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Functional associations between the cribellum spinning plate and capture threads of *Miagrammopes animotus* (Araneida, Uloboridae)

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Summary. Uloborid cribellar silk consists of torus-shaped puffs. In *Miagrammopes animotus* the width of these puffs is about 36% that of the cribellum of the spider and shows a 2.3-fold increase in surface area during development. The cribellar spigot number increase 5.7-fold during development, although, relative to spider mass, it decreases by 34%. Cribellum width is the best predictor of both cribellar silk puff width and length and is as good a predictor of puff surface area as is cribellum surface area. Relative to cribellum width, the length of the calamistrum comb responsible for drawing fibrils from the cribellum changes little during development. The attachment points of cribellar silk to a parallel frame thread become more widely spaced during development, although the number of puffs they delimit changes little.

A. Introduction

The purpose of this study is to determine how the shape and size of the cribellum of a spider influence the physical features of its cribellar silk and to describe developmental changes in the cribellum and its silk. By using data from a single species, the effects of interspecific differences in spinning behavior are eliminated. Measuring the parameters of both a cribellum and the actual cribellar silk it produced makes it possible to model the functional associations between cribellum shape, surface area, and spinning spigot density and cribellar silk dimensions and surface area.

The cribellar threads of all known uloborids consist of torus-shaped puffs (Figs. 2, 3; Comstock 1940; Opell 1979; Peters 1983, 1984, 1986). Each puff has been attributed to a single stroke of the calamistrum over the cribellum, followed by a backward movement as the cribellar sheet is combined with the axial fibers (Friedrich and Langer 1969; Langer and Eberhard 1969; Opell 1979). However, Peters (1984) suggests that constrictions occur when rhythmic abductions of the posterior spinnerets combine cribellar fibrils with axial fibers.

Miagrammopes animotus Chickering, 1968 (Ulobridae), was chosen for this study for three reasons. Firstly, each of its four, web-spinning developmental instars are continually present, making sampling easier. Secondly, the capture webs of this species consist of only one or a few diverging threads (Lubin 1986, Lubin et al. 1978), making it easy to collect undamaged samples. Finally, this species produces heteronomous capture threads by first spinning framework (foundation) threads and then depositing cribellar threads on them (Fig. 2, Peters 1983, 1986). This makes the dimensions of the silk less likely to be altered by stretching than the more typical, self-supporting autonomous cribellar threads of other ulobrids (Fig. 3).

B. Materials and methods

Field work was conducted during February and March 1987 at the Center for Energy and Environment Research's El Verde field station, located in the Luquillo National Forest of Puerto Rico. From each *M. animotus* web, I collected a 3 cm long cribellar silk sample on raised adhesive supports affixed to a labeled microscope slide and determined:

