

## Ontogenetic Changes in Cribellum Spigot Number and Cribellar Prey Capture Thread Stickiness in the Spider Family Uloboridae

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**ABSTRACT** Uloborids produce dry cribellar prey capture thread whose surface is formed of thousands of fine, looped fibrils. These fibrils are spun from spigots on an oval spinning plate termed the cribellum and handled by a setal comb on the fourth leg termed the calamistrum. Ontogenetic studies of the triangle-web species *Hyptiotes cavatus* and the simple-web species *Miagrammopes animotus* show that increases in the number of cribellar spinning spigots are associated with increases in the stickiness of cribellar threads. For *H. cavatus* this relationship is similar to that determined by a previous interspecific comparison. Relative to cribellum spigot number, *M. animotus* produces stickier threads than does *H. cavatus*. Differences in the features of these species' cribellar fibrils do not explain difference in thread stickiness. Cribellar threads produced by *M. animotus* have shorter, wider puffs than those produced by *H. cavatus* and, consequently, achieve a greater contact surface area per mm of length than do threads produced by *H. cavatus*. The more closely spaced cribellum spigots of *M. animotus* maximize the number of fibrils that contact a surface. *Miagrammopes animotus* also has a longer calamistrum and more closely spaced calamistrum setae than does *H. cavatus*. This demonstrates how small differences in spinning anatomy and behavior can fine-tune the physical characteristics of cribellar threads in ways that maximize their stickiness. © 1995 Wiley-Liss, Inc.

Cribellar thread is the most primitive type of prey capture thread produced by spiders (Fig. 1a). It appeared in the first aerial webs produced by members of the infraorder Araneomorphae, a group containing 86% of all spider families, 90% of all spider genera, and 94% of all living spider species (Coddington and Levi, '91). Cribellar thread is present in webs constructed by 22 families of spiders, where it increases the prey capture efficiency of these webs by preventing prey from escaping before a spider can locate, run to, and subdue it.

Unlike the viscous capture threads produced by more derived orb-weavers, the dry surface of a cribellar thread is formed of a cloud of thousands of fine, looped silk fibrils (Fig. 1a,b). Each of these fibrils has a diameter of about 18 nm and is spun from one of the spigots on an oval spinning plate, termed the cribellum (Fig. 1c,d), that is situated on the ventral surface of a spider's abdomen,

just anterior to its spinnerets (Eberhard and Pereira, '93; Kooor and Peters, '88; Opell, '93, '94a-c; Peters, '83, '84, '86, '92). These fibrils are drawn from the cribellum by a setal comb, termed the calamistrum (Fig. 1e), that is located on each of the spider's fourth legs (Eberhard, '88). Cribellar fibrils enfold two or four pairs of larger, supporting axial fibers produced by spigots on the posterior spinnerets to form a composite cribellar thread (Eberhard and Pereira, '93). In some species, a network of 30-56 smaller paracribellar fibrils appears to form a superstructure around the axial fibers (Peters, '84; Peters and Kooor, '80). In the Uloboridae, cribellar fibrils are deposited around a pair of axial fibers as a series of regularly spaced puffs (Fig. 1a; Eberhard and Pereira, '93; Opell, '89, '90; Peters, '84).

Even among related species, the stickiness of cribellar threads differs greatly (Opell, '94a). A comparison of the cribella and cribel-

