The Respiratory Complementarity of Spider Book Lung and Tracheal Systems

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ABSTRACT   Like most spiders, members of the orb-weaving family Uloboridae have a dual respiratory system. Book lungs oxygenate the hemolymph and tracheae carry oxygen directly to tissues. Most members of the family are characterized by an extensive tracheal system that extends into the prosoma, where branches enter the legs. A comparison of both absolute and size-specific indices of these two respiratory components in six uloborid species using the independent contrast method shows that their development is inversely related and indicates that these two systems are complementary. Species that more actively monitor reduced webs have tracheae with greater cross sectional areas and book lungs with smaller areas than do orb-weaving species that less aggressively manipulate their webs. Thus, the acuteness of a spider's oxygen demands appears to influence the development of its respiratory components. As the tracheae assume more responsibility for providing oxygen the book lungs become less well developed and vice versa. J. Morphol. *236*:57–64, 1998.   © 1998 Wiley-Liss, Inc.

KEY WORDS: book lung, independent contrast, spider, tracheae, Uloboridae

The respiratory system of primitive spiders, such as tarantulas and trapdoor spiders, consists of two pairs of opisthosomal book lungs. Oxygen diffuses across the cuticular leaves of the lungs into the hemolymph, which carries it to the tissues (Levi, '67; Moore, '76; Anderson and Prestwich, '80, '82; Hexter, '82; Foelix, '96). However, in most spiders (members of the Tracheospira clade, *sensu* Platnick, '77) the second pair of book lungs is replaced by a tracheal system that allows oxygen to diffuse directly to the tissues (Foelix, '96). Tracheae not only provide a more direct supply of oxygen, but, in spiders whose tracheae extend into the prosoma, a supply that is not interrupted during periods of activity when hemolymph exchange between the opisthosoma and prosoma is interrupted (Wilson and Bullock, '73; Anderson and Prestwich, '75). The development of the tracheal system differs greatly among spiders (Forster, '70; Bromhall, '87) and differences in tracheal development may be observed even within the members of a single family. For example, the plesiomorphic tracheal pattern in the orb-weaving spider family Uloboridae consists of a well-developed system whose tracheae extend into

the legs (Fig. 1; Opell, '79). In members of the genera that actively manipulate reduced webs, the tracheal branches that enter the legs are particularly large, presumably to meet the greater oxygen demands imposed by this prey capture strategy (Opell, '87a,b). In more derived orb-weaving genera, the tracheal system is confined to the opisthosoma.

As a spider's total respiratory needs are met by its book lung and tracheal systems, Opell ('90) has suggested that these are complementary systems. That is, in spiders where the more acute oxygen demands of certain tissues are met by a well developed tracheal system, the book lungs will be required to provide less oxygen and, therefore, will be less well developed than in spiders with less extensive tracheal systems. The data provided by Opell ('87a, '90) support this hypothesis, by showing that spiders with
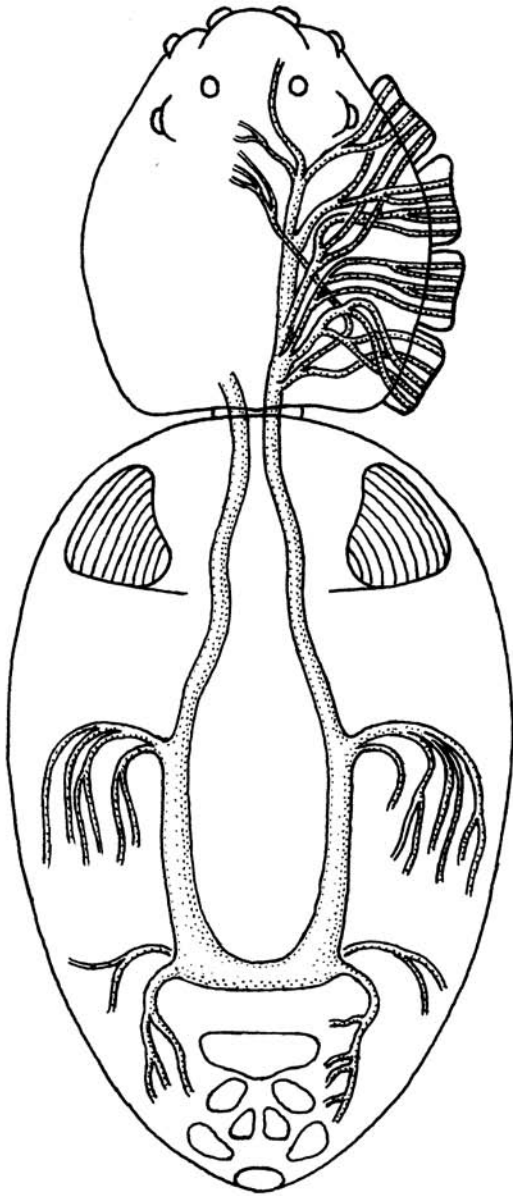
Fig. 1. The respiratory system of a *Uloborus glomosus* female, showing the book lungs in the anterior region of the opisthosoma and a well developed tracheal system extending into the legs.

