

The Relationship of Book Lung and Tracheal Systems in the Spider Family Uloboridae

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ABSTRACT The book lung surface areas of representatives of six genera were measured and divided by spider prosomal and leg mass and by the product of prosomal length and width to obtain two indexes of book lung area. Both indexes are greatest in species that have the simplest tracheal systems and smallest in those with the most extensive tracheal systems. When species are ordered phylogenetically and the lung area indexes of their hypothetical ancestors computed, a transformational increase in lung area is indicated. Neither the lung area of a species nor its phylogenetic position is significantly related to the general moisture regime of its habitat. The number of leaves in a book lung is positively correlated with both spider size and total lung area. However, leaf number is not correlated with tracheal development and shows no transformational change.

The Tracheospira (*sensu*, Platnick, '77) contains spiders that have two respiratory components: a pair of book lungs that oxygenate the hemolymph and a tracheal system that carries oxygen directly to tissues. A variety of spider tracheal patterns have been documented and their adaptiveness discussed (Bromhall, '87; Opell, '87a). However, the relationship between these patterns and book lung development has not been studied.

Spider book lungs reside in the anterior, ventral region of the opisthosoma. Each lung is formed of a stack of elongate, flattened, cuticle-lined leaves, between which hemolymph circulates. The air space between the two lamellae of each leaf is maintained by cuticular struts and communicates with a common atrium that opens to the outside via a spiracular slit (Levi, '67; Moore, '76; Anderson and Prestwich, '80; Hexter, '82). The width of the interlamellar air space within each leaf shows a negative allometric relationship with spider mass, an apparent adaptation to reduce the distance over which oxygen must diffuse to reach the hemolymph (Anderson and Prestwich, '80).

Members of the family Uloboridae exhibit the full range of tracheal development found in spiders (Opell, '79, '87a; Bromhall, '87). The orb-weaving genera *Waitkera* and *Uloborus*, the triangle-weaving genus *Hyptiotes*, and the irregular-web-weaving genus *Miagrammopes* retain the family's plesiomorphic pattern, characterized by two stout tracheal trunks that extend through the pedicel, into the prosoma, and

branch to enter the legs. Tracheae entering the prosomae of *Hyptiotes* and *Miagrammopes* have diameters that are, relative to combined prosomal and leg masses, nearly twice those of *Waitkera* and *Uloborus* (Table 1). This difference is attributed to the fact that they more actively monitor and manipulate their reduced prey capture webs (Opell '87a,b). Orb-weavers of the genera *Octonoba* and *Philoponella* have tracheae that are restricted to the opisthosoma (Opell, '79). Opell ('79) reported that the tracheoles in *Octonoba* extend into the prosoma, but none appeared in cross sections through the pedicels of North American *Octonoba sinensis* used in this study (unpublished observations).

Comparisons of the relative book lung surface areas in these taxa make it possible to determine how tracheal development, activity patterns, and phylogenetic position influence book lung development. If spiders with more extensive tracheal systems have greater book lung surface areas than those with more weakly developed tracheae, this would suggest that both systems act in consort to supply a spider's increased oxygen demands. If more extensive tracheal systems are associated with smaller book lung surface areas, this would indicate that the tracheae meet more acute or more specific oxygen demands (such as those imposed by web-monitoring behaviors) and, therefore have assumed a greater role in meeting a spider's total oxygen demands. Any transformational changes in book lungs of these species should be apparent when their relative surface areas are ordered phylogenetically.

TABLE 1. Comparison of tracheal development, spider size, book lung surface areas, and interlamellar air space widths (mean \pm standard deviation [sample size])

