

## Factors Governing the Stickiness of Cribellar Prey Capture Threads in the Spider Family Uloboridae

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**ABSTRACT** The surface of a cribellar prey capture thread is formed of thousands of fine, looped fibrils, each issuing from one of the spigots on an oval spinning plate termed the cribellum. This plesiomorphic capture thread is retained by members of the family Uloboridae, in which its stickiness differs among genera. An examination of five cribellar thread features in nine uloborid species shows that only the number of fibrils that form a thread explains these differences in thread stickiness. Neither the physical features of these fibrils, nor the manner in which they are combined to form threads differs among species. Threads produced by orb-weaving species contain fewer fibrils than those produced by species that build reduced webs. Relative to spider weight, the number of fibrils that form a cribellar thread is greatest in simple-web species of the genus *Miagrammopes*, less in triangle-web species of the genus *Hyptiotes*, and least in orb-weaving species representing five genera. A transformational analysis shows that change in the number of cribellum spigots is directly related to change in the stickiness of cribellar thread. This direct relationship between the material invested in a cribellar thread and its stickiness may have been a limiting factor that favored the switch from the dry cribellar threads of uloborids to the adhesive capture threads produced by other orb-weaving families. © 1994 Wiley-Liss, Inc.

Two types of prey capture thread are found in spider orb-webs, dry cribellar thread, and moist adhesive thread. Of the two, cribellar thread is more primitive. It is present in the aerial webs produced by the most primitive members of the largest spider infraorder, the Araneomorphae (Coddington and Levi, '91), and is retained in the orb-webs spun by members of the family Uloboridae (Opell, '79). The more speciose sister group of the Uloboridae-Deinopidae lineage contains six families of orb-weavers, the capture threads of which depend on droplets of adhesive for their stickiness (Foelix, '82; Vollrath, '92). This switch from cribellar threads, the stickiness of which appears to be derived from mechanical forces (Opell, '93), to adhesive capture threads, the stickiness of which appears to result from their chemical properties (Vollrath et al., '90), represents a major evolutionary change in the design of spider orb-webs. This study examines the physical composition of cribellar thread in an effort to determine which factors most affect its stickiness. A clearer understanding of this relation-

ship will provide a better understanding of how cribellar threads operate and what factors may have favored the switch from cribellar to adhesive capture threads.

The family Uloboridae is well suited for this study, both because it contains the only orb-weaving spiders that produce cribellar threads, and because the stickiness of these threads differs significantly among its members (Table 1; Opell, '94a). These differences in stickiness are associated with changes in web architecture. The family's plesiomorphic and most common web form is the orb-web (Coddington and Levi, '91), although two of its genera construct reduced webs. Members of the genus *Hyptiotes* construct triangle-webs that have four radii between which cribellar threads extend, whereas members of the genus *Miagrammopes* construct still simpler webs, on whose irregularly branching lines cribellar threads are deposited (Lubin, '86; Lubin et al., '78; Opell, '82, '90). As these webs become more reduced, their cribellar threads become stickier (Table 1; Opell, '94a). This study capitalizes on these differ-

ences in stickiness to determine how the features of a spider's spinning apparatus and of the silk that it produces determine the stickiness of cribellar thread.

The cribellar threads of Uloboridae each consist of three components: 1) a pair of central, supporting axial lines, each with an average diameter of 273 nm; 2) a network of 30–56 smaller paracribellar fibrils that appear to form a superstructure around the axial fibers; and 3) a cloud of thousands of very thin, looped fibrils, each with a diameter of about 18 nm, that form the outer sheath of the cribellar thread (Figs. 1a,b; Kovoor and Peters, '88; Peters, '83, '84, '86, '92; Peters and Kovoor, '80). The axial lines are spun from spigots on the posterior spinnerets, the paracribellar fibers from spigots on the leading edge of the median spinnerets, and the fibrils from spigots on the cribellum, an oval spinning field, located on the ventral surface of the abdomen, just anterior to the spinnerets (Fig. 1c). Each of the cylindrical spinning spigots of the cribellum (Fig. 1d) contributes one fibril to the cribellar thread. Using a setal comb on its fourth legs, a spider draws fibrils from the cribellum and combines them with axial lines to form a composite cribellar prey capture thread (Eberhard, '88).

