

What Forces Are Responsible for the Stickiness of Spider Cribellar Threads?

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ABSTRACT The surface of spider cribellar prey capture thread is formed of thousands of fine silk fibrils. The stickiness of this thread is often attributed to the ability of these fibrils to catch on irregular surfaces. However, 14-month-old cribellar threads of *Hyptiotes cavatus* (Uloboridae) were significantly less sticky than freshly spun threads. Slight changes in cribellar thread dimensions failed to fully explain this reduced stickiness, demonstrating that an auxiliary force contributes to the stickiness of cribellar threads. Because this force does not appear to rely on the snagging of fibrils, it may enhance the ability of cribellar threads to hold prey with smooth surfaces.

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The purpose of this study is to determine if the stickiness of spider cribellar prey capture thread is due solely to its physical features or if it results from a combination of physical and chemical features. If thread stickiness decreases with age and this change is not explained fully by changes in thread dimensions, then reduced stickiness must be attributed to the evaporation, breakdown, or contamination of material that contributes to thread stickiness. This would indicate that forces other than the thread's ability to snag a prey's surface irregularities contribute to its prey holding properties.

Spiders that possess a cribellum spinning plate (Fig. 1) use it to produce composite prey capture thread (Fig. 2) known as cribellar thread. The cribellum is beset with thousands of spinning spigots, each of which produces a fine silk fibril (Fig. 3). With the aid of setal combs on the fourth legs, the sheet of fibrils issuing from the cribellum is combined with two or four larger, supporting axial threads produced by the spinnerets (Fig. 1) to form a cribellar thread. The resulting capture thread consists of a cloud of loosely packed, looped cribellar fibrils (Figs. 2, 3) that form a sheath around the axial threads.

Cribellar thread is the most primitive type of prey capture thread found in spiders and is one of the autapomorphies that distinguish the largest spider infraorder Araneomorphae (Coddington and Levi, '91). The addition of these cribellar threads to spider webs probably made available a greater variety of insect prey and facilitated the diversification of web types, thereby contributing to the

early radiation of the Araneomorphae. Despite the significance of cribellar thread and its continued production by 22 araneomorph families, the mechanism of its operation is still not fully understood.

The structure of cribellar threads has been well documented (Comstock, '40; Friedrich and Langer, '69; Kullmann, '75; Kullmann and Stern, '81; Lehmensick and Kullmann, '57; Opell, '79, '89a, '90; Peters, '83, '84, '86; Peters and Kooor, '88), and Opell ('89a) has shown that the size and shape of the cribellum influences the dimensions and surface area of the cribellar threads it produces. However, the interaction between cribellar thread and prey is not fully understood (Eberhard, '80; Peters, '86), the principal question being whether the stickiness of this thread results from its physical properties or from a combination of its physical and chemical properties. Peters ('84, '86) suggested that electrostatic charges may contribute to the stickiness of cribellar threads and help maintain the configuration of fibrils around axial fibers, although no evidence is available to support this hypothesis.

The traditional and most obvious explanation is that an insect's setae and surface irregularities become snagged on the cloud of fibrils that form the cribellar thread's surface (e.g., Kaestner, '68; Opell, '79). Although this mechanism no doubt contributes to the operation of cribellar thread, it does not explain its ability to adhere to smooth surfaces such as glass, steel needles, or graphite (Eberhard, '80; Kullmann, '75; Peters, '86). Light and electron