well developed tracheal systems tend to have book lungs with smaller surface areas and those with simpler tracheal systems tend to have book lungs with larger surface areas. However, statistical tests have not been used to test this hypothesis.

This study uses the comparative method (Harvey and Pagel, '91) to more rigorously test in a phylogenetic context the hypothesis of respiratory complementarily in the book lung and tracheal systems of members of the spider family Uloboridae. The family Uloboridae provides an appropriate test of this hypothesis, as its members exhibit the full range of respiratory diversity found in tracheospira spiders (Opell, '79, '87a; Bromhall, '87) and as the relationship among its genera is known (Coddington, '90). Additionally, as members of this family exhibit a small range in body mass (6.8–14.5 mg for species included in this study), the effect of interspecific size difference is minimized. However, to account for these differences indices of both absolute and size-specific book lung and tracheal development are analyzed.

MATERIALS AND METHODS
Species studied

Six species are included in this study. The orb-weaving species *Waitkera waitakerensis* (Chamberlain, '46) and *Uloborus glomosus* (Walckenaer, 1841) exhibit the family's plesiomorphic tracheal condition, consisting of small tracheal trunks that extend from the opisthosoma into the prosoma and enter the legs. The triangle-web species *Hyptiotes cavatus* (Hentz, 1847) and the simple-line species *Miagrammopes amimotus* Chickering, '68 have very large prosomal tracheae that enter the legs. Tracheae of the orb-weaving species *Octonoba sinensis* (Simon, 1880) and *Philoponella tingena* (Chamberlin and Ivie, '36) are restricted to the opisthosoma.

Respiratory indices

This study compares both absolute and size-specific indices of book lung and tracheal systems (Table 1). Total book lung surface area was used as an index of book lung development, as it quantifies the surface over which oxygen can diffuse (Opell, '90). Opell ('87a) provides three indices of tracheal development: 1) the cross sectional area of tracheae that enter a spider's prosoma from its opisthosoma, 2) the cross sectional areas of tracheae that enter each of a spider's legs, and 3) the cross sectional area of the tracheae that enter each leg divided by the square root of the distance from the abdominal tracheal spiracle to the coxa of that leg. As the latter index accounts for both the distance over which oxygen must diffuse and the rate of diffusion (Schmidt-

Nielsen, '79; Anderson and Prestwich, '80), it is the best measure of the tracheal system's ability to supply oxygen to the active leg muscles. Therefore, I use the sum of this index for a spider's four legs as an index of the development of its tracheal system.

Opell ('90) does not provide a size specific index for tracheal development and the two size-specific indices that are given for book lung development (book lung area divided by prosomal and leg mass and book lung area divided by the product of carapace length and carapace width) do not account for the size of the spider's opisthosoma. To obtain a size-specific index of tracheal development, I divided the total cross sectional area of the tracheae entering each leg by the volume of the leg's femur and then divided this value by the square root of the distance from the spider's spiracle to that leg's coxa. The sum of these indices for a specimen's four legs was used as a size-specific index of a spider's tracheal development. Femur volume was chosen because, for all legs, this article has the greatest muscle mass and contributes significantly to the force of leg flexion. To determine femur volume, I measured a femur's length and its maximum and minimum dorsal-ventral width to the nearest 40 μm under a dissecting microscope and computed femur volume as the volume of a cylinder with a diameter equal to the femur's average width. The mean femur volumes of five specimens were used to calculate the size-specific tracheal development of each species (Table 2).

