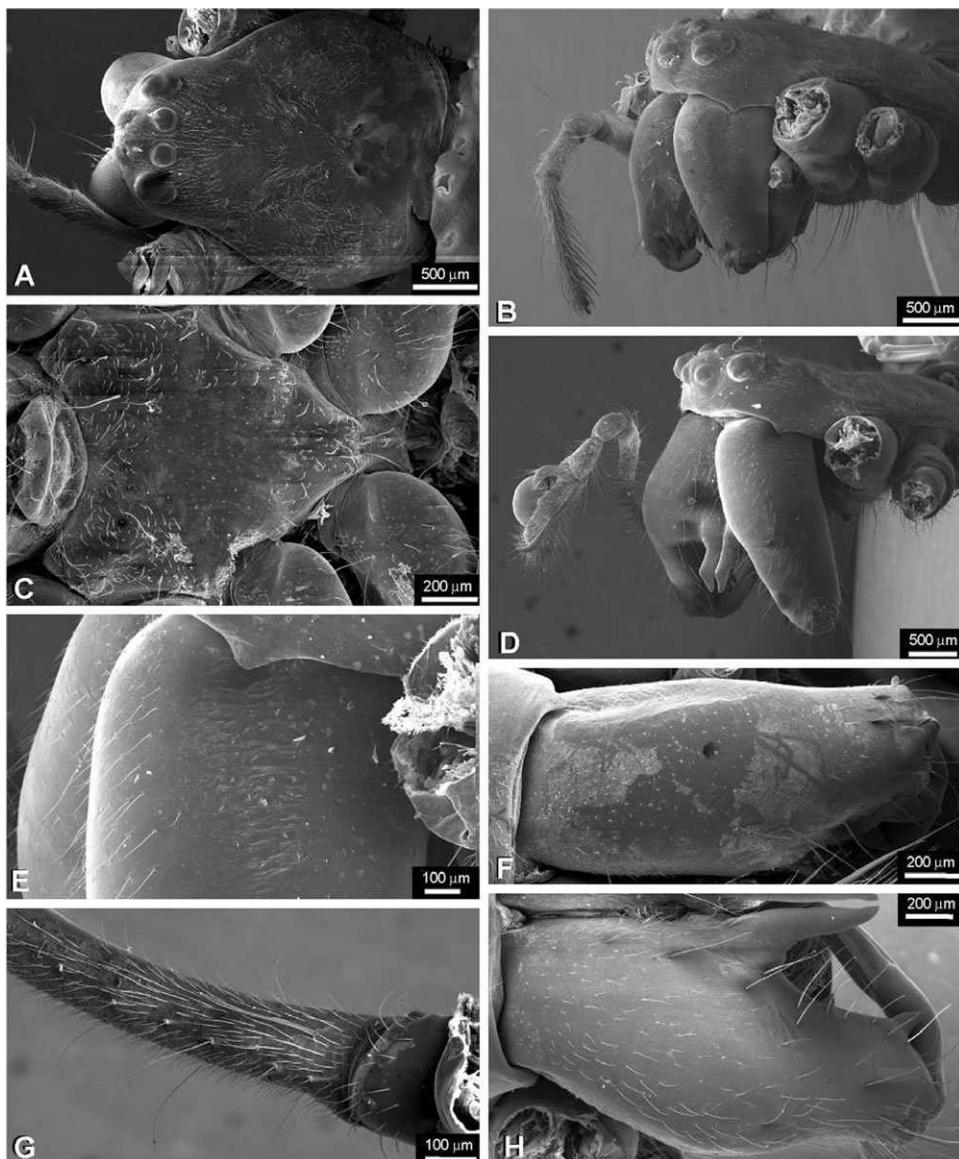
**Figure 100.** *Orsinome* cf. *vethi* abdomen: A, female booklung cuticle. B, anterior lateral spinnerets. C, tracheal system dorsal view. D, posterior lateral spinnerets. E, median tracheae bifurcation. F, epiandrous fusules. G, posterior median spinnerets. All images from SEMFAP040.

as lacking the translucent flap (coded differently in Kuntner, 2005, 2006; Kuntner *et al.*, 2008).

37. *Paracymbium*: (0) absent (*Asagena americana*, Fig. 138E); (1) present (*Argiope argentata*, Fig. 137E). The paracymbium is a basal process arising from the ectal edge of the cymbium and it has been postulated as synapomorphic for Araneoidea (Griswold *et al.*, 1998 and references therein). All tetragnathids, like most araneoids, have a paracymbium except *Homalomena* Simon, 1897 species (Levi, 1986: 206: figs 735–739). However, in the ‘reduced piroform clade’ the paracymbium has been lost several times in numerous taxa. Theridiids and many symphytognathoids lack paracymbia and thus the paracymbium is absent in taxa such as *Anapis* Simon, 1895 (Anapidae); *Maymena* Gertsch, 1960; *Mysmena* Simon,

1894 (Mysmenidae), and *Patu* Marples, 1951 (Symphytognathidae) (Griswold *et al.*, 1998, 2005; Agnarsson, 2004), whereas *Symphytognatha* Hickman, 1931 (Symphytognathidae); *Synaphris* Simon, 1894 and *Cepheia* Simon 1894 (Synaphridae); and some *Synotaxus* Simon, 1895 (Synotaxidae); *Nesticus* Thorell, 1869 (Nesticidae), amongst other taxa, have paracymbia (Harvey, 1992; Agnarsson, 2004; Lopardo, Hormiga & Melic, 2007; Lopardo & Hormiga, 2008). Topologically similar structures are found on spiders in other non-araneoid families (e.g. *Hypochilus* (Hypochilidae), Griswold *et al.* 2005: fig. 166A; *Tapinillus* (Oxyopidae), Griswold 1993: fig. 56) (L80, C90, H94, H95, S97, G98, T01, A04, G05, A07, DIP).

38. *Paracymbium morphology*: (0) hook-shaped (*Argiope argentata*, Fig. 137E); (1) cylindrical, longer than wide (*Meta menardi*, Fig. 59A);



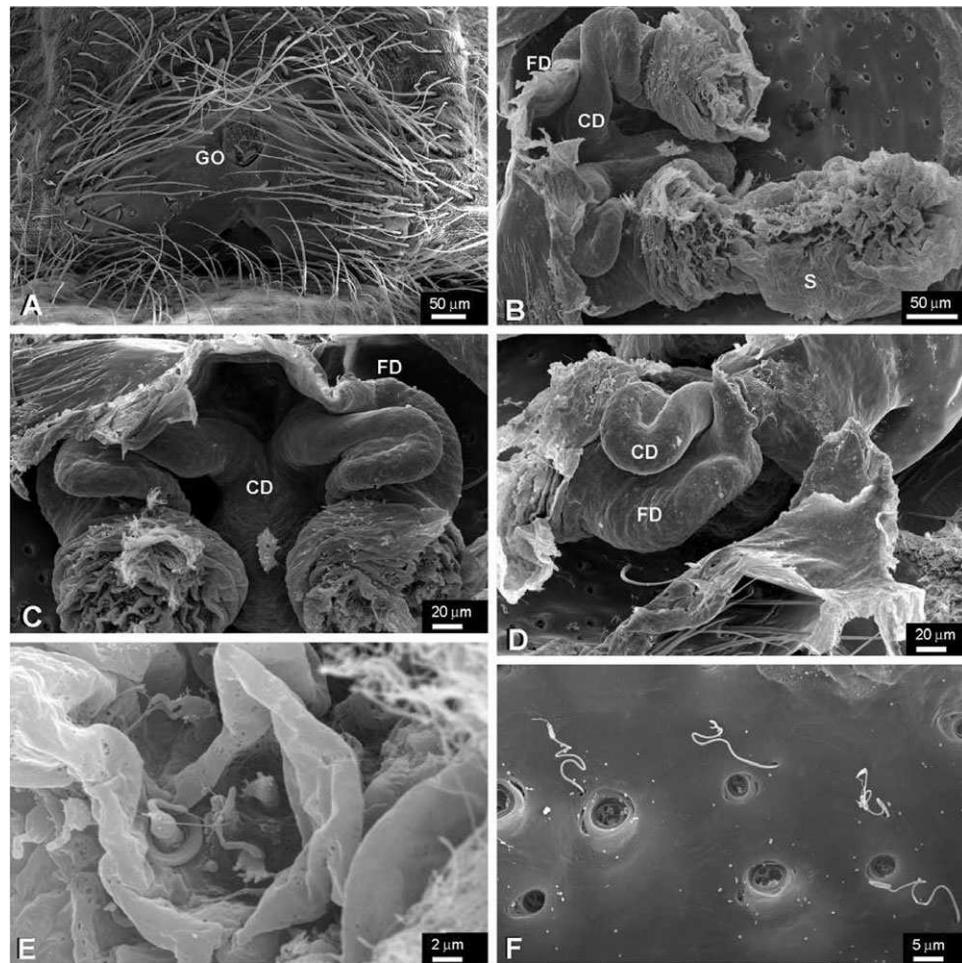
**Figure 101.** *Orsinome* cf. *vethi* cephalothorax: A, female dorsal view. B, female tangential view. C, female sternum. D, male tangential view. E, cheliceral paturon base. F, female chelicera. G, female femur IV dorsal view. H, male chelicera. All images from SEMFAP040.

(2) rectangular (*Nephilengys malabarensis*, Fig. 138D); (3) rim following tegular margin (*Phonognatha graeffei*, Fig. 125F); (4) U-shaped (*Linyphia triangularis*, Fig. 138A); (5) conical (*Mollemeta edwardsi*, Fig. 85C); (6) with protuberances (*Chrysometa alajuela*, Fig. 21C). The paracymbium morphology varies widely across araneoid taxa and it is particularly diverse amongst tetragnathids (see Hormiga *et al.*, 1995 and references therein) (H94, H95, G98, A04, K08, A07, DIP).

39. *Paracymbium length:* (0) shorter than half the cymbial length (*Mesida argentiopunctata*,

Fig. 54F); (1) longer (*Metellina segmentata*, Fig. 69D) (A07, DIP).

40. *Paracymbium articulation:* (0) integral (*Metabus ocellatus*, Fig. 65A); (1) articulated (*Chrysometa alajuela*, Fig. 22A); (2) intersegmental (*Linyphia triangularis* (Hormiga, 1994a: fig. 9C)). Integral paracymbia are those in which the base is as sclerotized as the cymbial edge and thus these paracymbia look like an extension of the cymbial cuticle. Articulated paracymbia are those in which attachment to the cymbium is membranous; however, they remain closer to the cymbium than to the tibia. Intersegmental para-



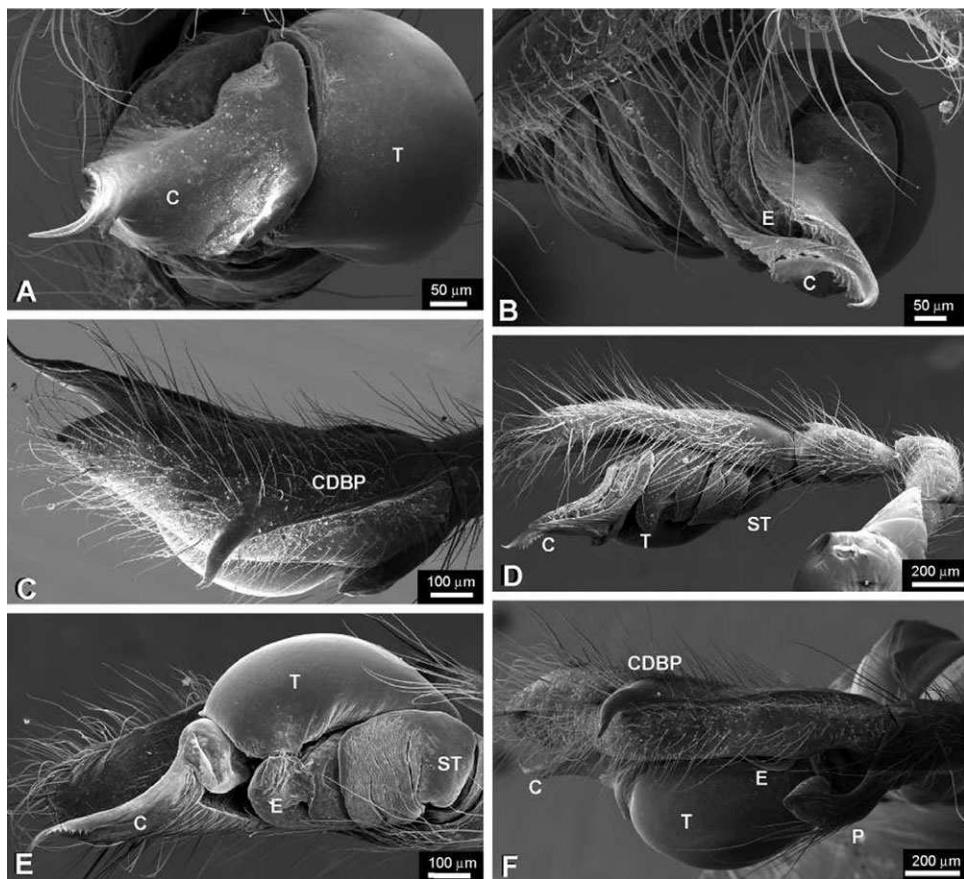
**Figure 102.** *Orsinome* cf. *vethi* epigynum: A, posterior view. B, dorsal view. C and D, copulatory and fertilization ducts. E, spermatheca accessory glands. F, abdomen cuticle gland ducts. All images from SEMFAP040.

cymbia are located on the membrane between the cymbium base and the tibia and are apomorphic for linyphiids (Hormiga, 1994a) (L80, C90, H94, H95, S97, G98, K08, A07, DIP).

41. *Paracymbium distal part*: (0) not swollen (*Azilia affinis*, Fig. 16D); (1) swollen (*Diphya spinifera*, Fig. 29C). The paracymbium apical edge is either proportionally of the same size as its base or wider (K08, A07, DIP).
42. *Paracymbium basal apophyses*: (0) absent (*Mesida argentiopunctata*, Fig. 54F); (1) present (*Tetragnatha versicolor*, Fig. 112D). Tetragnathid paracymbia can have one or several apophyses at their base (H95, K08, DIP, A07).
43. *Paracymbium margin fold*: (0) absent (*Metleucauge eldorado*, Fig. 80B); (1) present (*Nephilengys malabarensis*, Fig. 138D) (H95, K08, A07, DIP).
44. *Paracymbium setae*: (0) absent (*Micrathena gracilis*, Fig. 138B); (1) present (*Metellina segmen-*

*tata*, Fig. 69D). *Phonognatha graeffei* is coded as polymorphic, some specimens have no setae (Kuntner, 2005, 2006) whereas other specimens that we have studied have four setae evenly distributed (K08, DIP).

45. *Paracymbium setae distribution*: (0) only on the tip (*Orsinome* cf. *vethi*, Fig. 99F); (1) evenly distributed (*Metellina segmentata*, Fig. 69F); (2) only at the base (*Leucauge argyra* Fig. 49E); (3) only on the margins (*Chrysometa alajuela*, Fig. 21D). *Herennia multipuncta* has one macroseta at the paracymbium base (coded as ‘absent’ in Kuntner, 2005, 2006) (K08, DIP).
46. *Subtegulum position*: (0) under the tegulum (*Diphya spinifera*, Fig. 29A); (1) mesally displaced (*Metleucauge eldorado*, Figs 80A, 81C) (A07, DIP).
47. *Tegulum shape*: (0) spherical to oval (*Tetragnatha versicolor*, Fig. 112A); (1) disk-shaped (*Linyphia triangularis*, Fig. 138B). Tegulum shape varies



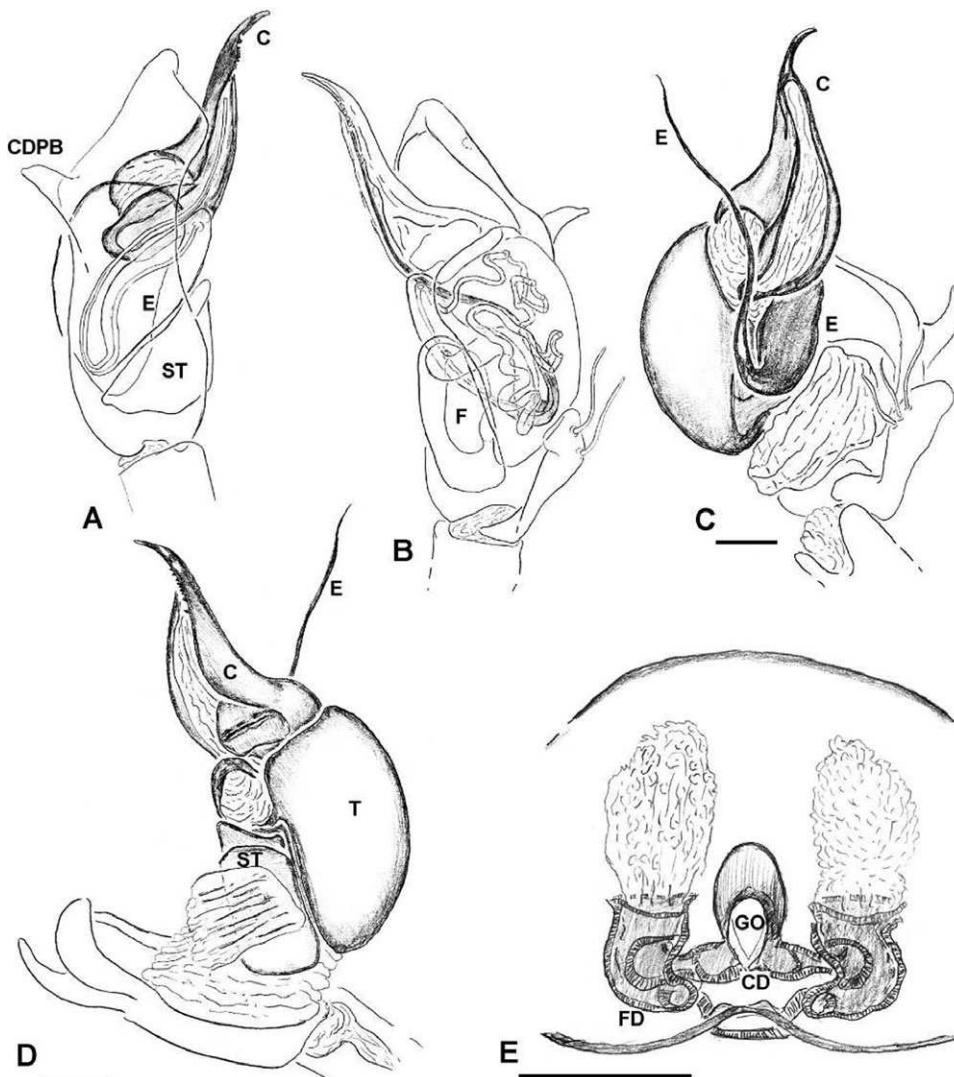
**Figure 103.** *Orsinome* cf. *vethi* male pedipalp: A and B, conductor. C, dorsal view. D, mesal view. E, ventral view. F, ectal view. All images from SEMFAP040.

considerably across Araneoidea and it is difficult to code. This diversity can be summarized in two basic morphologies: oval to spherical and disk-shaped. If tegulum height is less than one third of its diameter then it is considered here to be disk-shaped, otherwise it is considered to be oval to spherical.

- 48. *Tegulum ectal surface:* (0) same as mesal (*Azilia affinis*, Fig. 16A); (1) swollen (*Leucauge argyra*, Fig. 49F). The tegulum lateral sides can be either the same height or one side considerably higher (A07, DIP).
- 49. *Tegulum-subtegulum size:* (0) tegulum larger than subtegulum (*Mesida argentiopunctata*, Fig. 55B); (1) tegulum smaller than subtegulum (*Meta menardi*, Fig. 60A, B) (A04, K08, A07, DIP).
- 50. *Tegular sclerites insertion:* (0) apical (*Tetragnatha versicolor*, Fig. 112A, D); (1) subterminal (*Argiope argentata*, Fig. 140A). To code this character one needs to trace an imaginary perpendicular line to the tegular base at its centre.

If the insertion of the tegular sclerites crosses this line at the opposite end of the tegulum, then they are apically orientated, otherwise the sclerites are subterminally inserted (see also Hormiga *et al.*, 1995) (C90, H95, S97, G98, A07, DIP).

- 51. *Median apophysis:* (0) absent (*Pachygnatha autumnalis*, Fig. 105A); (1) present (*Araneus marmoreus*, Fig. 138F). In many araneoids two sclerites arise from the tegulum, the conductor and the median apophysis, although some taxa such as theridiids (Fig. 139D; Agnarsson, 2004 and references therein) can have more than two tegular sclerites. Often the median apophysis is distinguished from the conductor because it is separated from the embolus. During pedipalp development the median apophysis and the conductor originate from the dorsal lobe of the palpal claw fundament, while all other sclerites develop from the ventral lobe. During the last stages of pedipalp development all sclerites differentiate and insert into the tegulum; the scler-

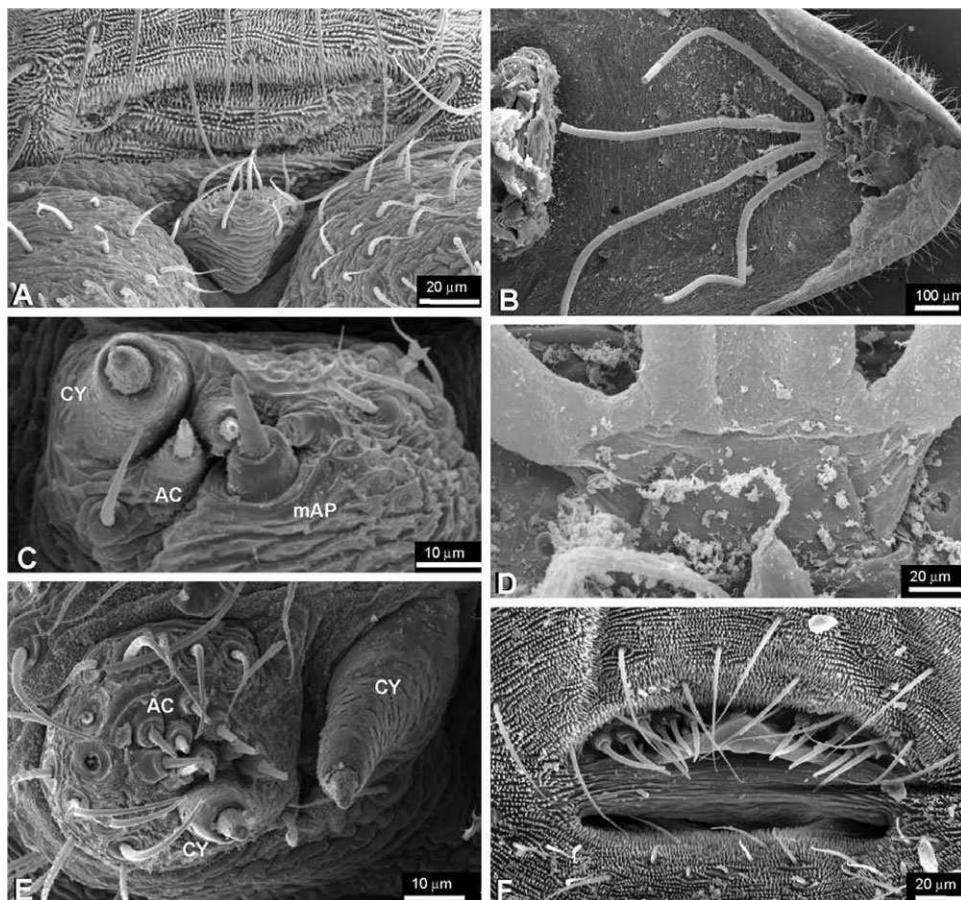


**Figure 104.** *Orsinome* cf. *vethi* genital anatomy illustrations: A, cleared male pedipalp bulb dorsal view. B, ventral view. C and D, pedipalp expanded. E, epigynum cleared ventral view.

- ite closest to the embolus is the conductor and the other is the median apophysis (Bhatnagar & Rempel, 1962). However, shifts of position during development amongst the median apophysis, the conductor, and any additional tegular sclerites could occur, complicating the discernment of the homology of these structures. All tetragnathids lack the median apophysis (*contra* Archer, 1951) (L80, C90, H94, H95, S97, G98, G05, A04, K08, A07, DIP).
52. *Median apophysis and sperm duct:* (0) duct loop inside MA (*Argyrodes argyrodes* (Agnarsson, 2004: fig. 91A, B); (1) apart (*Eidmannella pallida*, Agnarsson, 2004: fig. 89E). In theridiids the median apophysis, when present, may contain a loop of the sperm duct. This is a

synapomorphy of theridiids although some *Nesticus* spp. have this loop too (e.g. *Nesticus cellulanus*, see Huber, 1993: fig. 1). In all other araneoid taxa studied here the sperm duct does not go into the median apophysis. This character is coded as inapplicable for *Parasteatoda* because this species lacks both median apophysis and sperm duct loops (A04, K08, A07, DIP).

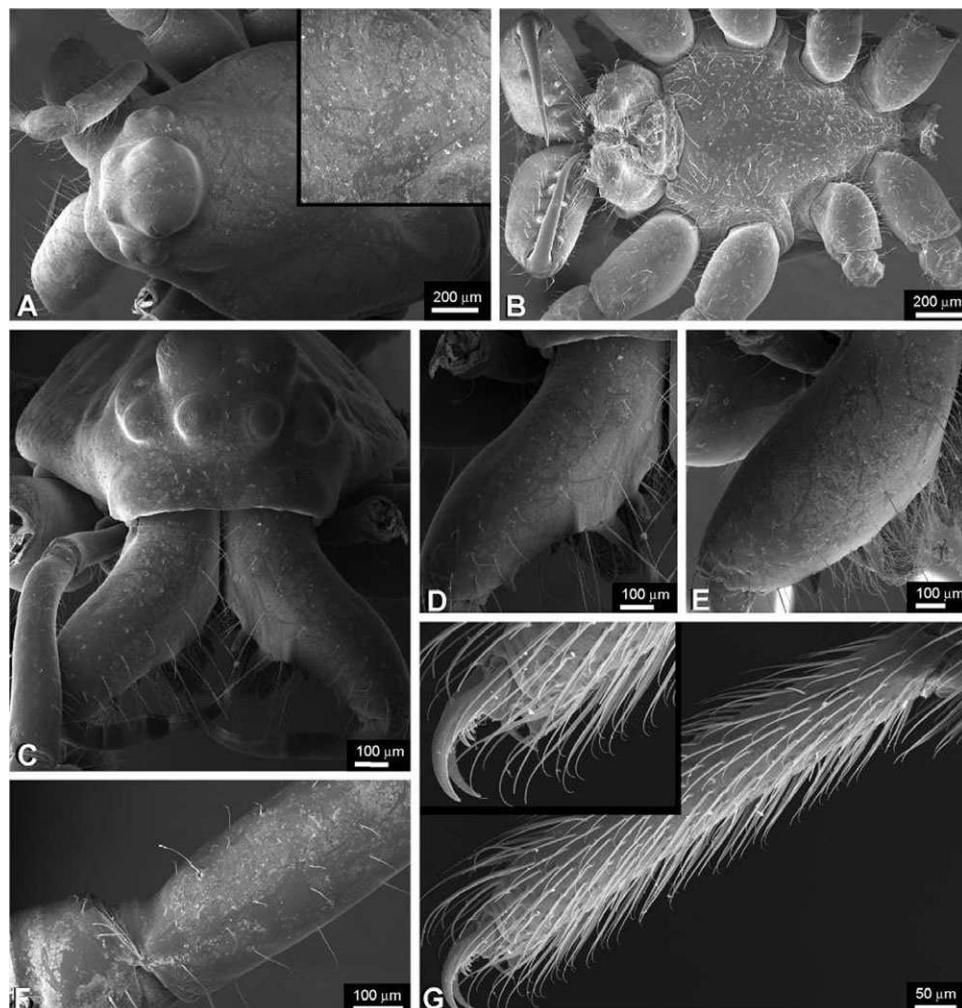
53. *Conductor:* (0) absent (*Azilia affinis*, Fig. 16F); (1) present (*Tetragnatha versicolor*, Fig. 112C, D). The conductor has been traditionally defined as the tegular sclerite associated with the embolus, presumably to protect it, at least its apical region (see discussion of character 51). In a recent study Kuntner (2005; Fig. 142A) interpreted the conductor of nephilids as a sclerite



**Figure 105.** *Pachygnatha autumnalis* abdomen: A, tracheal spiracle and colulus ventral view. B, tracheal system dorsal view. C, posterior median spinnerets. D, tracheal spiracle internal view. E, posterior lateral spinnerets. F, epiandrous fusules. All images from SEMFAP030.

unique to nephilids (which he named ‘embolic conductor’) and argued that the ‘embolic conductor’ was not homologous to the araneoid conductor, which he suggested that would be absent in nephilids. Kuntner’s (2005, 2006) rationale against homology to the araneoid conductor is based on the presence of a membrane that connects the ‘embolic conductor’ with the embolus membrane and the tegulum. In Kuntner’s view the ‘embolic conductor’ is part of the embolic division because of its membranous attachment to the tegulum (see character 59); this membrane is consequently interpreted as part of the embolus-tegulum membrane (see character 63). Both membranes in nephilids are contiguous (Kuntner, 2005, 2006). However, the conductor of many tetragnathids also has a membranous attachment to the tegulum, as can be seen in *Orsinome* cf. *vethi* (Fig. 104C, D), *Leucauge argyra* (Fig. 50A), *L. venusta* (Walckenaer, 1841), *L. mariana* and *Cyrtognatha* spp.

(Dimitrov & Hormiga, 2009: figs 6C, 41D, E). The conductor and the embolus of some tetragnathids, such as *Leucauge argyra* and *L. mariana*, are attached to the tegulum with a joint membrane (Dimitrov & Hormiga, 2009: 9) and thus present the same condition as described for nephilids. Consequently, we have interpreted this tegular sclerite of *Nephila* and its close relatives as a homologue of the araneoid conductor, following also Levi & Eckstedt (1989), Hormiga *et al.* (1995), Griswold *et al.* (1998), Álvarez-Padilla *et al.* (2009), Dimitrov & Hormiga (2009), and Dimitrov & Hormiga (2011). New light on the homology of the conductor of nephilids may come from studying the development of the pedipalp and establishing if this sclerite originates from the dorsal lobe of the claw fundament (conductor), or from the apical part of the ventral lobe of the claw fundament (‘embolic conductor’). Nevertheless, if the nephilids’ sclerite indeed originates from



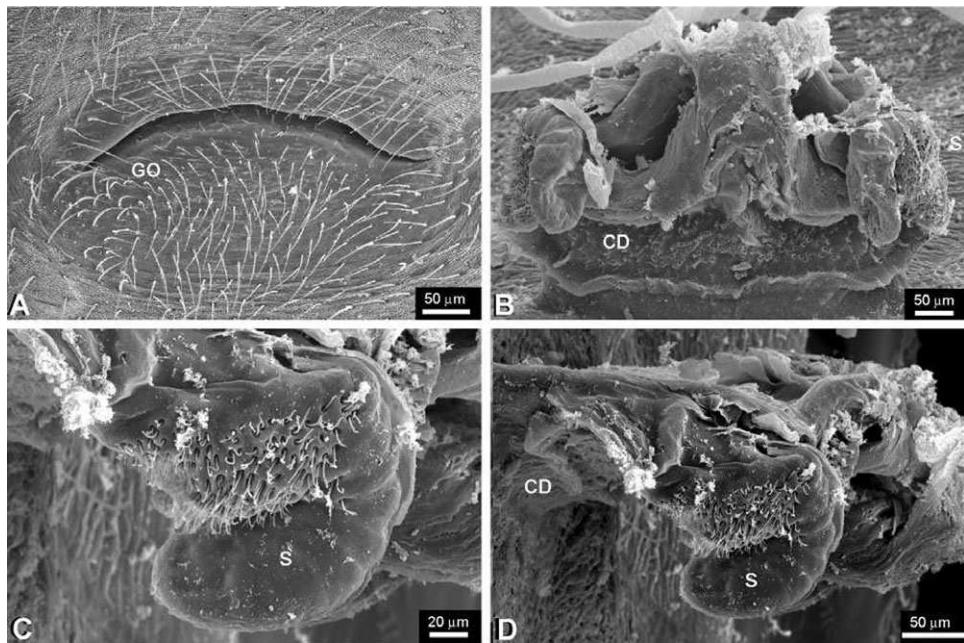
**Figure 106.** *Pachygnatha autumnalis* cephalothorax: A, female dorsal view; insert, close up of carapace cuticle. B, female ventral view. C, male anterior view. D, male chelicera. E, female chelicera. F, female femur IV base. G, female tarsus IV lateral view; insert, close up of claws. All images from SEMFAP030.

the ventral lobe, then it would be more parsimonious to homologize it to an existing embolic apophysis sclerite, such as the terminal or sub-terminal apophyses found in Araneidae, than to postulate its *de novo* origin (the latter also would require a secondary absence of the conductor). Finally, we have coded the conductor as present in *Nesticus* [Kuntner (2006) coded *Nesticus* as lacking a conductor; however, a conductor is clearly present in this genus: e.g. Huber, 1993; Griswold *et al.* 1998] (L80, C90, H94, H95, S97, G98, T01, A04, G05, A07, DIP).

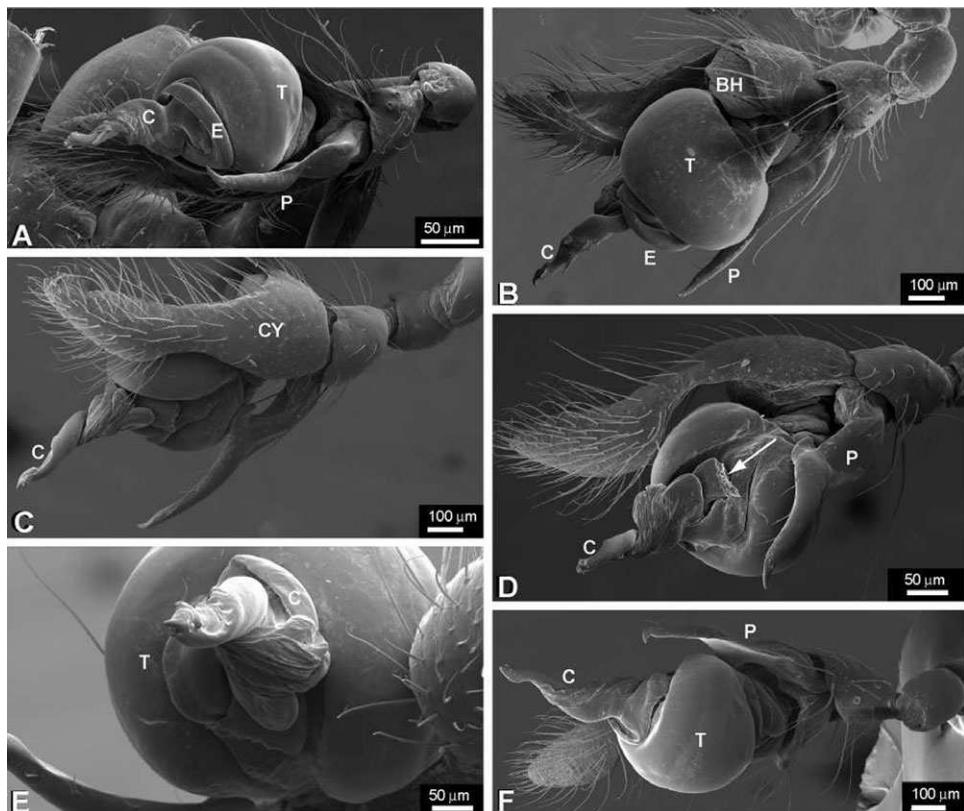
54. *Conductor and embolus:* (0) coiled with embolus (*Nanometa* sp., Fig. 90B, C); (1) separated (*Argiope argentata*, Fig. 140A, F). In tetragnathids the conductor encloses the embolus from its base to the apex and coils with it. The

conductor of all leucaugines and nephilids completely encloses the embolus, and to ‘see’ or dissect the embolus; it has to be manually separated from the conductor, e.g. in *Nephila clavipes* (Hormiga *et al.*, 1995: fig. 10) (L80, C90, H95, S97, G98, G05, T01, G05, K08, A07, DIP).

