

# The influence of web monitoring tactics on the tracheal systems of spiders in the family Uloboridae (Arachnida, Araneida)

Brent D. Opell

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061 USA

**Summary.** Uloborids that spin reduced webs more actively monitor them than those that construct orb webs. *Hyptiotes* use both their first and fourth legs to tense their triangle-webs, whereas *Miagrammopes* rely principally on their first legs to monitor and jerk the threads of their irregular webs. The respiratory systems of these spiders include tracheae that extend into the prosoma, bifurcate, and enter the legs. To determine if the legs responsible for active web-monitoring tactics have more extensive tracheal supplies, the total cross sectional area has been computed of the tracheae entering the legs of mature female orb web and reduced web uloborids. Each leg's value has been divided by the cross sectional area of the tracheal trunks that enter the prosoma. These indexes reveal no significant differences between the relative tracheal supplies of the orb weavers investigated (*Waitkera waitkerensis*, *Tangaroa beattyi*, *Uloborus glomus*). But the first, third, and fourth legs of *H. cavatus* and the first legs of *M. animotus* and *M. pinopus* have greater relative tracheal supplies than those of the three orb weaving species. Relative to leg volume, the first and fourth legs of *H. cavatus* have the greatest and the first legs of *Miagrammopes* species the next greatest tracheal supplies. When tracheal lengths are considered, these differences in potential oxygen supplies remain, showing that area differences do not simply compensate for differences in the distances over which oxygen must diffuse. These differences are leg-specific and not species-specific, and uloborids with the most extensive tracheal supplies are found in moist habitats. Thus the observed differences are best explained as adaptations to meet the greater oxygen demands of legs responsible for active web-monitoring tactics and not as adaptations to reduce respiratory water loss.

## A. Introduction

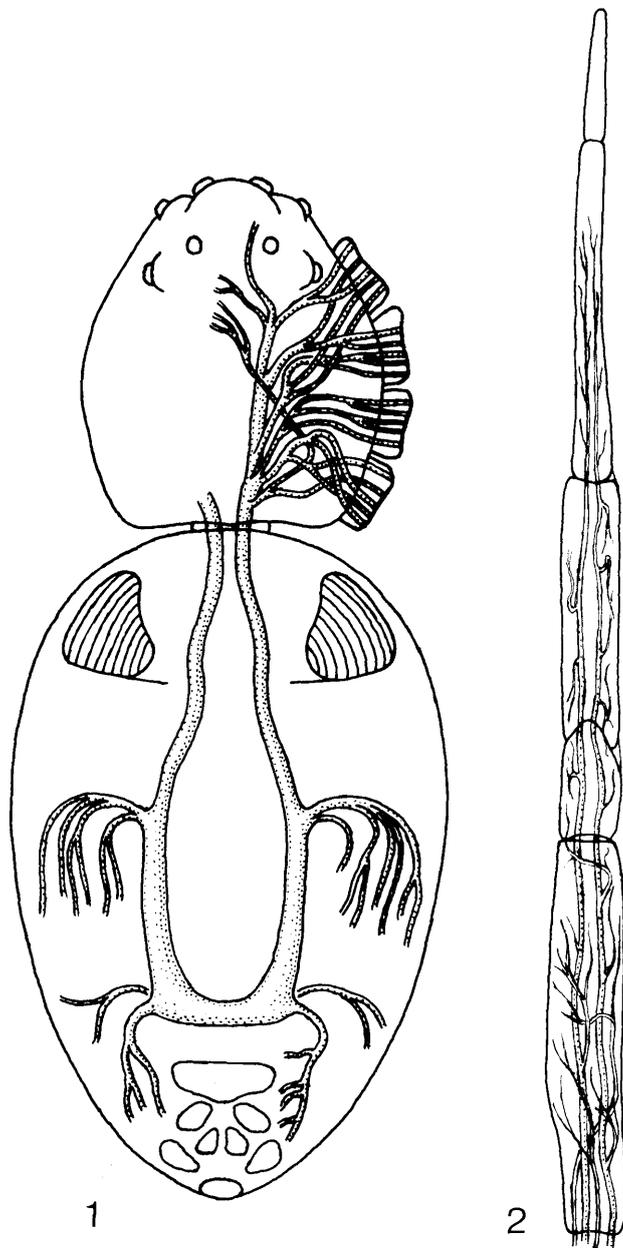
The respiratory systems of spiders exhibit much diversity. In the ground-plan of Araneida two pairs of book lungs are present, but in all members of the large subtaxon Tracheospira (Platnick 1977), tracheae replace the posterior pair of book lungs. Within this group and even within some families, e.g., Hahniidae (Forster 1970), Linyphiidae (Blest 1976; Millidge 1984, 1986), Uloboridae (Opell 1979), the tracheal system exhibits varying degrees of development, ranging from fine tracheae that are restricted to the opisthosoma to stout tracheal trunks that extend into the prosoma where they bifurcate and enter the appendages.