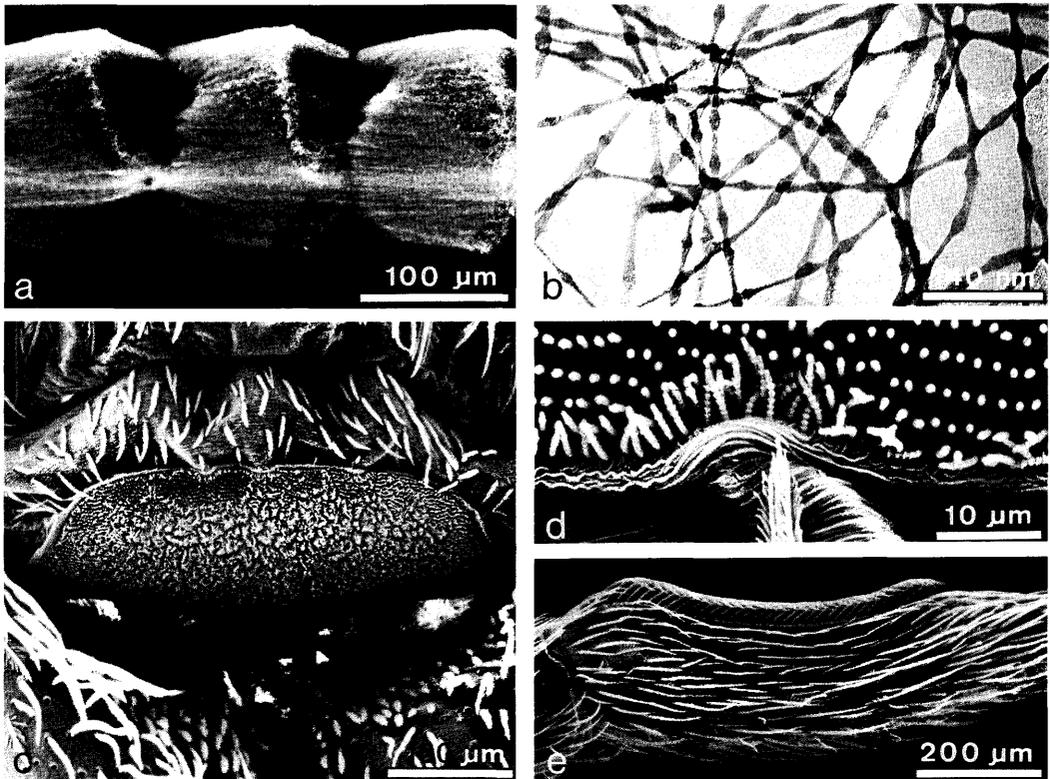


Fig. 1. *Miagrammopes animotus* cribellar thread and cribellar thread spinning apparatus. a: Cribellar thread. b: Cribellar fibrils. c: Cribellum. d: Border of cribellum showing spigots. e: Metatarsus of fourth leg, with calamistrum on its dorsal surface.

lar threads of adult females of nine species from the orb-weaving family Uloboridae showed that the stickiness of a cribellar thread is directly related to the number of fibrils that form the thread, as inferred from the number of spigots on a spider's cribellum. Neither the physical features of the cribellar fibrils nor the manner in which they were combined explained the differences in stickiness among these species' cribellar threads (Opell, '94c). One objective of this study is to verify this conclusion by examining ontogenetic changes in the cribellum spigot number and cribellar thread stickiness of two species of Uloboridae.

A second objective is to determine if spiders maximize the stickiness of their cribellar threads by fine-tuning features of their cribellum, calamistrum, or cribellar thread puffs. The species I studied are well suited for this, as they belong to sister genera (Coddington, '90) whose members construct webs that show different degrees of reduction from the

family's plesiomorphic orb-web and produce capture threads that have different stickinesses. Adult *Hyptiotes cavatus* construct triangle-webs (Lubin, '86; Opell, '82) and produce capture threads with an absolute stickiness value of 26.2  $\mu\text{N}/\text{mm}$  of contact and a spider weight-specific value of 3.4  $\mu\text{N}/\text{mm}/\text{mg}$  (Opell, '94a). Adult *Miagrammopes animotus* construct still simpler, irregular webs consisting of only a few capture lines (Lubin, '86; Lubin et al., '78; Opell, '89, '90) and produce capture threads with values of 31.5  $\mu\text{N}/\text{mm}$  and 6.9  $\mu\text{N}/\text{mm}/\text{mg}$ , respectively (Opell, '94a). The greater stickiness of *M. animotus* capture threads is associated with this species' greater absolute and weight-specific number of cribellum spinning spigots (Opell, '94c). However, there may be other factors that increase the stickiness of this species' cribellar threads.

A better understanding of factors that govern the stickiness of cribellar threads will clarify the mechanism by which this type of

thread operates. Compared to interspecific studies, developmental studies are able to track smaller changes in cribellum and cribellar thread features and to better control for interspecific differences in spinning behavior. Thus, they can determine how differences in cribellum shape and spigot density, calamistrum length and setal density, and the shape of a cribellar thread's puffs affect the stickiness of threads spun from a cribellum with a given number of spigots.

#### MATERIALS AND METHODS

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

This study included the triangle-web species *Hyptiotes cavatus* (Hentz, 1847) from southwestern Virginia and the simple-web species *Miagrammopes animotus* Chickerling, '68, from the Luquillo National Forest of Puerto Rico.

##### *Cribellar thread stickiness*

Because uloborids construct their webs in the early morning, I collected the threads of *Miagrammopes animotus* between 5:00 and 10:00 a.m. to obtain fresh threads that were not contaminated by dust or pollen or damaged by prey. The threads of *Hyptiotes cavatus* were collected from webs produced in the laboratory by spiders housed individually in plastic boxes. I collected thread samples on microscope slides to which five raised, parallel supports were glued at 4.8-mm intervals. Double-sided tape atop each support secured the threads to a sampler at their original tensions. After obtaining a thread sample from a spider's web, I collected the spider and preserved it in 80% ethanol. I measured the stickiness of four strands of thread from each spider's web 2–40 hr after collecting them and used the mean stickiness of these strands as the value for that spider's capture thread. All threads were examined under a dissecting microscope to assure that only undamaged threads were studied.