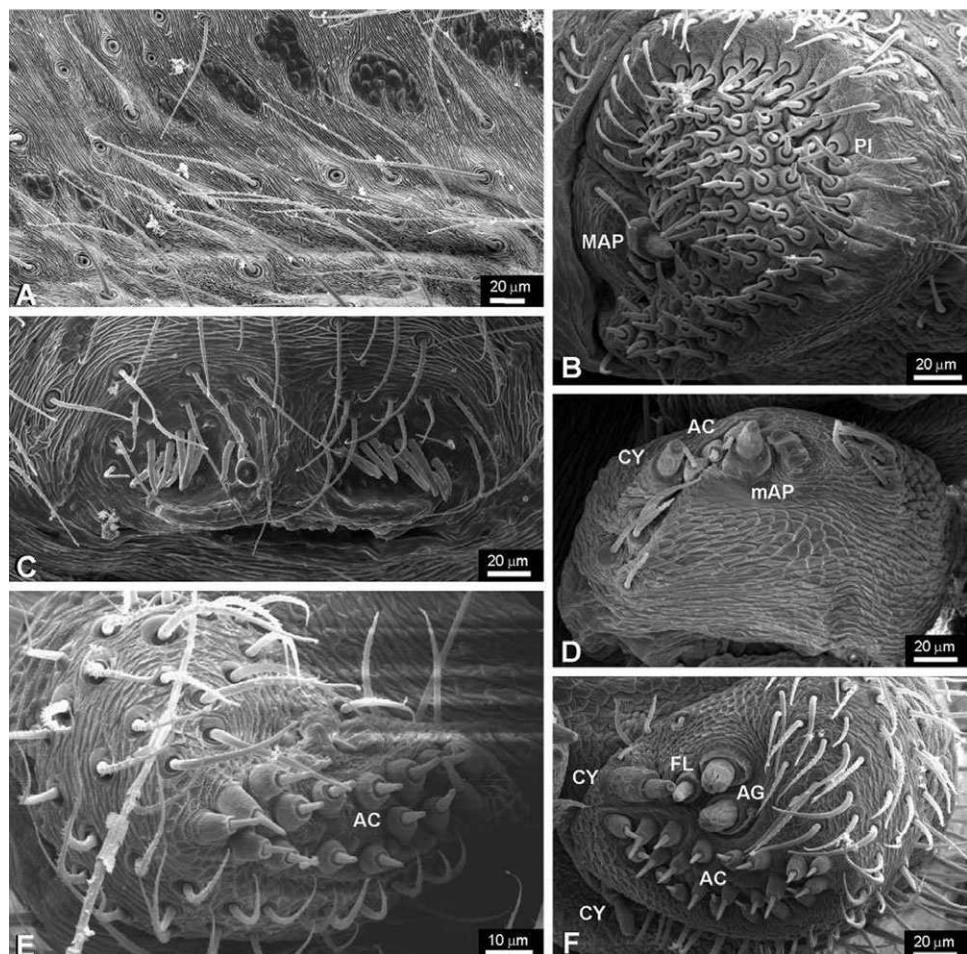
55. *Conductor tegular origin:* (0) centre (*Tetragnatha versicolor*, Fig. 112D); (1) lateral edges (*Araneus marmoreus*, Fig. 138D). The conductor can originate either at the centre of the tegulum or along the tegular lateral edges (G05, A07, DIP).
56. *Conductor end:* (0) straight (*Tetragnatha versicolor*, Fig. 112F); (1) sigmoid (*Nephilengys malabarensis*, Fig. 139C). The conductor tip of the araneoid taxa studied here is straight to slightly curved. In *Herennia* and *Nephilengys* the tip of the conductor coils, resembling a corkscrew (H95, K08, A07, DIP).



**Figure 107.** *Pachygnatha autumnalis* female genitalia: A, genital spiracle. B, genitalia dorsal view. C, close up of reduced spermatheca. D, genitalia lateral view. All images from SEMFAP030.

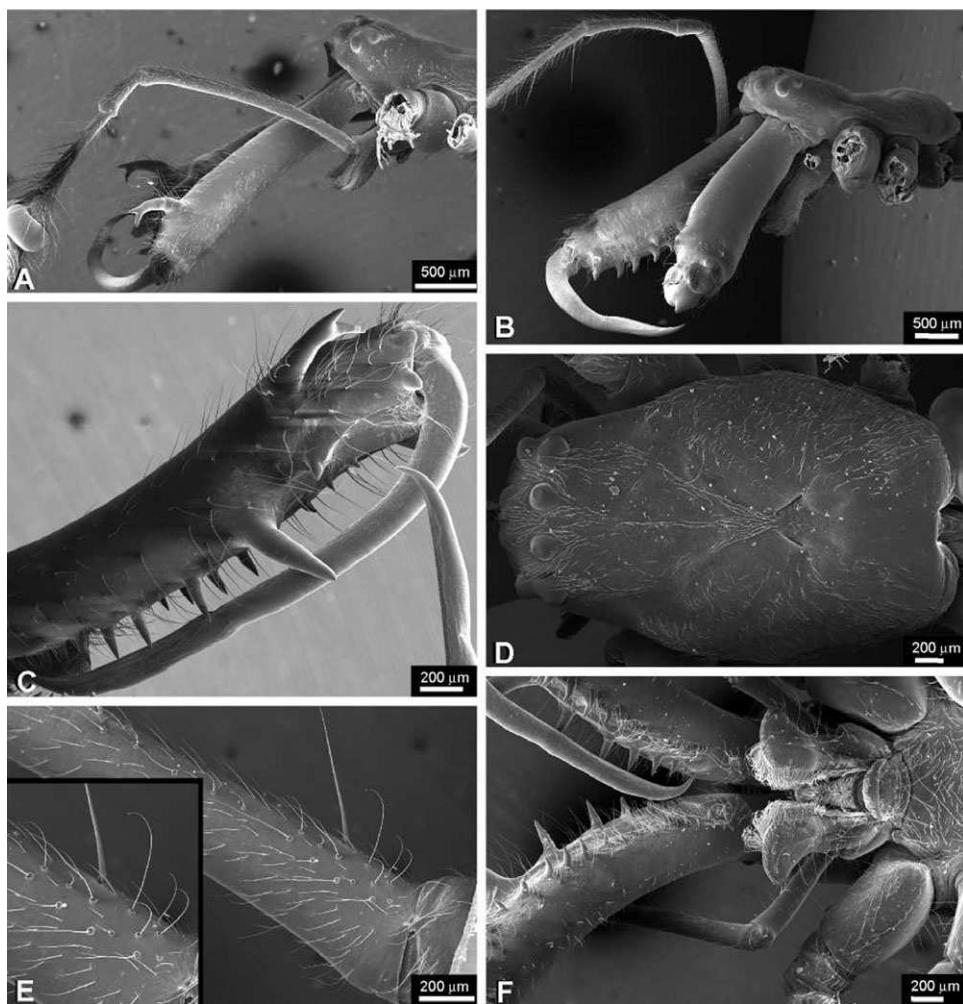


**Figure 108.** *Pachygnatha autumnalis* male pedipalp: A and B, ventral view. C, dorsal view. D, mesal view. E, apical view. F, ectal view. All images from SEMFAP030.



**Figure 109.** *Tetragnatha versicolor* abdomen: A, cuticle of the abdomen, close up of median lateral section. B, anterior lateral spinnerets, C, epiandrous fusules. D, posterior median spinnerets. E, male posterior lateral spinnerets. F, female posterior lateral spinnerets. All images from SEMFAP028.

- 57. *Conductor area covering the embolus:* (0) one third or less (*Uloborus glomosus*, Fig. 140D); (1) one side of the embolus (*Metellina segmentata*, Fig. 70B); (2) entire embolus (*Mesida argentiopunctata*, Figs 54A, 55C). In all araneoids studied here, except tetragnathids, the conductor area enclosing the embolus extends from the embolus base up to one third of the embolus length. In tetragnathids the conductor covers more than one third of the embolus and it can surround either only one side of the embolus or completely enclose it (A07, DIP).
- 58. *Conductor path:* (0) parallel to tegular margin (*Cyclosa, conica* Fig. 140E); (1) curving with tegular margin (*Meta menardi*, Fig. 59D); (2) apically distended (*Metabus ocellatus*, Fig. 64B); (3) ventrally distended (*Nephilengys malabarensis*, Fig. 139C). This character describes the path that the conductor follows relative to the tegulum distal surface (A07, DIP).
- 59. *Conductor tegulum attachment:* (0) solid uniform degree of sclerotization of tegulum and conductor (*Meta menardi*, Fig. 60A); (1) membranous (*Mesida argentiopunctata*, Fig. 55B). The conductor attachment to the tegulum can be either sclerotized or membranous. The conductors of *Nanometa* sp., *Nanometinae* sp., '*Orsinome*' *sarasini*, and *Mollemeta edwardsi* have a membranous appearance; however, their edges are sclerotized and fused to the tegulum (Fig. 91A, B). The conductor of the Australian taxa expands while submerged and transferred between a KOH solution and distilled water (Fig. 76A–C). Sclerotized attachments are found in several tetragnathids such as *Allende nigrohumeralis*, *Opadometa* sp., *Metellina segmentata*, and *Dolichognatha pentagona* (Figs 12B, 35A, 70B, 95C) as well as in some other araneoids. Membranous attachments are common amongst nephilids



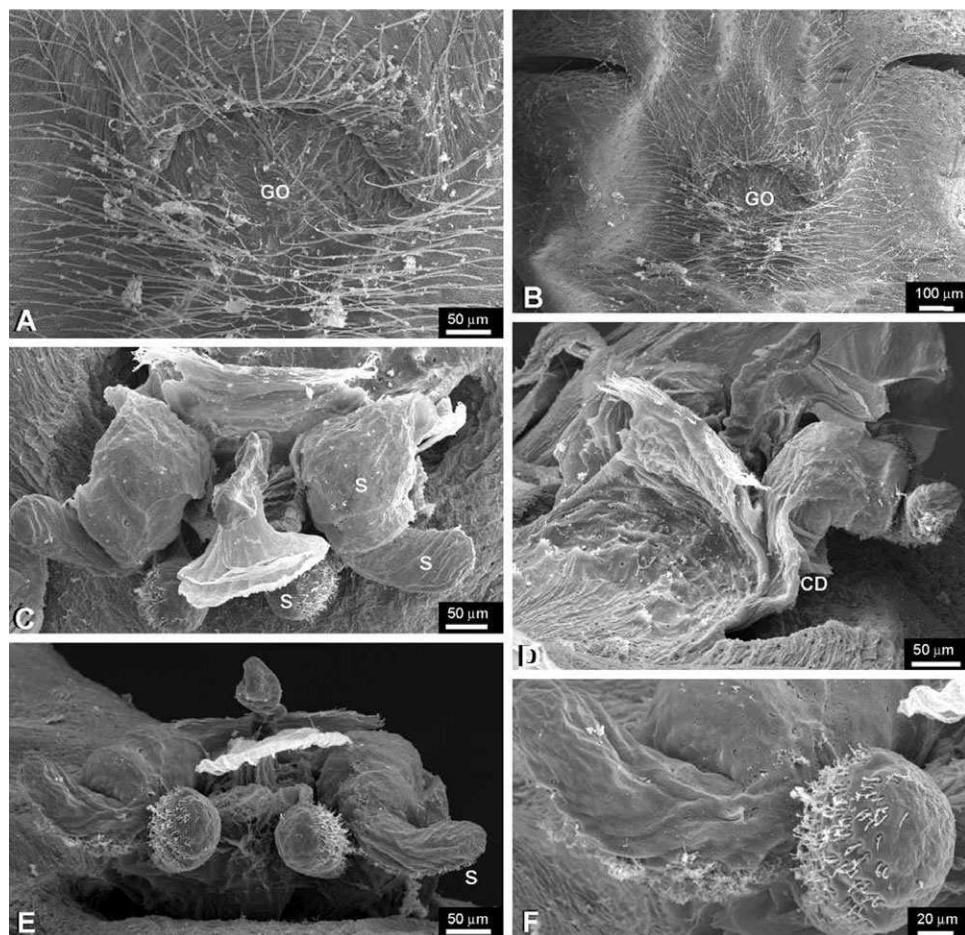
**Figure 110.** *Tetragnatha versicolor* cephalothorax: A, male lateral view. B, female lateral view. C, male chelicera. D, female carapace dorsal view. E, female femur IV trichobothria; insert, close up of trichobothria. F, female labium and endites. All images from SEMFAP028.

(Hormiga *et al.*, 1995: figs 9, 10) and leucaugines (A04, A07, DIP).

- 60. *Conductor size*: (0) shorter than half of the bulb longitudinal axis (*Zygiella x-notata*, Fig. 139F); (1) longer (*Orsinome cf. vethi*, Fig. 103E) (K08, DIP).
- 61. *Theridiid tegular apophysis*: (0) absent (*Parasteatoda tepidariorum*, Fig. 140E); (1) present (*Asagena americana*, Fig. 139D). The tegulum of theridioids has an additional sclerite besides the conductor and the median apophysis. This sclerite is unique to these spiders and synapomorphic for this clade, *Nesticus celulanus* also has this sclerite (e.g. Huber, 1993) (C90, H95, G98, A04, K08, A07, DIP).
- 62. *Embolus tegulum orientation*: (0) 90 degrees (*Nephilengys malabarensis*, Figs 139C, 140C);

(1) parallel (*Tetragnatha versicolor*, Fig. 113A). The embolus-conductor of nephilids is at a right angle to the longitudinal axis of the pedipalp (H95, G98, K08, DIP).

- 63. *Embolus tegulum membrane*: (0) absent (*Uloborus glomosus*, Fig. 139E); (1) present (*Orsinome cf. vethi*, Fig. 104D). The presence of an embolus attached to the tegulum by means of a membrane is optimized as synapomorphic for tetragnathids, and homoplastic in nephilids, *Linyphia triangularis*, *Deliochus* and *Phonognatha*; in all other taxa studied here the embolus attaches directly to the tegulum. The embolus tegulum membrane can be interpreted as homologous to the membrane connecting the radix to the tegulum of other araneoids, providing an alternative coding. We did not homologize this membrane with the



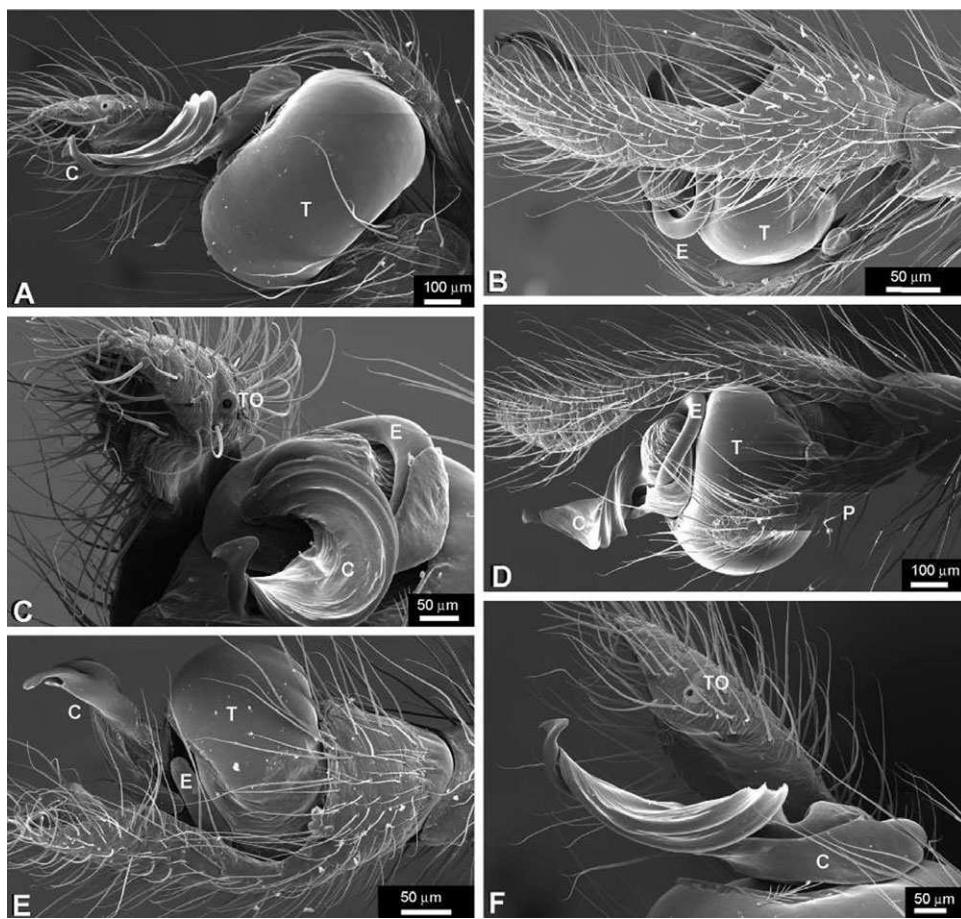
**Figure 111.** *Tetragnatha versicolor* female genitalia: A and B, genital spiracle. C, genitalia dorsal view. D, lateral view. E, posterior view. F, spermatheca.

radix-tegulum membrane because the embolus of araneids and linyphiids does not arise directly from the tegulum. The embolus tegular membrane can also be homologized with that connecting the ‘araneid radix’ to the tegulum. Variation in the coding of this primary homology in the character matrix did recover the same optimal topologies; refer to Character 71 discussion (C90, H95, S97, G98, K08, A07, DIP).

64. *Embolic basal apophyses:* (0) absent (*Tetragnatha versicolor*, Fig. 113A, B); (1) metine embolic apophysis (*Meta menardi*, Fig. 60A, B); (2) araneid basal apophyses (*Araneus marmoreus*, Fig. 138F); (3) linyphiid radical sclerites (such as the lamella *characteristica* and the terminal apophysis) (*Linyphia triangularis*, Fig. 139B). The embolus is a roughly tubular to rectangular sclerite that bears the apical part of the sperm duct and can have several apophyses at its base. The embolic apophyses of several araneoid taxa are homologous in position but different in morphology. Several araneids and

some *Cyrtognatha* species (Tetragnathidae) present one or more subdivided apophyses (Dimitrov & Hormiga, 2009: figs 6B, D, 39D, 27A, C, F). *Meta menardi*, *Metellina segmentata*, and other tetragnathids have only one apophysis. Finally, Linyphiidae also present embolic apophyses, which are usually treated as radical sclerites (e.g. Hormiga, 1994a, see also character 71) (C90, H95, S97, G98, T01, A04, K08, A07, DIP).

65. *Embolic apophysis attachment:* (0) membranous (*Allende nigrohumeralis*, Fig. 12A, B); (1) sclerotized (*Metellina segmentata*, Fig. 70B, C) (A07, DIP).
66. *Embolic base length:* (0) shorter than or equal to twice its width (*Parasteatoda tepidariorum*, Fig. 140E); (1) longer (*Leucauge venusta*, Fig. 45C).
67. *Embolus shape:* (0) tubular (Nanometinae sp., Fig. 67A–C); (1) flagelliform (*Leucauge venusta*, Fig. 45D, C); (2) lamelliform (*Azilia affinis*, Fig. 17A, C). The shape of the embolus of tetragnathids, in contrast to that of ara-

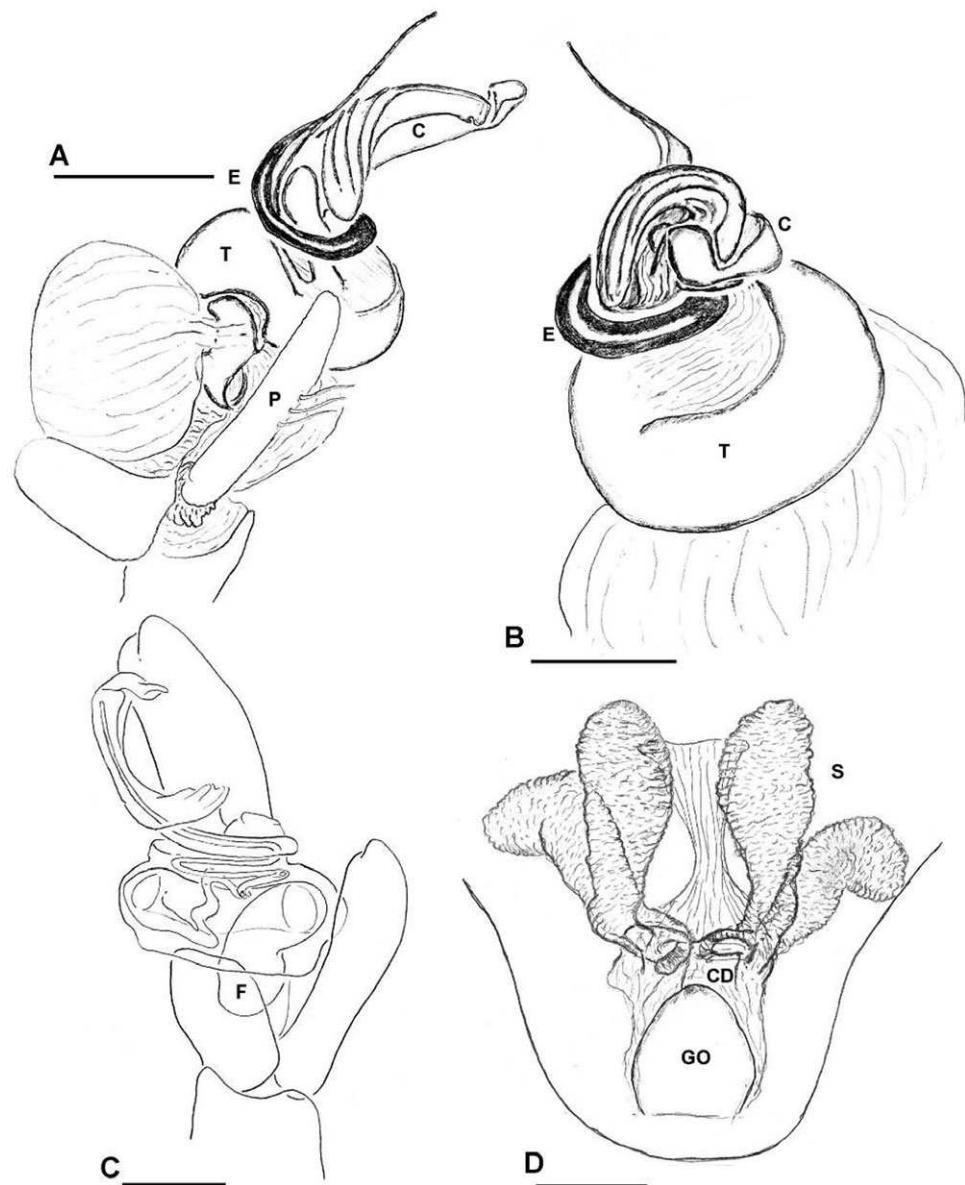


**Figure 112.** *Tetragnatha versicolor* male pedipalp: A, ventral view. B, dorsal view. C, apical view. D, ectal view. E, mesal view. F, conductor. All images from SEMFAP028.

neids, is not very variable but there are some general patterns. Tubular emboli are those roughly cylindrical for more than half of their length and gradually narrowing towards the apex (e.g. *Tetragnatha versicolor* Fig. 113A, B). Flagelliform emboli have a base considerably wider than the rest of the embolus, which is characteristic of nephilids and leucaugines. Lamelliform emboli are defined as flat rectangular sclerotized plates. *Meta menardi*, *Azilia affinis*, and *Allende nigrohumeralis* are considered as having lamelliform emboli (Figs 12A, B, 17C, 60B) (A04, K08, DIP).

68. *Embolus length:* (0) less than half cymbium length (*Azilia affinis*, Fig. 17C); (1) from 0.5 to 1.5 cymbium length (*Orsinome* cf. *vethi*, Fig. 104B–D); (2) greater than 1.5 cymbium length (*Nephila clavipes*, Hormiga *et al.*, 1995: figs 8G, 10, 13H). This character describes the length of the embolus relative to the cymbial length. *Nesticus cellularis* is coded as short (Huber, 1993: fig. 1) (K08, DIP).

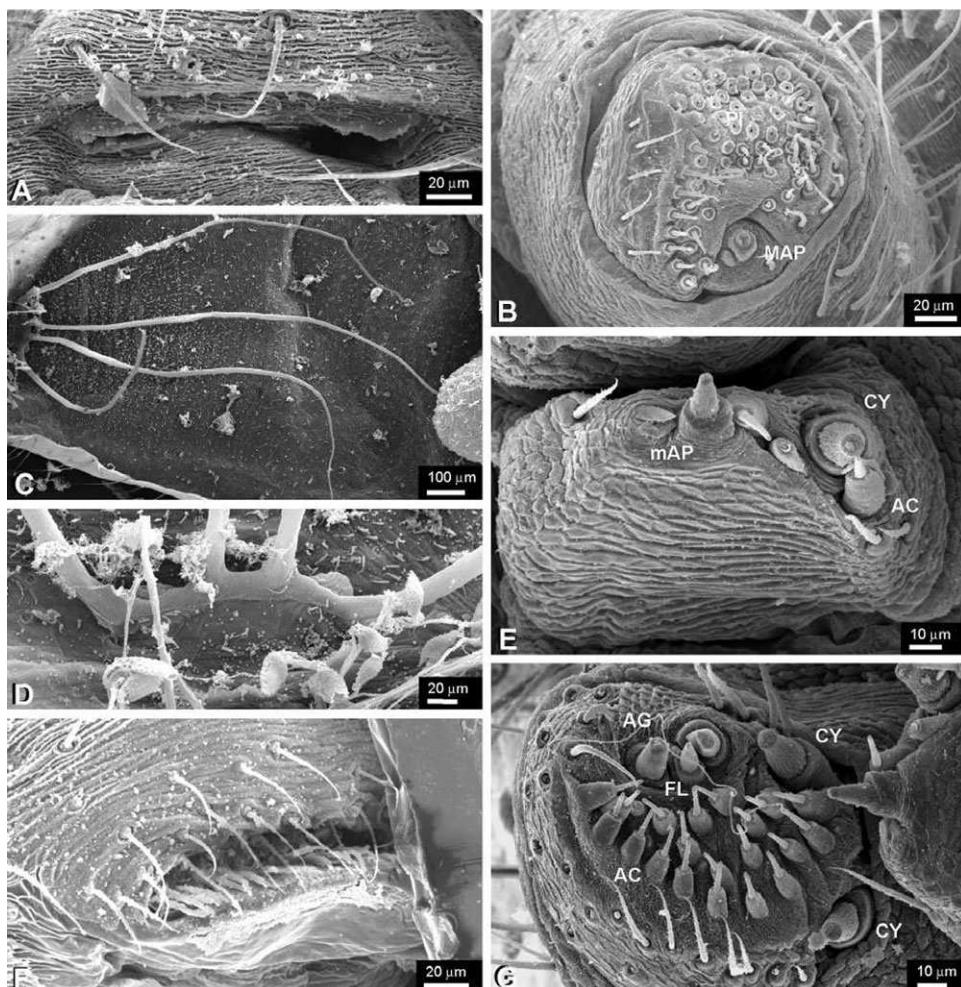
69. *Embolus path:* (0) less than half the circumference of curvature (*Araneus marmoreus* (Levi, 1971: figs 4–8); (1) more than half but less than the complete circumference (*Uloborus glomosus*, Fig. 139E); (2) more than the complete circumference (*Diphya spinifera*, Fig. 29E). This character is inapplicable to flagelliform emboli (see character 67).
70. *Embolus tip:* (0) cylindrical (*Nanometa* sp., Fig. 90C); (1) with caps or hooks (*Argiope argentata*, Fig. 140F). The diameter of the embolus of most araneoids decreases continuously in circumference towards its distal end. In some araneids the tip of the embolus has hooks or caps that presumably help to break this sclerite in the epigynum, blocking the female copulatory openings (A04, K08, DIM).
71. *Radix:* (0) absent (*Leucauge venusta*, Fig. 45C); (1) araneid radix (*Argiope argentata*, Levi, 1968: fig. 42); (2) linyphiid radix (*Linyphia triangularis*; Hormiga, 1994a: figs 8, 9). The araneid radix was defined by Scharff & Cod-



**Figure 113.** *Tetragnatha versicolor* genital anatomy illustrations: A and B, male pedipalp expanded. C, pedipalp cleared ventral view. D, cleared genitalia ventral view.

dington (1997) as an intermediate sclerite between the tegulum and the embolus; these authors coded linyphioids without such a radix. The radix can be differentiated from other embolic division sclerites by its relative position on the tegulum, by having the sperm duct running through it and by having a membranous attachment to more distal sclerites. Tetragnathids lack a radix. The absence of a radix is symplesiomorphic in Araneoidea with two independent origins, one of them synapomorphic for araneids (Scharff & Coddington, 1997). *Linyphia triangularis* (and linyphiids in

general) have an equally named sclerite but it is unclear whether it is homologous to the araneid radix (Hormiga, 1994a, 2000; Griswold *et al.*, 1998; Arnedo *et al.*, 2009). The linyphiid radix differs morphologically from the araneid radix, although the sperm duct also goes through it (e.g. Levi, 1971; Hormiga, 1994b). The radix can be defined as a basal modification of the embolus that interacts with a tegular membrane and that is crossed through its longitudinal axis by the sperm duct. If this definition of homology is applied, the basal modification of leucaugines (e.g. *Leucauge*



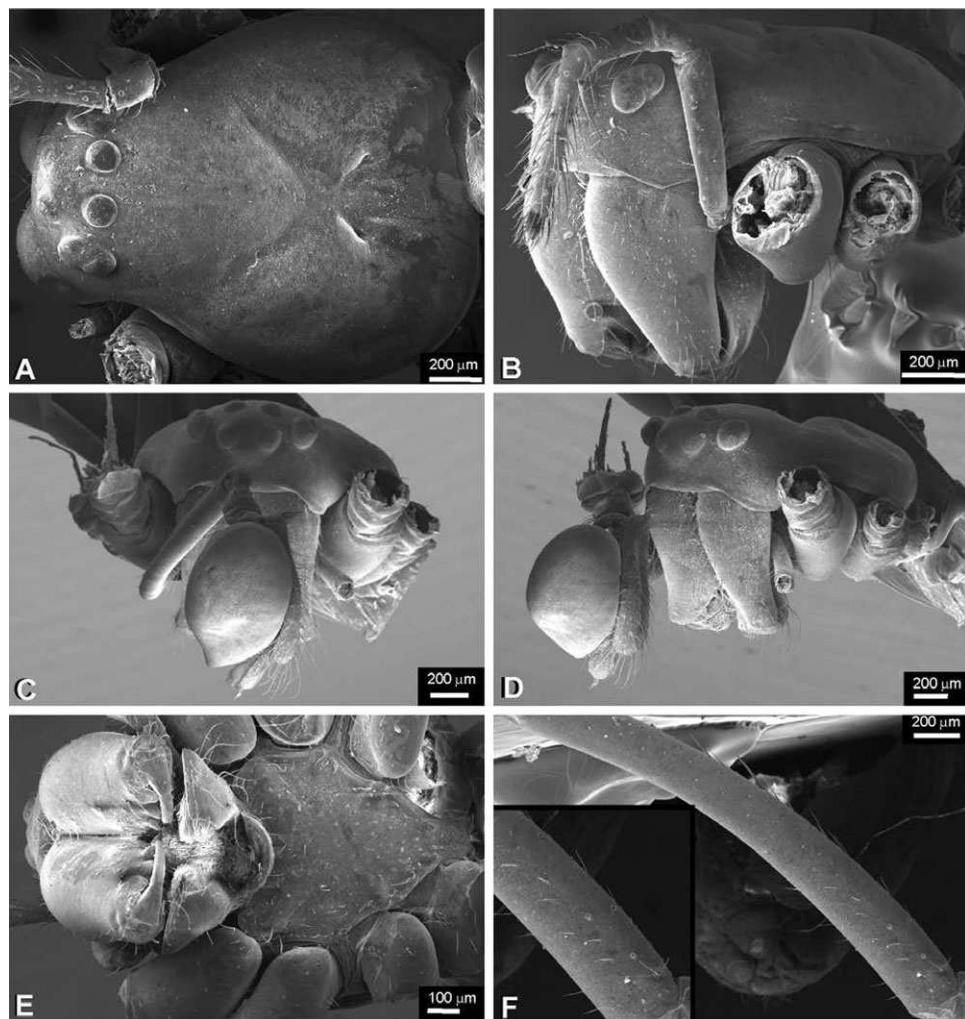
**Figure 114.** *Tylorida striata* abdomen: A, tracheal spiracle. B, anterior lateral spinnerets. C, tracheal system dorsal view. D, tracheal spiracle posterior view. E, posterior median spinnerets. F, epiandrous fusules. G, posterior lateral spinnerets. All images from SEMFAP052.

*venusta*, see Fig. 44D) and nephilids can be considered a radix; this alternative coding had no effects on the topologies of the optimal trees. We coded the linyphiid and araneid radices as homologous (C90, H94, H95, S97, G98, K08, A07, DIP).

72. *Stipes*: (0) absent (*Leucauge venusta*, Fig. 45C); (1) present (*Araneus marmoreus*, Levi, 1971: figs 4–8). The stipes is a sclerite between the radix and the embolus. As in the radix, the sperm duct also runs through it. This character is found only within some Araneidae (Scharff & Coddington, 1997 and references therein) (H95, S97, K08, A07, DIP).
73. *Distal hematodocha*: (0) absent (*Meta menardi*, Fig. 60A, B); (1) present (*Araneus marmoreus*, Levi, 1971: figs 4–8). The distal hematodocha is

a membranous sac located between the radix and the stipes. In some araneids the distal hematodocha is enlarged and associated with the terminal and subterminal apophyses (e.g. Scharff & Coddington, 1997: fig. 8) (H95, S97, A07, DIP).

74. *Araneid terminal apophysis*: (0) absent (*Leucauge venusta*, Fig. 45C); (1) present (*Araneus marmoreus*, Levi, 1971: figs 4–8). The terminal apophysis is defined as the most distal sclerite attached to the embolus via the distal hematodocha (Scharff & Coddington, 1997: fig. 10). Taxa without distal hematodocha are coded as inapplicable (i.e. *Argiope argentata* Fig. 140F). Taxa without this hematodocha but with embolic apophyses are coded as absent (i.e. *Meta menardi* and *Linyphia triangularis*



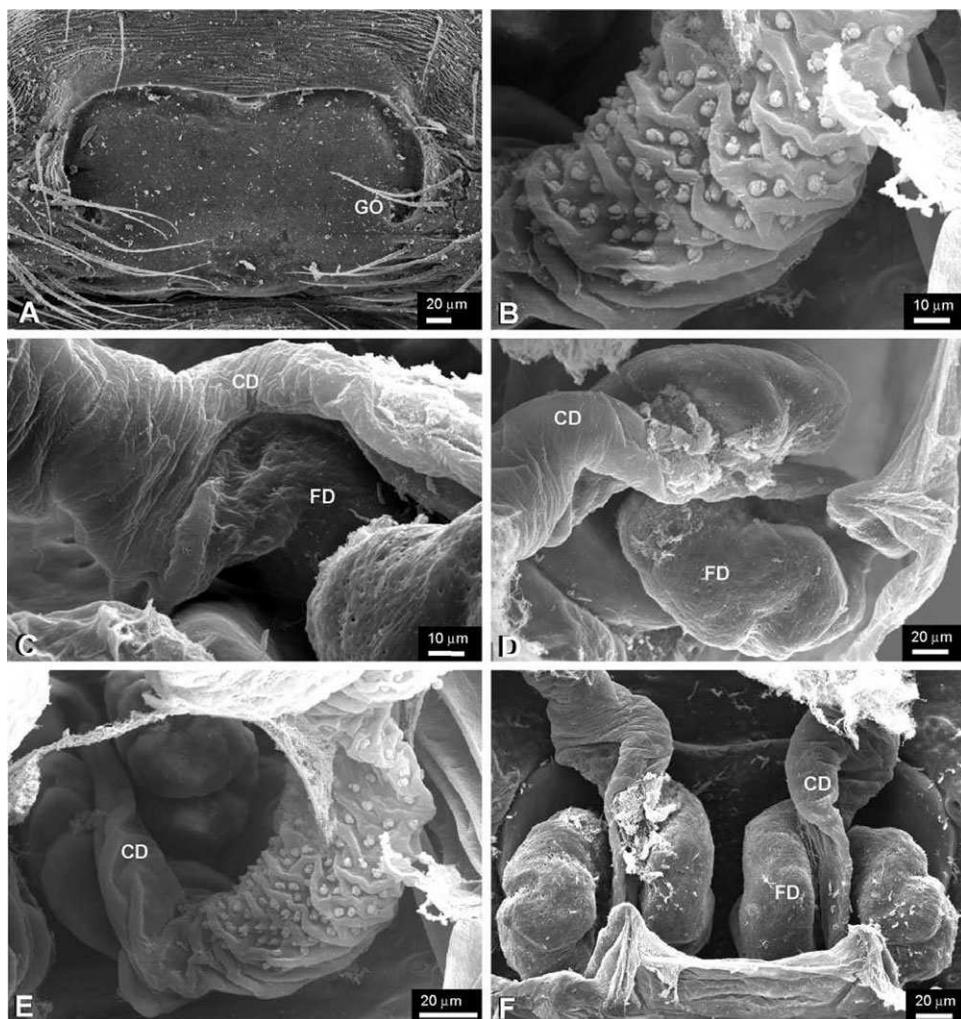
**Figure 115.** *Tylorida striata* cephalothorax: A, female dorsal view. B, female lateral view. C, male anterior view. D, male tangential view. E, male ventral view. F, female femora IV ectal view; insert, close up of trichobothria. All images from SEMFAP052.

