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Sub-units in the webs of *Dictyna meditata* (Arachnida: Araneae: Dictynidae): implications for studies of spider web evolution

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Abstract. Studies of web evolution in spiders generally focus on the overall designs of webs in the field. As has been typical for dictynids and several other cribellate families with "irregular" webs, this study detected few discernable patterns in the field regarding the spatial organization of the highly variable, three-dimensional and largely aerial webs of the dictynid *Dictyna meditata* Gertsch, 1936. Nevertheless, there were three consistent sub-unit designs in the additions that spiders made to their webs in captivity, and in webs that they built from scratch in captivity: "silk ladders", with a cribellum line that zig-zagged between a pair of approximately parallel non-sticky lines; "twig ladders", with a cribellum line that zig-zagged between a non-sticky line and the substrate; and long non-sticky lines that each supported a long, slightly looped cribellum line. I suggest, using examples from dictynids and other families with long-lived, geometrically irregular webs, that this pattern of using consistent behavior patterns to add geometrically regular "modules", is widespread and ancient, but has often been missed due to damage and additions to webs in the field, and to lack of direct behavioral observations. Recent attempts to link web evolution to studies of spider phylogeny could benefit from a change of emphasis, focusing on the additions that spiders make to their webs, rather than on the currently common but necessarily vague characterizations of overall web designs seen in the field.

Key words: Phylogeny, behavioral modules, combing behavior, categorizing web designs

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Spider prey-capture webs are an evolutionary success story in terms of both their long evolutionary history (on the order of 240 million years) (Vollrath & Selden 2007), and their present abundance and diversity (summary Eberhard 2020). Arachnologists have made many efforts to understand the evolutionary histories of webs. Many were based largely on the structure of the webs themselves (e.g., Kaston 1964; Comstock 1967; Coddington 1986a; Shear 1986; Vollrath 1988); some more recent attempts were based more on determining the phylogeny of the spiders by using powerful techniques that emphasize molecular traits (e.g., Blackledge et al. 2009; Dimitrov et al. 2011; Bond et al. 2014; Fernández et al. 2014, 2018a,b; Garrison et al. 2016; Coddington et al. 2019).

Analyses of the evolutionary history of webs and construction behavior depend on categorizing or typifying webs and behavior. The web design categories that have been used varied widely, ranging from simple systems designed to emphasize particular web properties such as the strength of attachment to supports (e.g., Wolff et al. 2019), to dissections of web construction into subroutines (Eberhard 1982; Coddington 1986b) and elaborate descriptions of the webs themselves (Shinkai 1989). The web categories that have been used in several recent studies of phylogeny that attempted to trace web evolution are intermediate in complexity. They have largely followed the categories recognized by Blackledge et al. (2009): brushed sheets; terminal lines; irregular ground sheets; irregular aerial sheets; orbs; cobs; stereotyped aerial sheets; and bolas (Table 1). I argue in this paper that these categories are inadequate for the task of elucidating web evolution. The paper has two parts: a study of the natural history of the web-building dictynid *Dictyna meditata* Gertsch, 1936; and a general discussion of some consequences of these observations for studies of web evolution. I propose a major shift of focus for attempts to understand web evolution and offer new ways to categorize web construction behavior that could improve this understanding.

The phylogenetic affinities of the large widespread family Dictynidae, with 470 species in 52 genera (World Spider Catalog version 21.0), are uncertain. Recent studies place it in the marronoid clade, not closely allied with orb weavers, and grouped most closely with Hahniidae, Agelenidae, Desidae and Amphinectidae (Garrison et al. 2016), or with Toxopidae, Hahniidae and Cybaeidae (Wheeler et al. 2017). Surprisingly little is known regarding the details of dictynid web designs, and their webs are not easily classified in any of the recent schemes. They have usually been described in vague terms, such as "irregular" (Emerton 1902; Comstock 1967), "three-dimensional tangled sheets" (Viera et al. 2007), "mesh webs" (Bristowe 1958; Adams 2014), a "meshed veil" (Bristowe 1958), "lacy lattices, meshes, and sheets" and "irregular mesh webs" (Chamberlin & Gertsch 1958), "mesh" and "nest" (Jackson 1978), "irregular ground sheet webs" (Blackledge et al. 2009), "lace webs" and "lace tent webs" (Shinkai 1989) (see also Emerton 1902; Comstock 1967; Eberhard 2019; below). It is often difficult to decipher any patterns in the lines of dictynid webs in the field. This is probably due, at least in part, to the webs being long-lived (e.g., Bond & Opell 1997); patterns in the original web's design can become obscured by the accumulated effects of damage from wind, prey, detritus, rain, and the spider's own movements, as well as by further additions to the web made by the spider (e.g., Lamoral 1968; Eberhard 1988, 2020). Although dictynid webs have usually been described in typological terms ("the" web of a given species), some species show quite substantial intra-specific variation (e.g., Jackson 1978 on the *Mallos niveus* O. Pickard-Cambridge, 1902). Chamberlin & Gertsch (1958) separated dictynid webs into those closely appressed to a substrate

Table 1.—Classifications of web types used in recent phylogenetic studies.

