

FACTORS AFFECTING THE DIAMETERS OF AXIAL FIBERS IN CRIBELLAR THREADS OF THE SPIDER FAMILY ULOBORIDAE

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ABSTRACT. The diameters of axial fibers that support the cribellar threads of uloborids are shown by electron microscopy to be related to web architecture. Cribellar threads produced by the simple-web species *Miagrammopes animotus* and *M. sp.* are supported by the radial threads along which they are deposited. The axial fibers of these threads have smaller diameters than those of the self-supporting cribellar threads that are deposited between radial threads by members of the orb-weaving species *Octonoba sinensis*, *Siratoba referena*, and *Uloborus glomosus* and the triangle web-species *Hyptiotes cavatus*. Among these six species, axial fiber diameter is directly related to the maximum distance that a cribellar thread spans in the web. However, in *O. sinensis* and *H. cavatus* there is no intraweb difference in the diameters of axial fibers from short and long cribellar thread spans.

Spider orb-webs are highly organized, minimum-design structures whose architectures and thread characteristics appear to be interdependent (Craig 1987; Denny 1976; Eberhard 1990). In the family Uloboridae, cribellar thread forms the web's spiral prey capture element. This thread has two components: small, looped cribellar fibrils that form its outer surface and a pair of larger axial fibers that lie within this sheath of cribellar fibrils and are thought to support the thread (Fig. 1; Peters 1983, 1984, 1986). In this family, reduction of the orb-web is correlated with an increase in the stickiness of the web's capture threads (Opell 1994), resulting from an increase in the number of cribellar fibrils that form their outer surfaces (Opell pers. obs.). The purpose of this study is to determine if these changes in web architecture are also associated with changes in the diameters of the cribellar thread's axial fibers.

As uloborid web architecture changes, the amount of support that the axial fibers of their cribellar fibrils must provide should also change. In orb-webs and in triangle-webs produced by members of the genus *Hyptiotes* Walckenaer, cribellar threads extend across radii (whose diameters are at least two times those of the cribellar threads' axial fibers) and are self-supporting (Lubin 1986). In the reduced webs produced by *Polenecia producta* (Simon) and by members of the genus *Miagrammopes* O. Pickard-Cambridge, cribellar threads are deposited on radii, which help support them (Lubin 1986; Lubin et al. 1978;

Opell 1990; Peters 1986). Peters (1986) has termed these two types of cribellar threads autonomous and heteronomous threads, respectively. In the family Uloboridae, the orb-web and its autonomous cribellar threads are plesiomorphic (Coddington 1990; Coddington & Levi 1991; Opell 1979).

Thus, two design features of uloborid webs have the potential to influence the diameter of the axial fibers within their cribellar threads: 1) the manner in which cribellar threads are supported and 2) the distance the cribellar threads span. In reduced webs with heteronomous cribellar threads, the axial fibers' support function appears to be largely redundant, as they have smaller diameters than do the frame thread on which they are deposited (Peters 1984). As these axial fibrils appear to contribute neither to the cribellar thread's strength nor its stickiness, selection for the conservation of silk invested in a web should favor a reduction in the diameter of these axial fibers to that needed simply to support the cribellar thread as it is being spun and deposited.

In webs with autonomous cribellar threads, differences in a web's diameter and the number of radii that it contains affect the distance that cribellar threads span. As this distance increases, these threads are more likely to bear the full impact of a prey that strikes the web and their ability to do so would be enhanced by stronger axial fibers. Therefore, in those uloborids that construct orb-webs and triangle-webs, the maximum