Tracheae, web type, species	Do not enter prosoma		Enter prosoma			
	Orb-web		Orb-web		Reduced-web	
	<i>P. tingena</i>	<i>O. sinensis</i>	<i>W. waitakeriensis</i>	<i>U. glomus</i>	<i>M. animotus</i>	<i>H. cavatus</i>
Pedicle tracheal area ¹ / prosomal and leg mass	0	0	410	448	761	840
Carapace length (μm)	1,460 \pm 158 (10)	1,484 \pm 126 (10)	1,252 \pm 88 (5)	1,364 \pm 49 (9)	1,507 \pm 112 (10)	1,017 \pm 69 (7)
Carapace width (μm)	1,358 \pm 145 (10)	1,394 \pm 134 (10)	1,168 \pm 70 (5)	1,171 \pm 45 (9)	1,073 \pm 57 (10)	1,151 \pm 32 (7)
Prosomal and leg mass (mg)	2.84 \pm 0.95 (10)	3.43 \pm 1.25 (10)	2.17 \pm 0.26 (7)	1.91 \pm 0.30 (9)	2.38 \pm 0.53 (10)	1.49 \pm 0.26 (7)
Book lung leaves	29.4 \pm 6.3 (10)	30.9 \pm 6.7 (9)	17.2 \pm 2.8 (5)	22.9 \pm 2.0 (7)	22.4 \pm 3.8 (9)	15.7 \pm 1.7 (7)
Number of lung leaves/ prosomal and leg mass (mg)	10.4 \pm 2.4 (10)	9.2 \pm 2.2 (9)	8.2 \pm 2.5 (5)	11.9 \pm 2.2 (7)	9.9 \pm 1.0 (9)	10.0 \pm 1.9 (7)
Book lung area (mm^2)	6.97 \pm 2.55 (10)	7.47 \pm 2.76 (9)	2.53 \pm 0.47 (7)	3.77 \pm 0.61 (8)	2.98 \pm 0.91 (10)	2.08 \pm 0.31 (7)
Lung area (mm^2)/ prosomal and leg mass (mg)	2.35 \pm 0.51 (10)	2.13 \pm 0.33 (9)	1.19 \pm 0.31 (5)	1.92 \pm 0.31 (8)	1.26 \pm 0.19 (10)	1.43 \pm 0.29 (7)
Lung area (μm^2)/ carapace length \times width	0.83 \pm 0.20 (10)	0.87 \pm 0.17 (9)	0.44 \pm 0.08 (5)	0.59 \pm 0.09 (8)	0.46 \pm 0.10 (10)	0.45 \pm 0.07 (7)
Live spider mass (mg)	—	14.52 \pm 3.63 (20)	—	9.93 \pm 4.65 (45) ²	6.39 \pm 3.36 (37) ²	6.76 \pm 3.06 (42) ²
Predicted interlamellar air space width (μm)	—	1.6	—	1.5	1.3	1.3
Measured interlamellar air space width (μm)	1.5 \pm 0.1 (5)	1.3 \pm 0.1 (5)	1.2 \pm 0.1 (5)	1.5 \pm 0.3 (5)	1.5 \pm 0.2 (5)	1.2 \pm 0.2 (5)

¹Mean values from Opell, '87a.

²Mean values from Opell, '87b.

METHODS AND MATERIALS

Adult females, representing 6 of the 18 described uloborid genera were studied: the orb-weavers *Waitkera waitakeriensis* (Chamberlain, '46) from northern New Zealand, *Uloborus glomosus* (Walckenaer, 1841) from Virginia, *Octonoba sinensis* (Simon, 1880) an introduced Asian species collected in Virginia, and *Philoponella tingena* (Chamberlain and Ivie, '36) from Panama and Colombia; the irregular-web weaver *Miagrammopes animotus* (Chickering, '68) from Puerto Rico; and the triangle-web weaver *Hyptiotes cavatus* (Hentz, 1847) from Virginia. These species were identified using the following revisions (Muma and Gertsch, '64; Chickering, '68; Opell, '79; and Yoshida, '80).

The anterior region of the opisthosoma containing the book lungs was removed, cleared in hot 10% (weight/volume) NaOH to remove non-chitinous tissue, rinsed in water, and stained to make the thin book lung leaves visible. One book lung from each specimen was dissected in a drop of mounting medium and its isolated leaves flattened under a coverslip.

The surface areas of the leaves of a book lung were measured with a digitizing tablet, summed, and this value multiplied by four to obtain a spider's total book lung surface area. The width of the air space separating a leaf's lamellae was measured from compound microscope photographs of a folded leaf (Anderson and Prestwich, '80). The shape of a species' book lung leaves was reconstructed from outline drawings of one of the three largest leaves of five specimens of each species. A midline was drawn from a leaf's tip to the center of a line connecting the corners of its base. The perpendicular distance from this midline to the leaf's left and right margins was measured at 15 equidistant points (Fig. 2). Mean values were used to reconstruct leaf shapes.

