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Combing and sticky silk attachment behaviour by cribellate spiders and its taxonomic implications

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Summary

Patterns in the distribution of behaviours involved in cribellate silk production and attachment in 27 species in 10 families suggest that some behavioural details may provide taxonomically useful characters. Possible synapomorphies linking Uloboridae and Deinopidae, and all familes examined except Hypochilidae and Filistatidae, are described.

Introduction

Several details of spiders' orb-web construction behaviour are both consistent within major taxonomic groups, and different between them, thus constituting useful taxonomic characters (Eberhard, 1982, 1987a; Coddington, 1986a, 1986b; Eberhard, in prep.). This note presents a further set of behavioural characters of both orb- and non-orb-weaving cribellate spiders that provide taxonomic information.

The cribellum is a plate with many tiny spigots on its surface. Fibrils are pulled from these spigots by movements of one leg IV which repeatedly passes a comb of modified setae, the calamistrum, across the cribellum (e.g., Foelix, 1982). The calamistrum apparently snags the fibrils momentarily as it moves posteriorly, then somehow disengages from them as the leg is moved anteriorly again to begin the next backward pass (see Peters, 1984).

There are scattered published drawings and photographs describing how the fourth leg is moved to brush the calamistrum over the cribellum. The present study assembles both published and new observations of behaviour, and analyses the taxonomic implications of the resulting patterns.

Methods

Observations were made on both captive and free-living adult or penultimate female spiders. Species that were particularly sensitive to direct illumination were observed in silhouette by lighting the substrate behind them, and were only occasionally lit directly. Both *Oecobius* species were observed spinning under a dissecting microscope. Still photographs were made of *Stegodyphus,* and video recordings were made of *Filistata* and *Tengella,* then analysed frame by frame. The exact number of individuals observed was not recorded for every species, but the approximate numbers are given in Table 1. In no case did different individuals of the same species vary with respect to the major aspects of their combing posture in more than the small details reported below, so published photographs and drawings made of other species spinning cribellate silk were also incorporated in Table 1.

The term "combing leg" is used in the descriptions to indicate the hind leg whose calamistrum was combing silk from the cribellum. The "supporting leg" was the leg upon which the combing leg rested as it combed. Legs are said to cross if the tip of the combing leg projected beyond the edge of the supporting leg when viewed from an angle perpendicular to the intersecting legs. "Sticky" silk is that which was pulled from the cribellum; the portion of sticky silk between two successive attachments is termed a "segment".

Results

Two basic combing techniques were observed (Fig. 1). The distributions of the techniques and of some of the associated details of spinning behaviour are given in Table 1. The following are descriptions of the species observed most carefully.

Position 1. Support with immobile leg III

Hypochilus thorelli Marx

The combing leg IV was flexed so that it lay on the retrolateral surface of the supporting leg, contralateral leg III, which maintained its contact with the substrate or a line in the web. The legs crossed slightly, with the middle portion of the tarsus of the combing leg lying near the tarsus-metatarsus joint of the supporting leg. The exact point of contact on the combing tarsus varied somewhat. The supporting leg was held immobile or nearly so while the combing leg "rocked" back and forth, combing silk from the cribellum.

Only one leg IV combed during the production of a single segment of sticky silk, and there was no clear tendency to alternate combing legs for successive segments. Typically the spider attached, combed for a brief period, moved forwards to where it would make the next attachment, combed some more without advancing further, and then attached again. Attachments were made when one leg III drew a non-sticky line towards the spinnerets; neither leg IV held any lines while attachments were made.