The mechanism by which a cribellar thread holds an object is not fully understood (Opell, '93). By catching on the setae and surface irregularities of prey, the coiled fibrils of the thread appear to act like the soft part of a Velcro fastener as it catches on its counterpart (Opell, '79). However, cribellar thread

also sticks to much smoother surfaces, such as glass, steel, graphite, and beetle elytra (Eberhard, '80; Peters, '86; Opell, '94b). Scanning and transmission electron microscope studies (e.g., Kullmann and Stern, '81; Opell, '79, '89, '90; Peters, '84, '86, '92) reveal no adhesive droplets on cribellar fibrils, indicating that unknown forces contribute to the stickiness. Electrostatic charge has been suggested as a possible force (Peters, '84, '86), although there are no data to support this hypothesis.

Regardless of the mechanisms involved, the stickiness of cribellar threads results from the interaction of its fibrils with the object that it holds. Using nine uloborid species, this study tests the hypothesis that the number of fibrils that form a thread is the principal factor determining its stickiness. I attempted to falsify this hypothesis by first determining if the manner in which cribellar fibrils were combined to form a thread affected thread stickiness and then by determining if the physical features of the fibrils themselves affected thread stickiness. Finally, I determined if fibril number accounted for cribellar thread stickiness.

Although it is possible to measure the features of cribellar fibrils, their small diameters and convoluted arrangement (Fig. 1b) make it impossible to count the number that form a cribellar thread (Fig. 1a). However, this number can be determined by counting the number of spigots on the cribellum that produced the thread (Figs. 1c,d).

TABLE 1. Comparison of cribellar thread and cribellar fibril features in nine species of Uloboridae<sup>1</sup>

	Cribellar thread stickiness: $\mu\text{N}/\text{mm}$ contact $\left(\frac{\mu\text{N}/\text{mm contact}}{\text{spider weight}}\right)$ in mg	Thread width Cribellum width	Node diam. nm	Internode diam. nm	Node spacing nm
Orb, webs					
<i>Waitkera waitakerensis</i>	15.5 (1.9)	$0.43 \pm 0.04$ (35)	$17.4 \pm 1.5$ (6)	$10.1 \pm 0.6$ (6)	$51.4 \pm 8.9$ (6)
<i>Siratoba referena</i>	11.5 (2.8)	$0.52 \pm 0.04$ (23)	$17.5 \pm 1.9$ (4)	$8.7 \pm 2.0$ (4)	$63.9 \pm 22.9$ (4)
<i>Uloborus glomusos</i>	15.4 (1.8)	$0.34 \pm 0.08$ (70)	$18.4 \pm 1.4$ (5)	$10.4 \pm 1.1$ (5)	$54.5 \pm 14.3$ (5)
<i>Octonoba sinensis</i>	17.0 (1.5)	$0.42 \pm 0.07$ (50)	$18.8 \pm 2.4$ (5)	$10.7 \pm 0.9$ (5)	$87.7 \pm 12.9$ (5)
<i>Philoponella arizonica</i>	15.0 (1.2)	$0.35 \pm 0.04$ (26)	—	—	—
Triangle-webs					
<i>Hyptiotes cavatus</i>	26.2 (3.4)	$0.39 \pm 0.04$ (51)	$19.4 \pm 1.0$ (5)	$10.3 \pm 0.3$ (5)	$63.1 \pm 10.0$ (5)
<i>Hyptiotes gertschi</i>	29.8 (3.2)	$0.40 \pm 0.04$ (33)	—	—	—
Simple webs					
<i>Miagrammopes animotus</i>	31.5 (6.9)	$0.43 \pm 0.12$ (104)	$16.2 \pm 0.5$ (4)	$8.6 \pm 0.7$ (4)	$42.3 \pm 11.1$ (4)
<i>Miagrammopes species</i>	24.4 (6.6)	$0.40 \pm 0.03$ (24)	$18.4 \pm 1.0$ (4)	$9.5 \pm 1.0$ (4)	$52.7 \pm 13.1$ (4)

<sup>1</sup>Cribellar thread stickiness values are taken from Opell ('94a). For other values: mean  $\pm 1$  standard deviation (sample size).

