1993. The Journal of Arachnology 21:161–174

ULTRASTRUCTURE OF CRIBELLATE SILK OF NINE SPECIES IN EIGHT FAMILIES AND POSSIBLE TAXONOMIC IMPLICATIONS (ARANEAE: AMAUROBIIDAE, DEINOPIDAE, DESIDAE, DICTYNIDAE, FILISTATIDAE, HYPOCHILIDAE, STIPHIDIIDAE, TENGELLIDAE)

William Eberhard: Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica; Cuidad Universitaria, Costa Rica

Flory Pereira: Escuela de Biología, Universidad de Costa Rica, Sede del Atlántico, Costa Rica

ABSTRACT. The ultrastructure of cribellum silk and associated fibers is described for nine species in eight families, and data from studies of 22 other species are summarized. Possible synapomorphies for filistatids (flattened cribellum fibers), for all cribellates other than hypochilids + filistatids (nodules on cribellum fibers), for deinopids + uloborids + dictynids, and for uloborids + dictynids (loss of reserve warp fibers) are described. Filistatid silk is distinctive and especially complex, and the spatial arrangement of different components is described for the first time.

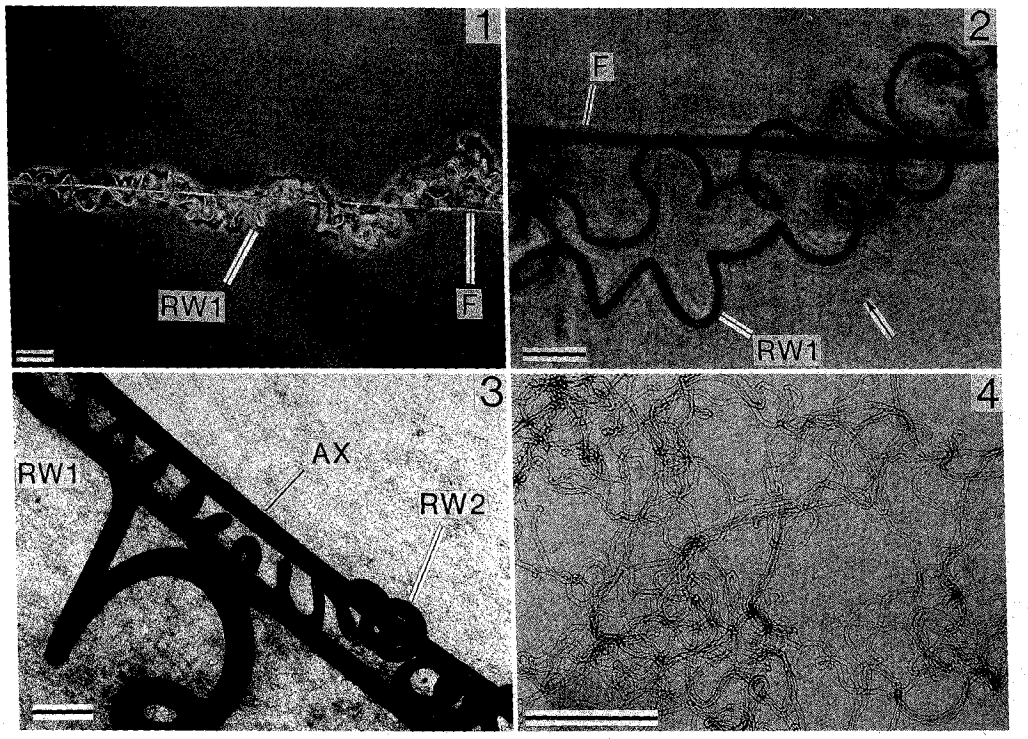
RESUMEN. Se describe la ultraestructura de la seda del cribelo y las fibras asociadas con ella de nueve especies en ocho familias, y se resumen además los datos de 22 otras especies. Se destacan posibles sinapomorfias para filistatidos, para todos los cribelados menos hypochilidos y filistatidos, para dinopidos + uloboridos + dictynidos, y para uloboridos + dictynidos. La seda de los filistatidos es especialmente distinctiva, y la ubicación espacial de los diferentes componentes de ella se describe por primera vez.

Nonviscous adhesive silk is produced by cribellate and some sicariid spiders. The ultrastructure of this silk and the lines associated with it have been described in six different families (Filistatidae, Uloboridae, Deinopidae, Eresidae, Oecobiidae, and Amaurobiidae), using both the light microscope and the scanning and transmission electron microscopes (Comstock 1948; Lehmensick & Kullmann 1957; Friedrich & Langer 1969; Kullmann 1970, 1975; Zimmermann 1975; Opell 1979, 1989a; Peters 1987, 1992a-c). This paper describes the cribellum silk and associated lines of species in five additional families, Desidae, Dictynidae, Hypochilidae, Stiphidiidae, and Tengellidae, and from additional species of Amaurobiidae, Deinopidae, Filistatidae and Uloboridae. We review data on the distribution of several characteristics of cribellum fibers and associated lines. Some characters are apparently consistent within taxonomic groups, and may be useful in systematic studies.

METHODS

No single technique is adequate for studying the complex arrays of fine fibers and lines in cribellate adhesive threads. The light microscope is incapable of resolving finer fibers, while the harsh preparation techniques and observation conditions of both the transmission electron microscope (TEM) and the scanning electron microscope can seriously distort arrays of silk (Peters 1987, 1992a). Both light microscope and TEM were used in the present study.

Silk was collected in the field from webs of mature or nearly mature females, using microscope slides to which three or four square plexiglass rods had been glued (Opell 1989b). The upper surface of each rod was covered with double-sided sticky tape. The web was pressed against the tape, taking care to minimize stress on threads between the rods, and scissors were used to cut the threads connecting the sample to the rest of



Figures 1–4.—Mature female *Hypochilus thorelli*: 1, Mass of cribellum fibrils (barely visible) and highly coiled primary reserve warp (RW1) laid on a foundation line (F) (light microscope); 2, same, with arrow showing edge of cloud of cribellum fibrils (light microscope); 3, one pair of straight axial lines (AX) and two highly curled reserve warp lines of different diameters (RW1, RW2), with fibrils in the background (TEM); 4, cylindrical cribellum fibrils lacking nodules (TEM). Note that fibril diameters do not vary along their lengths (compare with Fig. 9 of *Kukulcania*). Scale lines are, respectively, 50μ, 20μ, 2.6μ, and 0.5μ.

