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Changes in the mechanical properties of capture threads and the evolution of modern orb-weaving spiders

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ABSTRACT

The capture threads of spider orb-webs retain prey and contribute to a web's ability to absorb the forces generated when prey strike the web. Primitive orb-webs produced by the Deinopoidea clade are horizontally oriented and contain dry, fuzzy (cribellar) capture thread, whereas modern orb-webs constructed by the Araneoidea clade are vertically oriented and contain viscous adhesive threads. Independent contrast analyses find no relationships between spider mass or features of web architecture and the tensile strengths, Young's moduli and breaking energies of capture threads. Cribellar and adhesive threads have similar breaking energies, but the manner in which they resist breaking differs. The tensile strengths and Young's moduli of adhesive threads are smaller than those of cribellar threads, rendering adhesive threads weaker, but better equipped to dissipate force by stretching. This mode of absorbing force is advantageous for vertical orb-webs, which typically intercept faster flying prey than horizontal orb-webs. The greater extensibility of adhesive capture thread allows an orb-web to dissipate energy locally as capture threads stretch while transferring force and also enhances the web's overall extensibility, allowing it to flex and dissipate force through air resistance.

Keywords: adhesive thread, breaking energy, character evolution, cribellar thread, tensile strength, Young's modulus.

INTRODUCTION

The architecture and material properties of spider orb-webs provide a unique and interesting system for studying the dynamics of adaptation and key innovation, since many components of this complex system must function as a cohesive, integrated unit. Aspects of the evolution of spider orb-webs have been associated with changes in the sticky prey capture threads that help these webs capture and retain prey (Bond and Opell, 1998). The spirally arrayed capture threads of all orb-webs are internally supported by a pair of axial fibres, but the material that covers these fibres and imparts thread stickiness differs greatly. The axial

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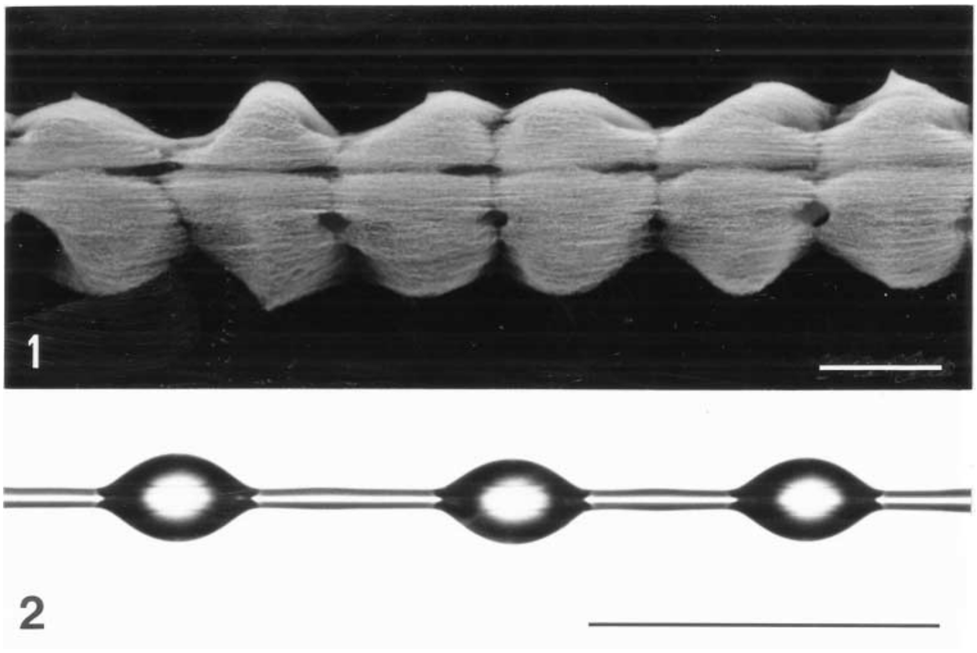
fibres of the primitive cribellar capture threads (Fig. 1) produced by members of the Deinopoidea are covered by a dry sheath formed of thousands of thin, coiled fibrils produced by the spigots of a spinning plate called the 'cribellum' (Eberhard and Periera, 1993; Opell, 1994, 1995, 1996, 1999a,b). In contrast, the axial fibres of the capture threads produced by the more derived Araneoidea are covered by a complex aqueous solution that coalesces into regularly spaced droplets soon after being deposited (Peters, 1986, 1995; Vollrath *et al.*, 1990; Vollrath, 1992; Opell, 1997, 1998) (Fig. 2).