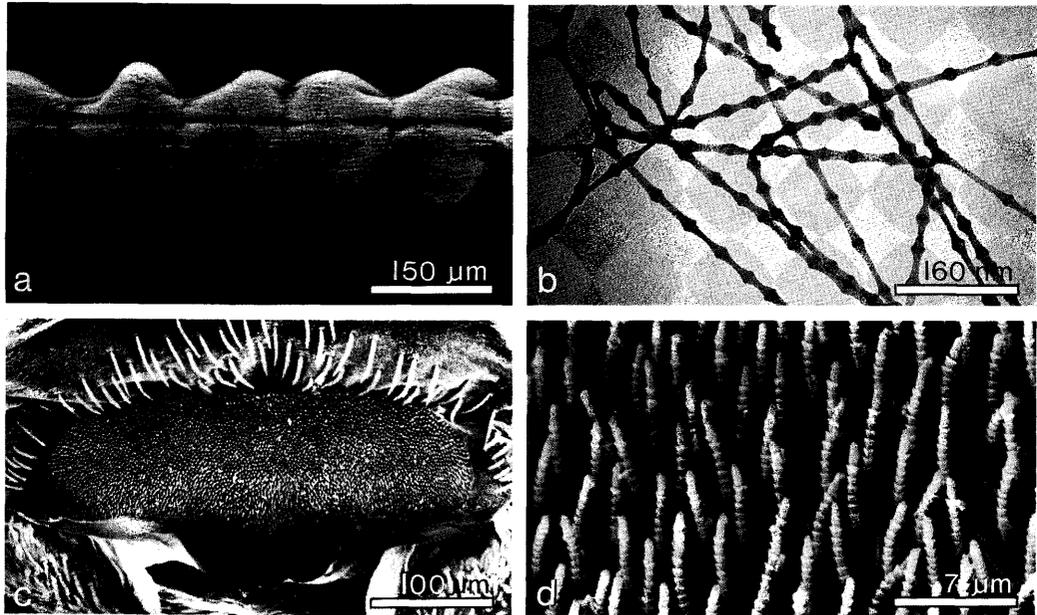


Fig. 1. Uloborid cribellar thread and cribellum features. **a:** Cribellar thread of *Hyptiotes cavatus*. **b:** Cribellar fibrils of *Miagrammopes* sp. **c:** Cribellum of *Waitkera waitakerensis*. **d:** Cribellar spigots of *Waitkera waitakerensis*.

#### MATERIALS AND METHODS

##### *Species studied and study sites*

I studied the cribellar threads and cribella of adult females (adult male uloborids do not construct capture threads) of nine species, representing seven of the family's 18 genera (Fig. 2). Included were five orb-weaving species: *Waitkera waitakerensis* (Chamberlain, '46) ( $\bar{X}$  live weight 8.79 mg, SD 2.99), from New Zealand's North Island; *Siratoba referena* (Muma and Gertsch, '64) ( $\bar{X}$  live weight 4.31 mg, SD 1.14) and *Philoponella arizonica* (Gertsch, '36) ( $\bar{X}$  live weight 13.35 mg, SD 4.49), from the Chiricahua Mountains of southeastern Arizona; *Uloborus glomus* (Walckenaer, 1841) ( $\bar{X}$  live weight 9.39 mg, SD 2.66) from southwestern Virginia; and *Octonoba sinensis* (Simon, 1880) ( $\bar{X}$  live weight 12.86 mg, SD 4.30), an introduced Asian species, collected from free ranging populations in greenhouses at Virginia Polytechnic Institute and State University. I also studied two triangle-web species: *Hyptiotes cavatus* (Hentz, 1847) ( $\bar{X}$  live weight 7.76 mg, SD 3.60), from southwestern Virginia, and *Hyptiotes gertschi* (Chamberlin and Ivie, '35) ( $\bar{X}$  live weight 9.68 mg, SD 2.95), from north-

western Washington; and two simple-web species: *Miagrammopes animotus* (Chickering, '68) ( $\bar{X}$  live weight 5.26 mg, SD 2.09), from the Luquillo National Forest of Puerto Rico and an undescribed green *Miagrammopes* species ( $\bar{X}$  live weight 3.92 mg, SD 1.36) from the Heredia Province of central Costa Rica.