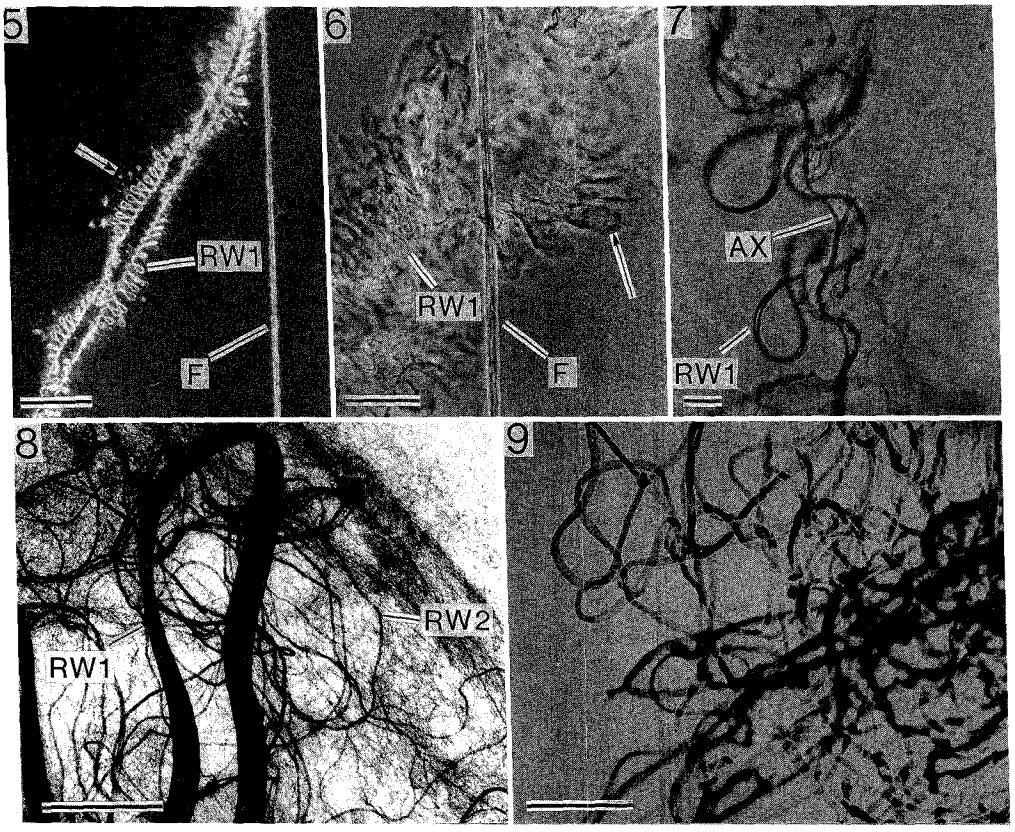
the web. Most observations with the light microscope were made on these slides.

Samples of silk for TEM study were carefully placed on untreated grids under a dissecting microscope, taking care to avoid stressing threads. None of the silk samples were coated or treated in any way before being examined. The silk of *Hyptiotes thorelli* Marx had been stored in sealed containers for 2–3 years; that of the other species was fresher (less than about six weeks old).

The terms "fiber" and "fibril" are used for the smallest units of silk (single cylinders); "line" refers to a combination of fibers of the same type running in parallel; "thread" and "band" refer to combinations of fibers and lines of different types. "Cribellum fibers" are presumed to emerge from the cribellum, while "cribellate" lines and threads ("calamistrated strands" of Peters 1987) contain cribellum fibers as well as other lines that presumably emerge from other spinnerets.

Terminology for different types of fibers and lines follows that of Peters (1987), with the exception that we have used the earlier, functionally descriptive term "reserve warp fibers" of Kullmann (1975) for the highly curled or undulating thicker fibers often associated with cribellum fibrils ("undulating fibers" and "U-fibers" of Peters 1987, 1992a). Identifications of different lines were based only on the morphology and location of the lines, so homologies are thus tentative. A straight or nearly straight fiber running in a pair (except when two separate cribellate threads were laid by a spider with a divided cribellum) in the midst of a mat of cribellum fibers was termed an axial fiber; curled fibers always in the midst of cribellum fibers, also generally in pairs, were termed reserve warp. Information on the glandular origins of different fibers, the spigots from which they emerge (e. g., Peters 1984, 1992a), and their chemical properties will be needed to establish more certain homologies.

Voucher specimens of the spiders are deposited in the Museum of Comparative Zoology



Figures 5–9.—Mature female *Kukulcania hibernalis*: 5, a pair of highly coiled primary reserve warp lines (RW1) and cribellum silk (barely visible) near a foundation line (F) to which they were attached (light microscope); 6, scalloped edge of mass of cribellum silk (arrow), primary reserve warp (RW1) and foundation line (F) composed of multiple fibers (light microscope); 7, "crinkled" axial line (AX) and primary reserve warp (RW1) in mass of cribellum fibrils (barely visible) (light microscope); 8, flattened primary reserve warp line (RW1) (note variation in diameter) and thinner secondary reserve warp lines (RW2) in mass of cribellum fibrils (TEM); 9, flattened cribellum fibrils (note that apparent diameters change where lines are folded (TEM). Scale lines are, respectively, 200μ, 100μ, 10μ , 5μ , and 0.3μ.

Cambridge, Massachusetts 02138. Collection sites for different genera were the following: *Hypochilus* - near Cullowhee, North Carolina, USA; *Kulkania*, *Tengella*, and *Dictyna* - near San Antonio de Escazu, Costa Rica; *Badumna* and *Paramatachia* - Lamington National Park, SW of Brisbane, Queensland, Australia; *Avella* and *Mahura* - Cape Tribulation, N of Cairns, Queensland, Australia; and *Stiphidium* - Gilles Highway W of Cairns near maximum elevation on way to Atherton, Queensland, Australia.

RESULTS

Table 1 summarizes our observations and those of other authors. More detailed descriptions of the species we studied follow.

Hypochilus thorelli Marx (Hypochilidae)—Observations with the light microscope revealed a more or less cylindrical mass of cribellum silk associated with a pair of linear axial fibers plus a pair of moderately coiled reserve-warp fibers (Figs. 1, 2). Additional, thinner secondary reserve warp fibers were revealed with the TEM (Fig. 3). The fibrils of cribellum silk were apparently cylindrical, and lacked nodules (Fig. 4).

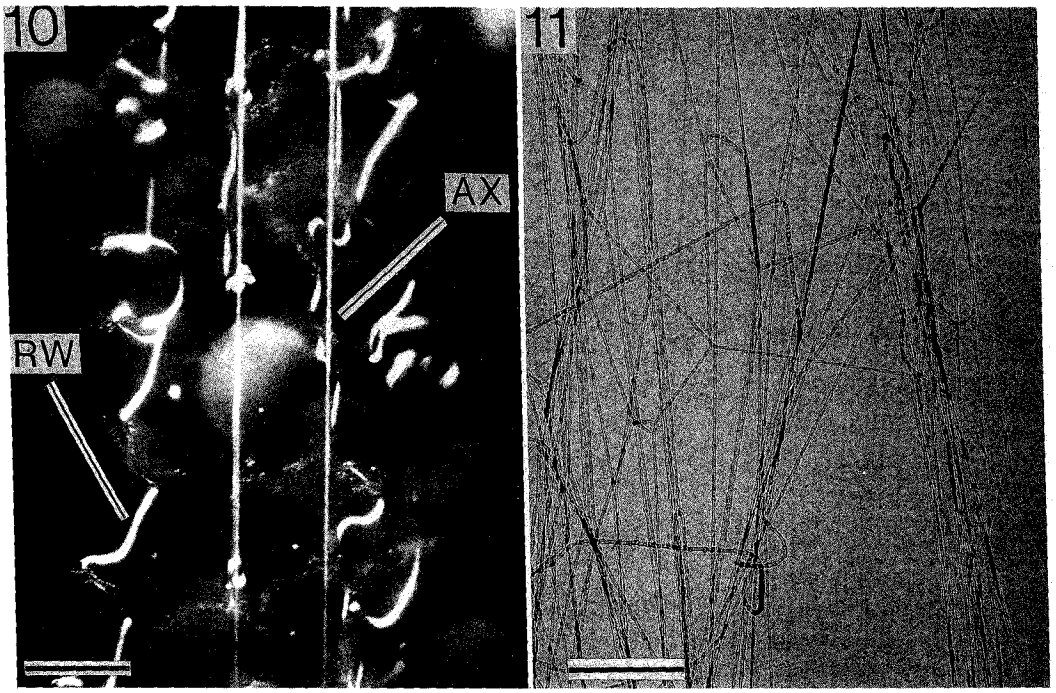
Kukulcania hibernalis (Hentz) (Filistatidae)—The band of cribellate silk was laid along a thick foundation line (Figs. 5, 6), to which it was attached periodically. The foundation line had multiple grooves (Fig. 6), suggesting it was composed of many different strands. The silk of the foundation line was unusual in being relatively rigid: when cut, the line did not sag or fold. The