More extensive tracheal systems are thought to reduce

respiratory water loss or to provide a greater and more direct supply of oxygen to prosomal and leg muscles (Levi and Kirber 1976). The former advantage is probably of particular benefit to small spiders (Levi 1967) and the latter to large spiders with higher metabolic rates or more energetic prey capture tactics (Anderson 1970; Cloudsley-Thompson 1957; Wilson and Bullock 1973; Davis and Edney 1952; Dresco-Derouet 1960). Extensive tracheal systems both provide a more direct supply of oxygen to the prosoma and prevent this supply from being interrupted during periods of activity when fluid exchange between opisthosoma and prosoma is interrupted (Anderson and Prestwich 1975).

Previous studies of tracheal development in arachnids have attempted to correlate major differences in tracheal patterns with size, habitat, and activity patterns. Most of these comparisons are between members of different families and even different orders. None attempts to quantify tracheal development. The purpose of this study is to compare the tracheal systems of similar sized spiders that belong to the same family and have the same grade of tracheal development, but that differ in their activity patterns. This comparison provides a conservative test of the hypothesis that tracheal evolution reflects change in respiratory demand. If this hypothesis is correct, not only should the most active spiders have the most well-developed tracheal systems, but these differences should be expressed in the legs that are specifically responsible for their greater activity.

The Uloboridae provide a good opportunity to evaluate the association of tracheal development and activity pattern. Although the full spectrum of tracheal patterns is found within this family (Opell 1979), the plesiomorphic and most common pattern is characterized by a pair of stout tracheal trunks that enters the prosoma and divides into smaller tracheae that extend into the appendages (Fig. 1). Within the legs, further branching supplies tracheoles to the muscles (Figs. 2, 4). This pattern is found in both orb weaving genera whose members simply hang from the hubs of their webs (Opell and Eberhard 1984) while waiting for prey as well as in genera whose members more actively monitor their reduced webs and more forcefully manipulate them when a prey is caught (Lubin 1986; Lubin et al. 1978; Opell 1982, 1984a; Peters 1938). Despite differences in web manipulation, all uloborids exhibit similar prey wrapping and handling behaviors (Lubin 1986). Lacking poison glands (Opell 1979), they attack-wrap ensnared prey, but neither bite nor grapple with struggling prey.



**Figs. 1, 2.** The opistosomal and prosomal (**Fig. 1**) and first leg (**Fig. 2**) tracheal systems of *Uloborus glomosus* as seen in dorsal views of a sodium hydroxide-cleared female specimen

If tracheal development reflects oxygen demand, the legs used by these reduced web uloborids to monitor and operate their webs should have more extensive tracheal supplies than the legs of orb weavers with the same type of tracheal pattern. To test this hypothesis I compared the tracheae of three orb web species, one triangle-web species whose members use both their first and fourth legs to tense their reduced webs (Opell 1982, 1985, 1987) and two "single-line-web" species that rely on their first legs to monitor and manipulate their webs (Lubin 1986; Lubin et al. 1978).