Web types	Blackledge et al. 2009	Dimitrov et al. 2011	Bond et al. 2014, Garrison et al. 2016	Fernández et al. 2018	Coddington et al. 2019
Orb	Y	Y	Y	Y	Y
Cob	Y	Y	Y	Y	Y
Brushed sheet	Y	Y	Y	Y	
Terminal line	Y	Y	Y		Y
Irregular ground sheet	Y	Y	Y	Y	Y
Irregular aerial sheet	Y	Y	Y	Y	Y
Stereotyped aerial sheet	Y	Y	Y	Y	Y
Bolas	Y	Y			
Trapdoor/burrow			Y	Y	Y
Sheet					Y
Aerial silk tube				Y	Y
Irregular tangle (not sheet-like)				Y	

(“surface” or “leaf” webs in what follows), and perhaps the most typical designs built at the tips of shoots or twigs where they span spaces between supports (“aerial webs” in what follows).

Close examination of some dictynid webs suggests that the lines within a web may show geometric regularities and that these patterns may vary between and within species. The most common pattern reported is a “ladder like” arrangement in which a cribellum line forms a zig-zag pattern between two more or less parallel non-sticky lines (summary Eberhard 2019). A second pattern in some species is that a cribellum line is attached repeatedly to a long, aerial non-sticky line, running along much of its length (Eberhard 2019 on *Dictyna bellans* Chamberlin, 1919) (possibly also in *Mexitlia trivittata* (Banks, 1901) and *Mallos pallidus* (Banks, 1904) (Bond & Opell 1997; Eberhard 2019). Additional designs described verbally or with a single photo include “a small opaque white sheet spun across the hollowed underside of a leaf” in *Nigma* (= *Dictyna*) *puella* (Simon, 1870) (Bristowe 1941), and a large extensive sheet with a relatively uniform, lace-like pattern of cribellum lines that lacked recognizable silk ladders except at one edge in *Emblyna* (= *Dictyna*) *sublata* (Hentz, 1850) (Comstock 1967).

Examination of recently built leaf webs that were coated with white powder to make the lines visible revealed still further patterns. The surface webs of *Emblyna* sp., *Mallos hesperius* (Chamberlin, 1916), and *Dictyna bellans* had cylindrical retreats with multiple entrances and also broad runways of non-sticky lines that extended from retreat entrances and led to areas with silk ladders of cribellum lines (Eberhard 2019, 2021). In the first two species, long “spanning lines” of non-sticky silk bridged curved leaves and often formed planar arrays that supported silk ladders.

The first section of the present paper presents the results of a study of the webs of an additional dictynid from Mexico and Central America, *Dictyna meditata*. Unexpectedly, the results of this small study led to the realization, discussed in the second section where observations of other species are included, that the focus on finished web designs, which has prevailed in recent discussions of web evolution, can be misleading. This section proposes a new focus on the behavioral subunits of web construction, that was inspired by the finding that the apparently irregular *D. meditata* webs observed in the field were nevertheless the result of quite orderly construction behavior. I argue that attempts to understand the evolution of both orb and non-orb spider webs may benefit from concentration on structural subunits, rather than on overall web design; this could increase the utility of attempts to trace web evolution that are based on clarifying spider phylogenies.

METHODS

All *D. meditata* spiders were observed in the field and in captivity at 1325–1400m near San Antonio de Escazu, San José Province, Costa Rica (9° 53′ 51.41″ N, 84° 08′ 15.99″ W) during the latter portion of the dry season in March and April, 2020 (during which only a single brief light drizzle of rain fell on one day) and the first week of the wet season. Nearly all were mature females or penultimate instar spiderlings. I photographed webs in the field between 10 AM and 1 PM after coating them with talcum powder. Additional photos were taken after repeatedly jarring the web supports to remove powder from non-sticky lines.

These webs and others that had not been powdered were collected by cutting the stem of the plant on which the web was built, carefully placing it in a jar whose depth matched the length of the stem, and bringing the web into the lab where individual lines could be observed under a dissecting microscope (Carl Zeiss 475002-9902, 8x – 80x) with a strong light and a black background. Many of these stems were then mounted vertically, with the base in a small plastic cylinder (a 35mm film canister) and placed in a closed container with water in the bottom (Fig. 1*b*), thus making it difficult for the spider to decamp, and checked on subsequent days for additional lines. New lines that had been built in captivity were easily distinguished from those laid in the field because they were clean, with no accumulations of detritus or (in the case of webs that had been photographed in the field) of powder (Fig. 1*c*). Some spiders were removed from their webs and allowed to build on simplified experimental supports that consisted of a plant stem (*Sida* sp.) from which all leaves, small branches, and schizocarps had been removed except for two small branches and a single empty schizocarp that was glued upside down at one intersection to form a shelter. The cadavers of apparent prey that were enmeshed in lines in or near the retreat were collected from some field webs examined