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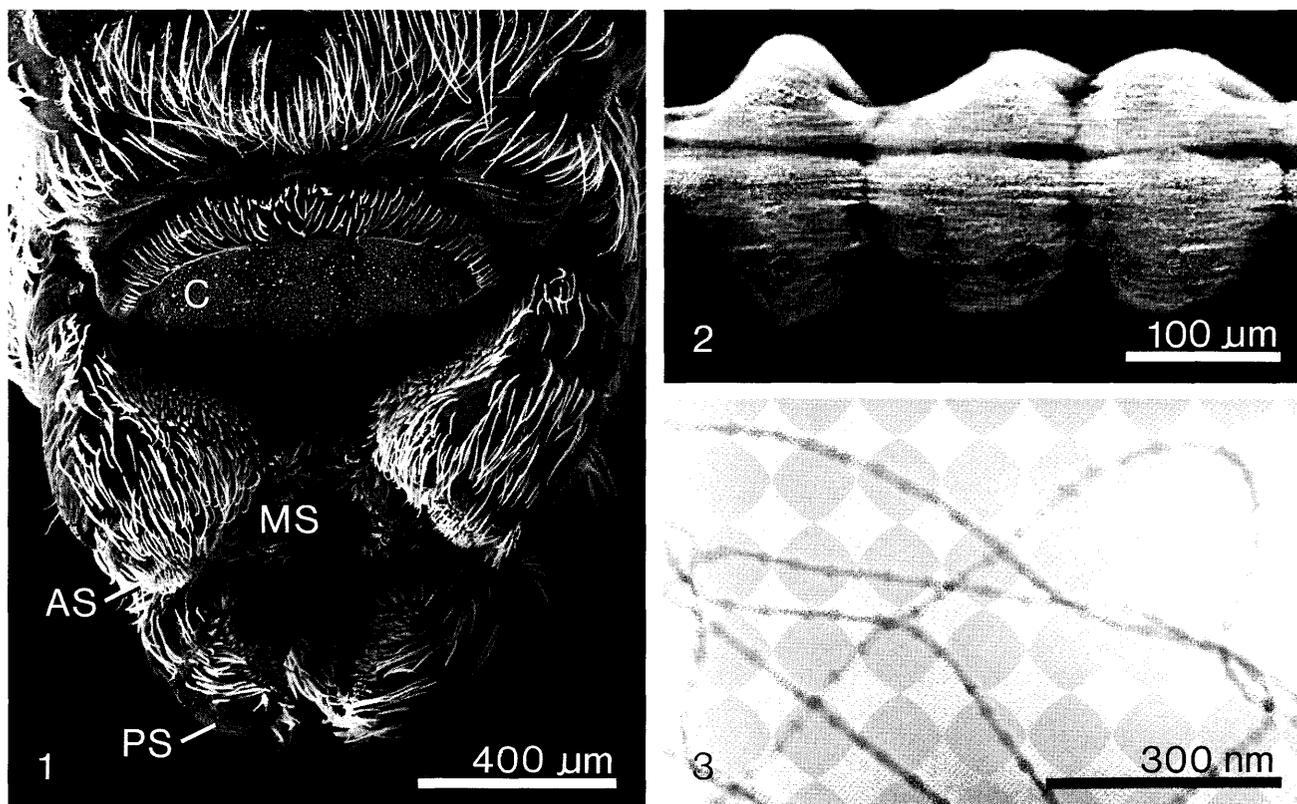


Fig. 1. The spinning apparatus of the uloborid *Zosis geniculatus* (Olivier, 1789). AS = anterior spinneret; C = cribellum; MS = median spinneret; PS = posterior spinneret.

Fig. 2. Cribellar thread spun by an adult female *Hyptiotes cavatus*.

Fig. 3. Cribellar fibrils from an aged cribellar thread spun by an adult female *Hyptiotes cavatus*.

microscope studies of cribellar threads reveal no adhesive droplets (Friedrich and Langer, '69; Kullmann, '75; Kullmann and Stern, '81; Lehmensick and Kullmann, '57; Opell, '79, '89a, '90; Peters, '83, '84, '86). Eberhard ('80) found that, unlike the viscous capture threads of more highly evolved orb-weavers that dry and lose their stickiness with age, the stickiness of cribellar threads produced by *Uloborus diversus* persisted after three months. From this, he concluded that "cribellar thread is probably dry, and it does not lose its stickiness on prolonged exposure to dry conditions." However, as he was unable to quantify stickiness, it is possible that stickiness diminished, but not to a noticeable degree.

A better understanding of the mechanism by which cribellar thread operates is more likely to come from experiments that compare its performance under different conditions than from additional light and electron microscope studies. Cribellar threads produced by members of the family Ulo-

boridae are particularly well suited for such studies. Unlike the capture threads of most cribellate spiders, which are secondarily coiled or folded as they are deposited along a previously placed supporting line, those of all uloborids except *Polonecia producta* and members of the genus *Miagrammopes* (Opell, '89a, '90; Peters, '83, '86; Peters and Koor, '88) are deposited as taut, self-supporting (autonomous, as opposed to heteronomous, according to the terminology of Peters, '86) strands that extend between non-sticky radii threads. Additionally, rather than being deposited in cylindrical fashion around axial fibers, the cribellar fibrils of uloborids form a regular series of contiguous, torus-shaped "puffs" (Fig. 2; Kullmann and Stern, '81; Opell, '79, '89a, '90; Peters, '83, '84, '86).