Cribellar thread stickiness was measured using methods describe more fully by Opell ('94a,b). The instrument used for these measurements incorporated a glass needle strain gauge with a 2-mm-wide contact plate glued to the needle's free tip. This plate was pressed against a cribellar thread strand at a speed of 13.5 mm per minute until a force of 19.61  $\mu\text{N}/\text{mm}$  was achieved. The motor was then reversed and the contact plate was withdrawn at a speed of 14.0 mm per minute until the contact plate pulled free of the thread. I

recorded the position of the glass needle on a calibrated scale at the instant the contact plate pulled free of the thread and multiplied this mg value by the accelerating force of gravity to determine the force in Newtons required to pull the thread from the contact plate. I then divided this force by the width of each contact plate (measured to the nearest 20  $\mu\text{m}$  under a dissecting microscope) to calculate stickiness, expressed as  $\mu\text{N}$  per mm of thread contact with the plate. The two glass needles used to measure the stickiness of *Hyptiotes cavatus* threads had a sensitivity of 1.88 and 1.91  $\mu\text{N}/\text{mm}$  contact. These two needles, plus another with a sensitivity of 1.82  $\mu\text{N}/\text{mm}$ , were also used to measure *Miagrammopes animotus* threads. After determining the stickiness of a spider's cribellar thread, I recorded the relative humidity (RH) at which these measurements were taken.

The contact plate on the tip of the strain gauge's needle consisted of a rectangle of 320 grit 3M waterproof silicon carbide sandpaper. The fine particles of this sandpaper have a uniform size and distribution and do not pull or accumulate cribellar thread fibrils in a way that affects subsequent measurements made with a plate (Opell, '93). Additionally, this surface registered the same stickiness as did similar-sized sections of fleshfly (*Sarcophaga bullata*) wings. Thus, the values recorded are representative of those that could be obtained with an actual insect surface.

Unlike other uloborids that deposit cribellar thread in the linear fashion shown in Figure 1, *Miagrammopes animotus* increases the surface area of some segments of its prey capture lines by depositing cribellar threads in a looped fashion (Opell, '90). However, this study measures the stickiness and features of only linear segments of this species' cribellar threads.

##### *Cribellar thread features*

I collected threads on the microscope slide samplers described above and determined mean puff length (dimension parallel to thread length) by measuring the lengths of either ten consecutive cribellar thread puffs or of three series of five puffs each at 125 $\times$  using a compound microscope equipped with Nomarski optics. I determined mean puff width (dimension perpendicular to thread axis) by measuring the width of four (or, in a few cases, three) puffs, one from each of a web sampler's four sectors.

I estimated the area of contact between a cribellar thread and an object by determining the planar surface area of one of the thread's puffs and multiplying this by the number of puffs per mm. I computed the surface area of a cribellar thread puff as the surface area of an ellipse, using the formula:  $\text{area} = \pi \times a \times b$ , where  $a$  = one-half mean puff length and  $b$  = one-half mean puff width. This approach makes the simplifying assumption that when a cribellar thread is pressed against an object, its puffs are fully flattened but maintain their previous dimensions.

The cribellar fibrils of uloborids have regularly spaced nodes (Fig. 1a). I compared the node diameters, internode diameters, and node spacing (the mean distance from the midpoint of one node to that of the next) of fibrils produced by adult *Hyptiotes cavatus* and *Miagrammopes animotus* using the data from Opell ('94c). I also used the raw data from this study to compute the surface area of a mm of cribellar fibril. To do this, I multiplied the surface area of a node-internode unit by the number of these units per mm of fibril. I determined the surface area of a node using the formula for the area of a sphere with a diameter equal to that of a node and the surface area of an internode region using the formula for the area of a cylinder with a diameter equal to internode diameter and a length equal to the difference between internode spacing and node diameter. By dividing 1 mm by node spacing, I determined the number of node-internode units per mm of fibril.

#### *Cribellum features*

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), length, and surface area of each cribellum and 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. From these three measurements I determined each cribellum's mean spigot density and multiplied this by its total surface area to calculate its total spigot number. This method assumes that either all or a constant percentage of the cribellum's spigots always operate and equates spigot number with the number of fibrils in the cribellar thread produced by that cribellum.

#### *Calamistrum features*

I removed each spider's left fourth leg and mounted it in water-soluble medium on a microscope slide, measured the length of the calamistrum, and counted the number of setae that formed it. From these measurements, I determined setal spacing and the ratio of calamistrum length to cribellum width.

### RESULTS

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

In both *Hyptiotes cavatus* and *Miagrammopes animotus* developmental increases in cribellum spigot number were associated with increased cribellar thread stickiness (Fig. 2a,b). In *H. cavatus* this relationship was very similar to that determined by interspecific comparisons (Fig. 2a). However, relative to cribellum spigot number, *M. animotus* produced threads that were stickier than predicted by previous interspecific comparisons (Fig. 2b). An analysis of covariance (ANCOVA) test showed that the regression slopes of *H. cavatus* and *M. animotus* did not differ ( $N = 300$ ,  $F = 0.62$ ,  $P = .43$ ), but that their  $Y$  intercepts did ( $F = 11.14$ ,  $P = .001$ ).