As a size-specific index of book lung development, I divided each species' book lung area by its live mass raised to a power of 0.80 (Table 1). This function describes the relationship between a spider's mass and its metabolic rate (Anderson and Prestwich, '82) and is, therefore, an appropriate measure of the book lung's ability to meet a spider's

respiratory demand. Opell ('90) does not give live masses for *Waitkera waitakerensis* and *Philoponella tingena*. The former value was added from Opell ('96) and the latter was estimated from the known live masses of the other three orb-weaving species and the prosomal and leg masses given by Opell ('90). For the three orb-weaving species, the mean ratio of live mass to prosomal and leg mass is 4.33. When this ratio is multiplied by the prosomal and leg mass of *P. tingena* (2.84 mg), an estimated live mass of 12.30 mg is obtained. Only orb-weaving species were used to compute this ratio, as their body shapes are very similar, whereas the shapes of *Hyptiotes* and *Miagrammopes* are quite different.

Comparative methodology

I used the independent contrast method of Felsenstein ('85), as implemented by the Contrast routine of the Compare 1.1 program of Martins ('95), to examine the relationship between book lung and tracheal development. Through a series of pair-wise contrasts between sister clades, this algorithm transforms interspecific comparative data into a set of normally distributed, independent, and standardized contrast values that meet the assumptions of parametric statistical tests (Harvey and Pagel, '91; Garland et al., '92).

The phylogeny used in this analysis (Fig. 2) was taken from Coddington ('90) and was pruned to include only the genera included in this study. As Coddington's phylogeny does not provide branch lengths, I determined these values using the trace all characters option of the MacClade 3.02 program of Maddison and Maddison ('92). For this, I used the 42 characters from Coddington's analysis (characters 3, 5, 9, 10, 11, 12, 13, 14, 15, 18, 19, 20, 24, 25, 26, 27, 28, 29, 30, 31, 32, 36, 37, 38, 41, 43, 53, 54, 55, 56, 57, 60, 62,

TABLE 1. *Absolute and size-specific indices of the book lung and tracheal development of six uloborid species*

	Waitkera waitakerensis	Hyptiotes cavatus	Miagrammopes animotus	Uloborus glomosus	Octonoba sinensis	Philoponella tingena
ε tracheal area μm² (Opell, '87a)	890	1252	1811	855	0	0
ε tracheal area μm²/√ distance μm (Opell, '87a)	17.32	30.07	31.28	20.62	0	0
ε Area/Volume/√ Distance of femurs of Legs (from Table 2)	125.73	265.18	267.29	189.53	0	0
Book lung area mm² (Opell, '90)	2.53	2.08	2.98	3.77	7.47	6.97
Spider mass mg	7.70 (Opell, '96)	6.76 (Opell, '90)	6.39 (Opell, '90)	9.93 (Opell, '90)	14.52 (Opell, '90)	12.30
Book lung area/spider mass$^{0.80}$	0.494	0.451	0.676	0.601	1.495	1.475

TABLE 2. *Values used to compute size specific indices of tracheal development for species with tracheae that extend into the prosoma*

	Waitkera waitakerensis	*Hyptiotes cavatus*	*Miagrammopes animotus*	*Uloborus glomosus*
Leg 1				
Tracheal area (μm^2)	331	387	891	289
Femur volume (mm^3)	0.339 ± 0.051	0.149 ± 0.017	0.451 ± 0.075	0.318 ± 0.092
Distance from spiracle (μm)	3072	2088	3772	2572
Area/volume/$\sqrt{}$ distance	17.62	56.83	32.18	17.93
Leg 2				
Tracheal area (μm^2)	133	159	21	157
Femur volume (mm^3)	0.098 ± 0.024	0.103 ± 0.011	0.064 ± 0.021	0.085 ± 0.030
Distance from spiracle (μm)	2796	1800	3388	2312
Area/volume/$\sqrt{}$ distance	25.65	36.41	113.03	38.40
Leg 3				
Tracheal area (μm^2)	110	153	83	101
Femur volume (mm^3)	0.0461 ± 0.009	0.041 ± 0.008	0.028 ± 0.002	0.036 ± 0.010
Distance from spiracle (μm)	2536	1572	3096	2004
Area/volume/$\sqrt{}$ distance	47.45	94.24	53.31	62.62
Leg 4				
Tracheal area (μm^2)	312	506	416	383
Femur volume (mm^3)	0.190 ± 0.039	0.185 ± 0.011	0.117 ± 0.017	0.133 ± 0.039
Distance from spiracle (μm)	2204	1240	2668	1664
Area/volume/$\sqrt{}$ distance	35.01	77.70	68.77	70.58
ϵ Area/volume/$\sqrt{}$ distance of four legs	125.73	265.18	267.29	189.53

Values for tracheal area and the distance from the tracheal spiracle to the coxa of each leg are from Opell ('87a). Values for femur volume are mean $\pm$ 1 standard deviation and are based on a sample size of five mature females per species.

