

Evolution of adhesive mechanisms in cribellar spider prey capture thread: evidence for van der Waals and hygroscopic forces

ANYA C. HAWTHORN and BRENT D. OPELL*

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061–0406, USA

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Sticky prey capture threads are produced by many members of the spider infraorder Araneomorphae. Cribellar threads are plesiomorphic for this clade, and viscous threads are apomorphic. The outer surface of cribellar thread is formed of thousands of fine, looped fibrils. Basal araneomorphs produce non-noded cribellar fibrils, whereas more derived members produce noded fibrils. Cribellar fibrils snag and hold rough surfaces, but other forces are required to explain their adherence to smooth surfaces. Threads of *Hypochilus pococki* (Hypochilidae) formed of non-noded fibrils held to a smooth plastic surface with the same force under low and high humidities. In contrast, threads of *Hyptiotes cavatus* and *Uloborus glomus* (Uloboridae) formed of noded fibrils held with greater force to the same surface at intermediate and high humidities. This supports the hypothesis that van der Waals forces allow non-noded cribellar fibrils to adhere to smooth surfaces, whereas noded fibrils, owing to the hydrophilic properties of their nodes, add hygroscopic forces at intermediate and high humidities. Thus, there appear to have been two major events in the evolution of adhesive mechanisms in spider prey capture thread: the addition of hydrophilic nodes to the fibrils of cribellar threads and the replacement of cribellar fibrils by viscous material and glycoprotein glue. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 1–8.

ADDITIONAL KEYWORDS: Araneomorph – character evolution – spider silk – thread stickiness