##### *Cribellar thread features*

Uloborids construct their webs at night or early morning. Therefore, I collected thread from webs between 5:00 and 10:00 a.m. to obtain fresh samples that were not contaminated or damaged. Threads were collected on microscope slides to which raised, parallel supports were glued at 4.8 mm intervals. Double-sided tape atop each support securely anchored the threads and maintained their original tensions. All threads used in this study were examined under a dissecting microscope to assure that only intact strands were included.

I measured the features of cribellar fibrils by transferring cribellar threads from microscope slide samplers to Formvar-coated copper grids and examining them without further treatment at  $\times 130,000$  under a

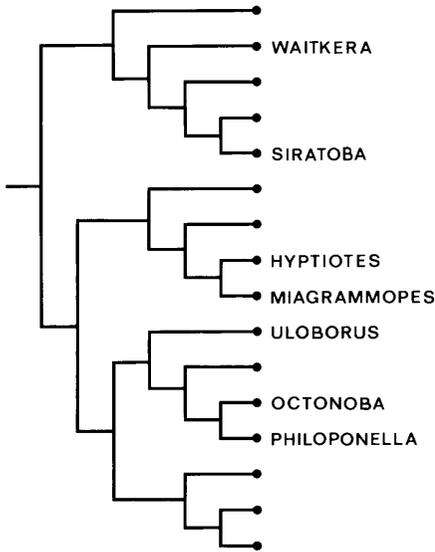


Fig. 2. Cladogram of the Family Uloboridae from Coddington (1990), showing the phylogenetic positions of the seven genera included in this study.

transmission electron microscope. From enlarged photographic prints, I measured 1–4 fibrils per specimen, including only fibrils that showed no evidence of having been stretched. From each fibril, I measured the width of three nodes and three internodes and the spacing of nodes in a fibril segment that contained 4–22 ( $\bar{X} = 9$ ) nodes (Fig. 1b).

On each of the 12 days that I examined these threads, I also photographed a grating replica (2,160 lines per mm) at  $\times 130,000$  to precisely calculate specimen magnification and determine if magnification was consistent from day to day. The standard error of the mean width of one of the replica's 463 nm wide lines, as measured from photographic negatives, was only 2.7 nm.

I evaluated the manner in which fibrils issuing from the cribellum are combined with axial threads to form a cribellar thread by comparing the cribellum's width with the width of the cribellar thread it produced. To determine the diameter of the puffs that form these threads, I measured the diameter of one puff from three regions of a thread and