Filistata hibernalis Hentz

Combing behaviour was very similar to that of *H. thorelli.* Confirming earlier observations (Eberhard, 1987b), the spider always combed while moving towards its retreat. The tarsus of the combing leg rested on the retrolateral surface of the tibia of the contralateral leg III. The exact point of contact on the combing leg's tarsus varied, but it was consistently near the tip, and the two legs did not cross. The supporting leg was held partly flexed under the spider; often it held the non-sticky line to which the sticky line would be attached, but sometimes it rested on the substrate (Fig. 1A). The combing leg rocked principally at the base (coxa-trochanter and/or trochanter-femur joint), and at the tarsus-metatarsus and tibia-metatarsus joints as it combed silk; the distal portion of the tarsus was very

nearly immobile. Usually the spider moved forwards (up to 2-3 cm but usually only a few mm) immediately after attaching a segment of sticky line and before beginning to comb again, then combed (usually for 2-3 minutes) without moving farther, then attached the sticky line again.

Two types of attachment occurred. In one the abdomen was moved ventrally while the supporting leg III lifted the line it was holding, and the attachment was made just posterior to the tip of tarsus III. Generally neither leg IV contacted either sticky or non-sticky lines during these attachments. In the other type of attachment, the spider seized the loose skein of sticky silk with the combing leg IV and moved it sideways, looping it over lines to the side of the combing site. Then it sometimes lowered its abdomen and attached to the line held by supporting leg III as above; in some cases this final attachment was not made. On some occasions I could not be sure whether a second attachment actually occurred or whether the spider had only made preliminary movements that would have led up to it.

The two types of behaviour resulted in quite different web patterns. Looping attachments using leg IV, which sometimes occurred in several successive segments, resulted in a zig-zag sort of dispersal of sticky silk. The other behaviour resulted in large accumulations of sticky silk along a single line running towards the retreat.

Position 2. Support with leg IV and move both legs IV synchronously

Psechrus sp. (prob. *torvus* (O. P.-C.))

The spider always moved underneath its sheet, where all sticky silk was added. The combing leg IV was held against the ventral surface of the supporting leg, contralateral IV. These legs crossed, with the proximal part of the tarsus or even the metatarsus of the combing leg IV touching the middle portion of the supporting metatarsus. The two legs were moved as a rigid unit anteriorly and posteriorly, combing out additional lengths of the paired cribellate silk lines which emerged from the cribellum.

Sticky silk was attached exclusively to non-sticky lines. The abdomen was bent so that the spinnerets touched the line held by the leg III ipsilateral to the combing leg just posterior to the tip of the tarsus. At

