

The web of *Dictyna bellans* (Araneae: Dictynidae)

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Abstract. Webs of *Dictyna bellans* Chamberlin, 1919 in captivity included several characteristics seen in other dictynid webs, including a fine-meshed tubular retreat of non-sticky lines with multiple exits, “runways” of dense, fine non-sticky lines that were continuous with the floor of the retreat, and “ladders” of cribellum silk that zig-zagged between more or less parallel non-sticky lines. They also included two traits not previously reported for dictynids: especially tightly spaced cribellum lines with tight zig-zags that were on and very close to the substrate at the edges of the web near the retreat; and extensive coiling of cribellum silk on a few long, elevated non-sticky lines. The webs of *D. bellans* argue against the supposition made in some studies of web evolution that webs built especially near the substrate lack complex organization. They also indicate that the degree of coiling of cribellum lines varies among dictynids and in other cribellate spiders, and may represent a useful axis of comparison that reflects adaptations for prey retention.

Keywords: Dictynid web, substrate web, non-orb design, cribellate, flexible behavior

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A recent summary (Eberhard 2019) cited published observations or photos of the webs of 22 species in 10 genera of the large family Dictynidae (469 described species) (World Spider Catalogue 20.5 2019), which is especially well-represented in the Nearctic and Palearctic regions (in a review published just over 60 years ago, about 75% of the 371 described species were from these regions) (Chamberlin & Gertsch 1958). While it has long been appreciated that dictynid webs show considerable regularity (Chamberlin & Gertsch 1958) and while a few published photos have clearly illustrated such regularity (Comstock 1967), nearly all the information on dictynid webs is superficial; few details of web designs are known. This lack of knowledge probably stems in part from the durability of dictynid webs in the field; they tend to accumulate damage from prey and detritus as well as subsequent additions by the spider over many days (Blackledge & Wenzel 2001; Eberhard 2019). The difficulties are compounded in some dictynids that build webs next to planar substrates such as leaves and walls (Emerton 1902; Nielsen 1932; Comstock 1967; Shinkai 1979) where it is especially difficult to observe structural details. Use of white powder to visualize lines in fresh webs built on leaves in the field and in captivity revealed unexpectedly elaborate designs in *Emblyna* sp. and *Mallos hesperius* (Chamberlin, 1916) webs (Eberhard 2019). These included non-sticky lines in fine-meshed tubular retreats with multiple openings, dense “runways” of non-sticky lines extending from these openings, long, strong non-sticky “spanning lines” that together formed approximate planes, and sticky lines, often in geometrically regular patterns, laid on the spanning lines (Eberhard 2019). The goal of the present note is to add observations of an additional dictynid, *Dictyna bellans* Chamberlin, 1919, that also builds webs on planar surfaces (in this case on vertical walls), by using the same technique; *D. bellans* webs resemble the leaf webs in some respects, but they also show a pair of previously undescribed characteristics.

METHODS

I collected specimens in Shreveport, Louisiana USA (32.5252°N, 93.7502°W, el. approximately 80 m), and studied web construction in captivity by placing each spider on a longitudinally folded, approximately 15 cm long and 6–7 cm wide strip of black construction paper or poster board. I braced the strip in a glass vial using pebbles and a cotton plug, and placed the vial in a closed aquarium with water in the bottom to discourage the spiders from decamping. I left spiders undisturbed for 1–14 nights before examining their webs under a dissecting microscope and photographing them. I checked some unpowdered webs under the microscope and then left them for additional days before adding powder. Most details could only be seen after the web was powdered, however, and I only powdered each web once; I thus did not follow web development in detail from day to day. Before photographing a powdered web, I removed most of the powder from the non-sticky lines and the strip by tapping the strip gently, and then illuminated the web from the side to increase the contrast. By controlling the tapping, I left a light coating on the non-sticky lines and a more abundant coating on the sticky cribellum lines, allowing them to be easily distinguished. Both powdered and unpowdered lines that bore highly coiled cribellum silk could be distinguished without magnification by their thicker, bumpy outlines (Figs. 1a–d, 2b, 3a).