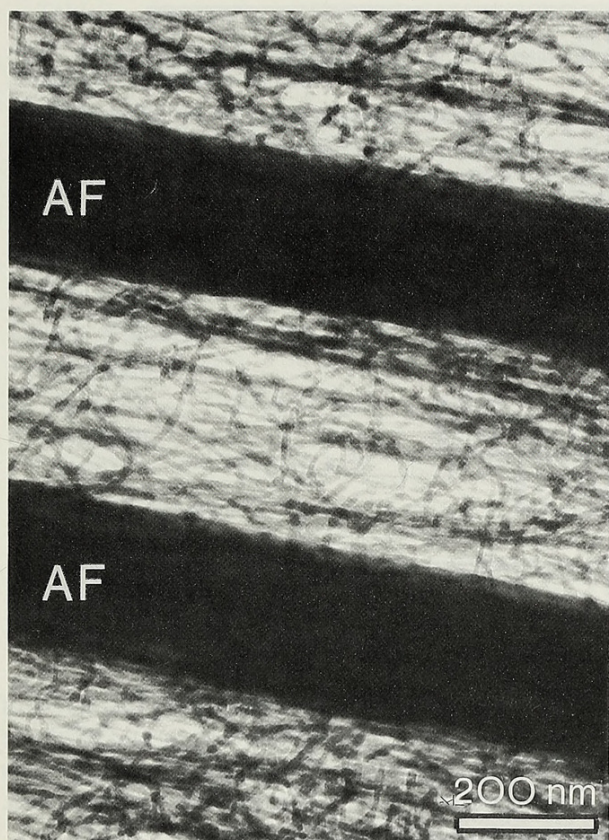


Figure 1.—A portion of a cribellar thread of *Waitkera waitakerensis*, showing two axial fibers (AF) surrounded by smaller cribellar fibrils.

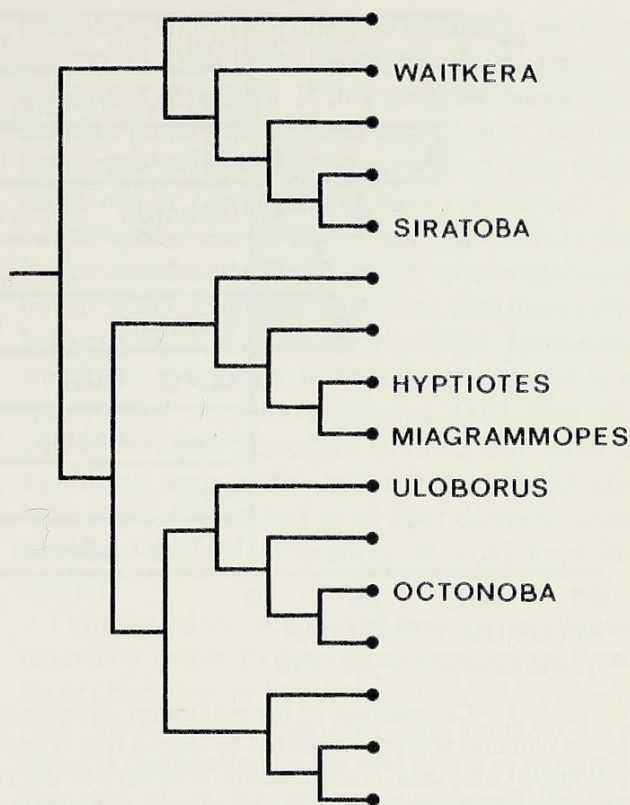


Figure 2.—A cladogram of the genera of Uloboridae from Coddington (1990), showing the phylogenetic positions of the six genera included in this study.

METHODS

Species studied.—As adult male uloborids do not construct capture webs, only the threads of adult females were measured. Four orb-weaving species were studied: *Waitkera waitakerensis* (Chamberlain), from New Zealand's North Island; *Siratoba referena* (Muma & Gertsch), from the Chiricahua Mountains of southeastern Arizona; *Uloborus glomosus* (Walckenaer), from southwestern Virginia; and *Octonoba sinensis* (Simon), an introduced Asian species, collected from free ranging populations in greenhouses at Virginia Polytechnic Institute and State University. Also included was the triangle-web species, *Hyptiotes cavatus* (Hentz), from southwestern Virginia. Two simple-web species were studied: *Miagrammopes animotus* Chickering, from the Luquillo National Forest of Puerto Rico and an undescribed green *Miagrammopes* species, from north central Costa Rica. The live weights in mg of these species, based on the individuals included in this study, are (mean, ± 1 SE, n): 6.52, 0.44, 18; 3.84, 0.23, 14; 7.73, 0.68, 18; 13.26, 0.83, 28; 7.60, 0.47, 30; 6.44, 0.38, 6; and 3.36, 0.51, 5, respectively. The relationship of the gen-

distance that cribellar threads must span should be directly related to the diameter of the axial fibers that support these threads.