The transition from deinopoid to araneoid orb-webs was also associated with a switch from horizontal to vertical web orientation (Bond and Opell, 1998). This change has the potential to enhance prey capture, since vertical artificial orb-webs capture more insects and retain them for longer periods of time than horizontal orb-webs with the same capture thread stickiness (Chacón and Eberhard, 1980). When the orientation of araneoid orb-webs was experimentally changed, vertically oriented webs retained prey longer than horizontally oriented webs (Eberhard, 1989). Additionally, insects that struggled free of vertical orb-webs were more often recaptured by the web's other threads than those that struggled free of horizontal orb-webs (Eberhard, 1989). However, the change to vertical orientation places additional demands on the araneoid web. Vertical orb-webs tend to intercept faster flying prey than horizontal orb-webs and must be better equipped to absorb and dissipate the greater kinetic energies generated when these prey strike the web (Denny, 1976; Eberhard, 1981, 1986; Craig, 1987).

Several mechanisms permit orb-webs to sustain the force of a prey strike. Webs that have more radii (higher radius-to-spiral ratio) rely on the tensile strength of their radial threads



Figs 1 and 2. Prey capture threads. (1) Cribellar thread of *Hyptiotes cavatus* Hentz. (2) Adhesive thread of *Argiope trifasciata* (Forskal). Scale bars are 100 μm long.

to withstand this force, whereas webs that have a lower radius-to-spiral index are more easily deformed and dissipate energy as they stretch (Craig, 1987). Lin *et al.* (1995) combined computer modelling and empirical data to show that the vertical web of *Araneus diadematus* absorbs a significant amount of force through aerodynamic dampening. This occurs when the force of a prey strike displaces a web and friction with the air helps dissipate the force of that strike.

The more stringent demands that are placed on the vertical orb-webs of Araneoidea suggest that the origin of these orb-webs was also associated with an increase in their ability to withstand the forces of prey strikes. Two factors equip a thread to do this, its tensile strength and its extensibility. Tensile strength is a measure of how much force can be applied to a thread before it breaks. Extensibility is a measure of how far a thread stretches before it breaks. These two indexes are used to compute a thread's elastic modulus, an index that describes a thread's stiffness. Threads with high elastic modulus values are stiff (e.g. a string) and those with low values are stretchy (e.g. a rubber band). Threads with high elastic modulus values must resist a breaking force, whereas those with low values are better equipped to dissipate some of this force through elongation. Breaking energy describes the total amount of energy necessary to break a thread. This index accounts both for a thread's ability to resist a breaking force by virtue of its tensile strength and its ability to dissipate force through stretching by virtue of its elastic modulus.

There is no clear evidence that the composition of adhesive capture threads makes them more extensible than cribellar threads. Vollrath and Edmonds (1989) proposed that each of the small droplets along an adhesive thread (Fig. 2) acts as a windlass mechanism to reel in a sector of silk and, when the thread is stretched, to play out this thread. However, Schneider (1995) found no microscopic or experimental evidence for the windlass mechanism and concluded that the way in which Vollrath and Edmonds prepared thread samples misled them. Köhler and Vollrath (1995) measured lower extensibilities in the cribellar threads of an adult female orb-weaver of the family Ulobiridae (Deinopoidea) than in the adhesive capture threads produced by a juvenile orb-weaver of the family Araneidae (Araneoidea) with the same mass. However, Opell and Bond (2000) found that the extensibility of capture threads of adult uloborid and adult araneoid species was directly related to spider mass and to architectural features of orb-webs. They did not find differences in the extensibilities of cribellar and adhesive threads after factoring in these relationships. However, these studies do not rule out the possibility that differences in the diameter and composition of the axial fibres of cribellar and adhesive threads may confer different mechanical properties to these capture threads.

We hypothesize that adhesive capture threads should have greater elastic moduli and breaking energies than cribellar capture threads, as they are typically required to withstand greater forces in the dynamic environment of a vertical orb-web. As the species we studied differ greatly in body mass and produce orb-webs with a range of architectural features, it was necessary to first refute the hypothesis that these features are associated with the mechanical properties of capture threads before comparing the mechanical properties of cribellar and adhesive capture threads. Independent contrast analyses uncovered no relationships between either spider mass or features of orb-web architecture and the tensile strengths, elastic moduli or breaking energies of capture threads. Therefore, we used parametric statistics to compare the mechanical properties of cribellar and adhesive capture threads. This showed that cribellar threads have greater tensile strengths and elastic moduli than adhesive threads, signifying that they are both stronger and stiffer than adhesive threads. Thus, adhesive capture threads are better equipped than cribellar threads to dissipate the force of a prey strike through elongation.