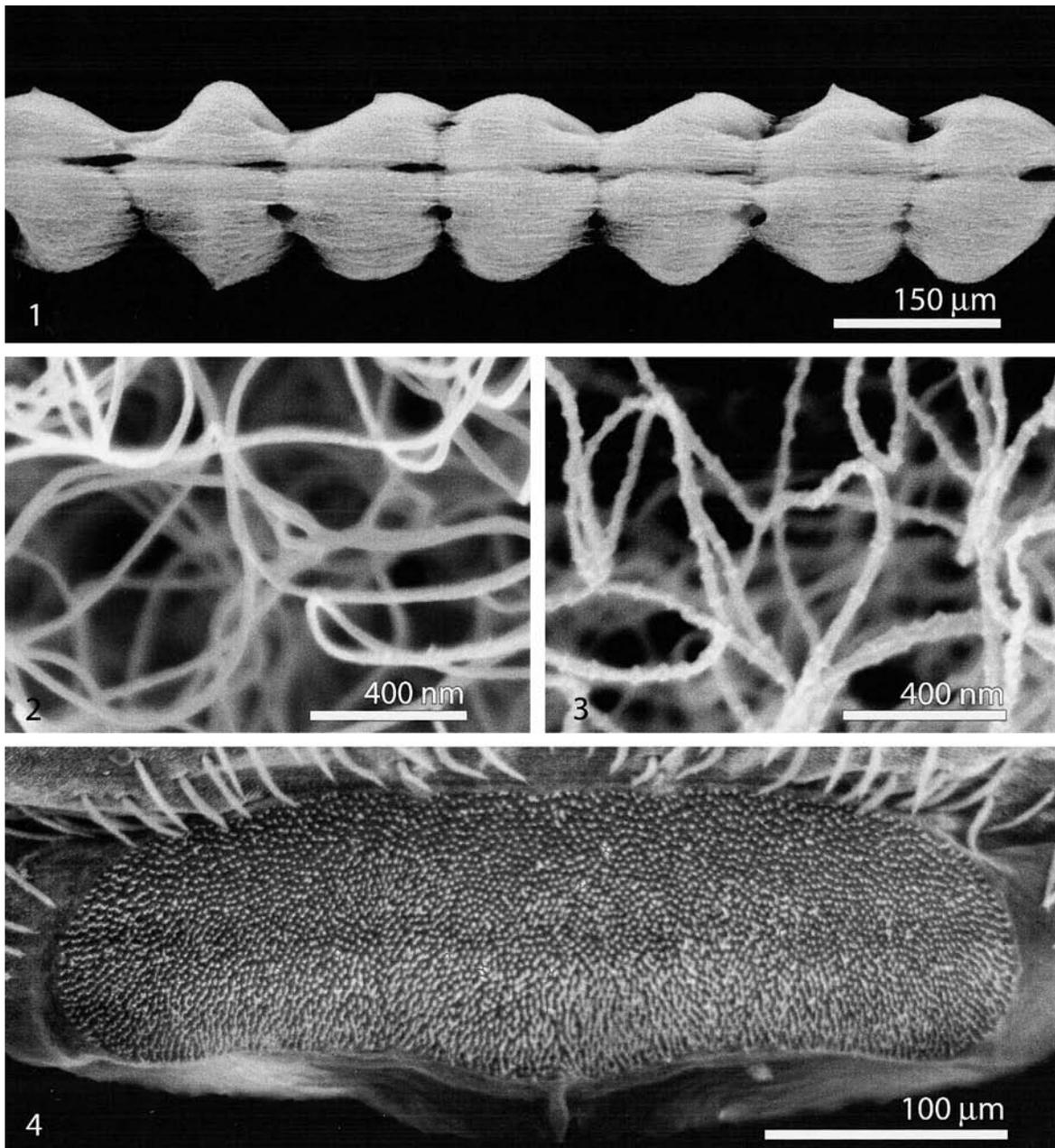
INTRODUCTION

An aerial web's sticky prey capture threads retain prey and buy time for a spider to respond. An insect that strikes a web is held and delayed for a time proportional to the stickiness of these threads, allowing a spider to subdue prey that would otherwise escape (Eberhard, 1989). The infraorder Araneomorphae contains the 'true spiders' that comprise the greater part of araneid diversity (Coddington & Levi, 1991). Unlike their sister clade, the Mygalomorphae, many araneomorphs produce sticky prey capture threads, the plesiomorphic type being cribellar thread (Fig. 1). Cribellar thread is a dry capture thread comprised of a wooly mass of fine fibrils with diameters of 10–20 nm (Figs 2 and 3; Eberhard & Pereira, 1993; Opell,

1994a) supported by a pair of larger, axial fibres and, in some groups, additional strands (Eberhard & Pereira, 1993). A spider produces cribellar thread by drawing fibrils from spigots on the cribellum (Fig. 4) using the calamistrum, a comb of setae on the metatarsus of the fourth legs. These fine fibrils are combined with supporting strands to produce wooly puffs (Eberhard & Pereira, 1993). The principle determinant of cribellar thread stickiness is the number of fibrils that form a thread, as gauged by the number of spigots on a spider's cribellum (Opell, 1994a, 1999a).

Cribellar thread is produced by the basal members of most major araneomorph clades and the phylogeny of cribellate families mirrors that of the complete araneomorph phylogeny (Coddington & Levi, 1991; Griswald *et al.*, 1999). Of the 90 araneomorph families, 22 contain cribellate members (Griswald *et al.*, 1999). Cribellar fibrils produced by members of the most primitive families are non-noded (Fig. 2) and

*Correspondence. E-mail: bopell@vt.edu



Figures 1–4. Scanning electron micrographs of: Fig. 1. *Hyptiotes cavatus* cribellar thread. Fig. 2. *Hypochilus pococki* non-noded cribellar fibrils. Fig. 3. *Hyptiotes cavatus* noded cribellar fibrils. Fig. 4. *Hyptiotes cavatus* cribellum.

those produced by the remaining families have regularly spaced nodes, except for one family that produces flat fibrils (Fig. 3; Eberhard & Pereira, 1993; Opell, 1994a). Although the taxon sample in Eberhard & Pereira (1993) is limited, the origin of noded fibrils appears to correspond to the origin of the Entelegynae clade (Griswald *et al.*, 1999). This clade is distinguished by features of male and female reproductive

anatomy, as well as the appearance of cylindrical silk spigots on the posterior median spinnerets.

Cribellar thread appears to rely on two stickiness mechanisms: mechanical interlock (snagging) and adhesion. The fibrils on its surface can snag on an insect's setae, and hold them like the soft, looped side of a Velcro fastener. However, cribellar thread also adheres to non-snagging surfaces by an unknown

mechanism. It holds more tightly to the smooth surface of a beetle elytra than to the heavily setose surface of a fly notum (Opell, 1994b). It also sticks to smooth surfaces such as glass, graphite, and polished steel (Eberhard, 1980; Hawthorn, unpublished observation) that are smooth even on a microscopic level (Autumn *et al.*, 2000).

