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RESPIRATORY SYSTEM MORPHOLOGY AND THE PHYLOGENY OF HAPLOGYNE SPIDERS (ARANEAE, ARANEOMORPHAE)

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ABSTRACT. The morphology of the respiratory system of basal araneomorph spiders, the Haplogynae and of Entelegynae with female haplogyne genitalia, is reviewed. The homology of cuticular respiratory structures is discussed in light of evidence from abdominal muscles and ontogeny. Ten morphological characters (13 transformations) were coded, mainly from the posterior pulmonary (or tracheal) segment, and other 7 non-respiratory characters here added. The new data were combined with those of a previously published analysis, resulting in a data matrix of 82 characters scored for 44 terminals. The evolution of the tracheal system is traced through the phylogeny of basal spiders and the Haplogynae, and new synapomorphies are provided. Elongate 3rd abdominal entapophyses are a synapomorphy of Araneomorphae. True median tracheae are a synapomorphy of Entelegynae (convergently with Austrochilinae), as is the extreme posterior displacement and narrowing of the tracheal spiracle. Tetrablemmidae, Pholcidae, Diguetidae and Plectreuridae are united by the absence of tracheae; and these taxa are united with Scytodidae, Sicariidae and Drymusidae by the fusion of 3rd entapophyses.

Keywords: Tracheae, cladistics, abdominal muscles

Since the seminal and detailed works of Bertkau (1872, 1878), much attention has been devoted to the respiratory system of spiders. Although the morphology and diversity of respiratory structures was repeatedly used in classifications (e.g., Bertkau 1878; Petrunkevitch 1933; Forster 1970), most attempts to depict the evolution of the respiratory organs in spiders were discouraging because of incongruity with other character systems, which led some authors even to negate the value of the respiratory organs to define higher groups (Lamy 1902; Levi 1967). The efforts were unable to overcome the obstacle of evaluating all character systems simultaneously. Fortunately, cladistic theory has provided the tools to manage all data globally; and the difficult task was recently achieved for basal araneomorphs and haplogyne spiders (Platnick et al. 1991). The aim of this contribution is to investigate once again the evolutionary transformations of the respiratory system through spider phylogeny, testing previous hypotheses of relationships in the light of new data.

Homology and ontogeny of respiratory structures.—Purcell (1909) convincingly demonstrated that lateral tracheae of araneomorph spiders originate as modifications of the posterior book lungs, and median tracheae as modifications of the entapophyses of the same segment. Median tracheae are distinguished from hollowed entapophyses (also called apodemal lobes) by their much more elongate shape, and by their thin cuticle; in some cases they still retain their connection with abdominal muscles (Lamy 1902). There has been some confusion in the literature about the ‘‘transverse duct’’ or ‘‘interpulmonary’’ or ‘‘inter-tracheal canal of communication.’’ In many spiders, the minute projections lining respiratory cuticles (called ‘‘spicules’’) also extend to cover the innermost part of the interpulmonary or inter-tracheal furrow. For the tracheal segment, Purcell (1909: 65) called this ‘‘intertracheal canal of communication,’’ defined as ‘‘a canal connecting the median trunks with one another and with the lateral trunks at their base,’’ and identified the structure as serially homologous with the interpulmonary canal of communication. Other authors (e.g., Forster & Platnick 1984) called the same structure ‘‘transverse duct.’’ If not topologically definite as a ''duct'' (as discussed by Hormiga 1994), this canal becomes a functional duct because the spicules prevent the smooth anterior and posterior walls of the furrow or tracheal vestibule from collapsing together (Purcell 1909: fig. 26). I will follow here the original and accurate wording of Purcell.

METHODS

Tracheae and other cuticular structures were observed after digestion of tissues with a 10–20% KOH solution at approximately 100 °C in a double boiler or hot plate. Dissections for muscle observations were made on regular alcohol-fixed specimens. Small structures were mounted in lactic acid or clove oil, and observed with a compound microscope. This analysis complements Platnick et al. (1991), and so numbers for characters follow that paper.