Figs 60B, 139B), although note that *Linyphia triangularis* has an equally named sclerite that is not homologous to the araneid terminal apophysis (e.g. van Helsdingen, 1969) (S97, A07, DIP).

- 75. *Subterminal apophysis*: (0) absent (*Leucauge venusta*, Fig. 45C); (1) present (*Araneus moreus*, Levi, 1971: figs 4–8). The subterminal apophysis is defined as the most basal sclerite attached to the embolus via the distal hematochela (Scharff & Coddington, 1997: fig. 10). Taxa without embolic apophyses are coded as inapplicable. This apophysis is present in some araneids (Figs 138F, 140B) (S97, A07, DIP).
- 76. *Sperm reservoir diameter*: (0) approximately uniform beyond the fundus (*Mesida argentiopunctata*, Fig. 55C); (1) medially wider (*Glenognatha foxi*, Fig. 40A).

The palpal sperm duct is divided in three distinct parts: the fundus, an enlargement forming a pouch at the proximal end; the reservoir, a long tube spiralling throughout the tegulum; and the ejaculatory duct that resides inside the embolus (Comstock, 1910). The sperm duct of most araneoids has approximately the same diameter for all its length (beyond the fundus). The median section of the sperm duct of *Glenognatha*, *Pachygnatha*, *Tetragnatha*, and *Cyrtognatha* is considerably wider in diameter between the fundus and the entry into the embolus. This widening of the sperm duct is a synapomorphy of Tetragnathinae (C90, H95, G98, A07, DIP).

- 77. *Sperm duct path*: (0) spiral (*Metellina segmentata*, Fig. 70C); (1) with switchbacks (*Meta*

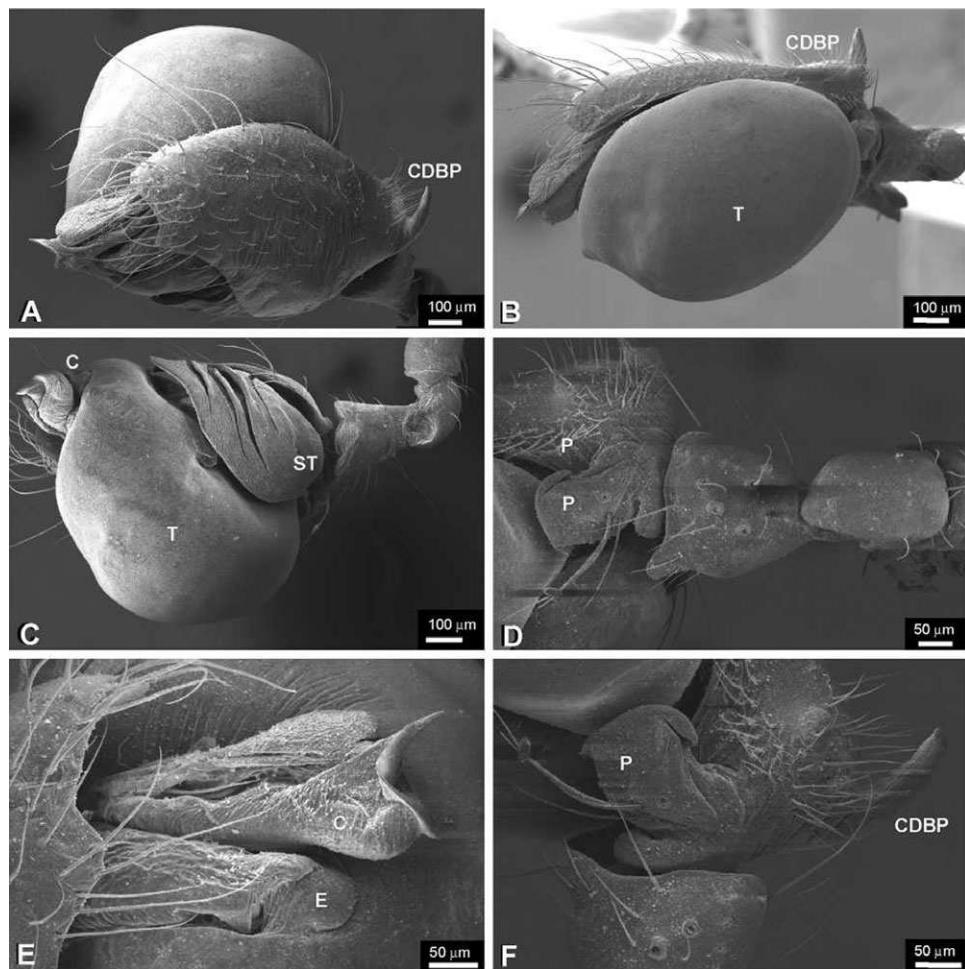


**Figure 116.** *Tylorida striata* epigynum: A, ventral view. B, accessory glands. C–F, copulatory and fertilization ducts. All images from SEMFAP052.

*menardi*, Fig. 60B). Spiral sperm ducts are optimized as plesiomorphic for Araneoidea (Coddington, 1990a and references therein); however in many araneoids the sperm duct trajectory widely varies in the amount of loops and switchbacks (Coddington, 1986a; Hormiga *et al.*, 1995; Griswold *et al.*, 1998; Agnarsson, 2004; Kuntner, 2005, 2006; Kuntner *et al.*, 2008). Coddington (1986a) and Agnarsson (2004) homologized individual switchbacks of the theridiosomatid and theridiid reservoir, and showed the systematic value of this character. We did not homologize individual loops of the sperm duct in leucaugines and some ‘metaine-tetragnathine complex’; however we expect that homologizing individual loops within leucaugines, combined with a larger taxonomic sample of these species, will be fruitful for the phylogenetics of these spiders as sug-

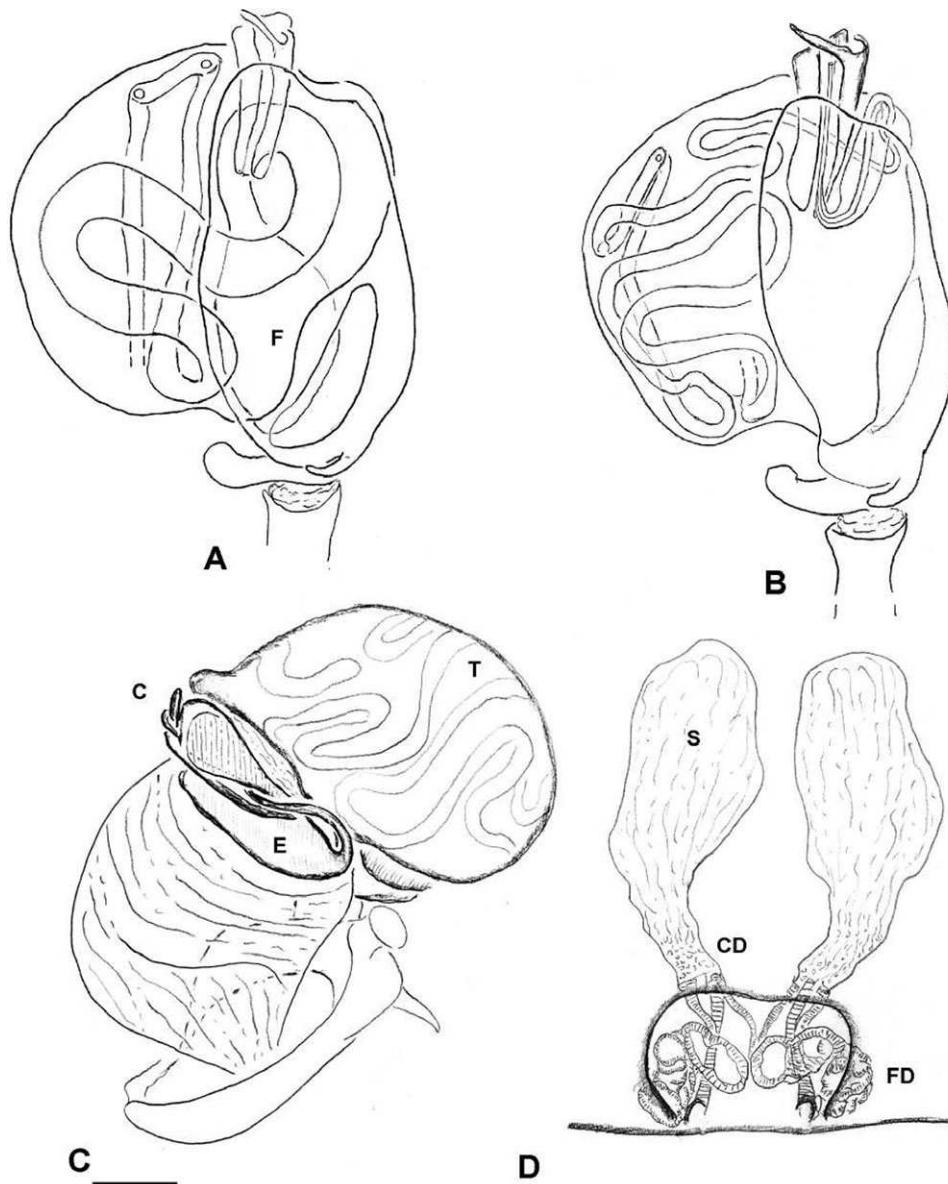
gested by previous studies (C90, H95, T01, A04, K08, A07, DIP).

78. *Sperm switchbacks*: (0) fewer than two switchbacks (*Dolichognatha pentagona*, Fig. 35C); (1) more than two (*Tylorida striata*, Fig. 133A, B). *Dolichognatha pentagona* has a few switchbacks although other congeneric species lack them (e.g. *Dolichognatha* sp. Hormiga *et al.*, 1995: fig. 13C). Some leucaugines, nephilids, and theridiosomatids have sperm ducts with several switchbacks (e.g. *Nephilengys cruentata*, Hormiga *et al.*, 1995: fig. 12D; *Epeirotypus brevipes* Coddington, 1986a: figs 62, 63) (A07, DIP).
79. *Sperm duct embolus joint*: (0) duct enters the embolus through the base (*Orsinome* cf. *vethi*, Fig. 104A); (1) duct joins embolus via a pars pendula (*Deliochus* sp., Fig. 45C). The pars pendula is a membrane that parallels the



**Figure 117.** *Tylorida striata* male pedipalp: A, dorsal view. B, ectal view. C, mesal view. D, male pedipalp patella and tibia. E, conductor and embolus. F, paracymbium. All images from SEMFAP052.

- embolus length. The sperm duct of *Tetragnatha versicolor* and *Argiope* species (Fig. 113C; Levi, 1968: figs 39, 55) are coded as entering through its base (coded differently in Kuntner *et al.*, 2008) (K08, DIP).
80. *Female cheliceral boss:* (0) absent (*Epeirotypus brevipes*, Fig. 131B); (1) present (*Micrathena gracilis*, Fig. 131D). The cheliceral boss is a swelling of the ectobasal part of the paturon (e.g. Griswold *et al.*, 2005). All taxa studied except the members of the ‘reduced piriform clade’ have cheliceral bosses (C90, A04, K08, DIP).
81. *Female cheliceral boss cuticle:* (0) striated (*Clytaera episinoides*, Fig. 131A); (1) as the paturon (*Mecynogea lemniscata*, Fig. 131C). In nephilids the boss cuticle is striated (Hormiga *et al.*, 1995: figs 27C, D, 28A, 29B) (H95, G98, K08, A07, DIP)
82. *Female cheliceral length:* (0) shorter than carapace margin width at the clypeus (*Gasteracantha cancriformis*, Fig. 130D); (1) same length (*Argiope argentata*, Fig. 130A); (2) longer (*Linyphia triangularis*, Fig. 130C). The cheliceral length is measured relative to the carapace margin clypeal width; the length of the carapace margin at the clypeus.
83. *Female chelicerae width:* (0) massive (*Gasteracantha cancriformis*, Fig. 130D); (1) slender (*Metleucauge eldorado*, Fig. 78G, C). Massive chelicerae are those in which their width is longer than half the paturon length; slender chelicerae have their widths shorter than the paturon length (K08, DIP).
84. *Female cheliceral denticles:* (0) absent (*Diphya spinifera*, Fig. 27F); (1) present (*Deliochus* sp., Fig. 130E). The area between the two cheliceral tooth margins can be either flat, or covered with



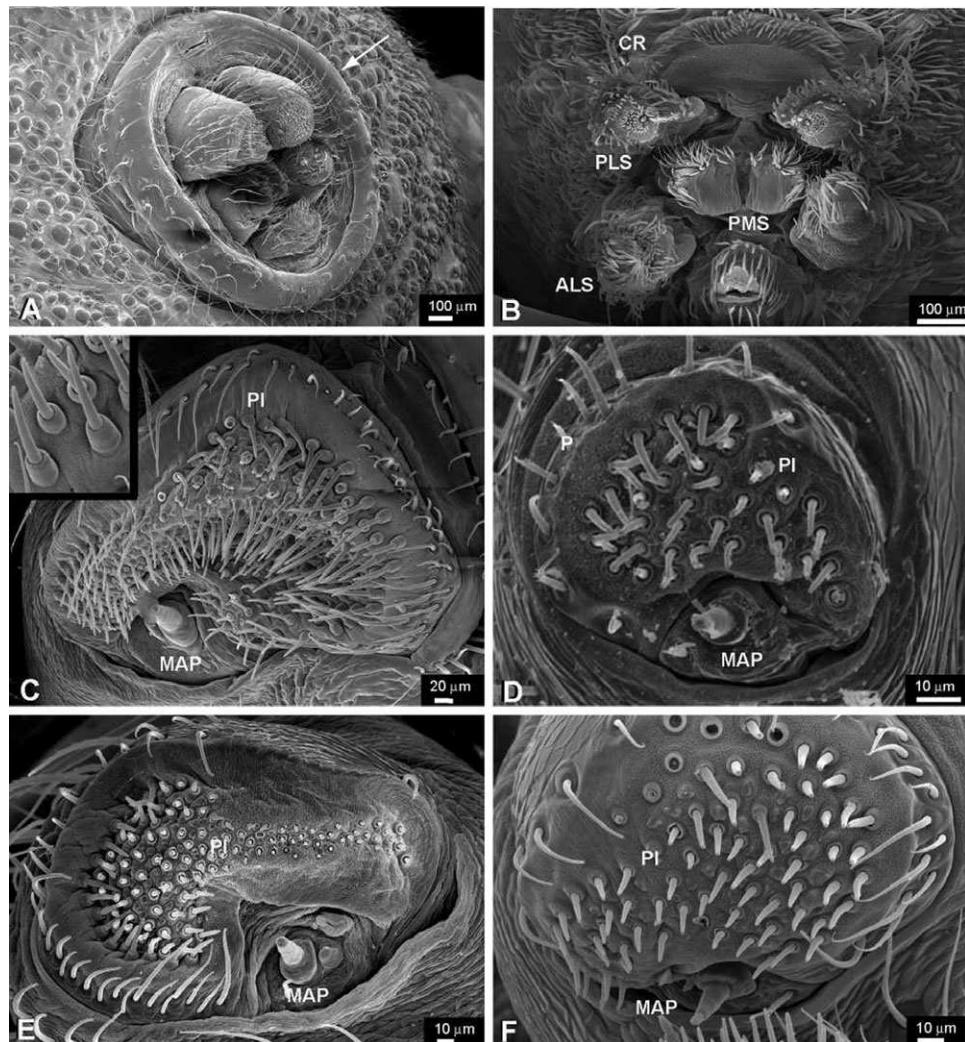
**Figure 118.** *Tylorida striata* genital anatomy illustrations: A and B, male pedipalp bulb cleared. C, male pedipalp expanded. D, cleared epigynum ventral view.

denticles. These denticles have been previously described in araneids and nephilids (Hormiga *et al.*, 1995; Scharff & Coddington, 1997 and references therein). All tetragnathids lack cheliceral denticles except the members of Nanometinae (Figs 73C, 88D) (C90, H95, S97, A04, K08, A07, DIP).

85. *Female chilum:* (0) absent (*Leucauge venusta*); (1) present (*Nephila clavipes*). The chilum is a small sclerotized plate between the clypeal margin and the chelicerae paturon membrane (G05, K08, DIP).

86. *Cheliceral promargin:* (0) toothed (*Diphya spinifera*, Fig. 27F); (1) without teeth (*Asagena americana*, Fig. 129C). In most araneoids studied the cheliceral promargin has teeth; the absence of these teeth is optimized as synapomorphic for theridiids (Agnarsson, 2004: figs 19C, 22E, 27F) (A04).

87. *Cephalothorax supracheliceral lobe:* (0) absent (*Epeirotypus brevipes*, Fig. 131B); (1) present (*Clitaetra episinooides*, Fig. 131A). The margin of the cephalothorax above the cheliceral boss area can either have a protuberance or be flat (K08, DIP).

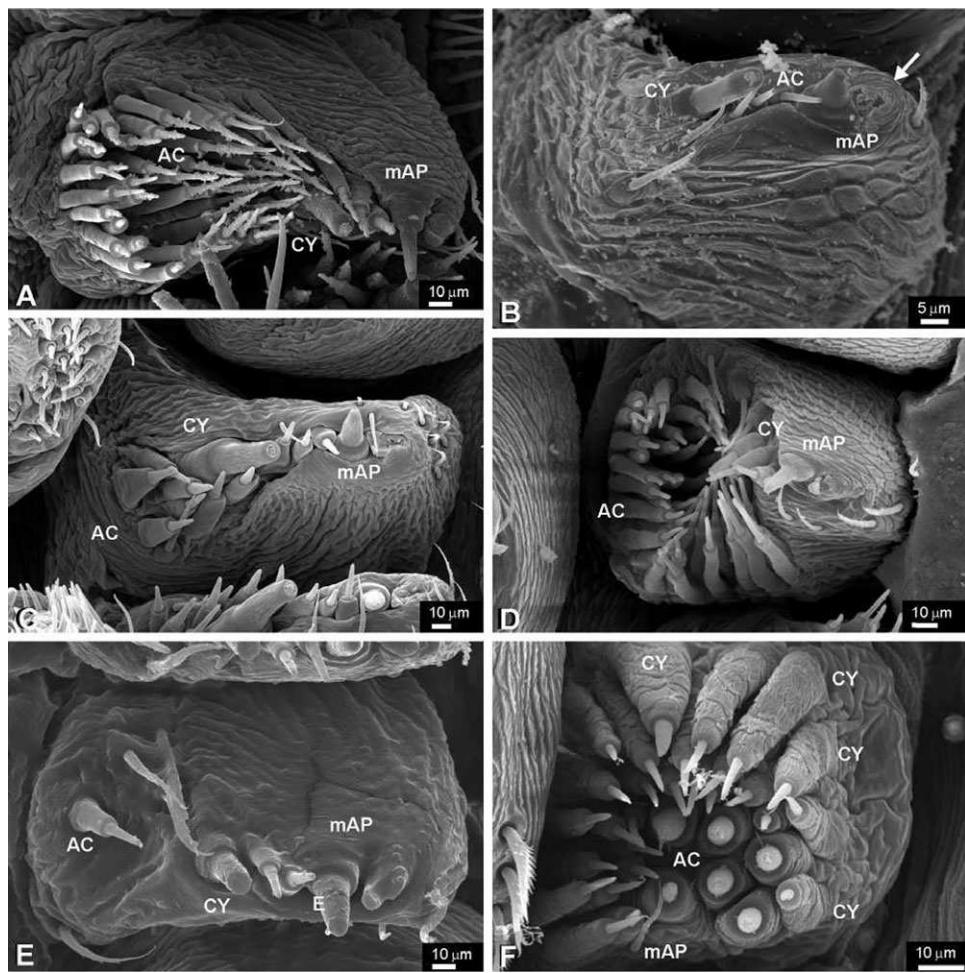


**Figure 119.** Spinnerets of outgroup taxa: A, *Gasteracantha cancriformis* (Araneidae), arrow indicates ring around the spinnerets (SEMFAP012). B, *Uloborus glomosus* (Uloboridae) spinnerets and cribellum (SEMFAP003). C, *Araneus marmoreus* (Araneidae) anterior lateral spinnerets; insert, close up of piriform spigot bases (SEMFAP009). D, *Epeirotypus brevipes* (Theridiosomatidae) anterior lateral spinnerets (SEMFAP020). E, *Mecynogea lemniscata* (Araneidae) anterior lateral spinnerets (SEMFAP011). F, *Zygiella X-notata* (Araneidae) anterior lateral spinnerets (SEMFAP005).

88. *Female ocular area height*: (0) low (*Leucauge argyra*, Fig. 47A); (1) high (*Metellina segmentata*, Fig. 67E). The ocular area position is defined by the ALE height relative to the carapace lateral margin. Low ocular areas are those in which the ALE are below the carapace lateral margin. High ocular areas are those in which ALE are above the carapace margin.
89. *Clypeus height*: (0) low (*Mangora gibberosa*, Fig. 130F); (1) intermediate (*Metellina segmentata*, Fig. 67E); (2) high (*Linyphia triangularis*, Fig. 130C). The clypeus is defined as the area between the anterior margin of the AME and the carapace's anterior margin. Clypeus height is

measured relative to the diameter of the AME. Low clypei are less than one AME diameter. Intermediate clypei are between one and two AME diameters. High clypei are more than two AME diameters. Male and female clypeal height are the same in all species studied here except in *Glenognatha foxi* and *Epeirotypus brevipes* where the male clypeus is high whereas the female clypeus is low; female specimens were coded for these two species (L80, H95, S97, G98, T01, A07, DIP).

90. *Separation between the lateral and median eyes*: (0) less than the PME area length (*Tetragnatha versicolor*, Fig. 110D); (1) more (*Araneus mar-*



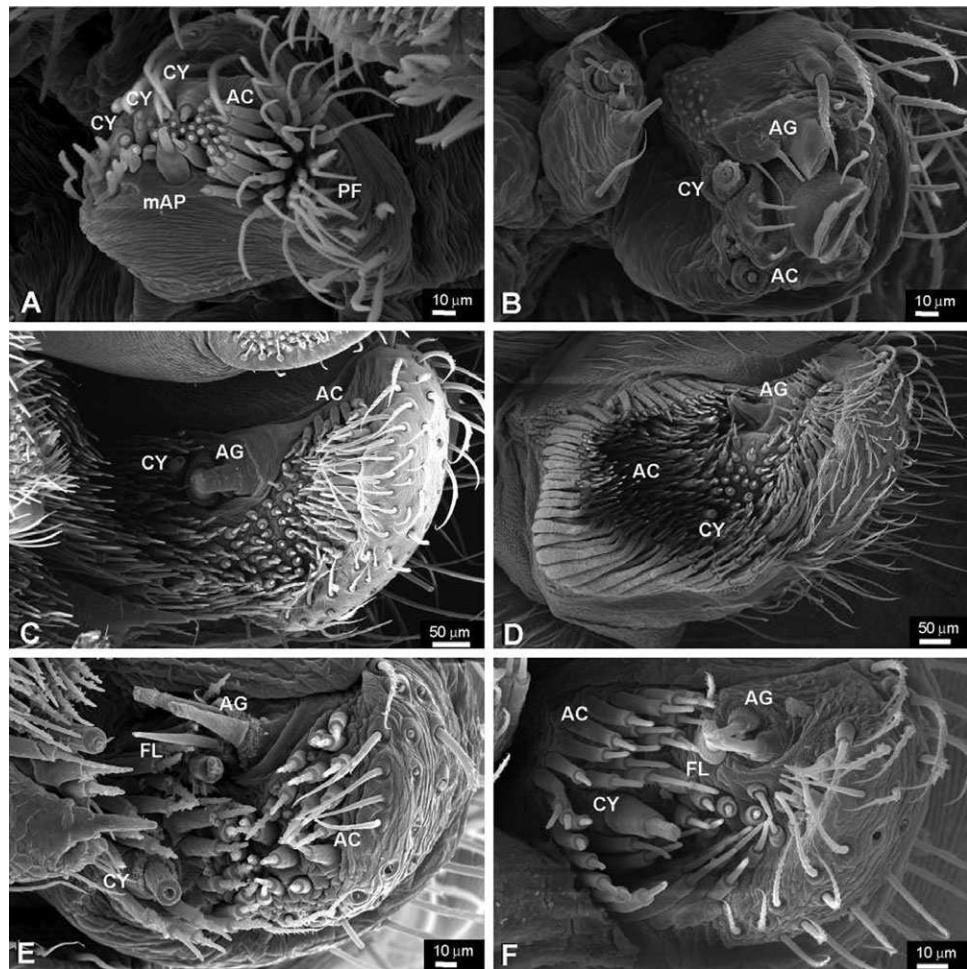
**Figure 120.** Posterior median spinnerets of outgroup taxa: A, *Cyclosa conica* (Araneidae) (SEMFAP008). B, *Epeirotypus brevipes* (Theridiosomatidae) (SEMFAP020). C, *Gasteracantha cancriformis* (Araneidae) (SEMFAP012). D, *Mangora gibberosa* (Araneidae) (SEMFAP014). E, *Micrathena gracilis* (Araneidae) (SEMFAP013). F, *Oncodamus decipiens* (Nicodamidae) (SEMFAP001).

*moreus*, Fig. 130A). The lateral eye separation is measured in relation to the separation of the PME (Scharff & Coddington, 1997) (S97, K08, DIP).

91. *PME separation*: (0) less than the PME diameter (*Cyclosa conica*, Fig. 126C); (1) equal to the PME diameter (*Meta menardi*, Fig. 57A); (2) more than the PME diameter (*Uloborus glomosus*, Fig. 127D). The separation between the PME is measured in relation to the lens diameter of one of these eyes (K08, DIP).
92. *PME canoe-shaped tapeta*: (0) absent (*Azilia affinis*, Levi, 1980: figs 299, 300); (1) present (*Argiope picta*, Scharff & Coddington, 1997: fig. 38). The tapetum is a reflective layer of guanine crystals found only in the secondary eyes. Its function is to amplify the amount of light received by the rhabdomes (Homann, 1971). In

most araneoids the tapetum, when present, is equally distributed along both sides of the mid line of the eye forming a canoe shape. Eyes without a tapetum have a uniform grey colour without any reflective coating. The tapetum deteriorates in dead and old museum specimens, but sometimes the canoe-shaped scar left by the tapetum can be seen. If this scar was identified then the studied species were coded as having a tapetum (L80, C90, S97, G98, G05, K08, DIP).

93. *PME canoe-shaped tapetum*: (0) broad (*Metleucocauge eldorado*, Levi, 1980: figs 139, 140); (1) narrow (*Argiope picta*, Scharff & Coddington, 1997: fig. 38). The canoe-shaped tapetum can be either evenly distributed along both sides of the middle line: covering more than one third of the eye area, or covering less than one third



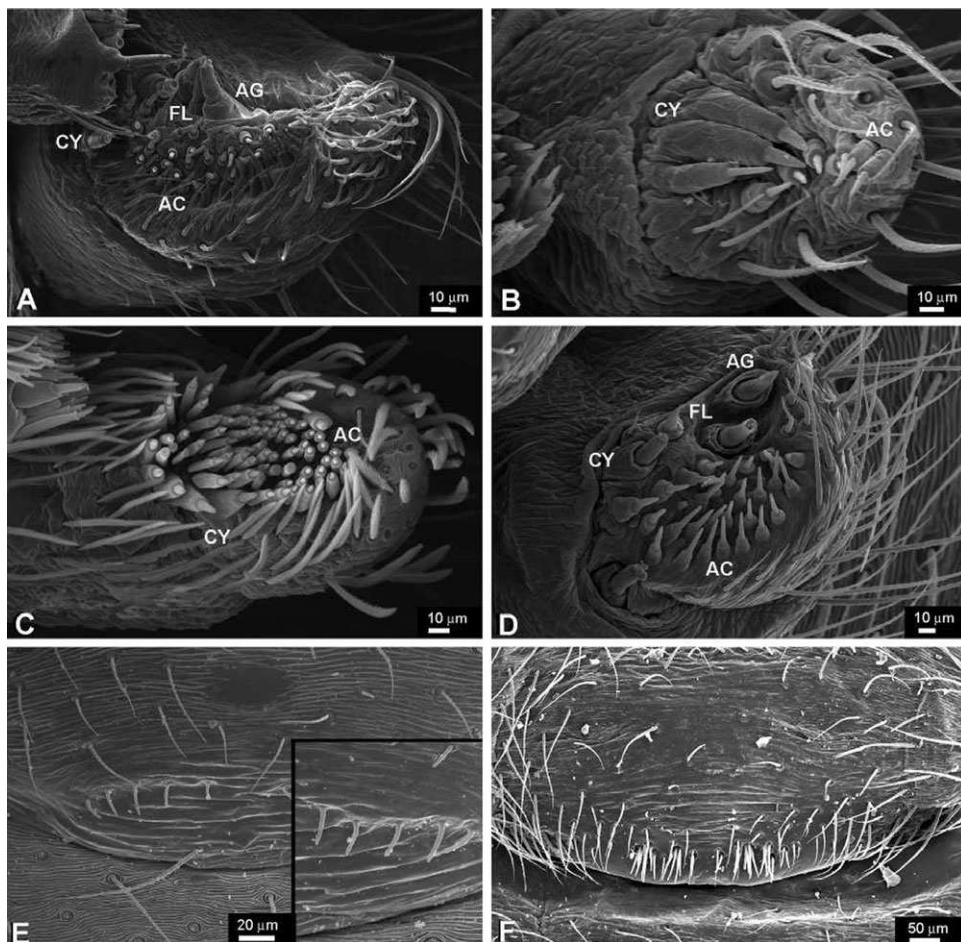
**Figure 121.** Spinnerets of outgroup taxa: A, *Uloborus glomosus* (Uloboridae) posterior median spinnerets (SEMFAP003). B, *Asagena americana* (Theridiidae) posterior lateral spinnerets (SEMFAP018). C, *Araneus marmoreus* (Araneidae) posterior lateral spinnerets (SEMFAP009). D, *Argiope argentata* (Araneidae) posterior lateral spinnerets (SEMFAP010). E, *Cyclosa conica* (Araneidae) posterior lateral spinnerets (SEMFAP008). F, *Mangora gibberosa* (Araneidae) posterior lateral spinnerets (SEMFAP014).

of the eye area. In araneids the tapetum is reduced to a thin line, this type of tapetum is synapomorphic for Araneidae (Scharff & Coddington, 1997) (L80, S97, G98).

94. *PLE canoe-shaped tapetum*: (0) absent (*Azilia affinis*, Levi, 1980: figs 299, 300); (1) present (*Argiope picta*, Scharff & Coddington, 1997: fig. 38). Araneoid spiders without a tapetum usually lack this structure in all secondary eyes, except in a few tetragnathids such as *Pachygnatha autumnalis* and *Glenognatha foxi* that have a tapetum in the PME but lack this structure in the PLE (L80, C90, S97, H95, G98, G05, K08, A07, DIP).
95. *PLE size relative to PME*: (0) smaller than PME (*Araneus marmoreus*, Fig. 128A); (1) same as PME (*Metellina segmentata*, Fig. 67E);

(2) larger than PME (*Dolichognatha pentagona*, 32A). This character was modified from Kuntner (2005), who coded two states for this character: (0) PLE diameter equal to or less than the PME diameter; (1) PLE diameter larger. Including the state PLE diameter equal to PME, either within state 0 or 1, resulted in different most parsimonious cladograms when analysed in previous versions of our data set. Therefore, this character was separated into the three states described above (K08, DIP).

96. *Female lateral eyes*: (0) separated (*Diphya spinifera*, Fig. 27A); (1) together on a single tubercle (*Opadometa* sp., Fig. 93A, B) (K08, DIP).
97. *Female posterior eye row*: (0) straight ('*Orsinome*' *sarasini*, Fig. 97A, B); (1) procurved (*Metepira labyrinthica*, Fig. 127B); (2) recurved



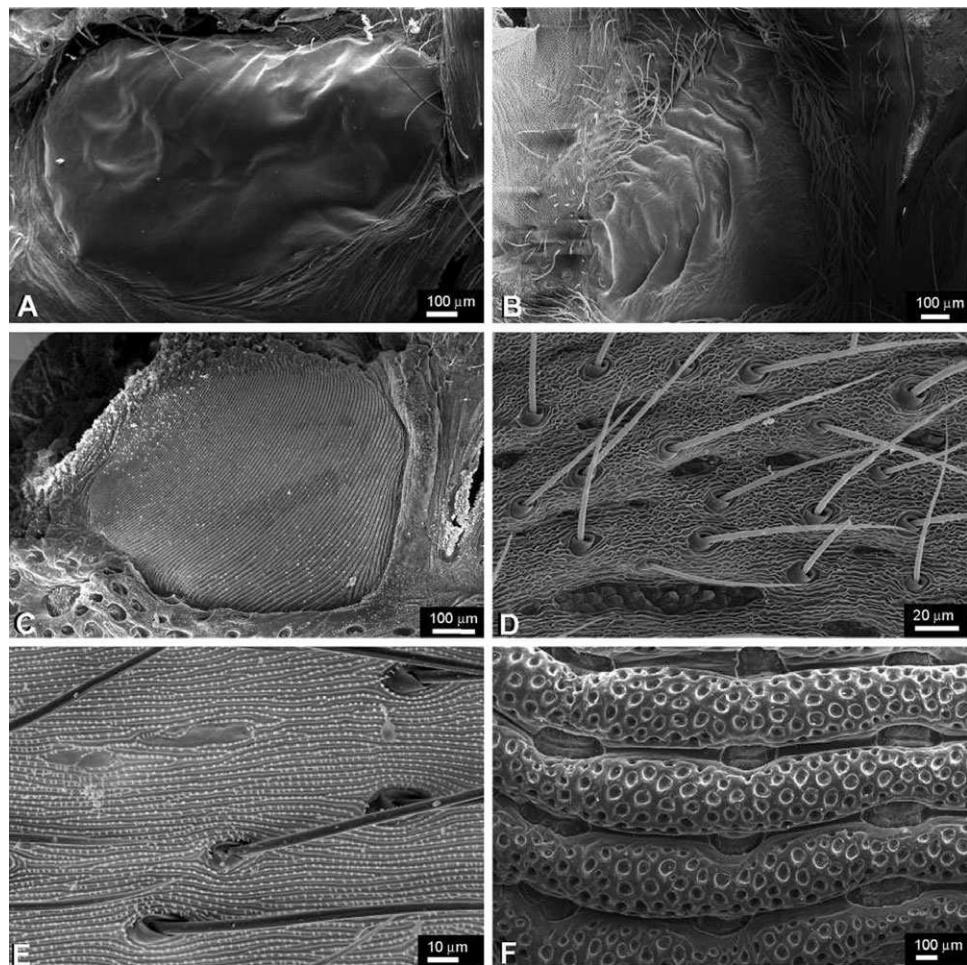
**Figure 122.** Spinnerets and epiandrous fusules of outgroup taxa: A, *Nephilengys malabarensis* (Nephilidae) posterior lateral spinnerets (SEMFAP027). B, *Oncodamus decipiens* (Nicodamidae) posterior lateral spinnerets (SEMFAP001). C, *Uloborus glomosus* (Uloboridae) posterior lateral spinnerets (SEMFAP003). D, *Zygiella x-notata* (Araneidae) posterior lateral spinnerets; insert, close up of fusules (SEMFAP005). E, *Epeirotypus brevipes* (Theridiosomatidae) epiandrous fusules; insert, detail of fusules (SEMFAP020). F, *Larinioides cornutus* (Araneidae) epiandrous fusules (SEMFAP004).