The stickiness of both species cribellar threads was measured at similar relative humidities (RH): *Hyptiotes cavatus*  $\bar{X}$  RH = 55%, SD 3%; *Miagrammopes animotus*  $\bar{X}$  RH = 62%, SD 3%. Adding relative humidity to spigot number had very little effect on the stickiness predicted by these regressions: For *H. cavatus* it improved the model's  $R^2$  value by 0.005 and for *M. animotus* it decreased the model's  $R^2$  by 0.006.

#### *Features that maximize cribellar thread stickiness*

I examined the following nine features to determine which were responsible for maximizing the stickiness of cribellar threads: 1) cribellum shape, 2) cribellum spigot density, 3) calamistrum length, 4) calamistrum setal density, 5) the ratio of cribellum width to cribellar thread width, 6) the ratio of cribellar thread puff width to puff length, 7) the ratio of cribellar thread contact area to cribellum area, 8) the ratio of cribellar fibril number to cribellar thread contact area, and 9) the ratio of cribellar thread stickiness to cribellar thread contact area. As summarized in Figure 3, differences in seven of these

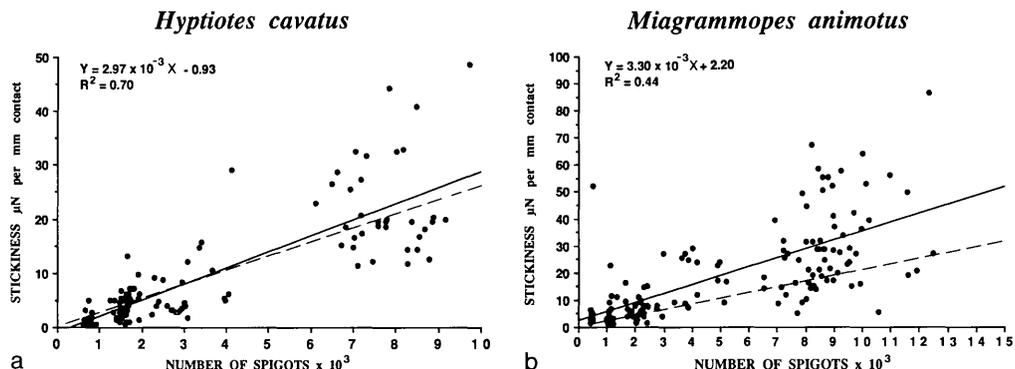


Fig. 2. *Hyptiotes cavatus* (a) and *Miagrammopes animotus* (b). Regression of cribellum spigot number and cribellar thread stickiness. Dashed lines depict the relationship between spigot number and stickiness determined by an interspecific comparison (Opell, '94c):  $Y = 2.64 \times 10^{-3} X + 0.25$ .

features appear to favor the production of stickier cribellar threads by *Miagrammopes animotus*.

Only cribellum shape, as measured by the relationship between the length and width of a cribellum, did not differ between the two species (Fig. 4a,b). An ANCOVA test showed the slopes and intercepts of these two species regressions to be the same (N = 394,

$F = 0.18, P = .67$  and  $F = 0.00, P = .98$ , respectively). There were statistical differences between regressions of the two species' cribellum width and cribellar thread width (Fig. 4c,d): Slopes differed (N = 364,  $F = 14.25, P = .0002$ ), but intercepts did not ( $F = 0.37, P = .54$ ). However, as these regression lines cross near their centers, it seems unlikely that these differences contribute to the ob-

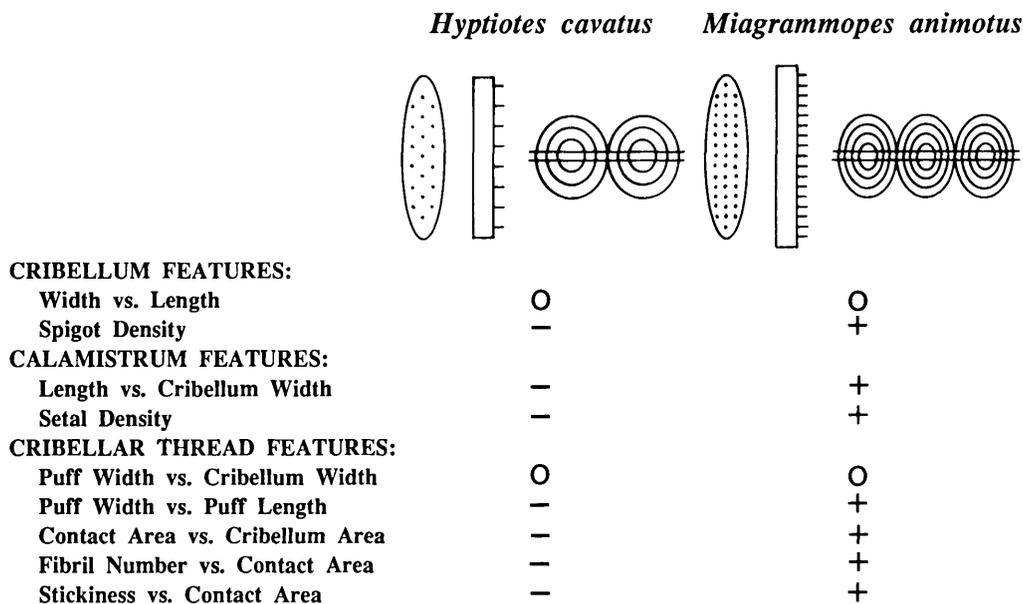


Fig. 3. *Hyptiotes cavatus* and *Miagrammopes animotus*. Summary of the differences in spinning anatomy and cribellar thread features. Diagrams depict the nature of differences but not actual values. Zero (0) indicates that values do not differ, minus (-) that the species has a lesser value, and plus (+) that it has a greater value.

served differences in the stickiness of the two species cribellar threads.