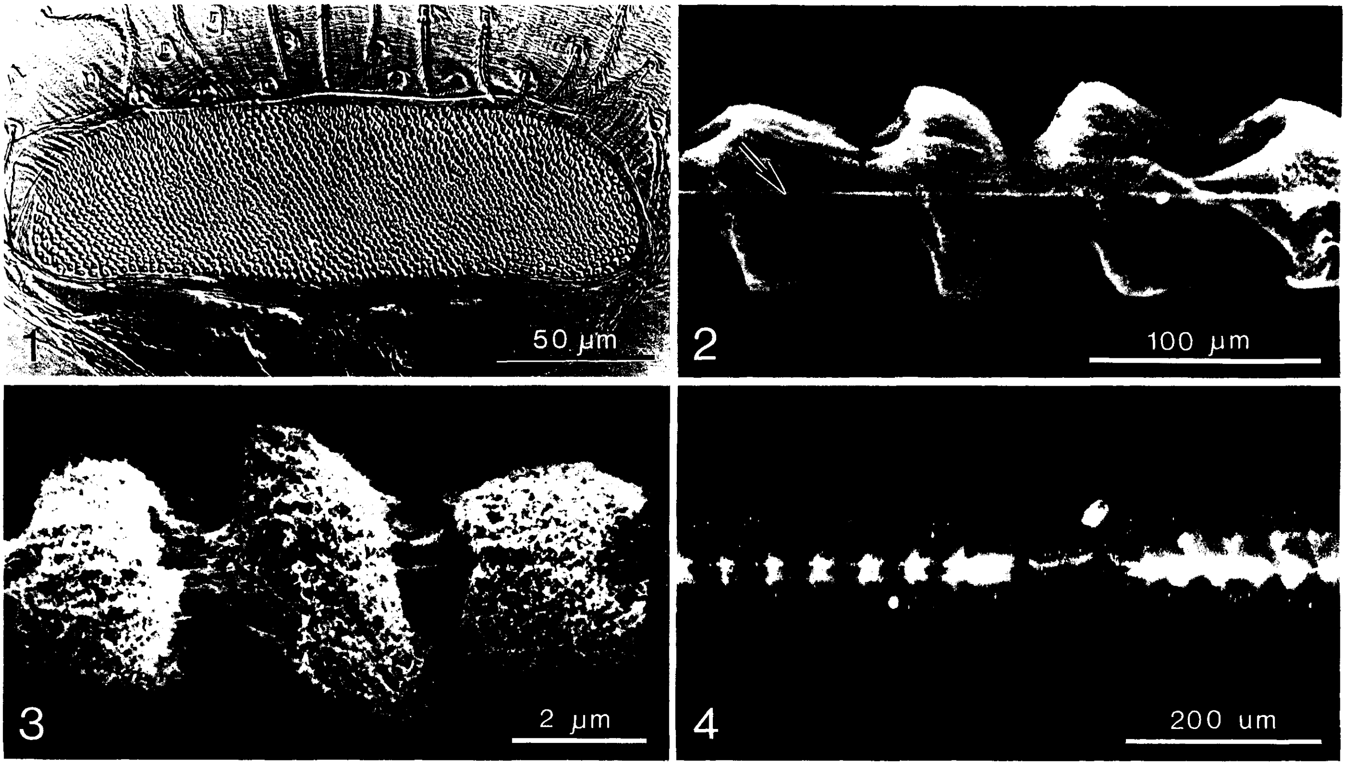
1. The width (dimension perpendicular to thread axis) of four cribellar puffs, each from a different "segment" (see below), and from this, the mean puff width of a sample.
2. The length of ten contiguous puffs (distance from the constriction preceding the first puff to the constriction following the tenth puff), and from this, the mean puff length of a sample.
3. The length and number of puffs in each of four cribellar silk "segments," from which I calculated the mean segment length of the sample and the mean number of puffs per segment.

Each segment is a length of cribellar silk bounded by short, flattened areas that interrupt the silk puffs (Fig. 4) and probably represent the points at which the spider pressed its cribellar thread against the framework thread. The surface area of each puff was computed using the formula for the area of a double cone:

$$\text{Area} = 2\pi R\sqrt{R^2 + h^2}$$

where R is the maximum radius of the cone (one-half the width of the puff) and h is the height of the cone (one-half the length of the puff). This value and the number of puffs per millimeter of cribellar silk determined the surface area in each millimeter of the silk of a spider.

Each spider that produced a web was collected, weighed to the nearest 0.01 mg, and preserved in 75% ethanol, and the lengths of its first femur and calamistrum (from the base of the first to the base of the last distinctly modified setae) measured to the nearest 0.02 mm under a dissecting microscope equipped with a micrometer. Its cribellum was removed, mounted in water-soluble mounting medium on a microscope slide (Fig. 1) and measured and photographed



Figs. 1–4. 1. Light micrograph (LM) of the cribellum of a third instar *Miagrammopes animotus*. **2.** Scanning electron micrograph (SEM) of the heteronomous cribellar thread of a fifth instar *M. animotus*, showing its supporting framework thread (*arrow*). **3.** SEM of the autonomous cribellar thread of an adult female *Tangaroa beattyi*. **4.** LM of the cibrellar thread of a fourth instar *M. animotus*, showing an interruption in the puffs where the cibrellar thread was pressed onto the frame thread

under a compound microcope equipped with Nomarski optics. With a Numonics digitizing tablet connected to an IMB PC running Sigmascan software, I measured the surface area of enlarged photographs of each cribellum. Spinning spigot density was determined by encircling three regions (one at the anterior midline, one at the posterior lateral margin, and one midway between these two) of the cribellum, measuring the surface area of each, counting the number of spinning spigots in each region, determining the mean area occupied by the spigots of each region, and then computing the grand mean spigot area. Mean spigot and total cribellum areas were used to calculate the total number of spinning spigots on a cribellum.