Table 1.—Characteristics of cribellum silk and associated lines in 31 species of spider. (a) Type of microscope: LM = light microscope; TEM = transmission electron microscope; SEM = scanning electron microscope. (b) Fibrils: C = cylindrical fibril; R = flattened, ribbonlike fibril; N = nodules along fibril. (c) Number of pairs of lines. (cc) C = cylindrical lines; R = flattened fibers. (d) Thick lines of two different diameters present in photo, but their arrangement (coiled, straight, etc.) unknown. (e) Opell 1979. (f) Eberhard 1972 for building behavior. (h) Eberhard 1982 for building behavior. (i) No direct observations, but builds typical orb—Wiehle 1928. (j) Marples & Marples 1937 for building behavior. (l) No direct observations, but spider spins typical orb—Opell 1987. (m) Coddington 1986. (n) Eberhard unpubl. (o) Eberhard unpubl. (p) Inclusion of this genus in Amaurobiidae is somewhat uncertain—R. Forster pers. commun.

Taxon	Type of microscope (a)	Fibrils (b)	Foundation line	Reserve warp (c)	Reserve warp (cc)	Axiall lines?	Puffs?	References
Hypochilidae								
Hypochilus thorelli	LM, TEM	C	?	≥2		yes	no	this study
Filistatidae								
Filistata insidiatrix	LM, TEM	R	Yes	1	C	yes?	no	Lehmensick & Kullman 1956; Peters 1987
Kukulcania arizonicus	TEM	R	?	≥2? (d)		?	?	Friedrich & Langer 1969
K. hibernalis	LM, TEM	R	yes	≥2?	R	yes? (2)	no	Comstock 1948; this study
Uloboridae								
Zosis plumipes	TEM	C + N	no (e)	?		?	?	Peters 1987
Uloborus diversus	LM, TEM	C + N	no (f)	0		yes	yes	Friedrich & Langer 1969
U. walckenaerius	LM, TEM	C + N	no	0		yes	yes	Peters 1987
U. penicillatus	SEM, TEM	C + N	no (h)	?		yes	yes	Opell 1979
U. plumipes	LM, TEM	C + N	no (i)	0		yes	yes	Peters 1984
U. sp. (Cairns, Aust.)	LM		no	0		yes	yes	this study
Polenecia producta	LM	C + N	yes	0		yes	yes?	Peters 1983, 1987
Miagrammopes sp.	LM	C + N	yes	0		yes	yes	Peters 1987
M. animotus	LM, SEM	?	yes	0		yes	yes	Opell 1989b
Hyptiotes paradoxus	LM, SEM	C + N	no (j)	0		yes	yes	Lehmensick & Kullmann 1956
H. cavatus	SEM	?	no (k)	?		yes	yes	Opell, Roth, & Cushing 1990
Tangaroa beattyi	SEM	?	no? (1)	?		?	yes	Opell 1989b

Table 1.—Continued.

Taxon	Type of microscope (a)	Fibrils (b)	Foundation line	Reserve warp (c)	Reserve warp (cc)	Axial lines?	Puffs?	References
Deinopidae								
Deinopus sp.	SEM	?	no (m)	1		yes	yes	Kullman 1975
D. subrufus	LM, SEM, TEM		no	1		yes	yes	Peters 1992c
Avella sp.	LM, TEM	C + N	no	1	C	yes	yes	this study
Eresidae								
Stegodyphus lineatus	LM	?	no/yes	4		yes	no (?)	Kullmann 1975; Peters 1987, 1992a
S. mimosarum				"several"		yes	?	Kullmann 1970
S. sarasinorum	LM, TEM	?	no (n)	3		yes	no	Kullman 1975
S. dumicola	LM, SEM	?	no/yes	3		yes		Peters 1992a
Seothyra henscheli	LM, TEM, SEM	?	no		C	yes	?	Peters 1992b
Oecobiidae								
Oecobius annulipes	TEM	C + N		1				Zimmerman 1975
Amaurobiidae								
Amaurobius sp.	LM			1 or 2		yes		Comstock 1948
A. sp.	TEM	C + N						Foelix 1982
Mahura sp. (p)	LM, TEM	C + N	no	1	C	no	?	this study
Tengellidae								
Tengella radiata	LM, TEM	C + N	no (o)	2		yes	no	this study
Dictynidae								
Dictyna sp.	LM, TEM	C + N	no/yes	0		no	yes	this study
Stiphidiidae								
Stiphidium sp.	LM, TEM	C + N	no	1	C	yes	no/yes	this study
Desidae								
Badumna sp.	LM, TEM	C + N	no	1		yes	no	this study
Paramatachia decorata	LM, TEM	C + N	yes	0		no	"yes"	this study



Figures 10–11.—Mature female *Tengella radiata*: 10, flat mass of cribellum fibrils (barely visible), with a pair of straight axial lines (AX) and a pair of folded reserve warp lines (RW) (light microscope); 11, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, and 0.5μ.

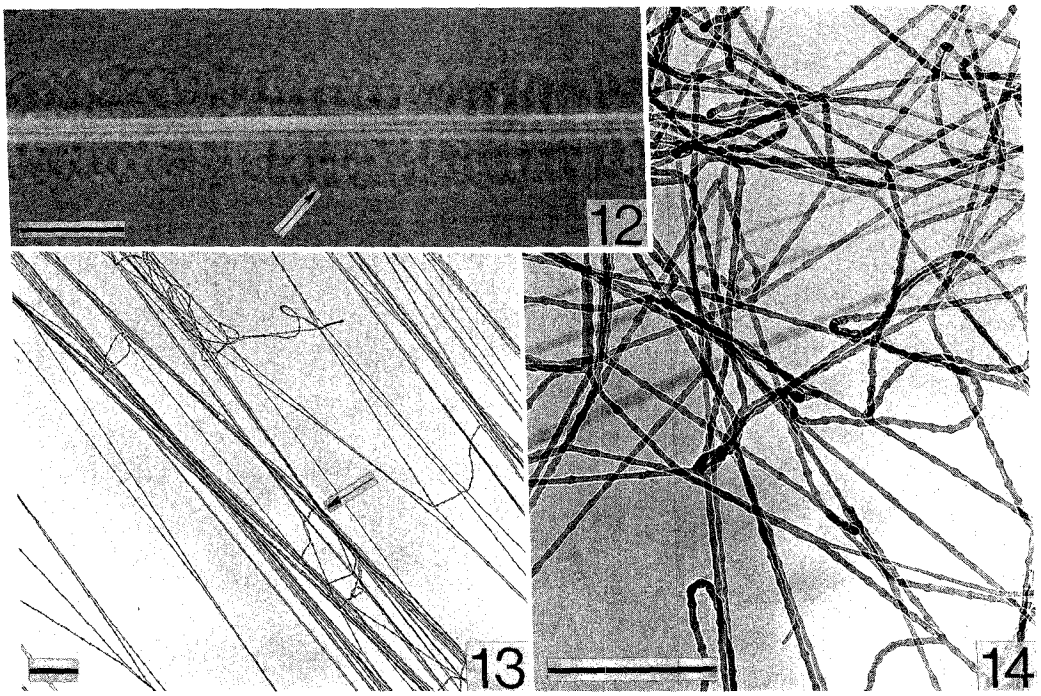
foundation line was laid as the spider moved away from its retreat, and the cribellum silk and associated fibers were laid during the return trip (Eberhard 1988). In some places the band of cribellate silk was more or less linear (Fig. 5), but more often it was piled up or coiled on itself, forming irregular loops.