Cribellum features

An ANCOVA test shows that cribellum spigot density is greater in *Miagrammopes animotus* than in *Hyptiotes cavatus*, as indicated by its greater regression slope and intercept (Fig. 4e,f;  $N = 357$ ,  $F = 11.23$ ,  $P = .0009$  and  $F = 1141.45$ ,  $P = .0001$ , respectively).

Calamistrum features

Relative to cribellum width, *Miagrammopes animotus* has a longer calamistrum than *Hyptiotes cavatus*, as indicated by its greater regression slope and intercept (Fig. 5a,b;  $N = 327$ ,  $F = 18.33$ ,  $P = .0001$  and  $F = 75.88$ ,  $P = .0001$ , respectively). The density of calamistrum setae is greater in juvenile *H. cavatus* than in juvenile *M. animotus*, as indicated by its greater y intercept (Fig.

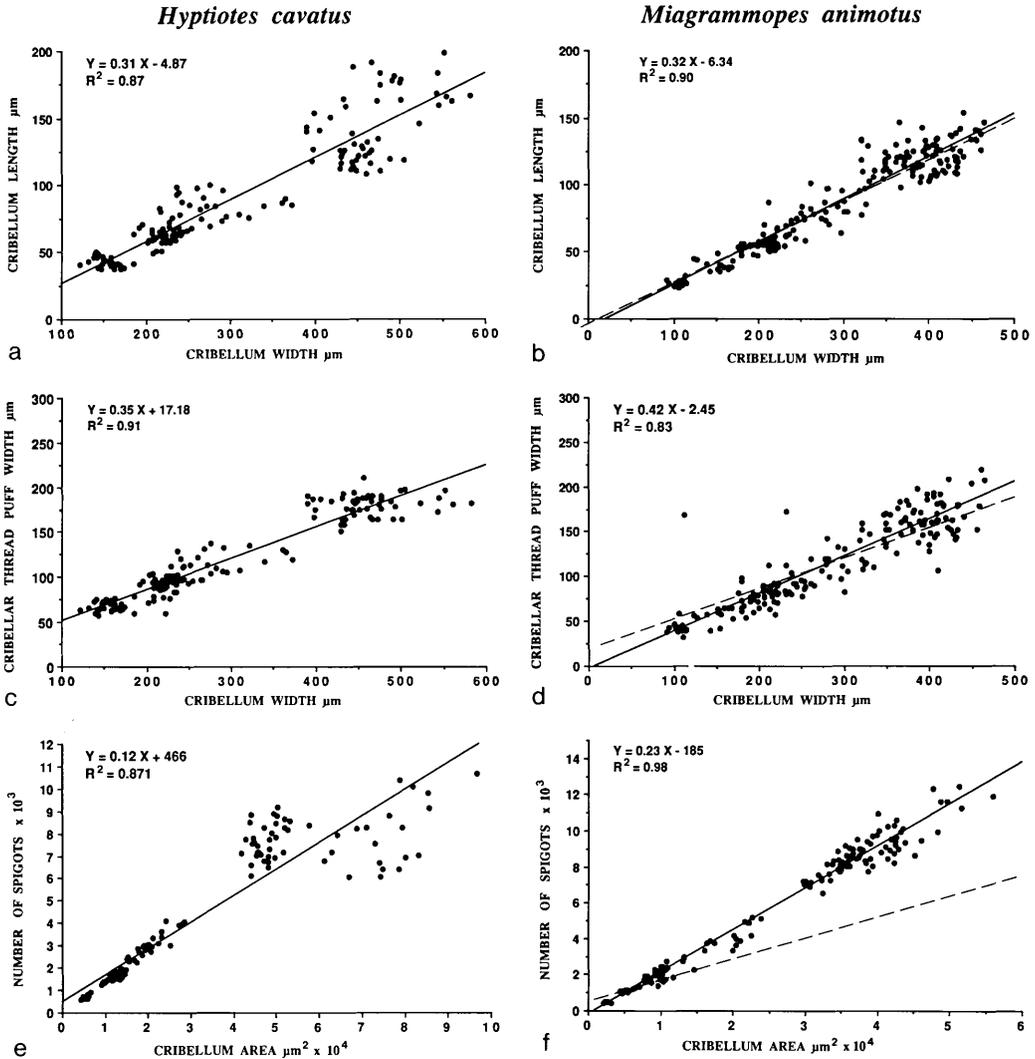


Fig. 4. *Hyptiotes cavatus* and *Miagrammopes animotus*. Regressions of cribellum and cribellar thread features. The dashed line on each *M. animotus* regression depicts the regression line for *H. cavatus*. a-f: Comparisons described in text.