RESPIRATORY SYSTEMS OF THE REPRESENTATIVE TAXA

Most data on tracheae, entapophyses and muscle attachments were extracted from the general works by Lamy (1902), Purcell (1909, 1910), Kästner (1929), and references therein. Data on particular groups were found in Forster et al. (1987: Austrochiloidea, Hypochiloidea), Ramírez & Grismado (1997: Filistatidae), Forster (1995: Scytodidae, Drymusidae, Sicariidae and Periegopidae), Platnick (1989: Diguetidae), Forster & Platnick (1985: Dysderoidea), Forster & Platnick (1984: Palpimanoidea), Platnick et al. (1999: Palpimanidae), and Forster (1970: Entelegynae). The new data are discussed below.

Austrochilinae: There is a wide furrow linking three paired structures (Fig. 4), described by Forster et al. (1987): ''the inner pair are in fact apodemes [. . .]. The middle pair of tubes (those immediately lateral to the apodemal lobes) could be homologous with one of the book lung lamellae, but the outer pair are more likely to represent the marginal extensions of the original atrial pouch, which in most spiders [. . .] tend to be arcuate.'' Their interpretation agrees with my observations. The inner pair connects with the median longitudinal muscles. In the early instars of *Thaida peculiaris* Karsch 1880 the intermediate pair arises during ontogeny as a flat outgrowth of the more lateral pair (Fig. 3). All these structures are lined with spicules, including an inter-tracheal canal. In subsequent stages the modified entapophyses are indistinguishable from the true median tracheae found in Entelegynae.

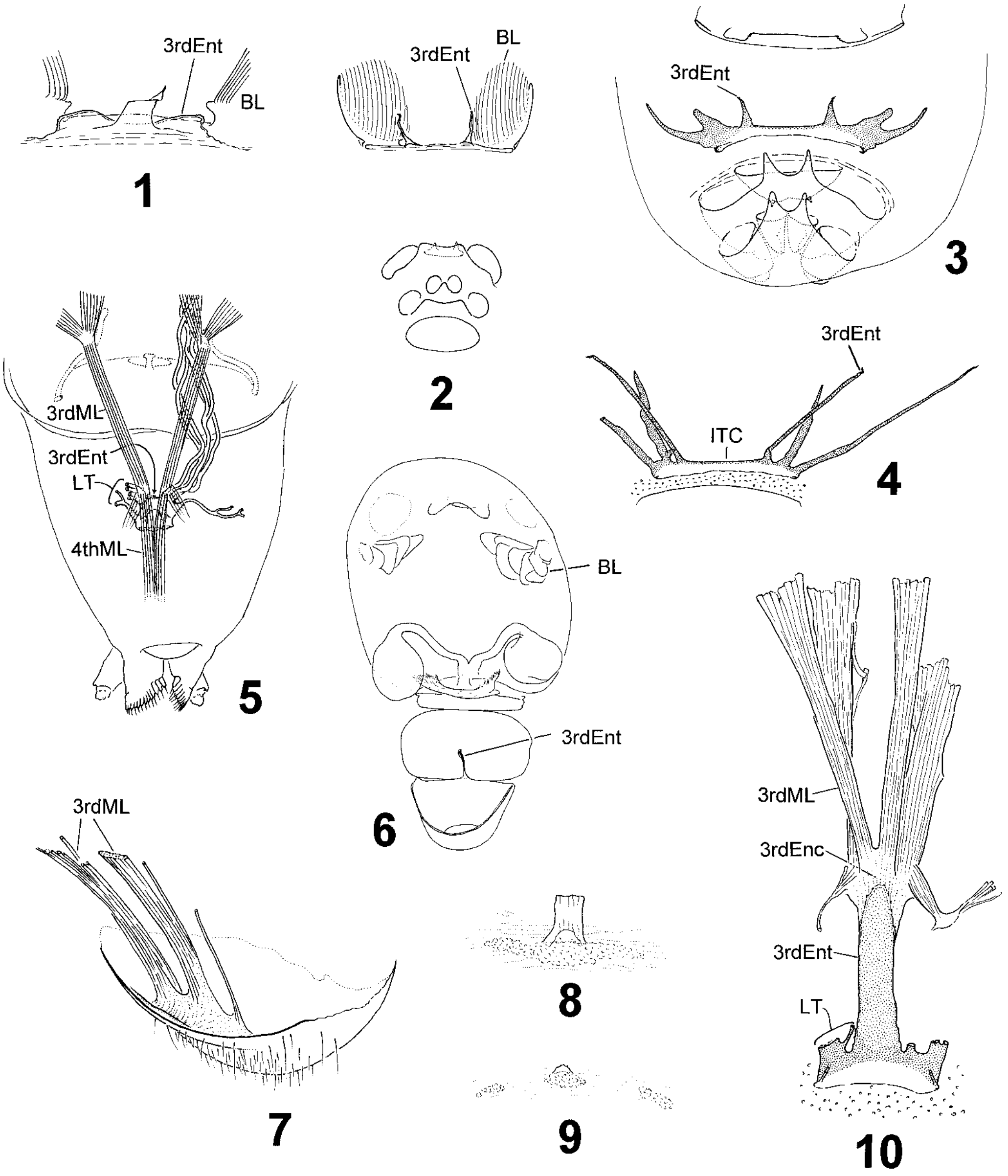
Sicariidae: In *Loxosceles laeta* (Nicolet 1849) and *Sicarius* Walckenaer 1847 spp. (from Argentina), there is a median structure homologous with the two fused entapophyses, similar to that found in *Drymusa* Simon 1891 and *Scytodes* Latreille 1804, but more elongate and thick. I found in both sicariids the expected attachment of the median longitudinal muscles that converge on the fused entapophyses (Fig. 10).