The internal structure of the band was complex. Under the light microscope a more or less looped and folded pair of helical fibers was seen (the helix is relatively extended in Fig. 5), with the mass of cribellum fibrils visible as a faint cloud (Figs. 5–7). Within each helix, a relatively thick, smooth primary reserve warp fiber was curled in a highly regular fashion that included a series of short, more or less straight basal portions alternating with longer loops (Figs. 5, 7). Each loop was oriented in nearly the same direction as the previous one. The axial line, which was thinner and apparently somewhat crinkled, ran near and approximately parallel to the straight basal portions of the loops of the primary reserve warp fiber (Fig. 7).

Under the TEM, the primary reserve warp proved to be flattened and ribbon-like, rather than cylindrical (Fig. 8). The axial line was seen to consist of a pair of lines, with the "crinkles" consisting of portions where one fiber was curled helically around the other. Additional, finer secondary reserve warp fibers (number uncertain) were folded loosely and irregularly in the area of the loops of primary reserve warp (Fig. 8). The cribellum fibrils were smooth and ribbon-like, rather than cylindrical (Fig. 9). They lacked the nodules seen in the silk of many other species (Table 1).

Tengella radiata (Kulczynski) (Tengellidae)—A more or less flat mat of cribellum silk lay on or around a pair of axial fibers plus a pair of kinked or somewhat curled reserve-warp fibers (Fig. 10) which were produced at the same time as the cribellum silk. The edges of the mat were not regularly scalloped, and the reserve warp fibers appeared to be cylindrical. The mat twisted from side to side as a relatively rigid unit in weak air currents under the light microscope. The fibrils of cribellate silk were apparently cylindrical, with many small nodules scattered along their lengths (Fig. 11).

Dictyna sp. (Dictynidae)—The cribellum silk formed a relatively flat mat with regularly scalloped edges (Fig. 12). In some cases the mat was



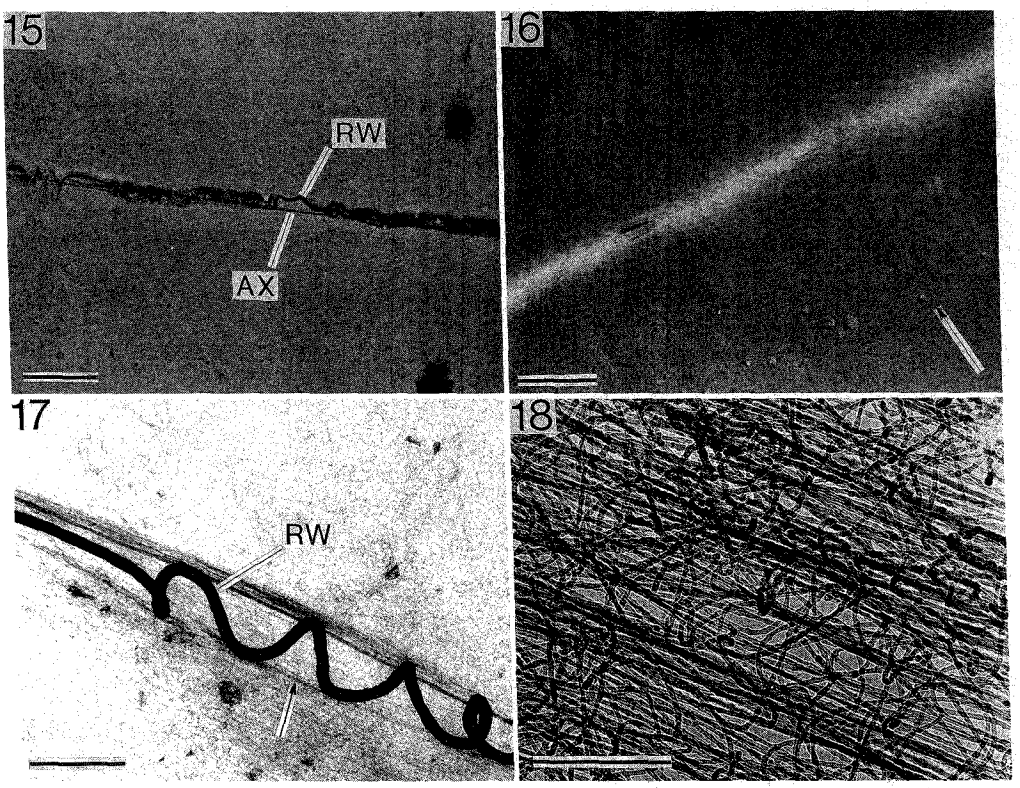
Figures 12–14.—Mature female *Dictyna* sp.: 12, mat of cribellum silk with scalloped edges (arrow) laid along a foundation line (light microscope); 13, cribellum fibrils clumped together in places to form cables (arrow) (TEM); 14, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, 1μ, and 1μ.

laid on a relatively thick foundation line (Fig. 12), while in others there was no foundation line. Careful searches using the TEM showed that there were neither axial nor reserve warp lines. Under the light microscope a pair of darker lines were sometimes visible in the central portion of the mat of cribellum fibers, but these presumably corresponded to cables composed of accumulations of cribellum fibrils (Fig. 13). Cribellum fibrils were cylindrical, with nodules along their length (Fig. 14).

Stiphidium sp. (Stiphidiidae)—The non-planar mass of cribellum fibrils was not laid along a foundation line (Fig. 15), and did not have a regularly scalloped outline (Fig. 16). Associated with the cribellum silk were a pair of straight, apparently cylindrical axial fibers and a pair of curled, cylindrical reserve warp fibers (Figs. 15, 16). The cylindrical reserve warp was curled tightly for short stretches which alternated with stretches of similar lengths in which it was relatively uncurled (Figs. 15–17). The cribellum fibrils were cylindrical, with nodules (Fig. 18).

Badumna sp. (Desidae)—In places two mats of cribellate silk ran in close parallel, presumably the product of the divided cribellum; in other places they were farther apart. The lateral outlines of mats were not regularly scalloped (Fig. 19). Each mat had a straight, relatively thin axial fiber, and a cylindrical reserve warp fiber in which the degree of coiling varied (Figs. 19–21). The cribellum fibrils were cylindrical, with nodules (Fig. 22).