Adhesion is most often achieved by a combination of several mechanisms. These can be classified as adsorption or van der Waals forces and electrostatic attraction (Allen, 1992a, b, c). Van der Waals forces technically encompass the hydrogen bonding facilitated by a thin film of water, but we will treat this separately as hygroscopic attraction. A third mechanism, diffusion of polymer chains across the interface of a bond (Allen, 1992a), requires the initial presence of a solvent and is unlikely to occur in dry, proteinaceous cribellar threads.

Van der Waals forces are the principle adhesive mechanism by which geckos can climb smooth, vertical surfaces. This is facilitated by very small, closely packed arrays of setae on the adhesive pads of their toes (Autumn *et al.*, 2000). Van der Waals forces are probably one mechanism utilized by cribellar thread, but the small diameter of its fibrils precludes accurate measurements of the force that each fibril exerts. Peters (1984, 1986) suggested that cribellar threads may derive at least part of their stickiness from electrostatic attraction. However, comparisons of the strength with which cribellar threads held to surfaces of different dielectric properties did not support this hypothesis (Opell, 1995a).

Opell (1995a) suggested that hygroscopic forces contribute to cribellar thread stickiness, although this hypothesis has not been tested. Water sticks to surfaces by adhesive forces and to other water molecules by cohesive forces, both of which involve hydrogen bonding. The forces of adhesion are usually stronger than cohesion, so the strength with which a thin film of water holds two surfaces together is determined by surface tension (Stork, 1979) and Laplace pressure (Israelachvili, 1992). It is not necessary for this film of water to be secreted by an organism, as a sufficiently hydrophilic substance can attract moisture from the atmosphere. This has been documented in the viscous adhesive capture threads that, in higher araneomorphs, have replaced cribellar threads. At typical ambient humidities, hydrophilic compounds in these threads draw water from the air to increase the volume of glue droplets on these threads (Townley *et al.*, 1991).

In this study we examine the mechanisms by which cribellar thread sticks to smooth surfaces. We test two hypotheses: (1) van der Waals forces contribute to thread stickiness, and (2) The nodes on fibrils of more advanced cribellate spiders are hydrophilic and

increase thread stickiness by implementing hygroscopic forces.

The majority of cribellate species spin thread with noded fibrils (Fig. 3), but these nodes are absent in the most ancestral cribellate spiders (Fig. 2; Eberhard & Pereira, 1993). As nodes appear to reduce the area of fibril contact to a series of points, this would tend to reduce the stickiness of the cribellar thread with noded fibrils. However, as selection has favoured an increase in thread stickiness (Opell, 1997, 1998, 1999a, b) this seems unlikely. As hygroscopic forces are stronger than van der Waals forces (Israelachvili, 1992), we hypothesize that the nodes of these fibrils incorporate hydrophilic amino acid groups that facilitate hygroscopic adhesion by adsorbing water from the atmosphere, thus increasing thread stickiness.

Cribellar threads produced by different spider species are comprised of different numbers of fibrils and have different surface configurations. Therefore interspecific comparisons of stickiness are less useful for testing our hypotheses than are comparisons of the stickiness registered by threads produced by the same spider under different humidity regimes. Our hypotheses predict that threads made of noded fibrils are stickier at high humidities than at very low humidities and that threads made of non-noded fibrils show little or no difference in stickiness under these conditions. Additionally, at near zero humidity noded threads should have a residual (van der Waals) stickiness that is similar to the stickiness of non-noded threads.

This approach also provides information about the operation of electrostatic force. If this force contributes significantly to thread stickiness, then it should diminish because electrostatic charges dissipate more readily at higher humidity. If electrostatic force is weak or nonexistent, then its effect will be overcome by an increase in hygroscopic force at higher humidity.