This study tests the hypothesis that the diameters of the axial fibers of uloborid cribellar threads are correlated with the loads that these threads must bear, as determined by differences in web architecture. If verified, this hypothesis lends credibility to the putative support function of these axial fibers and demonstrates that the axial fiber and cribellar fibril components of cribellar threads respond independently to changes in web architecture. To test this hypothesis, I compared the diameters of axial fibers in cribellar threads produced by seven uloborid species. This hypothesis assumes that axial fiber diameter is uniform within a web. However, as the distance spanned by cribellar threads is greater at the perimeter of a web than near its center, this may not be true. Therefore, for two species I also tested the hypothesis that, within a web, axial fiber diameter is greater in long than in short cribellar thread spans.

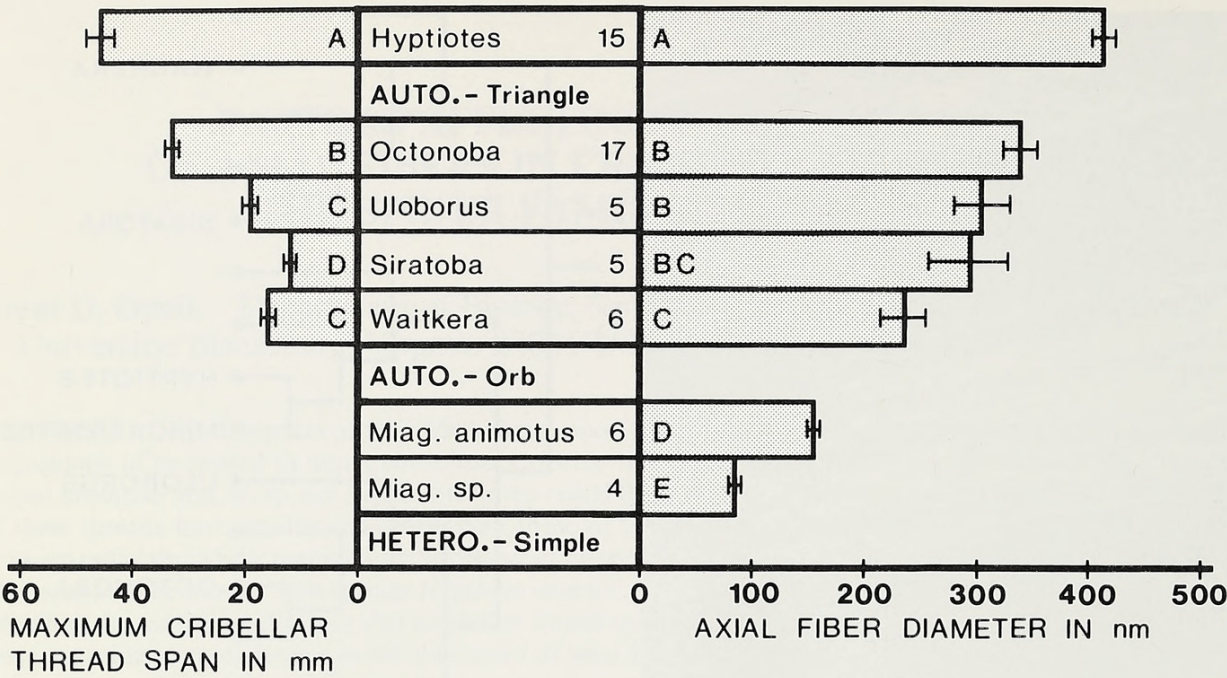


Figure 3.—Comparison of the maximum cribellar thread spans and cribellar thread axial fiber diameters of seven uloborid species, organized by thread type (Hetero. = heteronomous, Auto. = autonomous) and web type (Simple-, Orb-, and Triangle-web). Numbers to the right of each taxon represent the number of axial fibers measured. For each species, the maximum cribellar thread span of webs spun by 12 individuals was measured. Letters within each rectangle designate the Duncan test ranking of means and error bars denote + 1 SE.

era to which these species belong is shown in Fig. 2.

Intraweb differences in axial fiber diameter.—For this comparison, I chose *H. cavatus* and *O. sinensis*, as their autonomous cribellar threads spanned the greatest distances (Fig. 3). I collected webs or web regions on 18 cm diameter aluminum rings, whose 5 mm diameter rims were covered with double-sided plastic “Scotch” tape. I then isolated the half of the ring containing short spans of cribellar thread from that containing long spans by placing a thread across the ring. This permitted me to collect threads from one half without damaging those in the other half. Before collecting cribellar thread samples, I measured the distance between the adjacent radii that supported them.

