Construction behaviour of non-orb weaving cribellate spiders and the evolutionary origin of orb webs

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Summary

Preliminary observations of certain non-orb weaving cribellate spiders show some general patterns of order and location of thread placement that also occur in the building behaviour of orb weavers. These patterns may be plesiomorphic, and their presence in uloborid and araneoid orb weavers thus is not strong evidence that these two groups are related.

Introduction

The question of whether the orb webs of Uloboridae and Araneoidea represent an astounding evolutionary convergence or the legacy of a single orb-weaving ancestor has been a point of controversy for over 100 years (see Coddington, 1986a for a summary). A particularly striking similarity between the orbs of the two groups is that they are all built using the same overall sequence of behaviour: (1) first the spider lays a network of non-sticky supporting lines (radii and frames); (2) then it fills in the supports, starting at the hub and laying a non-sticky spiral line connecting the radii as it moves outwards; and finally (3) it attaches the sticky spiral to the radii, starting near the edge of the web and moving gradually inwards. This similarity has been cited as evidence of a single origin for orb webs (e.g. Wiehle, 1931).

The present note reports observations of the construction behaviour of several cribellate spider species which make non-orb webs. Their behaviour resembles that of orb weavers in some of these patterns, suggesting that the behaviour may be very ancient and thus making the dual origin hypothesis of orb evolution less implausible. Details of leg movements are described, since similar details in other groups have proved to be useful taxonomic characters (Eberhard, 1982; Coddington, 1986b).

Sites and Methods

The observations on *Psechrus* sp. were made in the field at Top Slip in the Annamalai Wildlife Sanctuary (alt. approximately 1300 m) about 35-40 km W. of Pollachi in Tamil Nadu, India. A series of about 20 webs was destroyed except for the retreat tubes on one afternoon, and the spiders were observed as they rebuilt their webs in the evening. No single spider was observed throughout the complete web construction process; instead the entire series of spiders was checked repeatedly, and the sequence of web construction was deduced from observing the order of appearance of lines and the spiders' behaviour as they built.

Stegodyphus sp. (a colonial species — probably *S. sarasinorum* Karsch although lack of taxonomic expertise and an adequate revision of the genus precluded certain identification) was observed using a similar technique except that colony retreats were collected and placed at convenient sites, and were also observed in captivity. These spiders were collected and studied about 22 km N. of Ootacamund near the southern edge of Mudumalai National Park, Tamil Nadu, India. In this species each spider contributes only a part of the colony's web, and sequences of behaviour were determined by following about 40 individual spiders and by watching changes in the behaviour of groups when they emerged at dusk to repair their webs.

Dictyna sp. and *Filistata* sp. were observed as they rebuilt damaged webs indoors near San Jose, Costa Rica.

Those species that ceased building when illuminated directly (*Filistata, Stegodyphus*) were observed by illuminating a surface behind them and observing their silhouettes, making occasional brief checks of thread positions with direct illumination.

Numbers after genus names refer to labels in the vials of voucher specimens that have been placed in the Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138, U.S.A.

Results

Psechrus sp.

Webs of *Psechrus* sp. (#2299) were similar to the web of *P. argentatus* (Doleschall) (Robinson & Lubin, 1979). The sheet was often but not always slightly elevated or domed near the centre, and was continuous with the upper surface of a tube-like retreat at one edge. The sheets of undisturbed webs had sectors of apparently different ages, and spiders probably often replace only part of the sheet at once. The meshwork above the sheet was variable in density and extent. There were numerous lines of sticky, cribellate silk in the sheet, but none in the mesh above. I observed only the construction of the sheet proper, and only briefly; undoubtedly many details were missed.

There were three more or less discrete stages in sheet construction. First the spider laid a sparse array of lines that formed in effect the skeleton of the new sheet. Many lines were relatively long, and they were connected to others by only a few cross lines. They were not consistently arranged in radial patterns, but in some cases (e.g. Fig. 1) there was a suggestion of radial symmetry around the peak of the sheet. Construction of this stage was not observed. Some skeleton arrays were built soon after nightfall, while others were not begun until after about 22.00.