Tetrablemmidae: Platnick et al. (1991) coded the respiratory characters of *Caraimatta* Lehtinen 1981 according to the description of *Brignoliella* Shear 1978 given by Forster & Platnick (1985). It seems that they confused the ducts of the female genitalia, or the paired pits of the preanal plate, with tracheae or spiracles. In *Brignoliella* cf. *carmen* Lehtinen 1981 (from New Caledonia), and in *Caraimatta* cf. *cambridgei* (Bryant 1940), the only remnant of tracheal system is a median apodeme (Fig. 6), in agreement with Shear (1978). I also found a similar apodeme in an unidentified Pacullinae from Borneo.

Diguetidae and Plectreuridae: A transverse external mark indicates the place where longitudinal muscles attach, on a wide line of the abdominal cuticle (Fig. 7). The entapophyses appear to have lost, in some degree, their function of main site of muscle attachment. In *Kibramoa* Chamberlin 1924 (Fig. 8) and *Plectreurys* Simon 1893 (Fig. 9) the entapophyses are still recognizable as a short median lobe. In *Diguetia catamarquensis* (Mello-Leitão 1941) and *Segestrioides tofo* Platnick 1998 the marks on the cuticle are similar to those of Fig. 9, but the median lobe is almost unrecognizable.

Telemidae: My dissections of *Usofila* sp. (from California) showed a tracheal pattern like that of *Telema* Simon 1882, as described by Fage (1913).

Ochyroceratidae: Ochyrocera Simon 1891 sp. has two groups of 4–5 tubes each arising from each anterior corner of a characteristic trapezoidal vestibule (Fage 1912: fig. 73), one of them posteriorly directed. In the space between these groups, I found a pair of short