Paramatachia decorata (Dalmas) (Desidae)—The lateral outlines of mats of cribellum silk were often regularly scalloped, although the thickenings ("puffs") often did not occur at the same point on either side of the mat (Fig. 23). Mats of cribellate silk were usually but not always associated with foundation lines (Figs. 24, 25). When viewed with the light microscope a pair of straight axial fibers seemed to be present (Fig. 23), but no reserve warp fibers were seen. In some places the mat of cribellum fibrils was coiled on the axial line. Neither axial nor reserve warp fibers were found using the TEM, however. Over short stretches, cribellum fibrils came together to form cables which gave the false impression of thicker fibers (Fig. 25), but these differed from the axial fibers seen in the light microscope in being only relatively short. It appears that axial fibers were absent from some samples, but it is



Figures 15–18.—Mature female *Stiphidium* sp.: 15, straight axial line (AX) and reserve warp line (RW) with alternating highly curled and straighter regions (light microscope); 16, same, showing non-scalloped edge of mat of cribellum fibrils (arrow) (light microscope); 17, curled cylindrical reserve warp line (RW) with cribellum fibrils, some of which clump together to form cables (arrow) (TEM); 18, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, 100μ, 5μ, and 0.5μ.

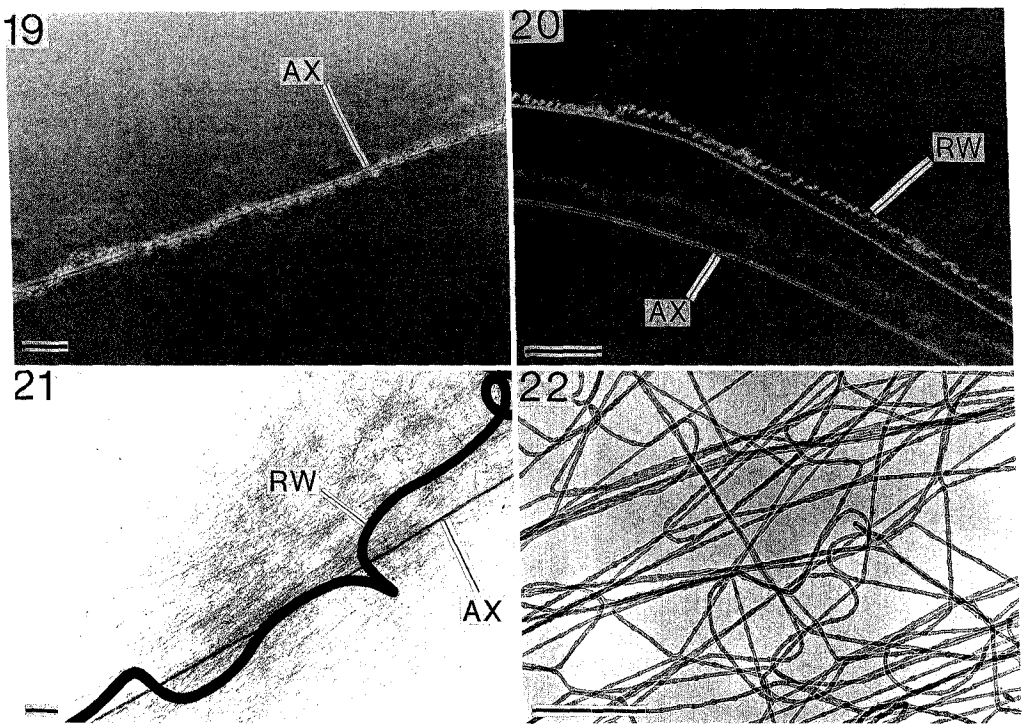
uncertain whether they were present in others. The cribellum fibrils were cylindrical, with nodules (Fig. 26).

Mahura sp. (Amaurobiidae)—Many mats of cribellate silk in the sheet of this spider's web were composed of parallel double bands, presumably due to the divided cribellum. In contrast, mats of cribellate silk in the mesh above the sheet were usually single. Each cribellate mat collected from the sheet had a single cylindrical reserve warp fiber, which was alternately tightly coiled and relatively uncoiled (Fig. 27). Axial fibers were not clearly visible in the light microscope (appearing to be present only in short stretches), and no axial lines were seen with the TEM. In places cribellum fibrils came together to form cables, and presumably these were the "axial fibers" seen in the light microscope. Cribellum fibrils were cylindrical, with nodules (Fig. 28).

Avella sp. (Deinopidae)—The lateral margins of each mat of cribellum silk were strongly scalloped (Fig. 29). A pair of linear axial fibers and a pair of loosely coiled, cylindrical reserve warp fibers ran through the central portion of the mass (Figs. 29, 30). Cribellum fibrils were cylindrical, with nodules (Fig. 31).

DISCUSSION

The data available to date suggest that some ultrastructural characteristics of cribellate capture silk are relatively constant within and between taxa (Table 1). The consistency is especially clear in the cylinder plus nodule structure of cribellum fibrils, and the lack of reserve warp fibers in the best studied family, Uloboridae. It should be born in mind that the changes in cribellum fibril morphology in the TEM (electron bombardment in a vacuum) are not known. Thus the morphology of fibrils described here may differ from that of fibers under normal conditions. The tentative nature of homologies of the lines

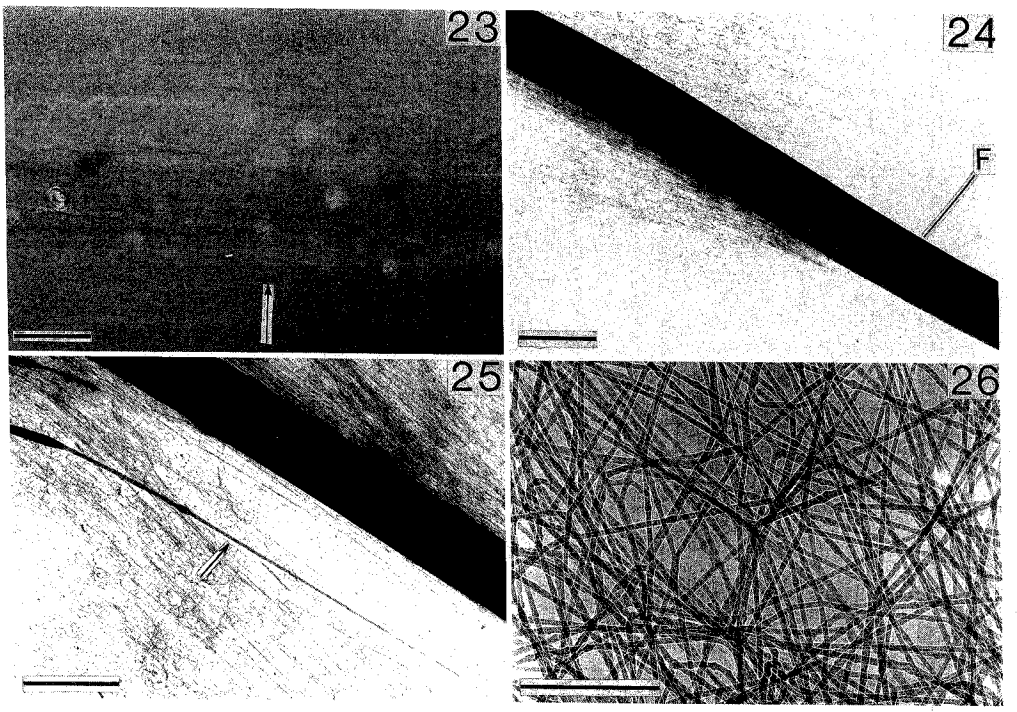


Figures 19–22.—Mature female *Badumna* sp.: 19, mat of cribellum fibrils with irregularly scalloped edges, axial lines (AX), and curled reserve warp line (light microscope); 20, pair of axial lines (AX) and pair of alternately curled and uncurled reserve warp lines (RW), with a more regularly scalloped mat of cribellum fibrils (light microscope); 21, curled cylindrical reserve warp line (RW) and straight axial line (AX) with cribellum fibrils (TEM); 22, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 150μ, 100μ, 2μ, and 0.5μ.

associated with cribellum silk should also be kept in mind.