This note is meant to document the types of design features in *D. bellans* webs; it probably does not document the entire range of designs or the frequencies of different design traits in the webs that this species builds; dictynid web designs are thought to vary substantially at sites with different geometric arrays of potential attachment points (Bond & Opell 1997; Eberhard 2019). Because it is not yet clear which web traits will prove most informative in comparing different dictynid webs, I include multiple photographs and present only qualitative analyses. I use the term “cribellum line” in the descriptions below to designate what is likely a complex combination of fibers that includes probably hundreds of fine

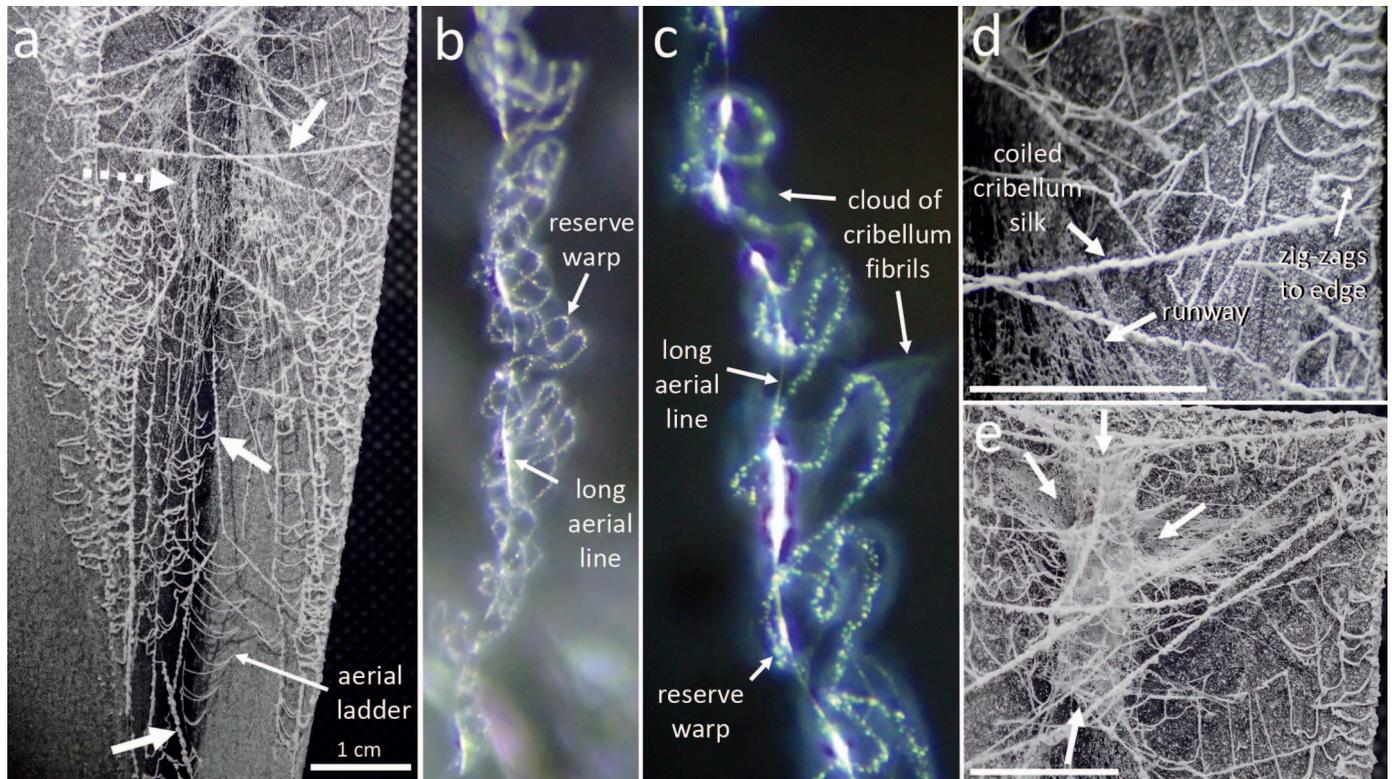


Figure 1.—This five day-old web of a mature female *Dictyna bellans* built on folded black paper, seen in general overview (*a*) and at closer range (*b–e*), illustrates three web traits not previously documented in other dictynids: long aerial silk lines with thick, coiled accumulations of cribellum silk and reserve warp lines that glinted in the light (thick arrows in *a*; closeups in *b* and *c*); closely spaced zig-zag cribellum lines attached directly to the substrate (*d*); and a cylindrical retreat with multiple entrances (*e*) (four are marked with arrows). Two traits shared with other dictynid species are also visible: aerial zig-zag cribellum lines between more or less parallel non-sticky lines (“aerial ladder” in *a*), and a runway of non-sticky silk lines continuous with the floor of one retreat exit (dotted arrow in *a*; closeup in *d*). Silk lines in *a*, *d* and *e* were powdered; those in *b* and *c* were not powdered. Scale bars = 1.0 cm; the approximate maximum width of the coiled cribellum silk in *b* and *c* was 0.5 mm.