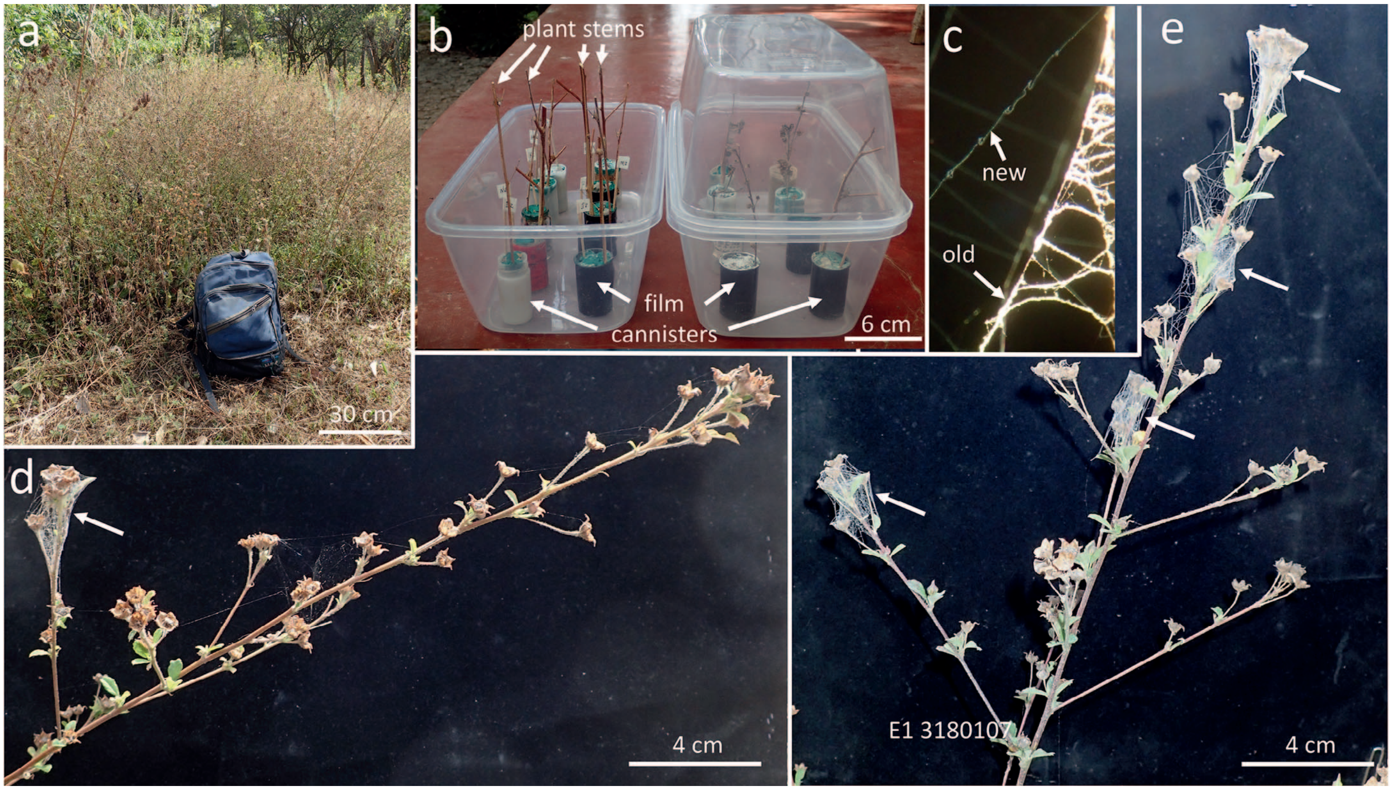

Figure 1.—(*a*) A dense stand of *Sida* sp. in an open field. There were at least 40 webs in about 10 m^2 in this patch. (*b*) Stems of *Sida* sp. inserted into film canisters resting in plastic containers (open on left, enclosed on right) where spiders built webs in captivity. (*c*) A cribellum silk line newly built in captivity (arrow on left) was easily distinguished from previous lines in a web that had been powdered the previous day (arrow on right). (*d*) and (*e*) Branches of *Sida* sp. plants with *D. meditata* webs (arrows).

under the microscope. Spiders were fed at irregular intervals with small chironomid flies. Nocturnal construction behavior was analyzed frame-by-frame from 30 fps recordings made in captivity at room temperature (about 24°C) using the "night-shot" infra-red illumination option of a SONY FDR-AX53 camera equipped with a +2 closeup lens. Individual lines were only visible occasionally in these recordings, when they were fortuitously illuminated at favorable angles.

In the descriptions below, the term "cribellum line" designates the complex of fibers that includes hundreds or thousands of fibrils from the cribellum, a baseline (perhaps the pair of axial lines of Eberhard & Pereira 1993), and bright coils (perhaps the "reserve warp" lines of Eberhard & Pereira 1993). Because I could not resolve the number of lines present in either the "baseline" or the "bright coils", and in view of the diversity of lines that accompany cribellum fibers in different species (e.g., Opell 2013; Grannemann et al. 2019; Ramírez & Michalik 2019; below) and even in the same species (Eberhard 2018 on *Mallos hesperius*), and because I could not associate particular lines with particular spinnerets and spigots, I have side-stepped questions of homology and use only descriptive terms for different types of line, rather than the terms in previous publications. Cribellum lines were termed "lax" when unpowdered lines in a web were curved rather than straight and swung perceptibly in gentle air currents (a probable bias is that longer sticky lines were almost certainly more likely to be judged to be lax than short lines). Production of sticky lines was distinguished from production of non-sticky lines in behavioral descriptions by the distinctive combing behavior of legs IV in the production of cribellum lines. "Distal" and "basal" locations on plants refer to locations with respect to the plant stem on which the web was built. I employed the illusion that all spiders are females (as in Spanish, German, French and other languages) to improve the clarity of behavioral descriptions by avoiding the less specific "it" (in any case, most behavioral observations were made using adult females). Some observations of web forms are presented quantitatively, in order to give an idea of sample sizes and the degree of variation; but the numbers themselves are probably of little general significance because the effects of the environment (e.g., the branching patterns of the plant) on web design are apparently very strong (below). Means are followed by ± one standard deviation.