METHODS AND MATERIALS

Species studied

We measured the tensile strength of cribellar capture threads produced by adult females of three species of the Uloboridae, five species of the family Araneidae and one species of the family Tetragnathidae (Table 1). These species were identified using the studies of Berman and Levi (1971), Levi (1968, 1971, 1976, 1977), Muma and Gertsch (1964) and Opell (1979). Voucher specimens are deposited in the Museum of Comparative Zoology at Harvard University. These spiders were collected from the same populations as individuals whose web parameters were determined by Opell (1999a) and Opell and Bond (2000). The phylogenetic relationship of these species is given in Fig. 3. In this pruned phylogeny, *Leucague venusta* occupies a basal phylogenetic position among the six araneoid species. However, in the context of a complete phylogeny, it is clear that vertical orb-web orientation is plesiomorphic for the Araneoidea and that the horizontal orientation of *L. venusta* webs is secondarily derived (Bond and Opell, 1998).

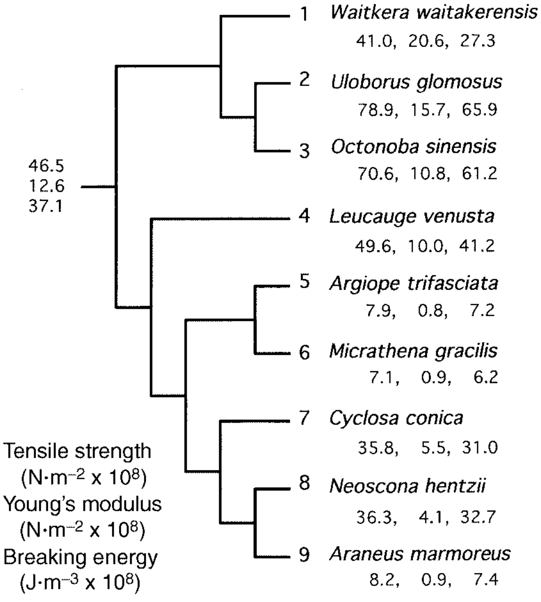


Fig. 3. The phylogenetic relationships of species included in this study. This composite phylogeny was produced by combining the phylogeny of uloborid species from Coddington (1990b) and the araneoid phylogeny of Scharff and Coddington (1997). The mean mechanical properties of each species' capture thread is given. For the three cribellate species, these values were computed from the cross-sectional areas of the axial fibres and half the cribellar fibrils. Ancestral values are given at the base of the tree.

Table 1. Spider mass, conditions under which thread features were measured and measurements used to compute the mechanical properties of threads (mean ± 1 standard error)

Species	Sample size	Mass (mg)	Temperature (°C)	% Relative humidity	Axial fibre diameter (μm)	Breaking strength (μN)	Extensibility[a] (% original length)
Araneidae							
Araneus marmoreus (Clerck)	10	692.10 ± 85.45	22.80 ± 0.13	59.90 ± 0.10	4.50 ± 0.43	483.79 ± 41.16	1039
Neoscona hentzii (Keyserling)	21	538.43 ± 41.75	23.43 ± 0.11	60.00 ± 0.00	3.41 ± 0.27	1352.10 ± 141.91	997
Cyclosa conica (Pallas)	16	7.23 ± 0.38	25.19 ± 0.2	62.13 ± 0.29	1.25 ± 0.13	198.19 ± 6.53	749
Argiope trifasciata (Forskal)	19	303.89 ± 27.06	22.68 ± 0.11	59.58 ± 0.12	5.37 ± 0.42	679.49 ± 69.18	1100
Micrathena gracilis (Walckenaer)	19	101.93 ± 6.56	24.16 ± 0.09	59.95 ± 0.21	3.44 ± 0.25	288.06 ± 16.67	857
Tetragnathidae							
Leucague venusta (Walkenaer)	19	25.91 ± 2.31	25.05 ± 0.12	60.00 ± 0.55	1.03 ± 0.05	292.77 ± 13.38	586
Uloboridae							
Ocotonoba sinensis (Simon)	16	12.13 ± 1.72	22.81 ± 0.16	60.69 ± 0.48	0.38 ± 0.01	383.25 ± 30.08	753
Uloborus glomosus (Walckenaer)	17	7.23 ± 0.66	23.88 ± 0.17	61.12 ± 0.51	0.32 ± 0.03	440.41 ± 18.97	604
Waitkera waitakerensis (Chamberlain)	20	7.85 ± 0.54	25.00 ± 0.38	70.60 ± 1.32	0.31 ± 0.01	428.27 ± 13.31	299

[a] Extensibility values are from Opell and Bond (2000).

Tensile strength

Tensile strength describes the extension force per cross-sectional area at which a filament breaks. Therefore, both the breaking strength and diameter of a thread must be measured. We collected web samples in the morning, a few hours after spiders constructed them. We measured breaking strengths within 12 h (usually within 4 h) of threads being collected and recorded the temperature and relative humidity at which these measurements were made (Table 1). Thread samples were collected, examined and handled as described by Opell and Bond (2000).