In the second, "fill-in" stage, the spider laid shorter non-sticky lines connecting the skeleton lines. The spider moved slowly, grasping each line, to which it would attach its trail line, with only a single leg III and bending its abdomen upwards towards the sheet and (sometimes) to the side so that its spinnerets touched the line just posterior to the point held by the leg. The anterior spinnerets may have sometimes touched the posterior edge of the leg. Sometimes the spider made successive attachments to lines held by the same leg III, while in others it alternated from side to side. Paths taken by spiders as they laid fill-in lines were not consistent, but in several cases the central, uppermost portion of the sheet was filled in first, and subsequent filling in was concentrated (though not restricted to) near the periphery.

Only after both skeleton and fill-in lines had been laid did spiders begin to lay sticky lines. As in some other cribellates (Szlep, 1966; Robinson & Lubin, 1979), the sticky lines were produced in pairs. The most surprising aspect of this behaviour was that in four of the five cases in which I determined the sites of the first sticky lines laid in completely new sheets (as opposed to partial replacements), these lines ran near and more or less parallel to the border of the sheet (Figs. 1,2). Thus there appeared to be a tendency to start laying sticky silk near the web's edge, and move gradually inwards towards more central portions. The spider's path was not always strictly parallel to the web's edge, and in one case a spider that had been moving along the edge circled inwards and eventually turned through 180°.

Attachments were consistently made to the line held by the leg III that was ipsilateral to the leg IV that combed silk from the cribellum. The other leg IV supported the combing leg as it combed cribellate silk, and at least on some occasions neither leg IV held any line at the moment of attachment. The leg III that had held the attachment line probed forwards and laterally after each attachment. The more anterior legs moved less often and did not appear to be involved in locating the site of the next attachment, though one leg I was sometimes held at the margin of the sheet and may have served to sense the position of the edge.

Spiders tended to lay sticky lines in zig-zag patterns rather than straight lines (Figs. 1, 2). The sizes of the zig-zags were small compared with the size of the spider, and resulted from movements of the abdomen from side to side. Spiders consistently attached sticky lines to non-sticky lines rather than to other sticky lines. In one case a spider tapped a sticky line several times with one leg III until it touched a non-sticky line, then immediately grasped this line and attached the sticky line to it.

Some spiders reverted to fill-in behaviour after having laid some sticky lines. Later sticky lines also tended to intersect or be laid over earlier ones, so the relatively orderly arrangement of early lines was gradually obscured.

Stegodyphus sp.

Colony webs consist of a central retreat made of a mass of silk and prey remains honeycombed with tunnels, and a set of more or less planar trapping webs around the retreat (e.g. Kullmann, 1970: fig. 29). Construction of trapping webs is described here.

As noted by Jambunathan (1905) and Bradoo (1972) for *S. sarasinorum*, the first stage of construction by a given spider involved placement of non-sticky lines. I was unable to distinguish patterns in the spiders' movements during this stage other than their tendency to use ipsilateral legs III and IV to hold the line to which an attachment was about to be made, with one leg on each side of the point where the new line was to be attached. Occasionally only leg III held the line.

Sticky cribellate silk was laid during the second stage of a given spider's activity. There were two clear tendencies. The overall orientation of the sticky lines tended to be radial, converging on the retreat; spiders usually started near an outer edge and moved towards the retreat. Of 20 spiders in the field whose orientation with respect to the retreat was noted, 15 were moving towards the retreat, one away from it, and 4 moved more or less parallel to it. Of 25 observations in captivity, 21 spiders moved towards the retreat, 2 away, and 2 more or less parallel to it ($p < 0.01$ with Chi Squared for both sets of observations assuming random orientations). The second outstanding characteristic was that many of the sticky lines zig-zagged, often in quite regular patterns (Fig. 3) (see also Bradoo, 1972). The displacements in this case were large in relation to