cribellum silk fibrils, a pair of baselines, and curled “reserve warp” lines (Opell 2013; Grannemann et al. 2019).

I observed attack behavior by touching small live flies to sticky lines just above the retreat (spiders rejected ants and cicadellids). Darrell Ubick kindly identified specimens; I have deposited vouchers in the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica.

RESULTS

Webs of *D. bellans* in the field were in 90° corners between planar surfaces on the outer walls of a building that were sheltered above by a roof. The webs were dense, approximately oval three-dimensional tangles loaded with the bodies of dead insects and other detritus; the spider, which rested in the central area where the surfaces intersected, was not visible. I did not note any pattern in the lines of these webs, but the contrast with the background was very poor and I could not easily discern individual lines.

In captivity, the 14 webs built by seven individuals all had a retreat near the top of the strip, but showed substantial variation in some other details despite the relatively uniform supports (Figs. 1–4). As in other dictynids (Blackledge & Wenzel 2001; Eberhard 2019), some spiders added lines to

webs from one night to the next. Even after only a single night, all webs (including one built by a mature male) had a retreat; the retreat was composed of fine, densely meshed non-sticky lines, with two to five circular exit holes, and lacked cribellum lines (Figs. 1e, 2b, 4a). In at least some retreats, the side nearest the substrate (the “floor”) appeared to be less dense than the roof. During the day, the spider crouched in the retreat, usually on the floor (Fig. 3a); one individual observed at dusk rested on the runway just beyond the bottom exit of its retreat with its legs more extended. All retreats had a nearby, relatively sparse three-dimensional tangle of non-sticky lines, and (except in the male) aerial cribellum lines were attached to these lines. In at least some places, the sticky lines formed zig-zags running back and forth between approximately parallel non-sticky lines (Figs. 1–4).

The most elaborate webs included additional traits. The retreat floor extended beyond some exits, forming an approximately planar sheet or “runway” that was composed of many fine, more or less parallel non-sticky lines (Figs. 1a, 2a,b, 3b). Cribellum lines were laid at and beyond the farthest (lower) edge of the longest, more or less vertical runway (Figs. 2a,b); occasionally cribellum lines were also placed in zig-zag patterns on the outer portion of the runway