I collected threads on raised supports glued to microscope slides. Double-sided plastic “Scotch” tape atop these supports maintained the natural tension of these threads. I then sub-sampled threads on Formvar-coated copper grids and examined them at 66,000× with a transmission electron microscope without further treatment. From each short and long span of cribellar thread I photographed two axial fibers, being careful to include only those strands that had a uniform

diameter and showed no signs of being damaged by the microscope’s electron beam. On each photographic negative, I measured the axial fiber’s diameter at its center and both ends. The mean of these six measurements was used as the diameter of an axial fiber in a short or long cribellar thread span.

On each of the four days that I photographed threads, I also photographed a grating replica (2160 lines per mm) at 66,000× to precisely determine specimen magnification and confirm that it was consistent from day to day. The standard error of the mean measured width of one of the replica’s 463 nm wide lines was 4.3 nm.

Interspecific differences in axial fiber diameter.—Cribellar threads were collected from the webs of the seven species listed above. Those from orb-webs and triangle-webs were usually taken midway between the web’s hub or apex and its perimeter, although this sampling procedure was not employed consistently. These threads were collected and studied as described above, except that one to three axial fibers were measured from each web. On the 12 days that I photographed these axial fibers, the measured width of the 463 nm diffraction gradient spacing had a standard error of 1.6 nm.

Table 1.—Comparison of axial fiber diameter in short and long spans of cribellar thread from the same web. Mean ± 1 standard deviation.

| | <i>Hyptiotes cavatus</i> (n = 10) | <i>Octonoba sinensis</i> (n = 12) |
|-----------------------|--|--|
| Spider weight (mg) | 7.24 ± 2.84 | 12.50 ± 3.44 |
| Length of thread | | |
| Short span (mm) | 14.8 ± 4.6 | 7.1 ± 1.6 |
| Long span (mm) | 41.1 ± 8.5 | 21.5 ± 5.5 |
| Axial fiber diameter | | |
| Short span (nm) | 412 ± 60 | 308 ± 52 |
| Long span (nm) | 400 ± 40 | 319 ± 45 |
| Paired <i>t</i> -test | | |
| <i>t</i> value | 0.735 | 1.024 |
| <i>P</i> value | 0.481 | 0.328 |

Cribellar thread span.—I determined the maximum distance a cribellar thread spanned in the orb-webs and triangle-webs produced by 12 adult females of each of these five species. These webs were dusted with corn starch, photographed, and enlarged prints made. On each print I measured the three longest cribellar threads and used the mean of these measurements as that web’s maximum cribellar thread span. Only cribellar threads extending between radii were measured; those that were connected to or that ran along frame lines were not included.

Phylogenetic analysis.—As the species included in this study are related to differing degrees (Fig. 2), phylogenetic position alone may contribute to differences in the diameters of their axial fibers. Species that share a more recent common ancestor would also be expected to have more similar axial fiber diameters. Thus, the values obtained for these species are not strictly independent, making it inappropriate to analyze them with traditional regression techniques (Harvey & Pagel 1991). Therefore, I employed the method described by Huey & Bennett (1986, 1987) for evaluating the direction and rate of evolution of two continuous variables whose states are hypothesized to be coadapted. This method has two steps: 1) the inference of ancestral character states from the states of its extant

members, and 2) the analysis of change in these characters from these hypothetical ancestors to the extant members. If this analysis shows that changes (both positive and negative) in the two characters are significantly correlated, then their states can be considered to have coevolved.

I computed the states of three characters in the hypothetical ancestors of the six species included in this study: axial fiber diameter, maximum cribellar thread span, and spider weight. I included weight in this analysis because it represents a feature that may have affected axial fiber diameter. Unless this effect is ruled out, even a significant association between maximum cribellar thread span and axial fiber diameter may not fully explain differences in axial fiber diameter.

I employed the scheme of iterative averaging described below to determine the state of these three characters in hypothetical ancestors A₁–A₅ (Fig. 4). In these equations, the value of each genus is represented by the first initial of its name. For each character, the mean value of the two *Miagrammopes* species are used because all other genera are represented by only a single species.

$$\begin{aligned} A_1 &= W + S + A_4/3. \\ A_2 &= H + M + ((U + O)/2)/3. \\ A_3 &= U + O + ((H + M)/2)/3. \\ A_4 &= A_2 + A_3 + ((W + S)/2)/3. \\ A_5 &= A_1 + A_4/2. \end{aligned}$$

Next, I computed the change that occurred between the most recent ancestor of each genus and that genus. For example, the transition from hypothetical ancestor A₁ to *Waitkera* involved a 35 nm reduction in axial fiber diameter, no change in maximum cribellar span, and a 0.63 mg increase in spider weight. Changes in axial fiber diameter were then regressed against changes in weight and changes in maximum cribellar thread span to determine if one or both of these latter two parameters satisfactorily explained changes in axial fiber diameter.