Darrell Ubick very kindly identified specimens; vouchers are deposited in the Museo de Zoología of the Universidad de Costa Rica, and the California Academy of Sciences. Other species and genus names were checked against the World Spider Catalog Version 21.0 (online at https://wsc.nmbe.ch).

RESULTS

Prey.—Eight insect orders were represented in the 205 bodies of apparent prey collected from field webs. In order of abundance, prey were Hymenoptera (57.6%), Diptera (19.0%), Coleoptera (5.9%), Thysanoptera (5.4%), Psocoptera (3.9%), Homoptera (2.9%), Hemiptera (2.9%), Neuroptera (0.5%) and

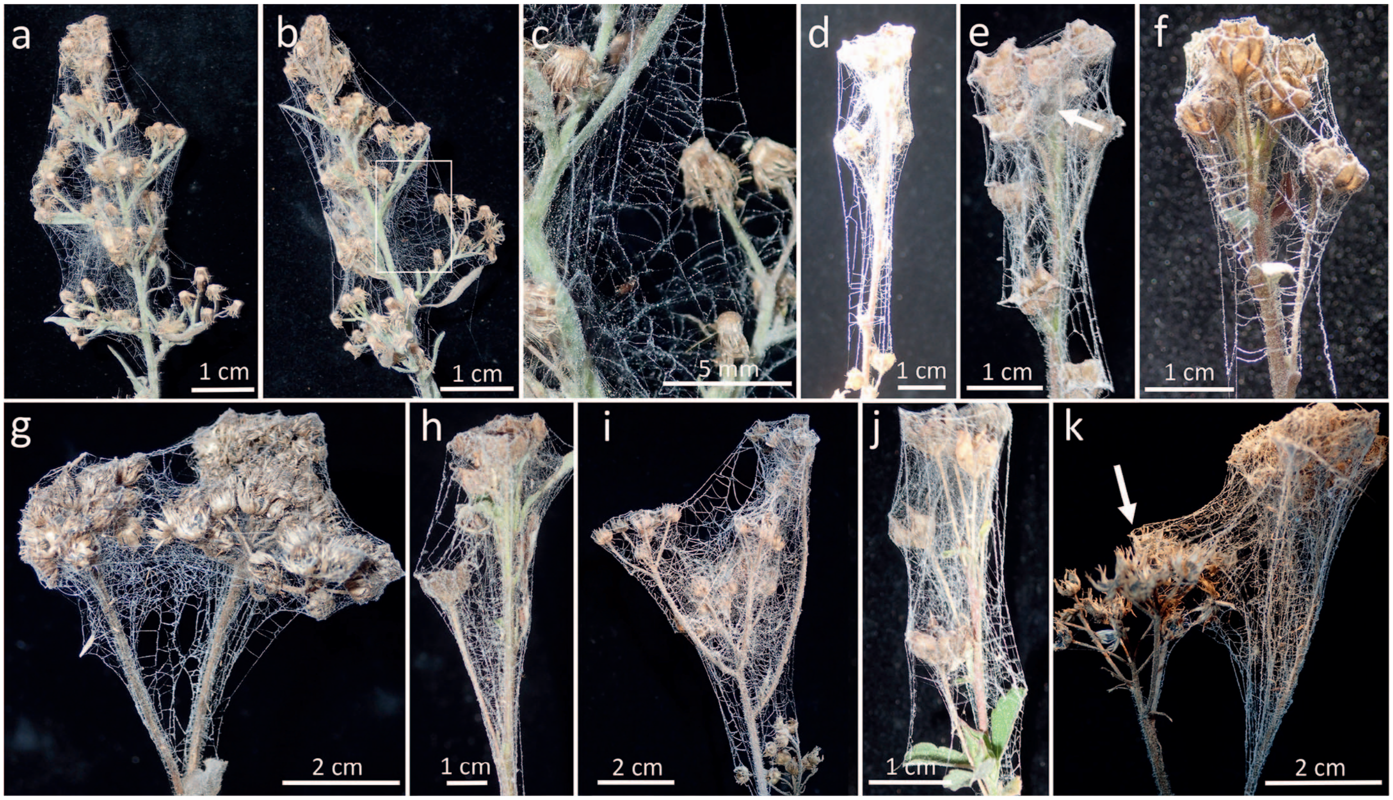

Figure 2.—The designs of these field webs of *D. meditata* varied widely. *a*, *b* and *c* are the same three-dimensional web seen from two sides (*a* and *b*); *c* is a close-up view of the portion marked in *b*; *d–f*, *h,* and *j* are on *Sida* sp. plants. Some webs (*i*) were much nearer to planar than others (*a–b*); some narrowed sharply basally (*d, h*), others less sharply (*e*), and others were more nearly cylindrical in form (*j*), apparently depending on the availability of attachment sites; the web in *k* was especially irregular, as nearby objects offered attachment sites (arrow in *k*). In some webs, the spider's retreat (the circular mouth of one retreat is indicated by an arrow in *e*) was near the middle (*a–c, i*), while in others it was much nearer the distal end (*d–h, j*). While most field webs photographed in the dry season had no clear ladder patterns (*a–e, g–k*), webs photographed the morning following the first rain showed clear ladders (*f*).

Lepidoptera (0.5%). Strikingly, small parasitic wasps (mostly diverse species of Chalcidoidea) were by far the most common group (37.6 %). Only 2.4% of the prey lacked wings (three worker ants, a theridiid spider, and a small mite). Many prey were somewhat dismembered, and it was not possible to measure their individual sizes. The largest prey were winged, and belonged to the orders Hymenoptera and Diptera.