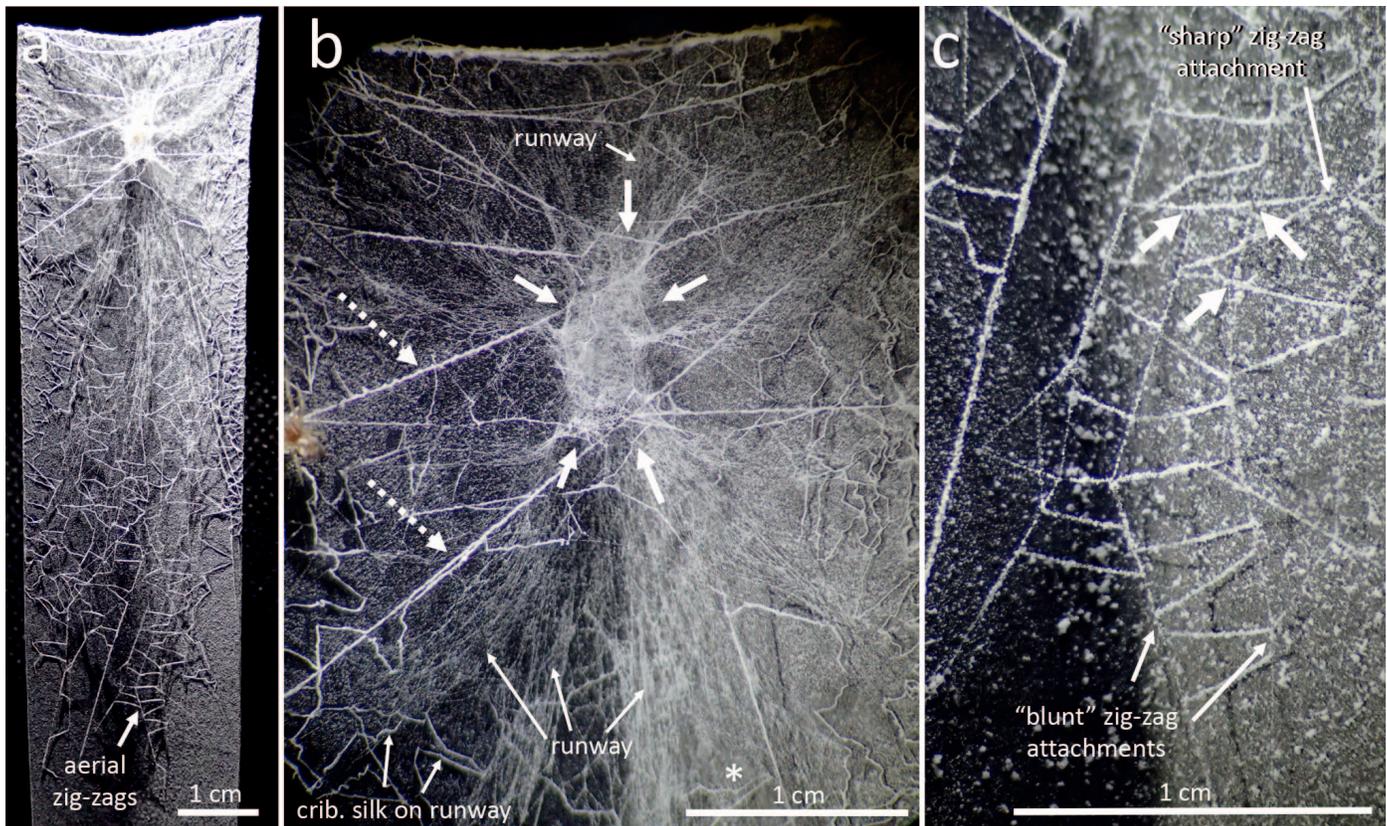


Figure 2.—(a) This four-day old powdered web of a second *Dictyna bellans* individual seen in overview in *a* and in closeups in *b* and *c* illustrates variations with respect to the web in Fig. 1. (b) The retreat has five exits (thick solid arrows); the runways near the retreat are relatively more extensive; the long lines with coiled cribellum silk (dotted arrows) are limited to lines in the upper portion that cross over the retreat; and some zig-zag sticky lines are on runways (thin arrow in lower portion). (c) A closeup of a ladder shows how zig-zag cribellum lines sometimes skipped over non-sticky lines (marked with arrows) or that some non-sticky lines were added after the cribellum lines were laid.

itself (Fig. 2b). Cribellum lines were also laid in the upper portion of the web. They were especially dense at the edges of the web near the retreat, where they were often laid directly on and very near the substrate; many of these cribellum lines also had perceptible zig-zag patterns (Figs. 1a, 2a). When loaded with powder, some cribellum lines that had been previously seen to be just above the substrate before they were powdered sagged into direct contact with the substrate (e.g., Fig. 1e).

An additional feature was that webs generally had a few especially long compound lines that were farther from the substrate and consisted of a non-sticky baseline bearing highly coiled bands of cribellum silk (Figs. 1b,c, 3a). In unpowdered webs, the baseline reflected light intermittently when illuminated from the side (Figs. 1b, c), the fine fibrils (presumably from the cribellum spigots) had a bluish tinge, and the coiled reserve warp fibers (perhaps the “undulating” fibers of Grannemann et al. 2019) glittered brightly within the mass of cribellum fibrils (Figs. 1b,c). When coated with powder, these long lines with coiled cribellum silk had a thicker, bumpy outline (Figs. 1d, 2b). Usually the long bumpy lines spanned the space over the retreat (Fig. 3a), but some had more nearly radial orientations (Fig. 1a). In some (but not other) blunt zig-zags, there was apparently less extensive coiling, as the portion of the cribellum line that ran

along the non-sticky line was slightly thicker and bumpy (Fig. 3b).