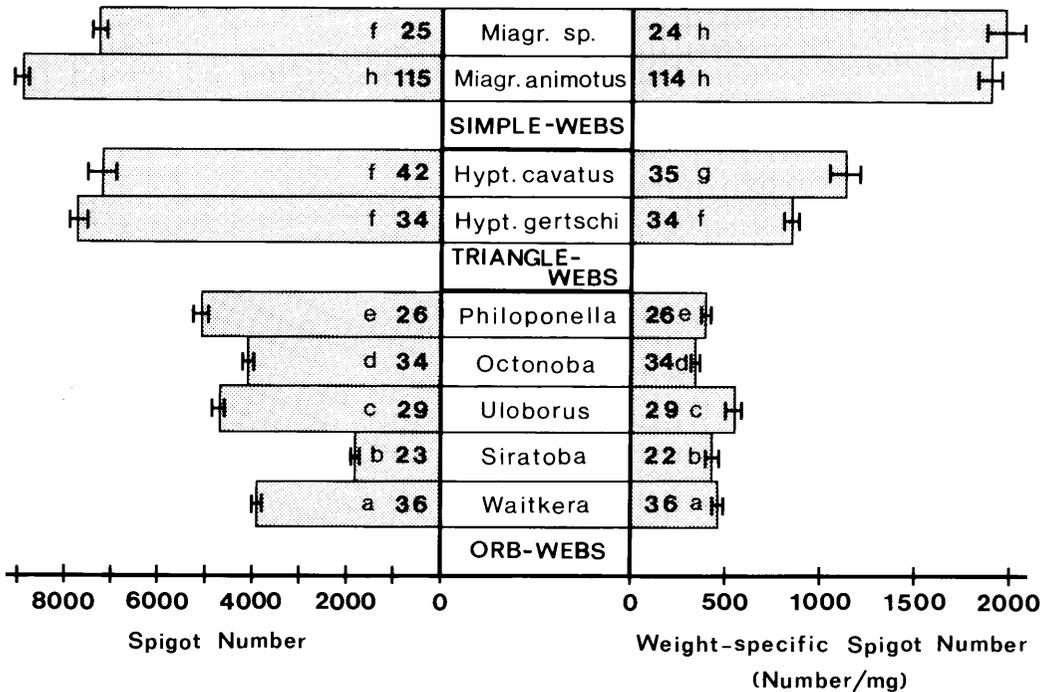


Fig. 3. Comparison of the absolute (left) and weight-specific (right) cribellar spigot numbers of nine uloborid species. Numbers within each box indicate sample size; species with different letters have values that differ statistically; error bars denote  $\pm 1$  standard error.

used their mean value as a spider's value. After a sample of a spider's cribellar thread was taken, the spider was collected and its live weight determined before it was preserved in 80% ethanol. I removed the cribellum of each preserved spider, mounted it in water-soluble medium on a microscope slide, and examined it under a compound microscope equipped with differential phase contrast optics. With a computerized digitizing apparatus, I measured the width (transverse dimension) and surface area of each cribellum and determined the density of spinning spigots in three regions of the cribellum: one at its anterior midline, one at its posterior lateral margin, and one midway between these two regions. I then multiplied the mean spigot density of each cribellum, as determined from these three density measurements, by its total surface area to determine the total number of spigots on its surface. This method of determining the number of fibrils that form a cribellar thread assumes that either all or a constant percentage of the cribellum's spigots always operate.

All values were tested with a Shapiro-Wilk W-statistic to determine if they were normally distributed ( $P > 0.05$ ). If they were, T-tests (T) were used for pair-wise comparisons and analysis of variance tests (ANOVA) for multiple comparisons. If one or more values being compared were not normally distributed, Wilcoxon 2-sample tests (W) were used for pair-wise comparisons and Kruskal-Wallis K-sample tests (KW) for multiple comparisons. Values were considered to be significantly different if  $P < 0.05$ .

#### *Cribellar thread stickiness*

The individuals, the cribellar thread and features of which were measured in this study, are the same individuals of which the cribellar thread stickiness was measured earlier (Opell, '94a). As described more fully in that study, stickiness was measured by first pressing with a standard force a 2 mm wide piece of fine sandpaper against a 4 mm long strand of cribellar thread and then pulling the sandpaper plate away from the thread at a slow, constant rate. The force required to pull the plate from a strand of cribellar thread was then divided by the width of the plate (measured to the nearest 20  $\mu\text{m}$ ) and stickiness was reported as  $\mu\text{Newtons}$  of force per mm of thread contact with the sandpaper plate. Values obtained with a sandpaper plate

are the same as those obtained with a section of a fleshfly (*Sarcophaga bullata*) wing (Opell, '94a) and, therefore, provides a reasonable estimate of the performance of a cribellar thread. However, different insect surfaces yield significantly different stickiness values (Opell, '94b).

#### *Relationship of spigot number and thread stickiness*

As the species included in this study are evolutionarily related to different degrees (Fig. 2), their values are not strictly independent. Species that are more closely related would be expected to be more similar than those that are less closely related, making it inappropriate to analyze the associations of weight, cribellum spigot number, and cribellar thread stickiness with traditional regression techniques (Harvey and Pagel, '91). Therefore, I employed the method described by Huey and Bennett ('86, '87) for evaluating the direction and rate of evolution of two continuous variables, the states of which are hypothesized to be functionally linked or co-adapted. This method has two steps: 1) the inference of a group's ancestral character states from the states of its extant members and 2) the analysis of changes in these characters from these hypothetical ancestors to the extant taxa descended from them. If this analysis shows that changes (both positive and negative) in the two characters are significantly correlated, then their states can be considered to be functionally linked or to have coevolved.