The instar of each spider was determined from its first femur length, using values given by Opell (1987): third instar <1.20 mm, fourth instar 1.20–1.63 mm, fifth instar 1.64–2.04 mm, sixth instar >2.04 mm. Mature males do not spin capture webs and were excluded from this study. To evaluate developmental changes in cribellum shape, I selected ten cribellum photographs of each instar (except the fifth instar, for which only seven were available), traced the outline of each, and drew in its sagittal midline. Using as an origin the point where this midline intersected the anterior margin of the cribellum, I drew reference lines at 5-degree intervals through the margin of the cribellum (Fig. 5), measured the length of each line, and divided it by the sagittal length of the cribellum to obtain relative distance measurements for the 18 marginal points. I used the mean values of each instar to reconstruct its cribellum shape (Fig. 5), and measured the surface areas of these outlines with a digitizing tablet.

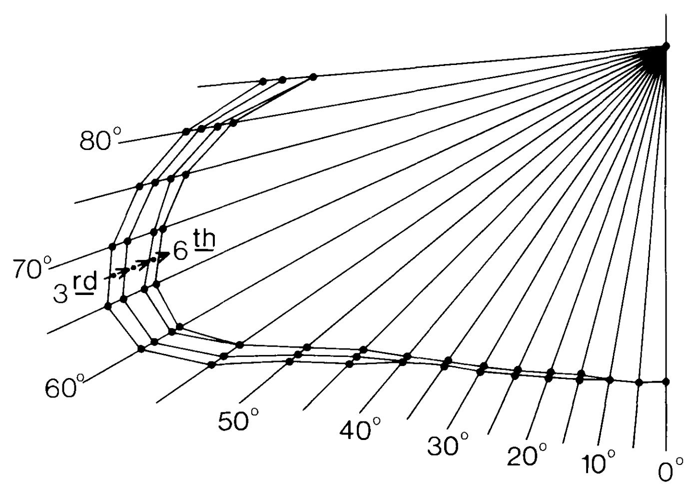


Fig. 5. Reconstructions of the left halves of third through sixth instar *Miagrammopes animotus* cribellae. Points along each reference angle represent the mean relative distance (actual distance/cribellum length) for each instar

To determine whether the cribellum grows allometrically, I compared developmental changes in its weight-specific surface area with those of a hypothetical oval plate whose width was set equal to the length of the first femur and whose length was half this value. The area of this oval was computed using the formula:

$$\text{Area} = \pi \times (\text{length}/2) \times (\text{width}/2).$$

The first femur was chosen because it is not functionally linked with cribellar silk production.

Opell (1982a) used the mean area of a rectangle and an ellipse, each having the width and length values of the cribellum, to compute the cribellum area and spigot number of the triangle-web uloborid *Hyptiotes cavatus* (Hentz, 1847). To compare these results with those for *M. animotus*, I established a correction factor for *H. cavatus* instars by using the earlier method to compute *M. animotus* cribellum areas and compared these values with their actual surface areas.

Duncan's multiple range tests were used to rank the mean cribellum, calamistrum, and cribellar silk parameters of each instar. Instars whose values do not differ significantly ($P<0.05$) are enclosed in parentheses. Maximum R^2 Improvement Stepwise Regression tests determine which cribellum parameters (width, length, surface area, or spinning spigot number) best predict cribellar silk features (puff width, length, and surface area).

C. Results

Mean cribellum, calamistrum, and cribellar silk values are presented in Table 1. Cribellum width, length, area, and spigot number rank: $3<4<5<6$. Mean spigot area ranks: $(4, 5, 6)<3$. Relative to the mass of a spider, spigot density does not differ among instars.