Figures 1–10.—Posterior respiratory system and abdominal structures. 1. *Liphistius sumatranus* Thorell 1890, exuvia of female, detail of 3rd abdominal entapophyses on posterior interpulmonary furrow; 2. *Hypochilus* cf. *gertschi* Hoffman 1963, female from Virginia, Giles County, posterior respiratory system and spinneret's bases; 3. *Thaida peculiaris*, first free instar, posterior respiratory system and spinneret's bases; 4. *Thaida peculiaris*, subadult male, detail of posterior respiratory system; 5. *Ochyrocera* sp., female from Minas Gerais, dissected and cleared abdomen, showing median longitudinal muscles and tracheal system; 6. *Caraimatta* cf. *cambridgei*, female from Costa Rica, digested abdomen, dorsal view; 7. *Diguetia catamarquensis*, female, dissected abdomen, anterior-lateral view, showing insertion of median longitudinal muscles; 8. *Kibramoa* sp., female from California, 3rd entapophysis and muscle insertion area; 9. *Plectreurys* sp., female from Costa Rica, muscle insertion area; 10. *Loxosceles laeta*, posterior respiratory system showing muscle insertions (lateral tracheae broken). *Abbreviations:* 3rdEnc = entochondrite at hind end of third median longitudinal muscle; 3rdEnt = third entapophysis; 3rdML = third median longitudinal abdominal muscle; 4thML = fourth median longitudinal abdominal muscle; BL = book lung; ITC = inter-tracheal canal; LT = lateral tracheae.

entapophyses, where the longitudinal muscles connect (Fig. 5).

Archaeidae: The reduced tracheal system of *Archaea workmani* (O. P.-Cambridge 1881) consists of two separate spiracles each leading to a slender median tracheae, without a transverse furrow (Forster & Platnick 1984). I found the apex of these structures widened and fibrose, typical of muscle insertions.

CLADISTIC ANALYSIS

The present data matrix includes the 43 terminals from Platnick et al. (1991), plus *Pikelinia roigi* Ramírez & Grismado 1997 (Filistatidae, Prithinae) and a root vector, all scored for 80 characters. The first 67 characters are those used in that paper; only modifications and additional characters are listed below. The root vector specifies the states plesiomorphic for Mygalomorphae and Liphistiomorphae. Polymorphisms were used to express variability in the taxa represented by the selected exemplars, and internal steps were added to account for the homoplasy while computing weights. If a representative species does not has a condition known to occur in the family it represents, I followed a strategy similar to that of Platnick et al. (1991), but coding polymorphic entries. Polymorphisms were assigned according to notes in Platnick et al. to characters 23 (in *Oecobius* Lucas 1846), 36 (in *Dysdera* Latreille 1804 and *Otiothops* Macleay 1839), and 65 (in *Pholcus* Walckenaer 1805), and checked to ensure none required illogical optimizations. Except as noted, all characters were treated as unordered.