These characteristics make it possible to collect intact, isolated strands of uloborid cribellar thread and to compare the effect of aging on their dimensions and stickiness (Opell, '89a,b, '90; Opell et al., '90). If the stickiness of a thread is due solely to

the catching of its cribellar fibrils on the irregularities of surfaces with which they come into contact, then the thread's width should be a good index of how many fibrils contact a surface and, hence, the stickiness of the thread. If width changes with age, then a model of the relationship between cribellar thread width and stickiness should satisfactorily predict the effect of aging on cribellar thread stickiness. If the stickiness of aged thread is less than that predicted by this model, then support is provided for the operation of auxiliary forces, such as electrostatic charges, that diminish with age.

MATERIALS AND METHODS

I chose to study the triangle-web uloborid *Hyptiotes cavatus* (Hentz, 1847) because its cribellar thread is stickier than that of orb-weaving uloborids (Opell, unpublished observations). Therefore, its thread should be a more sensitive indicator of changes that occur with aging. From May through September 1990, I collected cribellar threads from the triangle-webs (Lubin, '86; Opell, '82) of *H. cavatus* living in the forests of Montgomery and Giles counties, Virginia. Threads from third (first web-spinning) through sixth (adult) instars were used to determine the relationship of cribellar thread puff width to cribellar thread stickiness. As mature males do not spin capture webs, only the threads of adult females were used to evaluate the effect of aging on cribellar thread stickiness and puff dimensions. I compared the stickiness of fresh and aged cribellar threads spun by adult females rather than that of threads spun by a developmental series of spiders because pair-wise comparisons promised to be more sensitive to small changes than did regressed analyses of developmental series.

The method I used for collecting cribellar thread samples permitted me to measure several cribellar thread strands from a spider web at the beginning of this experiment and several undisturbed strands from the same web at the end. From each web, I collected two to five cribellar thread strands (depending on their spacing in the web) on a microscope slide to which five raised, parallel, 4.8 mm wide, 2 cm long brass supports were glued at 4.8 mm intervals. Double-sided Scotch tape atop each support assured that threads were securely anchored and that their original tensions were maintained. Initial puff dimensions and cribellar thread stickiness were measured 2–40 hours after thread samples were collected. During the 14 months between initial and final measurements, cribellar thread samples were stored in a closed microscope slide box at 75–85°C and 30–60% relative humidity (RH).

Before taking measurements, I examined each web sample under a dissecting microscope and removed cribellar threads that were damaged or intersected by radii. The lengths (dimensions parallel to thread axis) of three series of five puffs, each from a different sector of the sampler, were measured at 125× using a compound microscope equipped with Nomarski optics. From these measurements, I determined mean puff length. I determined a sample's mean puff width (dimension perpendicular to thread axis) from measurements of three puffs, each from a different sector of the web sampler.

Four initial and four final stickiness measurements were taken from the threads on each sampler and their mean values were used as the web's initial and final stickiness values, respectively. The stickiness meter used in this study is a modification of that described by Opell ('89b). It incorporated a silk sample holder that can be both rotated and moved along X and Y axes, permitting orientation of the cribellar thread sampler. A glass needle strain gauge mounted in a horizontal plexiglass frame was positioned so that the contact plate on the needle's protruding tip could be brought into contact with a cribellar thread. A motorized screw advanced the thread sample toward the 2 mm wide, 4–5 mm long contact plate at a speed of 13.5 mm per minute and withdrew it at 14.0 mm per minute. Using 5 mg weights, I calibrated the arbitrary scale over which the needle's free end passed. By multiplying these scale values by the accelerating force of gravity, I determined the force in Newtons required to deflect the needle. The width of the contact plate used for initial measurements was 2,175 μm and that used for the final measurements 2,040 μm . The needle used for the initial measurements had a sensitivity of 0.192 $\mu\text{N/mm}$ of contact width and that used in the final measurements 0.186 $\mu\text{N/mm}$.