Cribellar threads were placed on formvar-coated copper grids and examined (uncoated) under a scanning electron microscope, where their dense axial fibres could easily be seen through the outer cloud of fine cribellar fibrils. We photographed the widely spaced axial fibres of these threads and measured their diameters from the negatives under a dissecting microscope. We measured the diameter of an axial fibre at three points along its length and used the mean diameter to compute the cross-sectional area of that fibre. We doubled this value to yield the cross-sectional area of a thread's supporting elements.

As noted by Köhler and Vollrath (1995), the aqueous coating of both the droplet and inter-droplet regions of viscous threads poses a problem to measuring thread diameter. In both fresh threads and those that have been desiccated for study under the electron microscope, this coating exaggerates the diameter of the inner axial fibres that provide the thread's strength. We found that this problem could be overcome by anchoring a thread strand to a microscope slide, placing a drop of 'Super Glue' on it, and then adding a cover slip to this preparation. After the glue hardened, the supporting strand formed from the paired axial fibres could be easily distinguished from the surrounding aqueous material, which was effectively cleared by the glue. We photographed these fibres at 1250× under a compound microscope and then measured the width of this image on 35 mm colour slides using a dissecting microscope. Each strand was measured at three points along its length and the mean width used in computations. Previous studies of tensile strength (e.g. Criag, 1987) have treated the width of the paired axial fibres as the diameter of a single strand in computing the cross-sectional area of the supporting elements of a capture thread. However, we believe that this tends to overestimate the cross-sectional area; consequently, we used a more conservative approach. We divided the width of the paired axial fibres by 2 to obtain the width of a single axial fibre, computed the cross-sectional area of this fibre, and then doubled this value to determine the combined cross-sectional area of both axial fibres.

Our technique for measuring the breaking strength of capture threads differs from that used in other studies (e.g. Köhler and Vollrath, 1995). It increases the force applied to a thread at a constant rate rather than elongating the thread at a constant rate. We followed the procedure of Opell and Bond (2000) by beginning these measurements with threads under their native web tensions rather than by first relaxing them. Thus, the values we measured reflect a thread's performance after it has been incorporated in an orb-web. We believe that this provides an appropriate comparison of the mechanical properties of threads, as these properties have been selected in the context of a functioning orb-web.

The instrument we used to measure the breaking force of a thread was constructed from an analog electrical meter to which voltage was supplied by a motor-driven rheostat. The thread sample was suspended between a plate on the meter's tip and a stationary support. Double-sided tape on these two surfaces held the thread securely. Force was applied at a rate of 11.34 $\mu\mathrm{N \cdot s^{-1}}$ until the thread broke, at which time the needle opened a contact that stopped the rheostat motor which was increasing the voltage applied to the meter. A digital voltmeter recorded the voltage at the instant the thread broke. We calibrated this instrument by determining the voltage required to lift weights of known masses, computing the regression formula of these values, and using this linear regression to convert the breaking voltage of a thread first to milligrams and then to micro-Newtons of force. Values were recorded to the nearest millivolt, which resulted in a resolution of 0.98 μN. We measured the breaking value of three thread samples from each spider's web and used the mean value for analysis.

From these measurements, we computed a thread's tensile strength as its true stress (S_T) at the time it broke using the formula: $S_T = S_e \times (L/L_0)$, where S_e = engineering stress = force applied to thread at breaking point/initial cross-sectional area of thread, L = length of thread at breaking point and L_0 = initial length of thread. For elastic materials like spider threads, true stress is a more appropriate measure of the breaking strength than engineering stress, because it is based on an approximation of the instantaneous cross-sectional area of a thread (Köhler and Vollrath, 1995). If a material does not stretch as force is applied, engineering stress and true stress are identical, but the more elastic a material is, the more it stretches before breaking and the smaller its diameter at the time of breaking. Multiplying engineering stress by the expression (L/L_0) increases true stress as elasticity increases.

Elastic modulus

We used the following formula to compute elastic modulus (E_T) based on the true stress of a thread at the point of breaking: $E_T = S_T/(\mathrm{d}L/L_0)$, where d$L$ = difference between the initial and final lengths of a thread. The values of thread extensibility are taken from Opell and Bond (2000) and were measured from the same webs from which the tensile strength of capture threads was measured.

Breaking energy

Breaking energy (BE) was computed as $\mathrm{BE} = F \times D/V$, where F = the force in Newtons required to break a thread, D = the distance over which the thread stretched before it broke and V = the volume of the thread.