Web designs.—*Webs in the field:* Webs were found at open, sunny sites on small branches or shoots of living and dead herbaceous plants, including *Sida* sp. (Malvaceae) (Figs. 1*a*,*d*,*e*), an unidentified melostome, and the dried flower heads of composites. Webs tended to be at the tips of the plant structures. In a sample of 47 webs on *Sida* sp. plants, for instance, all but one web was at the tip of a branch (e.g., Figs. 1*d*, 2*d–f*,*h*,*j*). I had the strong impression that the branch tips that bore webs tended to project farther from the rest of the plant and other surrounding vegetation than did other tips (e.g., Fig. 1*d*) (I was unable to devise a convincing objective measure to test this idea, however). Another strong but quantitatively untested impression was that *Sida* sp. plants at moderately shaded sites lacked *D. meditata* webs, even when they were only a few meters away from populated conspecific plants in a sunnier area.

I photographed 30 webs of adults and penultimate nymphs in the field. They had a wide variety of designs, including more or less planar (at least in portions; Fig. 2*i*), nearly cylindrical (Fig. 2*j*), and other more irregular three-dimensional forms (Figs. 2*a*,*b*,*e–h*,*k*). All webs had a denser area where the spider rested; often this retreat area was near the distal end of the web (Figs. 2*d*,*e*,*f*,*j*), but some retreats were nearer the web's geometric center (Figs. 2*a*,*b*,*g*). Many webs were intermediate with respect to these variables.

The only consistent overall geometric pattern in the lines in dry season webs in the field was that the lines were closer together in the internal area where the spider rested. This dense portion often included one or more finely meshed tubular structures made of non-sticky silk that were in close contact with the plant. These retreats were consistently located in portions of the webs where plant structures such as schizocarps or leaves offered shelter. In *Sida* sp. for example, retreats were often among the schizocarps at the tips of branches (Fig. 2), where the spider was hidden from view. A few other retreats were more exposed, alongside a twig (Fig. 3*a*)

The overall forms of webs seemed to correlate with available attachment sites. For instance, when a *Sida* sp. stem lacked leaves or reproductive structures just basal to its tip, the web was long and narrow (Fig. 2*d*); when there was a cluster of schizocarps or flowers in this area, the web was wider (Fig. 2*e*). When another object was near the tip of the branch, the web

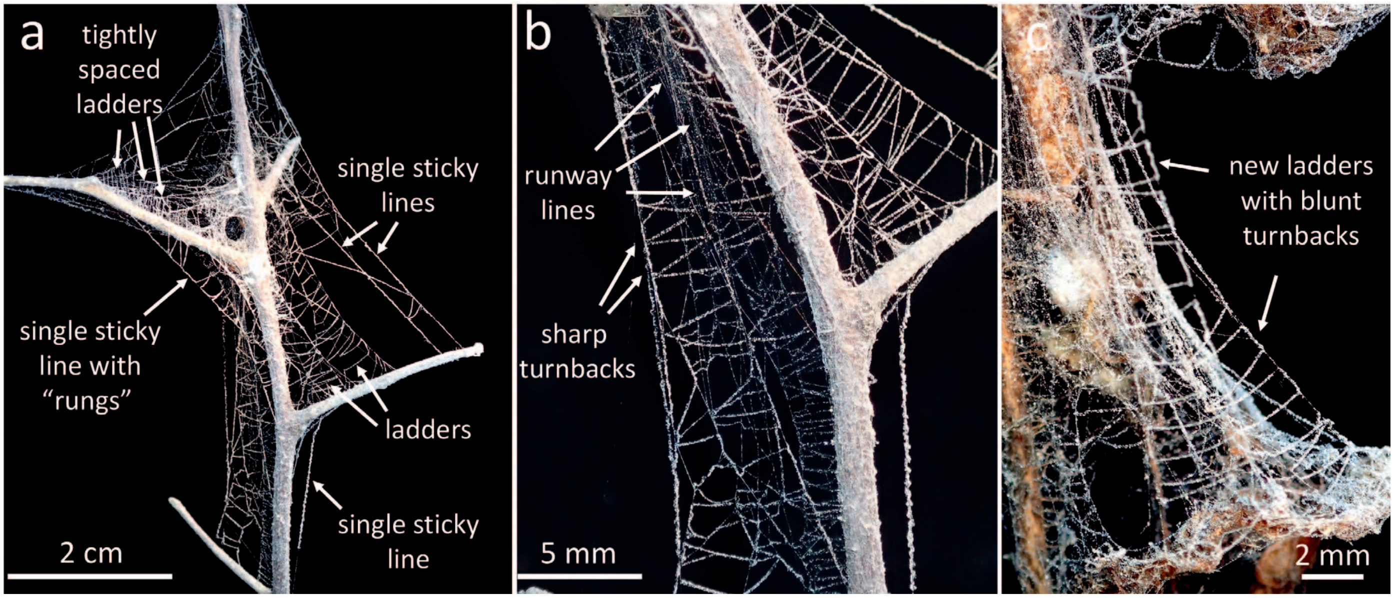

Figure 3.—Several subunits are distinguishable in these webs. The web in (*a*) and (*b*), which was photographed ten days after it was initiated from scratch in captivity, shows the following: a tubular retreat (hole next to the twig in *a*); multiple ladders and single sticky lines (*a, b*); a single sticky line with several "rungs" (*a*); ladders with especially tightly spaced sticky lines (*a*); and a small runway of fine non-sticky lines below the retreat (*b*). The web in (*c*) is a field web to which two silk ladders with blunt turnbacks were added the night after the spider and its web were brought into captivity (all other lines were part of the field web). This web illustrates how new additions were placed just beyond the external edges of previous webs.