## B. Materials and methods

Only mature female specimens were used in this study. The three orb weaving species studied were: *Waitkera waitkerensis* (Chamberlain, 1946) from northern New Zealand,

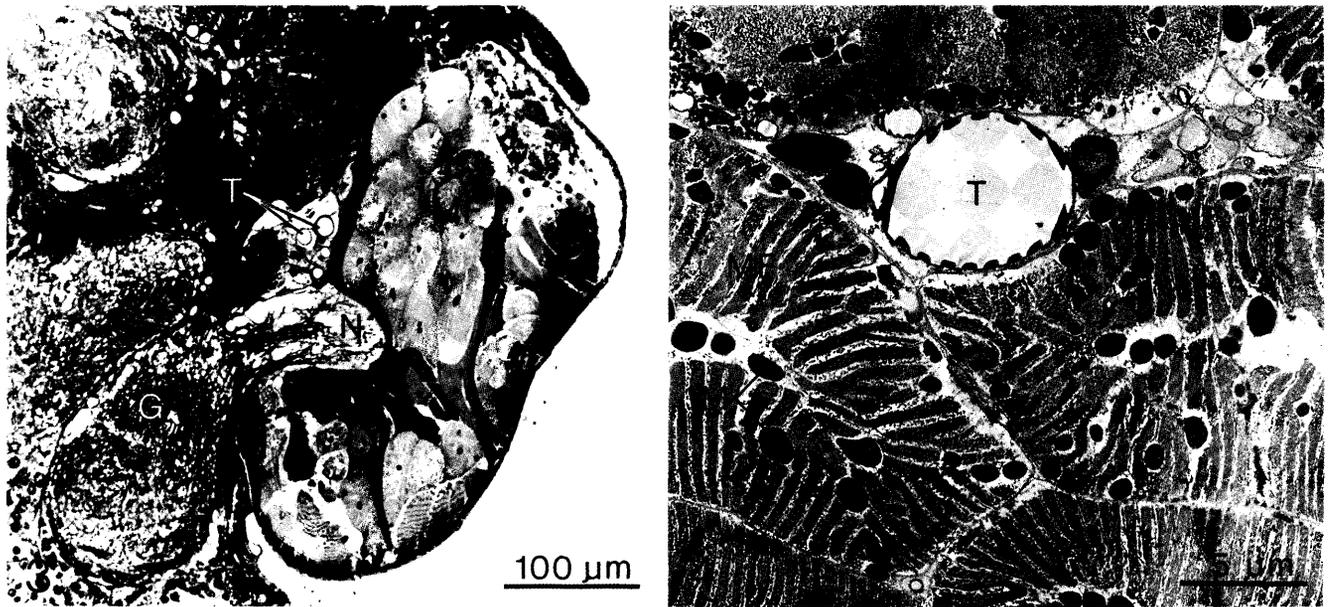
*Tangaroa beattyi* Opell, 1983, from the Caroline Islands, and *Uloborus glomosus* (Walckenaer, 1841) from Virginia. The triangle-web species *Hyptiotes cavatus* (Hentz, 1847) was collected from Virginia, the "single-line-weaver" *Miagrammopes animotus* Chickering, 1968, from the Center for Energy and Environment Research's El Verde, Puerto Rico field station, and an undescribed member of the *Miagrammopes aspinatus* species group (Opell 1984a) from the Organization for Tropical Studies' La Selva, Costa Rica field station. Mean carapace lengths of these species are: 1312  $\mu\text{m}$ , 760  $\mu\text{m}$ , 1372  $\mu\text{m}$ , 906  $\mu\text{m}$ , 1512  $\mu\text{m}$ , and 1138  $\mu\text{m}$ , respectively. *Waitkera* and *Tangaroa* exhibit the most primitive grade of genitalic development found in the Uloboridae and *Uloborus* has the most advanced grade found in orb weaving genera that retain an extensive tracheal system (Opell 1979). *Hyptiotes* and *Miagrammopes* are sister taxa (Opell 1984b).

Tracheal measurements were taken from plastic-embedded specimens cross sectioned with a Sorvall JB-4 microtome. Prior to sectioning, specimens were fixed in 3% glutaraldehyde/3% formaldehyde in 0.1 M sodium cacodylate buffer (pH 7.3) at 20°–26° C for 12–18 h, rinsed in 0.1 M sodium cacodylate buffer, dehydrated through a graded series of acetone, and embedded in Spurr's epoxy resin. 1  $\mu\text{m}$  thick cross-sections were stained with 1% toluidine blue.