Attacks on prey ($n = 11$) always began with a bite; spiders never wrapped their prey. In six attacks, however, the spider pulled a captured prey backward through the web into its retreat soon after biting it. This caused web lines to snag and accumulate on the prey; in the other five attacks, the spider returned quickly to the retreat after biting the prey, leaving the prey in the web. The collapsed bodies of two prey were later attached to the upper edge of the web, just beyond the upper exit of the retreat.

DISCUSSION

The webs of *D. bellans* shared several traits seen in other dictynid webs that were summarized by Eberhard (2019): ladders of sticky silk strung between pairs of non-sticky lines (many species); a more or less tubular retreat with dense walls of fine non-sticky lines and an opening at either end (as in *Emblyna* sp. and *Mallos hesperius* (those of *D. bellans* differed in often having additional openings); long, multi-strand non-sticky lines that splayed apart where they were attached individually to the substrate (as in *Emblyna* sp. and *M. hesperius* (these lines differed in *D. bellans*, however, in being less numerous, having fewer attachments to the substrate, and

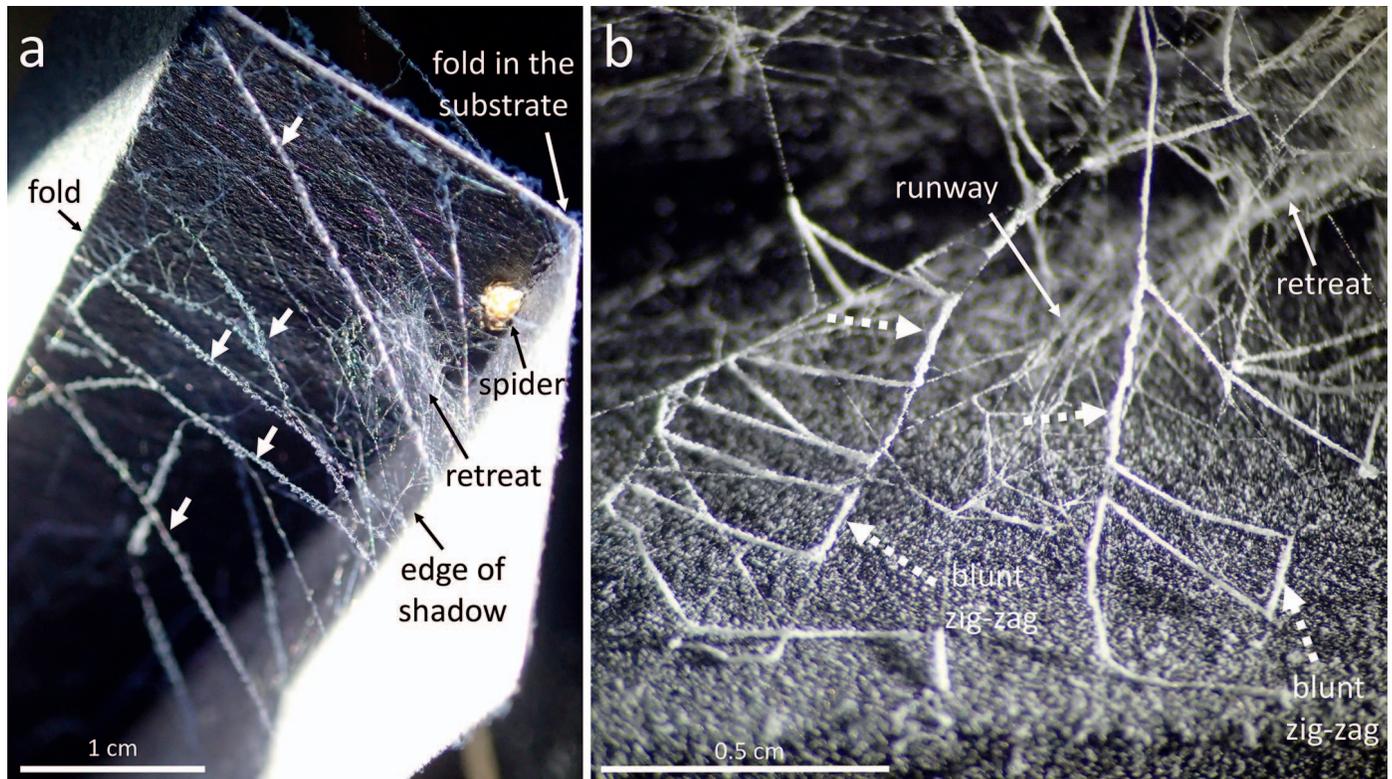


Figure 3.—(a) The aerial nature of long lines with highly coiled cribellum silk (thick white arrows) is illustrated by lines in an unpowdered five-day old web built in the fold of black construction paper (the web, seen from above, was illuminated from the left; the lines are visible against the shadow cast by the fold on the left). (b) In this web, in which a reduced runway extended from the floor of the retreat, the thick dotted arrows mark sites where cribellum lines that ran along non-sticky lines (in a “blunt zig-zag” pattern) were thicker than adjacent segments of cribellum silk, producing a slightly thicker, bumpy outline; the dotted arrow at the lower left indicates a site where the cribellum line laid on a non-sticky line was not thicker and was smooth.

bearing cribellum silk); and runways of approximately parallel non-sticky lines that formed extensions of the retreat floor (as in *Emblyna* sp.).