63, 64, 67, 69, 71, 83, 85, 86, and 87) that were informative for the superfamily Deinopoidea (Deinopoidea + Uloboridae). I excluded Coddington's character 35 (cheliceral denticles) because it was scored for only one uloborid genus. The length of the resulting tree shown in Figure 2 is 42.

I computed independent contrast values for both absolute and size-specific indices of book lung and tracheal development using
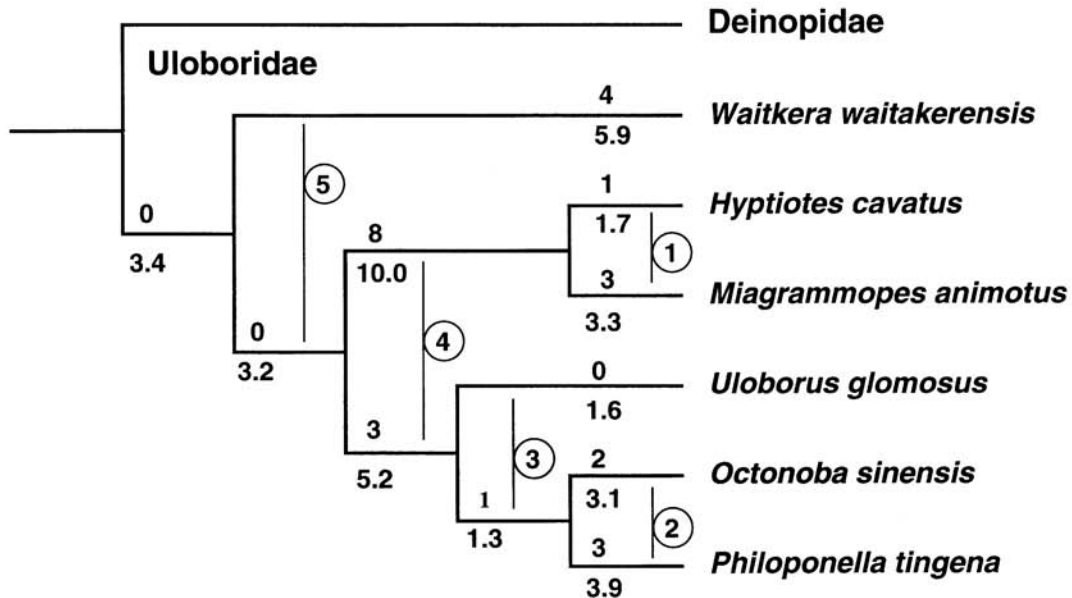

Fig. 2. Phylogeny of the six species included in this study. Minimum branch lengths appear above and average branch lengths below lines. Circled numbers identify the contrast values plotted in Figures 3–6.

branch lengths determined by two methods (Fig. 2) to confirm that the results of this study were robust. I used the "unambiguous changes only" and the "average over all reconstructions" options for this purpose. The first option determines minimum branch length by excluding questionable characters. As some of these excluded characters are probably valid, the true branch lengths of these clades are probably greater than those reported by this option. In contrast to the "all possible changes" option that almost certainly overestimates branch length, the average changes option appears to be a more reasonable estimator of true branch length.

RESULTS

Pearson correlation shows that indices of absolute book lung and tracheal development are inversely related ($r = -0.92$, $P = 0.009$), as are those of size-specific book lung and tracheal development ($r = -0.87$, $P = 0.024$). Although these comparisons do not account for the influence of phylogenetic relationship (Harvey and Pagel, '91), independent contrasts computed using both minimum and average branch lengths show significant ($P < 0.05$), negative relationships between both absolute and size-specific indices of book lung and tracheal development (Figs. 3–6). In all cases, the independent contrast values used in these analyses were truly independent, as confirmed by the absence of a significant correlation ($r = -0.17-$ $-0.71, P = 0.18-0.78$) between the standard deviation and absolute values of independent contrasts. The 95% confidence limits of each regression (Figs. 3–6) encompass its origin. Thus, those uloborids that have more extensive tracheal systems have book lungs with lower areas and species whose tracheae are confined to the opisthosoma have book lungs with the greatest surface areas.