5c,d;  $N = 337$ ,  $F = 25.81$ ,  $P = .0001$ ). However, the greater slope of the regression of *M. animotus* shows that this species has more closely spaced calamistrum setae during most of its development (Fig. 5c,d;  $F = 42.47$ ,  $P = .0001$ ).

Cribellar thread features.

Throughout development, *Miagrammopes animotus* produces cribellar threads that have a greater puff width-to-length ratio than those of *Hyptiotes cavatus*, as indicated by the

former species' greater regression slope and intercept (Fig. 5e,f;  $N = 432$ ,  $F = 7.09$ ,  $P = .008$  and  $F = 30.96$ ,  $P = .0001$ , respectively). Relative to cribellum area, the wider, shorter cribellar thread puffs of *M. animotus* give its cribellar threads more surface area per mm of length than those of *H. cavatus* (Fig. 6a,b). An ANCOVA test shows that both the slopes and intercepts of these two species' regression lines differ ( $N = 361$ ,  $F = 60.37$ ,  $P = .0001$  and  $F = 5.59$ ,  $P = .0186$ , respectively). Probably as a consequence of the greater

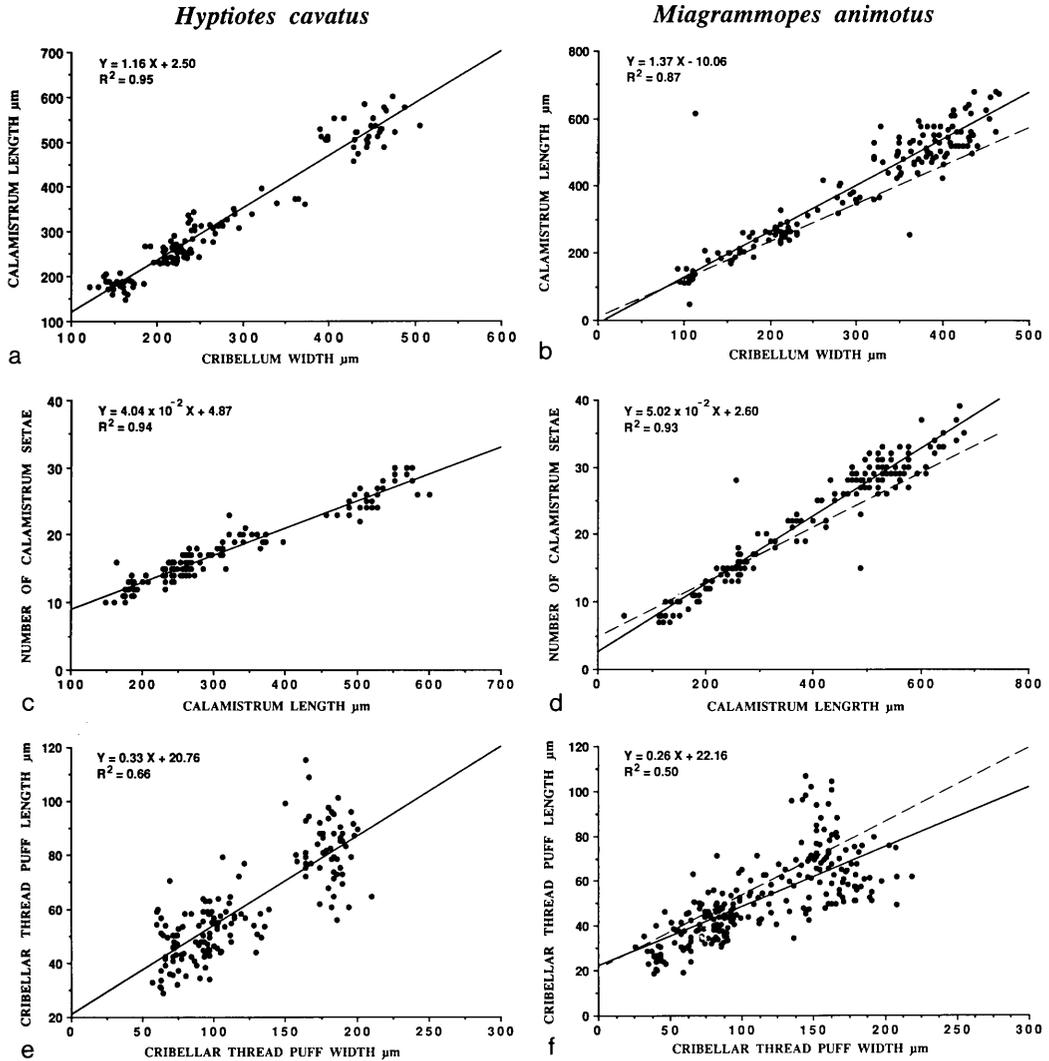


Fig. 5. *Hyptiotes cavatus* and *Miagrammopes animotus*. Regressions of cribellum, calamistrum, and cribellar thread features. The dashed lines on each *M. animotus* regression depicts the regression line for *H. cavatus*. a-f: Comparisons described in text.