(*Argiope argentata*, Fig. 126B). To score this character one needs to trace an imaginary straight line through the centre of the PLE, the carapace must be in dorsal view. If this line crosses the PME near the centre, then the posterior eye row is considered straight (state 0). If the line crosses near the posterior edge of the PME, it is considered procurved (state 1). Finally, if it crosses near the anterior edge of the PME, then it is considered recurved (state 2). The posterior eye row is similarly arranged in females and males, except in *Herennia multipuncta*, *Nephilengys malabarensis*, and *Opadometa* sp. Female specimens were used to code these three species (S97, K08, DIP).

98. *Female cephalothorax setae*: (0) glabrous, macrosetae covering less than 10% of the carapace dorsal surface (*Nanometa* sp., Fig. 88B); (1)

moderately hirsute, macrosetae covering more than 10% but less than 50% of its surface (*Phonognatha graeffei*, Fig. 125E); (2) hirsute, macrosetae covering more than 50% of its surface (*Herennia multipuncta*, Fig. 126E) (S97, K08, DIP).

99. *Female carapace shape*: (0) piriform (*Argiope argentata*, Fig. 126B); (1) oval (*Phonognatha graeffei*, Fig. 125E). Piriform carapaces are considered as having the cephalic region width less than 70% of the thoracic region width. Oval carapace is defined as the cephalic region wider than 70% (S97, A04, K08, DIP).
100. *Female anterior gut caeca*: (0) absent (*Argiope aurantia*); (1) present (*Tetragnatha versicolor*). Enlarged anterior gut caeca are midgut projections that extend inside the chelicerae and coxae. *Tetragnatha* and *Pachygnatha* have



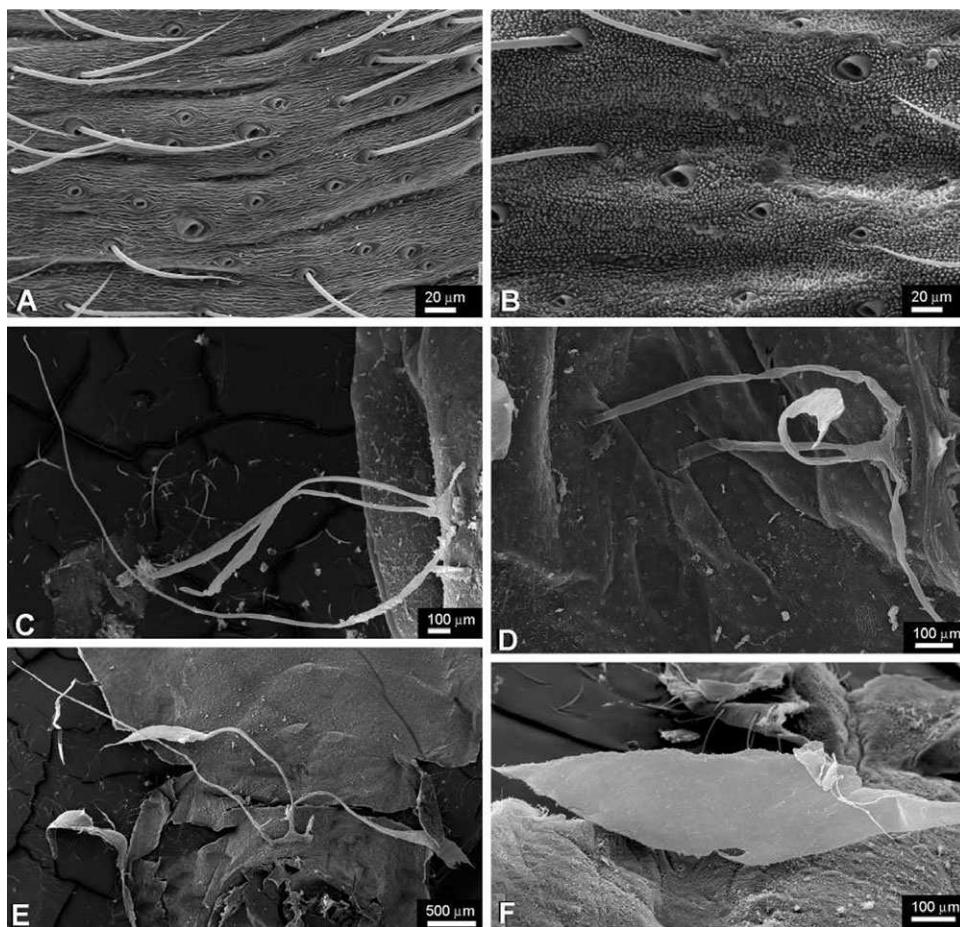
**Figure 123.** Abdomens of outgroup taxa: A, *Nephilengys malabarensis* (Nephilidae) female booklung cuticle (SEM-FAP027). B, *Argiope argentata* (Araneidae) female booklung cuticle (SEM-FAP010). C, *Micrathena gracilis* (Araneidae) female booklung cuticle (SEM-FAP013). D, *Mangora gibberosa* (Araneidae) cuticle of the female abdomen, close up of median lateral section. E, cuticle of the male abdomen, close up of median lateral section (SEM-FAP014). F, *Micrathena gracilis* (Araneidae) cuticle of the female abdomen, close up of median lateral section (SEM-FAP013).

bulkier ventral caeca. Normal anterior gut caeca do not extend into the chelicerae and pedipalp coxae. Anterior gut caecae have been observed in *Leucauge*, *Pachygnatha*, and *Tetragnatha*, and are absent in *Meta* (Pallgrem, 1978a, b; Hormiga *et al.*, 1995) (L80, H95, G98, G05, A07, DIP).

101. *Cephalothorax fovea*: (0) absent (*Glenognatha foxi*, Fig. 37A, B); (1) present (*Metleucauge eldorado*, Fig. 78A). The cephalothorax fovea or furrow is a cuticular depression located at the centre of the carapace (it is the external manifestation of the apodeme for the stomach muscles). In the taxonomic sample studied here this character did not exhibit sexual dimorphism. This character was coded with observations of specimens preserved in alcohol and

SEM preparations, as both methods complement each other, in particular with shallow depressions difficult to interpret by one method alone (K08, DIP).

102. *Female fovea shape*: (0) transversely elongate (*Metellina segmentata*, Fig. 67A); (1) longitudinally elongate (*Mangora gibberosa*, Fig. 126F); (2) two deep transverse pits (*Tetragnatha versicolor*, Fig. 110D); (3) shallow oval depression (*Mecynogea lemniscata*, Fig. 127A); (4) single deep hole (*Micrathena gracilis*, Fig. 127C). The morphology of the cephalic fovea varies considerably; we used five states to code variation in this character. Shallow foveae are better seen with alcohol preserved specimens than with SEM, the pigmentation of the cephalic fovea is considerably darker than the surrounding cuticle. The



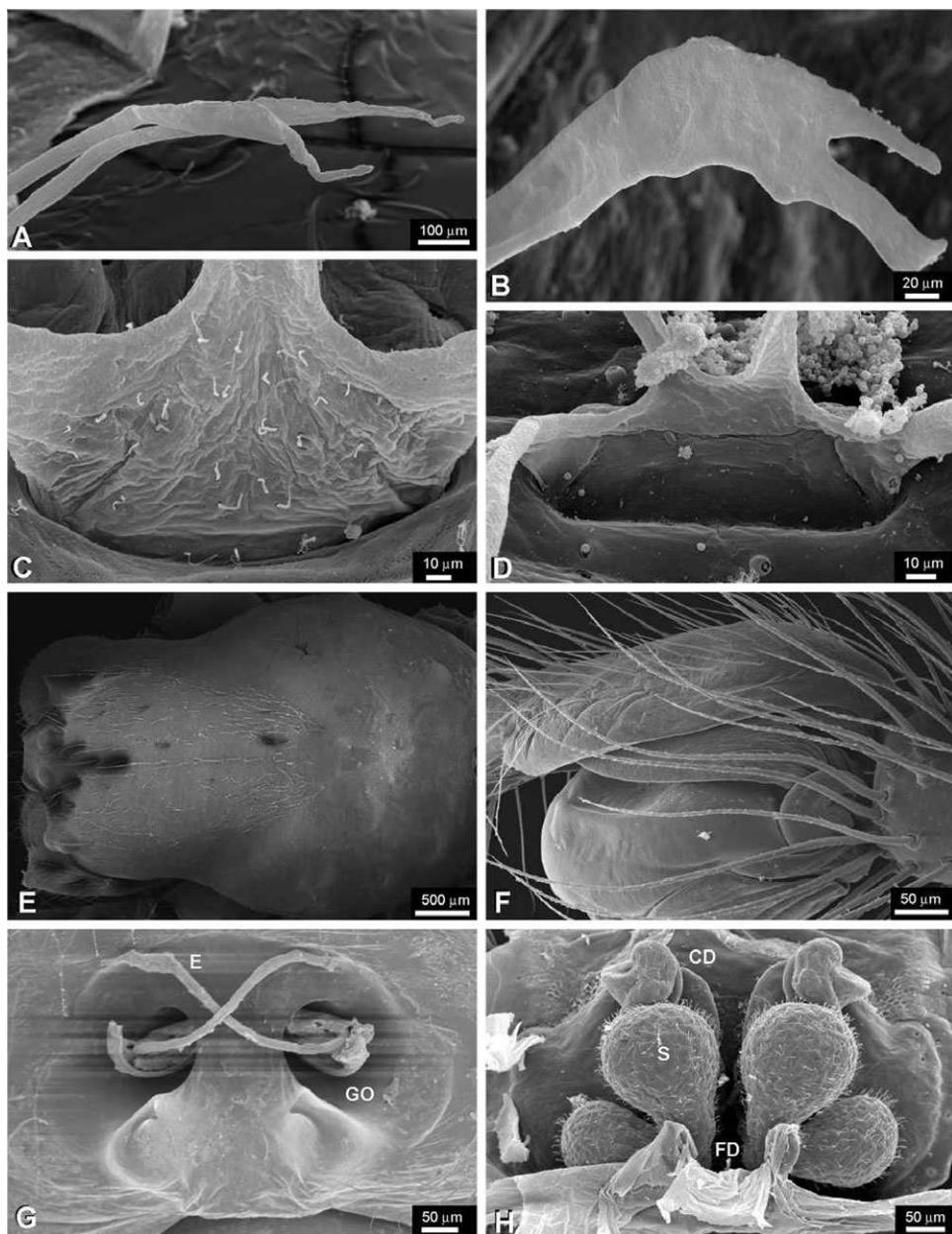
**Figure 124.** Abdomens of outgroup taxa: A, *Neoscona domiciliorum* (Araneidae) cuticle of the male abdomen, close up of median lateral section. B, cuticle of the female abdomen, close up of median lateral section. C, tracheal system dorsal view (SEMFAP006). D, *Metepeira labyrinthica* (Araneidae) tracheal system dorsal view (SEMFAP007). E, *Nephilengys malabarensis* (Nephilidae) tracheal system dorsal view. F, median trachea tip (SEMFAP027).

shape of the fovea may vary amongst sexes (see character 112) (K08, DIP).

- 103. *Carapace pits*: (0) absent (*Tylorida striata*, Fig. 115A); (1) present (*Leucauge argyra*, Fig. 47B). Usually the only depression on the cephalic area is the cephalic fovea; some leucaugines however have an additional pair of pits anterior to the fovea. This character has no sexual dimorphism.
- 104. *Labium edge*: (0) slightly swollen (*Araneus marmoreus*, Fig. 128A); (1) rebordered (*Tetragnatha versicolor*, Fig. 110F). The labium edge of most araneoid spiders is slightly swollen and pointed; however, in all tetragnathids studied this edge folds back (re bordered). This character presented no variation between females and males.
- 105. *Labium shape*: (0) pentagonal (*Gasteracantha cancriformis*, Fig. 128F arrow); (1) trap-

ezoidal (*Allende nigrohumeralis*, Fig. 9F arrow). The labium apical edge of many araneids and nephilids is roughly triangular giving the appearance of a pentagonal labium. The labium apical edge of most tetragnathid is flat giving the appearance of a trapezoidal labium. This character has no variation between females and males.

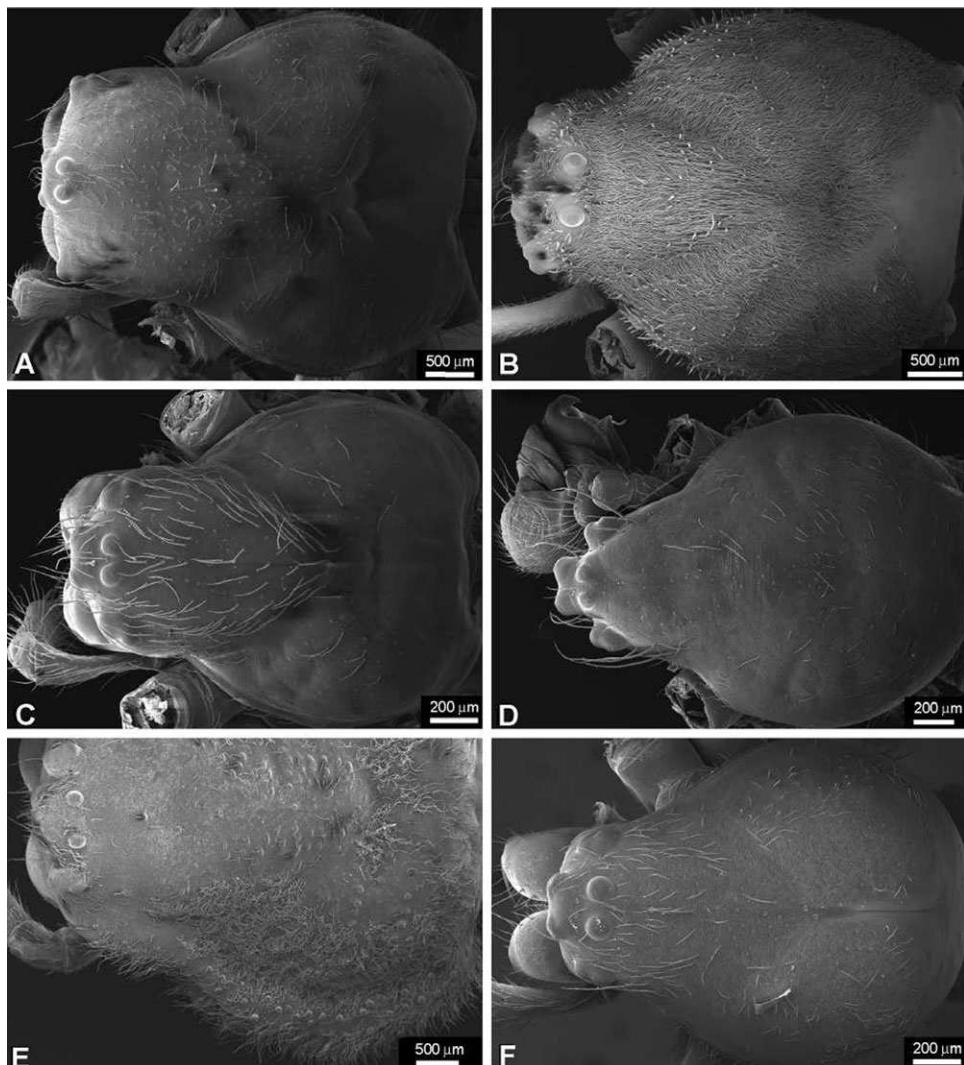
- 106. *Female sternum*: (0) longer than wide (*Metaphenardi*, Fig. 53C); (1) as wide as or wider than long (*Herennia multipuncta*, Fig. 128E).
- 107. *Female sternal surface*: (0) flat (*Dolichognatha pentagona*, Fig. 32F); (1) tubercles I to IV present ('*Orsinome*' *sarasini*, Fig. 97G); (2) tubercles I to III (*Herennia multipuncta*, Fig. 128E); (3) tubercles I, III, and IV (*Orsinome* cf. *vethi*, Fig. 101B); (4) tubercles III and IV (*Chrysometa alajuela*, Fig. 19G); (5) tubercles I and II (*Leu-*



**Figure 125.** Anatomy of outgroup taxa: A, *Neoscona domiciliorum* (Araneidae) median tracheal tips (SEMFAP006). B, *Metepeira labyrinthica* (Araneidae) median tracheal tip (SEMFAP007). C, *Gasteracantha cancriformis* (Araneidae) tracheal spiracle posterior view (SEMFAP012). D, *Mangora gibberosa* (Araneidae) spiracle posterior view (SEMFAP014). E, *Phonognatha graeffei* (Araneidae) female cephalothorax dorsal view. F, male pedipalp cymbium ectal view (SEMFAP023). G, *Deliochus* sp. (Araneidae) epigynum ventral view. H, dorsal view (SEMFAP022).

cauge *argyra*, Fig. 47G); (6) only tubercle I (*Diphya spinifera*, Fig. 27F); (7) tubercle only III (*Zygiella x-notata*, Fig. 128D); (8) only tubercle IV (*Mollemeta edwardsi*, Fig. 83F). The sternum of most araneoids is covered with several tubercles that vary in their position relative to the coxae. A tubercle is defined as a dome-shaped ventral protuberance of the sternum in which the

cuticle is the same as the rest of the sternum and is covered with macrosetae. *Clitaetra episinoides* lacks all tubercles but has small apodemes instead (Fig. 128B). Kuntner (2005, 2006) was the first to report on this interesting character complex and we have combined these serial homologues into a single multistate character (K08, DIP).

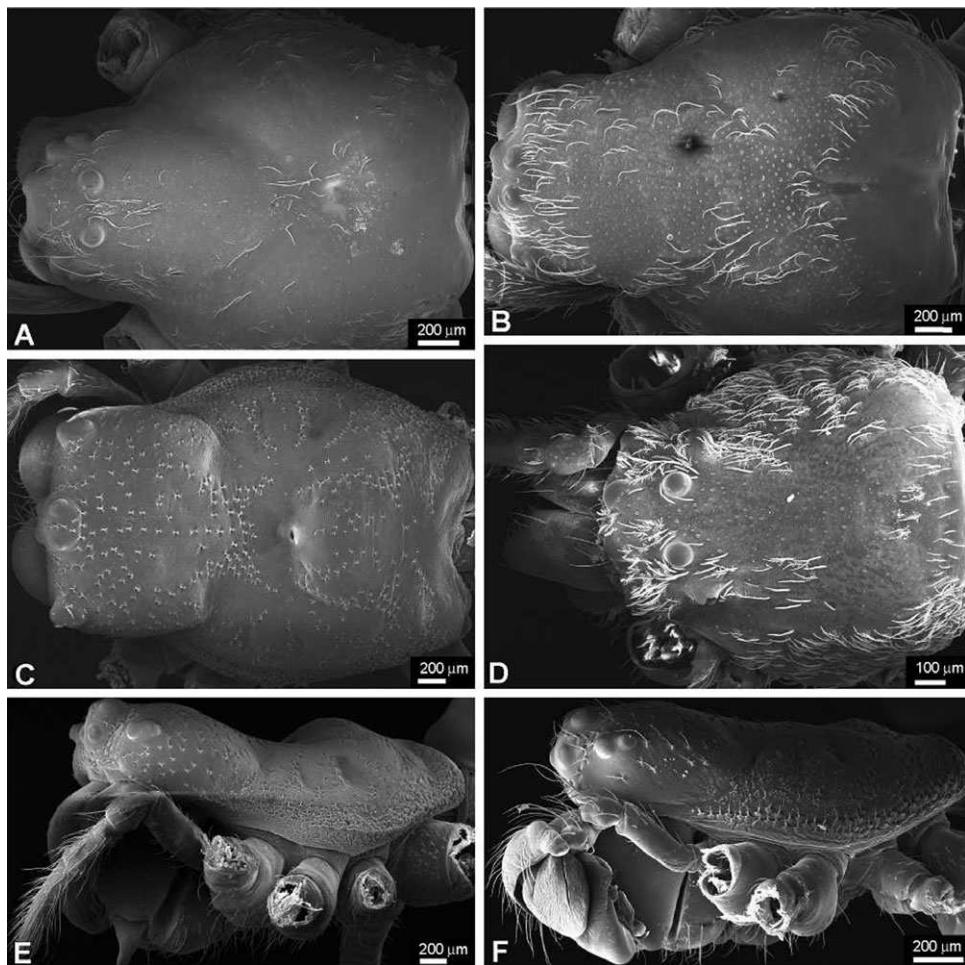


**Figure 126.** Cephalothorax of outgroup taxa dorsal view: A, *Araneus marmoreus* female (SEMFAP009). B, *Argiope argentata* female (Araneidae) (SEMFAP010). C, *Cyclosa conica* female (SEMFAP008). D, male (SEMFAP070). E, *Herennia multipuncta* (Nephilidae) female (SEMFAP026). F, *Mangora gibberosa* (Araneidae) female (SEMFAP014).

- 108. *Male cheliceral length*: (0) cheliceral length less the clypeal width (*Argiope argentata*, Fig. 130B); (1) chelicerae same length as the clypeal width (*Azilia affinis*, Fig. 14D); (2) chelicerae longer (*Metleucauge eldorado*, Fig. 78D). Cheliceral length is measured in relation to the width of the carapace margin at the clypeus (see character 82 description) (A07, DIP).
- 109. *Female frontal sternal tubercle*: (0) absent (*Leucauge argyra*, Fig. 47G); (1) present (*Meta menardi*, Fig. 57C). In addition to the paired tubercles located at the edge of the sternum, there can be an anterior median tubercle (K08, DIP).
- 110. *Male cheliceral boss*: (0) absent (*Leucauge venusta*, Fig. 42H); (1) present (*Dolichognatha pentagona*, Fig. 32E).

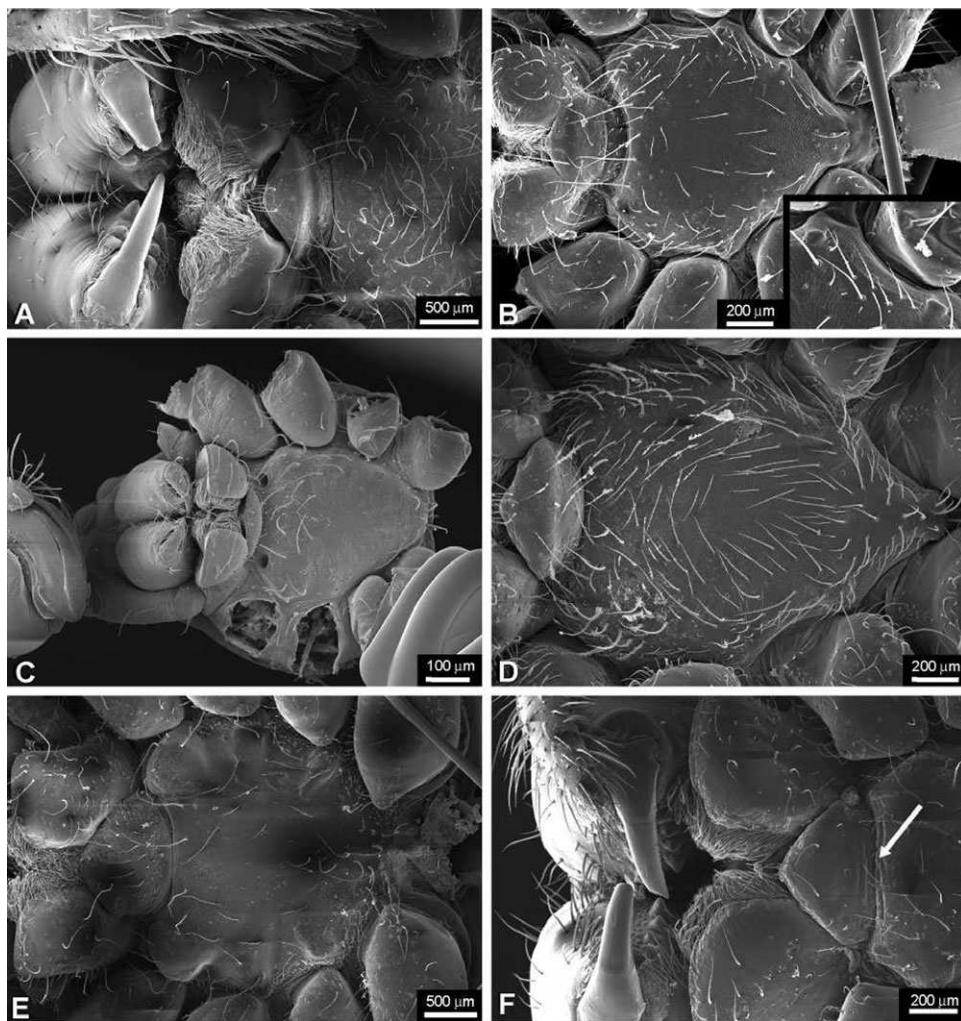
*pentagona*, Fig. 32E). Both males and females have a cheliceral boss, except in the ‘reduced piriform clade’. The males of other araneoids, including some tetragnathids and *Uloborus glomosus* also lack cheliceral bosses (see character 81 definition).

- 111. *Male cheliceral distal curvature*: (0) straight, less than twice the clypeus width (*Azilia affinis*, Fig. 14D); (1) greater (*Pachygnatha autumnalis*, Fig. 106C). The cheliceral curvature is measured by comparing the width between the distal ectal surfaces of the chelicera, with the clypeus width.
- 112. *Male cheliceral macroseta bases*: (0) base size as those in the clypeal area. (*Dolichognatha pentagona*, Fig. 32B); (1) bases larger (*Mesida argentiopunctata*, Fig. 52H).



**Figure 127.** Cephalothorax of outgroup taxa: A, *Mecynogeia lemniscata* (Araneidae) dorsal view female (SEMFAP011). B, *Metepeira labyrinthica* (Araneidae) dorsal view female (SEMFAP007). C, *Micrathena gracilis* (Araneidae) dorsal view female (SEMFAP013). D, *Uloborus glomosus* (Uloboridae) dorsal view female (SEMFAP003). E, *Micrathena gracilis* (Araneidae) lateral view female. F, male lateral view (SEMFAP013).

- 113. *Male ectal cheliceral cuticle*: (0) as in the anterior surface (*Metellina segmentata*, Fig. 67C); (1) rugose ('Orsinome' *sarasini*, Fig. 97H).
- 114. *Male cheliceral mesomedian apophysis*: (0) absent (*Metellina segmentata*, Fig. 67F); (1) present (*Tetragnatha versicolor*, Fig. 110C).
- 115. *Male cheliceral distal apophysis*: (0) absent (*Metellina segmentata*, Fig. 67F); (1) present and glabrous (*Glenognatha foxi*, Fig. 37D); (2) present and covered with setae (*Cyrtognatha espaniola*, Fig. 23E). The cheliceral apex near the fang-paturon junction can bear several apophyses in addition to the mesomedian apophysis (see character 114). These apophyses can be either smooth or be covered with macrosetae (DIP).
- 116. *Male paturon basal tubercle*: (0) absent (*Asagena americana*); (1) present (*Meta menardi*). This tubercle is found on the cheliceral surface, just anterior to the mouth (K08, DIP).
- 117. *Cheliceral cuticle sexual dimorphism*: (0) same texture in male and females (*Pachygnatha autumnalis*, Fig. 106D, E); (1) different (*Allende nigrohumeralis*, Fig. 9B, C). In some species the anterior surface paturon cuticle is more wrinkled in males than in females.
- 118. *Cheliceral length sexual dimorphism*: (0) male chelicerae smaller (*Neoscona domiciliorum*, Fig. 129E, F); (1) same length (*Metellina segmentata*, Fig. 67C, E); (2) male chelicerae larger (*Dolichognatha pentagona*, Fig. 32E, G). The male chelicerae of *Metellina curtisi* are larger than the female chelicerae but not in *Metellina*



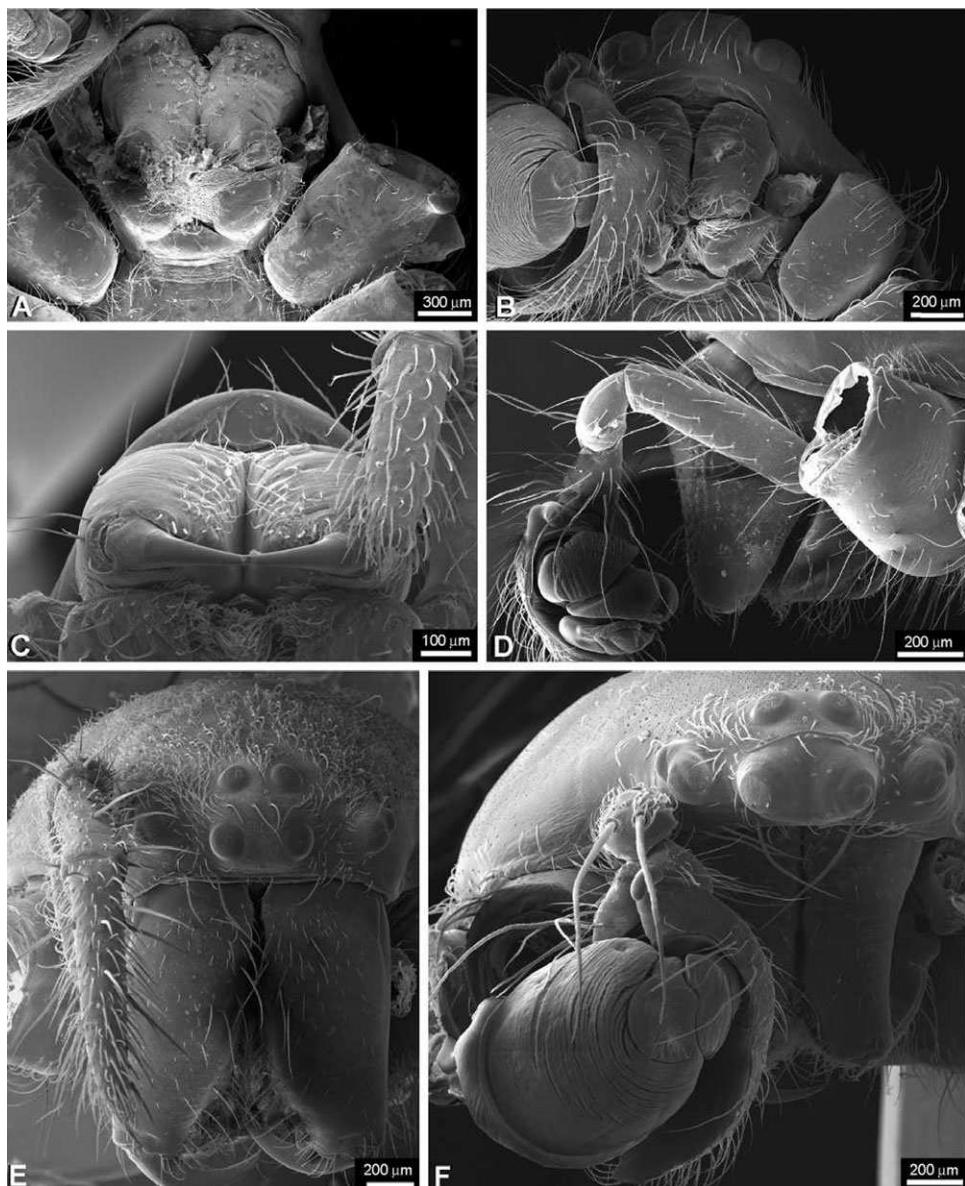
**Figure 128.** Cephalothorax of outgroup taxa: A, *Araneus marmoreus* (Araneidae) labium and endites (SEMFAP009). B, *Clitaetra episinoides* (Nephilidae) ventral view female (SEMFAP024). C, *Epeirotypus brevipes* (Theridiosomatidae) female sternum (SEMFAP020). D, *Zygilla x-notata* (Araneidae) female sternum (SEMFAP005). E, *Herennia multipuncta* (Nephilidae) female sternum (SEMFAP026). F, *Gasteracantha cancriformis* (Araneidae) labium and endites (SEMFAP012).

*segmentata* (Levi, 1980; Figs 72, 73). Both sexes of *Dolichognatha pentagona* have chelicerae longer than the carapace margin at the clypeus; however the male's chelicerae are considerably longer than the female's.

119. *Carapace shape sexual dimorphism:* (0) same shape in males and females (*Leucauge venusta*, Fig. 42A, B); (1) cephalic region narrower in males (*Cyclosa conica*, Fig. 126C, D). Proportions between the cephalic and thoracic regions in males and females are the same in most of the taxa studied. In some araneids and nephilids the cephalic region of the male is considerably narrower than the female cephalothorax. Carapace sexual dimorphism within our sample of Tetrag-

nathidae is present only in *Chrysometa alajuela* (Fig. 19A, B).

120. *Ocular area height sexual dimorphism:* (0) same height in male and females (*Micrathena gracilis*, Fig. 127E, F); (1) male ocular area higher (*Orsinome cf. vethi*, Fig. 101B, D); (2) male ocular area lower (*Neoscona domiciliorum*, Fig. 129E, F). The ocular area position is a comparison between the ALE height in relation to the carapace lateral margins (see character 89 description). The ocular area in male and females is the same in almost all taxa.
121. *Fovea shape sexual dimorphism:* (0) same in male and females (*Mollemeta edwardsi*, Fig. 83A, B); (1) different (*Cyclosa conica*, Fig. 126C, D).

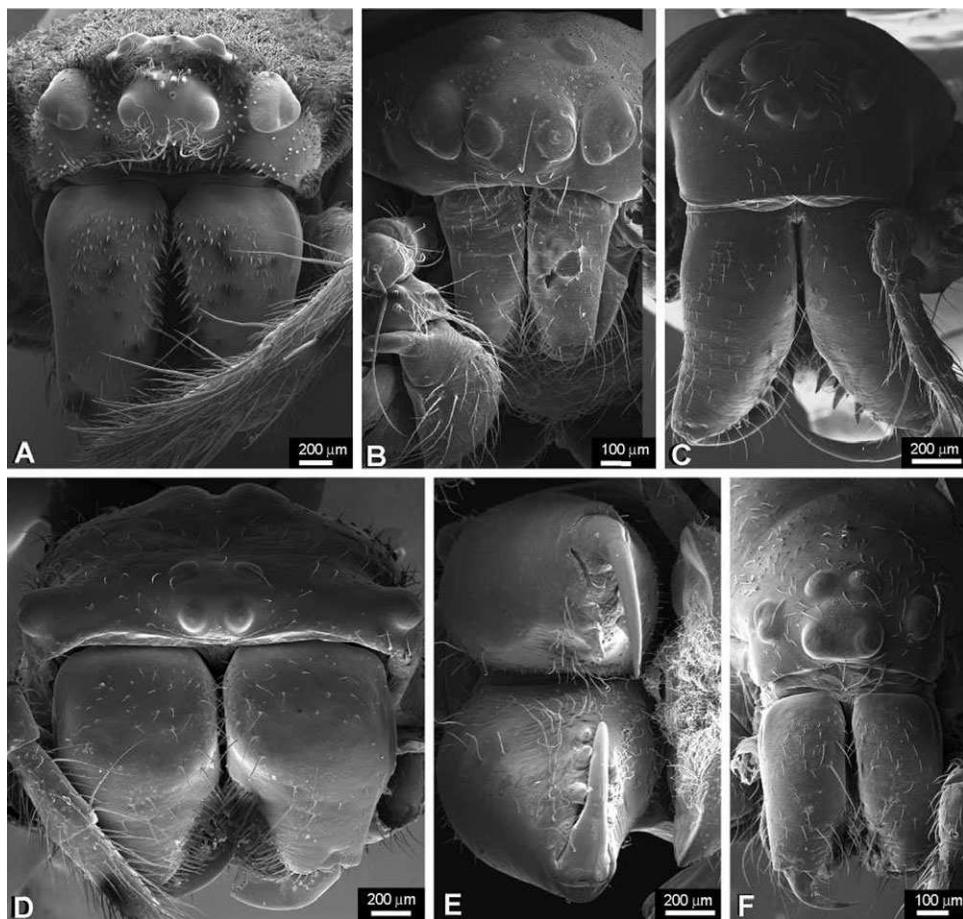


**Figure 129.** Cephalothorax of outgroup taxa: A, *Araneus marmoreus* (Araneidae) male coxa I (SEMFAP072). B, *Argiope argentata* (Araneidae) male coxa I (SEMFAP073). C, *Asagena americana* (Theridiidae) female cheliceral margins (SEMFAP018). D, *Zygiella x-notata* (Araneidae) male palpal femur (SEMFAP069). E, *Neoscona domiciliorum* (Araneidae) female anterior view. F, male anterior view (SEMFAP006).