I computed the states of three characters in the hypothetical ancestors of the seven genera included in this study: spider live weight, number of cribellar spigots, and cribellar thread stickiness. I included weight in this analysis to permit evaluation of the effect of spider size on cribellar thread stickiness. Unless this variable is ruled out, even a significant association between spigot number and cribellar thread stickiness may not fully account for cribellar thread stickiness.

I employed the scheme of iterative averaging described below to determine the state of these three characters in hypothetical ancestors A1-A6 (Fig. 4). In these equations, the value of each genus is represented by the first initial of its name. All genera but *Hyptiotes* and *Miagrammopes* are represented by a single species. Therefore, the mean values of the two *Hyptiotes* and the two *Miagram-*

*mopes* species are used in order not to over-represent these genera.

$$A1 = A2 + A3/2$$

$$A2 = W + S + A3/3$$

$$A3 = (W + S)/2 + A4 + A5/3$$

$$A4 = H + M + ((U + ((O + P)/2))/2)/3$$

$$A5 = (((H + M)/2) + U + ((O + P)/2))/3$$

$$A6 = U + O + P/3$$

Next, I computed the change that occurred between the most recent hypothetical ancestor of each genus and that genus. For example, the transition from hypothetical ancestor A2 to *Waitkera* involved a 1.86 mg increase in weight, the addition of 303 cribellum spigots, and an increase in cribellar thread stickiness of 0.13  $\mu$ N per mm of contact. Changes in cribellar thread stickiness were then regressed against changes in spider weight and changes in cribellum spigot number to determine if one or both of these parameters were associated with changes in cribellar thread stickiness.

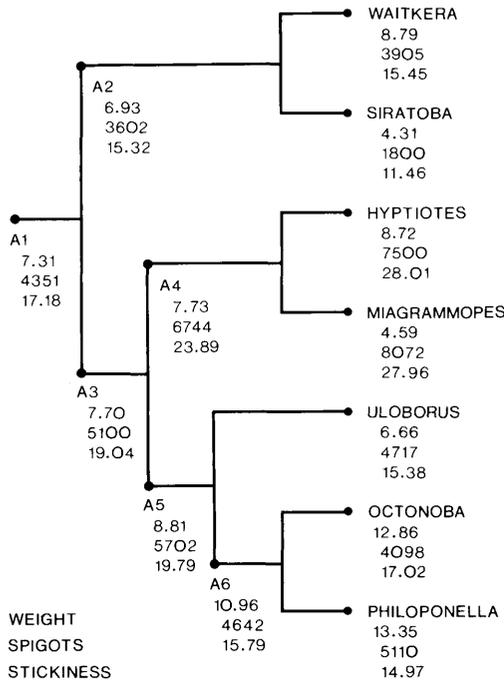


Fig. 4. Transformational analysis of spider weight in mg, cribellum spigot number, and cribellar thread stickiness in  $\mu$ N per mm of contact based on the values of seven genera.

RESULTS

*Cribellar thread width and fibril features*

Table 1 presents the ratios of cribellar thread width to cribellum width and the three features of cribellar fibrils that were measured in the nine species studied. Both the absolute and weight-specific stickiness values of reduced-web species are greater than those of orb-web species (Table 1; Opell, '94a). Therefore, the simplest and most liberal indication that differences in the way in which cribellar fibrils are combined to form a thread or that differences in the fibrils themselves affect cribellar thread stickiness is the demonstration that one or more of these variables differs significantly between threads produced by reduced-web and orb-web species. These differences are not found in the four features that were investigated: 1) cribellar thread width to cribellum width, ( $W, P = 0.47$ ), 2) diameter of fibril nodes (ANOVA,  $P = 0.93$ ), 3) diameter of fibril internodes (ANOVA,  $P = 0.24$ ), and 4) spacing of fibril nodes (ANOVA,  $P = 0.12$ ). Therefore, these features can be eliminated as major determinants of cribellar thread stickiness.