Character 1: Cribellum: present (0); absent (1). *Gradungula* Forster 1955 and *Pianoa* Forster 1987 are coded as 1, although the primitive state for the gradungulids should be 0. This coding does not produce an illogical optimization, as the lost cribellum appears as synapomorphy of both genera. *Character 16:* Posterior book lungs or modifications: pair of normal book lungs (0); pair of book lungs reduced to two lamellae (1); pair of lateral tracheae (2); absent (3). Filistatines are coded [012] because the homology of their short, flattened lateral structures are unclear (Purcell 1910: 558; Forster et al. 1987: 93). *Character 18:* Opening(s) of posterior respiratory system, or position of 3rd abdominal entapophyses: about midway between anterior book lungs and spinnerets (0); just behind openings of anterior respiratory system (1); just anterior to spinnerets (2). The root is coded as [02] because the openings of posterior book lungs are just anterior to the spinnerets in Liphistiomorphae, but separated from them in Mygalomorphae. *Character 20:* Cheliceral gland mound: absent (0); present (1). The putative parallelism in *Crassanapis* Platnick & Forster 1989 was coded as 1 (Platnick & Forster 1989: fig. 11). *Character 32:* Posterior spiracles or origin of 3rd abdominal entapophyses: separate (0); contiguous (1); fused (2). This character expresses the degree of fusion of the formerly bilateral posterior respiratory organs, and is, accordingly, coded as ordered. The position of apodemes serves to discriminate between states in those cases where there is a median transverse furrow, but two interpretations (a wide median spiracle, or two spiracles linked by a furrow) are possible. *Diguetia* Simon 1895 and *Segestrioides* Keyserling 1883 are coded as uncertain because they lack definite cuticular apodemes, and the longitudinal muscles insert on a wide line. *Appaleptoneta* Platnick 1986 is also coded as uncertain because its respiratory system is unknown, and *Leptoneta* Simon 1872 has no evidence of apodemes (Lamy 1902: fig. 16). *Otiothops* is coded [12] because of the variability found in Otiothopinae (Platnick et al. 1999). *Character 45:* Cribellum: entire (0); divided (1). *Gradungula* and *Pianoa* Forster 1987 are coded as inapplicable, with the same provisions as in character 1. Gray (1995) noted the curious optimization of the entire cribellum as primitive, given that it is homologous with paired anterior median spinnerets. Interestingly, first free instars of *Thaida peculiaris* show a bilobate cribellum, with only one spigot on each side (Fig. 3). *Character 67:* 3rd abdominal entapophyses: short, flat or absent (0); elongate (Fig. 2) (1). I added one internal step to the character because other pholcids lack the entapophyses (Lamy 1902). *Character 68:* Shape of fused 3rd abdominal entapophyses: short, slender (0) (Lamy 1902: fig. 14); elongate, broad (1) (Fig. 10). *Character 69:* Median tracheae: absent (0); present (1). *Character 70:* Transverse furrow between posterior spiracles: present (0); absent (1). The furrow is present in arachnid outgroups and Liphistiomorphae (Fig. 1), but absent in all Mygalomorphae (e.g., Purcell 1910: 525; Forster et al. 1987: 93). It is coded as present in those groups with a single median spiracle whenever it is still possible to discern a furrow not lined with spicules. Some authors that overlooked that furrow interpreted the structures as two separate spiracles (e.g., Millidge 1986; revised by Hormiga 1994). *Character 71:* Inter-tracheal canal: absent (0); present (1). Scored as uncertain in those terminals without spicules through the tracheal system. *Mallecolobus* Forster & Platnick 1985 is coded [01], as the canal is present in *Orsolobus* Simon 1893 and *Falklandia* Forster & Platnick 1985, but absent in *Mallecolobus* and other orsolobids (Forster & Platnick 1985: 225). The same is true for *Segestria* Latreille 1804, as the canal is present in *Ariadna* Audouin 1826 (op. cit.). *Character 72:* Dysderoid lateral tracheae: absent (0); present (1). Each tracheal spiracle connects with a broad trunk anteriorly directed. At its base arises a small trunk that provides tracheoles to the posterior part of the abdomen. Also present in caponiids (Purcell 1910). *Character 73:* Bunch of prosomal tracheoles on lateral tracheae: absent (0); present (1). Typical of dysderoids and Caponiidae. *Character 74:* Anterior book lungs: present (0); transformed into tracheae (1). *Ochyrocera* is coded as [01], as *Theotima* sp. (from Argentina) have tracheae (pers. obs.), but at least some *Ochyrocera* have lung leaves still recognizable. *Character 75:* 3rd dorsoventral abdominal muscles: present (0); absent (1). Although present in Liphistiomorphae and related arachnids, it is coded as [01] for the root, because some Mygalomorphae (at least) seem to lack these muscles (*Acanthogonatus centralis* Goloboff 1995, and unidentified Theraphosidae, pers. obs.). Abdominal musculature was studied in only a few taxa. The muscles were not found in normal dissections of *Gradungula sorenseni* Forster 1955, *Scytodes* sp. (from Buenos Aires), *Diguetia catamarquensis*, *Mecysmauchenius segmentatus* Simon 1884 and *Otiothops birabeni* Mello-Leitão 1945, but these observations must be considered preliminary until more refined techniques are employed. Filistatids were coded according to Ramírez & Grismado (1997). All other codings are from Millot (1936). *Character 76:* Leg autospasy: between coxa and trochanter (0); between patella and tibia (1). *Hypochilus* Mark 1888 is coded as uncertain, because it lacks definite regions for leg autospasy (Petrunkevitch 1933: 347). *Character 77:* Excavation between male palpal femur and trochanter, into which the embolus fits (Ramírez & Grismado 1997): absent (0); present (1). *Character 78:* Three synapomorphies for Filistatidae (Gray 1995; Ramírez & Grismado 1997): absent (0); present (1). *Character 79:* Supra-anal organ: absent (0); present (1). A synapomorphy of Diguetidae (Lopez 1983; Platnick 1989). *Character 80:* Bipectinate claws: absent (0); present (1). Coded as [01] in *Dysdera* because the single row of teeth in dysderids seems to retain traces of two rows (Forster & Platnick 1985: 218). *Character 81:* Proprioceptor bristles on tarsi: absent (0); present (1). A synapomorphy of orsolobids plus at least some oonopids (Forster & Platnick 1985: 219, 227; Platnick et al. 1991: 67).