Almost all cases of fovea sexual dimorphism refer to longitudinal foveae in males in contrast to the transversal foveae found in the females were common amongst nephilids and araneids.

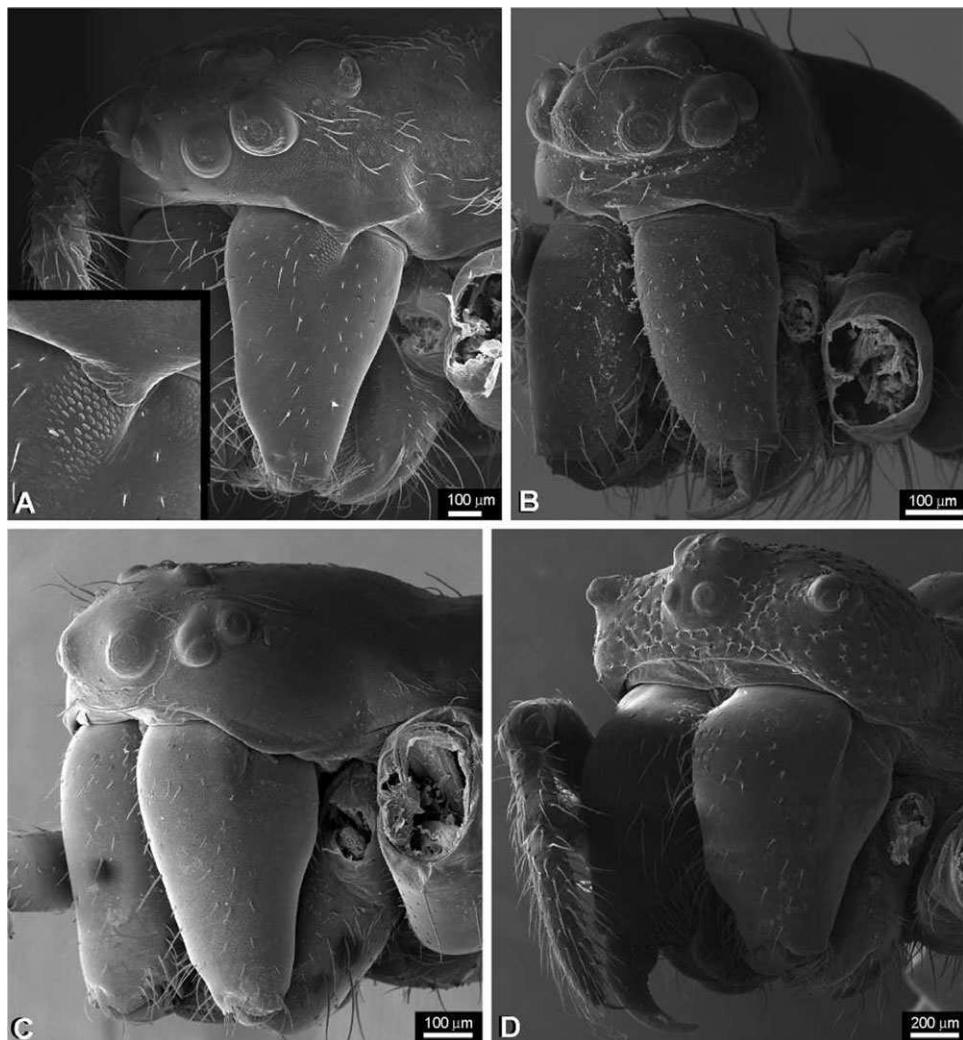
122. *Body size sexual dimorphism:* (0) male length more than half of the female body length (*Leucauge venusta*, Fig. 42A, B); (1) male less than half of the female body length (*Herennia multipuncta*, Fig. 2C). For this character the longitudinal body length was taken into consideration. Sexual size dimorphism in araneoid spiders has been the

subject of numerous studies (e.g. see references in Hormiga, Scharff & Coddington, 2000 and in Moya-Laraño, Halaj & Wise, 2002). The evolution of size dimorphism in Araneoidea has been studied recently from a cladistic perspective, concluding that female gigantism has been responsible for many cases of size dimorphism in orb-weaving spiders, including *Nephila* and their close relatives, although several cases of male dwarfism exist (e.g. *Kaira* spp.) (Hormiga *et al.*, 1995, 2000; Coddington, Hormiga & Scharff,



**Figure 130.** Cephalothorax of outgroup taxa: A, *Argiope argentata* (Araneidae) female anterior view (SEMFA010). B, male anterior view (SEMFA073). C, *Linyphia triangularis* (Linyphiidae) female anterior view (SEMFA015). D, *Gasteracantha cancriformis* (Araneidae) female anterior view (SEMFA012). E, *Deliochus* sp. (Araneidae) female chelicera apex (SEMFA022). F, *Mangora gibberosa* (Araneidae) female anterior view (SEMFA014).

- 1997, Scharff & Coddington, 1997; Kuntner *et al.*, 2008) (H95, S97, G98, K08, A07, DIP).
123. *Epigynum:* (0) absent (*Tetragnatha versicolor*, Fig. 111A, B); (1) present (*Opadometa* sp., Figs 94A, 95E). The epigynum is a sclerotized cuticular plate surrounding the female genital area where the copulatory ducts open. All araneoids in our study have an epigynum except tetragnathines, which instead have a nonsclerotized spiracle-shaped copulatory opening (H95, S97, A04, G07, A07, DIP).
124. *Epigynal plate level:* (0) same height as the surrounding cuticle (*Mesida argentiopunctata*, Fig. 53A, B); (1) bulging at least one third of the epigynal plate width (*Meta menardi*, Fig. 58A, B) (A07, DIP).
125. *Epigynal plate atrium:* (0) absent (*Metellina segmentata*, Fig. 68A, B); (1) present (*Metabus ocellatus*, Fig. 63A, B). The copulatory openings can be either separated by the epigynal cuticle or located in a depression of the epigynal plate. This depression is shallow in *Opadometa* sp., *Tylorida striata*, and *Mesida argentiopunctata* (Figs 53A, B, 94A, 116A) (C90).
126. *Cuticular area anterior to the epigynum:* (0) flat or rounded (*Leucauge venusta*); (1) excavated (*Meta menardi*). The area between the pedicel and epigynal plate can be either the level of the surrounding cuticle or excavated (K08, DIP).
127. *Scape:* (0) absent (*Tylorida striata*, Fig. 116A); (1) present (*Larinoides cornutus*, Fig. 135A). The scape is a projection of the ventral epigynal plate found in some araneids. A similar projection is present in *Mollemeta*, but we deemed it not to be homologous to the scape of araneids (Fig. 84A, B). *Linyphia triangularis* and many other linyphiids have a scape that originates from the dorsal epigynal plate. In previous studies both apophyses of the epigynal plates, either dorsal or ventral, have been considered as scape (Hormiga,



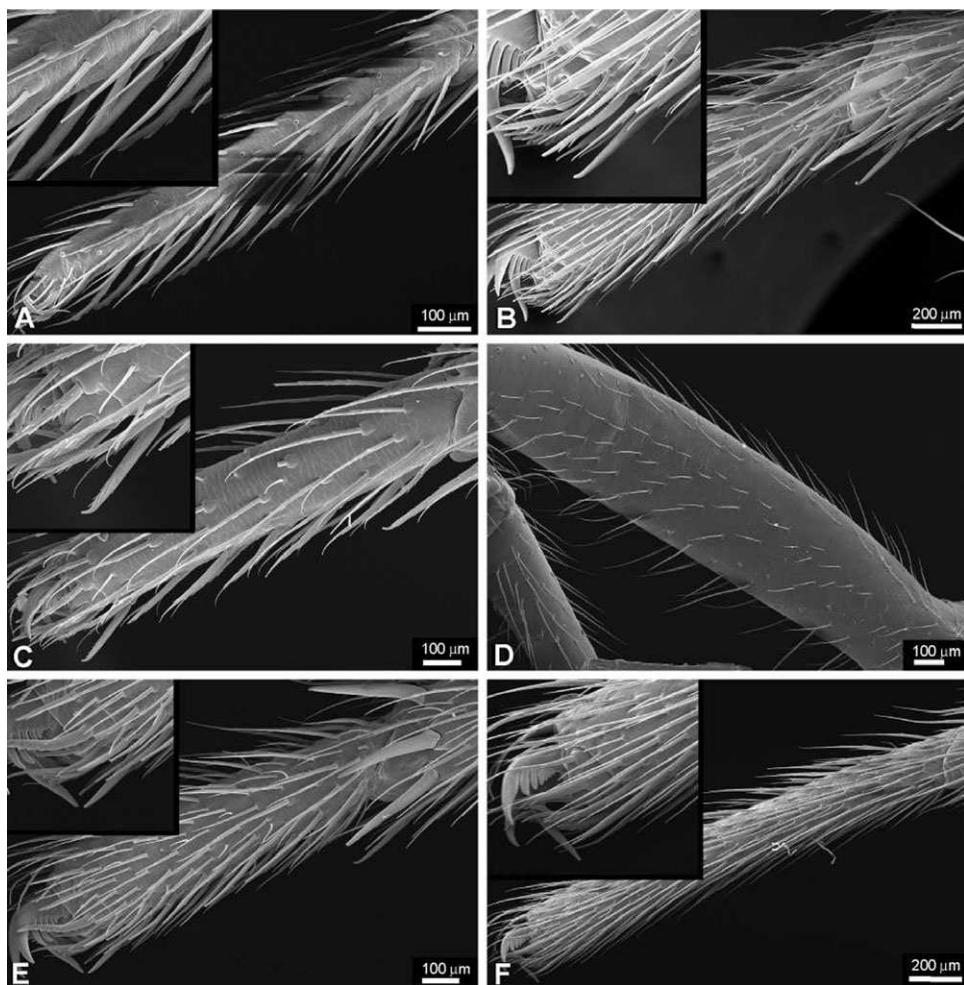
**Figure 131.** Cephalothorax of outgroup taxa: A, *Clitaetra episinoides* (Nephilidae) female tangential view; insert, close up of cheliceral boss with striated cuticle (SEMFAP024). B, *Epeirotypus brevipes* (Theridiosomatidae) female tangential view (SEMFAP020). C, *Mecynogeia lemniscata* (Araneidae) female tangential view (SEMFAP064). D, *Micrathena gracilis* (Araneidae) tangential view female (SEMFAP013).

1994a, 2000). In this study we have restricted the term scape to only those projections of the anterior edge of the ventral plate (H94, S97, A07, DIP).

128. *Scape cuticle texture:* (0) smooth (*Gasteracantha cancriformis*, Fig. 133E); (1) wrinkled (*Araneus marmoreus*, Fig. 133A). The scape cuticle of *Mollemeta* is smooth (Fig. 84A, B) (S97).
129. *Scape apex:* (0) tapering towards the end (*Cyclosa conica*, Fig. 133C); (1) with a pocket (*Mangora gibberosa*, Fig. 134B) (S97).
130. *Copulatory opening shape:* (0) resembling pits (*Deliochus* sp., Fig. 125G); (1) longitudinal grooves (*Meta menardi*, Fig. 58A, B); (2) transverse grooves (*Epeirotypus brevipes*, Fig. 133G).

131. *Copulatory opening orientation:* (0) ventral (*Nanometa* sp., Fig. 89A); (1) posterior (*Metellina segmentata*, Fig. 68D); (2) anterior (*Metepeira labyrinthica*, Fig. 134C). This character compares the copulatory opening position in relation to the body's longitudinal plane (C90, A04, K08, DIP).

132. *Copulatory opening plugs:* (0) never plugged (*Mesida argentiopunctata*, Fig. 53A, B); (1) often plugged with broken embolus (*Argiope argentata*, Fig. 133B); (2) plugged with embolus and conductor (*Herennia multipuncta*, Fig. 133F); (3) plugged amorphous material (*Nanometinae* sp., Fig. 74A). The origin of the plugs can be from secretions produced by one or both sexes (Knoflach, 2004; Uhl, Nessler & Schneider, 2010). This character was modified from Kuntner (2005),



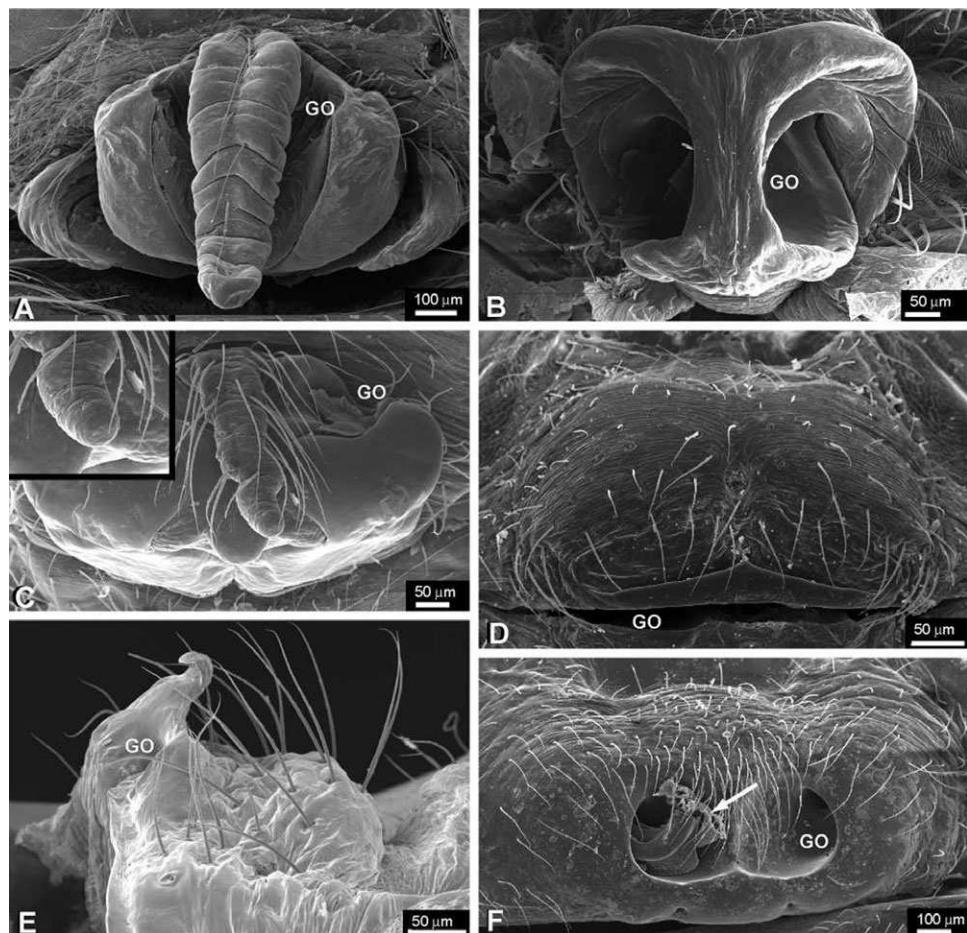
**Figure 132.** Female tarsi and femora IV of outgroup taxa: A, *Parasteatoda tepidariorum* (Theridiidae) tarsus IV ectal view; insert, close up of serrated setae (SEMFAP017). B, *Araneus marmoreus* (Araneidae) tarsus IV ectal view; insert, close up of sustentaculum (SEMFAP009). C, *Cyclosa conica* (Araneidae) tarsus IV ectal view; insert, close up of sustentaculum. D, female femur IV mesal view (SEMFAP008). E, *Larinioides cornutus* (Araneidae) tarsus IV ectal view; insert, close up of sustentaculum (SEMFAP004). F, *Nephilengys malabarensis* (Nephilidae) tarsus IV ectal view; insert, close up of sustentaculum (SEMFAP027).

2006) by adding more character states; nephilids usually have plugs made of parts of the male bulb (Fig. 133F) (K08, A04, DIP).

- 133. *Uterus externus modified with an enlarged chamber:* (0) absent (*Diphya spinifera*, Fig. 28C); (1) present (*Cyrtognatha espaniola*, Fig. 24D). This membranous chamber is located between the spermathecae, when present, and could be a transformation of the uterus externus walls into a sac. This membranous sac is unique to tetragnathines (Dimitrov *et al.*, 2007), and thus it is synapomorphic for this subfamily (DIP).
- 134. *Posterior sac:* (0) absent (*Glenognatha foxi*, Fig. 38C, D); (1) present (*Cyrtognatha espaniola*, Fig. 24D). Some tetragnathines have in addition to the spermathecae a posterior sac (e.g. *Tetrag*

*natha versicolor*, Fig. 111C, D). This membranous sac has been homologized to an enlargement of the uterus externus (Dimitrov *et al.*, 2007) (DIP).

- 135. *Epigynal plate:* (0) apart from the spermathecae (*Metellina segmentata*, Fig. 68C); (1) enclosing the spermathecae (*Larinioides cornutus*, Fig. 136D). The epigynum is a sclerotized plate where the spermathecae and copulatory ducts connect (see character 123). The epigynal plate of most araneoids is flat and the ventral surface of the spermathecae is surrounded by accessory glands and the uterus externus. In some araneids the epigynal plate folds, surrounding the spermathecae (e.g. *Neoscona domiciliorum*, Fig. 135A). In these



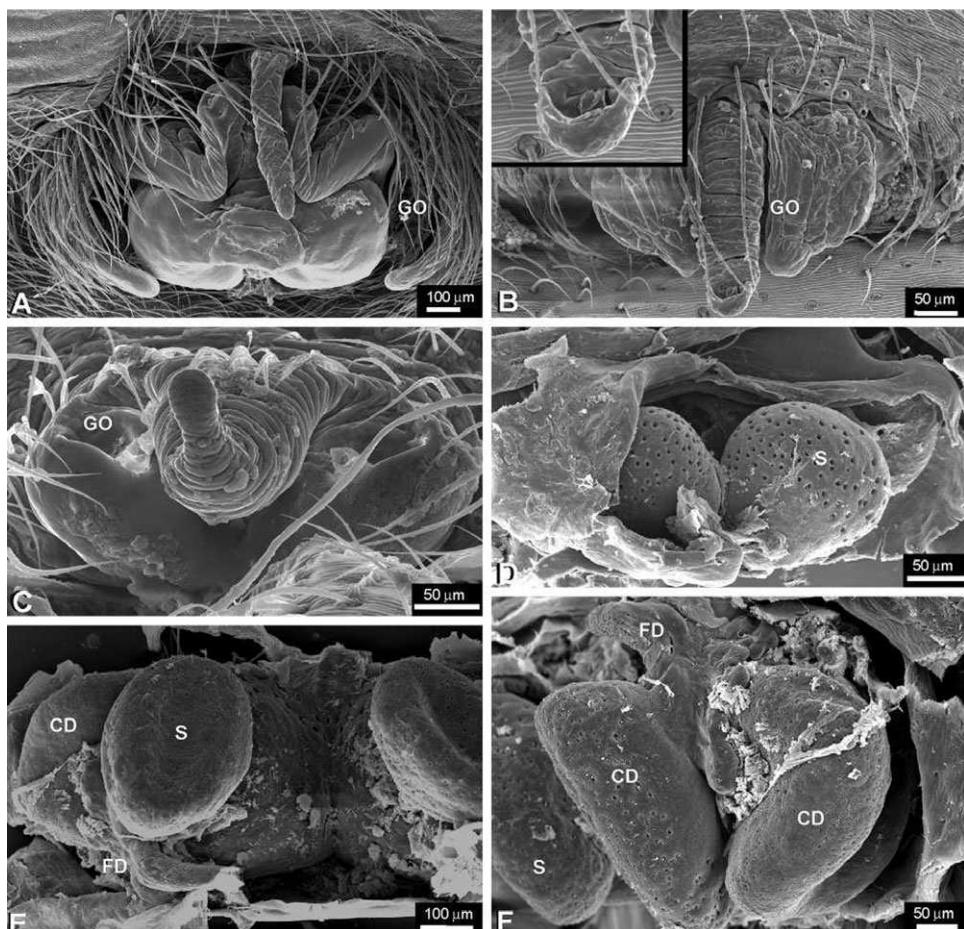
**Figure 133.** Epigyna of outgroup taxa: A, *Araneus marmoreus* (Araneidae) ventral view (SEMFAP009). B, *Argiope argentata* (Araneidae) ventral view (SEMFAP010). C, *Cyclosa conica* ventral view; insert, close up of apical end of scape (SEMFAP008). D, *Epeirotypus brevipes* (Theridiosomatidae) ventral view (SEMFAP020). E, *Gasteracantha cancriformis* (Araneidae) lateral view (SEMFAP012). F, *Herennia multipunctata* (Nephilidae) ventral view, arrow indicates broken embolus obstructing the female genital opening (SEMFAP004).

taxa, parts of the curved plate had to be removed to observe the copulatory ducts and spermatheca junction (e.g. *Cyclosa conica*, Fig. 134D).

136. *Epigynal sclerotized arch:* (0) absent (*Deliochus* sp., Fig. 125H); (1) present (*Nephilengys malabarensis*, Fig. 135B). The presence of this sclerotized arch has been found to be synapomorphic for *Nephilengys* and *Herennia*. This arch is a sclerotized ridge that runs parallel to the interior and anterior spermathecal edges and can be seen on a dorsal view of the epigynum (K08, DIP).
137. *Spermathecae sclerotization:* (0) sclerotized (*Meta menardi*, Fig. 60C); (1) not sclerotized, membranous (*Metleucauge eldorado*, Fig. 81D). The spermathecae cuticle can be either hard or soft (resembling a membranous sac) as a result

of different degrees of sclerotization of its walls (T01, A07, DIP).

138. *Spermathecae separation:* (0) separated more than two spermatheca diameters apart (*Metellina segmentata*, Fig. 68C); (1) under two diameters apart (*Neoscona domiciliorum*, Fig. 135A) (K08, DIP).
139. *Spermathecal chambers:* (0) each spermatheca consisting of a single chamber (*Nephilengys malabarensis*, Fig. 136F); (1) two chambers (*Deliochus* sp., Fig. 125H). Although there is always a continuous space inside the spermathecae, in some species the spermathecae have constrictions and loops that create more chambers (A04, K08, DIP).
140. *Accessory gland distribution:* (0) isolated (*Mesida argentiopunctata*, Fig. 53D); (1) grouped (*Metellina segmentata*, Fig. 68E). The spermathecae



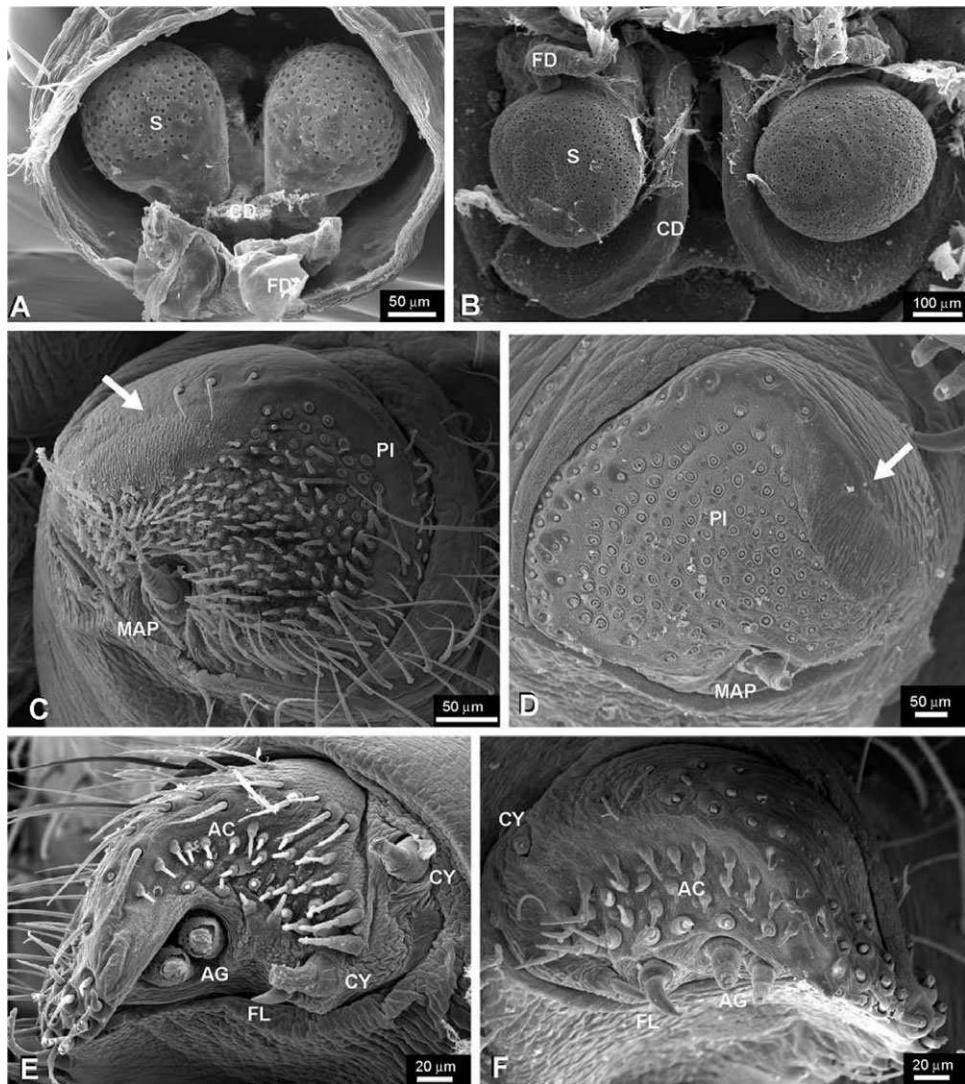
**Figure 134.** Epigyna of outgroup taxa: A, *Larinioides cornutus* (Araneidae) ventral view (SEMFAP004). B, *Mangora gibberosa* (Araneidae) ventral view; insert, close up of scape tip (SEMFAP014). C, *Metepeira labyrinthica* (Araneidae) ventral view (SEMFAP007). D, *Cyclosa conica* (Araneidae) spermathecae (SEMFAP008). E and F, *Herennia multipunctata* (Nephilidae) spermathecae (SEMFAP026).

accessory gland openings usually arise from an orifice that can bear one or more gland ducts. Isolated glands are those in which a single duct originates per pit, clustered glands are those in which more than one duct arises. The number of orifices with more than one duct usually varies within a single individual; in such cases, the more common type is taken into account. All taxa studied have accessory glands (C90).

141. *Accessory gland base diameter:* (0) less than one and a half times the duct diameter (*Mollemeta edwardsi*, Fig. 84D); (1) wider (*Glenognatha foxi*, Fig. 37B). After the glandular tissue is digested, only the gland duct remains at the base of the accessory gland opening; this character compares both diameters.
142. *Accessory gland base shape:* (0) tubular (*Metabus ocellatus*, Fig. 63F); (1) acorn-shaped (*Leucauge venusta*, Fig. 43F). The accessory gland bases are

particularly large in some leucaugines, giving the appearance of an inverted acorn. Wider, but not acorn-shaped, accessory gland bases are present in *Tetragnatha versicolor* and *Metabus ocellatus*, amongst other taxa (Figs 63F, 111F).

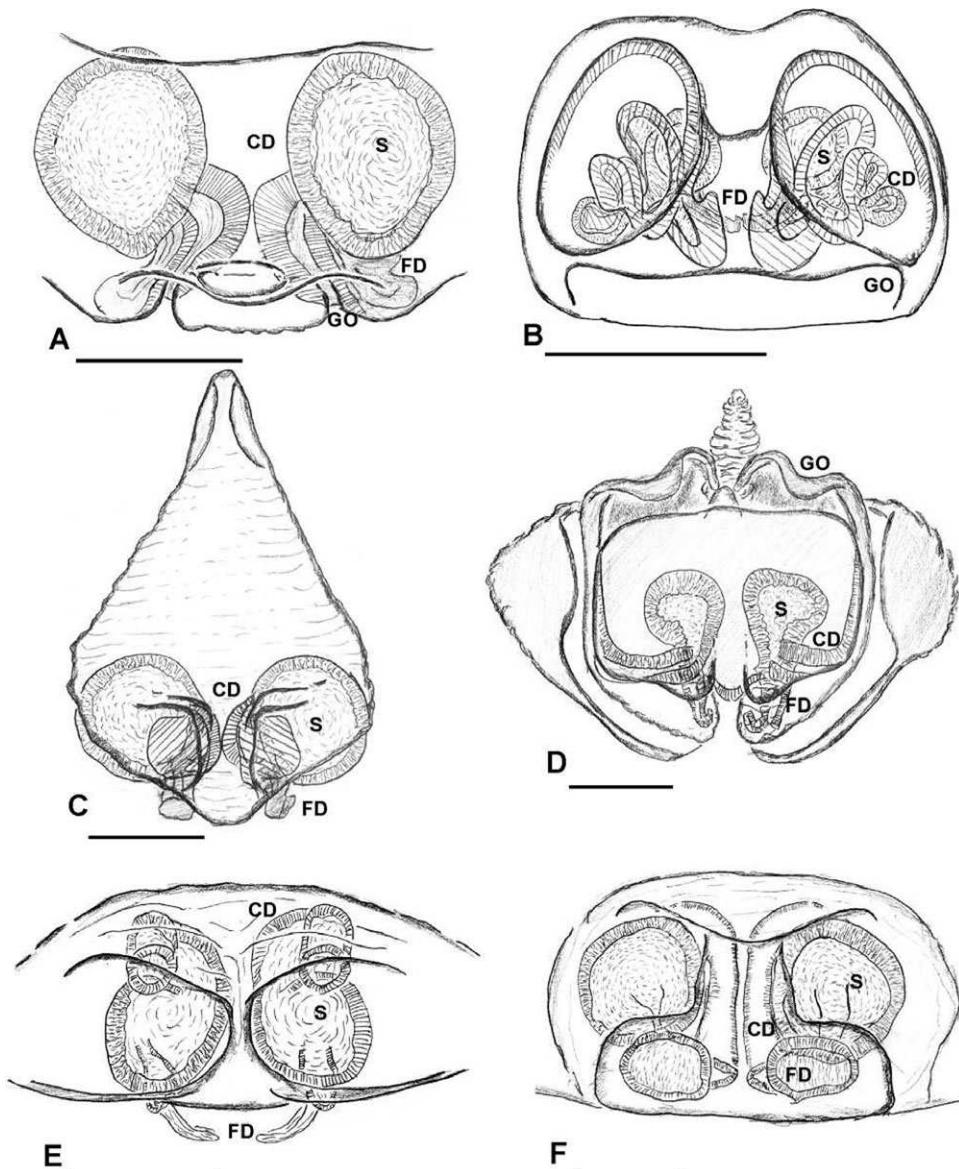
143. *Accessory gland distribution:* (0) evenly over the spermatheca (*Deliochus* sp., Fig. 125H); (1) clustered near the fertilization duct (*Nanometa* sp., Fig. 89B, C); (2) clustered near the copulatory ducts (*Glenognatha foxi*, Fig. 38B).
144. *Copulatory duct path:* (0) curved less than half the circumference (*Opadometa* sp., Fig. 95E); (1) curved more than half the circumference but less than a complete turn (*Gasteracantha cancriformis*, Fig. 136A); (2) coiled more than one turn (*Asagena americana*, Fig. 136B); (3) L-shaped (*Larinioides cornutus*, Fig. 136D). This character was coded based upon diagrams of cleared epigyna (A04, K08).



**Figure 135.** Anterior lateral spinnerets and epigyna of outgroup taxa: A, *Neoscona domiciliorum* (Araneidae) spermathecae (SEMFAP006). B, *Nephilengys malabarensis* (Nephilidae) dorsal view (SEMFAP027). C, *Phonognatha graeffei* (Araneidae) anterior lateral spinnerets (SEMFAP023). D, *Deliochus* sp. (Araneidae) anterior lateral spinnerets, arrows indicate the sclerotized plates that interrupt the piriform spigot field (SEMFAP022). E, *Phonognatha graeffei* (Araneidae) posterior lateral spinnerets (SEMFAP023). F, *Deliochus* sp. (Araneidae) posterior lateral spinnerets (SEMFAP012).

- 145. *Copulatory duct shape:* (0) cylindrical (*Dolichognatha pentagona*, Fig. 35D); (1) modified as a sac (Nanometinae sp., Fig. 74F) (A07, DIP).
- 146. *Copulatory duct length:* (0) less than half the spermathecae length (*Metellina segmentata*, Fig. 70D); (1) more than half the spermathecae length but less than its total length (*Tylorida striata*, Fig. 118D); (2) longer than the spermathecae length (*Nephilengys malabarensis*, Fig. 136F).
- 147. *Copulatory duct cuticle:* (0) well sclerotized (*Orsinome* cf. *vethi*, Figs 102C, D, 104E); (1) membranous (*Mesida argentopunctata*, Figs 53E, F,

- 55D). This character was coded with cleared epigyna. The degree of sclerotization in the cuticle varies from well sclerotized, opaque, thick, with walls that are brown when made translucent to less sclerotized with thin, clear duct walls.
- 148. *Female genitalia:* (0) entelegyne (*Metellina segmentata*, Fig. 70D); (1) haplogyne (*Glenognatha foxi*, Fig. 40B). Entelegyne female genitalia are those in which the spermathecae have two pairs of ducts, one for insemination and the other for fertilization; whereas, haplogyne spermathecae have only one pair. The fertilization duct is a



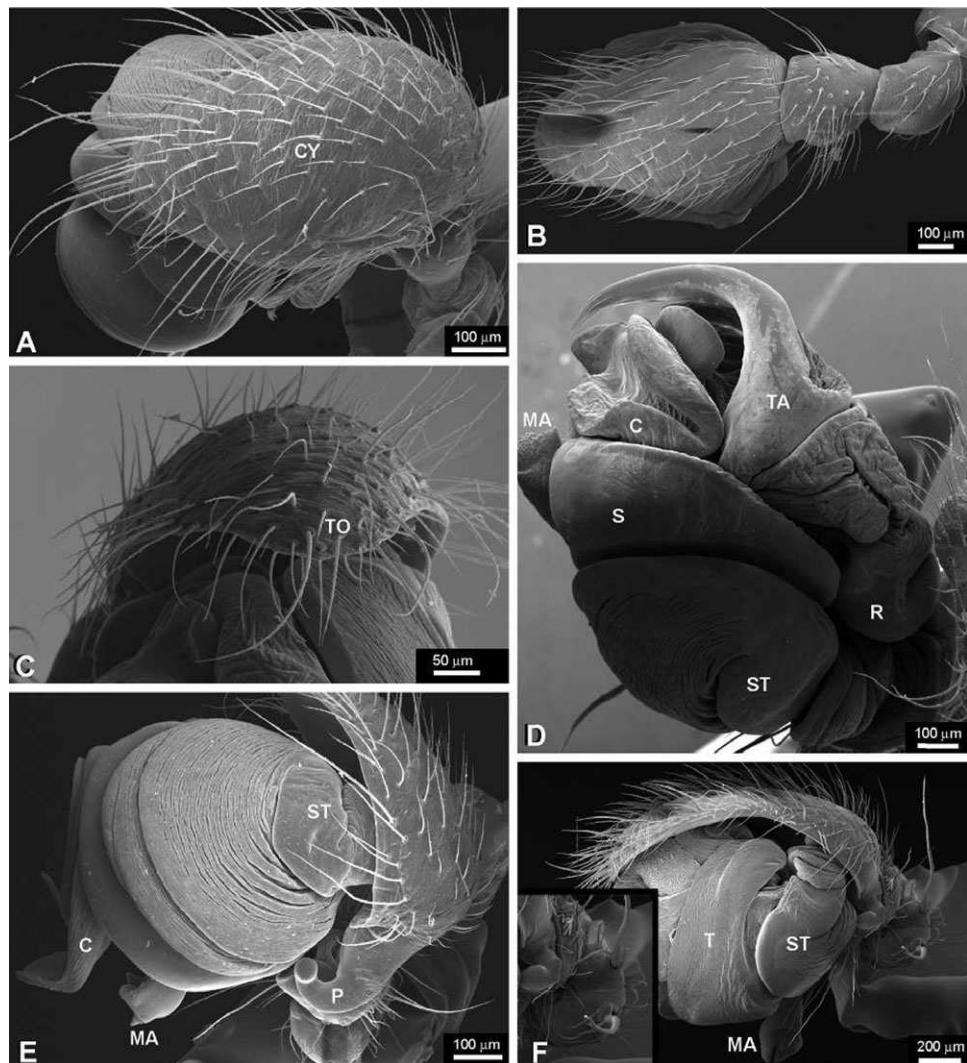
**Figure 136.** Outgroup taxa cleared epigyna illustrations: A, *Gasteracantha cancriformis* (Araneidae) ventral view. B, *Asagena americana* (Theridiidae) ventral view. C, *Micrathena gracilis* (Araneidae) ventral view. D, *Larinioides cornutus* (Araneidae) ventral view. E, *Phonognatha graeffei* (Araneidae) ventral view cleared. F, *Nephilengys malabarensis* (Nephilidae) ventral view.

sclerotized fold of the uterus externus (Sierwald, 1989; Uhl, 2002 and references therein). Tetragnathids present both types of female reproductive systems. Haployne genitalia are synapomorphic for Tetragnathinae. Furthermore, some genera have completely lost the spermathecae, e.g. all *Cyrtognatha* species (Dimitrov *et al.*, 2007; Dimitrov & Hormiga, 2009) (L80, C90, H95, S97, G98, G05, A07, DIP).