*Fibril number*

Figure 3 presents the absolute and weight-specific numbers of cribellum spinning spigots for each species, numbers that are considered equivalent to the absolute and weight-specific number of fibrils in the threads produced by these species. In contrast to the four features just discussed, these two indexes differ with web type. The absolute number of spigots differ among orb-weavers (ANOVA,  $P = 0.0001$ ), but each species has fewer than the pooled numbers of the two triangle-web species ( $W, P = 0.0001$  in all cases). The number of spigots do not differ between the two triangle-web species ( $W, P = 0.46$ ) and their mean pooled value (7,476, SD 1510) does not differ from that of the Costa Rican species of *Miagrammopes* ( $W, P = 0.12$ ). This simple-web species had fewer spigots than *M. animotus* ( $W, P = 0.0001$ ).

Weight-specific spigot number differs among the orb-weaving species ( $KW, P = 0.0001$ ), but each has fewer than *Hyptiotes gertschi* ( $T, P = 0.0001$  for *Philoponella arizonica*;  $W, P = 0.0001$  for all other species). *Hyptiotes gertschi* has fewer spigots than *Hyptiotes cavatus* ( $W, P = 0.020$ ). Values of the two species of *Miagrammopes* do not differ ( $W, P = 0.35$ ) and their combined

mean (1,917/mg, SD 647) is greater than that of *H. cavatus* ( $W, P = 0.0001$ ).

Regardless of their phylogenetic position, orb-weaving species have both absolute and weight-specific cribellar spigot numbers that are more similar to one another than to those of either triangle-web or simple-web species. Thus, like changes in cribellar thread stickiness, changes in cribellum spigot number appear to reflect changes in web architecture, not phylogenetic relationships within the family (Fig. 2). This is demonstrated by comparisons of the sister orb-web genera *Octonoba* and *Philoponella* and the sister reduced-web genera *Hyptiotes* and *Miagrammopes*. Weight-specific cribellar spigot number differs by only 64 spigots/mg between the orb-weavers, whereas it differs by an average of 949 spigots/mg between *Hyptiotes* and *Miagrammopes*. The greater similarity between the values of *Octonoba* and *Philoponella* is best explained by the fact that they produce the same type of web, whereas *Hyptiotes* and *Miagrammopes* produce different web types.

#### *Effect of fibril number on thread stickiness*

Congruent changes in the number of cribellum spigots and cribellar thread stickiness (Fig. 3, Table 1) support the hypothesis that increased cribellar thread stickiness is achieved by an increase in cribellum spigot number. More rigorous support for this functional association comes from the transformational analysis of spider weight, cribellum spigot number, and cribellar thread stickiness. When change in the stickiness of cribellar thread is regressed against change in spider weight, no relationship is found ( $DF = 5, t = 0.54, P = 0.62$ ). In contrast, change in cribellar thread stickiness and change in cribellum spigot number produces a significant regression (Fig. 5;  $DF = 5, t = 3.51, P = 0.017$ ). This analysis indicates that the cribellum spigot number and cribellar thread stickiness of *Octonoba*, *Philoponella*, and *Waitkera* have changed little from their ancestral values, whereas the values of *Hyptiotes* and *Miagrammopes* have increased and those of *Siratoba* and *Uloborus* have decreased from their ancestral values.

#### DISCUSSION

##### *Relationship between fibril number and thread stickiness*

Of the five features examined, only the number of spigots on the cribellum of a spi-

der relates to the stickiness of its cribellar thread. Thus, differences in the number of fibrils that form a cribellar thread and not differences in the fibrils themselves appear to govern the stickiness of the thread.

A two-fold increase in fibril number doubles the thread's stickiness (Fig. 5). Consequently, in the Uloboridae, the increased cribellar thread stickiness that is associated with web reduction is achieved at the cost of greater material investment in cribellar threads. Relative to spider weight, the cribellar threads of triangle-web species have, on average, 2.3 times more cribellar fibrils than those spun by orb-weavers and the threads of simple-web species have 2.0 times more cribellar fibrils than those of triangle-web species (Fig. 3). Thus, the increased cribellar thread stickiness that is associated with web reduction in the uloborids is achieved at the cost of increased investment in cribellar fibrils. As web architecture becomes simpler, these changes may serve to reallocate silk from the web's non-sticky supporting elements to its sticky prey capture threads.