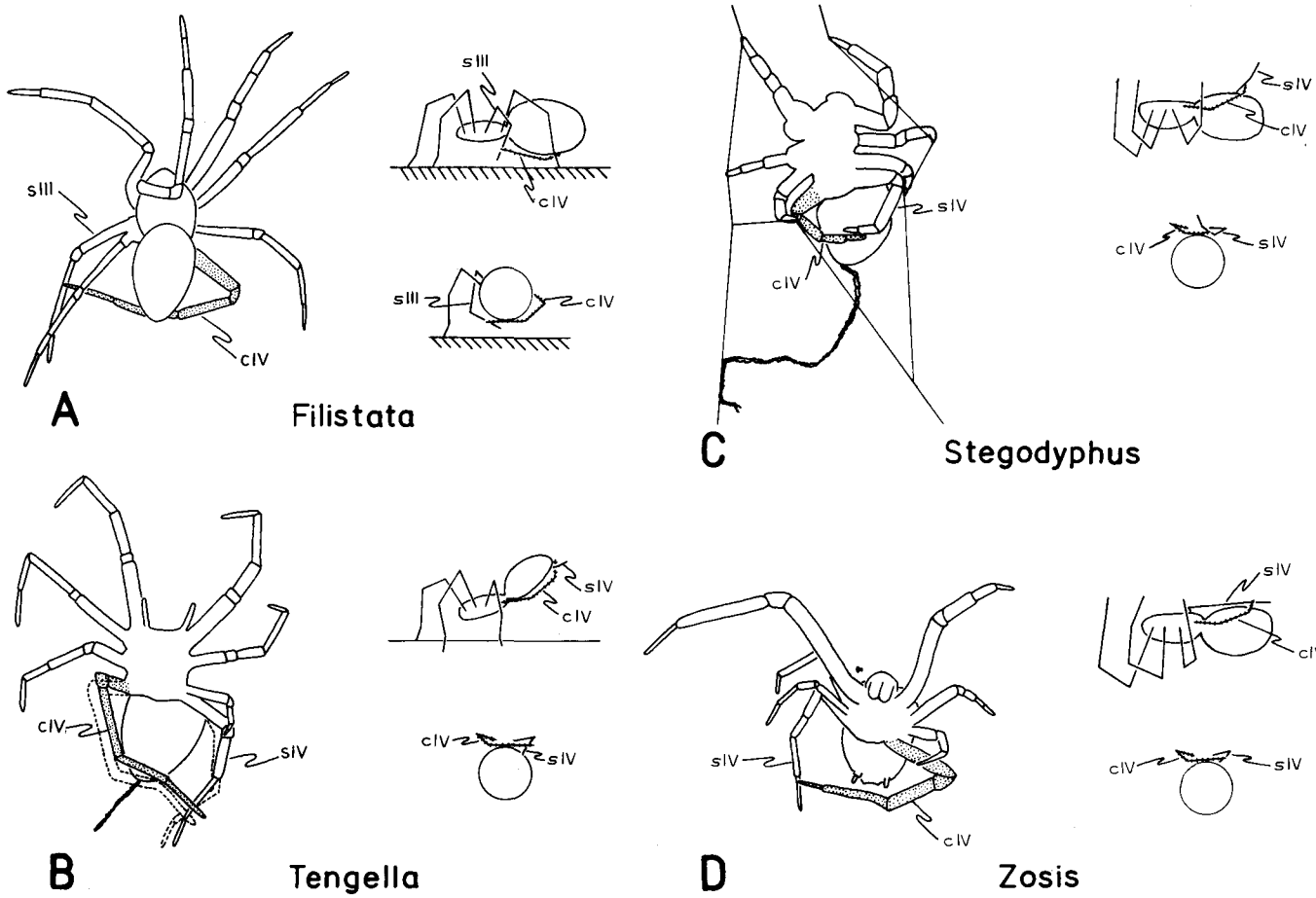

Fig. 1: Positions in which spiders combed cribellate silk (c = combing leg (stippled or cross-hatched), s = supporting leg). **A** *Filistata hibernalis*, posterior-dorsal view drawn from a videotape (left), and diagrammatic lateral and posterior views (right); **B** *Tengella radiata*, ventral and slightly anterior view (left) drawn from a videotape (solid lines show positions of legs at start of one combing movement, dotted lines those of legs IV at the end of a combing movement), and diagrammatic lateral and posterior views (right); **C** *Stegodyphus sarasinorum*, ventral and slightly posterior view drawn from a photograph (left), and diagrammatic lateral and posterior views (right); **D** *Zosis geniculatus*, anterior-ventral view (left) drawn from a photograph (Opell, 1979), and diagrammatic lateral and posterior views (right).

the moment of attachment the combing leg IV was held near the attachment site, but it appeared that it did not grasp any line there. As the spider moved forwards after an attachment, the leg III that was to grasp the next line to which the sticky line would be attached sometimes made small probing movements. This leg did not follow (in the sense of Eberhard, 1972) any other legs. If this leg III touched a sticky line already laid, it continued to probe until it contacted a non-sticky line.

The spider did not shift combing legs between attachments, and often laid several consecutive segments using the same combing leg. When it did change combing legs, the change was preceded by attaching just behind the "wrong" leg III (i.e. the leg III contralateral to the combing leg). The leg used to comb was not correlated with the spider's position on the web (i.e. nearest the edge, or nearest the centre) as in uloborids (see below).

Tengella radiata (Kulczynski)

T. radiata added cribellate silk to both the upper surface of the sheet of its web and to the mesh above the edges of the sheet. The tarsus of combing leg IV contacted the distal portion of the metatarsus of contralateral IV; sometimes the tip of the tarsus made contact, but in others the point of contact was near the basal portion of the tarsal segment and the legs crossed slightly (Fig. 1B). The two legs IV were moved as a unit. In all cases the same combing IV was used for the entire segment.