While much more data need to be gathered to determine whether the patterns of distribution will hold up, it may be useful to attempt a tentative comparative analysis. If one superimposes the data on silk ultrastructure on a recently proposed pylogeny of cribellate spiders (Coddington & Levi 1991), several hypotheses result (Fig. 32): 1. Ribbon-like cribellum fibrils are a derived character of filistatids (*Filistata*, *Kukulcania*). 2. Nodules on cribellum fibrils are a synapomorphy linking all cribellates other than filistatids and hypochilids; 3. Lack of "reserve-warp" lines is a derived character, present in the single dictynid, one of the two desids, and all of the 12 uloborids. Since several details of web construction behavior link Uloboridae and Deinopidae (which has reserve warp fibers), the loss either occurred independently in Uloboridae and Dictynidae (Fig. 32) (with subsequent reacquisition of both axial and reserve warp lines in *Badumna* and loss of axial fibers in *Mahura*), or dictynoids are the sister group of uloborids + deinopids, and deinopids and *Badumna* secondarily re-acquired reserve warp lines (with a loss of axial lines in dictynoids and *Mahura*).

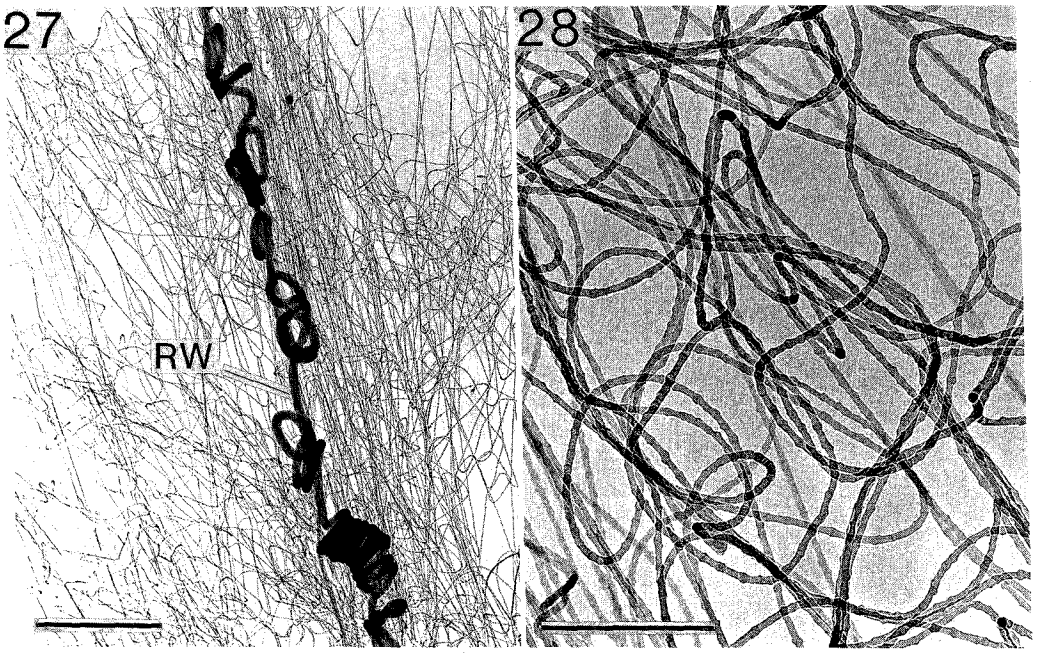
An additional character, noted by other authors, is the scalloped outline of the mass of cribellate silk ("puffs"), which may unite Uloboridae, Deinopidae, Dictynidae and the desid *Paramatachia* (in at least some uloborids, a puff is actually shaped more nearly like a twisted torus). This character may be somewhat less useful, however, since: 1) intermediate degrees of "scalloping" occur (e. g., Figs. 12, 20, 23), and it is not clear how regular scalloping must be to be condsidered a puff; and 2) some uloborid mats are only barely scalloped (Peters 1984, 1987). We were unable to confirm the presence of paracribellar fibrils (Peters 1984, 1987) in any of our species (unless they correspond to the "cables" of cribellum fibrils seen in *Dictyna*, *Paramatachia*, and *Mahura*).



Figures 23–26.—Mature female *Paramatachia decorata*: 23, mat of cribellum silk with scalloped edges (arrow) (apparent axial lines are slightly out of focus except at right and left margens) (light microscope); 24, foundation line (F) to which cribellum silk was attached (note multiple fibers) (TEM); 25, foundation line with cables formed by multiple cribellum fibrils (arrow) (TEM); 26, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, 5μ, 5μ, and 0.5μ.

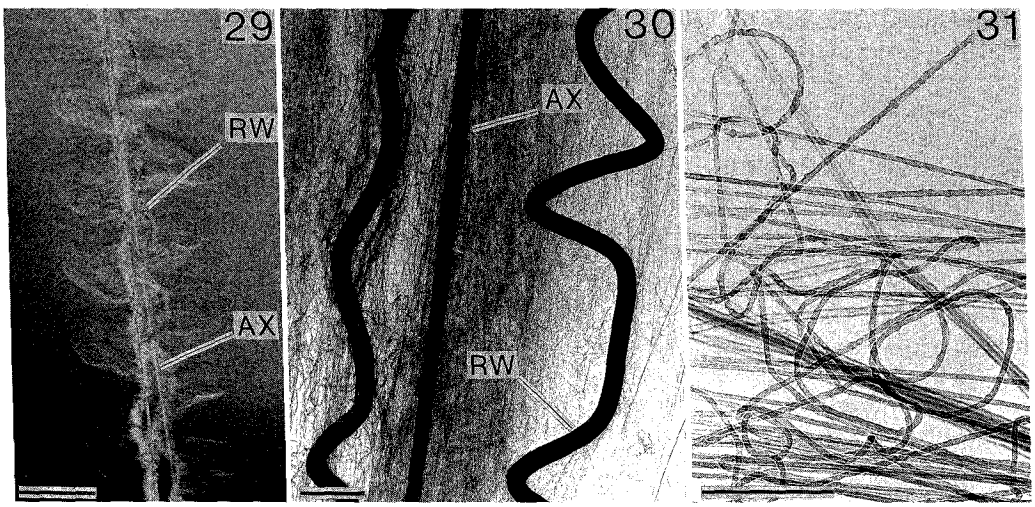
The positions of the fibers associated with cribellum silk help clarify some details of combing behavior. Assuming that spider silk is polymerized by being pulled (e. g., Foelix 1982), the presence of highly curled reserve warp fibers, which are presumably pulled out by strokes of the calamistrum and then fold or coil upon themselves, suggests that cribellum silk *per se* is piled on itself in the sticky threads of all species with curled reserve warp fibers. In some cases the tendency of reserve warp fibers to curl up may even cause clumping to occur. For instance, the secondary helices of *Filistata* and *Kukulcania* may result from curling of the axial fibers and/or the primary reserve warp lines. In species such as *Tengella radiata*, where the reserve warp fibers curl less, they appear to have little influence on the shape of the mass of cribellum fibrils. In both these groups (as well as in *Stegodyphus* - see Eberhard 1988), the spiders do not pull the cribellate silk threads taut in their webs. Rather, silk accumulates and sags free behind the spider as it is combed from the cribellum with the calamistrum. The thread is under no tension other than that resulting from its own weight and friction with air currents, and is actually often piled on itself in *Kukulcania* and *Stegodyphus* webs. Presumably when cribellum fibrils accumulate in this way, the force of adhesion is increased by bringing more silk surface into contact with the prey (Opell 1990). The effective length of the silk is probably also increased, making escape more difficult when the prey attempts to pull away.