##### *Implications for origin of adhesive capture thread*

This study demonstrates the constraints of producing cribellar capture threads: any change in thread stickiness requires changes in both the spider's spinning apparatus and the amount of silk that it must produce. In contrast, studies of adhesive threads show that their adhesive droplets have complex chemical properties (Townley et al., '91; Vollrath et al., '90) and suggest that changes in the chemical composition of these droplets can affect the thread's stickiness. Unlike cribellar threads, the stickiness of which can be increased only by quantitative changes in thread composition, both qualitative and quantitative changes probably alter the stickiness of adhesive threads. Additionally, changes in the stickiness of cribellar threads must be achieved by anatomical changes in the cribellum and associated changes in the setal comb that cards the fibrils from it. In contrast, changes in both the composition and amount of adhesive deposited on a thread could be achieved with little or no change in the morphology of a spider's spinning apparatus.

The energetic (behavioral) costs of spinning cribellar and adhesive threads have not been compared, although cribellar thread appears to be more costly to produce. The pro-

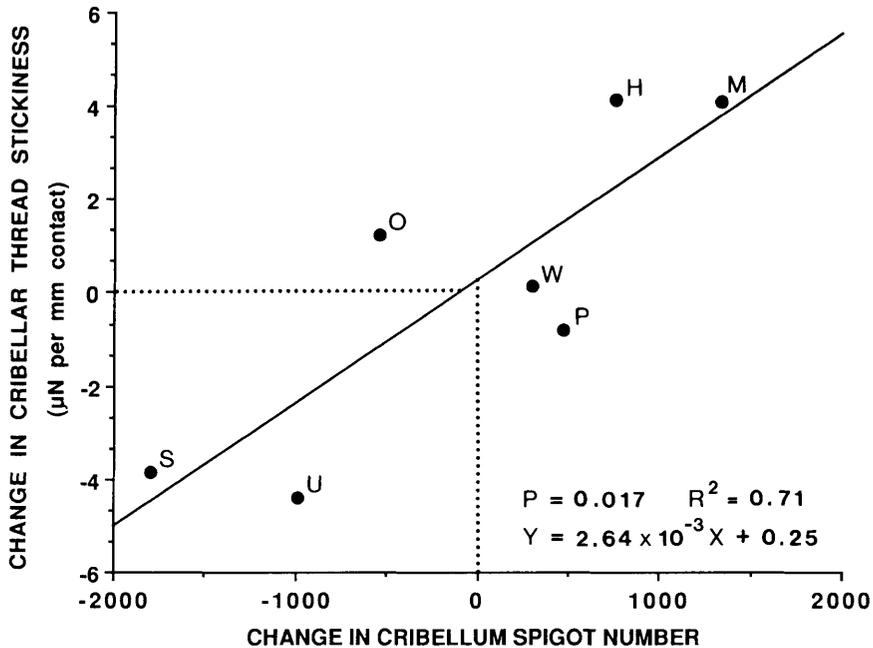


Fig. 5. Regression of changes in the values of cribellum spigot number and cribellar thread stickiness from hypothetical ancestors A2, A4, A5, and A6 to their decedent genera, as determined from values presented in

Figure 4. Letters are the first initials of the genera whose values are plotted: *Hyptiotes*, *Miagrammopes*, *Octonoba*, *Philoponella*, *Siratoba*, *Uloborus*, and *Waitkera*.

duction of an adhesive thread requires only that, as axial fibers are spun, they are coated with adhesive from adjacent spigots on the same spinnerets. However, when a cribellar thread is spun, cribellar fibrils must first be drawn from the cribellum's spigots with sufficient force to polymerize them and then be combined with the axial fibers. Increasing the amount of adhesive added to axial threads does not appear to have a very large energetic cost. However, more energy is probably required to polymerize and manipulate a greater number of cribellar fibrils. Along with the material costs of producing more cribellar fibrils, this energetic cost may have further constrained increases in cribellar thread stickiness and favored the origin of adhesive thread.

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