Two indexes of spider size were used for comparisons: 1) the product of prosomal length and width and 2) combined prosomal and leg masses. The former index accounts for differences in uloborid prosomal shape (Opell, '84) and the latter for differences in a spider's feeding and the mass of forming eggs in its opisthosoma. For example, in *Octonoba sinensis*, prosomal length is poorly correlated with live weight ($r = 0.60$, $P > 0.09$, $N = 9$) but more strongly correlated with combined prosomal and leg mass ($r = 0.94$, $P < 0.0003$, $N = 9$).

Specimens of *Philoponella tingena* were stored in ethanol and transferred to buffer one day before being weighed. All others were fixed in 3% glutaraldehyde/3% formaldehyde and stored in sodium cacodylate buffer. This treat-

ment leaches little material from tissue, has little effect on mass, and coagulates hemolymph, preventing its loss when a specimen's pedicel is severed. Prior to weighing, specimens were blotted and air dried for 30 seconds. The masses of eight *Miagrammopes animotus* so treated averaged 103% (range 95–105%) of their live weights.

Species were assigned to one of three groups of increasing tracheal development, one of four phylogenetic groups, and one of three habitat groups of increasing moisture availability (Fig. 1). Within the limited context of this study, *Hyptiotes* and *Miagrammopes* and *Philoponella* and *Octonoba* are sister taxa, making it inappropriate to assign one member of the pair a more advanced status than the other. One factor analysis of variance (ANOVA) and Kruskal-Wallis K-sample ranking (K-W) tests were used to determine if tracheal type and habitat explained the differences in relative book lung surface area.

Phylogenetic tracts were evaluated using ANOVA tests, K-W tests, and transformational analysis. The latter approach infers from terminal (living) taxa the states of hypothetical ancestral taxa and determines if these states exhibit directional changes indicative of an evolutionary trend (Lauder, '81; Huey, '87; Huey and Bennett, '87). Hypothetical ancestors are used in an attempt to neutralize the unique selective forces that have operated on each terminal taxa since its origin. I used the following scheme of iterative averaging to determine the states of hypothetical ancestors H_1 – H_4 .

$$H_1 = \textit{Hyptiotes} + \textit{Miagrammopes}/2.$$

$$H_2 = (H_1 + \textit{Waitkera}) + (H_1 + \textit{Uloborus}) \\ + (\textit{Waitkera} + \textit{Uloborus})/6.$$

$$H_3 = (H_1 + \textit{Uloborus}) + (\textit{Uloborus} + \textit{Octonoba}) \\ + (H_1 + \textit{Octonoba})/6.$$

$$H_4 = (\textit{Uloborus} + \textit{Octonoba}) + (\textit{Octonoba} + \textit{Philop.}) \\ + (\textit{Uloborus} + \textit{Philop.})/6.$$

RESULTS

Table 1 presents mean values for the six species studied. Habitat differences do not confound the interpretation of these results. Neither the tracheal patterns of the six study species nor the two indexes of relative book lung surface area are affected by habitat (ANOVA $P > 0.18$). Likewise, phylogenetic position has no effect on the habitat of a species (ANOVA $P < 0.35$).

The three tracheal groups of increasing tracheal development are characterized by decreasing book lung surface area. When book lung surface area is divided by combined prosomal and leg mass, the mean ratios for tracheal groups 1–3 are 2.25, 1.64, and 1.33 mm²/mg, respec-