Movements that occurred before and after combing were consistent. After attaching the previous segment, the spider walked a short distance away (approximately 1-3 cm). As it did this a thin line or lines emerged from its spinnerets. The spider then assumed the combing posture, often raising its abdomen somewhat when on its sheet (Fig. 1B), and began combing sticky silk which was connected to (was continuous with?) the proximal end of the line running from the last attachment, in effect lengthening it. After combing steadily in this position for several minutes, the spider paused, then walked several cm (in one case > 10 cm), often partly forwards and partly sideways, and attached. It did not hold the new sticky line with any leg as it walked or as it attached. When on the interior portion of its sheet, the spider usually attached the sticky line by lowering its abdomen, without bringing any legs near the attachment point. When near the edge of the sheet (where lines were more sparse) or in the mesh above the sheet, the spider usually grasped with one or more legs the line to which it would attach the sticky line. Two combinations of legs held the line at the moment of attachment: one III just anterior to the attachment; or ipsilateral III and IV just anterior to the attachment. Sometimes when there were several lines in the immediate vicinity, the attachment was made to a line near to a leg but not being held by it. In summary, attachment behaviour was variable; the leg most consistently involved in holding the line to which the sticky line was attached was III.

Stegodyphus sarasinorum Karsch

The tip of the tarsus of combing leg IV rested on the dorsal surface of contralateral IV, just distal to the tibia-metatarsus junction. The metatarsus and tarsus of the supporting leg were bent ventrally so that they lay ventral to the abdomen and more or less directly ventral to the tarsus and metatarsus of the combing leg (Fig. 1C). Combing and supporting legs moved as a unit forwards and backwards as the spider combed out silk. Because of the close juxtaposition of the hind legs, careful attention was needed to determine which hind leg combed and which supported.

When the segment was complete, one or sometimes both legs IV seized the loose skein of cribellate silk and quickly looped it over the non-sticky line a mm or so posterior to the tip of the spider's abdomen. Occasionally an attempt at an attachment of this sort failed when the hind leg failed to encounter a non-sticky line. Neither leg IV gripped the non-sticky line to which the attachment was made. Often this was the only attachment made, but in some cases the spider then dabbed its spinnerets to the non-sticky line which was being held by one leg III. The result of this combination of behaviours was a double attachment, and when the spider was zig-zagging between two different non-sticky lines, a "blunt" zig-zag (Eberhard, 1987b) was produced.

Uloborus diversus Marx

The following account is extracted from more detailed descriptions in Eberhard (1972). The combing leg IV was bent across the abdomen and its tarsus held the metatarsus (the original description of contact with the tibia is in error) of the supporting leg, contralateral leg IV (as in Fig. 1D, *Zosis geniculatus*). Both combing and supporting legs were moved as a rigid unit anteriorly and posteriorly as the calamistrum combed out cribellate silk. After attaching the sticky line to a radius, the spider always began to comb immediately with the "outer" leg IV (on the side nearest the web's edge) as it moved away from that attachment. About halfway to the next attachment (the exact site varied), the spider, with hardly a break in its rhythm, switched and began combing with the inner leg IV and continued in this way until making the next attachment. Usually the spider combed continually as it walked from one attachment to the next, and continued to comb for a brief period (approximately one second) after arriving at the next attachment site, before turning and attaching by applying its spinnerets to the radius. The spider held the radius with both legs IV, one on either side of the attachment point as it attached.