Statistical analysis.—In both intraweb and interspecific comparisons, axial fiber diameter was normally distributed (*P* > 0.05), as determined by a Shapiro-Wilk *W*-statistic. However, as maximum cribellar thread span was not normally distributed for all five species, statistical tests were performed using log-transformed data. *P*-values of < 0.05 are considered significant.

RESULTS

Intraweb differences in axial fiber diameter.—Table 1 compares the diameters of axial fibers from short and long spans of cribellar threads taken from the webs of *H. cavatus* and *O. sinensis*. Although the length of long spans was, on average, three times greater than that of short spans, in neither species did axial thread diameter differ significantly between long and short spans. These results falsify the hypothesis that there are intraweb differences in axial fiber diameters. Additionally, they indicate that any bias in the web region from which cribellar threads were taken in the interspecific comparison is not likely to affect the results of this study.

Interspecific comparisons of axial fiber diameter.—Figure 3 compares the diameters of the seven species' axial fibers. A one-way analysis of variance test shows that axial fiber diameter differs among the species ($df = 6$, $F = 34.12$, $P < 0.0001$). These differences are not explained by differences in spider weight, as demonstrated by an insignificant Pearson correlation coefficient ($df = 5$, $T = 1.46$, $r = 0.55$, $P > 0.20$) between the mean weight of the species and their mean axial fiber diameters. When the two *Miagrammopes* species are excluded, the Pearson correlation remains insignificant ($df = 3$, $T = 0.78$, $r = 0.41$, $P > 0.49$). Therefore, the ranking of axial fiber diameter by a Duncan test (Fig. 3; $df = 51$, $\text{Alpha} = 0.05$) supports the hypothesis that the heteronomous cribellar threads of the two *Miagrammopes* species have axial fibers with smaller diameters than do the autonomous cribellar threads of orb- and triangle-web genera. It also shows that, even among species that produce autonomous cribellar threads, axial fiber diameter differs.

Cribellar thread span.—Figure 3 also presents the maximum cribellar thread span for the five species that produce autonomous cribellar threads. An analysis of variance test shows that the log base ten of maximum cribellar thread span differs significantly among these species ($df = 4$, $F = 81.96$, $P = 0.0001$). The ranks assigned to these species by a Duncan test ($df = 56$, $\text{Alpha} = 0.05$) are similar to those based on axial fiber diameter. Among these species, weight fails to explain maximum cribellar thread span, as indicated by an insignificant Pearson correlation coefficient ($df = 3$, $T = 1.17$, $r = 0.56$, $P = 0.33$). However, among these species, maximum cribellar thread span is positively correlated with

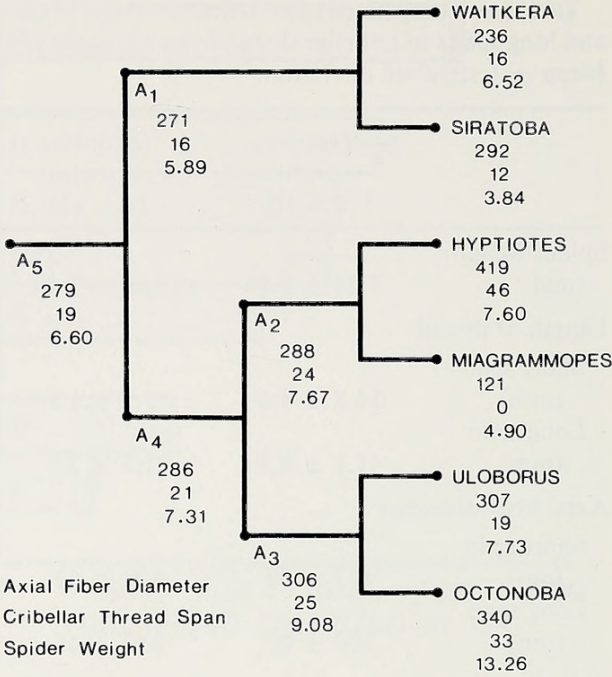


Figure 4.—Transformational analysis of axial fiber diameter, maximum cribellar thread span, and spider weight based on the values of six genera.

axial fiber diameter ($df = 3$, $T = 3.71$, $r = 0.91$, $P = 0.03$), indicating that these two features are functionally linked.