The data matrix of Table 1 was analyzed under parsimony using implied weights (Goloboff 1993, 1995), using Pee-Wee version 3.0 (Goloboff 1999). This program assigns lower weight to characters with more homoplasy. Internal steps of characters were assigned as implied by polymorphic terminals with command *ccode=*. The same tree of Fig. 11 is found for any value of the constant of concavity *K* ($1 \leq K \leq 6$). Under $K = 3$, 80% of the independent replications of Wagner trees followed by TBR branch swapping (command *mult*N;*) produces the same optimal tree, thus it is likely an exact solution. The tree is 243 steps long, which is two steps longer than the 20 trees obtained under equal weights with Nona (Goloboff 1999). In these trees, steps are saved in some homoplasious characters (like the anterior median eye loss, and the inter-tracheal canal) at expenses of less homoplasious ones (independent acquisition of retrolateral tibial apophysis, and reversion to a primitive tapetum).

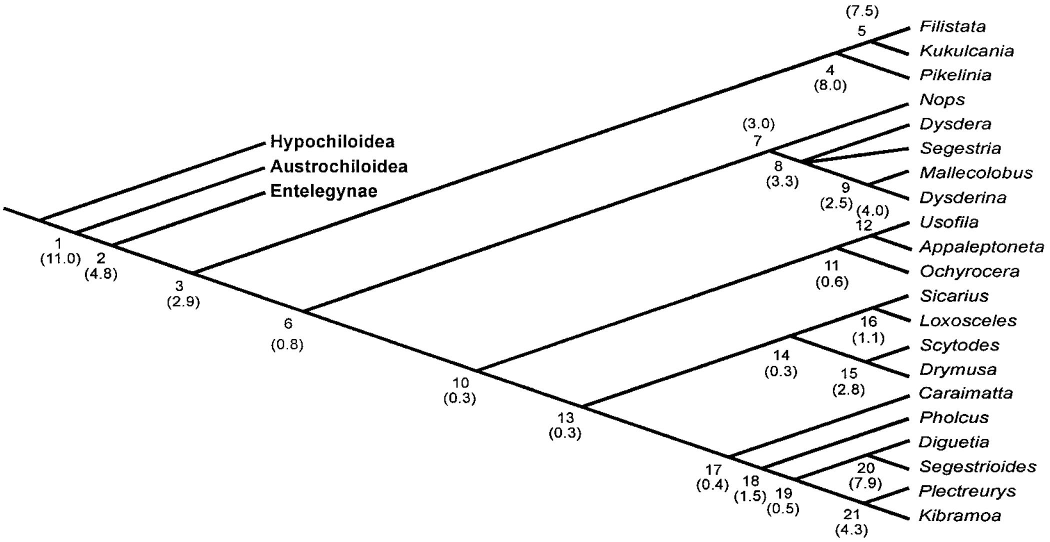
DISCUSSION

Forster (1995) discussed the phylogeny of haplogyne spiders proposed by Platnick et al. (1991) in the light of additional characters from the tracheal system. He proposed the group Sicarioidea coincident with Simon's (1893) Sicariidae, composed by Sicariidae, Scytodidae, Periegopidae, Drymusidae, Plectreuridae, and Diguetidae, all united by the fusion of the third entapophyses. The present analysis that takes into account all characters