DISCUSSION

The results of this study support the hypothesis that spider book lung and tracheal systems are complementary respiratory structures. When the plesiomorphic tracheal condition of the family Uloboridae, as represented by *Waitkera waitakerensis* and *Uloborus glomosus,* becomes more well developed, as in the case of *Hyptiotes cavatus* and *Miagrammopes animotus,* book lung surface area decreases. Conversely, when the tracheal system becomes less extensive, as in the case of *Octonoba sinensis* and *Philoponella tingena,* book lung surface area increases.

These respiratory changes appear to be driven by changes in the acuteness of oxygen demand by certain tissues. The more active web monitoring and manipulation tactics of *Hyptiotes cavatus* and *Miagrammopes animotus* (Lubin et al., '78; Lubin, '86; Opell, '87b) suggest that their leg muscles (particularly those of the first two pairs of legs) may have a more acute demand for oxygen that can be better supplied by direct diffusion of oxygen through the tracheae than by oxygen transported by the hemolymph. Thus, the lungs of these spiders probably serve to provide oxygen principally to other tissues. The absence of prosomal tracheae in the more derived orb-weaving spiders such as *Octonoba sinensis* and *Philoponella tingena* suggests that these spiders less actively monitor and manipulate their orb-webs than do other uloborids, such as *Waitkera waitakerensis* and *Uloborus glomosus.* Although there are differences in the web-monitoring postures of orb-weaving uloborids (Opell and Eberhard, '83), differences in their web manipulation have not been quantified. As all uloborids lack poison glands and must, therefore, subdue prey by actively wrapping it with silk (Opell, '79; Lubin, '86), there is little reason to believe that differences in this phase of prey capture have influenced the development of the tracheal system.

Differences in the cribellar prey capture threads produced by uloborids may also influence the tracheal systems of uloborids. Cribellar threads are composite threads formed of an outer mantel of thousands of fine, coiled cribellar fibrils that surrounds a pair of larger, supporting axial fibers (Peters, '83, '84, '86; Eberhard and Periera, '93; Opell, '94a, '95). These cribellar fibrils are polymerized as they are pulled from spigots on an oval abdominal spinning plate, termed the cribellum, with the aid of a setal comb on the spider's fourth leg (Eberhard, '88). The web reduction that leads to the triangle-webs of *Hyptiotes* and the simple-webs of *Miagrammopes* is associated with increased capture thread stickiness (Opell, '94b, 96). This, in turn, is associated with a large increase in the number of cribellar fibrils that form a thread and is achieved by an increase in the number of cribellum spinning spigots (Opell, '94a). The greater force required to polymerize the increased number of cribellar fibrils produced by *Hyptiotes* and *Miagrammopes* species may be another factor that favored greater development of the tra-
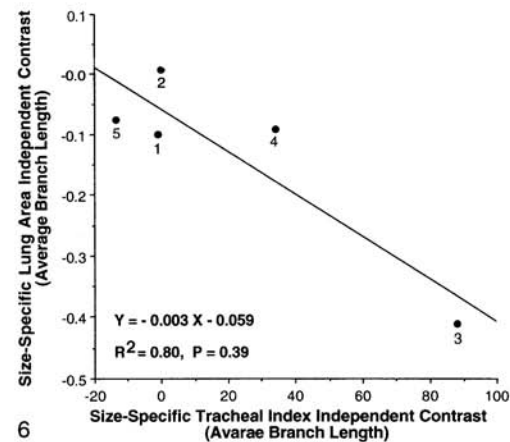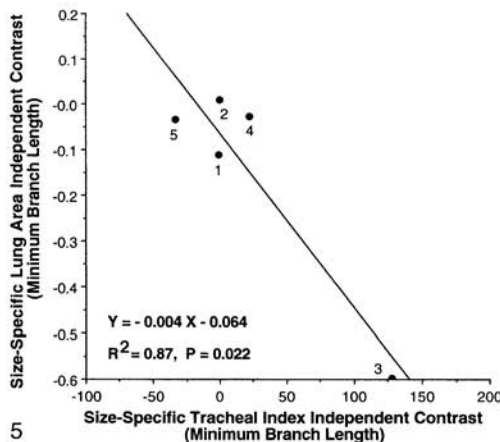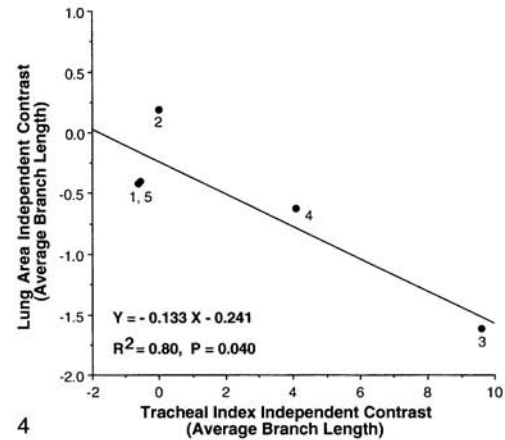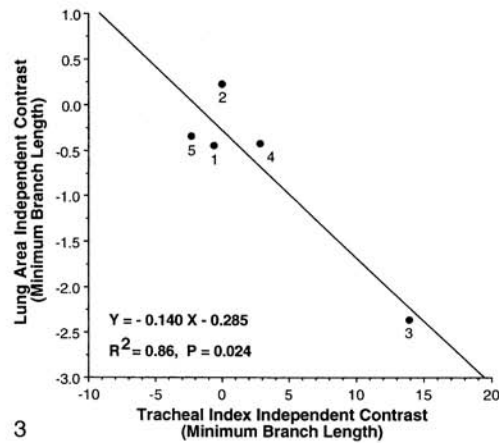
Figs. 3–6. Regressions of independent contrast values for absolute and size specific indices of tracheal and book lung development. Fig. 3. Values for absolute indices computed with minimum branch lengths. Fig. 4. Values for absolute indices computed with average branch lengths. Fig. 5. Values for size-specific indices computed with minimum branch lengths. Fig. 6: Values for size-specific indices computed with average branch lengths. Absolute tracheal development is given as Σ cross sectional area in μm^2 of tracheae entering leg coxa/$\sqrt{}$ distance from spiracle to coxa in μm. Absolute book lung development is given as lung area in mm^2. Size-specific tracheal development is given as Σ cross sectional area in μm^2 of tracheae entering leg coxa/ volume of femur in $mm^3/\sqrt{}$ distance from spiracle to coxa in μm. Size-specific book lung development is given as lung area in μm^2/spider mass in $mg^{0.80}$.