Many authors have thought that each of the puffs in a mass of cribellum fibrils is produced by a single combing movement of the calamistrum (Eberhard & Langer 1969; Friedrich & Langer 1969; Opell 1979; Peters 1992c), but Peters (1984) attributed puffs to rhythmic clamping movements of the posterior spinnerets. The presence of many helical turns of reserve warp fibers between each pair of puffs in the sticky threads of *Deinopus* sp. and *Deinopus subrufus* (Kullmann 1975; Peters 1992c), and *Avella* sp. (this study) indicates that the second hypothesis is more likely. The combing movement necessary to produce a puff would be too short to pull out such lengths of reserve warp fiber.



Figures 27–28.—Mature female *Mahura* sp.: 27, reserve warp line (RW) which is more tightly curled in some places than others (TEM); 28, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 2μ and 0.5μ.

Similar reasoning indicates that combing movements of the calamistrum in many species are not responsible for pulling out axial fibers. The looped and tangled cribellar fibrils (presumably pulled by the calamistrum) are substantially longer than the axial fibers. Probably many axial fibers are pulled out as the spider moves away from the last attachment point. This mechanism is not possible, however, in spiders such as *K. hibernalis* and *Stegodyphus gregalis*, which do



Figures 29–31.—Mature female *Avella* sp.: 29, highly scalloped mat of cribellum silk with pair of axial lines (AX) and reserve warp lines (RW) (light microscope); 30, axial line (AX) with pair of reserve warp lines (RW) and cribellum fibrils (TEM); 31, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, 5μ, and 0.5μ.

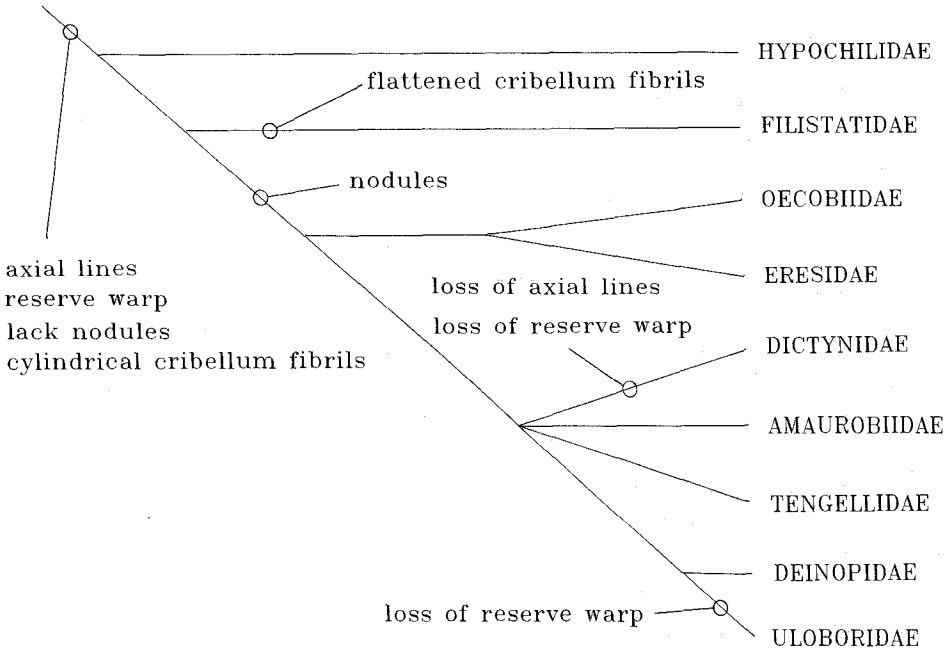


Figure 32.—Phylogeny of the families in which the ultrastructure of cribellum silk and associated lines has been studied (after Coddington & Levi 1991), with data on silk morphology (Table 1) superimposed to show possible transitions.

not move forward during most of the time cribellum silk is being combed (Eberhard 1988; see also Opell 1990 on *Miagrammopes*). It is not clear how axial fibers are pulled from the spinnerets in these species.

Comstock (1948) speculated that the helix of threads (he saw them as loops) of *Kukulcania hibernalis* (under the name *Filistata*) result from movements of the spinnerets, while the very regular loops of the primary reserve warp are made by combing movements of the calamistrum. Given the much longer length of the secondary reserve warp fibers, however, it seems more likely that their irregular folding may be associated with the combing movements of the calamistrum. The highly ordered folding of the primary reserve warp and the helical coiling of the swath itself is presumably due to their intrinsic curliness (but see below), and the fact that spider moves forward very little as it combs out silk, so that cribellate silk "piles up" between attachments to the foundation line.

Comstock also thought that the axial fibers of *K. hibernalis* are highly elastic, stretching "to fifty times their first length". We were unable to confirm this. Instead, when a swath was pulled under the light microscope, a process of sequential breaking occurred (possibly of the axial fibers), bringing the reserve warp fibers under tension as described by Kullmann (1975) for *Stegodyphus*. As the swath was slowly pulled, it extended: the primary reserve warp began to unfold, but did so unevenly, in little starts. It became completely unfolded in some places before others. Eventually the primary reserve warp became completely extended. If the tension was then relaxed, the reserve warp remained extended, and did not recoil to its original position (thus failing to show the intrinsic curliness postulated above). Further extension caused the primary reserve warp fiber to break, and with that the entire thread usually broke. Thus the finer, secondary reserve warp fibers of *K. hibernalis* apparently serve in adhesion (of the cribellum silk to the primary reserve warp? to the prey?) rather than to increase the tensile strength and elongation of the array of lines as do the secondary reserve warp fibers of *Stegodyphus* (Kullmann 1975). Presumably the extension Comstock observed was the extension of the entire array of cribellum silk and associated fibers.

The most complex and distinctive arrays of cribellum silk and associated fibers are those of filistatids. These may show intergeneric differ-

ences. Lehmensick & Kullmann (1956) describe a two-part mass of adhesive silk in *Filistata insidiatrix*, laid in small accumulations on a previously built foundation line, just as in *K. hibernalis*. Although they did not mention that each of the two parts has a helical form, this seems to be the case in the light microscope photo of Peters (1987) of the same species. Lehmensick & Kullmann also noted a pair of axial fibers, which seem (in their light microscope photo, plate 2, fig. 3) to be thicker and straighter than those of *K. hibernalis*. The fiber labelled axial line in their TEM micrograph (plate 2, fig. 4) may, however, may not correspond to the light microscope axial fiber: it does not run through the mass of cribellum fibers and curled reserve-warp fibers; and a thinner fiber, which is more appropiately located and which resembles the axial fiber of *K. hibernalis*, is unlabelled. Perhaps the line they labelled as an axial line in their TEM micrograph was a foundation line.