An index of relative tracheal development was obtained by dividing the total cross sectional area of the tracheae entering a leg by the cross sectional area of the tracheal trunk serving that half of the prosoma (Fig. 1). Each of the two tracheal trunks entering the prosoma serves only one side of the body, and so right and left legs of the same specimen were treated as separate samples. The diameters of tracheal trunks entering the prosoma and of tracheae entering leg coxae (Fig. 3) were measured at  $\times 500$  with the ocular micrometer of a compound microscope. In one *U. glomosus* specimen, damage prevented me from measuring the legs on one side of the body. To avoid using duplicate measurements of looped tracheae, measurements were taken during the course of a careful posterior-to-anterior examination of serial sections. If a trachea's perpendicular profile deviated noticeably from a circle, I measured its diameter in at least three axes and used the average diameter for calculations. If a trachea was obliquely sectioned, I used the maximum width of its lumen as its diameter. From these measurements, I computed the cross sectional area of each tracheae and then summed the cross sectional area of tracheae serving each leg.

To estimate the volume of the first and fourth leg muscle served by the tracheae of these legs, I determined the mean volumes of the right legs of five mature female specimens of each species except *T. beattyi*. The volume of each leg article was determined by multiplying its mean cross sectional area by its length. The diameters used to compute this cross sectional area were obtained as follows: coxa, mean central width and height; trochanter, mean central width and height; femur, mean width and height at proximal 25% of length, center, and distal 25% of length; patella, mean central width and height; tibia, same measurements as femur; metatarsus, mean width and height at proximal 33% and distal 33% of length; tarsus, same measurements as metatarsus.

The cross sectional area of the tracheae serving a leg is not the only factor influencing the availability of oxygen to the leg muscles. If oxygen moves principally by diffusion,



**Figs. 3-4.** Fig. 3. Cross-section through the origin of the right first coxa of *Uloborus glomus*, showing two large and two small tracheae entering the leg Fig. 4. First leg muscle fibers of *Miagrammopes animotus* and a large and small tracheole supplying them with oxygen. *T* trachea or tracheole; *MF* muscle fiber; *G* first leg ganglion of subesophageal ganglion; *N* nerves enervating the first leg; *M* mitochondria

**Table 1.** Sample size, number of tracheae entering each leg coxa, total cross sectional area of tracheae serving each leg, and first and fourth leg volumes. Mean and (standard deviation) are presented

	<i>Waitkera waitkerensis</i>	<i>Tangaroa beattyi</i>	<i>Uloborus glomus</i>	<i>Hyptiotes cavatus</i>	<i>Miagrammopes animotus</i>	<i>Miagrammopes</i> sp.
Leg 1: Spiders/sides	2/4	1/2	2/3	2/4	1/2	3/6
Tracheae	2 or 3	1	6 or 9	2 or 3	1	1 or 2
Area ( $\mu\text{m}^2$ )	331 (45)	128 (28)	289 (23)	387 (37)	891 (109)	597 (122)
Leg 2: Spiders/sides	2/4	1/2	2/4	2/4	1/2	3/6
Tracheae	1 or 2	1	4 or 6	2	6	1-3
Area ( $\mu\text{m}^2$ )	133 (39)	62 (19)	157 (51)	159 (40)	421 (13)	161 (43)
Leg 3: Spiders/sides	2/3	1/2	2/3	2/3	1/2	3/6
Tracheae	1	1	4	2	1	1
Area ( $\mu\text{m}^2$ )	110 (36)	38 (15)	101 (31)	153 (30)	83 (11)	88 (33)
Leg 4: Spiders/sides	2/3	1/2	2/3	2/4	1/2	3/6
Tracheae	1 or 3	1	8 or 14	3 or 5	1	1-3
Area ( $\mu\text{m}^2$ )	312 (16)	92 (23)	383 (33)	506 (100)	416 (25)	302 (14)
Total leg areas ( $\mu\text{m}^2$ )	890 (24)	318 (85)	855 (9)	1252 (122)	1811 (107)	1148 (166)
Pedicle: Spiders/sides	2/4	1/2	2/4	2/4	1/2	3/6
Total tracheae	2	2	2	2	2	2
Area/tracheae ( $\mu\text{m}^2$ )	1948 (198)	720 (64)	1549 (131)	1747 (359)	3355 (138)	2461 (357)
Leg 1 volume ( $10^4 \mu\text{m}^3$ )	62798 (11483)	-	48822 (19435)	27438 (2020)	104188 (15300)	46905 (5404)
Leg 4 volume ( $10^4 \mu\text{m}^3$ )	43327 (8339)	-	33069 (12133)	29375 (6264)	40253 (4175)	36387 (11953)

the speed of its movement is directly proportional to the square root of tracheal length (Anderson and Prestwich 1980; Schmidt-Nielsen 1979). Therefore, a short, small diameter trachea could supply as much oxygen as a long, large diameter trachea. To evaluate this interaction, I divided the total cross sectional area of tracheae entering each leg by the square root of the distance from the spiracle to the leg base (Fig. 1). I estimated the latter by measuring the distance from the tracheal spiracle to a point on the sternum midline perpendicular to each coxa and added to this the distance from this sternal point to each leg's coxa.