extended asymmetrically toward that side (Fig. 2*k*). The capture portion of webs at the tips of branches of *Sida* sp. that was basal to the retreat averaged 79 ± 9% (range 42–93%) (Figs. 2*d*,e,*f*), but in other webs in which the web did not reach the tip of a branch (one on a *Sida* sp. plant and three others on other species of plants), the tendency for the basal portion to be larger disappeared (the mean fraction of the web basal to the retreat was 42 ± 12%) ($P = 0.0015$ with Mann-Whitney U Test).

At a more detailed level, I could not discern any consistent patterns of lines within field webs, other than two general trends that had multiple exceptions: lines near the edge of the web appeared to be longer (Figs. 2*c*,*g*); and a few short segments of sticky lines were often more or less parallel to each other (e.g., Figs. 2*c*,*g*,*i*). Eight webs photographed the morning after the first rain were all exceptional, however, in having clear ladders of sticky silk (Fig. 2*f*).

Webs in captivity: The sites where cribellum lines were added to field webs that had been brought into captivity showed a consistent trend to be located at the external edges of the webs (Figs. 3*c*, 4*a*). This impression might be thought to be due to an observational bias (lines in the interior would be more difficult to see); but the lax sticky lines often moved under the microscope, making them easy to see, and no moving lines were ever seen in the interior of a web; in addition, powdering of the web did not reveal previously unobserved sticky lines in the interior.

These additions to webs that had been brought in from the field, as well as the webs that were built from scratch in captivity (Figs. 3*a*, 4*b*–*d*, 5, 6), resembled field webs in lacking consistent overall forms. Although there was variation in the sites at which lines were added (some additions of sticky and non-sticky lines were near the retreat, some above it, some below it), these webs contrasted strongly with dry season field webs in that there were clear, consistent patterns of individual sticky lines that formed sub-units. At a rough estimate, >80% of the cribellum silk lines in the webs that were built from scratch had one of three forms: (1) a "silk ladder" formed by a zig-zag cribellum line built between a pair of long, approximately parallel non-sticky lines (Figs. 3–6); (2) a "twig-ladder" formed by a zig-zag cribellum line built between a twig and a long non-sticky line that was more or less parallel to a plant surface (Fig. 4*c*); and (3) a single cribellum line that was laid along a long, single non-sticky line (Figs. 4*b*,*d*; 5*a*,*c*) and attached to it at more or less regular intervals (Fig. 7*a*–*d*). In some twig ladders, I was unable to be absolutely sure that the cribellum line was attached to the plant surface rather than to non-sticky lines very close to the surface; in some cases, however, attachment to the plant seemed certain (arrows in Fig. 4*c*). The mean numbers of "rungs" in silk and twig ladders were 7.0 ± 4.3 ($n = 25$, range 3–18) and 7.2 ± 4.9 ($n = 30$, range 2–22) respectively; the mean number of attachments of the cribellum line to the non-sticky line in a single sticky line was 12.4 ± 5.7 ($n = 22$, range 3–20). It was not uncommon for a given cribellum line to form part of more than one arrangement: thus a cribellum line that formed a ladder sometimes continued as a "single" line along one of the two non-sticky lines of the silk ladder (Figs. 4*d*, 6*b*,*d*, 7*f*), or as a twig ladder (Fig. 5*c*), or continued from a twig ladder to a silk ladder. The distances between the zig-zag rungs in ladders sometimes varied dramatically in the same web (Fig. 3*a*).

In 17 webs that were built over one or two days in captivity, the mean numbers of different types of arrangements of sticky lines were the following: 1.7 ± 1.2 silk ladders; 1.6 ± 1.4 twig ladders; 1.6 ± 1.6 single sticky lines; and 1.3 ± 1.2 other arrangements. "Other" arrangements commonly involved zig-