density of spigots on the cribella of *M. animotus*, this species has more cribellar fibrils (as inferred from cribellum spigot number) per contact area of cribellar thread than does *H. cavatus* (Fig. 6c,d). The slopes of these two species regressions do not differ ( $N = 329$ ,  $F = 1.53$ ,  $P = .22$ ), although their intercepts do ( $F = 2161$ ,  $P = .0001$ ). Probably as a consequence of their greater cribellar fibril number, the cribellar threads of *M. animotus* are stickier relative to their area of contact

than those of *H. cavatus* (Fig. 6e,f). Both the slopes and intercepts of these species regressions differ ( $N = 311$ ,  $F = 12.91$ ,  $P = .0004$  and  $F = 72.48$ ,  $P = .0001$ , respectively).

As Table 1 shows, a Wilcoxon statistical analysis shows that cribellar fibrils produced by *Hyptiotes cavatus* have significantly greater node and internode diameters than those of *Miagrammopes animotus*, although neither node spacing nor the surface area per mm of fibril differs significantly between these

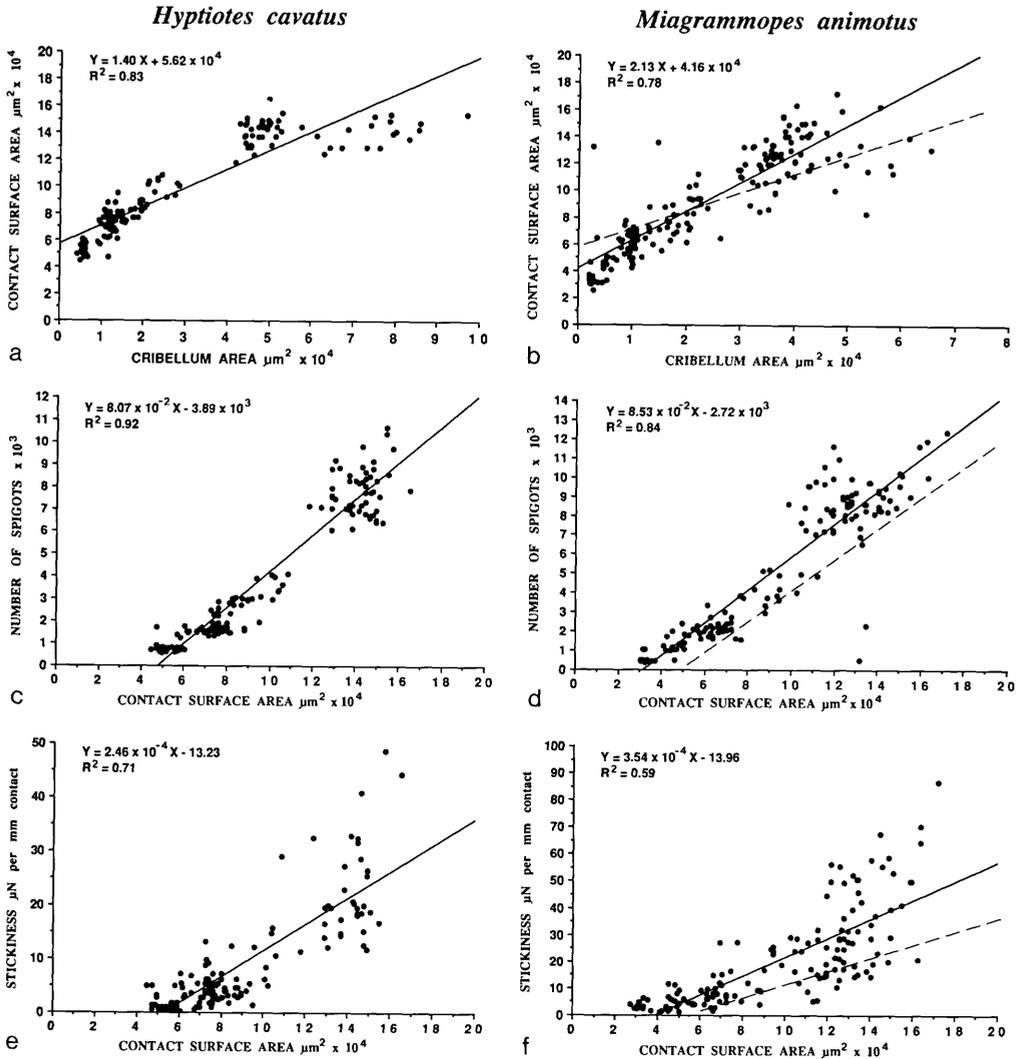


Fig. 6. *Hyptiotes cavatus* and *Miagrammopes animotus*. Regressions of cribellum, calamistrum, and cribellar thread features. The dashed lines on each *M. animotus* regression depicts the regression line for *H. cavatus*. a-f: Comparisons described in text.

species. Consequently, differences in structural features of cribellar fibrils do not appear to contribute to the greater stickiness of cribellar threads produced by *M. animotus*.