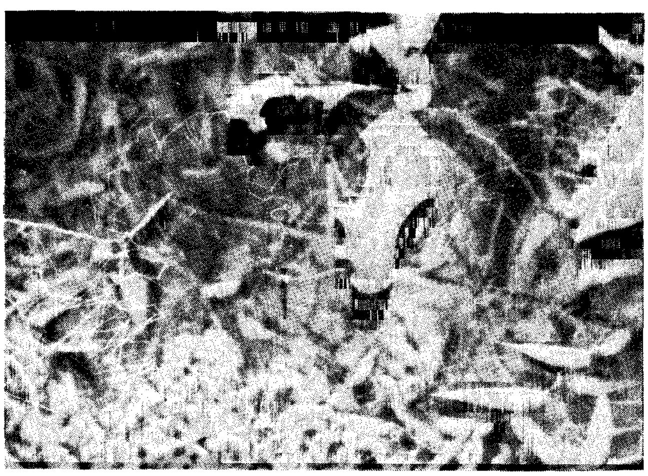

Fig. 1: Sheet of *Psechrus* sp. (#2299) with old portion at far right, and new, partially complete portion at left. The spider had laid a single "loop" of paired sticky lines near the edge in the upper part of the photograph, and two "loops" in the lower part. Newer part is approximately 20 cm wide from top to bottom.

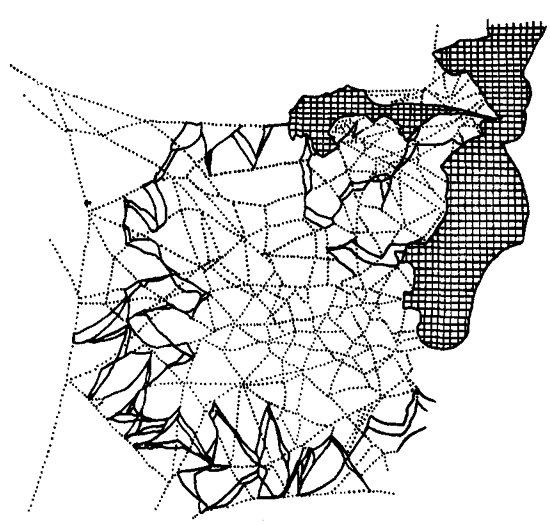

Fig. 2: Diagrammatic representation of newer portion of web in Fig. 1, showing non-sticky (dotted), and sticky lines (solid). Note wider mesh of non-sticky lines near edge.

the spider's size, and the spider moved from side to side as it moved gradually towards the retreat.

In some cases the spider's legs spanned the lines between which the sticky line zig-zagged, but in others the space was wider, and the spider had to reach across with its front legs. In about one third of the cases the spider laid sticky silk on a single dry line. In all cases the spider moved forwards slowly soon after making an attachment until it reached the spot where the next attachment would be made, then continued combing there for several seconds before attaching. As a result, sticky lines were invariably slack. Often (I could not be sure in some cases) the attachment was to a line held by one leg III. The spiders did not make obvious tapping movements as they moved between attachments as do orb weavers, and did not avoid attaching to cribellate silk (or at least lines with cribellate silk on them) as did *Psechrus* sp.

As in *Psechrus* sp., subsequent spinning activities both on the same night and on later nights generally resulted in deposition of additional sticky and non-sticky lines near or on lines already laid, thus obscuring early patterns.

Filistata sp. and *Dictyna* sp.

Brief observations of spiders renovating webs suggest that these species also tend to lay sticky lines radially, and tend to move towards the retreat as they spin them (12 of 12 cases in *Filistata* sp., 5 of 5 in *Dictyna* sp.).

Discussion

Two of the most striking points of similarity between uloborid and araneid orb construction behaviour patterns noted in the introduction are that a non-sticky spiral is laid from the hub outwards, and that the sticky spiral is then laid from the edge of the web inwards. It might seem difficult to explain these similarities in orb weavers' behaviour as convergences, since other sequences and patterns of behaviour could be imagined that would result in similar final web designs. The brief observations presented above show, however, that rough approximations of both of these behaviour patterns may also occur in other, non-orb weavers. *Psechrus* sometimes performs both a filling-in behaviour that starts in the centre and moves peripherally, and sticky silk production that begins at the edge and moves parallel to the edge, only slowly progressing towards the centre. The other three species all tend to initiate sticky lines near the periphery and direct them more or less towards the centre of the web. In addition, the adults of another psechrid, *Fecenia,* also begin laying sticky lines near the edge of their web and more or less parallel to it, and gradually move inwards (Y. D. Lubin, pers. comm.).