MATERIAL AND METHODS

We examined the cribellar threads of *Hyptiotes cavatus* (Hentz 1847) and *Uloborus glomosus* (Walckenaer 1841) (Family Uloboridae) that are formed of noded fibrils, and of *Hypochilus pococki* (Platnick 1987) (Family Hypochilidae) that are formed of non-noded fibrils. Only threads spun by adult females were used in this study. *Uloborus glomosus* threads were collected on the Virginia Tech campus from July to September, and *H. cavatus* threads were collected from the Virginia Tech campus, the forests of Montgomery and Giles Co. VA (hereafter referred to as the Virginia population), and near the town of Roan Mountain, Craig Co., TN from September to October (hereafter referred to as the Tennessee population). Adult females of both uloborid species were collected and housed individu-

ally in large plastic boxes, where they attached their webs to wooden dowel rods glued around the perimeter the boxes. These boxes were kept in an environmental chamber under conditions of 13 h dark/11 h light, 24 °C, and RH that ranged from 80% during the dark phase to 70% during the first and last two hours of the light phase to 60% during the remainder of the light phase. Spiders were misted with water daily and those kept for longer than two days were fed flightless fruit flies every other day. Threads from adult female *H. pococki* webs were collected in September and October from near the town of Roan Mountain, Craig Co., TN and on the eastern slope of Grandfather Mountain, Avery Co., NC. All hypochilid threads were collected in the field, because these spiders could not be induced to spin webs in the lab. Unlike the uloborids that take down and replace their webs nightly, *H. pococki* continues to repair and add cribellar threads to its web. This allowed us to collect newly spun threads from the outer edges of *H. pococki* webs.

We collected threads from webs on microscope slides with parallel raised supports. Double-sided tape atop each support securely anchored threads, ensuring that threads crossing between supports maintained their initial tension when they were cut away from the web. We examined all threads under a dissecting microscope and discarded any that appeared damaged, were intersected by another thread, or were contaminated with dirt or pollen. We also removed older *Hypochilus* threads, which, under the dissecting microscope, could be distinguished from more recently spun threads by their contracted, collapsed structure.

Stickiness was measured using an instrument that was a modification of the one described by Opell (1989) and was used in previous studies of thread stickiness (Opell, 1993, 1994a, 1994b, 1995a, 1995b, 1999b). This consisted of a stainless steel needle strain gauge

mounted in a plexiglass frame, positioned so that the contact plate on the needle's protruding tip could be brought into contact with the cribellar thread. A motorized screw advanced the thread toward the 2 mm wide contact plate at a constant speed of 10.4 mm per minute, and withdrew it at 10.7 mm per minute. The arbitrary scale over which the needle's free end passed was calibrated using 5 mg weights, and the force in Newtons required to deflect the needle was calculated by multiplying the scale values by the accelerating force of gravity.

The contact plate was made of aluminium surfaced with acetate from the non-sticky side of Scotch® Magic™. Tape (3M Co., 2002). We chose this surface because scanning electron microscope examination showed it to be fairly smooth even at the scale of tens of nanometers, at which the cribellar fibrils operate. It also has a non-polar surface that does not attract moisture and allows small water droplets to bead up. Cribellar thread sticks to this surface with a force that is comparable to the force with which it holds fleshfly wings and 320 grit silicon carbide sandpaper, surfaces used in previous studies of capture thread stickiness (Opell, 1993, 1994a, 1994b, 1995a, 1995b, 1999b). Contact plates were prepared by sticking the tape to aluminium strips cut from weighing pans, cutting strips that were approximately 2 mm wide (final widths were measured to the nearest 20 µm under a dissecting microscope), cutting these strips into 4–5 mm lengths, and sealing all edges with silver paint to ensure that none of the tape's adhesive was exposed.

The stickiness of most threads was measured within 2 weeks after being collected and of all threads within 38 days (Table 1). Each strand was orientated so that it was perpendicular to the long axis of the contact plate. A motorized screw advanced the thread holder