Web features

Values for spiral spacing and capture area were taken from Opell (1999a) and for capture area per radius from Opell and Bond (2000). Web parameters were not available for *Neoscona hentzii*. The number of radii per spiral turn was determined from the web photographs used in these two studies. Values of this index are (mean ± 1 standard error, sample size): *Araneus marmoreus* 0.73 ± 0.03, 13; *Cyclosa conica* 1.64 ± 0.09, 17; *Argiope trifasciata* 1.10 ± 0.04, 22; *Micrathena gracilis* 1.17 ± 0.04, 20; *Leucague venusta* 0.99 ± 0.06, 15; *Ocotonoba sinensis* 2.98 ± 0.12, 23; *Uloborus glomosus* 2.79 ± 0.12, 27; *Waitkera waitakerensis* 2.32 ± 0.09, 25. Spiral spacing is an index of spiral density. The greater this index, the fewer the spirals that an insect will strike and the greater the stress that each spiral will experience. Capture area is a measure of a web's ability to intercept prey. It is the area of a web occupied by a web's capture threads and is computed by subtracting the area inscribed by the web's innermost capture spiral from that inscribed by its outermost capture spiral. Capture area per radius and radii per capture spiral turn are indices of how well a web's capture threads are supported. Webs with small values for area per radius and large values for radii per capture spiral are better supported by radii and, consequently, their capture spirals will experience less stress than those of webs with greater area per radius and smaller radii per capture spiral indices.

Phylogenetic analysis

Relationships between spider mass or web architecture and the mechanical properties of capture threads could compromise the comparisons between cribellar and adhesive capture threads that we wish to make. Therefore, we sought to uncover these relationships using the comparative method. We examined associations between the five independent variables of spider mass, spiral spacing, capture area, radii per spiral turn and capture area per radius and the three dependent variables of tensile strength, Young's modulus and breaking energy. *Neoscona hentzii* was excluded from this analysis because its web features were not measured. In these analyses, the mechanical properties of cribellar threads are computed from the cross-sectional areas of their axial fibres and half of their cribellar fibrils. As species interrelationships are 'manifestly nonindependent' (Felsenstein, 1985), it is inappropriate to examine these relationships with traditional regression techniques. Therefore, we used the Comparative Analysis of Independent Contrasts program of Purvis and Rambaut (1995) to compute normally distributed independent contrast values.

We also estimated the values of tensile strength, Young's modulus and breaking energy for a hypothetical ancestor at the base of the tree consisting of the nine species that were studied (Fig. 3). For this we used the rooted minimized sum of squared changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison and Maddison, 1992). We then computed the changes from these ancestral values to those of each extant species and compared the mean changes of each index for cribellate and adhesive threads. For all statistical analyses we used programs of the SAS Institute, Inc.

RESULTS

Table 1 presents data used to compute mechanical properties of the nine species included in this study. Table 2 gives the cross-sectional areas of the cribellar fibrils of uloborid species used to adjust the indices of these species. Figures 4–6 present the mean tensile strengths, Young's moduli and breaking energies of each species' capture thread.

Phylogenetic analyses

Regression analyses of independent contrast values showed that neither spider mass nor the four indices of orb-web architecture were related to the mechanical properties of capture threads ($n = 7$, $F = 0.00$–3.91, $P = 0.950$–0.105).

Interspecific comparisons

Having found no evidence that either spider mass or web architecture is related to the tensile strength, Young's modulus or breaking energy of a web's capture threads, we examined the

Table 2. Number of cribellar spigots and diameter of cribellar fibrils for uloborid species[a]

Species	Number of cribellar spigots	Diameter of cribellar fibrils (nm)	Total cross-sectional area of cribellar fibrils (μm^2)
Octonoba sinensis	3905	10.1	0.313
Uloborus glomosus	4717	10.4	0.401
Waitkera waitakerensis	4098	10.7	0.368

[a] Spigot number is taken from Opell (1996) and is equated with the number of cribellar fibrils in a species' capture thread. Cribellar fibril diameter is the internodal (minimal) diameter of cribellar fribrils and is taken from Opell (1994).