The contact plate was made of 320 grit 3M waterproof silicon carbide sandpaper. Both plates were cut from a single strip of sandpaper. I chose fine sandpaper to replace the smooth aluminum contact plate described by Opell ('89b) for three reasons. First, it seemed to better model an arthropod's setose surface. Second, its surface provided a fairly uniform series of projections (Fig. 4), unlike an aluminum plate, most of whose surface is smooth, but whose edges tend, even when polished, to catch on cribellar thread. Therefore, the sandpaper plate's width is a truer index of the area of contact than that of an aluminum plate. Third, a preliminary study of the stickiness of cribellar threads spun by an orb-weaving uloborid showed that a sandpaper

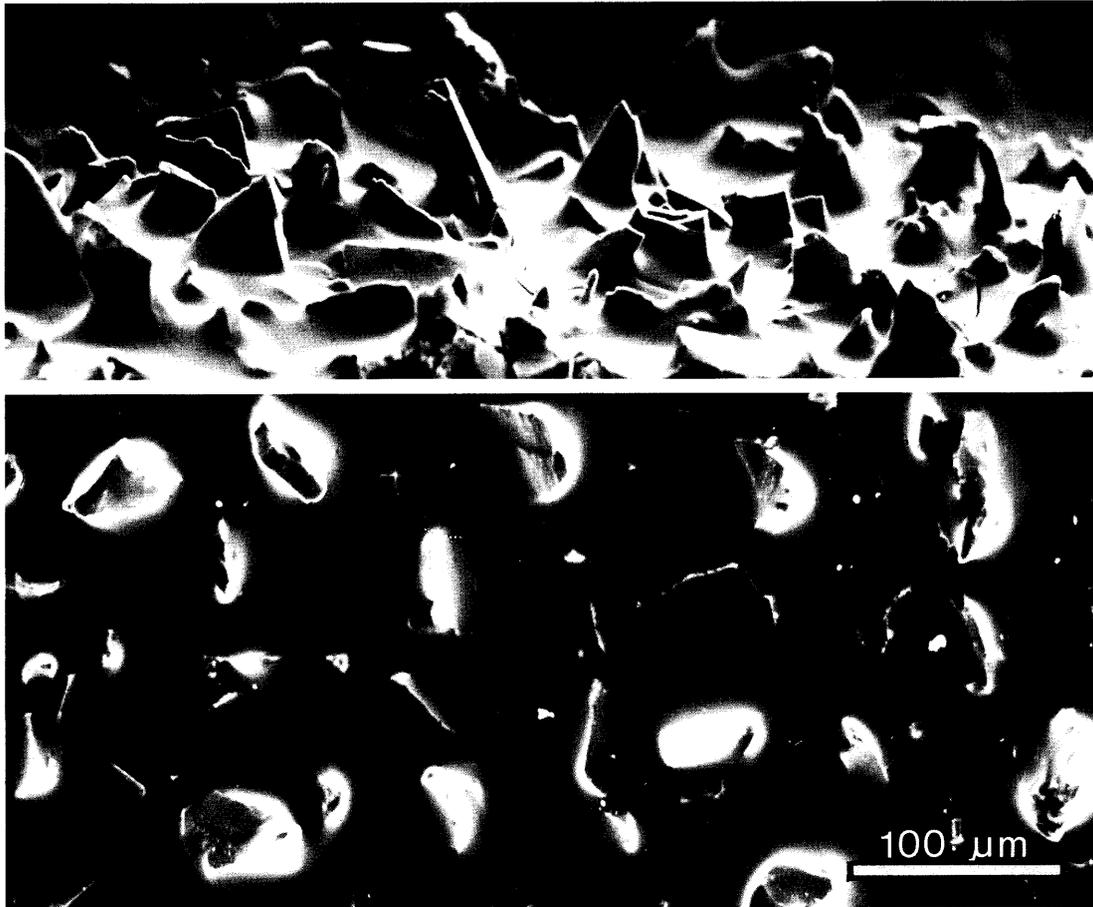


Fig. 4. Surface of contact plates made of 320 grit 3M sandpaper in side view (upper) and top view (lower).

contact plate was more sensitive to developmental changes in thread stickiness than was an aluminum plate.