The webs of *D. bellans* also had two traits not previously described in dictynid webs, both of which may represent ways of increasing the amount of stickiness beyond that provided by a single cribellum line. Some cribellum lines laid on long, aerial non-sticky lines were highly coiled rather than straight, giving the line a thicker, bumpy outline; this contrasted with the smooth outline of other cribellum lines in the same webs that hung free between supporting non-sticky lines or that ran short distances along supporting non-sticky lines (Figs. 2c, 3b). None of the cribellum lines in the leaf webs of the dictynids *Emblyna* sp. or *M. hesperius* were coiled this way; most hung free, and those laid on non-sticky lines (in “blunt zig-zags”) were not perceptibly coiled (Eberhard 2019). In contrast, the dictynid *Mexitlia trivittata* (Banks, 1901) and also the uloborid *Miagrammopes* O. Pickard-Cambridge, 1870 produce coiled (or “looped”) cribellum lines on non-sticky lines (Opell 2002). Direct measurements showed that coiling increases the stickiness of cribellum lines and thus their ability to retain prey (Opell 2002, 2013; Grannemann et al. 2019). The filistatid *Kukulcania hibernalis* (Hentz, 1842) produced loose piles of highly coiled sticky lines by performing long bouts of combing while standing immobile or moving forward very

slowly (Eberhard 1987, 2020; Grannemann et al. 2019). This suggests that the coiled cribellum lines of *D. bellans* were probably produced when the spider moved forward more slowly while it combed out cribellum silk. As outlined in Fig. 5, differences in web designs with respect to the degree of coiling of sticky silk (and that thus affect stickiness and prey retention) may constitute a dimension along which the webs of different cribellate spiders can be profitably compared, complementing previous comparisons involving the numbers of spigots on the cribellum (Opell 2013). In addition, the spinnerets of *K. hibernalis* execute complex, highly coordinated movements that pack the axial fibers, undulating fibers, and supporting fibers together in complex arrays (Grannemann et al. 2019), and the overall morphology of these arrays varies substantially in different families (Opell 2013). Further exploration of the hitherto poorly studied diversity of behavioral mechanisms employed by different cribellate spider groups to produce cribellum silk and to place it on their webs may reveal differences in prey retention strategies.

Secondly, the cribellum lines of *D. bellans* were often especially close to each other and especially close to the substrate in areas near the retreat along the edge of the substrate (Figs. 1a,d,e, 2a). Some of these densely spaced zig-zag lines were attached directly to the substrate, while others were just slightly above it. Presumably these dense arrays of