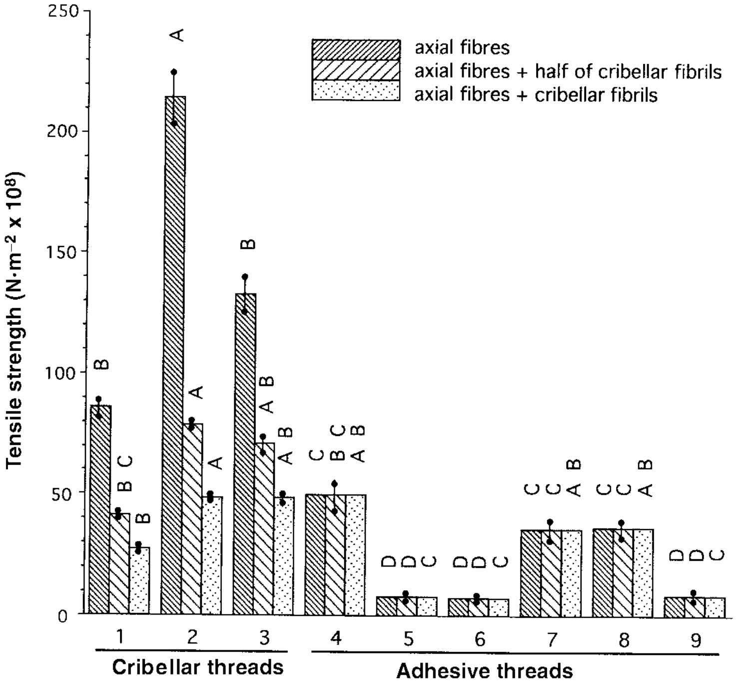


Fig. 4. Comparison of the tensile strengths of cribellar and adhesive threads. Species are identified by numbers given in Fig. 3. Error bars represent ± 1 standard error. Letters refer to similar mean values, as determined for Log $_n$ tensile strength by a Ryan Q-test with an alpha of 0.05.

alternative hypothesis that there is a phylogenetic difference in the mechanical properties of the capture threads of deinopoid and araneoid orb-weavers. We compared the mean change from ancestral values for cribellar and adhesive threads and the mean values of cribellar and adhesive threads. We also ranked the mean values of the nine species.

We report the mechanical properties of capture threads computed under three assumptions: (1) axial fibres alone are responsible for thread properties; (2) for cribellar threads,

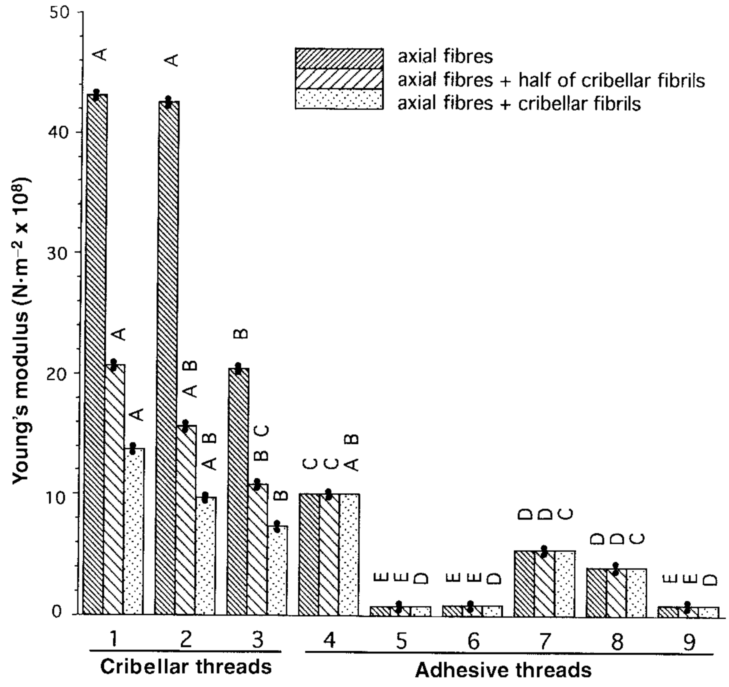


Fig. 5. Comparison of the Young's moduli of cribellar and adhesive threads. Species are identified by numbers given in Fig. 3. Error bars represent ±1 standard error. Letters refer to similar mean values, as determined for Log $_n$ Young's modulus by a Ryan Q-test with an alpha of 0.05.

both axial fibres and cribellar fibrils are responsible for these properties; and (3) for cribellar threads, axial fibres and half of the cribellar fibrils are responsible for these properties (Figs 4–6). There are no data on the proportion of the cribellar fibrils that remain intact as a cribellar thread is stretched to different lengths. Scanning electron microscope images show that some cribellar fibrils often unravel and break when a thread is stretched slightly as it is being prepared for study, so it is clear that not all of the fibrils contribute to a thread's mechanical properties. Therefore, we believe that values based on the assumption that half of the fibrils are present when the thread breaks are somewhat conservative but probably the most appropriate for interspecific comparisons.

For cribellar thread, the mean change from ancestral tensile strength (Fig. 3) was 17.0 $N \cdot m^{-2} \times 10^8$ and for adhesive thread −22.4 $N \cdot m^{-2} \times 10^8$, a difference that was shown to be significant by a Kruskall-Wallis test ($H = 4.267$, $P = 0.039$). For Young's modulus, these changes (2.9 and −8.9 $N \cdot m^{-2} \times 10^8$, respectively) were also significantly different ($H = 5.445$, $P = 0.020$). However, for breaking energy, these changes (14.4 and −16.2 $J \cdot m^{-3} \times 10^8$, respectively) did not differ ($H = 2.400$, $P = 0.121$).