Discussion

Several of the behaviours described here may provide useful taxonomic characters (Fig. 2). The character with most extensive data (direct observations of 24 species in 10 families) is the position of the combing and supporting legs (Table 1). The family Hypochilidae is generally thought to be the sister group of all other araneomorphs (e.g. Platnick, 1977); the fact

that it shares with Filistatidae a combing position and movement (leg III immobile and supporting the tip of combing leg IV as it rocks back and forth) suggests that this position and movement are ancestral for cribellate spiders. The other position (support with leg IV and move both hind legs synchronously) may thus be a synapomorphy shared by Uloboridae, Deinopidae, Dictynidae, Amaurobiidae, Psechridae, Tengellidae, Eresidae and Oecobiidae. The combing position of hypochilids and filistatids also seems primitive from a functional point of view, since the length of each brushing stroke is relatively short, and the immobility of leg III means that the spider can comb out cribellate silk only while standing still. More data will be needed to determine whether other details of combing positions (e.g. the strange posture of *Stegodyphus* in which the dorsal rather than the ventral portion of supporting leg IV supports the combing IV, and the crossed legs IV of *Psechrus* and *Tengella*) are of taxonomic value.

Other behaviours may also provide useful characters, though conclusions must be more tentative owing to smaller sample sizes. The use of only a single leg III to hold the non-sticky line to which a sticky line is being attached is probably primitive. The alternate use of both legs IV to comb out a single segment of sticky line occurs consistently in uloborids and deinopids, and may be a synapomorphy linking them.

Species	Combing position	Legs holding non-sticky line	Pause in combing to walk?	Alternate combing legs between attachments?	Combing and support legs cross?	Reference
Hypochilidae						
Hypochilus thorelli Marx (3-5)	1	contra III	yes	no	no	
Filistatidae						
Filistata hibernalis Hentz (> 20)	1	contra III/IV(a)	yes(b)	no	no	
Psechridae						
Psechrus sp. prob. *torvus* (O. P.-C.) (5-10)	2	contra III		no	yes	
Tengellidae						
Tengella radiata (Kulczynski) (> 10)	2	III/IV(c)	yes	no	yes (usually)	
Eresidae						
Stegodyphus sarasinorum Karsch (> 30)	2	III/IV(d)	no	no	no	
Oecobiidae						
Oecobius annulipes Lucas (1)	2	none	no	no	no	
O. sp. (1)	2	none	no	no		
Amaurobiidae						
Amaurobius fenestralis (Stroem)	2					Nielsen, 1932
A. similis (Blackwall)	2				no	Bristowe, 1958; Jones, 1983
Dictynidae						
Mallos gregalis Simon (3)	2					
Dictyna sp.	2					
D. sp. (SA1-114) (> 5)	2	none(?)(e)		no		
D.(?) sp. (SJ1-98) (5)	2					
Uloboridae						
Uloborus diversus Marx (> 20)	2	IV, IV	no	yes	no	Eberhard, 1972
U. walckenaerius Latreille	2	IV, IV		yes	no	Wiehle, 1927; Peters, 1984
U. glomosus (Walckenaer)	2	IV, IV	no	yes		
U. plumipes Lucas	2					
U. trilineatus Keyserling (0-21-3) (2)	2	IV, IV	no	yes	no	
Philoponella vicina (O. P.-C. (> 20)	2(f)	IV, IV	no	yes	no	
P. tingena (Chamberlin & Ivie) (2)	2	IV, IV	no			
Zosis geniculatus (Olivier)	2	IV, IV(?)		yes	no	Opell, 1979; this study
Hyptiotes cavatus (Hentz) (1)	2(g)	prob. IV, IV				
H. paradoxus (C. L. Koch)	2					Wiehle, 1927
Polenecia producta (Simon)	2					Wiehle, 1931
Deinopidae						
Deinopis sp. (#2203) (2)	2	IV, IV(h)		yes		
D. spinosa Marx	2(?)	ipsi III, IV	no	yes	no (usually)	Coddington, pers. comm.
D. sp.	2	ipsi IV, III	no	yes		Coddington, 1986a