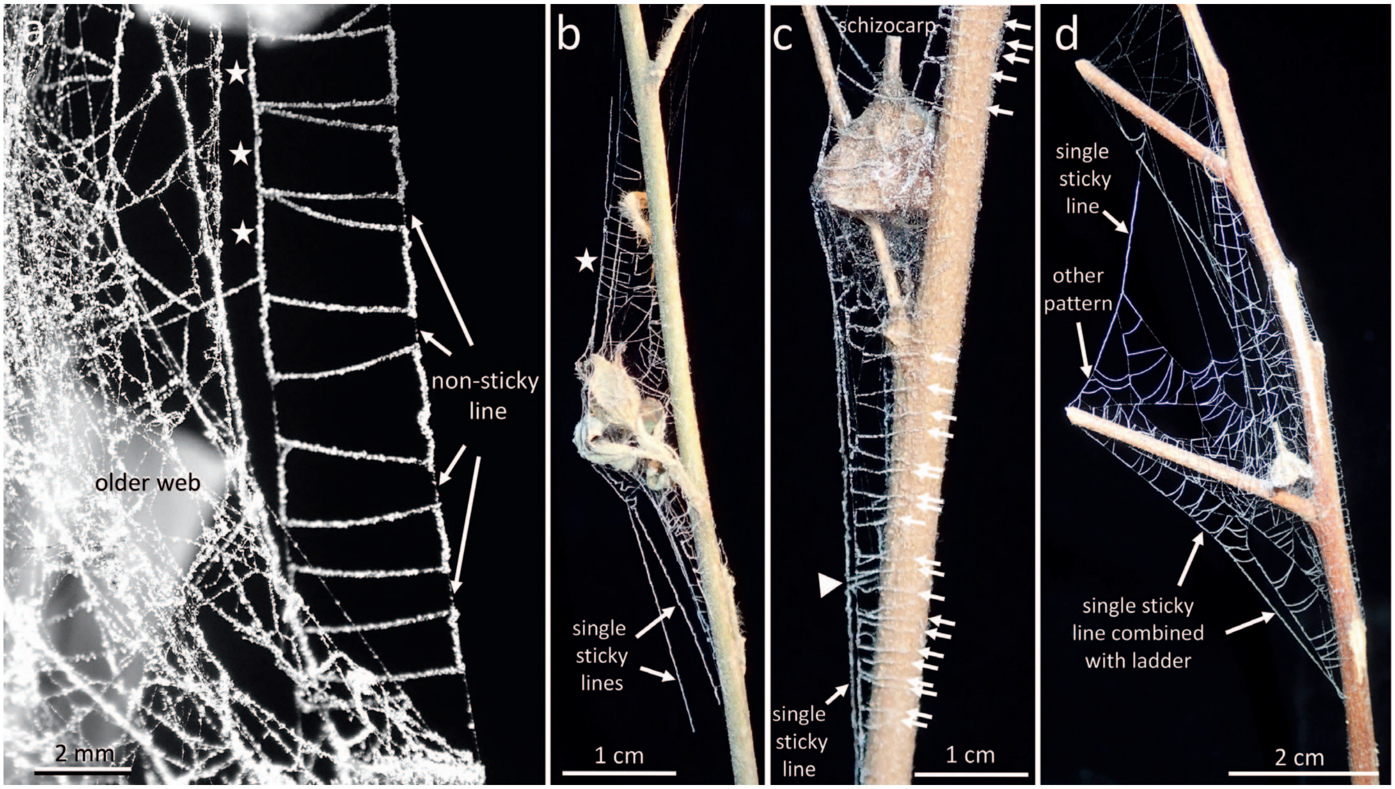

Figure 4.—These webs of *D. meditata* illustrate several subunits. (*a*) This silk ladder with blunt turnbacks was added in captivity to the right edge of a field web ("older web"). In the portions of the ladder's left border, a sticky line was presumably already present on the line when the spider built zig-zag cribellum line (indicated with stars). (*b*) This web, built from scratch in captivity, had two long single sticky lines below the retreat, and two above it; sticky zig-zag lines of a silk ladder were attached to one of these lines (star). (*c*) This web built on an experimental *Sida* sp. stem had twig ladders (arrows) below and above the retreat where the spider rested (under the inverted schizocarp glued to a fork), and a single sticky line with a single zig-zag (triangle). (*d*) This two day web built on an experimental *Sida* sp. twig had several long single sticky lines, the lowest of which was combined with a silk ladder. Also illustrated is an irregular pattern of sticky lines ("other pattern"); such patterns often showed partial resemblances to zig-zag patterns of sticky silk. Powder was removed from non-sticky lines by jarring the twig in (*b–d*).

zag cribellum lines attached to more than two non-sticky lines that were not necessarily parallel to each other (Figs. 4*d*), or short sticky lines attached to lines near the retreat (Fig. 5*c*). The most extensive set of additions made in a single night in captivity included eight silk ladders, two single sticky lines, short sticky lines near the retreat, and numerous non-sticky lines both near the retreat and farther away.

The cribellum lines in ladders made both "sharp" turn backs where the cribellum line contacted the non-sticky line at only one point (Figs. 3*b*, 7*e*,*f*), and "blunt" attachments where the cribellum line made an approximately 90° angle and ran along the non-sticky line for a short distance before returning to the other non-sticky line (Figs. 3*c*, 4*a*, 6*b*,*d*, 8*a*,*b*). Both configurations were common (16% sharp and 84% blunt in a sample of 45), and both sharp and blunt turn backs sometimes occurred in the same ladder (e.g., Figs. 4*a*,*d*, 7*e*,*f*). The portion of the cribellum line that ran along the non-sticky line in a blunt configuration was sometimes slightly coiled (Figs. 7*f*,*g*, 8*b*). but more often straight (Figs. 3*c*, 8*a*) (96% of 27).

Most commonly, the cribellum line in a single line had a small loop near the site of attachment to the line (Figs. 7b,c); much less commonly, it was folded more substantially (Figs. 7d, 8c,d); even less commonly, the cribellum line was straight, with no coiling at all (Fig. 7a).

Each cribellum line consisted of a complex combination of lines. In unusually highly coiled lines, where the components separated from each other in places, it was possible to distinguish different components: a straight non-sticky line on which the cribellum line was laid; a slightly undulating thin line ("baseline"); a thicker, glittering line or lines that were apparently coiled helically (bright coil); and a weakly scalloped bluish or greyish mat of cribellum fibrils (Figs. 8*c*,*d*). Apparent attachment discs fastening the cribellum line to the non-sticky lines were formed by small bright masses (Figs. 7*a*–*d*,*h*, 8*d*). In a few places the mat of cribellum fibrils separated slightly from the bright coils (Fig. 7*h*).