These differences are also reflected by comparisons of the mean values of cribellate and adhesive species. Mean tensile strength values (63.5 and 24.2 $N \cdot m^{-2} \times 10^8$, respectively) differed ($H = 4.267$, $P = 0.039$), as did mean Young's modulus values (15.7 and

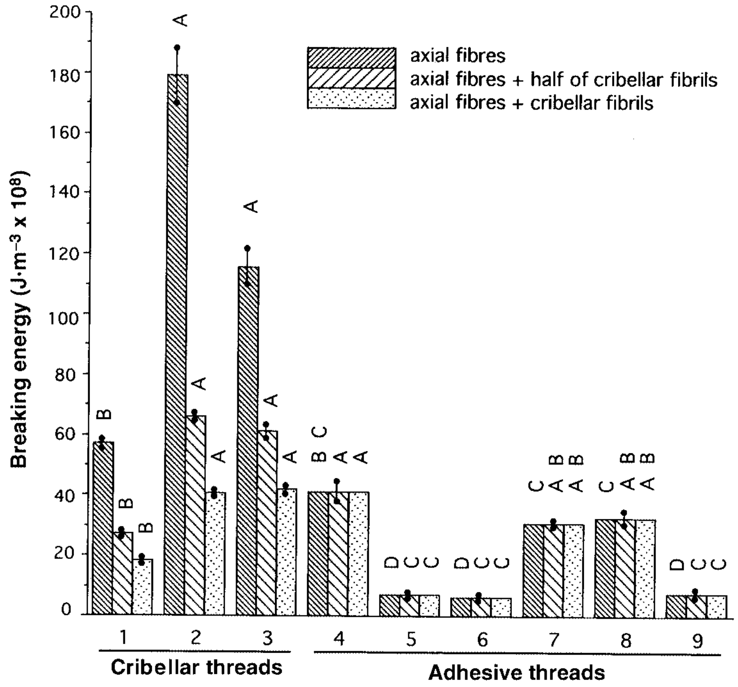


Fig. 6. Comparison of the breaking energy of cribellar and adhesive threads. Species are identified by numbers given in Fig. 3. Error bars represent ±1 standard error. Letters refer to similar mean values, as determined for Log $_n$ breaking energy by a Ryan *Q*-test with an alpha of 0.05.

3.7 $N \cdot m^{-2} \times 10^8$, respectively; $H = 5.445$, $P = 0.020$). However, mean values for breaking energy (51.5 and 21.0 $J \cdot m^{-3} \times 10^8$, respectively) did not differ ($H = 2.400$, $P = 0.121$).

Shapiro-Wilk tests show that, for some of the nine species, tensile strength, Young's modulus and breaking energy were not normally distributed ($P < 0.05$). However, all values became normal when log-transformed. Therefore, all of the interspecific comparisons presented in Figs 4–6 and discussed below are based on log-transformed data.

Analyses of variance (ANOVA) showed significant interspecific differences between tensile strength, Young's modulus and breaking energy ($F > 46.78$, $P = 0.0001$) computed under each of the three assumptions described above. Using Ryan-Einot-Gabriel-Welsch multiple range tests (alpha = 0.05; Day and Quinn, 1989), we ranked the tensile strengths, Young's moduli and breaking energies of the nine species (Figs 4–6). When only the axial fibres of cribellar threads were considered, the values of cribellar threads were greater than those of adhesive threads. However, as cribellar fibrils are considered to play a greater role, the values of cribellar threads became more similar to those of the adhesive threads, particularly to the threads from the vertical orb-webs of *L. venusta*. These comparisons show that cribellar threads tend to be strong but stiff, as indicated by high values for both tensile strength and Young's modulus, and that adhesive threads, particularly those from vertical orb-webs, are weak but elastic (Figs 4–6). The breaking energies of cribellar and adhesive threads were not very different.

DISCUSSION

Previous studies have shown that the transition from cribellar to adhesive capture thread was marked by changes in the light-reflecting properties of threads, the mechanism by which stickiness is achieved and the material economy with which this stickiness is achieved (see Bond and Opell, 1998, for a summary). As summarized in Fig. 7, this study shows that the origin of adhesive capture threads was also accompanied by changes in the mechanical properties of these threads. Cribellar and adhesive capture threads resist breaking in different ways, although they have similar breaking energies. Cribellar threads are strong but stiff, whereas adhesive threads are weaker but more extensible. Adhesive threads are better equipped to absorb energy through stretching, a characteristic that is advantageous for vertical orb-webs. Our failure to find a direct association between the mechanical properties of capture threads and either spider mass or features of web architecture indicates that these differences in thread properties cannot be explained simply as ecological differences common to all orb-weavers. Instead, the features of adhesive threads must be characterized as adaptations of the Araneoidea, following the reasoning of Coddington (1988, 1990a, 1994) and Baum and Larson (1991) that defines an adaptation as an apomorphic character that appears to have a positive selective value for a particular selective regime when compared to the plesiomorphic condition.