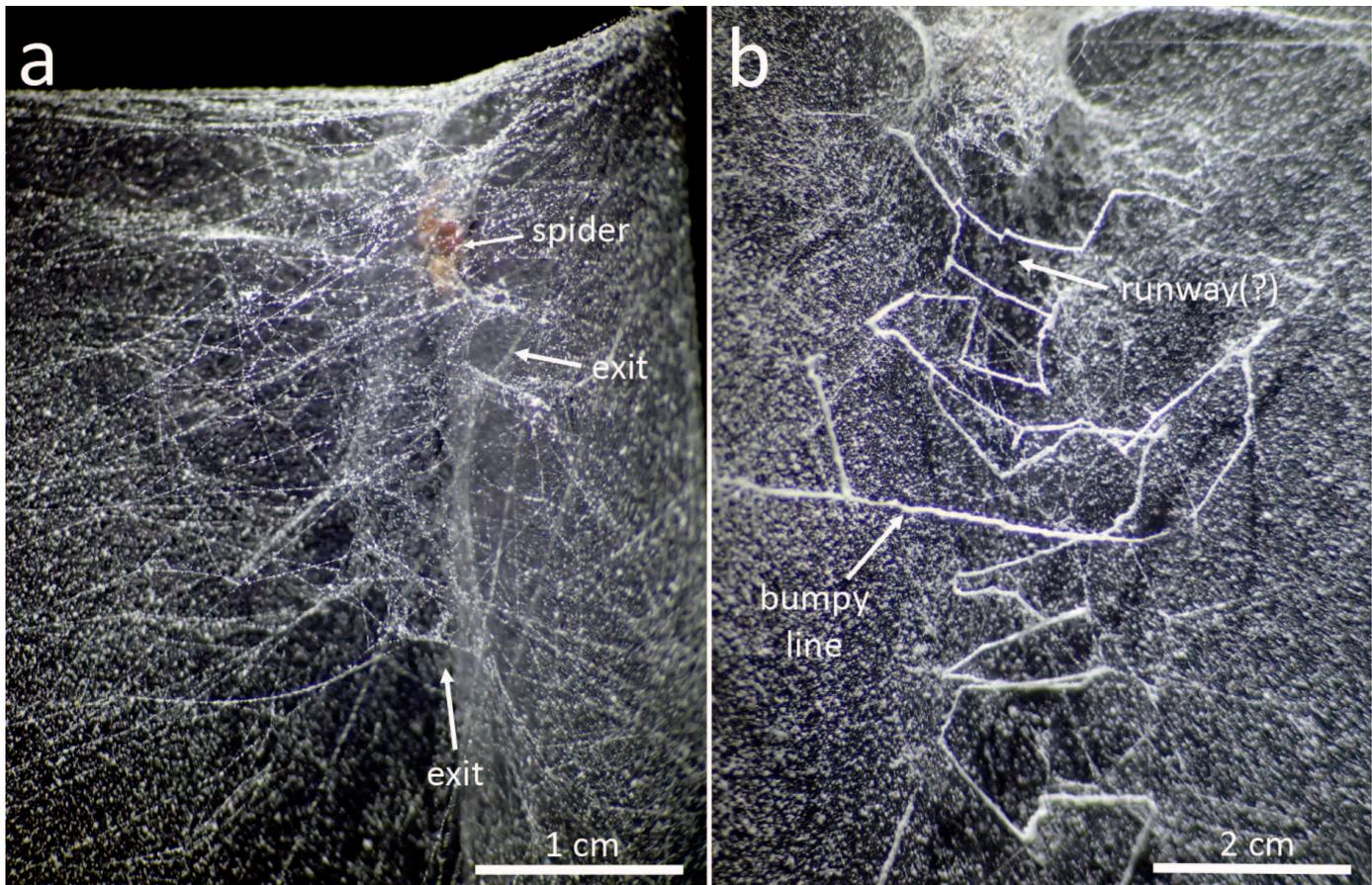


Figure 4.—(a) A lightly powdered retreat of non-sticky lines built by a mature male (two exits are indicated by arrows). (b) A web of a mature female after two weeks. There is only a single short aerial bumpy line (arrow), and only one skimpy, possible runway below the retreat.

tightly-spaced zig-zag sticky lines, which to my knowledge have not been described in any other spider, serve to capture walking prey, thus resembling the approximately circular bands of cribellum silk on the substrate in webs of the oecobiid *Oecobius annulipes* Lucas, 1846 (Solano-Brenes et al. 2018). By dragging prey through the web soon after biting them (as also occurs in the filistatid *K. hibernalis*), *D. bellans* may “wrap” prey by increasing its entanglement, and thus improve retention. The common attacks in which the spider bit the prey only briefly and then left it briefly to hide in the retreat resemble the attacks by the titanoecid *Titanoeca quadriguttata* (Hahn, 1833) (Tsai & Pekár 2019), and suggest that the webs of both species are highly effective in retaining prey.