Also unique to filistatids is the non-cylindrical, ribbon-like form of the primary reserve warp fiber. Judging by the flattened tips of the paracribellar spigots on the posterior median spinnerets of *K. hibernalis* (figs. 56–58 in Platnick et al. 1991), these spigots may be the source of primary reserve warp fibers. This speculation is supported by the existence of a somewhat similar, slit-shaped opening of the "major ampullate gland spigot" on the anterior lateral spinneret of *Loxosceles rufescens* and *L. reclusa* (Platnick et al. 1991), and the fact that *L. rufescens* also makes a wide, ribbon-like band of silk (Lehmensick & Kullmann 1956; Kullmann 1975). It is in apparent conflict with the lack of paracribellar spigots in hypochilids, eresids, and *Tengella* (Platnick et al. 1991). Peters (1992a) has established that reserve warp fibers are secreted from spigots on the posterior median spinnerets in *Stegodyphus*. Further work is needed to establish which spigots produce these and other fibers.

The band-like cribellum fibrils of *K. hibernalis* may be associated with their bladder-shaped "claviform" cribellar spigots (fig. 52 of Platnick et al. 1991), which are quite different from the more sharply-tipped "strobilate" spigots known for other cribellates (Kullmann 1975; Opell 1979; Peters 1984, 1987, 1992; Platnick et al. 1991). A second possible silk-spigot association, between the presence of nodules on cribellum fibrils and nodule-like expansions on the cribellum spigots, is apparently ruled out, however, by the presence of expansions on the spigots of *Hypochilus pococki* (Platnick et al. 1991), and the absence of nodules on the fibrils of *H. thorelli*.

Homologies of the filistatid fibers with those of other species are somewhat uncertain. Comstock (1948) apparently also noted the axial fibers, and both primary and secondary reserve warp fibers in *K. hibernalis* (calling them, respectively, primary looped threads, secondary looped threads, and irregular threads). We have designated as "axial lines" the least folded lines within the helices, but the double nature of these lines is unique. If, instead, the wider, regularly looped "primary reserve warp" fibers are homologous to the axial fibers of other species, the characteristics of *Kukulcania* in Table 1 and the position of filistatids in Fig. 32 would be little altered.

ACKNOWLEDGMENTS

Fred Coyle kindly sent carefully packed samples of *Hypochilus* silk. Herb Levi helped with identifications. Robert Raven facilitated work in Australia. Brent Opell, M. J. West-Eberhard and especially Charles Griswold made helpful comments on preliminary drafts of the manuscript. The Vicerrectoría de Investigación of the Universidad de Costa Rica provided financial support. We thank all for their help.

LITERATURE CITED

Coddington, J. A. 1986. Orb webs in "non-orb-weaving" ogre-faced spiders (Araneae: Dinopidae): a question of genealogy. Cladistics, 2:53–67.

Coddington, J. A. & H. W. Levi 1991. Systematics and evolution of spiders (Araneae). Ann. Rev. Ecol. Syst., 22:565–592.

Comstock, J. 1948. The Spider Book. Comstock Publ. Assoc., Ithaca, New York. 729 pp.

Eberhard, W. G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). J. Zool., London, 166:417–465.

Eberhard, W. G. 1988. Combing and sticky silk attachment behaviour by cribellate spiders and its taxonomic implications. Bull. British Arachnol. Soc., 7:247–251.

Eberhard, W. G. & R. Langer. 1969. Laboratory photography of spider silk. American Zool. 9:97–101.

Foelix, R. 1982. Biology of spiders. Cambridge, Harvard Univ. Press.

Friedrich, V. & R. Langer. 1969. Fine structure of cribellate spider silk. American Zool., 9:91–96.

Kullmann, E. 1970. Bemerkenswerte Konvergenzen im Verhalten cribellater und ecribellater Spinnen. Freunde Kolner Zoo, 4:123–150.

Kullmann, E. 1975. Die Produktion und Funktion

von Spinnenfaden und Spinnengeweben, Pp. 318–378, *In* Netz in Natur und Technik. (Inst. Leichte Flachentragwerke, ed.). Stuttgart-Vaihingen.

Lehmensick, R. & E. Kullmann. 1956. Uber den Feinbau der Faden einiger Spinnen (Vergleich des Aufbaues der Fangfaden cribellater und ecribellater Spinnen). Zool. Anz., Suppl.: 123–129.

Lehmensick, R. & & E. Kullmann. 1957. Uber den Feinbau der Spinnenfaden. Proc. Stockholm Conf. Electron Microscopy. Pp. 307–309.

Marples, M. J. & B. J. Marples. 1937. Notes on the spiders *Hyptiotes paradoxus* and *Cyclosa conica*. Proc. Zool. Soc. London, 107A:213–221.

Opell, B. D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. Bull. Mus. Comp. Zool., 148:443–549.

Opell, B. D. 1987. The influence of web monitoring tactics on the tracheal systems of spiders in the family Uloboridae (Arachnida, Araneida). Zoomorph., 107:255–259.

Opell, B. D. 1989a. Functional associations between the cribellum spinning plate and capture threads of *Miagrammopes animotus* (Araneida, Uloboridae). Zoomorph., 108:263–267.

Opell, B. D. 1989b. Measuring the stickiness of spider prey capture threads. J. Arachnol., 17:112–114.

Opell, B. D. 1990. Material investment and prey capture potential of reduced spider webs. Behav. Ecol. Sociobiol., 26:375–381.

Opell, B. D., Roth, G., & P. 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. 1983. Struktur und Herstellung der Fangfaden cribellater Spinnen (Arachnida: Araneae). Verh. Naturwiss. Ver. Hamburg, 26:241–253.

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

Peters, H. 1987. Fine structure and function of capture threads, Pp. 187–202, *In* Ecophysiology of spiders. (W. Nentwig, ed.). Springer, New York.

Peters, H. 1992a. Uber Struktur und Herstellung von Fangfaden Cribellater Spinnen der Familie Eresidae (Arachnida, Araneae). Verh. Naturwiss. Ver. Hamburg, 33:213–227.

Peters, H. 1992b. On the burrowing behaviour and the production and use of silk in *Seothyra*, a sand-inhabiting spider from the Namib Desert (Arachnida, Araneae, Eresidae). Verh. Naturwiss. Ver. Hamburg, 33:191–211.

Peters, H. 1992c. On the spinning apparatus and the structure of the capture threads of *Deinopus subrufus* (Araneae, Deinopidae). Zoomorph., 112:27–37.

Platnick, N. I., Coddington, J. A., Forster, R. R., & C. E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Mus. Novitates, 3016:1–73.

Wiehle, H. 1928. Beitrage zur Biologie der Araneen, insbesondere zur Kenntnis des Radnetzbaues. Z. Morph. Okol. Tiere, 11:115–151.

Zimmerman, W. 1975. Biologische und rasterelektronenmikroskopische Festellungen an Oecobiinae, Uroecobiinae und Urocteinae (Araneae: Oecobiidae) als Beitrag zum "Cribellaten-Ecribellaten-Problem". Thesis, Univ. Bonn.

Manuscript received 7 May 1993, revised 19 July 1993.