149. *Fertilization duct origin:* (0) posterior (*Mollemeta edwardsi*, Fig. 86D); (1) anterior (*Chrysometa*

*alajuela*, Fig. 22D). This character describes where the fertilization ducts join the spermathecae. Most of the araneoid studied have fertilization ducts originating on the posterior edge of the spermatheca (A07, DIP).

150. *Fertilization duct length:* (0) shorter than the spermatheca width (*Nephilengys malabarensis*, Fig. 135B); (1) longer (*Chrysometa alajuela*, Fig. 22D) (A07, DIP).
151. *Fertilization duct path:* (0) curved (*Metleuauge eldorado*, Figs 79C, 81D); (1) coiled (*Tylorida*



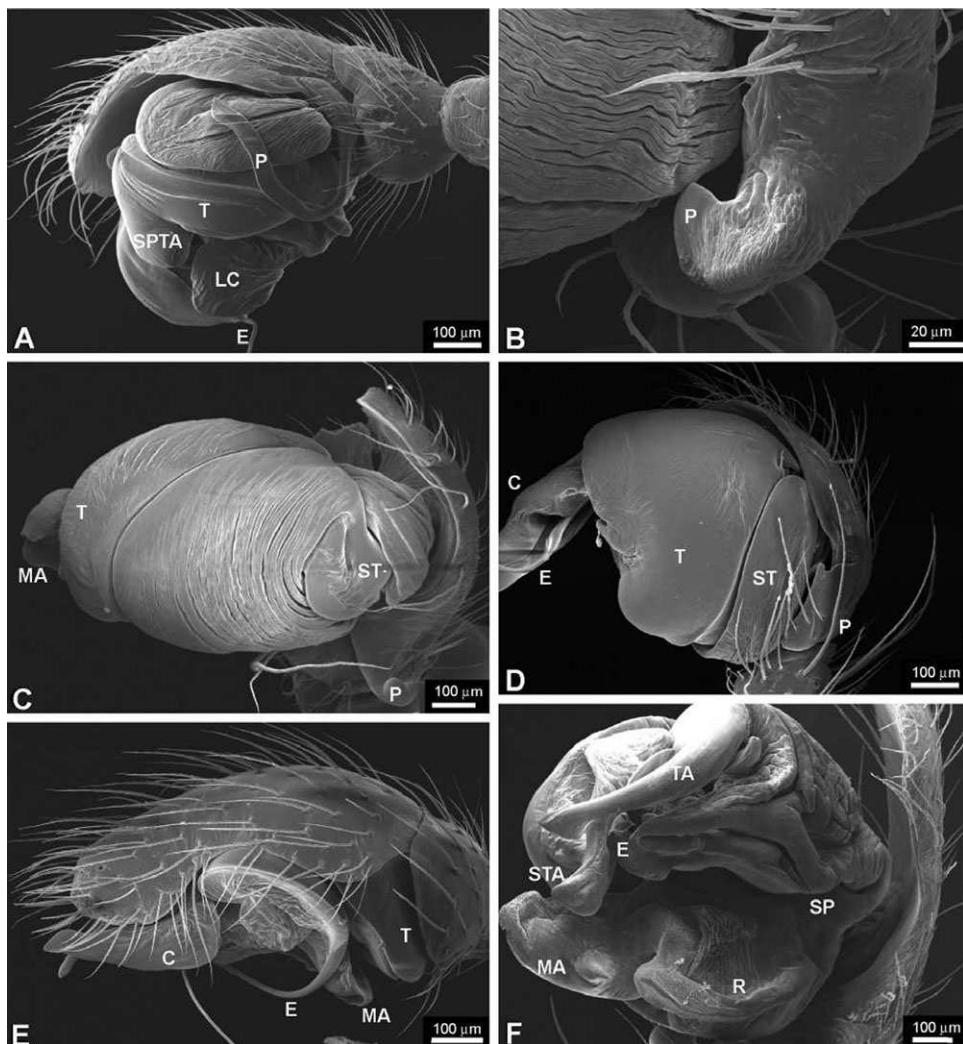
**Figure 137.** Male pedipalps of outgroup taxa: A, *Argiope argentata* dorsal view (SEMFAP073). B, *Linyphia triangularis* (Linyphiidae) dorsal view (SEMFAP015). C, *Argiope argentata* (Araneidae) apical view (SEMFAP073). D, *Araneus marmoreus* (Araneidae) apical view (SEMFAP072). E, *Argiope argentata* (Araneidae) ectal view (SEMFAP073). F, *Larinioides cornutus* (Araneidae) ectal view; insert, close up of palpal tibia (SEMFAP004).

*striata*, Figs 116F, 118D). Curved fertilization duct paths are C-shaped, coiled ducts have more than one turn.

152. *Fertilization duct and copulatory duct paths*: (0) separated (*Herennia multipuncta*, Fig. 134E, F); (1) fertilization ducts coiled around the copulatory ducts (*Opadometa* sp., Fig. 95E).
153. *Fertilization duct path and spermathecae*: (0) separated (*Herennia multipuncta*, Fig. 134F); (1) crossing over (*Meta menardi*, Figs 58D–F, 60C).
154. *Female abdominal dorsal surface*: (0) without guanine silver patches (*Meta menardi*, Fig. 1D); (1) with guanine silver patches (*Leucauge venusta*, Fig. 1C–E). The white abdominal pattern is created by clusters of guanine, a meta-

bolic by-product that can be either excreted or diverted towards storage (Collatz, 1987; Seitz, 1987). These guanine patches can be either white and opaque or silver and reflective. Silver guanine crystals may help to prevent overheating by reflecting light (Oxford & Gillespie, 1998 and references therein).

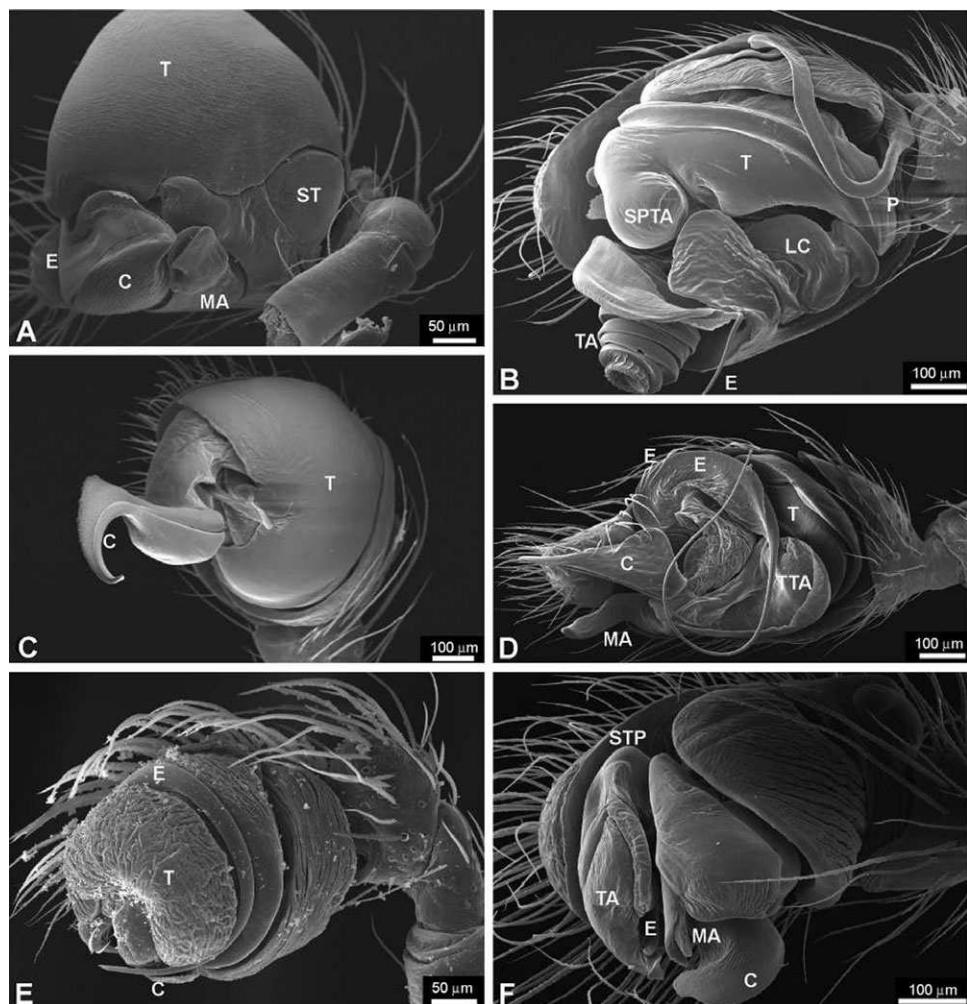
155. *Female abdominal ‘spines’*: (0) absent (*Phonognatha graeffei*, Fig. 2D); (1) present (*Micrathena gracilis*, Fig. 2E). The surface of the abdomen of *Gasteracantha* and *Micrathena* is characteristically decorated with sharp, thorn-like cuticular apophyses or ‘spines’ (S97, A07, DIP).
156. *Female abdominal cuticle microsculpture*: (0) made of flaps (*Diphya spinifera*, Fig. 26C); (1)



**Figure 138.** Male pedipalps of outgroup taxa: A, *Linyphia* (Linyphiidae) ectal view (SEMFAP015). B, *Micrathena gracilis* (Araneidae) paracymbium (SEMFAP013). C, *Neoscona domiciliorum* (Araneidae) ectal view (SEMFAP006). D, *Nephilengys malabarensis* (Nephilidae) ectal view (SEMFAP074). E, *Asagena americana* (Theridiidae) ectal view (SEMFAP071). F, *Araneus marmoreus* (Araneidae) mesal view (SEMFAP72).

made of cylinders (*Pachygnatha autumnalis*, Fig. 105A). The abdominal cuticle pattern is made of either a ‘fingerprint’ pattern or small cuticular cylinders (c. 1 µm). The cuticle of many araneoids, although very variable (e.g. compare *Diphya* with *Tetragnatha*, Figs 26C, 109A) is made of cuticular flaps. The cuticle of *Mangora gibberosa* and *Neoscona domiciliorum* is composed of small cylinders (Figs 123E, 141B), but considerably more spread out than in *Pachygnatha autumnalis* and *Glenognatha foxi* (Fig. 36A, B). The cuticle microsculpture flaps of *Micrathena gracilis* are swollen, and although this condition is highly modified it was coded as state 0 (Fig. 123F).

157. *Female anterior abdominal tubercles:* (0) absent (*Meta menardi*, Fig. 1D); (1) present (*Dolichognatha pentagona*, Fig. 35D) (K08, DIP).
158. *Female booklung surface:* (0) flat (*Leucauge venusta*, Fig. 41A); (1) grooved (*Argiope argenteata*, Fig. 123B); (2) covered with transverse lines (*Micrathena gracilis*, Fig. 123C). The booklung grooves were coded using both SEM images and observing the specimens in alcohol because both techniques complement each other well. The SEM images of *Nephilengys malabarensis* may suggest that this species lacks grooves (Fig. 23A), whereas these grooves are easily observed in alcohol-preserved specimens (Kuntner, 2006), appearing as more sclerotized than the surround-



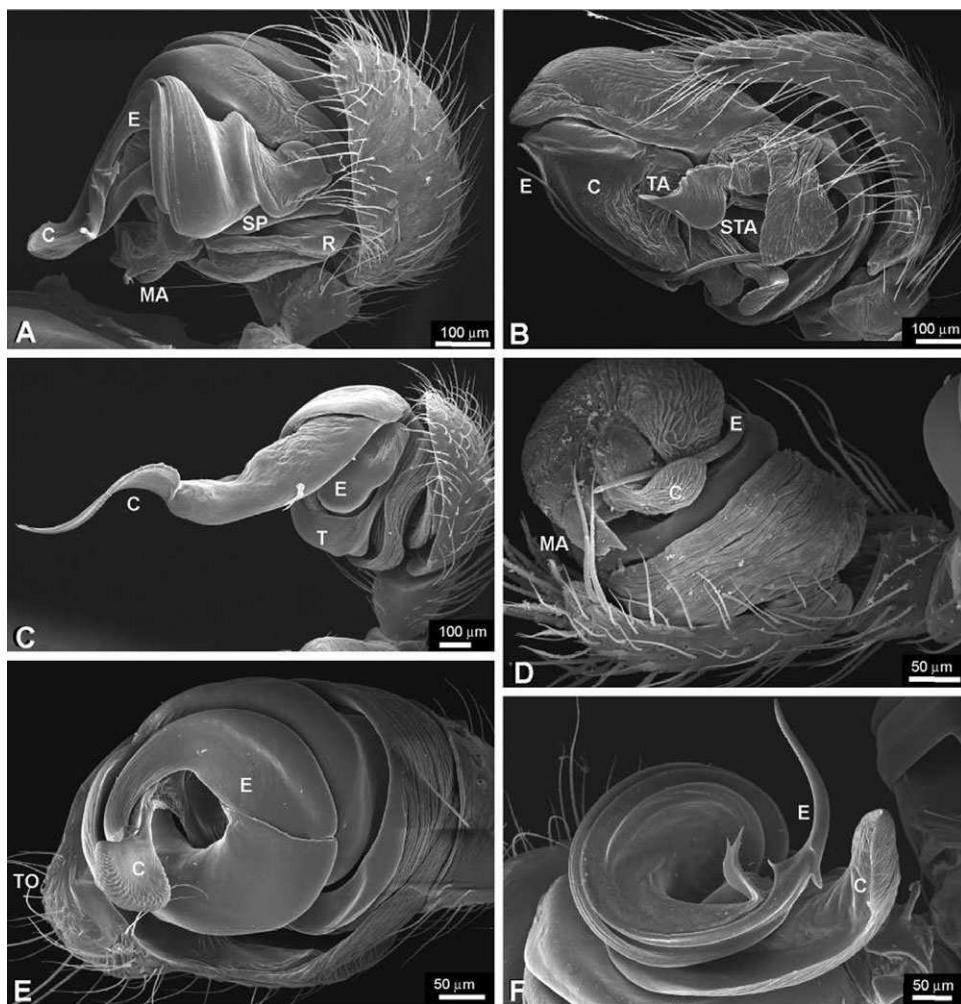
**Figure 139.** Male pedipalps of outgroup taxa: A, *Epeirotypus brevipes* (Theridiosomatidae) ventral view (SEMFAP020). B, *Linyphia triangularis* (Linyphiidae) ventral view (SEMFAP015). C, *Nephilengys malabarensis* (Nephilidae) ventral view (SEMFAP074). D, *Asagena borealis* ventral view (SEMFAP067). E, *Uloborus glomosus* (Uloboridae) ventral view (SEMFAP065). F, *Zygilla x-notata* (Araneidae) ventral view (SEMFAP069).

ing cuticle. *Micrathena gracilis* females have booklungs that are covered with parallel lines that resemble a stridulatory organ that could be a transformation from these grooves (Levi, 1985). (H95, S97, G98, T01, K08, A07, DIP).

159. *Female abdominal tip colour:* (0) as the subapical part (*Mollemeta edwardsi*); (1) with paired white dots around spinnerets (*Metellina segmentata*); (2) lighter than the subapical part (*Oncodamus decipiens*). This character is from Kuntner (2006), but state 2 was added to accommodate the variation exhibited in our taxonomic sample (K08).
160. *Female light pigmented pattern form on abdominal venter:* (0) one central white area (*Leucauge venusta*); (1) transverse lines (*Argiope argentata*); (2) four large spots (*Nephilengys malabarensis*);

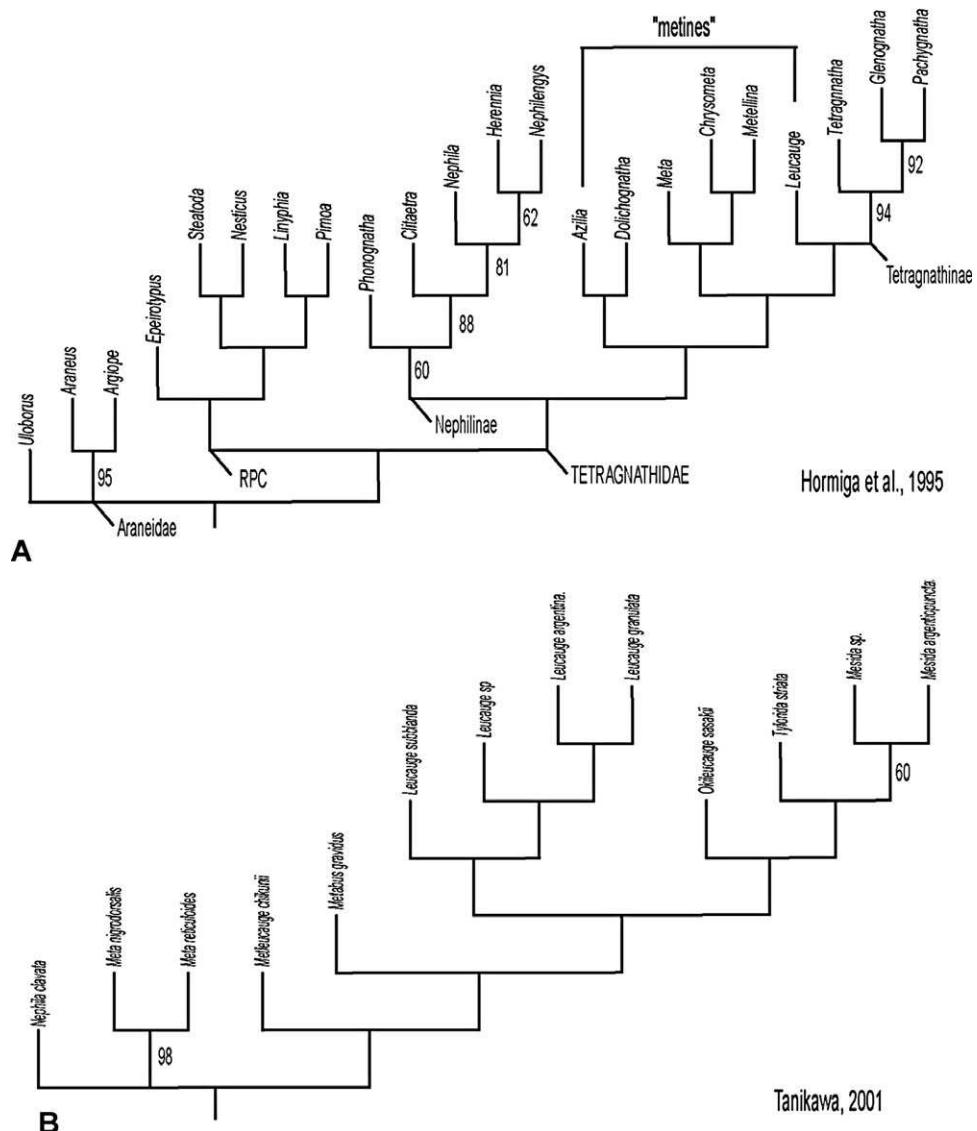
(3) numerous spots (*Nephila clavipes*); (4) longitudinal line (*Clitaetra episinoides*); (5) same pattern as lateral sides (*Mangora gibberosa*). The ventral pattern of the abdomen can be decorated with patches of various shapes (Kuntner, 2005, 2006) (K08).

161. *Median tracheal morphology:* (0) cylindrical (*Neoscona domiciliorum*, Fig. 125A); (1) tracheal trunk divided into broad tracheoles (*Nanometa* sp., Fig. 87B); (2) tracheal trunk divided in several small tracheoles (*Glenognatha foxi*, Fig. 36C, D). Although in most araneoids the median tracheal trunks are cylindrical and undivided (and restricted to the abdomen), in some groups the median tracheae are divided into tracheoles (e.g. in some linyphiids, see Lamy, 1902) (G05).



**Figure 140.** Male pedipalps of outgroup taxa: A, *Argiope argentata* (Araneidae) mesal view (SEMFAP073). B, *Cyclosa conica* (Araneidae) mesal view (SEMFAP070). C, *Nephilengys malabarensis* (Nephilidae) mesal view (SEMFAP74). D, *Uloborus glomosus* (Uloboridae) mesal view (SEMFAP065). E, *Parasteatoda tepidariorum* (Theridiidae) ventral view (SEMFAP071). F, *Argiope argentata* (Araneidae) conductor and embolus (SEMFAP073).

- 162. Apical end of median tracheal trunks: (0) leaf-shaped (*Nephilengys malabarensis*, Fig. 124E, F); (1) round (*Leucauge venusta*, Fig. 41C, D); (2) bifurcated (*Metepeira labyrinthica*, Fig. 125B).
- 163. Median trachea length: (0) shorter than half the lateral tracheae length (*Dolichognatha pentagona*, Fig. 31A); (1) longer (*Tylorida striata*, Fig. 114C). As we excised and dissected the abdomen for enzymatic digestion to study the tracheal morphology, we could not always determine whether or not these tracheae extended into the cephalothorax.
- 164. Tracheal atrium gland: (0) absent (*Mangora gibberosa*, Fig. 125D); (1) present (*Gasteracantha cancriformis*, Fig. 125C). The internal surface of the tracheal atrium can be either smooth or covered with slender cylindrical glands.
- 165. Tracheal gland abundance: (0) fewer than four on each side (*Mesida argentiopunctata*, Fig. 51C); (1) more than four (*Nanometinae* sp., Fig. 71D).
- 166. Male abdominal scutum: (0) absent (*Leucauge venusta*, Fig. 1E); (1) present (*Nephila clavipes*, Kuntner, 2006: fig. 8a). The abdominal scutum is defined as a sclerotized plate that covers the abdomen. In some nephilids the scutum is located on the dorsal surface of the abdomen. This character is synapomorphic for *Nephila*, *Herennia*, and *Nephilengys*. Other araneoids may also have an abdominal scutum such as the species of the araneid genus *Hypognatha* Guérin, 1839 (Levi, 1996) as well as some theridiids, malkarids, and linyphiids, amongst others. (H95, G98, K08, A07, DIP).

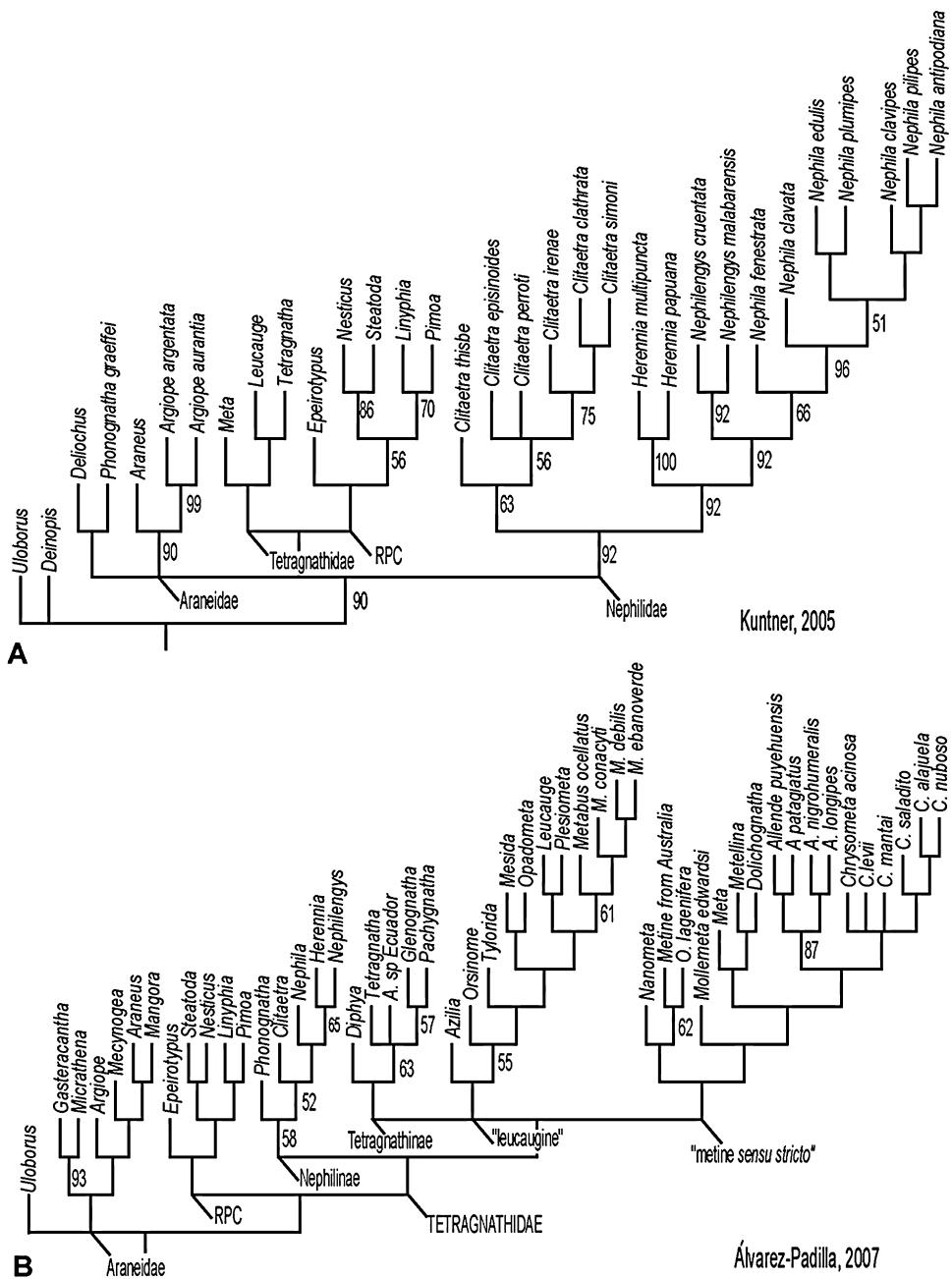


**Figure 141.** Cladograms from previous studies on tetragnathid phylogeny: A, Hormiga *et al.* (1995) most parsimonious cladogram [130 steps, consistency index (CI) = 56, retention index (RI) = 72] based on morphological and behavioural data. B, Tanikawa (2001) most parsimonious cladogram (39 steps, CI = 61, RI = 71) based on morphological data. Jackknife support values above 51% are given under their corresponding nodes.

167. *Male abdominal cuticle microsculpture:* (0) made of flaps (*Neoscona domiciliorum*, Fig. 124A); (1) made of cylinders (*Pachygnatha autumnalis*, Fig. 105F). Male abdominal cuticle made of cylinders is synapomorphic for *Glenognatha* and *Pachygnatha*; cuticle made of flaps was found in all other taxa studied (see character 156 definition). The males of *Mangora gibberosa* and *Neoscona domiciliorum* lack these cuticular cylinders (Fig. 123D).
168. *Male booklung stridulatory groove:* (0) absent (*Metellina segmentata*, Fig. 66A); (1) present (*Nanometa* sp., Fig. 87A). The anterior edge of

the booklung cuticle can be either smooth or modified with a stridulatory organ. In our analysis this stridulatory organ is synapomorphic of Nanometinae (Forster & Forster, 1999; but see Dimitrov & Hormiga, 2011). Forster & Forster suggest that these grooves could be a stridulatory organ because they correspond topologically with a line of denticles on the fourth coxae.

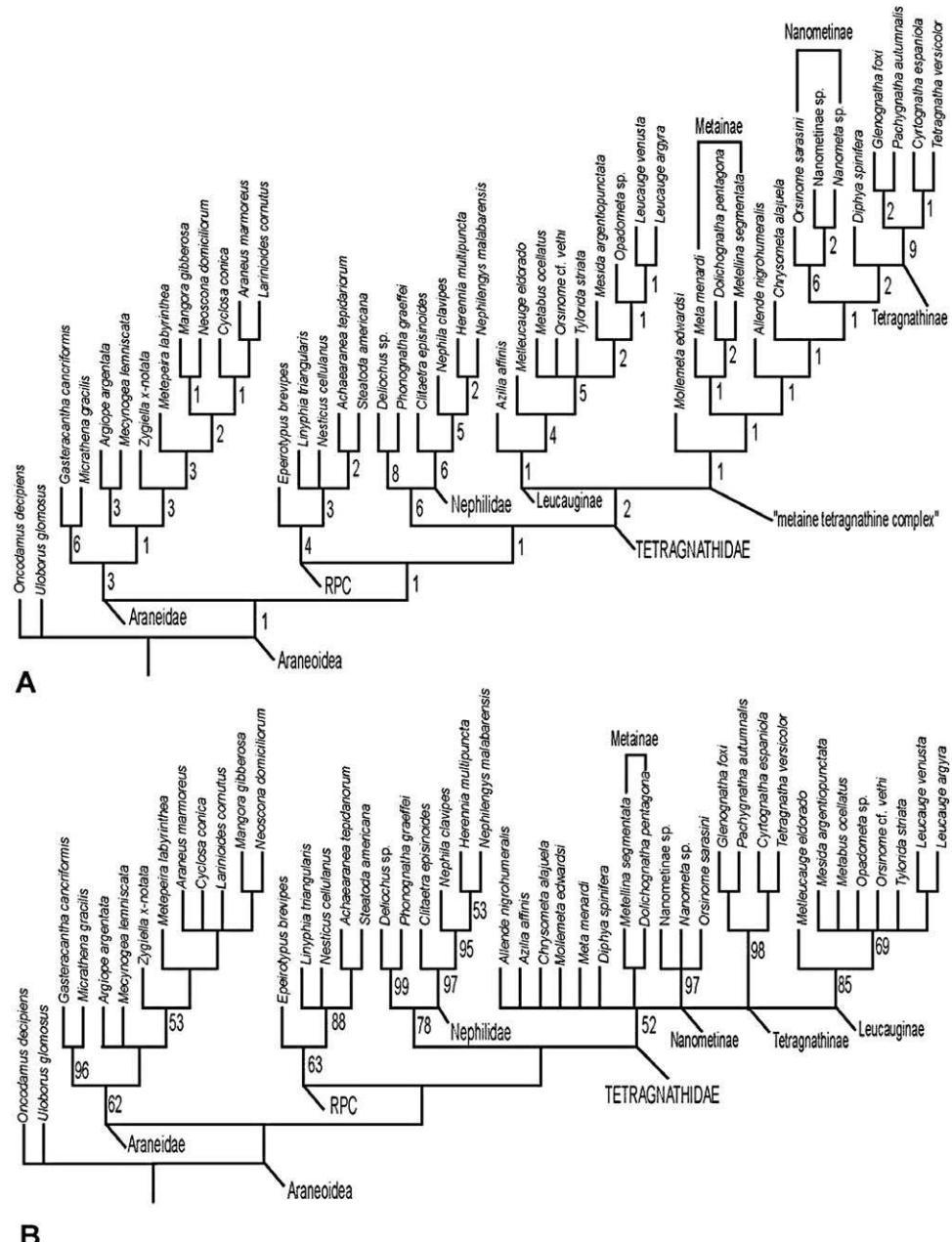
169. *Femur IV trichobothria:* (0) absent (*Metellina segmentata*, Fig. 67H); (1) present (*Leucauge venusta*, Fig. 42E, F). The basal surface of the fourth femora may bear trichobothria. These trichobo-



**Figure 142.** Cladograms from previous studies on tetragnathid phylogeny: A, Kuntner (2005) strict consensus of eight most parsimonious cladograms [531 steps, consistency index (CI) = 42, retention index (RI) = 70]. B, Álvarez-Padilla (2007) strict consensus of ten most parsimonious cladograms (322 steps, CI = 45, RI = 75). Both studies were based on morphological and behavioural data. Jackknife support values above 51% are given under their corresponding nodes.

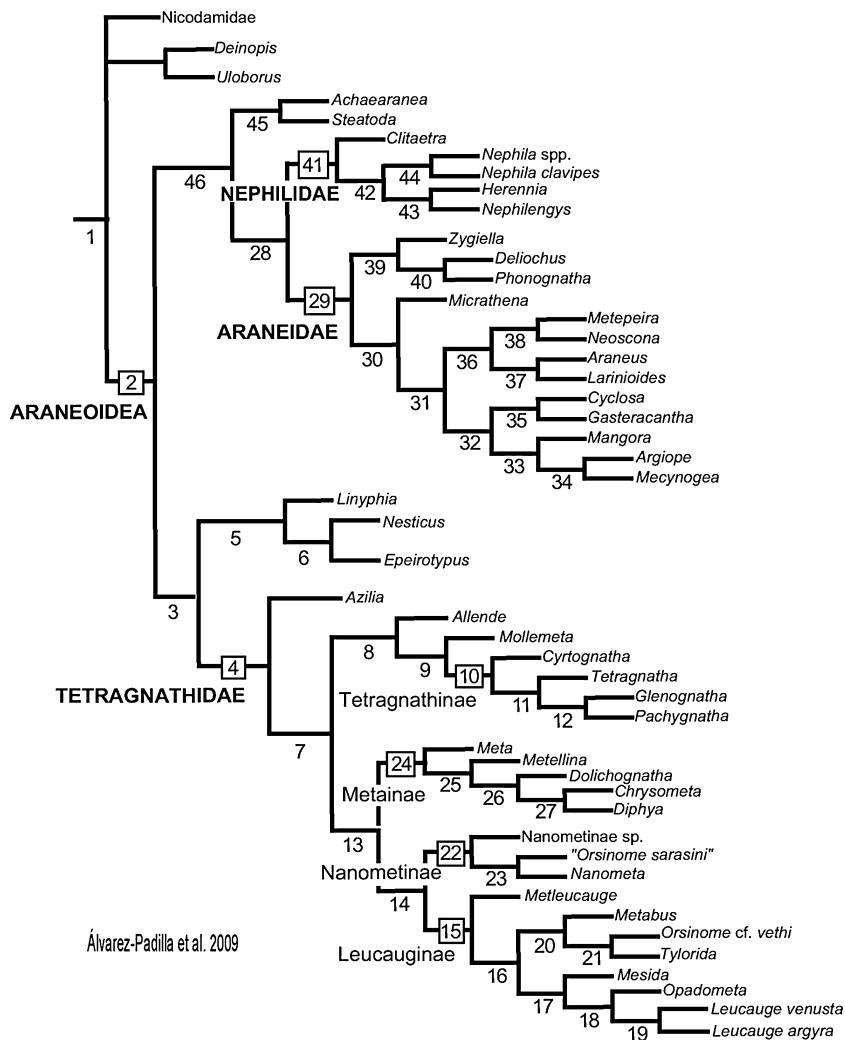
thria are common within tetragnathids and rare in other araneoids. Coddington (1990a) coded *Uloborus glomosus* as having femoral trichobothria (without specifying which femora); we did not find trichobothria on the fourth femora of this species (L80, H95, S97, G98, T01, A07, DIP).