In preparation for taking a stickiness measurement, I oriented the thread sampler so that the length of a cribellar thread sector was perpendicular to that of the contact plate. I then advanced the web sampler until the thread was pressed against the plate with a force of $19.61 \mu\text{N}$ and then immediately reversed the direction of the sampler's travel. I observed the position of the strain gauge's needle as the cribellar thread was pulled away from it and recorded the value registered at the instant the thread pulled free of the contact plate. After measuring the stickiness of a thread sector, I removed it from the sampler so that it would not be mistakenly remeasured.

I recorded the RH at which each sample's initial stickiness measurement was taken. Mean initial RH was used to determine the RH at which final puff dimension and stickiness measurements were taken. I measured the final lengths and widths of

cribellar thread puffs at an RH similar to that of the initial measurements and, one day later, at a much lower RH. On the next day, I measured thread stickiness at an RH similar to that at which initial measurements were taken. After measuring the dimension and stickiness of each sample, I recorded RH. Because initial puff measurements were made shortly before stickiness measurements, the latter's RH was also used for initial puff measurements.

Using the scanning electron microscope (SEM), I evaluated two properties related to the ability of sandpaper contact plates to consistently measure cribellar thread stickiness: the uniformity of the size and distribution of the silicon carbide particles on the surfaces of these plates and the potential for fragments of cribellar fibrils to accumulate on the plate's surface after repeated use. For the latter purpose, I examined a plate that had been used to measure the stickiness of over 520 cribellar thread sectors produced by females from a total of four uloborid species. The last 104 thread sectors measured prior to the plate's examination were the aged cribellar threads of *H. cavatus*.

To quantify within and between plate differences in particle size, I used 8.0×11.5 cm photographic prints, each representing a 410×575 μm region of a contact plate. Over each print, I aligned an 8.0×11.5 cm piece of clear acetate, across whose shorter dimension three evenly-spaced lines had been drawn. I then counted the number of particles each of these lines touched and measured in mm the lengths of the particles over which each line passed. In this way, I quantified both the number of projections that would contact a cribellar thread and the length of this contact. I used a line rather than a band, as I considered the former to be a more sensitive index of potential differences. From one plate I measured seven regions and from nine other plates one region each, for a total of 48 line intercepts. In tests of intra- and inter-plate differences, I treated each of the three line intercepts from a region as a separate measurement. By totaling the values from a region's three lines, I obtained indexes for the particles crossed by a 1,230 μm line, a length slightly greater than the width of a contact plate. I then compared mean particle number and length for the sub-sampled plate with the means of the nine other plates. This comparison should be a sensitive test of differences between contact plates that takes into account both intra- and inter-plate variance.

RESULTS

When the seven sectors of a single contact plate were compared, Kruskal-Wallis tests show no significant difference in either the number of particles crossed by a line ($P > 0.094$) or the total length of these particles ($P > 0.707$). Likewise, when nine plates were compared, this test showed no significant inter-plate difference in the number ($P > 0.150$) or total length ($P > 0.763$) of particles crossed by a line. For the sub-sampled plate, the mean number of particles crossed by a 1,230 μm line was 11.0 ($N = 7$, $SD = 1.8$) and the mean total length of these particles was 44.4 mm ($SD = 7.6$). The means of the nine other plates were, respectively, 12.3 ($N = 9$, $SD = 1.9$) and 41.4 mm ($SD = 8.0$). When these means are compared, a Wilcoxon 2-sample test shows that neither the number of particles nor their total length differs ($P > 0.104$ and $P > 0.202$, respectively). These results demonstrate that the distribution and size of particles on sandpaper contact plates are functionally uniform. This suggests that there should be no difference among repeated stickiness measurements made with the same contact plate and measurements made with different contact plates.