Table 1: Combing and attachment behaviour of cribellate spiders. Data without references are original observations. Position numbers are illustrated in Fig. 1 and described in the text. "Contralateral" and "ipsilateral" are with reference to the leg IV combing cribellate silk. Blank spaces indicate no observations were recorded; code numbers of voucher specimens deposited in the Museum of Comparative Zoology follow some names; other numbers in parentheses are numbers of individuals observed.
(a) one leg IV sometimes looped sticky line over other line;
(b) spider moved forwards to next attachment site before beginning to comb out sticky line;
(c) when attaching to a sheet, no legs held lines near attachment; when attaching to single lines, leg III and sometimes also ipsilateral IV usually held the line to which the sticky line was attached;
(d) often used one or both legs IV to loop sticky line over non-sticky line; leg III was used only occasionally;
(e) only one leg IV was ever near attachment site, perhaps not on the line to which the sticky line was attached;
(f) combing leg IV was nearly perfectly flat over ventral surface of abdomen and moved nearly perfectly forwards and backwards;
(g) point of contact of combing leg on supporting leg not certain;
(h) attachment much nearer to one IV than to the other.

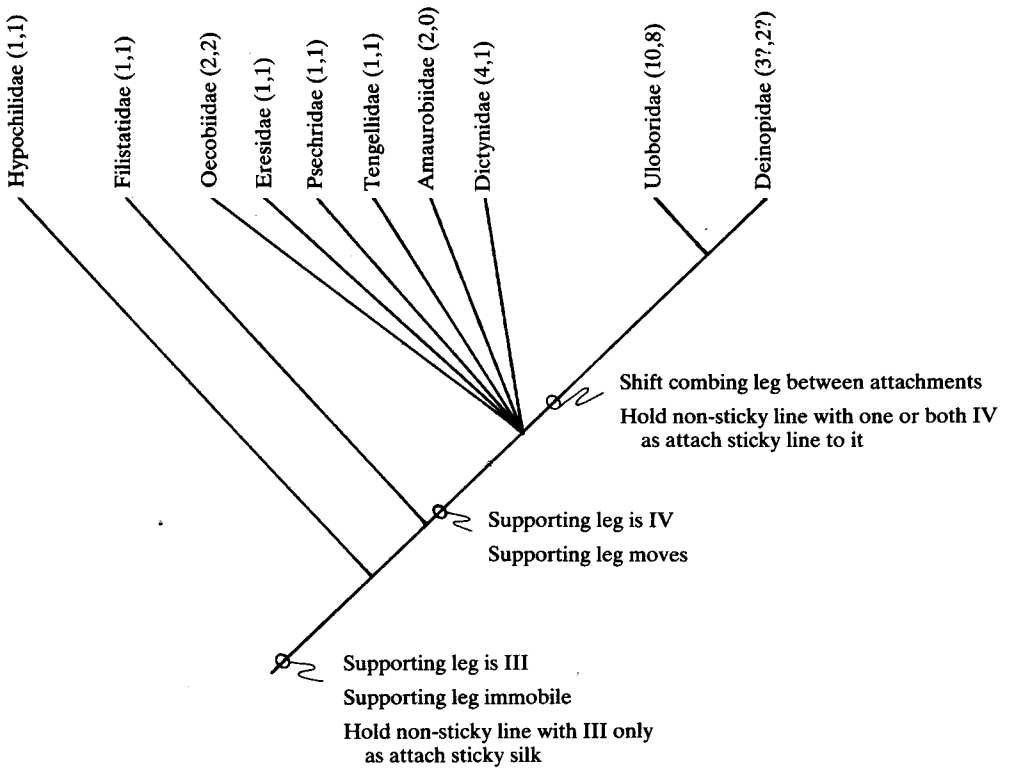

Fig. 2: Tentative cladogram summarising observations reported in this study (Hypochilidae is placed as a sister group to the others on the basis of information in Platnick, 1977). Numbers in parentheses are numbers of species whose combing position is known, followed by the number of species in which other details of combing and attachment behaviour were observed in this study.

In summary, it must be emphasised that the cladogram in Fig. 2 is tentative, owing to the small sample sizes in most groups. In addition, other cribellate and ecribellate araneomorph families must be added. It is presented as a target for future critical observations of other arachnologists.

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