170. Femoral trichobothria position: (0) dorsal (*Tylorida striata*, Fig. 115F); (1) ectal (*Mesida argentiopunctata*, Fig. 52G) (A07, DIP).
171. Femur IV trichobothria organization: (0) one irregular line (*Tetragnatha versicolor*, Fig. 110E);



**Figure 143.** Strict consensus trees of parsimony analyses of the morphological and behavioural data set presented in Appendix 2: A, strict consensus cladogram of the five cladograms of minimal length obtained under equal weights of 1033 steps (consistency index = 26, retention index = 58); the consensus tree is ten steps longer. Bremer support values are given under the nodes. B, strict consensus of 11 optimal cladograms obtained with implied weights at concavities 1 to 100; the consensus tree is 101 steps longer than the equal weighted optimal cladograms. Symmetric resampling support values above 51% are given under each node. See text for additional details.

- (1) two parallel rows (*Opadometa* sp., Fig. 93E) (A07, DIP).
- 172. *Femur IV trichobothria distribution*: (0) less than one third of femur (*Tylorida striata*, Fig. 115F); (1) more than one third of femur (*Opadometa* sp., Fig. 93F) (A07, DIP).
- 173. *Trichobothrium shaft morphology*: (0) smooth (*Tetragnatha versicolor*, Fig. 110E); (1) branched (*Leucauge venusta*, Fig. 42F) (A07, DIP).
- 174. *Female femur IV mesal surface*: (0) with setae (*Cyclosa conica*, Fig. 132D); (1) without setae (*Azilia affinis*, Fig. 14H). In most araneoids the



**Figure 144.** Preferred optimal cladogram from the study of Álvarez-Padilla *et al.* (2009). This tree is based on a combined analysis, using direct optimization methods, of multigene DNA sequences and the morphological and behavioural data set presented in Appendix 2. The single most parsimonious tree was 54 536 steps when all the data were analysed simultaneously. Numbers under each node correspond to the node numbers in Table 1 where all support values are plotted and the synapomorphies mapped.

mesal and ectal basal surfaces of the femur IV have similar setae densities; whereas, in most tetragnathids the mesal surface of the femur IV at its base has a wide area without setae.

- 175. *Female IV tibia:* (0) without bristles (*Meta menardi*, Fig. 1D); (1) with bristles (*Nephila clavipes*; Levi, 1980: fig. 31). These bristles are made of modified setae that cover the basal part of the tibia in *Nephila clavipes* and *Opadometa* sp. (K08, A07, DIP).
- 176. *Sustentaculum:* (0) absent (*Pachygnatha autumnalis*, Fig. 106G); (1) present (*Araneus marmoreus*, Fig. 132B). The sustentaculum is a modified macroseta on the ventral tip of tarsus IV ventral tip, between the serrated bristles. Rei-

moser (1917) was the first to notice this modified macroseta (Griswold *et al.*, 1998 and references therein). In addition to the sustentaculum some araneids have a line of similar macrosetae on the ventral surface of the tarsus and metatarsus IV. The sustentaculum can be distinguished from other setae because its cuticle is sculpted and can have some small indentations (Fig. 132C). The sustentaculum differs from the serrated bristles in being less pigmented and in lacking the ventral line of teeth characteristic of these bristles (Foelix, 1970). Taxa without sustentaculum only have serrated bristles and thin, smooth setae. All tetragnathids studied lack a sustentaculum (H95, S97, G98, K08, A07, DIP).

177. *Sustentaculum tip*: (0) straight (*Nephilengys malabarensis*, Fig. 132F); (1) bent (*Cyclosa conica*, Fig. 132C).
178. *Tarsus IV theridioid comb*: (0) absent (*Larinoides cornutus*, Fig. 132E); (1) present (*Parasteatoda tepidariorum*, Fig. 132A). The theridioid comb is formed by a ventral line of curved serrated macrosetae located on the distal end of the fourth tarsus. These macrosetae help handling the sticky silk drops while wrapping the prey (Nielsen, 1932; Kirchner & Kullmann, 1972; Griswold *et al.*, 1998: fig. 6); this comb does not interact with the silk during web building (Benjamin & Zschokke, 2004). Spiders lacking this comb only have regular setae or a line of macrosetae beneath tarsus IV. This comb is reduced in some theridioid males and is also present in *Synotaxus* (Synotaxidae) (Agnarsson, 2004 and references therein) (C90, H95, G98, A04, A07, DIP).
179. *Male tibia II macrosetae*: (0) as in tibia I (*Cyclosa conica*, Levi, 1977: fig. 12); (1) thicker (*Neoscona domiciliorum*, Berman & Levi, 1971: fig. 127) (S97).
180. *Male palpal patella macrosetae*: (0) none (*Dolichognatha pentagona*, Fig. 32E); (1) one (*Diphya spinifera*, Fig. 29F); (2) two (*Larinoides cornutus*, Fig. 129F). The male patella usually bears a small seta on its surface; palpal patellar macrosetae are located near the distal edge when present, are at least twice as thick as the surrounding setae and their cuticle is sculpted (H95, S97, T01, A07, DIP).
181. *Male palpal tibia length*: (0) approximately as long as the widest point of the tibia (*Linyphia triangularis*, Fig. 137B); (1) approximately twice the maximum width of the tibia (*Metellina segmentata*, Fig. 69C); (2) approximately three times the maximum width of the tibia or more (*Metleucauge eldorado*, Fig. 78F). This character codes the ratio of the tibia length to its maximum width.
182. *Male palpal femur length*: (0) under four times its width (*Zygiella x-notata*, Fig. 129D); (1) longer (*Metleucauge eldorado*, Fig. 78F). This character codes the length of the femur relative to its maximum width. Most tetragnathids have long femora.
183. *Male palpal trochanter length*: (0) less than twice its width (*Epeirotypus brevipes*, Fig. 128C); (1) more (*Tetragnatha versicolor*, Fig. 110F). This character codes the length of the trochanter relative to its maximum width. (K08, DIP).
184. *Male coxa I hook*: (0) absent (*Argiope argentata*, Fig. 129B); (1) present, *Araneus marmoreus*,
- Fig. 129A). See also Scharff & Coddington (1997: figs 26, 27, 98) (S97).
185. *Male coxa IV*: (0) smooth (*Diphya spinifera*, Fig. 27F); (1) with denticles (*Nanometa* sp., Fig. 88F). In the males of *Nanometa* and its relatives the mesal surface of the coxa IV is covered with rows of denticles. It has been suggested that these teeth interact with striae found in the booklung covers to form a stridulatory organ (Forster & Forster, 1999: 166, see also character 168) (A07, DIP).
186. *Capture web*: (0) absent (*Pachygnatha autumnalis*); (1) present (*Dolichognatha pentagona*, Fig. 3E). Spiders either directly hunt their prey or build webs to catch them. Orb webs are characteristic for Orbiculariae; however, capture webs have been lost several times independently during the diversification of orbicularians. For example, adult females of *Pachygnatha* do not build webs to capture prey (Levi, 1980).
187. *Web architecture*: (0) orbicular (*Mesida argentiopunctata*, Fig. 3A); (1) as a sheet (*Linyphia* sp., Fig. 6D); (2) gum foot (*Parasteatoda* sp., Fig. 5F). Orbicular webs are composed of a radial frame from which is suspended a spiral of sticky silk; although some araneids such as cyrtophorines make orb webs without a sticky silk spiral (e.g. Kullmann, 1958; Levi, 1980). Orb webs are plesiomorphic for Araneoidea and are also found in Deinopoidea (Coddington, 1986b). The highest diversity of web architectures is found within the reduced piriform clade (Figs 5F, 6A–C, 7B). Araneoids with web architecture similar to that of Tetragnathidae are found mostly in Araneidae (Fig. 7C, D). Somewhat similar ‘orbicular’ webs also exist outside of Araneoidea, such as the ‘pseudo-orb’ of the psechrnid *Fecenia* sp. (Fig. 6C), but these webs are clearly convergent and quite different in their details and the building behaviours (Robinson & Lubin, 1979; Levi, 1982). The modification of the ancestral orb web into sheet webs or gum foot webs has been proposed as synapomorphic for a clade that included the linyphioids, theridioids, synotaxids, and cyatholipids (Griswold *et al.*, 1998). Subsequent analyses have not been able to corroborate the monophyly of the ‘araneoid sheet web weavers’ (Blackledge, Coddington & Gillespie, 2003; Lopardo & Hormiga, 2008; Arnedo *et al.*, 2009; Álvarez-Padilla *et al.*, 2009) (C90, H95, S97, G98, A04, K08, A07, DIP).
188. *Web frame*: (0) two dimensional (*Nanometa* sp., Fig. 4F); (1) three dimensional (*Linyphia* sp., Fig. 6D). Webs have most of their main struc-

- tural threads in an *x* and *y* plane; structural threads of three-dimensional webs extend to the *z* plane. Three-dimensional webs are optimized as synapomorphic for the ‘reduced piriform clade’ with four homoplasious occurrences, two in araneids and two in nephilids.
189. *Web posture*: (0) legs I and II extended (*Cyrtognatha* sp., Fig. 2A); (1) flexed (*Herennia multipuncta*, Fig. 2C). This character refers to the position of the legs when the spider is at the centre of the web or resting inside its retreat. Extended legs I and II has also been referred to as the ‘metine resting posture’ (L80, C90, H95, S97, G98, K08, A07, DIP).
190. *Stabilimentum*: (0) absent (*Ocrepeira* sp., Fig. 7C); (1) present, *Argiope versicolor* (Seah & Li, 2002; Fig. 1). The stabilimentum consists of silk decorations on the web of some araneoids. The function of web decorations remains unresolved. At least seven different functional explanations have been proposed, but only a few functions have been tested. The foraging function has been the most tested hypothesis (e.g. Eberhard, 1990b and Herberstein *et al.*, 2000 and references therein). It has been noticed that stabilimenta reflect UV light – studies tested the function of the stabilimenta as either an attraction to insects (Craig & Bernard, 1990; Blackledge and Wenzel, 2000 and references therein) or protection from wasps and other predators such as birds (Blackledge & Wenzel, 2001; Zschokke, 2002; Bruce, 2006 and references therein). This character has a retention index of zero: the four occurrences of web decorations are homoplastic in *Uloborus*, *Nephila*, *Argiope*, and *Cyclosa conica* (Tso, 1998; Zschokke, 2002: figs 3, 4D; but see also Scharff & Coddington, 1997) (K08, DIP).
191. *Orb web angle*: (0) horizontal (*Leucauge venusta*, Fig. 3F); (1) vertical (*Mesida argentiopunctata*, Fig. 4A). Horizontal webs are considered those with fewer than 45 degrees of slope; vertical webs are those with greater angles (K08, DIP).
192. *Barrier web*: (0) absent (*Orsinome* cf. *vethi*, Fig. 5C); (1) present (*Linyphia* sp., Fig. 6D). The orb web can be exposed from both sides, or one side may be covered with a net of threads. This net of threads is defined as a barrier web and it differs from the stabilimentum in that it does not reflect UV light (see character 189). Barrier webs can be considered a byproduct of the web architecture (Lubin, 1975), although they have been suggested as protective mechanisms (Comstock, 1948; Robinson & Robinson, 1970). Barrier webs are optimized as synapomorphic for a clade that includes all members of the ‘reduced piriform clade’ except *Epeirotypus* with the molecular and behavioural partition. The absence of barrier webs is common amongst tetragnathids; the only species that have barrier webs are *Leucauge venusta* and *L. argyra*. Barrier webs are also present in *Nephila* (Higgins, 1992) and *Nephilengys* (K08, DIP).
193. *Partial web renewal*: (0) new web build each day or shortly after damage (*Chrysometa* sp.); (1) webs repaired (*Nephila clavipes*). Most araneids and all tetragnathids build a new web each day or remove the complete web after it is damaged; other araneoids, such as linyphiids or nephilids, repair their webs after damage (e.g. see images in Hormiga, 2002: fig. 9D; Kuntner, 2006: fig. 34C) (K08, DIP).
194. *Hub*: (0) closed (*Wagneriana* sp., Fig. 7F); (1) open (*Opadometa* sp., Fig. 5B). The hub consists of a series of silk loops in the centre of the web where all radii converge. The hub construction can be either integrated with radii construction, or radii construction can be interrupted while hub loops are added to the unfinished web. However, hub construction is not finished until the last stages of web building, after the spider has spun the sticky spiral. Four adjustments can be carried out on the hub: the hub can either be left intact, have only its centre removed, be removed and replaced, or be completely removed and the radii attached directly. Furthermore, some spiders such as *Ogulnius* sp. (Theridiosomatidae) never build a hub (Eberhard, 1982). In tetragnathids the hub can either be left intact or have only its centre removed (open hubs). Open hubs are common within tetragnathids; of the taxa that we have studied only *Mollemeta*, *Azilia*, and *Dolichognatha* have closed hubs (Figs 3C, 4E) (L80, C90, H95, G98, K08, A07, DIP).
195. *Hub bite-out*: (0) absent (*Phonognatha graeffei*); (1) present (*Araneus marmoreus*). The centre of the hub can be either left intact or removed by biting it out; after hub removal the spider can either rebuild the hub or leave it open (Eberhard, 1982) (C90, H95, G98, K08, A07, DIP).
196. *Hub against substrate*: (0) absent (*Nanometa* sp., Fig. 4F); (1) present (*Nephilengys malabarensis*, Fig. 6B). The hub is either unconnected to the substrate or connected to it by means of a mesh of threads. The hub of *Phonognatha* (Araneidae) is coded as against the substrate because it is attached to a leaf that the spider places in the centre of the web (Hormiga *et al.*, 1995); an alternative coding for *Phonognatha* is to treat it as having the substrate unconnected to the hub. This character was coded as ‘free hub’ by (Kuntner, 2005, 2006; Kuntner *et al.*, 2008). The

- only tetragnathid that presents a hub attached to the substrate is *Mollemeta*. *Glenognatha* has intact hubs that are very close to the substrate but not attached (Hormiga & Döbel, 1990; G. Hormiga, unpubl. data) (K08, DIP).
197. *Hub loop – nonsticky spiral shift*: (0) gradual (*Nephilengys malabarensis*); (1) abrupt (*Metellina segmentata*). The last loop of silk in the hub can be either continuous with the nonsticky spiral, or discontinuous. This behaviour must be observed before web building completion, that is, before the spider removes the nonsticky spiral (Eberhard, 1982). Gradual transition between the hub loops and the nonsticky spiral is synapomorphic for *Deliochus*, *Phonognatha*, and nephilids; this character is coded as unknown (?) for *Deliochus*. Just a few tetragnathids are coded for this character, amongst them *Mollemeta* is the only species that has a gradual transition between these two web components (H95, K08, A07, DIP).
198. *Hub cup*: (0) absent (*Nanometa* sp., Fig. 4F); (1) present (*Herennia multipuncta*, Fig. 2C). The hub can also be modified into a silken cup, this cup is unique and synapomorphic for *Herennia* and *Nephilengys* (Kuntner, 2005) (K08, DIP).
199. *Hub relative position on the web*: (0) central (*Metamenardi* Fig. 4C); (1) displaced up (*Phonognatha graeffei* Fig. 7A); (2) displaced down (*Deliochus* sp., Kuntner, 2005, 2006). The hub of all taxa studied here except *Deliochus*, *Phonognatha*, and the nephilids is approximately in the centre of the web; some araneids such as *Scoloderus* Simon, 1877 have hubs displaced above the web (Levi, 1995; Kuntner, 2005, 2006) (K08, DIP).
200. *Radii construction*: (0) radii singly attached (*Araneus marmoreus*); (1) radii attached twice (*Nephila clavipes*). Radial construction starts when the spider attaches a new radius to the hub, then walks over an existing radius until it reaches the edge of the web; if the spider replaces this radius while returning to the hub, then only one point of attachment exists for this radius to the hub (state 0). Few tetragnathids and *Phonognatha* are coded for this character, and all of them have a single attached radius. By contrast, nephilids do not replace the previous radius while returning to the hub and attach this second radius to the same junction of the previous one, creating a double attachment (state 1) (Eberhard, 1982) (C90, H95, G98, K08, A07, DIP).
201. *Radii construction*: (0) radii not cut and reeled (*Nephila clavipes*); (1) radii cut and reeled (*Araneus marmoreus*). When the spider knits a new radius, it can cut the original radius and knit a new one while returning to the hub (state 0), or leave intact that radius (state 1) (see also character 199 definition). *Uloborus glomosus* have a single attached radius that is not cut and reeled (Eberhard, 1982) (C90, H95, G98, K08, A07, DIP).
202. *Secondary split radii*: (0) absent (*Nanometa*, Fig. 4F); (1) present (*Phonognatha graeffei*, Fig. 7A). Radii can follow a straight path to the web perimeter or divide (K08, DIP).
203. *Tertiary split radii*: (0) absent (*Nanometa* sp., Fig. 4F); (1) present (*Nephilengys malabarensis*, Fig. 6B) (K08, DIP).
204. *Sticky spiral location*: (0) oL1 (*Argiope argentata*); (1) iL1 (*Leucauge venusta*); (2) oL4 (*Nephila clavipes*). This character refers to the leg that the spider uses to measure where to attach the sticky silk line to the radii. oL1 means the leg one pointing away from the hub, iL1 internal leg one towards the hub, and oL4 the leg four away from the hub (Eberhard, 1982). Leg oL1 is optimized as plesiomorphic for Araneoidea; *Uloborus glomosus* also uses this leg to measure where to attach the sticky silk. The use of iL1 is synapomorphic for a clade that includes Tetragnathidae, ‘the reduced piriform clade’, *Deliochus*, *Phonognatha*, and nephilids. Finally, the use of leg oL4 is synapomorphic for *Phonognatha* and nephilids. This behaviour has not been documented for *Deliochus* or *Clitaetra* (L80, C90, H95, S97, G98, K08, A07, DIP).
205. *Nonsticky spiral*: (0) removed from finished web (*Tetragnatha versicolor*); (1) remains in finished web (*Nephila clavipes*). This is the first spiral that the spider builds after radial construction, from the hub to the edge of the web. The spider uses this frame to produce the sticky silk spiral, starting from the perimeter towards the centre (Eberhard, 1982) (H95, S97, G98, K08, A07, DIP).
206. *Nonsticky spiral contacts first sticky spiral construction*: (0) absent (*Nephilengys malabarensis*); (1) present (*Leucauge venusta*). The first line of sticky silk can be either separated from the first line of nonsticky silk or continuous (Hormiga *et al.*, 1995 and references therein).
207. *Retreat*: (0) absent (*Epeirotypus brevipes*, Fig. 6A); (1) off web (*Nephilengys malabarensis*, Fig. 6B); (2) in web (*Phonognatha graeffei*, Fig. 7A). Many araneoids are found either hanging on the hub, or build a retreat where they wait until a prey is caught in the web. The placement of the retreat can be either in the web or away from it. Usually retreats in the web are made of leaves (*Phonognatha graeffei*, Fig. 7A), ‘dirt’ or remains from previous meals (*Cyclosa caroli*, Levi, 1977: pl. 3; Tso, 1998). Retreats off the web are usually located above the web and

- are made on the surrounding substrate, usually leaves or pieces of bark, mosses, etc. on tree trunks or rocks. Retreats off the web are connected to the web by telegraphic silk threads (*Chrysometa* spp., Fig. 3D; Levi, 1986: pl. 1–2). Within Tetragnathidae *Azilia*, *Dolichognatha*, and *Chrysometa* build retreats off the web. No tetragnathines build retreats on the web, although the webs of some *Tetragnatha* species are in close contact with twigs and branches that run through the hub (Levi, 1981). Retreats on the web are found within Araneidae in some *Metepeira* species (Levi, 1977: pl. 1; Piel, 2001) and *Cyclosa*, and within nephilids in *Herennia* (Kuntner, 2005) (K08, DIP).
208. *Retreat form*: (0) silken tube (*Nephilengys malabarensis*, Fig. 6B); (1) utilization of a leaf (*Phonognatha graeffei*, Fig. 7A). Refer to character 206 description. The utilization of leaves as a retreat is synapomorphic for *Deliochus* and *Phonognatha*, and homoplastic in *Metepeira* (K08, DIP).
209. Wrap-bite attack: (0) the spider first bites the prey then wraps it (*Meta menardi*); (1) the spider first wraps the prey with silk (*Tetragnatha elongata*). This character describes the sequence in which the spider immobilizes and injects venom into the prey. Eberhard (1982) identified four types of attack behaviour that can be summarized in two general patterns: the spider first bites the prey injecting venom and then wraps it with silk, or the spider first wraps the prey and then injects venom. The other two patterns refer to whether the spider rotates the prey while wrapping it or not. We coded presence of wrap-bite attack without taking into account the prey rotation as specified in Eberhard's I4 behaviour category. This character was also included in Griswold *et al.* (2005), referred to as 'wrapping with legs IV', and coded for a variety of araneoid and non-araneoid spiders (C90, H95, G98, A04, K08, A07, DIP).
210. *Wrap bite silk*: (0) dry (*Araneus diadematus*); (1) sticky (*Asagena* sp.). This character codes whether or not the spider uses sticky silk to wrap the prey. The use of sticky silk while wrapping is optimized as synapomorphic for theridiids in our analysis; however, this character has been scored only for six terminals. The use of sticky silk while wrapping the prey has been postulated as a synapomorphy for the 'spineless femur clade' (Griswold *et al.*, 1998; Agnarsson, 2004) (G98, A04, K08, DIP).
211. *Body shake*: (0) absent (*Asagena* sp.); (1) present (*Argiope argentata*). This refers to a behaviour exhibited when the spider is disturbed, and it

forcefully shakes the web (Kuntner, 2005) (K08, DIP).

212. *Bulbus detachment*: (0) absent (*Nephila clavipes*); (1) present (*Nephilengys malabarensis*). Some spiders, including species of some nephilids, block the epigynum by detaching the complete pedipalp bulb (Robinson & Robinson, 1980, see also the recent review by Uhl *et al.*, (2010) on mating plugs and genital mutilation in spiders). This character is synapomorphic for *Herennia* plus *Nephilengys* and it is also present in some theridiids (Agnarsson, 2004) (A04, K08, DIP).
213. *Cheliceral clasp*: (0) absent (*Araneus diadematus*); (1) present (*Tetragnatha* sp., Fig. 1B). Males and females interlock their chelicera while mating in some *Tetragnatha* (Levi, 1981: pl. 4) and *Leucauge* species. Cheliceral clasp does not occur in *Meta* and *Nephila* (Robinson, 1982; Eberhard & Huber, 1998a and references therein).

#### ACKNOWLEDGEMENTS

The authors would like to acknowledge Marc Allard, Jim Clark, Diana Lipscomb, Jonathan Coddington, and Lara Lopardo for comments and revisions on early versions of this manuscript. Special thanks to Charles Griswold for proofreading the final version of the manuscript. Also thanks to Dimitar Dimitrov for the numerous discussions, comments and contributions to this paper. Our gratitude to Nikolaj Scharff, Volker W. Famenau, and an anonymous reviewer for their useful comments of an earlier version of this paper. Thanks to Tamas Szuts for his help in translating some of the German language references. We would like to thank the curators of the following museums for making specimens available and allowing us to perform dissections and SEM preparations: N. Platnick (American Museum of Natural History), G. Giribet (Museum of Comparative Zoology); J. Coddington (National Museum of Natural History, Smithsonian Institution), R. Raven (Queensland Museum), C. Griswold (California Academy of Sciences), M. Gray (Australian Museum) and C. Ribera (Universitat de Barcelona). We also would like to thank the following people for their valuable help during our fieldwork: R. Raven, V. Davies, N. Scharff, S. Larsen, and M. Kuntner (Australia); J. Coddington and J. Miller (Chile); N. Scharff, M. Ramírez, J. Birkedal, J. Coddington, D. de Roche, and P. Wongprom (Thailand); N. Scharff (Denmark); K. Guerrero, S. Benjamin, and the staff of the scientific reserves 'Ébano Verde' and 'Loma Quita Espuela' (Dominican Republic); L. Lopardo, J. Castelo-Calvillo, T. Pérez, G. Montiel, and the

IBUNAM staff for the logistic support and resources (Mexico). We thank the Willi Hennig Society and P. Goloboff for the free use of the program TNT. Support for this project was provided by a NSF-PEET grant to G. Hormiga and G. Giribet (DEB-0328644), a scholarship from the Consejo Nacional de Ciencia y Tecnología of México (CONACYT) to F. Álvarez-Padilla, by Research Enhancement Funds and Selective Excellence grants from The George Washington University to G. Hormiga, and by a Schlänger Chair of Arachnology postdoctoral fellowship from the California Academy of Sciences to F. Álvarez-Padilla. Additional support was provided by an AToL grant from the US National Science Foundation (EAR-0228699) to W. Wheeler, J. Coddington, G. Hormiga, L. Prendini, and P. Sierwald. This paper was completed during the second author's stay at the Zoologisk Museum (University of Copenhagen) thanks to the generous support of Nikolaj Scharff and a grant from Danmarks Nationalbank.

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APPENDIX 1  
MORPHOLOGICAL AND BEHAVIOURAL DATA SET

Characters 1 to 110.

<i>Oncodamus decipiens</i>	001111101-	000--10001	0000000-0--	0--010---	----01010	1011101201	0100-00000	000--00-01	1100001120	20-021000?	1000010101
<i>Parasteatoda tepidariorum</i>	1010-00011	0110000100	000100-0--	0--1010---	----01010	0-11101101	0100-02010	000--00-00	-110110120	010111210?	1300102100
<i>Allende nigrohumeralis</i>	0110-01010	0110100010	0001010121	0--0001111	1001100000	0-10101101	0111002010	0000000-11	1100001110	110111120?	1001113201
<i>Araneus marmoreus</i>	0011101000	1110100001	0010000-0--	0--0111000	0000-01001	1011100010	0102002001	1111100-01	1101101101	0111011200	1000001000
<i>Argiope argentata</i>	0011101000	1110100001	0010000-0--	0--0011000	0000-01001	1011101010	0100-02121	110--00-01	1111101000	2111112200	1300012000
<i>Asagena americana</i>	1010-00011	0110100101	0000000-0--	0--1000---	----01011	1111101011	1100-011-0	000--00-00	-110110120	110121200?	1300110000
<i>Azilia affinis</i>	0111101010	0110000001	000100-0--	0--0011000	0001100000	0-0-----	0110-02010	000--01101	1100001000	00-010110?	1201101101
<i>Chrysometa alajuela</i>	0110-01010	0110000001	0001010100	0--0011611	1101300000	0-10001111	0111102020	0000000-11	1100001110	010111110?	1001114201
<i>Clitaetra episinoides</i>	0111001010	0110100001	000100-0--	0--0011200	0011200000	0-10102311	0010-012-0	000--01101	0001001100	20-020120?	1000010001
<i>Cyclosa conica</i>	0111101000	1110100001	0010000-0--	0--0011000	0000-01001	1011101001	01200111-0	1011100-01	1101101100	011111110?	1300001000
<i>Cyrtognatha espaniola</i>	0110-01010	0110000001	110110-0--	0--0101111	1001100000	0-10001210	0110-02120	000--010-1	12000001000	1101111001	1001100201
<i>Deliochus sp.</i>	0101001010	0111000???	??0?00-0--	0--0011310	0000-00010	0-10002211	0110-011-1	000--00-11	1101101100	010101101?	0-00003201
<i>Diphya spinifera</i>	0110-01010	0110000001	000100-100	0--0001100	1101000000	0-10002101	0110-02120	000--00-01	1110001120	00-010100?	1001116201
<i>Dolichognatha pentagona</i>	0110-01010	0110000101	00010110--	0--0111100	0001101000	0-10101201	0111102000	0000001001	1210001100	00-020100?	1001110201
<i>Epeirotypus brevipes</i>	1110-00010	0110000000	0000000-0--	0--0011200	0000-00101	1011101101	0100-02110	000--01100	-101100110	010101100?	1300006000
<i>Gasteracantha cancriformis</i>	0011001010	1110101???	?11000-0--	0--0011200	0000-01001	1011100010	0100-00100	100--00-01	1001101101	211121121?	0-00001001
<i>Glenognatha foxi</i>	0110-01110	0110000000	110110-0--	0--0101111	1001000000	0-10002200	0110-00120	000--010-1	1200000100	10-111100?	0-01110200
<i>Herennia multipuncta</i>	0011001010	1110100001	000100-0--	0--0011200	0011200000	0-10112311	0010-012-0	000--01101	0001101110	20-001020?	1000011101
<i>Larinoides cornutus</i>	0011101000	1110100001	001000-0--	0--0011000	0000-01001	1011100010	012002101	1111100-01	1001101101	011101120?	1000001001
<i>Leucauge argyra</i>	0110-01010	0110100010	100100-0--	1010011000	0001210100	0-10102211	0110-111-0	000--01101	1100001010	110101100?	1211005101
<i>Leucauge venusta</i>	0110-01010	0110100010	100100-0--	0--0001000	0001110100	0-10102211	0110-111-0	000--01101	1100001010	2101110001	1211015100
<i>Linyphia triangularis</i>	1010-00110	0110100001	0000000-0--	0--0011412	0001201000	0-0-----	01130012-0	2000000-00	-210000120	2101011000	1101100200
<i>Mangora gibberosa</i>	0111101000	111010101	001000-0--	0--0011000	0000-01001	1011100000	012002000	1011100-01	1101101000	011101120?	1100012000
<i>Mecynogea lemniscata</i>	0?11101000	1110100001	001000-0--	0--0011000	0000-01001	1011100000	01200111-0	1001100-01	1111101000	211101210?	1300001100
<i>Mesida argentopunctata</i>	0110-01010	0110100010	110100-0--	1100011000	0001210100	0-10102211	0110-111-0	000--01101	12000001010	110111101?	1201110201
<i>Meta menardi</i>	0011101010	0110100000	0001011110	0--0001100	0001101010	0-10101101	0111102000	00000001001	1210001110	110111110?	1201101211
<i>Metabus ocellatus</i>	0110-01010	0110100010	110100-0--	1110011000	00011110100	0-10102211	0110-111-0	000--01101	1210001010	110111020?	1201116201
<i>Metellina segmentata</i>	0110-01010	0110100101	000101110--	0--0111110	0001101000	0-10101101	0111102000	0000000-01	1110001110	110111110?	1001111201
<i>Metepeira labyrinthica</i>	0011101000	111010101	001000-0--	0--0111000	0000-01001	1011100010	0102002001	1011100-01	1101101000	111111120?	1100001111
<i>Nanomete sp.</i>	0110-01010	0110100000	0001010111	0--0011000	0001100000	0-10001101	0110-00120	000--00-01	1111001110	010111110?	1001110201
<i>Metleucauge eldorado</i>	0110-01010	0110100000	0001001100-100	1000111200	10011110100	0-10102211	0110-10000	000--00-01	1210101010	210111120?	1201111201
<i>Micrathena gracilis</i>	0011001010	1110101010	001000-0--	0--0011100	1000-01001	1011100010	012002100	1000100-01	1001101111	211101120?	1400003001
<i>Mollemeta edwardsi</i>	0010-01010	0110100001	0001011100	0--0001500	0001101000	0-10101211	0110-00100	000--00-01	1100101110	1101111210?	1001108101
<i>Nanometa sp.</i>	0110-01010	0110100101	0001010110	0--0001000	0001100000	0-10001101	0110-00120	000--00-01	1101001110	1101111000?	0-01110101
<i>Neoscona domiciliorum</i>	0011101000	1110100001	001000-0--	0--0011000	0000-01001	1011100000	012002000	1111000-01	1111101100	111101120?	1100002000
<i>Nephila clavipes</i>	0011001010	1110100001	010100-0--	0--0011200	0011200000	0-10102311	0010-012-0	000--01101	0001101110	2101?1121?	1000012011
<i>Nephilengys malabarensis</i>	0011001010	1110100001	000000-0--	0--0011200	0011100000	0-10112311	0010-012-0	000--01101	0001101110	210101121?	1200002001
<i>Nesticus cellulanus</i>	1010-00011	0110000???	?11000-0--	0--0011110	1101201001	1111100010	1100-00010	000--01000	-111100120	110111200?	1000100100
<i>Opadometa sp.</i>	0110-01010	01101000???	?11000-0--	1100111000	1001011100	0-10102201	0110-111-0	000--00-01	1100101010	110111110?	1201011201
<i>Orsinome cf. vethi</i>	0110-01010	0110100010	000100-0--	1000111000	1001010100	0-10102211	0110-111-0	000--01101	1210101010	210111120?	1201113201
<i>Orsinome sarasini</i>	0110-01010	0110000000	0001010111	0--0001110	0101100000	0-10001101	0110-00120	000--00-01	1111001110	110111000?	1301111201
<i>Pachygnatha autumnalis</i>	0110-0011-	000--00000	110110-0--	0--0101111	1101100000	0-10002201	0110-00120	000--10-01	1210001110	20-1010101	1301100201
<i>Phonognatha graeffei</i>	0001001010	0111000000	000100-0--	0--0101310	000?101000	0-10002211	0110-00220	000--00-01	1101101100	010111111?	1300003201
<i>Tetragnatha versicolor</i>	0110-01010	0110000101	000110-0--	0--0101111	0101100000	0-10002201	0110-00120	000--10-01	1210001010	20-0001201	1201100201
<i>Tylorida striata</i>	0110-01010	0110100010	?00100-0--	1000011200	1001110100	0-10102210	0110-111-0	000--01101	12000001010	0101?1000?	1201113200
<i>Uloborus glomosus</i>	011111100-	100--10000	0000000-0--	0--0000---	----01011	1011100010	0100-00020	000--00-01	1001001100	20-010120?	1300000000
<i>Zygiella x-notata</i>	0011001010	0111000001	001000-0--	0--0011000	0000-01011	1011100010	0102002000	1111100-01	1101101100	011111120?	1100007101

APPENDIX 1 *Continued*

Characters 111 to 213.