Table 1. Conditions for stickiness comparisons

Species	<i>N</i>	RH mean ± SD (%)	Mean age (days)	RH Range (%)	Temperature mean ± SD (°C)
<i>Hypochilus pococki</i>	9	Low: 0.60 ± 0.48	13	0.0–1.45	24.5 ± 0.35
		High: 99.78 ± 0.36	14	99.0–100	23.5 ± 0.48
<i>Hyptiotes cavatus</i> (Virginia)	8	Low: 1.89 ± 0.51	32.3	1.40–2.85	22.3 ± 0.27
		High: 99.55 ± 1.0	28.8	97.15–100	21.9 ± 0.24
<i>Hyptiotes cavatus</i> (Roan Mt. TN)	8	Low: 0.28 ± 0.28	5.1	0.0–0.75	25.1 ± 0.38
		Medium: 46.93 ± 1.45	8.3	44.5–48.5	25.7 ± 0.61
Uloborus glomusos	7	Low: 1.25 ± 0.58	12	0.25–1.8	24.8 ± 0.45
		Medium: 46.6 ± 0.81	12.5	45.3–47.5	24.7 ± 1.01
		High: 99.98 ± 0.38	17	99.9–100	25.2 ± 0.38
	9	Low: 1.1 ± 0.37	2.3	0.55–1.60	26.4 ± 0.29
		Medium: 48.4 ± 2.54	3.8	45.45–52.9	26.1 ± 0.46

towards the contact plate until it pressed against the plate with a force of 19.61 μN , and then immediately reversed the direction of the thread holder. We observed the position of the strain gauge needle along the calibrated scale, and recorded the value at the moment it pulled away from the thread. The stickiness of each web is the mean stickiness of three or four threads taken from that web. The force in μN required to pull the plate from the thread was divided by the width of the plate to give the stickiness in $\mu\text{N mm}^{-1}$ of thread contact. The number of webs sampled per spider varied from 1 to 3, depending on how readily that individual spun in the lab.

To determine the effect of atmospheric water on the stickiness of cribellar thread, we compared the stickiness of threads from individual webs under conditions of high (near 100% RH), intermediate (between 45 and 50% RH), and low (under 3% RH) relative humidities. To control humidity the entire stickiness measuring apparatus was placed inside a sealed clear plexiglass box. A port in the side admitted the probe of a digital humidity gauge, and another port was connected to a tube through which the chamber could be flushed. The low humidity was achieved by flushing the chamber with pure, dry nitrogen. High and intermediate humidities were achieved by bubbling the nitrogen through distilled water. A small fan in the chamber ensured thorough mixing of the atmosphere in the box. For the high humidity measurements a piece of cloth dampened with distilled water was placed over the fan. We recorded the humidity and temperature at the start and finish of the stickiness measurements of each thread sample and averaged these to determine the mean humidity for each trial.

The conditions under which stickiness was measured are given in Table 1. The cribellar threads spun by *H. cavatus* adult females from Roan Mountain were narrower and less sticky under low humidity than those spun by Virginia specimens (data were normal: Shapiro–Wilke W statistic > 0.1. Width: Tennessee 142 μm , SD = 32, $N = 6$ vs. Virginia 204 μm , SD = 27, $N = 8$, t -test $P = 0.002$. Stickiness: Tennessee 8.2 $\mu\text{N mm}^{-1}$, SD = 3.6, $N = 8$ vs. Virginia 27.3 $\mu\text{N mm}^{-1}$, SD = 15.9, $N = 8$, t -test $P = 0.0051$). Therefore, the values of these two populations are treated separately. As the stickiness of capture threads spun by different individuals of the same species differ, the stickiness of threads spun by the same individual were compared at different RHs using paired tests. The statistical programs SAS and JMP (SAS Institute, Carry, NC) were used to analyse these data. P -values ≤ 0.05 were considered significant. All data analysed with parametric statistics were first tested for normality using the Shapiro–Wilk W statistic; values >0.05 were considered normally distributed.

RESULTS

NODED THREAD

The stickiness of threads from Virginia *H. cavatus* populations measured in high RH was greater in all cases than the stickiness of threads from the same webs measured in low RH (Fig. 5; \bar{x} difference = 10.4 $\mu\text{N mm}^{-1}$, SD = 3.7, paired t -test: $t = 5.399$, $P = 0.0005$, $N = 8$). The stickiness of *H. cavatus* threads from the Tennessee population showed a similar difference in stickiness. Although the overall stickiness of the threads from the Tennessee population was lower, each thread was stickier when measured at intermediate RH than at low RH (Fig. 5; \bar{x} difference = 13.7 $\mu\text{N mm}^{-1}$, SD = 1.6; paired t -test: $t = 9.676$, $P = 0.0001$, $N = 9$). The increase in stickiness from low to intermediate RH (Tennessee population) and the increase from low and high RH (Virginia Population) did not differ (t -test: $t = 1.396$, $P = 0.1845$). That is, beyond a RH of 47%, there was no demonstrable increase in thread stickiness.