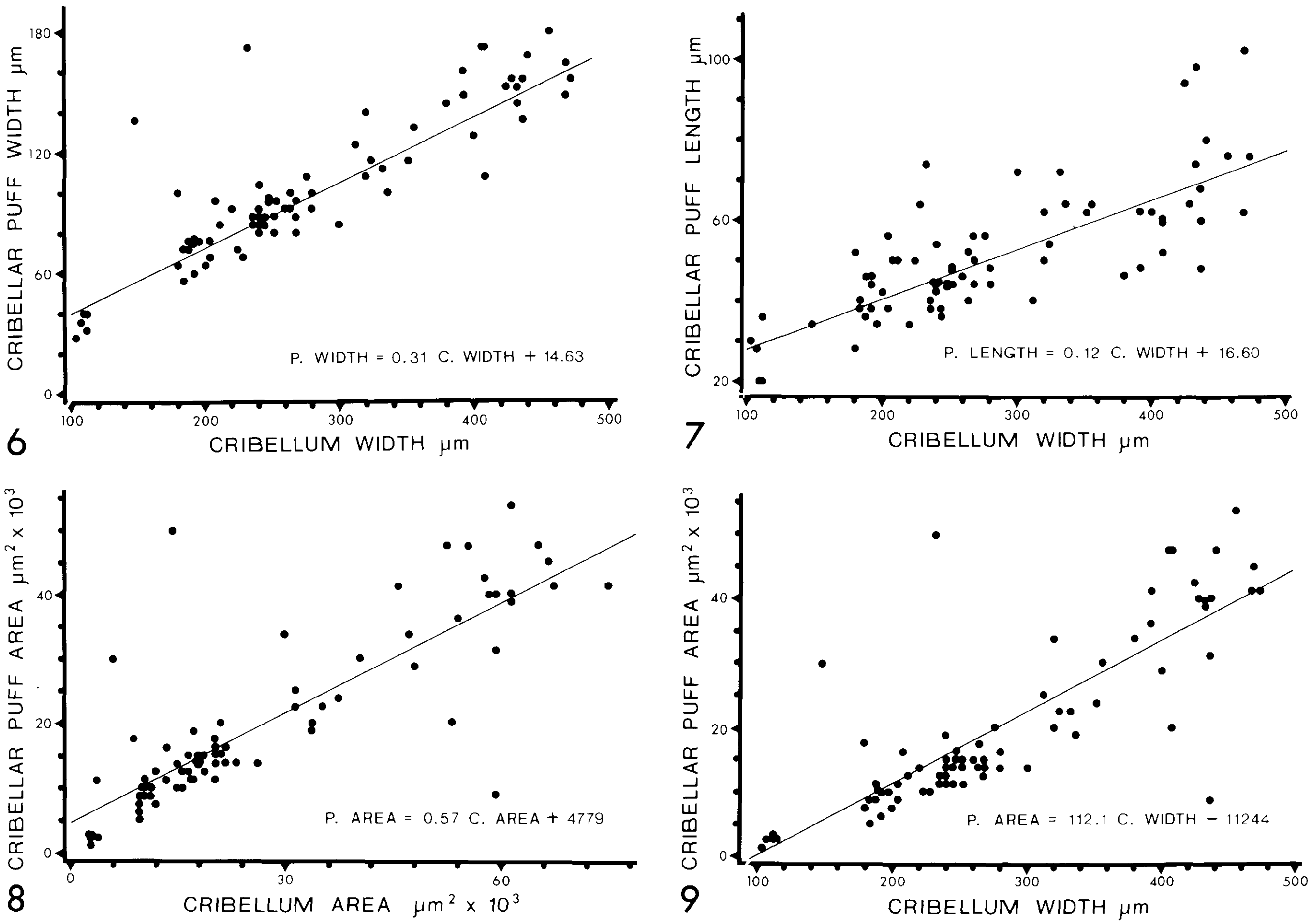
Calamistrum length ranks: $3<4<5<6$, although, relative to cribellum width, it does not change during development. Linear regressions show that cribellum width and the lengths of the fourth femur, patella, tibia, and metatarsus are equally good predictors of calamistrum width ($P<0.0001$, R^2 0.95–0.97). By failing to show that cribellum width is not the best predictor of calamistrum length, this study does not support a developmental linkage of these two structures.

Cribellar silk puff width ranks: $3<4<5<6$ and puff area: $(3, 4)<5<6$. Cribellar silk puff length and area per Millimeter of length rank: $(3, 4)<(4, 5)<6$. Relative to its length, mean cribellar silk puff width increases during development (1.81, 1.95, 2.06, 2.33). However, these values rank: $(3, 4, 5)<(4, 5, 6)$, indicating that only third and sixth instars differ. Relative to spider mass, cribellar thread surface area per millimeter of length ranks: $3<(4, 5, 6)$. The mean number of puffs per segment of cribellar silk does not change during development.