When examined under the SEM, only 50 cribellar

fibrils were seen on the surface of the used contact plate. This is an average accumulation of 0.096 fibril per thread measured for a final density of 1 fibril per 15.5×10^4 μm^2 of contact plate surface. At this density, a 2 mm strand of *H. cavatus* cribellar thread with a puff width of 177 μm would contact 2.28 residual fibrils on the sandpaper contact plate. Fibrils were uniformly distributed along the plate's width, as shown by the number counted in each of the seven length-wise scans required to examine the plate: 10, 4, 10, 8, 2, 8, and 8, the first and last values being those of the plate's edges. This demonstrates that the accumulation of cribellar fibrils is so slight as to not have an effect on the measurement of thread stickiness.

Table 1 presents the results of this study. All data were tested for normality using a Shapiro-Wilk W-statistic. When the initial and final values of an index were normally distributed ($P > 0.05$), a paired T-test was used to compare their means. When one or both indexes were not normally distributed, a Wilcoxon signed rank test was used. Mean puff length was unaffected by aging, but mean puff width showed slight (3.9%) but significant decreases with aging, although there was no significant difference in the humidity at which initial and final measurements were made. However, puff width/length ratio did not change significantly during the course of the study. Cribellar thread stickiness showed a significant decrease of 55% during the 14 months between measurements, although the humidity at which initial and final measurements were made did not differ.

After aging, cribellar thread stickiness decreased much more than did the length and width of cribellar thread puffs. Therefore, it is difficult to attribute this reduction in stickiness solely to a decrease in cribellar thread surface area. However, it is possible to further test this explanation. As Figure 5 shows, there is a clear relationship between the width of a cribellar thread's puffs and its stickiness. Using this regression formula, initial and final stickiness values can be computed for each thread sample based on its mean puff width. These computed values can then be used to determine if changes in stickiness attributable to changes in puff width are sufficient to explain the observed decrease in cribellar thread stickiness.

As Table 1 shows, computed final stickiness is still significantly less than computed initial stickiness. However, in this case, final stickiness was 82% that of initial stickiness, rather than only 45%, as was the case for measured stickiness. The remaining 37% decrease in stickiness must be attrib-

TABLE 1. The effect of aging upon the puff dimensions and stickiness of *Hyptiotes cavatus* cribellar threads¹

Parameter	Time		N	Test and P Value
	Initial	14 Months Later		
% Relative Humidity for Puff Measurements	58.7 ± 1.0	58.6 ± 1.7	25	W, 0.733
Mean Puff Length (μm)	81.4 ± 9.1	79.9 ± 8.7	26	T, 0.118
Mean Puff Width (μm)	181.5 ± 16.0	174.5 ± 15.0	26	W, 0.001
Puff Width/Length	2.25 ± 0.27	2.20 ± 0.23	26	T, 0.114
% Relative Humidity for Stickiness	58.7 ± 1.0	58.2 ± 1.7	25	W, 0.167
Measured Stickiness: μN/mm contact	28.4 ± 16.7	12.9 ± 5.0	26	W, 0.001
Stickiness Computed from Puff Width: μN/mm contact	26.3 ± 11.4	21.5 ± 7.7	26	W, 0.001
Measured-Computed Stickiness	4.8 ± 20.6	-7.1 ± 7.0	24	W, 0.005

¹Means values are followed by standard deviations. Statistical tests: T = paired T-test, W = Wilcoxon signed rank test.

uted to the aging process. Furthermore, Wilcoxon signed rank tests show that initial measured and computed stickiness values did not differ significantly ($P = 0.380$), whereas final measured stickiness was significantly less ($P < 0.001$) than computed stickiness. The difference between measured and computed stickiness differed significantly between initial and final trials.

Paired T-tests show that the two sets of final cribellar puff dimensions were measured at significantly different RHs ($58.7\% \pm 1.7$ and $35.0\% \pm 0.0$, respectively; $P < 0.001$). However, a paired T-test showed that this difference in RH did not signifi-

cantly alter mean puff length (79.4 ± 8.1 and 79.8 ± 8.7 , respectively; $P = 0.53$) and a Wilcoxon signed rank test showed that it did not affect mean puff width (173.1 ± 14.0 and 169.4 ± 14.3 , respectively; $P = 0.06$).