Phylogenetic analysis.—An analysis of maximum cribellar thread span and axial fiber diameter within a phylogenetic context also supports the relationship of these two features. Figure 4 presents the values of these two variables and of spider weight for the six genera included in this study and for their hypothetical ancestors. Changes in the values of these features between hypothetical ancestors A₁–A₃ and the genera derived from them are plotted in Fig. 5. Change in spider weight is not significantly related to change in axial fiber diameter (Fig. 5A), whereas change in maximum cribellar thread span is significantly related to change in axial fiber diameter (Fig. 5B). In the latter regression, values of *Siratoba*, *Uloborus*, and *Waitkera* are shown to have changed little from those of their ancestors, whereas values of *Hyptiotes* and, to a lesser degree, *Octonoba* have increased and those of *Miagrammopes* have decreased.

DISCUSSION

The results of this study support the hypothesis that the switch from autonomous to heteronomous cribellar threads was accompanied by a reduction in the diameter of the cribellar thread's

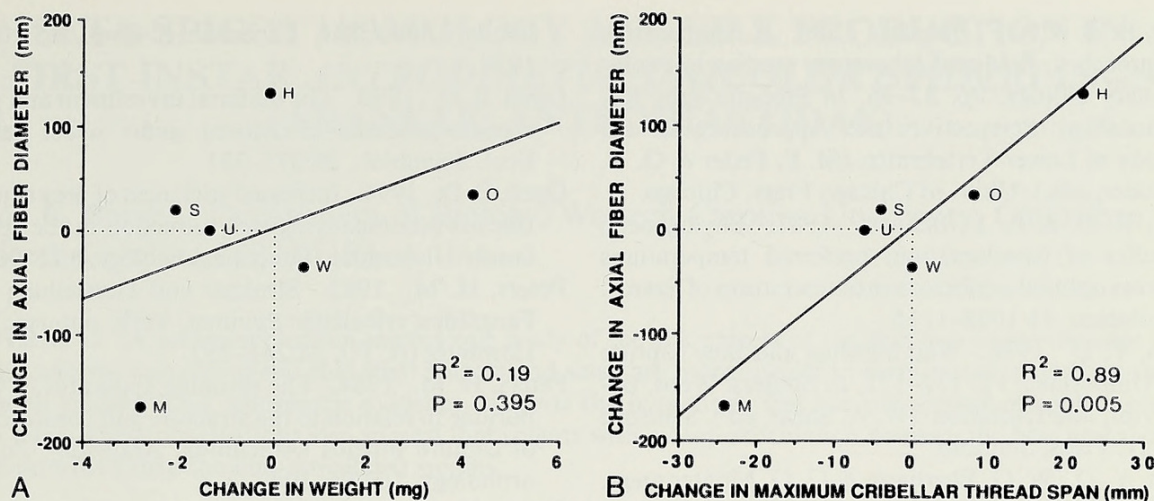


Figure 5.—Regressions of changes in values from hypothetical ancestors A_1 – A_3 to their descendant genera as determined from values presented in Fig. 4. A. The relationship of spider weight and axial fiber diameter ($df = 4$, $T = 0.95$). B. The relationship of maximum cribellar thread span and axial fiber diameter ($df = 4$, $T = 5.65$). Letters denote the genus whose values are plotted.

axial fibers. They also show that the diameter of the axial fibers in autonomous cribellar threads is affected by web architecture. Species whose cribellar threads span larger distances produce axial fibers that have greater diameters. However, there is no evidence that within a web axial fiber diameter differences between short and long cribellar thread spans.

These observations provide further evidence that changes in web architecture are associated with changes in the properties of the threads that form a web. In conjunction with other studies, they also demonstrate that selection can act independently on different components of a single thread. Although the heteronomous threads of *Miagrammopes* contain axial threads that are smaller in diameter than the other five species that were studied, they contain the greatest absolute and weight-specific number of cribellar fibrils and, therefore, hold prey more strongly than do the threads of the other species (Opell in press, pers. obs.).

The principle underlying these differences in axial fiber diameter appears to be the parsimonious investment of silk in a spider's web. This supports the arguments of Craig (1987) and Denny (1976) that only as much material is invested in each component of a spider's web as is necessary for that component to function properly.

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