Such uniformity in initiating cribellate sticky lines is not expected. At least some ecribellate spiders, such as the pholcid *Modisimus* sp. (Eberhard & Briceño, 1985; Briceño, 1985) and the theridiid *Synotaxus turbinatus* Simon (Eberhard, 1977) do not place sticky silk in their webs starting near the edge and moving inwards

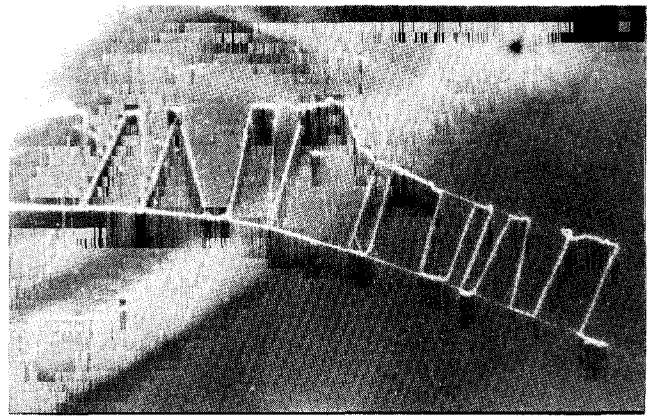

Fig. 3: Portion of the web of *Stegodyphus* sp. showing the zig-zag pattern of sticky silk laid by a single spider.

towards a retreat or some other central area. Others do, however, e.g. the *Latrodectus* species that spin "gum foot" lines (Szlep, 1965) and *Chrysso ecuadorensis* Levi, which makes long sticky lines more or less radiating from a retreat under a leaf (Eberhard, unpub.).

All of the species observed here conform to the orb weavers' pattern of laying scaffolding or skeletons of non-sticky lines before producing sticky lines, but this is not really unexpected since one of the apparent functions of the non-sticky lines is to support the sticky lines and the spider as it spins them, and to do this they must be in place before the sticky lines are laid. In fact very similar behaviour patterns have been described in such different spiders as *Modisimus* (Eberhard & Briceño, 1985), *Latrodectus* (Szlep, 1965) and *Synotaxus* (Eberhard, 1977), the amaurobiid *Titanoeca* (Szlep, 1966), and the psechrid *Fecenia* (Robinson & Lubin, 1979). The web designs of *Stegodyphus lineatus* (Latreille) and *Dictyna arundinacea* (L.) figured by Wiehle (1929, 1931) and that of *Titanoeca nipponica* Yaginuma (Shinkai, 1979) also suggest that sticky lines were laid after non-sticky lines.

If both uloborids and araneids are descended from a cribellate ancestor or ancestors, and if these patterns of web construction were present in these ancestors, then their possession by both uloborids and araneids may be a symplesiomorphy, and similarity in these aspects of web construction cannot be used to indicate relatedness between the two groups (Wiehle, 1931). Of course the behaviour patterns of the non-orb weavers are only tendencies rather than the strict stereotyped patterns seen in orb weavers. Even the transition from non-sticky to sticky line production, a clear and nearly irreversible step in orb web construction, was sometimes reversed in *Psechrus* sp. (reversals also occur in *Hypochilus gertschi* Hoffman (Eberhard, unpub.) and probably in *H. thorelli* Marx — see Comstock, 1948: fig. 234). But this comparative lack of stereotypy is to be expected since presumably one aspect of the evolution of orb web construction was the progressive fixation of particular behaviour patterns that were present in pre-orb weaving ancestors.

The zig-zag pattern of sticky lines in *Psechrus* and *Stegodyphus* webs (also present in those of *Dictyna* — Nielsen, 1932) is shared by many uloborid orb weavers

(Lubin, 1986) (e.g. *Uloborus* — Szlep, 1961; Eberhard, 1972; Lubin *et al.*, 1982; *Hyptiotes* — Nielsen, 1932; Opell, 1982; *Zosis* — Shinkai & Takano, 1984; Eberhard unpub.; *Philoponella* — Eberhard, unpub.), but is very rare in araneoid webs (present only in the highly derived "saw tooth" web of *Eustala* sp. — Eberhard, 1985). Unless one argues that the common ancestor of araneoids built orb webs (Levi & Coddington, 1983), this character would link uloborids more closely to these other cribellates than to araneoids.

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