Cribellum width is the best single predictor of cribellar silk puff width (Fig. 6, $P<0.0001$, $R^2=0.664$). The best two-variable model, with cribellum width and length as variables, increases R^2 by only 0.0004. Cribellum width is also the best single predictor of cribellar silk puff length (Fig. 7, $P<0.0001$, $R^2=0.566$), with the best two-variable model (cribellum width and length) increasing R^2 by only 0.0046. Cribellum area is the best predictor of cribellar silk puff area (Fig. 8, $P<0.0001$, $R^2=0.667$), with the best two-variable model, cribellum area and cribellum width, increas-

Table 1. Miagrammopes animotus cribellum, calamistrum, and cribellar silk values

	Stadium											
	Third			Fourth			Fifth			Sixth		
	N	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*	Mean	SD
Cribellum:												
Width (µm)	29	190	45	23	273	52	7	356	37	17	419	44
Length (µm)	24	60	11	23	83	20	7	113	14	17	137	16
Area (µm²)	24	12488	3926	23	22896	12993	7	39414	8433	17	56067	10774
Spigot area (µm²)												
Posterior lateral	24	6.28	1.41	24	6.13	0.78	7	6.41	0.21	17	6.33	0.84
Central	24	5.23	1.04	24	4.70	0.74	7	4.23	0.43	17	4.24	0.35
Dorsal midline	24	7.46	0.92	24	6.08	0.99	7	6.83	1.23	17	5.57	0.83
Mean	24	6.33	0.73	24	5.64	0.53	7	5.83	0.44	17	5.38	0.31
Spigot no.	23	1824	795	23	4128	2285	7	6852	1890	17	10454	2103
Spigot no. / Mass (mg)	21	2737	810	23	2778	1719	7	2252	483	17	2040	853
Calamistrum:												
Length (mm)	30	0.24	0.05	25	0.33	0.06	7	0.44	0.03	22	0.50	0.06
Length / Cribellum width	28	1.25	0.15	23	1.21	0.07	7	1.23	0.05	17	1.18	0.09
Cribellar Silk:												
Puff width (µm)	30	76	26	25	96	18	7	117	11	22	152	26
Puff length (µm)	30	42	11	25	48	13	7	58	9	22	68	18
Puff area (µm²)	30	11506	8850	25	16851	6996	7	24181	4048	22	40724	10827
Puffs/mm	37	25.8	8.3	25	20.6	3.7	7	17.5	3.2	22	15.5	3.8
Area × 10³ µm²/mm	37	265	168	25	386	242	7	425	108	22	618	203
Area µm²/mm / Mass (g)	35	466.9	416.8	25	232.7	67.0	7	143.5	43.9	22	116.5	45.9
Segment length (mm)	18	2.16	0.64	13	2.44	0.69	3	3.29	0.55	9	3.81	1.22
Puffs/segment	12	48	6	25	46	10	3	53	7	9	54	12



Figs. 6–9. Plots of cribellum parameters (bottom axes) against cribellar thread puff features (*left axes*). The formula for the regression line of each plot appears above its lower axis

ing R^2 by only 0.0018. However, a simple linear regression of cribellar puff area and cribellum width (Fig. 9) produced an R^2 value (0.677) equal to the value of the stepwise regression for cribellum area, showing cribellum surface area and width to be equally good predictors of cribellar silk puff area.

The cribellum shows a small, continuous decrease in relative width throughout development (Fig. 5). The mean width-to-length ratios for its instars are 3.54, 3.32, 3.16, and 3.07. These values rank: $(6, 5) < (5, 4) < 3$. When the surface areas of the scaled reconstructions shown in Fig. 5 are compared, the fourth instar cribellum has 96% the surface area of the third, the fifth instar 91%, and the sixth instar 89%. The mean angular measurements on which these reconstructions are based all have comparative values (CVs) lower than 17 and 68% have CVs less than 5.

A *t*-test shows no signficant difference ($0.50 < P < 0.90$) between the slopes of linear regressions of the log of cribellar surface area on the log of spider mass:

Cribellum area $= 9.620$ Mass$^{0.745}$, $N = 73$, $R^2 = 0.77$,

and the regression of the log of the area of the hypothetical oval on the log of spider mass:

Oval area $= 13.135$ Mass$^{0.765}$, $N = 442$, $R^2 = 0.90$.

Thus, relative to spider mass, cribellum surface area shows neither positive nor negative allometric growth.

The method used by Opell (1982a) tended to underestimate the cribellum area of *H. cavatus*. Third instars were reported to have 89% (SD 3%) their actual values, fourth instars 1.03% (SD 61%), fifth instars 92% (SD 2%), and sixth instars 92% (SD 2%). When these correction factors are used and the mean instars weights reported by Opell (1987) are employed, the corrected absolute and relative cribellum spigot numbers for *H. cavatus* are: third instar 1049 and 3085 per milligram, fourth instar 1489 and 1519 per milligram, fifth instar 2581 and 1053 per milligram, and sixth instar 4860 and 719 per milligram. Relative to spider mass, the third, fourth, fifth, and sixth instars of *M. animotus* have, respectively, 0.89, 1.83, 2.14, and 2.84 times more cribellar spinning spigots than the same instars of *H. cavatus*.