The fibrils of aged cribellar thread (Fig. 3) possess the nodes characteristic of recently spun threads (Lehmensick and Kullmann, '57; Friedrich and Langer, '69; Kullmann and Stern, '81; Opell, '79; Peters, '83, '84). However, this comparison is probably meaningless, as the high vacuums and voltages to which these fibrils are subjected when they are examined under transmission and scan-

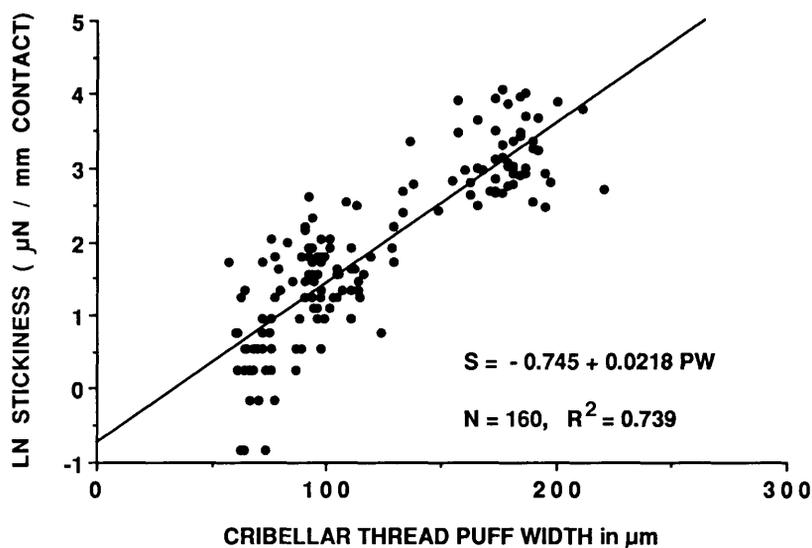


Fig. 5. Relationship of the cribellar thread puff width and cribellar thread stickiness in *Hyptiotes cavatus*. Stickiness is expressed as the natural log of force in μN per mm contact plate width.

ning electron microscopes are much harsher than the aging process employed in this study.

DISCUSSION

The results of this study fail to support the hypothesis that the stickiness of cribellar thread does not change with age. Instead, they show that after 14 months the length and width of cribellar thread puffs decrease slightly and the thread's stickiness decreases markedly. A reduction in puff width accounts for only part of the reduction in stickiness, leaving a 37% reduction in stickiness that must be attributed to the degradation with age of auxiliary forces.

As cribellar thread samples were stored in a closed box and housed in a closed cabinet, dust contamination can be eliminated as the cause of reduced cribellar thread stickiness. This means that reduced stickiness resulted from changes in the properties of the cribellar thread fibrils. Their surfaces may initially be covered by a thin layer of material that acts as an adhesive and, over time, either evaporates or, through adsorption, is covered by or deactivated by contaminants. Alternatively, these cribellar fibrils may contain compounds that favor the retention of electrostatic charges, the maintenance of moisture films, or molecular adhesion and, as these compounds degrade over time, the attractive forces they foster diminish.

The fact that cribellar thread becomes less sticky as it ages is not, by itself, likely to be ecologically important for members of the family Uloboridae. Most of these species, including *H. cavatus*, replace their webs every night and even those that are more tolerant of web damage replace them every few days (Lubin, '86; Opell, '82, unpublished observations). It is unlikely that cribellar thread loses much of its stickiness over these short periods. However, the dual mechanisms that appear to contribute to the stickiness of cribellar thread do have important implications for its prey capture potential. The ability of a cribellar thread's fibrils to catch on insect setae and spines allows it to hold prey with rough surfaces. The auxiliary force documented by this study does not appear to rely on this snagging mechanism and may adapt cribellar thread to hold smooth surfaces, such as the elytra of beetles or the hemelytra of hemipterans.

Two factors may explain why these results are at variance with Eberhard's ('80) findings. First, the cribellar threads he examined had aged for only three months and the changes observed in this study may not have taken place. Second, he was able only to estimate how sticky the threads were before

and after aging and probably would have been unable to detect changes of the magnitude observed in this study.

Changes in the dimensions of cribellar thread puffs may have resulted from compaction due to slight changes in thread tension as RH fluctuated. If Peters' ('84) suggestion that electrostatic charge helps maintain the configuration of fibrils around axial threads is correct, then the dissipation of this charge over time might allow these fibrils to settle closer together and reduce puff dimensions.