<i>Oncodamus decipiens</i>	0000000100	0010000--0	0300000000	0-23020000	0000000025	000110000-	--000-000	100000---	-----	-----	-0?
<i>Parasteatoda tepidariorum</i>	0000000110	0010100--0	0000000101	0-03020000	0000000005	00?0-0000-	--000-100	00100121?-	-11-----	------??-?	00?
<i>Allende nigrohumeralis</i>	0010001100	0011010--1	1300000101	0-00000001	1010000000	001110000-	--100-001	2110010???	??1?0?0???	?00?0?0???	00?
<i>Araneus marmoreus</i>	0000001002	1011011110	2100100100	0-00020000	0000000114	0????0000-	--0011012	0001010010	1000100000	1000001000	000
<i>Argiope argentata</i>	0000000000	1111010--0	0100100110	0-01010000	0000001101	00?100000-	--0011001	0000010011	1000100000	1000000-00	100
<i>Asagena americana</i>	0000000100	0010100--2	1000000101	0-12020000	0000000005	000100000-	--000-100	010001211-	-11-----	------0-11	00?
<i>Azilia affinis</i>	0000000100	0010000--0	1000001101	0-20001000	1100000000	001110000-	--10?001	1010010000	00?0101000	10010?10??	00?
<i>Chrysometa alajuela</i>	0010001210	1010000--0	1000000101	0-12020011	0011000005	000100000-	--100-001	00000100?0	10?1?0?00?	?00?0?10??	00?
<i>Cliatetra episinoides</i>	00000?0100	1010000--1	1000000100	0-00010000	000000014	010100000-	--0010001	0000010?0?	10????1???	??????????	00?
<i>Cyclosa conica</i>	0000000012	1011001100	2300100100	0-02020000	0000001014	2000-0000-	--0011012	0010101011	1000?0?000	?0000?20??	00?
<i>Cyrtognatha espaniola</i>	1010201200	000----2	1011----1	0-200-01--	--1001014	0101100011	011?00-001	0110010000	001?0?00?	?00?0?0-??	00?
<i>Deliochus sp.</i>	0110001200	-110000--0	0100001110	0-02021000	0000000015	011100?00-	--000-001	0100010?0?	100????02?	?10???11??	01?
<i>Diphya spinifera</i>	0000011200	0010000--0	0300000110	0-20000000	0000000014	000100000-	--000-001	00000?????	???????????	???????????	00?
<i>Dolichognatha pentagona</i>	0000010200	0010010--1	1000000000	0-00010000	0000001014	000100000-	--100-000	1100010010	00?0101000	10010110??	00?
<i>Epeirotypus brevipes</i>	0000000000	0011000--2	1000001101	1020001000	0000000005	0110-0000-	--000-001	0000010110	1000101000	1001000-1?	00?
<i>Gasteracantha cancriformis</i>	00000?1000	-110011001	1000000100	0-01010000	0000101005	0?0110?00-	--001-000	0000010010	1000?01000	10000?0-??	00?
<i>Glenognatha foxi</i>	0000110200	-00----2	0010----0	102000101--	--0010015	1?2110100-	--100-000	0010010000	000-0?000	10010-0-??	00?
<i>Herennia multipuncta</i>	00?000011?	0110110--0	0200010100	0-02020000	0000001110	000111000-	--0010001	0?00010010	10?0010111	0??21?20??	?1?
<i>Larinoides cornutus</i>	0000000002	1011011100	2000100100	0-03020000	0000000114	0????0000-	--1010002	0001010010	1?0????000	?0000?0000?	00?
<i>Leucauge argyra</i>	0100011100	0011000--0	1300001100	1111000001	1101000014	0111100011	111100-001	11100100?0	0101?0?00?	?00?0?0-??	00?
<i>Leucauge venusta</i>	0000000100	0010100--0	0000001100	1110011001	1101000010	0111100011	111100-001	2110010000	0101101000	1001010-00	001
<i>Linyphia triangularis</i>	1000010200	0011100--0	1000000000	0-12020011	0000000005	00?0-0000-	--000-000	011001111-	-11-----	-0-1?	00?
<i>Mangora gibberosa</i>	0000000000	0011001111	1000100100	0-02020000	0000001015	021100000-	--0011011	0001010010	1000100000	1000000-??	00?
<i>Mecynogea lemniscata</i>	0000000100	0011110--1	1000000110	0-03010000	0000001114	0010-0000-	--0011001	00000010110	01?0?0000?	?00?1?0000?	00?
<i>Mesida argentopunctata</i>	0101011200	0010100--0	00000001100	1010011001	1101000004	0111100011	111000-001	01100100??	?001?0?00?	?00?0?0-??	00?
<i>Meta menardi</i>	00000001100	0011010--1	1000000001	0-00000001	1010000114	?????0000-	--100-001	1110010000	1001101000	1001010-00	000
<i>Metabus ocellatus</i>	0000000100	0010110--1	0000001100	1010011001	1101000004	000110000-	--100-001	21100100?0	0?1?0?00?	????0?????	00?
<i>Metelella segmentata</i>	0000000100	0010000--1	1000000001	0-20000011	0000000014	001100000-	--100-001	1100010000	100110100?	?00?0?0-??	00?
<i>Metepeira labyrinthica</i>	0000000100	0111011100	0100100100	0-02020000	0000000110	020100000-	--0011012	0000010110	11?0?0?000	?0000?21??	00?
<i>Nanometine. sp.</i>	0010011200	0010000--0	0300000101	0-12121000	0001000004	1?11101010-	--100-000	11101100?0	?001?0?00?	?00?0?0-??	00?
<i>Meteleauge eldorado</i>	0010011100	0010000--0	03000001101	1-00011000	0000000004	001100000-	--100-001	2110010?0?	0001?0?00?	?00???????	00?
<i>Micrathena gracilis</i>	0000000100	0111011000	1000100100	0-01010000	0000101205	000110010-	--000-001	0000010010	1001?01000	10000?0-??	00?
<i>Mollemeta edwardsi</i>	0000000100	00100111000	1300000101	0-20010001	0000000104	000110000-	--100-001	21100100?0	10?0?1000?	?00?0?0000?	00?
<i>Nanometea sp.</i>	0010000100	-010000--0	0100000101	0-12121000	0001000004	1010-0010-	--000-000	00001100?0	0001?0?00?	?00?0?0-??	00?
<i>Neoscona domiciliorum</i>	0000000010	0011011010	1000100100	0-03020000	0000001014	000100000-	--001?012	0001010010	1000?0?000	?0000?0000?	00?
<i>Nephila clavipes</i>	0000000210	1111110--1	1000000100	0-00010000	0000000113	?????1000-	--?110001	00000010111	1110000011	01121?0-1?	100
<i>Nephilengys malabarensis</i>	0000000210	1110010--0	00000010100	0-02020000	0000000112	0000001000-	--0010001	00000010110	11?0010111	011210101?	?10
<i>Nesticus cellulanus</i>	01?0010100	10110100--2	1000000010?	??2?010011	0000000000	0?????000-	--?00-100	1?000121--	-11-----	-0-??-1	000
<i>Opadometa sp.</i>	01000001201	0110100--1	00000001100	1110011001	1100000104	0??110?011	111110-000	11100100?0	1001?0?00?	?00?0?0000?	00?
<i>Orsinome cf. vethi</i>	1001000201	00101100--0	03000001100	1112010001	1101000004	0?11000011	110100-001	01100100?0	0001?0?00?	?00?0?0-??	00?
<i>Orsinome sarasini</i>	00100001100	00100?0--0	03000001000	0-12121000	0000000004	0?1110010-	--100-000	1110110???	???????????	???????????	00?
<i>Pachygnatha autumnalis</i>	10010?0100	000----2	0010--0011	0-000001--	--0010005	0?11001010	000100-000	010000---	-----	-0-??-	-0?
<i>Phonognatha graeffei</i>	0100011200	1010000--0	0100000111	0-00000000	0000000004	001110000-	--000-001	1100010010	1100010010	?11210211?	00?
<i>Tetragnatha versicolor</i>	1001210200	000----2	1011--0111	10000001--	--1000014	0????00010	000000-001	2110010000	0001101000	1001010-1?	001
<i>Tylorida striata</i>	0000000100	0010100--0	00000001100	1110011001	1101001005	0111100010	010000-001	01100100?0	0001?0?00?	?00?0?0000?	00?
<i>Uloborus glomosus</i>	0000000100	0011000--0	1000000000	0-01021000	00000001014	1????0000-	--000-000	0000010001	001-00-000	0000000-0?	00?
<i>Zygiella x-notata</i>	0100001100	0011000--0	1000000100	0-01020000	0000000104	020100000-	--0011002	00000100?0	100?0?00?	?0000?0000?	00?

## APPENDIX 2

### SPECIMENS EXAMINED

#### *Label data organization*

The museum where specimens are deposited is given first, next the locality data transcribed from the labels and finally the specimens museum codes (if available; e.g. 'QMS: S45254'). This information is mentioned to facilitate location of the specimens studied for additional examination. Specimens used for scanning electron microscopy (SEM) and photo vouchers are indicated at the end of its respective locality data and marked with a code that starts with the letters 'SEMFAP.' All SEM stubs are deposited at the Laboratory of G. Hormiga at The George Washington University. A small label with this code was inserted in each vial to indicate that specimens were dissected for SEM study; these codes correspond to those used in the figure legends. The total number of specimens examined for the phylogenetic data set (Appendix 1) and the morphological atlas is given at the end (e.g. 'n = 6'). Asterisks indicate if the specimens studied belong to the type species. Museum and university names are abbreviated as follows: AMNH, American Museum of Natural History, New York. AUM, Australian Museum, Sydney. CAS, California Academy of Sciences, San Francisco. CNAN, Colección Nacional de Arácnidos Instituto de Biología UNAM, Mexico, D.F. GWU, The George Washington University, Department of Biological Sciences, Washington, D.C. QMS, Queensland Museum, Brisbane. MACN-Ar, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires. UBA, Universitat de Barcelona, Departament de Biología Animal, Facultat de Biología, Barcelona. USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

#### *Araneidae*

##### *Araneus marmoreus* Clerck, 1757

USNM: USA Georgia: Rabun Co. Ellicott Rock Wilderness, 1 km SW Ellicott Rock, cove hardwood fort. 750–800 m. 16.ix.1991 34°59'46"N: 83°06'54". Two female specimens SEMFAP009. USA Iowa: Loop of Little Sioux 22.vii.1916 T. C. Stephens. One male specimen SEMFAP072. Mass. Berkshire Co., Lenox W. Mtn. Road. Pleasant Valley Wildl. Sanctuary J. Coddington 3.vii.–26.vii.1976. USA Palomar Mt. Ca. 4.vii.1967. t. Y. Sandoval In wasp mud nest W. Young, Dellinger, McGarity. Aerial 3D. n = 6.

##### *Argiope argentata* (Fabricius, 1775)

AMNH: MEXICO Cuernavaca Morelos x.1944 N. L. H. Krauss. Two female specimens SEMFAP010. ECUADOR: Tungurahua: Banos, 10.iii.1971 BRMSA

Near Hot bath house. Ray A. Sweet. One male specimen SEMFAP073. MACN-Ar: ARGENTINA Buenos Aires, Pulla Rosa. ii.1964. n = 5.

##### *Cyclosa conica* (Pallas, 1772)\*

USNM: USA Palomar Mt. Ca. 4 Jul 1967. t. Y. Sandoval In wasp mudd nest. Two female specimens SEMFAP008. USNM USA S. D. Custer Co. Harney Peak trail 13 June 1964 B and C Durden. One male specimen SEMFAP070. n = 6.

##### *Deliochus* sp.

QMS: S45254 AUSTRALIA: East Pt. Darwin N. T. 9.xi.1979. One female and one male specimens SEMFAP022. n = 4.

##### *Gasteracantha cancriformis* (Linnaeus, 1758)\*

USNM DOMINICA Roseau. x.1967 N. L.H. Krauss. Two female SEMFAP012 and one male specimens illustrated (Fig. 136A). PANAMA: Canal Zone, Colon 2–14.vii.1979 E. Broadhead *et al.* Humid forest Canopy fogging. n = 4.

##### *Larinoides cornutus* (Clerck, 1757)

USNM USA WI, Winn. Co. 5788 Bittersweet 18 June 1974 B. R. H. Two female and one male specimens SEMFAP004 and one female illustrated (Fig. 136D). USNM USA WI, Winn. Co. Pt. Comfort S. of Oshkosh 30–31.v.1957 JLK, BRH leg. n = 8.

##### *Mangora gibberosa* (Hentz, 1847)

GWU: USA: VA, Fairfax County Parkway, Bull Run/Occoquan Trail. vi-viii.2003 Álvarez, F. Two female and two male specimens SEMFAP014. USNM: Massachusetts: Barnstable Co., Hatchville, FCWMA. 8.vi.1979. L. Edwards leg. n = 10.

##### *Mecynogea lemniscata* (Walckenaer, 1841)

GWU: USA: VA, Vienna Metro Station. 29.ix.2005 Álvarez, F. Two female specimens SEMFAP011. USNM: S. Carolina. Oconee, Co. Chattooga River landing just below Rt. 28 bridge, 1580' elev., 22.vii.1988. USA: SC. Oconee Co. Yellow Branch Picnic Area on Rt. 28, 2.9 mi S intersect with Rt. 107. 1300' elev., 22.vii.1998 K. Smith. one male specimen SEMFAP064. Alabama. Jefferson, Co. Birmingham, Birmingham Zoo grounds. 20.vi.1984. J. Coddington leg. n = 9.

##### *Metepira labyrinthaea* (Hentz, 1847)

GWU: USA: VA, Fairfax County Parkway, Bull Run/Occoquan Trail. 28.viii.2005 Álvarez, F. One male and two female specimens SEMFAP007. n = 7.

##### *Micrathena gracilis* (Walckenaer, 1805)

GWU: USA: VA, Fairfax County Parkway, Bull Run/Occoquan Trail. vii.2005 Álvarez, F. Two females and

one male. SEMFAP013. One female illustrated (Fig. 136C) and one female photo voucher (Fig. 2E) DSCN3350.  $n = 6$ .

*Neoscona domiciliorum* (Hentz, 1847)

GWU: USA: VA, Fairfax County Parkway, Bull Run/Occoquan Trail. 28.viii.2005 Álvarez, F. Three males and three female specimens SEMFAP006.

*Ocrepeira* sp.

MCZ: DOMINICAN REPUBLIC: Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth. N  $18^{\circ}05'54.8''$ ; W  $71^{\circ}11'22.0'$ , 1220 m, 6–9.iv.2005. G. Hormiga, F. Alvarez and S. Benjamin. Web of female photo voucher (Fig. 7C) DSCN7326.  $n = 1$ .

*Phonognatha graeffei* (Keyserling, 1865)\*

QMS: S45617 West Burleigh, SEQ 12.ii.1953. Two female and one male specimens SEMFAP023. S45460 Mudgerabah, W. on road to Springbrook. St ORT 21.ii.1986. One female illustrated (Fig. 136E). S33973 Conway NP. Nr. Site 34. Nighth colln. Swamp at start Mt. Rooper walk. 8.xi.1991. One male specimen SEMFAP068. USNM: AUSTRALIA: SE QLD.; Noosa National Park. Dry forest,  $26^{\circ}23'32''S$   $153^{\circ}06'41''E.$ , 50 m. 5.iv.2002. M. Kuntner, F. Alvarez, M. Rix. Photo vouchers Neph001 (Fig. 2D) and Neph002 (Fig. 7A).  $n = 8$ .

*Wagneriana* sp.

MCZ: MEXICO: Chiapas, Ocosingo, Reserva Comunal El Cartón,  $16^{\circ}47' 21.4''$  N,  $90^{\circ}55' 48.4''$  W, EPE07 207 m. 26.x-2.xi.2005. F. Alvarez, L. Lopardo and J. Castelo leg. Web photograph of female specimen (Fig. 7D) photo voucher DSCN8014.  $n = 1$ .

*Zygiella x-notata* (Clerck, 1757)

USNM: USA S. D. 19 January 69 Steve Johanson. Two female specimens SEMFAP005. Myanmar Sagaing Division. Cattin Wild life Sanct. Takontaing Camp Lake 23 37' 20" N. 95 31" 52" E. 7-12.x.1998 Coddington & Baptista leg. One male specimen SEMFAP069. SWITZERLAND: Bern; Gals, field, meadows.  $47^{\circ}02' N.$   $7^{\circ}02'E.$  16.viii.1989 JA Coddington leg.  $n = 6$ .

*Linyphiidae*

*Linyphia triangularis* (Clerck, 1757)\*

USNM: DENMARK: Hestehaven, Rønde 22 km NE of Århus  $56^{\circ}17.46' N$   $10^{\circ}28.50' E$  30.viii.1994, Bjørn, Christiansen, Coddington, Griswold, Hormiga, Krat, Langemark, Scharff and Sørensen leg. Two females and one male specimens SEMFAP015.  $n = 6$ .

*Lomaita* sp.

MCZ: DOMINICAN REPUBLIC: La Vega Prov., Constanza, Reserva Científica Valle Nuevo, pine forest, N

$18^{\circ}46'39.2''$ ; W  $70^{\circ}38'22.4''$ , 2277 m, 11.iv.2005. F. Alvarez and S. Benjamin. Web photograph of female specimen (Fig. 6D) photo voucher DSCN7476.  $n = 1$ .

*Nephiliidae*

*Clitaetra episinooides* Simon, 1889\*

USNM: These specimens have no label except the species identification by M. Kuntner. Two female specimens SEMFAP024. GWU: SOUTH AFRICA: Kawa Zulu-Natal, Fanies Is., 40–50 m, 31.iii.2001, Hormiga leg. One male specimen examined.  $n = 4$ .

*Herennia multipuncta* (Doleschall, 1859)\*

USNM: Los Banos P.I. 1909 No777-0- 1909 Leonadr leg. Two female specimens SEMFAP026. THAILAND: Surat Thani Prov., Khao Sok NP, Wing Hin Waterfall trail, N  $8^{\circ}55'0.4''$ ; E  $98^{\circ}31'40.9''$ , 300 m 19–20.x.2003. ATOL Expedition 2003 leg. Female and male specimens (Fig. 2C) Photo voucher DSCN4400.  $n = 6$ .

*Nephila clavipes* (Linnaeus, 1767)

USA: Florida, Hillsborough Co., Tampa, 1.ix.1984, Larcher leg. Two female and two male specimens examined.  $n = 4$

*Nephilengys* sp.

USNM: AUSTRALIA: NE QLD.; Mission Beach. Rainforest at the Sanctuary. 1.v.2002. M. Kuntner, F. Alvarez. Web of a female specimen (Fig. 6B) photo voucher DSCN1442.JPG.  $n = 1$ .

*Nephilengys malabarensis* (Walckenaer, 1841)\*

QMS: S45227 N.T. East Alligator Xing 12.25 S. 132.58 E 16–18.vii.1979 G. Monteith and D. Cook leg. Two female specimens SEMFAP027. S45220 NE.Q. Ellis Beach 22.xii.1979 S45220. One female illustrated (Fig. 136F). One male specimen SEMFAP074. USNM: THAILAND: Surat Thani Prov., Khao Sok NP, Wing Hin Waterfall trail, N  $8^{\circ}55'0.4''$ ; E  $98^{\circ}31'40.9''$ , 300 m 19–20.x.2003, ATOL Expedition 2003 leg.  $n = 6$ .

*Nesticidae*

*Nesticus cellulanus* (Clerck, 1757)\*

UBA: España Barcelona Cus. De Sta. Crev d' Olorde 18.vi.1987 Ribera-Serra leg. Two male and two female specimens revised.  $n = 4$

*Nicodamidae*

*Oncodamus decipiens* Harvey, 1995

QMS: S15410 Mt. Bartle-Frere, N. Qld. fifth peak summit 1620 m 6–8.xi.1981 Earthwatch/QLD. MUS. Two female specimens SEMFAP001. S15310 Victoria

park, via Alstonville NSW Australia. GM 41A/4' Rainforest pitfalls 3 3.viii.-16.xi.1975. G and S. Monteith. One male specimen SEMFAP066.  $n = 6$ .

#### *Psechridae*

*Fecenia* sp.

GWU: THAILAND: Surat Thani Prov., Khao Sok NP, Wing Hin Waterfall trail, N  $8^{\circ}55'0.4''$ ; E  $98^{\circ}31'40.9''$ , 300 m, 19-20.x.2003, ATOL Expedition 2003. Web of a female specimen (Fig. 6C) photo voucher DSCN4354.  $n = 1$ .

#### *Sympytognathidae*

*Sympytognathid* sp.

GWU: THAILAND: Chiang Mai Prov., Doi Inthanon NP, nr. intersect. rd. to Mae Chaem and checkpoint, wet primary forest, N  $18^{\circ}31'33.2''$ ; E  $98^{\circ}29'57.7''$ , c. 1800 m, 3.x.2003, ATOL Expedition 2003. Web of a female specimen (Fig. 7B) photo voucher DSCN3937.  $n = 1$ .

#### *Tetragnathidae*

*Allende nigrohumeralis* F. O. P.-Cambridge, 1899  
AMNH: CHILE Region de Valparaíso V Viña del Mar i.1979 Tobar, A. Female trachea preparations, SEMFAP047. CHILE Metropolitana de Santiago Santiago El Golf 9.iv.1961 Archer, A. F. Two male specimens illustrated (Fig. 12A-C) and SEMFAP057. CHILE Region del Bío Bío VIII Ñuble 8-9.xi.1993 Peña, L. E. Two female specimens one illustrated (Fig. 12D), the other used for external anatomy SEMFAP058.  $n = 6$ .

#### *Azilia affinis* O. P.-Cambridge, 1893

AMNH: USA, FL Alachura Co. Dudley Caves 18-iii.1938. Two male and two female specimens, one couple illustrated (Fig. 17A-C) the other SEMFAP032.  $n = 6$ .

#### *Azilia* sp.

MCZ: DOMINICAN REPUBLIC: La Vega Prov., Constanza, Reserva Científica Valle Nuevo, pine forest, N  $18^{\circ}46'39.2''$ ; W  $70^{\circ}38'22.4''$ , 2277 m, 11.IV.2005. F. Alvarez and S. Benjamin. One female specimen (Fig. 2B) photo voucher DSCN7469. MEXICO: Chiapas, Ocósingo, Arroyo Nayte Loc 1, Sierra de la Cojolita,  $16^{\circ}47' 36.2''$  N,  $91^{\circ}02' 35.3''$  W EPE06, 202 m. 26.x-2.xi.2005. F. Álvarez, L. Lopardo and J. Castelo leg. Photo voucher (Fig. 3C) DSCN3350.  $n = 1$

#### *Chrysometa alajuela* Levi, 1986

GWU: COSTA RICA: Puntarenas, P. N. (ACLA) Estación Pittier 009°01' N  $82^{\circ}5''$  W. 1800 m. 8-11.iv.1995 G. Hormiga. Two male and two female specimens, one couple illustrated (Fig. 22A-D) the other SEMFAP046.  $n = 12$ .

#### *Chrysometa nuboso* Levi, 1986

GWU: COSTA RICA: Puntarenas, P. N. (ACLA) Estación Pittier 009°01' N  $82^{\circ}5''$  W. 1800 m. 8-11.iv.1995 G. Hormiga.  $n = 5$ .

#### *Chrysometa saladito* Levi, 1896

GWU GH COSTA RICA: Puntarenas, P. N. (ACLA) Estación Pittier 009°01' N  $82^{\circ}5''$  W. 1800 m. 8-11.iv.1995 G. Hormiga.  $n = 2$ .

#### *Chrysometa* sp.

MCZ: DOMINICAN REPUBLIC: Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth.  $18^{\circ}05'54.8''$ N:  $71^{\circ}11'22.0''$ W, 1220 m, 6-9.iv.2005. G. Hormiga, F. Álvarez and S. Benjamin. Photo voucher Figure 2A DSCN7358. Photo voucher (Fig. 3D) DSCN7336.  $n = 1$ .

#### *Cyrtognatha espaniola* Bryant, 1945

MCZ: DOMINICAN REPUBLIC: Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth. N  $18^{\circ}05'54.8''$ : W  $71^{\circ}11'22.0''$ , 1220 m, 6-9.iv.2005. G. Hormiga, F. Álvarez and S. Benjamin. One male and one female specimens SEMFAP031. Photo voucher Figure 2A DSCN7358.  $n = 12$ .

#### *Diphya spinifera* Tullgren, 1902

AMNH: CHILE Región VII Bío-Bío. Ñuble Prov. E. Recinto las Trancas, 1100 m. ii.1987, L. E. Peña. One female used for trachea preparations SEMFAP051. AMNH CHILE Cautín Chacamo NW of Nueva Imperial/W. of Temuco 16-24.ii.1981 L. E. Peña. Two male and two female specimens, one couple illustrated (Fig. 30A-C) the other SEMFAP053.  $n = 7$ .

#### *Diphya* sp.

USNM: TANZANIA: Iringa Distr.; Uzungwa Scarp For. Res., 11 km SE Masisiwe, Kihanga Strm.  $8^{\circ}22'5.7''$ S:  $35^{\circ}58'41.6''$ E, 1800 m 17-27.v.1997. Sweeping. ZMUC-SI Exp. 1997.  $n = 23$ .

#### *Dolichognatha* sp.

MCZ: Chiapas, Ocósingo, Arroyo Nayte Loc 1, Sierra de la Cojolita,  $16^{\circ}47' 36.2''$  N,  $91^{\circ}02' 35.3''$  W EPE06, 202 m. 26.x-2.xi.2005. F. Álvarez, L. Lopardo and J. Castelo leg. Female and web (Fig. 3E) photo voucher DSCN7723  $n = 1$ .

#### *Dolichognatha pentagona* (Hentz, 1850)

AMNH: USA, Miss Forrest Co. Cam = p Shelby. 1945-46 Archer, A. F. Two male and two female specimens, one couple illustrated (Fig. 35A-D) the other SEMFAP045.  $n = 6$ .

*Glenognatha foxi* (McCook, 1894)

AMNH: USA: LA, Hamburg Co. 29.iv.1963. Two male and two female specimens, one couple illustrated (Fig. 40A, B) the other SEMFAP029.  $n = 8$ .

*Leucauge venusta* (Walckenaer, 1841)

GWU: USA: VA, Fairfax County Parkway, Bull Run/Occoquan Trail.vi.-viii.2003 Álvarez, F. One male and two female specimens SEMFAP033. USA, Virginia, Luray, Sheridan School's Mnt. Campus,  $38^{\circ}44'10.40''$  N  $78^{\circ}23'28.81''$  W. 241 m. 3–4.vi.2006. D. Dimitrov, S. Benjamin leg. Male and female specimens illustrated (Fig. 45A–D). USA VA Fairfax Co. Allison Cr. 22030. vi-vii.2003, Álvarez, F. photo vouchers DSCN3055 (Fig. 1C), DSCN3506 (Fig. 1E) and female web (Fig. 3F) DSCN3599.  $n = 16$ .

*Leucauge argyra* (Walckenaer, 1841)

CAS: USA FLA Highlands Co. Archbold Biol. Sta. 11.x.1964 P. H. Arnaud Jr. One male specimen SEMFAP034. MEXICO Nayarit: Highway 15 near Acaponteta 7 mi N junction of Highways 15 and 23 16.x.1973 S. c. Williams, K. B. Blair and Mullinex c. L. #346 (1). Two female specimens SEMFAP054. MCZ DOMINICAN REPUBLIC: La Altagracia Prov., Hoyo Azul, c. 10 km W of Punta Cana. N  $18^{\circ}33'26.5''$ : W  $68^{\circ}26'43.1''$ , 120 m, 5.IV.2005. G. Hormiga, F. Álvarez and S. Benjamin. Male and female specimens illustrated (Fig. 50A–D).  $n = 7$ .

*Mesida argentiopunctata* (Rainbow, 1916)

QMS: S27777, AUSTRALIA North Queensland, Bellender Ker Range, NQ Cable Tower 7, 500 m. 1-7.xi.1981 EARTHWATCH/QLD. MUSEUM. Two female specimens SEMFAP061. S26253 AUSTRALIA North Queensland, Davies, V. E and D Marshall xi.1981. One male specimen SEMFAP037. USNM: AUSTRALIA: SE QLD.; Noosa National Park. Rainforest,  $26^{\circ}23'06''$ S  $153^{\circ}06'01''$ E., 30 m. 5–7.iv.2002. M. Kuntner, F. Álvarez, M. Rix. One male and one female specimens illustrated (Fig. 55A–D). Photo voucher (Fig. 4A) Leuc004b.  $n = 14$ .

*Meta menardi* (Latreille, 1804)\*

UBA: España Vizcaya Sima Europa, galdawes 20.xi.1983 C. Ribera leg. One female specimen SEMFAP042. UBA España Andorra Forat Dorau, Ariusal 24.x.1978 C. Ribera leg. One male specimen SEMFAP076. USNM: USA Conn. From cedar in light field. 5.i.1935 R. Woodbury leg. One female specimen illustrated (Fig. 60C). USNM FRANCE: Pyrenees Orientales; Vernet-les-Bains.  $42^{\circ}33'$  N,  $2^{\circ}23'$  E 22.viii.1989. J.A. Coddington. One male specimens illustrated (Fig. 60A, B).  $n = 6$ .

*Metabus ebanoverde* Álvarez-Padilla, 2007

DOMINICAN REPUBLIC: Constanza, La Vega, Ébano Verde, Loma La Sal,  $18^{\circ}41'49.4''$ N,  $70^{\circ}35'3023.7''$ W, 2274 m, 16.iv.2005, F. Álvarez and B. Suresh leg. photo voucher (Fig. 4B) DSCN7567.  $n = 1$ .

*Metabus ocellatus* (Keyserling, 1864)\*

AMNH: MEXICO Chiapas Prusia iv.-v.1942 1000 m H. Wagner. Two male and two female specimens, one couple illustrated (Fig. 65A–D) the other SEMFAP036.  $n = 20$ .

*Metellina segmentata* (Clerck, 1757)

USNM: DENMARK: Hestehaven, Ronde 22 km NE of Arhus  $56^{\circ}17.46'$  N  $10^{\circ}28.50'$  E 30.viii.1994, Bjorn, Christiansen, Coddington, Griswold, Hormiga, Krat, Langemark, Scharff and Sorensen leg. Two male and two female specimens, one couple illustrated (Fig. 70A–D) the other SEMFAP044.  $n = 4$ .

*Nanometinae* sp.

USNM: AUSTRALIA: SE QLD.; Lamington NP, tracks near O'Reilly's. Rain forest.  $28^{\circ}14'05''$ S  $153^{\circ}08'13''$ E., 920 m. 13–17.iv.2002. G. Hormiga, M. Kuntner, F. Álvarez. Two male and two female specimens, one couple illustrated (Fig. 76A–F) the other SEMFAP049. Photo voucher (Fig. 4A) Nano005.  $n = 8$ .

*Metleucauge eldorado* Levi, 1980\*

AMNH: USA: CA, Cedar Grove King's Canyon 5.vii.1956 W. Gertch and V Roth leg. Two female specimens SEMFAP041. USA: CA. Tulare Co. Cedar Grove 4633 ft. King's River Canyon 16.vii.1956 W. Gertch and V Roth leg. One male specimen SEMFAP075. One female and another male illustrated (Fig. 81A–D)  $n = 6$ .

*Mollemeta edwardsi* (Simon, 1904)

AMNH: CHILE Region de los Lagos X Osorno P. N. Puyehue, Aguas Calientes  $40^{\circ}44'0''$ S  $72^{\circ}18'0''$ W 480 m 21.xi.1993 Platnick, Catley, Ramírez and Allen leg. External anatomy one male (except pedipalp) and one female specimen SEMFAP043. CHILE Region de los Lagos X Osorno P. N. Puyehue, Aguas Calientes 450 m 27 January 86 Platnick, N. I. Goloboff, P. A and R. T. Schuh. Internal anatomy one female specimen SEMFAP060. MACN-AR CHILE: Reg. IX, Prov. Osorno P. Nac. Puyehue, Aguas Calientes. 13–17.xii.1998. M. Ramírez, L. Compagnucci, c. Grismado, L. Lopardo leg. One male and one female specimens illustrated (Fig. 86A–D). USNM: CHILE: Region de los Lagos X. Osorno P. N. Puyehue, Aguas Calientes,  $40^{\circ}44'0''$ S,  $72^{\circ}18'45''$ W, 450 m. 12.xii.2000–2.i.2001. Hormiga, G. leg. Male pedipalp SEMFAP056.  $n = 10$ .

*Nanometa* sp.

QMS: S26367 Bellender Ker Range, NQ Cable Tower 3, 1054 m. 17-24.x.1981 EARTHWATCH/QLD. MUSEUM. Two male and two female specimens, one couple illustrated (Fig. 91A-D) the other SEMFAP048. USNM AUSTRALIA: SE QLD.; Lamington NP, tracks near O'Reilly's. Rain forest. 28°14'05"S 153°08'13"E., 920 m. 13-17.iv.2002. G. Hormiga, M. Kuntner, F. Alvarez. Photo voucher (Fig. 4F) DSCN0492. n = 8.

*Opadometa* sp.

AMNH: PAPUA NEW GUINEA: Louisiade Arch. Misima Island, North slopes of Mt. Misima 350 M. Camp #7. 16-30.vii.1956. Fifth Archbold Exp. To Papua New Guinea L. J. Bass leg. Two female specimens SEMFAP038. PAPUA NEW GUINEA: Louisiade Arch. Misima Is, north slopes of Mt. Misima, 350 m, Camp 7. 16-30.vii.1956, Fifth Archbold Expedition, Brass leg. One female illustrated (Fig. 95E). SOUTH WEST PACIFIC: 1986-87, Krauss leg. One male illustrated (Fig. 95A-D). GWU: THAILAND: Chiang Mai Prov., Doi Chiang Dao WS, Amphen Chiangdao, below guest house along road, N 19°19'13.2"; E 98°49'47.0", c. 1500 m, 2.x.2003, ATOL Expedition 2003. Photo voucher (Fig. 5A, B) DSCN3876. n = 4.

## 'Orsinome' sarasini Berland, 1924.

AUM: KS20172 Tasmania Frollentine Valley Punishment Pot 373. 1988. Twilight threshold. S. Eberhard leg. AUM KS28644 Tasmania O, Grady's falls Mt. Wellington 18.viii.1951 W Hickman. One male and two female specimens SEMFAP050. n = 7.

*Orsinome* cf. *vethi* (Hasselt, 1882)\*

AMNH PNG: Louisiade Arch. Rossel Is: south slopes of Mt. Rossel, 400 m., Camp 13 12-20.x.1956. Two male and two female specimens, one couple illustrated (Fig. 104A-E) the other SEMFAP040. GWU: THAILAND: Yala Prov., Bang Lang NP, N 6°11'47.5"; E 101°9'50.9", 270 m, 15.X.2003, ATOL Expedition 2003. Photo voucher (Fig. 5C) DSCN4297. n = 6.

*Pachygnatha autumnalis* Marx, 1884

USNM: USA, MA Quisset Co. 24.iii.1989 R.L. Edwards. One male and two female specimens SEMFAP030. n = 6.

*Tetragnatha* sp.

GWU: Australia: NE QLD. Daintree NP. Cape Tribulation, Marrdja Boardwalk. Mangrove forest.

24.iv.2002 S16.08'16"0.5 m. E 145.26'26" 0.5 m. G. Hormiga, M. Kuntner, F. Alvarez. Photo voucher (Fig. 1B) DSCN1180. n = 1.

*Tetragnatha versicolor* Walckenaer, 1841

GWU: FAP USA: VA, Waterlik 5.5 miles S of 678 rd. 4.v.2005 F. Alvarez. Photo voucher (Fig. 1A) DSCN7721 and (Fig. 5D) DSCN3180. FAP USA: VA, Fairfax County Parkway, Bull Run/Occoquan Trail. vi.-viii.2003 Alvarez, F. Two male and two female specimens, one couple illustrated (Fig. 113A-D) the other SEMFAP028. n = 8.

*Tylorida striata* Thorell, 1877

AMNH: NIGERIA, Abeokouta Prov. Ilugun. 11.xii.1948. SEMFAP039. AUM KS66865 PNG Kairiru Is. 03°20' S 143°33' E. 28.x.1981 O. W. Borrell. KS66865. Two male and two female specimens, one couple illustrated (Fig. 118A-D) the other SEMFAP052. GWU: THAILAND: Nakhon Si Thammarat Prov., Khao Luang NP, N 8°43'25.2"; E 99°40'7.7", 355 m, 10-12.x.2003, ATOL Expedition 2003. Photo voucher (Fig. 5E) DSCN4091. n = 10.

*Theridiidae**Parasteatoda tepidariorum* (C. L. Koch, 1841)

USNM: USA Pennsylvania: Montgomery Co. Bryn Mawr, 629 Pembroke Road. Two female specimens SEMFAP017. USA NC: New Hanover Co. Willmington. Alleys in downtown area. 31.viii.1986. W.F. Adams and C.R. Wilson. Lot 3. One male specimen SEMFAP071 USA Mass. West Concord 4.viii.1957 R. E. Carbill leg. Windows of garage. n = 6.

*Parasteatoda* sp.

MCZ: MEXICO: Chiapas, Ocosingo, Reserva Comunal El Cartón, 16°47' 21.4" N, 90°55' 48.4" W, EPE07 207 m. 26.x-2.xi.2005. F. Alvarez, L. Lopardo and J. Castelo leg. Web of female specimen (Fig. 5F) photo voucher DSCN7996. n = 1.

*Asagena americana* (Emerton, 1882)

USNM: USA Mt. Carmel, Ct. 2.viii.1937 col. By K. Sommerman in nest of Sceliphron. Two female specimens SEMFAP018. One female illustrated (Fig. 136B) n = 6.

*Asagena borealis* (Hentz, 1850)

USNM: USA WV Berkeley County Sleepy Creek Hunt and Fish Area 20-27.vi.1986 Third hill Mtn. Oak-Pine Forest. P. J. Martinat unbaited pitfall trap. One male specimen SEMFAP067. n = 1.

*Theridiosomatidae*

*Epeirotypus brevipes* O. P.-Cambridge, 1894\*

CNAN: MEXICO: Chiapas, Ocosingo, Arroyo Nayte Loc 1, Sierra de la Cojolita, 16°47' 36.2" N, 91°02' 35.3" W EPE06, 202 m. 26.x-2.xi.2005. F. Álvarez, L. Lopardo and J. Castelo leg. Three female and one male specimens SEMFAP020. Female specimen (Fig. 2F) photo voucher DSCN7740; and female web (Fig. 6A) photo voucher DSCN7732.  $n = 8$ .

*Uloboridae*

*Uloborus glomosus* (Walckenaer, 1841)

AMNH: USA: CA, Los Angeles Co. Elizabeth Lake Can. 16.viii.1952. R. X. Schick. Two female specimens SEMFAP003. USA: CA. Fresno San Joaquin Valley. 16.vii.1955. Robert Schick. One male specimen SEMFAP065.  $n = 6$ .