### C. Results

Table 1 presents mean leg cross sectional areas and volumes, Table 2 indexes of the relative tracheal supplies to the legs of each species. The indexes presented in Table 3 account for differences in the lengths of tracheae serving the legs. From Table 2, four trends are apparent: (1) the first and fourth legs of orb weavers have similar relative tracheal supplies and these supplies exceed those of the second and third legs; (2) reduced web uloborids have better developed first leg tracheae than do orb weaving uloborids;

**Table 2.** Indexes of each leg's tracheal supply relative to the area of tracheae entering the prosoma and, for first and fourth legs, total leg volume  $\times 10^4 \mu\text{m}^3$ . Mean and (standard deviation) of the former index are presented. The latter index is derived from means presented in **Table 1**

	<i>Waitkera waitkerensis</i>	<i>Tangaroa beattyi</i>	<i>Uloborus glomosus</i>	<i>Hyptiotes cavatus</i>	<i>Miagrammopes animotus</i>	<i>Miagrammopes</i> sp.
Leg 1:						
Area/pedicle area	0.17 (0.03)	0.18 (0.05)	0.18 (0.03)	0.23 (0.03)	0.27 (0.02)	0.25 (0.09)
Volume/trach. area	190	–	169	71	117	79
Leg 2:						
Area/pedicle area	0.07 (0.02)	0.09 (0.03)	0.10 (0.04)	0.10 (0.04)	0.13 (0.001)	0.07 (0.02)
Leg 3:						
Area/pedicle area	0.06 (0.01)	0.05 (0.03)	0.06 (0.02)	0.09 (0.01)	0.03 (0.002)	0.04 (0.02)
Leg 4:						
Area/pedicle area	0.16 (0.03)	0.13 (0.04)	0.24 (0.04)	0.29 (0.04)	0.12 (0.01)	0.13 (0.02)
Volume/trach. area	139	–	86	58	97	121
<hr/>						
Total leg trach. area 0.5 Pedicle trach. area	0.47 (0.05)	0.45 (0.16)	0.52 (0.04)	0.71 (0.12)	0.54 (0.01)	0.48 (0.13)

**Table 3.** Mean estimates of the lengths of tracheae serving each leg and indexes of potential oxygen availability. Values in parentheses are the standard deviations of distance measurements. Cross sectional areas used in these calculations are those means presented in **Table 1**

	<i>Waitkera waitkerensis</i>	<i>Uloborus glomosus</i>	<i>Hyptiotes cavatus</i>	<i>Miagrammopes animotus</i>	<i>Miagrammopes</i> sp.
Leg I:					
Distance ( $\mu\text{m}$ )	3072 (326)	2572 (538)	2088 (230)	3772 (464)	2804 (248)
Area/ $\sqrt{\text{distance}}$	5.97	5.70	8.47	14.51	11.28
Leg II:					
Distance ( $\mu\text{m}$ )	2796 (330)	2312 (506)	1800 (197)	3388 (471)	2580 (220)
Area/ $\sqrt{\text{distance}}$	2.52	3.27	3.37	7.23	3.17
Leg III:					
Distance ( $\mu\text{m}$ )	2536 (305)	2004 (483)	1572 (209)	3096 (445)	2348 (207)
Area/ $\sqrt{\text{distance}}$	2.18	2.26	3.86	1.49	1.82
Leg IV:					
Distance ( $\mu\text{m}$ )	2204 (273)	1664 (472)	1240 (161)	2668 (399)	2028 (218)
Area/ $\sqrt{\text{distance}}$	6.65	9.39	14.37	8.05	6.71

(3) in *Hyptiotes* the fourth legs have the most highly developed tracheal systems, whereas in *Miagrammopes* the first leg tracheae are most highly developed; and (4) the prosomal tracheal system of *H. cavatus* is more extensive than those of the other species.