Our finding that the cross-sectional area of axial fibres is not related to a thread's mechanical properties is not surprising given Craig's proposal that the molecular properties

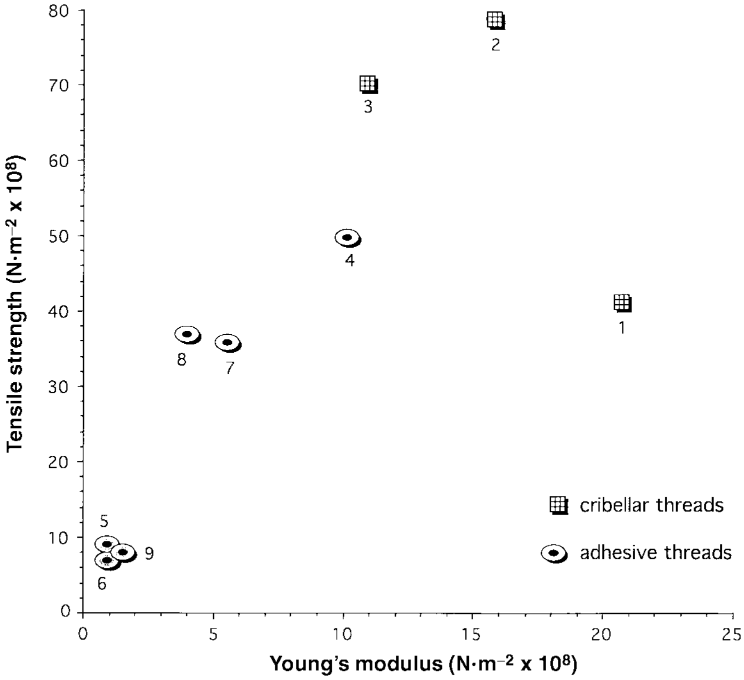


Fig. 7. Comparison of the tensile strengths and Young's moduli of cribellar and adhesive threads. Points are identified by the species numbers given in Fig. 3.

of threads differ among species in ways that alter their functional properties and their cost of production (Craig, 1992, 1997; Craig and Weber, 1998; Craig *et al.*, 1999). We found a dichotomy among araneoid species that construct vertical orb-webs: The threads of *C. conica* and *N. hentzii* have greater tensile strengths, Young's moduli and breaking energies than those of *A. trifasciata*, *M. gracilis* and *A. marmoreus*. *Cyclosa conica* has the smallest capture area per radius value and the largest radii per spiral value among the six araneoid species whose web features were measured. Thus, the orb-webs of *C. conica* are what Craig (1987) characterizes as 'high energy absorbing webs' by virtue of having a higher radius-to-spiral ratio. This species may rely more on web strength than on web flexibility for absorbing the force of a prey strike.

Craig (1987) also noted that the webs of *Cyclosa caroli* have many radii, but found that this was not correlated with the kinetic energy of the prey that these webs typically intercepted. She attributed this high radius-to-spiral ratio to these spiders suspending their egg sacs and prey remaining in a line that passes through the web's hub, a practice that is 'important to the provision of a protected site for the spider's egg sacs'. An increase in the number of radii would not appear to protect or camouflage the egg sacs along a spider's stabilamentum. However, the presence of this linear stabilamentum may constrain overall web extensibility, thereby requiring these webs to rely more heavily on thread strength than on aerodynamic dampening to resist forces generated by prey strikes.

The mechanical properties of adhesive threads from the horizontal orb-webs of *L. venusta* are intermediate between those of other adhesive threads and those of cribellar threads. We attribute similarities in the adhesive threads of *L. venusta* and cribellar threads to the derived horizontal orientation of *L. venusta* orb-webs. This apparent shift in the mechanical properties of these adhesive threads provides additional compelling evidence that the conclusions drawn from this study are plausible. Our conclusions predict that the capture threads of horizontal webs are strong and stiff, whereas those of vertical webs are weaker but more elastic.

This study models capture threads as simple elastic fibres and measures their tensile strengths, Young's moduli and breaking energies at their points of failure. Both cribellar and adhesive threads dissipate force through the extensibility of their axial fibres, but each also appears to employ a different ancillary mechanism. When a cribellar thread is stretched, its outer fibrils unravel, create friction as they rub and snag on one another, and eventually break as force sufficient to cause failure of the axial fibres and remaining cribellar fibrils is generated. When an adhesive thread is deposited, a thin film of aqueous material extends between droplets to completely cover the axial fibres, causing these fibres to supercontract (Work, 1985). When these threads are partially restrained in an orb-web, their supercontraction is limited and they are under retractive tension. Force is dissipated as an adhesive thread's axial fibres are stretched to a length equivalent to their dry length. Thus, it appears that the mechanical properties of capture threads have been affected by the orientation of orb-webs, the molecular structure of axial fibres and the performance of ancillary mechanisms that resist thread elongation.

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