The failure of changes in relative humidity to affect the puff dimensions of aged cribellar thread suggests that electrostatic repulsion may not be an important factor in maintaining the configuration of fibrils that form cribellar thread puffs. If it were, then the charge should decrease at higher relative humidities and the fibrils repel each other less, resulting in a decrease in puff dimensions. However, these results should be interpreted cautiously. If the cribellar thread fibrils have been altered by age and their electrostatic charge has already been lost or reduced, then conclusions drawn from these observations may not apply to freshly spun cribellar threads.

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LITERATURE CITED

- Coddington, J.A., and H.W. Levi (1991) Systematics and evolution of spiders (Araneae). *Annu. Rev. Ecol. Syst.*, 22:565-592.
- Comstock, J.H. (1940) *The Spider Book*. Doubleday, Doran, and Co., Inc., New York, pp. 1-729.
- Eberhard, W.G. (1980) Persistent stickiness of cribellum silk. *J. Arachnol.*, 8:283.
- Friedrich, V., and R. Langer (1969) Fine structure of cribellate spider silk. *Am. Zool.*, 9:91-96.
- Kaestner, A. (1968) *Invertebrate Zoology*, Vol. 2 (trans. and adapted by H. Levi and L. Levi). John Wiley and Sons, Inc., New York, pp. 1-472.
- Kullmann, E. (1975) The production and function of spider threads. In: *Netze in Natur und Technik*. E. Kullmann, W. Nachtigall, J. Schurig, K. Bach, D. Blümel, T. Braun, B. Burkhardt, R. Graefe, G. Gröbner, U. Hangleiter, J. Hennicke, M. Kreuz, F. Otto, and R. Raccanello, eds. *Inst. Leichte Flächentragwerke*, Stuttgart, pp. 319-378.
- Kullmann, E., and H. Stern (1981) *Leben an seidenen Fäden*. Vindler Verlag, München, pp. 3-300.
- Lehmensick, R., and E. Kullmann (1957) Über den Feinbau der Spinnenfäden. In: *Electron Microscopy: Proceedings of Stockholm Conference*, Sept. 1956. F. Sjöstrand and J. Rhodin, eds. Academic Press, New York, pp. 307-309.
- Lubin, Y.D. (1986) Web building and prey capture in Uloboridae. In: *Spiders: Webs, Behavior, and Evolution*. W.A. Shear, ed. Stanford Univ. Press, Stanford, pp. 132-171.

- Opell, B.D. (1979) Revision of the genera and tropical American species of the spider family Uloboridae. *Bull. Mus. Comp. Zool.*, *148*:433–549.
- Opell, B.D. (1982) Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). *J. Arachnol.*, *10*:185–191.
- Opell, B.D. (1989a) Functional associations between the cribellum spinning plate and capture threads of *Miagrammopes animotus* (Araneida, Uloboridae). *Zoomorphology*, *108*:263–267.
- Opell, B.D. (1989b) Measuring the stickiness of spider prey capture threads. *J. Arachnol.*, *17*:112–114.
- Opell, B.D. (1990) The material investment and prey capture potential of reduced spider webs. *Behav. Ecol. Soc. Biol.*, *26*:375–381.
- Opell, B.D., G. Roth, and P.E. Cushing (1990) The effect of *Hyptiotes cavatus* (Uloboridae) web-manipulation on the dimensions and stickiness of cribellar silk puffs. *J. Arachnol.*, *18*:238–240.
- Peters, H.M. (1983) Struktur und Herstellung von Fangfäden cribellater Spinnen. *Verh. naturw. Ver. Hamburg (N.F.)*, *26*:241–253.
- Peters, H.M. (1984) The spinning apparatus of Uloboridae in relation to the structure and construction of capture threads (Arachnida, Araneida). *Zoomorphology*, *104*:96–104.
- Peters, H.M. (1986) Fine structure and function of capture threads. In: *Ecophysiology of Spiders*. W. Nentwig, ed. Springer-Verlag, New York, pp. 187–202.
- Peters, H.M., and J. Koor (1988) The spinning apparatus of *Polenecia producta* (Araneae, Uloboridae): Structure and histochemistry. *Zoomorphology*, *108*:47–59.