When intraspecific differences in relative tracheal supplies are analyzed with a two-tailed *t*-test, there is no significant difference ( $P > 0.05$ ) between the first and fourth legs of each of the three orb weavers. By contrast, these values differ significantly ( $P < 0.05$ ) in *H. cavatus*, where the fourth leg has a relative tracheal supply that is 1.26 times greater than that of the first leg, and in the two *Miagrammopes* species, where the first legs have tracheal supplies that average 2.09 times greater than those of the fourth legs. Only in *Miagrammopes* do relative tracheal supplies to the second and third legs differ significantly. In both species the third leg has a smaller relative tracheal supply than the second. In all species but *M. animotus* the second and third leg tracheal supplies are smaller than those of both the first

and fourth legs. In *M. animotus* there is no significant difference between tracheal supplies to the second and fourth legs.

When interspecific differences are analyzed with a two-tailed *t*-test, there is no significant difference between the relative tracheal supplies to the legs of orb weavers, although the greater supply to *U. glomosus* fourth legs ( $P = 0.051$ ) closely approaches statistical significance. When relative tracheal values for the three orb weaving species are pooled and compared with those of reduced web species using a two-tailed *t*-test, the tracheal supplies of all but the second leg of *H. cavatus* are significantly greater ( $P < 0.05$ ) than those of the orb weavers. All *M. animotus* legs differ significantly from those of orb weavers, but only the third legs of *M. sp.* differ significantly from those of orb weavers. However, *P* values for all but the second pair of *M. sp.* legs are less than 0.09, indicating that they do not differ fundamentally from those of *M. animotus*. In *Miagrammopes* only the first pair of legs have consistently

greater relative tracheal supplies than those of orb weavers. The third and fourth legs of *Miagrammopes* have smaller relative values than those of orb weavers.

#### D. Discussion

The results support the hypothesis that web monitoring tactics have influenced uloborid tracheal development, causing more actively monitoring spiders to have more well-developed tracheal supplies to those legs that are responsible for this activity. Indexes of potential oxygen availability (Table 3) show that cross sectional differences are not simply compensatory changes related to differences in tracheal lengths. The first legs of *H. cavatus* and the two *Miagrammopes* species have the greatest values, despite the fact that *H. cavatus* has the shortest tracheae and *Miagrammopes* have the longest. Likewise, leg proportions do not affect the leg volume served by each  $1 \mu\text{m}^2$  of tracheal cross-section (Table 2). The smallest values (most extensive supplies) are found in *H. cavatus* which has short, stout legs and in the two *Miagrammopes* species which have long, slender legs.

Two observations suggest that tracheal differences are not primarily adaptations to reduce respiratory water loss. First, there is no clear association of tracheal development with habitat moisture: *T. beattyi*, *H. cavatus*, and the two *Miagrammopes* species are found in forest habitats with the greatest moisture and *W. waitkerensis* and *U. glomosus* in more exposed habitats (personal observations, personal communications from James Berry, Joseph Beatty, and David Court). Second, tracheal development is leg-specific rather than species-specific, as would be expected if it were primarily a response to water conservation.

Likewise, differences in relative tracheal supply to the legs cannot be attributed to differences in tracheal branching patterns. For example, the first legs of both *H. cavatus* and *W. waitkerensis* have two to three tracheae, but the former has significantly greater relative cross sectional area. Similarly, a single trachea serves the first legs of both *T. beattyi* and *M. animotus*, but the latter has a significantly greater relative cross sectional area. These observations suggest that tracheal branching patterns are conservative and that increased oxygen demands are met principally by increases in tracheal diameters.

The differences in tracheal development documented in this study strongly suggest that reduced web uloborids expend more energy in monitoring their webs than do orb web uloborids. The specific way in which the tracheal system adapts to these demands suggests that the spiders' basal (resting) metabolic rates may not differ. In light of Anderson's (1970) findings that the resting metabolism of spiders correlates highly with their book-lung surface areas, this hypothesis predicts that there will be little difference in the relative book lung surface areas of the spiders studied here. However, the less active web monitoring tactics of orb weavers may impose less acute oxygen demands that can be more easily met by oxygen dissolved in the hemolymph. If this is the case, orb weaving uloborids may rely more extensively on their book lungs and, consequently, have relatively larger book lung surface areas.

