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

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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, Di- guetidae and Plectreuridae are united by the absence of tracheae; and these taxa are united with Scytodidae, Sicaridae 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 araneomorph 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 to-
Pologically 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), Käästner (1929), and references therein. Data on particular groups were found in Forster et al. (1987: Austrochiloidea, Hypochiloidea), Ramirez & Grismado (1997: Filistatidae), Forster (1995: Scytodidae, Drymusidae, Sicariidae and Periegosipidae), Platnick (1989: Duguetidae), Forster & Platnick (1985: Dysderoidea), Forster & Platnick (1984: Palpimanidae), Platnick et al. (1999: Palpimanoidea), 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 apodermal 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 *Drymusia* 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).

**Tetramelemmidae:** Platnick et al. (1991) coded the respiratory characters of *Caramaitta* 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 *Caramaitta* 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.

**Duguetidae 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 *Plectreurus* Simon 1893 (Fig. 9) the entapophyses are still recognizable as a short median lobe. In *Diguettia* 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 *Usofita* 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
entapophyses, where the longitudinal muscles connect (Fig. 5).

Archaea: The reduced tracheal system of Archaea workmani (O. P.-Cambridge 1881) consists of two separate spiracles each leading to a slender median trachea, 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 Pinikelinia 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 pleisiomorphic 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 have 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 Liphistiomorphae), but separated from them in Mygalomorphae. Character 20: Cheliceral gland mounding: 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. Diguettia 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). Gradingula 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, slender (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: Intert-tacheal 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 Forster & Platnick 1985 is coded colobus spicules through the tracheal system. Scored as uncertain in those terminals without ter-tracheal canal: absent (0); present (1).

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 dorso-ventral 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 Millott (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 (Petrunkевич 1933: 347).

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 Sicariioidea coincident with Simon’s (1893) Sicariidae, composed by Sicariidae, Scytodidae, Periegopidae, Drymusidae, Plectreuridae, and Diguetiidae, all united by the fusion of the third entapophyses. The present analysis that takes into account all characters
from both sources (but revises some observations), yields intermediate results. In agreement with Forster’s hypothesis, my analysis retrieves a monophyletic group with fused en-
tapophyses, 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
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 relic 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-Leota), 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 re-examination of the tracheal system of tetrableminds. 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 cu-
ticle 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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