DISCUSSION

This study shows that developmental increases in the cribellum spigot number of *Hyptiotes cavatus* and *Miagrammopes animotus* are directly related to increases in the stickiness of their cribellar threads. The relationship between cribellum spigot number and cribellar thread stickiness depicted by these developmental changes is in general agreement with that derived from an interspecific comparison of adult uloborids (Opell, '94c). However, relative to cribellum spigot number, *M. animotus* produces stickier cribellar threads than does *H. cavatus*.

Differences in the features of the two species' cribellar fibrils do not explain this difference in the stickiness of their cribellar threads. Although this study did not compare the fibrils of juvenile spiders, the surface areas of fibrils produced by adults did not differ. The differences in node and internode diameters that were observed would seem to favor greater stickiness in the threads of *Hyptiotes cavatus* and not, as observed, in *Miagrammopes animotus*.

The ultimate cause of this difference in cribellar thread stickiness appears simple: A thread produced by *Miagrammopes animotus* brings more cribellar fibrils into contact with a surface than does a thread of the same length produced by *Hyptiotes cavatus*. However, the mechanisms by which this is achieved are more complex and result from differences in the dimensions of cribellar thread puffs, features of the calamistrum, and the density of cribellum spigots (Fig. 3). Differences in the spinning behavior that shape a cribellar thread's puffs probably also help determine the thread's stickiness, although this was not studied.

By producing cribellar threads whose puffs are shorter (dimension parallel to thread length) relative to their widths than those of *Hyptiotes cavatus*, *Miagrammopes animotus* achieves a greater contact area per mm of cribellar thread than does *H. cavatus*. Because the cribella of *M. animotus* also have greater spinning spigot densities, their cribellar threads have more cribellar fibrils per contact area than do those of *H. cavatus*. The longer calamistra and closer calamistrum setal spacing of *M. animotus* are probably associated with this species' cribellar fibril combing behavior and greater cribellum setal density.

It appears that *Miagrammopes animotus* produces cribellar threads that have greater stickiness by producing threads that contain more silk. The shorter puffs and greater cribellar fibril density of its threads appear to maximize thread stickiness by maximizing the length and number of cribellar fibrils invested per unit length of cribellar thread. Therefore, the cribellar thread stickiness achieved per volume of cribellar fibril silk invested may not differ between *Hyptiotes cavatus* and *M. animotus*.

The conclusions of this study are in fundamental agreement with recent investigations of cribellar thread function which show that the stickiness of cribellar thread is determined by the number of fibrils that it contains (Opell, '94c) and is influenced by features of the surface it contacts (Opell, '94b). Threads with more fibrils hold surfaces more strongly and surfaces whose features minimize the area of contact with cribellar fibrils without eliciting fibril snagging are held less strongly by a thread. Although the number of spigots on a spider's cribellum plays a major role in determining the stickiness of its cribellar thread, the total surface area contacted by the fibrils of this thread is the final determinant of thread stickiness. Differences in cribellum spigot density, calamistrum features, and probably also thread spinning be-

TABLE 1. Comparison of cribellar fibrils produced by adult female *Hyptiotes cavatus* and *Miagrammopes animotus*.<sup>1</sup>

	Node diam.* (nm)	Internode diam.* (nm)	Node spacing* (nm)	Surface area per mm fibril length (μm <sup>2</sup> )
<i>Hyptiotes cavatus</i>	19.4 ± 1.0(5)	10.3 ± 0.3(5)	63.1 ± 10.0 (5)	41.27 ± 1.76(5)
<i>Miagrammopes animotus</i>	16.2 ± 0.5(4)	8.6 ± 0.7(4)	42.3 ± 11.1(4)	36.47 ± 3.86(4)
Wilcoxon test <sup>2</sup>				
Z	2.34	2.33	1.84	1.35
P	.02	.02	.07	.18

<sup>1</sup>Values are for mean ± standard deviation; sample sizes in parentheses. Values for parameters marked \* are taken from Opell ('94c).  
<sup>2</sup>Wilcoxon 2-sample test for pair-wise comparisons, z and P values. Values significant if P < .05.

havior affect the surface configuration of cribellar threads and, thereby, govern their stickiness.

The adaptive significance of the greater stickiness of cribellar threads produced by *Miagrammopes animotus* appears to be related to this species' web architecture. The simple-webs produced by adult female *M. animotus* contain an average of 125 mm of cribellar thread per mg of spider weight, whereas the triangle-webs produced by adult female *Hyptiotes cavatus* contain an average of 209 mm of cribellar thread per mg of spider weight (Opell, unpublished observations). Thus, *M. animotus* appears to produce stickier capture threads to compensate for the shorter length of cribellar thread in its simple-web.

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