*Acknowledgements.* David Court collected and fixed *Waitkera waitkerensis* specimens and Joseph Beatty and James Berry collected

*Tangaroa beattyi* specimens. Paula E. Cushing, Amy D. Ware, and Elizabeth M. Reinoehl sectioned specimens and assisted with measurements. National Science Foundation grants No. DEB-8011713 and BSR-8407979 to the author supported this study.

#### References

- Anderson JF (1970) Metabolic rates of spiders. *Comp Biochem Physiol [A]* 33:51–72
- Anderson JF, Prestwich KN (1975) The fluid pressure pump of spiders (Chelicerata, Araneae). *Z Morphol Tiere* 81:257–277
- Anderson JF, Prestwich KN (1980) Scaling of subunit structures in book lungs of spiders (Araneae). *J Morphol* 165:167–174
- Blest AD (1976) The tracheal arrangement and the classification of linyphiid spiders. *J Zool* 180:185–194
- Cloudsley-Thompson J (1957) Nocturnal ecology and water regulations of the British cribellate spiders of the genus *Ciniflo*. *J Linn Soc London* 43:133–152
- Davis ME, Edney EB (1952) The evaporation of water from spiders. *J Exp Biol* 29:571–582
- Dresco-Derouet L (1960) Étude biologique comparée de quelques espèces d'Araignées lucicoles et troglodiles. *Arch Zool Exp Gen* 98:271–354
- Forster RR (1970) The spiders of New Zealand: III. *Otago Mus Zool Bull* 3:1–184
- Levi HW (1967) Adaptations of respiratory systems of spiders. *Evolution* 21:571–583
- Levi HW, Kirber WM (1976) On the evolution of tracheae in arachnids. *Bull Brit Arach Soc* 3:187–188
- Lubin YD (1986) Web building and prey capture in Uloboridae. In: Shear WA (ed) *Spiders: webs, behavior, and evolution*. Stanford University Press, Stanford, pp 132–171
- Lubin YD, Eberhard WG, Montgomery GG (1978) Webs of *Miagrammopes* (Araneae: Uloboridae) in the neotropics. *Psyche* 85:1–23
- Millidge AF (1984) The taxonomy of the Linyphiidae, based chiefly on the epigynal and tracheal characters (Araneae: Linyphiidae). *Bull Brit Arach Soc* 6:229–267
- Millidge AF (1986) A revision of the tracheal structures of the Linyphiidae (Araneae). *Bull Brit Arach Soc* 2:57–61
- Opell BD (1979) Revision of the genera and tropical American species of the spider family Uloboridae. *Bull Mus Comp Zool Harv Univ* 148:433–549
- Opell BD (1982) Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). *J Arach* 10:185–191
- Opell BD (1984a) Phylogenetic review of the genus *Miagrammopes* sensu lato (Araneae: Uloboridae). *J Arach* 12:229–240
- Opell BD (1984b) Comparison of the carapace features in the family Uloboridae (Araneae). *J Arach* 12:105–114
- Opell BD (1985) Force exerted by orb-web and triangle-web spiders of the family Uloboridae. *Can J Zool* 65:580–583
- Opell BD (1987) Changes in web-monitoring forces associated with web reduction in the spider family Uloboridae. *Can J Zool* 65:1028–1034
- Opell BD, Eberhard WG (1984) Resting postures of orb-weaving uloborid spiders. *J Arach* 11:369–376
- Peters HM (1938) Über das Netz Der Dreieckspinne, *Hyptiotes paradoxus*. *Zool Anz* 121:49–59
- Platnick NI (1977) The hypochiloid spiders: a cladistic analysis with notes on the Atypoidea (Arachnida, Araneae). *Am Mus Novitates* 2627:1–23
- Schmidt-Nielsen K (1979) *Animal physiology: adaptation and environment*, 2nd edn. Cambridge University Press, London
- Wilson RS, Bullock J (1973) The hydraulic interaction between prosoma and opistosoma in *Amaurobius ferox* (Chelicerata, Araneae). *Z Morphol Tiere* 74:221–230

Received January 7, 1987