D. Discussion

The cribellar silk of *Miagrammopes animotus* is only 0.33–0.40 times as wide as the cribellum (Table 1). Because calamistrum length is 1.18–1.25 times greater than cribellum width (Table 1), the width of this comb probably does not limit the width of completed cribellar threads. Even when the metatarsus of the fourth leg extends laterally from the cribellum at a 33° angle, the calamistrum still spans a transverse distance equal to the width of the cribellum. Three factors contribute to the narrowing of the cribellar fibril sheet produced by the cribellum:

1. It must enfold the axial fibers to form the three-dimensional configuration shown in Figs. 2–4.

2. Fibrils become looped after passing over the calamistrum, either as a result of being twisting by the curved grooves in calamistral setae (Peters 1984) or of having their tension reduced when they are freed from the calamistrum.

3. The cribellar sheet is pressed against the axial fibers by the movement of the calamistrum and/or the abduction of the posterior spinnerets.

Both the shape of the cribellum and the combing behavior of the spider may influence the physical properties of the cribellar silk. Although cribellum width establishes the maximum width of cribellar silk puffs, the manner in which the cribellar fibrils are combined with axial fibers determines the actual dimensions of the puff. If the fibril sheet is stretched more tightly and attached at greater intervals to the axial fibers, its puffs should be narrower and longer (as illustrated by Opell 1979, plate 1-F and Peters 1984, Fig. 3-d for two *Uloborus species*) than if the sheet were stretched less tightly and attached at more frequent intervals to the axial fibers, as they are in *M. animotus*.

There is evidence for minor developmental changes in the spinning behavior of *M. animotus*. Whereas the cibrellum width-to-length ratio decreases during development, the cribellar puff width-to-length ratio increases. Unless spiders adjusted their spinning behavior to produce more compact cribellar silk puffs, changes in cribellum morphology would dictate a decrease rather than an increase in relative puff width.

Cribellar silk with wider puffs has more surface area per unit length and, consequently, is better able to hold prey. Therefore, selection favoring greater prey retention should act both on the spinning behavior of a spider and on the dimensions of its cribellum. This may explain why *M. animotus* has more cribellar spigots relative to its size than does *H. cavatus*. Prey striking *H. cavatus* webs (Opell 1982b) are likely to contact several capture threads, whereas those striking *M. animotus* webs contact only a single thread. To compensate for their reduced webs, *M. animotus* should have stickier cribellar threads.

The greater mean spinning spigot area of third instar *M. animotus* is explained by the smaller size of the cribellae of these spiders, resulting in their having proportionally more peripheral spigots. In all instars these peripheral spigots have greater surface areas (Table 1), but in earlier instars they constitute a greater percentage of the total spigot number of the cribellum. Despite this difference, third instars have, relative to their mass, as many spigots as do later instars. The proportionately wider cribellae of the third instars may explain this.

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References

Comstock JH (1940) The spider book. Doubleday, Doran, New York

Friedrich V, Langer R (1969) Fine structure of cibrellate spider silk. Amer Zool 9:91–96

Langer RM, Eberhard WG (1969) Laboratory photography of spider silk. Amer Zool 9:97–102

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

Opell BD (1979) Revision of the genera and tropical American species of the spider family Uloboridae. Bull Mus Comp Zool 148:433–549

Opell BD (1982a) Cribellum, calamistrum, and ventral comb ontogeny in the spider family Uloboridae. Bull Brit Arach Soc 5:338–343

Opell BD (1982b) Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Ulboridae). J Arach 10:185–191

Opell BD (1987) Changes in web-monitoring forces associated with web reduction in the spider family Uloboridae. Canadian J Zool 65:1028–1034

Peters HM (1983) Struktur und Herstellung von Fangfäden cribellater Spinnen. Verh Naturw Ver Hamburg (NF) 26:241–253

Peters HM (1984) The spinning apparatus of Uloboridae in relation to the structure and contruction of capture threads (Arachnida, Araneida). Zoomorphology 104:96–104

Peters HM (1986) Fine structure and function of capture threads. In: Nentwig N (ed) Ecophysiology of spiders. Springer, Berlin Heidelberg New York, pp 187–202

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