Perhaps the most appropriate comparison of the webs of *D. bellans* is with those of other dictynids such as the *Dictyna uncinata* Thorell, 1856 (Nielsen 1932) and *Emblyna* (= *Dictyna*) *sublata* (Hentz, 1850) (Comstock 1967) that build in similarly vertical planar sites like grooves in board fences and window corners. An especially clear photograph of an *E. sublata* web (Comstock 1967: Fig. 265) shows similar zig-zag cribellum lines; but it has a sheet with an apparently uniform “lacework” of cribellum lines covering the entire web, a pattern never seen in *D. bellans*. With respect to the dictynids *Emblyna* sp. and *M. hesperius* that

build webs on planar (but not vertical) websites (leaves), the webs of *D. bellans* also lacked the long aerial, non-sticky “spanning” lines that formed the approximate planes on which sticky lines were laid (Eberhard 2019). These preliminary indications of diversity suggest that observations of the webs of other dictynid species would be profitable. It should also be noted that the strips of substrate provided in this study may have affected the web designs. In captivity, the retreats were consistently located near the top of the web, but spiders in the field were found in more central positions in their webs.

In sum, details of the webs of *D. bellans* suggest that they are designed to capture walking and perhaps also flying prey. The geometric regularity of their webs reaffirms the assertion (Eberhard 2020) that the suppositions in some studies of web evolution that webs that are built on or near the substrate lack regular patterns (e.g., the “irregular ground sheet web” category of Blackledge et al. 2009, 2011, and Bond et al. 2014) are imprecise.

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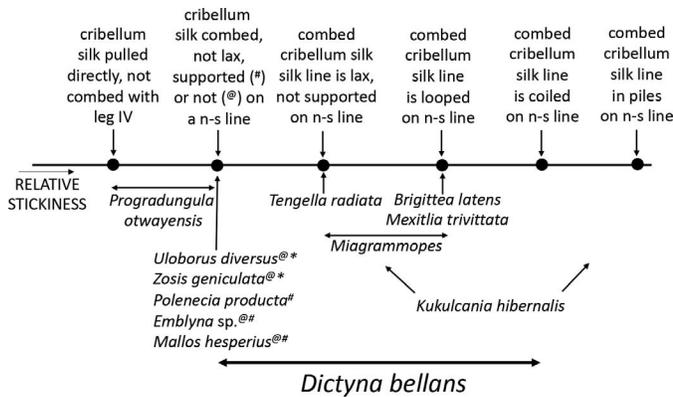


Figure 5.—Schematic representation of the likely order of relative stickiness (and thus the prey retention abilities) of cribellum lines that have a given composition (e.g., equal numbers of fibrils) when they are placed on webs in different configurations (the horizontal distances between the dots are not to scale); a few representative species that use the different configurations are included. The “n-s line” = non-sticky line or the “foundation” line of Opell (2013). “Looped” refers to cribellum lines that are folded back on themselves along at least a portion of their length; “coiled” refers to lines like those in Fig. 1b and 1c; “in piles” refers to much greater numbers of coiled cribellum lines, as in *Kukulcania hibernalis*. For the category “Cribellum silk combed, not lax”, “*” indicates that even though the spider extended the cribellum line by combing out additional cribellum silk just before attaching it to a non-sticky line, the cribellum line nevertheless did not sag or coil perceptibly in the finished web; “@” indicates that most cribellum lines hang free or, occasionally, are laid along radii for short distances in the uloborids *Uloborus diversus* Marx, 1898 and *Zosis geniculata* (Olivier, 1789); and “#” indicates that the cribellum line is laid along a non-sticky line. The sources of information are: Nielsen 1932 on *Brigittea* (= *Dictyna*) *latens* (Fabricius, 1775); Lubin et al. 1978 on *Miagrammopes*; Peters 1995 on *Polenezia producta* (Simon, 1873) (Uloboridae); Eberhard 1987, Opell 2002 and Grannemann et al. 2019 on *Kukulcania hibernalis*; Eberhard et al. 1993 on *Tengella radiata* (Kulczyński, 1909) (Zoropsidae); Opell 2002 on *Mexitlia trivittata*; Michalik et al. 2019 on *Progradungula otwayensis* Milledge, 1997 (Gradungulidae); Eberhard 2019 on *Emblyna* sp. and *M. hesperius*; Eberhard 2020 on *U. diversus*, *Z. geniculata*.

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