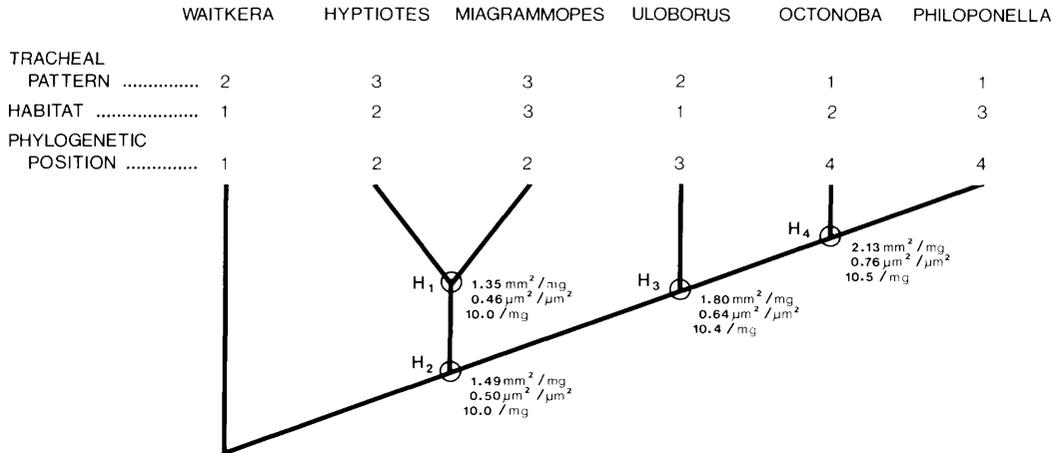


Fig. 1. Phylogenetic, tracheal, and habitat categories of the genera studied. To the right of H₁–H₄, estimated values are given for: 1) book lung area relative to prosomal and leg mass (upper), 2) book lung area relative to the product of prosoma length and width (middle), and 3) the number of book lung leaves relative to prosomal and leg mass (lower). Tracheal categories: 1) tracheae restricted to the opistho-

soma, 2) smaller tracheae enter the prosoma and legs, 3) stout tracheae enter the prosoma and legs (Opell '79; '87b). Habitat categories: 1) dry temperate shrubby and forest underbrush, 2) moist temperate forests and buildings, and 3) wet tropical forests (Comstock '40; Forster '67; Opell '79, '82, '87a,b; Peaslee and Peck '83; David Court and Denis Gibbs, personal communication).

tively. When book lung surface area is divided by the product of prosomal length and width, the mean ratios for tracheal groups 1–3 are 0.85, 0.53, and 0.45 μm²/μm², respectively. These inverse relationships between both indexes of book lung surface area and tracheal development are significant (ANOVA, K-W $P < 0.0001$), as are those between orb-weavers with different tracheal patterns (tracheal groups 1 and 2; ANOVA, K-W $P < 0.0013$).

Transformational analyses of changes in hypothetical ancestors H₂–H₄ show increases in both indexes of lung area (Fig. 1). The ratio of lung area to prosomal and leg mass increases by a mean of 20% and the ratio of lung area to prosomal length and width increases by a mean of 24%. These results are supported by comparisons of book lung surface areas across phylogenetic groups. The mean ratios of lung area to prosomal and leg mass for phylogenetic groups 1–4 (Fig. 1) are: 1.19, 1.33, 1.92, and 2.25 mm²/mg, respectively. The mean ratios of lung area to the product of prosomal length and width for these phylogenetic groups are: 0.31, 0.45, 0.59, and 0.85 μm²/μm², respectively. The interactions between phylogenetic position and both indexes of lung area are significant (ANOVA, K-W $P < 0.0001$). When only the four orb-weavers were compared, phylogenetic position also significantly affected both indexes of book lung surface area (ANOVA, K-W $P < 0.0008$).

When all six species are considered, the number of leaves per book lung correlates positively with spider prosomal and leg mass ($r = 0.76$, $P < 0.0001$, $N = 47$) and with total book lung area ($r = 0.91$, $P < 0.0001$, $N = 47$). Therefore, mass-specific indexes (Table 1) were used in comparisons of leaf number. A transformational analysis of the number of leaves per prosomal and leg mass shows an average change of only 3% (Fig. 1). Likewise, ANOVA tests show an insignificant effect ($P > 0.51$) of the three tracheal and four phylogenetic categories on the ratio of book lung leaves to prosomal and leg mass.

The shape of the six species' book lung leaves is similar, although those with greater book lung areas and more leaves have narrower leaves (Fig. 2). When the mean value of a leaf's 16 width measurements is divided by its length, the resulting index is inversely related to both the number of a specimen's book lung leaves ($r = -0.55$, $P < 0.002$, $N = 30$) and to its book lung area ($r = -0.41$, $P < 0.024$, $N = 30$). However, this index of leaf width is not correlated with a specimen's combined prosomal and leg mass ($P < 0.11$).