Table 1.—Modifications and additional characters for the data matrix of Platnick et al. (1991). *Pikelinia* scores as *Kukulcania* for all characters not shown here. v = [01], w = [012], x = [12], y = [02], ? = unknown, − = inapplicable. Prior weight applied as: character 27 (weight 10), 28(14), 28(2), 51(5), 76(3). Internal steps implied by polymorphisms as: character 23, 32, 33, 39, 65, 67, 74, 80 (1 step); 36, (2 steps); 70 (4 steps); 71 (3 steps).

Character	16	18	32	67	70	75	80
root	0	y	0	000	00000	v0000	00-
Hypochilus	0	0	0	1-0	00000	0-000	000
Ectatostisca	0	0	0	1-0	0?000	10000	00?
Gradungula	0	0	0	1-0	00000	10000	00-
Pianoa	0	0	0	1-0	0?000	?0000	00-
Hickmania	0	0	0	1-0	0?000	?0000	00?
Austrochilus	1	0	0	1-1	01000	?1000	001
Thaida	1	0	0	1-1	01000	?1000	001
Pikelinia	3	0	0	1-0	1-000	01100	00?
Filistata	w	0	0	1-0	01000	01110	000
Kukulcania	w	0	0	1-0	01000	01110	000
Scytodes	2	0	2	100	01000	10000	10-
Sicarius	3	0	2	110	––000	10000	00-
Drymusa	2	0	2	100	01000	?0000	00-
Loxosceles	2	0	2	110	01000	10000	00-
Diguetia	3	0	?	000	––000	10001	00-
Segestrioides	3	0	?	000	––000	?0001	00-
Plectreurys	3	0	2	000	––000	?0000	00-
Kibramoa	3	0	2	000	––000	?0000	00-
Pholcus	3	0	1	000	––000	10100	00-
Caraimatta	3	0	2	100	––000	?0000	00-
Nops	2	1	0	000	01111	?0000	00-
Ochyrocera	2	0	1	000	0-00v	?0000	00-
Segestria	2	1	0	000	vv110	10000	00-
Dysdera	2	1	0	000	10110	10000	v0-
Mallecolobus	2	1	0	000	vv110	?0000	11-
Dysderina	2	1	0	000	01110	?0000	11-
Appaleptoneta	2	0	?	?-?	0?000	?1000	00-
Usofila	2	0	0	?-?	10000	?0000	00-
Archaea	3	0	0	1-1	10000	?0000	00-
Mecysmauchenius	2	0	1	1-1	01000	10000	00-
Tricellina	2	2	1	1-1	01001	?0000	00-
Huttonia	2	0	2	111	01000	?0000	00-
Othiotops	2	0	x	000	01000	10000	00-
Waitkera	2	0	1	1-1	01000	00000	001
Tetragnatha	2	2	1	1-1	01000	10000	00-
Crassanapis	2	2	1	1-1	01000	?0000	00-
Oecobius	2	2	1	1-1	01000	00000	001
Stegodyphus	2	2	1	1-1	01000	00000	001
Deinopis	2	2	1	1-1	01000	?0000	001
Dictyna	2	0	1	1-1	01000	00000	001
Callobius	2	2	1	1-1	01000	?0000	001
Araneus	2	2	1	1-1	01000	00000	00-
Mimetus	2	2	1	1-1	01000	?0000	00-
Pararchaea	2	2	1	1-1	01000	?0000	00-

from both sources (but revises some observations), yields intermediate results. In agreement with Forster's hypothesis, my analysis retrieves a monophyletic group with fused entapophyses, but including Tetrablemmidae, after the re-examination of their tracheal system. However, the placement of Pholcidae coincides with that of Platnick et al. 1991. It must



Figures 11.—Optimal cladogram for the representative taxa. Bremer support in terms of Fit are given on each node.

be noticed that the differences between my results and those of Platnick et al. involve groups with relatively low Bremer support (Bremer 1994; values on Fig. 11), which might be the most prone to change should new characters (e.g., from female genitalia) or representatives (e.g., from Pacullinae and Theotiminae) be added.