cheae that serve the third and fourth legs, which are responsible for the manipulation of cribellar fibrils (Eberhard, '88).

The arguments presented above attribute differences in uloborid book lung and tracheal systems to differences in spider activity patterns. Tracheal development increases in response to the more acute oxygen demand associated with greater activity and decreases with reduced activity. Development of the book lungs compensates for these changes: as more oxygen is supplied by the tracheae, book lung area diminishes and

as less oxygen is provided, book lung area increases. Some authors suggest that, particularly in small spiders, more extensive tracheal development serves to reduce respiratory water loss by permitting a lower book lung surface area or reducing the flow of air over the lung surfaces (Davis and Edney, '52; Cloudsley-Thompson, '57; Levi, '67; Levi and Kirber, '76). Although this adaptation may explain the well-developed tracheal systems of some spiders, it does not appear to account for differences in the tracheal development of uloborids (Opell, '90). The most ex-

tensive tracheal systems of the uloborids studied are found in *Hyptiotes cavatus* and *Miagrammopes animotus,* which are found in moist temperate and tropical forests, respectively (Opell, personal observations). Members of the genera *Octonoba* and *Philoponella* have the least well developed tracheal systems in the family. *Philoponella tingena* is found in moist tropical forests, but *P. oweni* and *P arizonica* occupy arid habitats in Arizona (Opell, personal observations). Consequently, differences in activity pattern provide the only consistent explanation for differences in tracheal development in the family Uloboridae.

The arguments presented above assume that intergeneric differences in uloborid respiratory anatomy are genetically determined and are not induced by differences in web-monitoring behavior. However, this has not been confirmed in this or any other group of spiders. Differences in acute oxygen demand may stimulate the tracheal development in certain tissues and this may explain some of the differences in the number and diameters of tracheae that enter the legs of uloborids. However, this provides a less plausible explanation of the major differences in tracheal patterns that distinguish uloborid genera.

ACKNOWLEDGMENTS

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