Uloborus glomus threads showed similar differences in stickiness. Threads from one set of webs were measured at low and intermediate RH and threads from another set were measured at low, intermediate, and high RH. Threads from the first set of webs were stickier at intermediate RH than at low RH (Fig. 5; \bar{x} difference = 15.7 $\mu\text{N mm}^{-1}$, SD = 3.8; paired t -test: $t = 12.536$, $P = 0.0001$, $N = 9$). The stickiness of threads from the second set of webs also differed among RH's (Fig. 5; ANOVA: $F = 24.521$, $P = 0.0001$, $N = 7$). Pairwise comparisons using the Tukey–Kramer Honest Significant Difference (Sokal & Rohlf, 1969) revealed a difference between low and intermediate RH and between low and high RH, but not between intermediate and high RH at the $\alpha = 0.05$ level experiment-wise (difference between low and intermediate RH's = 12.3 $\mu\text{N mm}^{-1}$, SD = 4.8, $N = 7$; difference between low and high RH's = 18.4 $\mu\text{N mm}^{-1}$, SD = 5.7, $N = 7$; \bar{x} difference between intermediate and high RH's = 6.1 $\mu\text{N mm}^{-1}$, SD = 5.1, $N = 7$).

NON-NODED THREAD

Threads from six of the nine webs of *H. pococki* showed an increase in stickiness when measured at low and high RH (Fig. 5). However, there was no significant difference in the stickiness of threads measured under these two conditions (difference = 0.4 $\mu\text{N mm}^{-1}$, SD = 5.3, $N = 9$); paired t -test: $t = 2.100$, $P = 0.839$).

DISCUSSION

This study found that the stickiness of cribellar threads with noded fibrils increased as RH increased, whereas the stickiness of primitive cribellar threads

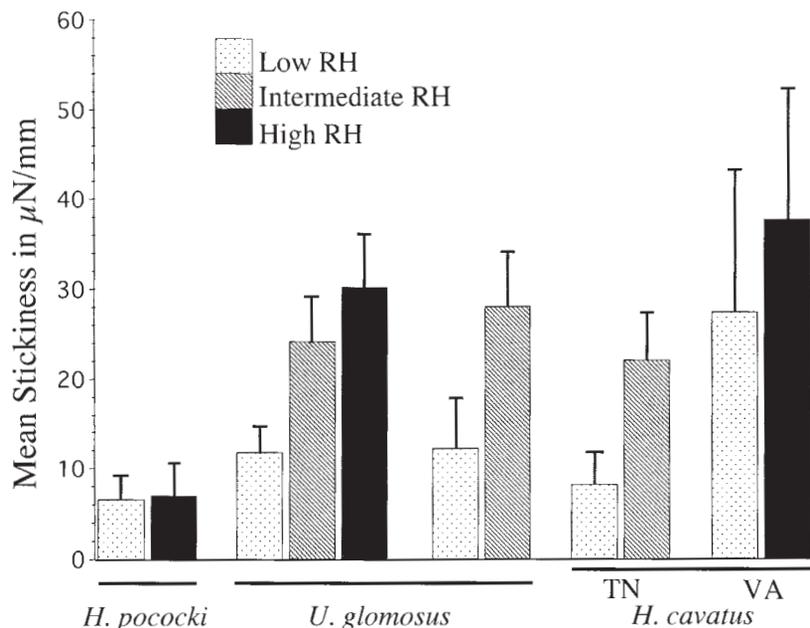


Figure 5. Mean stickiness in $\mu\text{N mm}^{-1}$ of *Hypochilus pococki* threads in low vs. high RH, *Uloborus glomosus* threads in low vs. intermediate vs. high and low vs. intermediate RH, and *Hyptiotes cavatus* threads in low vs. intermediate RH (Tennessee population) and low vs. high RH (Virginia population). Error bars represent 1 standard deviation.