The elongate entapophyses (char. 67) are a synapomorphy of Araneomorphae, with a subsequent reversion in the Haplogynae other than filistatids (node 6), and regain in Scytodidae, Sicariidae and Tetrablemminae as a central, fused element (see below). Confirming the hypothesis of Purcell (1909), the short apodemes of Segestriidae (and their relatives) are reduced entapophyses rather than reduced median tracheae. As supposed by the same author, the loss of the transverse furrow (char. 70) is a synapomorphy of the suborder Mygalomorphae, with parallelisms in some isolated araneomorph groups. Although homoplasy seems to be rampant in this character, no parallel gains of a transverse furrow have been mapped. The inter-tracheal canal appears in Araneoclada or Neocribellatae (ambiguous optimization), and is independently lost in several araneocladan clades. Lateral tracheae (char. 16 -state 2) are a synapomorphy of Araneoclada (node 2), whereas the reduction of posterior book lungs to two pulmonary leaves (char. 16-1) is a synapomorphy of Austrochilinae.

Within the Haplogynae, filistatines (node 5) were repeatedly described as having some relict of book lungs instead of lateral tracheae. Because the optimization of the character gives state 2 at the base of Filistatinae, the congruence criterion suggests that these structures are homologous with lateral tracheae. The 3rd dorsoventral abdominal muscles (char. 75) have been lost several times in this tree, but were never found in haplogynes other than Filistatidae. The loss of lateral tracheae (char. 16-3) is a synapomorphy of node 17, with parallelism at least in Prithinae (*Pikelinia* Mello-Leotão), *Sicarius*, and dictynids. The advanced spiracles (char. 18-1) are a synapomorphy of caponiids (*Nops* MacLeay 1838) and Dysderoidea (node 8), but the placement of Tetrablemmidae (*Caraimatta*) is different from that of Platnick et al. because of the reexamination of the tracheal system of tetrablemmids. The fused entapophyses (char. 32-2) are a synapomorphy of node 13 plus Periegopidae; this last group was not included here but seems to be the undisputed sister group of Scytodidae (Forster 1995). For this data matrix there is a reversion to state 1 in *Pholcus*, but conditions in other pholcids range from a pair of contiguous entapophyses linked by a furrow, to the smooth concave cuticle serving directly as the site for muscle attachment. Further elongation of the fused entapophyses is a synapomorphy of Sicariidae. All book lung reductions (char. 74) have independent origin for this data set.

Three characters of the respiratory system are synapomorphies of Entelegynae: The first is the extreme posterior displacement of the spiracle (char. 18-2), with homoplasy in several palpimanoids, dictynids, Uloboridae, and many derivative groups not included in the analysis. The second is the contiguous median tracheae (homologous with 3rd entapophyses, char. 32-1), although the same state appears to arise convergently (but without true median tracheae) in *Ochyrocera* and *Pholcus*. The third is true median tracheae (char. 69), with a notable convergence in Austrochilinae.

A scenario of the morphological transformations leading to the median tracheae can be traced by optimizing characters on the phylogeny. Basal spiders (and closer outgroups) have hollowed thick entapophyses, arising from an interpulmonary furrow. The entapophyses elongated in Araneomorphae. The spicules typical of respiratory cuticles extended from posterior book lungs (in an ancestor of the Neocribellatae) or from lateral tracheae (in an ancestor of Araneoclada) to line the furrow, forming an inter-tracheal canal. At the same time, or later in some ancestor of the Entelegynae, the spicules lined also the interior surface of entapophyses, that became elongated and slender, with thin cuticle, forming the median tracheae. This transformations series was hypothesized by Purcell as early as 1909.

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