DISCUSSION

In the Uloboridae, increased book lung area is achieved by increases in leaf number and area. Tracheae and book lungs are complementary

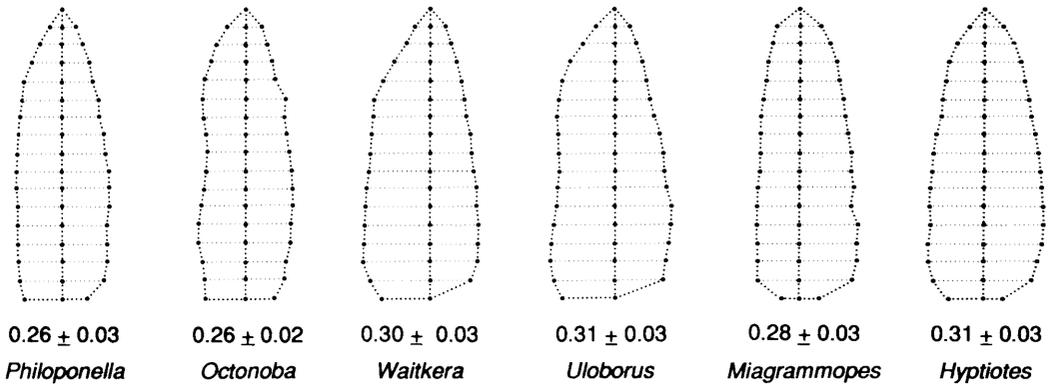


Fig. 2. Reconstructed shapes of book lung leaves. The lengths of the leaves have been made equal and their mean right and left widths at each reference point along the midline

are expressed relative to their lengths. Below each leaf is its mean width-to-length ratio followed by the standard deviation of this ratio.

respiratory mechanisms; when one system is better developed the other provides less of a spider's total oxygen. The inverse relationship between these two systems suggests that their development is governed not only by a spider's total respiratory demands, but also by the specificity of these demands.

The tracheae of *Hyptiotes cavatus* and *Miagrammopes animotus* extend into the prosoma and legs (Opell, '87a), where they can directly meet the oxygen demands imposed by these spiders' active web monitoring and manipulation tactics (Lubin et al., '78; Lubin, '86; Opell, '87b). These species' smaller relative book lung areas probably supply their non-locomotor respiratory demands. In contrast, the tracheae of *Octonoba sinensis* and *Philoponella tingena* are confined to the opisthosoma, requiring all locomotor oxygen demands to be met by hemolymph-borne oxygen. These spiders' book lungs must meet both locomotor and non-locomotor respiratory demands. Not surprisingly, these orb-weavers have the largest relative book lung areas of the six species studied.

Within the Uloboridae, there is a transformational increase in book lung area. This is seen despite the fact that *Hyptiotes* and *Miagrammopes* have more well developed tracheae to accommodate the active web-monitoring behaviors their reduced-webs demand. In these genera, increased behavioral involvement compensates for the reduced material (silk) invested in capture webs. The inverse may be true in orb-weavers that demonstrate an increasing reliance upon book lungs to supply their respiratory needs. In these spiders, oxygen demand appears to become less acute in more derived taxa. Sev-

eral factors may contribute to this trend. These spiders may spin wider cribellar capture threads that more securely hold prey and, therefore, require less rapid and less vigorous behavior to subdue prey. They may possess more aciniform spigots, responsible for producing the wrapping silk used to swath struggling prey, and therefore, be able to thoroughly wrap prey with fewer leg movements.

Across spiders of different sizes, book lung area is directly related to metabolic rate (Anderson, '70; Anderson and Prestwich, '82). However, this measurement does not include the area of fine tracheoles across which oxygen diffuses directly into tissues and, therefore, underestimates total respiratory surface area, particularly of spiders with well developed tracheal systems. Therefore, it is inappropriate to conclude that uloborids with the greatest book lung areas also have the highest metabolic rates.

On average, Anderson and Prestwich's ('80) formula: width of interlamellar air space = 0.90 body mass^{0.21} predicts to within 10% the mean interlamellar separation of the four species whose adult masses are known (Table 1). Considering that the standard deviations of the six species' measured interlamellar separations average 12% of their mean values, the generality of Anderson and Prestwich's model is supported by this study.

Orb-weavers of the families Uloboridae and Araneidae have similar relative book lung surface areas. The four large araneids studied by Anderson and Prestwich ('82) [*Acanthepeira stellata*, *Argiope aurantia*, *Mecynogea lemniscata*, and *Metazygia wittfeldae*; mean mass of about 382 mg] had a mean value of 0.54 mm² of book lung area per milligram of live mass. The

uloborid *Octonoba sinensis*, with a poorly developed tracheal system similar to those found in the four araneid species, has a value of 0.51 mm²/mg. *Uloborus glomosus*, with a more extensive tracheal system, has a value of 0.38 mm²/mg. However, before it can be concluded with certainty that the metabolic costs of operating an orb-web is similar in both families, the lung areas of smaller araneid species must also be measured.

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