with non-noded fibrils was unaffected. These observations support the hypotheses that both van der Waals and hygroscopic forces contribute to the stickiness of cribellar threads and that the fibril nodes of derived cribellar threads facilitate the hygroscopic mechanism. They also provide no evidence for the operation of electrostatic force. These findings reveal an innovation in spider evolution that was comparable to the replacement of cribellar capture threads by the viscous capture threads spun by modern orb-weaving (Araneoidea) spiders (Opell, 1997, 1998; Opell & Bond, 2001). Just as this latter event is associated with increased species numbers (Bond & Opell, 1998), the replacement of non-noded fibrils by noded fibrils is also associated with increased spider diversity. The family that produces non-noded fibrils is comprised of 2 genera and 11 species, whereas those that spin noded fibrils are comprised of 369 genera and 3595 species (Eberhard & Pereira, 1993; Platnick, 2000). Although these numbers include members of cribellate families that have lost their cribellum, they highlight the disparity between the numbers that spin noded and non-noded fibrils.

Only cribellar threads with noded fibrils show an increase in stickiness with increased humidity, thus the appearance of these nodes was most probably associated with the inclusion of hydrophilic amino acids at these sites on the fibrils. This innovation allowed spiders to spin stickier threads and construct webs that were characterized by a greater stickiness

per capture area, a feature that enhances the web's prey capture potential (Eberhard, 1989; Opell, 1999b). As cribellar thread with non-noded fibrils appears to rely only on van der Waals forces for their stickiness, stickiness can only be increased by increasing the number of fibrils that contact a surface. This can be achieved by either increasing the number of fibrils that form a cribellar thread (Opell, 1994a, 1995a, 1999b) or by folding and looping the thread before it is placed in the web (Opell, 2002). Both of these strategies require a spider to invest more material (protein) to increase thread stickiness. Only when noded cribellar fibrils that were capable of implementing hygroscopic forces appeared was the direct link between silk investment and silk stickiness broken. Even if the amino acids whose incorporation was necessary to implement hygroscopic forces were more metabolically costly (Craig & Weber, 1998) than those they replaced, the benefit appears to be disproportionately great. Under the intermediate RH typical of many habitats noded threads are 30–50% stickier than they are under low RH, where we believe that van der Waals forces account for most of the stickiness. As we did not measure thread stickiness at RHs between 2 and 50%, it is possible that noded threads may implement hygroscopic adhesion at values considerably less than 50%.

Evidence for the incorporation of a different suite of amino acids in noded fibrils comes from the configuration of cribellar fibrils. The size of these fibrils

(diameter 10–20 nm, compared to 1.5 nm for a single collagen fibre; Stryer, 1995) suggests that they may represent individual fibrous proteins or a quaternary assembly of protein fibres, and that the nodes are produced by protein folding and aggregation. Hygroscopic proteins would incorporate hydrophilic polar or charged amino acids such as serine, lysine and aspartate, causing them to fold and assemble to form nodes. These amino acids may also be capable of hydrogen bonding directly with a substrate in the absence of environmental humidity, resulting in a somewhat higher stickiness even in dry environments. However, molecular studies of fibril composition are necessary to confirm this hypothesis. The complex structure of cribellar thread, which incorporates silks from many glands makes direct amino acid analysis impractical, but the product of the cribellar glands could be determined sequencing its mRNA.

The transition from cribellar capture threads spun by members of the Deinopoidea to viscous capture threads spun by its sister clade, the Araneoidea, has been problematic as transitional states are difficult to envision. Like cribellar threads, viscous threads have a pair of supporting axial fibres (Griswald *et al.*, 1998; Opell & Bond, 2001). However, rather than being sheathed by cribellar fibrils, these fibres are covered by an aqueous solution that contains hydrophilic compounds (Townley *et al.*, 1991) as well as glycoproteins which coalesce to form granules that confer thread stickiness (Tillinghast *et al.*, 1993). It is plausible that the hygroscopic nodes of noded cribellar threads are one step along the path to viscous thread. The secretion of even a small amount of moisture onto threads would further enhance this mechanism and subsequent increases in this material would eliminate the need for relatively expensive cribellar fibrils, leading to the loss of the cribellum and the production of modern viscous threads.

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