Freshly built cribellum lines in ladders were often lax: in a sample of 328 segments, 57% were lax (e.g., Fig. 8*a*). In contrast, the non-sticky lines were not lax in these or other ladders. Judging by the movements of the lax sticky lines in the weak air movements under the microscope, few of them would have lasted more than a few minutes before swinging into contact with another nearby line in the moderate dry season winds that occurred nearly every day at the study sites.

Building behavior.—One spider was videotaped for a total of 19.4 minutes during the first hour after nightfall while she added lines to a web that was brought into captivity after it had been damaged by rain earlier that day. Although nearly

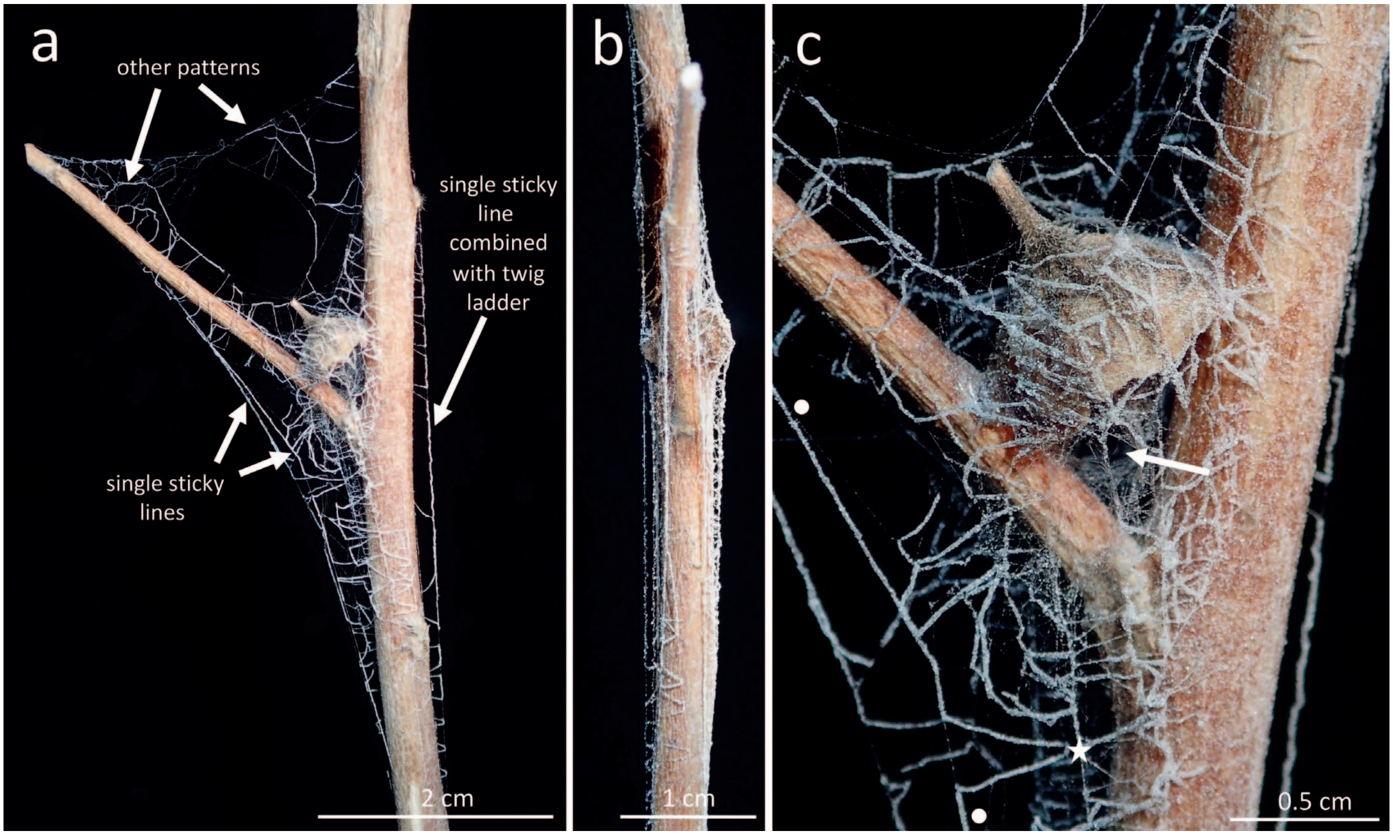

Figure 5.—This two-day web, built on a *Sida* sp. twig in which most potential supports had been removed, was nearly perfectly planar (the images in (*a*) and (*b*) differ by 90° in orientation). The web had one single sticky line combined with a twig ladder, and at least two other single sticky lines (*a*), and an unusual number of shorter sticky lines with no clear pattern (*c*). The spider used the empty schizocarp glued to the fork as a retreat (the arrow in (*c*) marks the mouth of the tubular retreat); numerous short sticky lines were near this shelter (*c*). The star in *c* marks a single zig-zag that was associated with a single sticky line (marked with dots). Powder was removed from non-sticky lines by jarring the twig.

all the lines were invisible in the video, it was nevertheless possible to distinguish several consistent details. The spider repeatedly returned to her retreat briefly between bouts of moving around her web. There was no sign that she removed lines: her legs and palps did not move as if packing lines together, nor did her anterior legs move as if dropping or flicking away an object. Most movements appeared to involve laying non-sticky lines. During this behavior near the retreat, her spinnerets were often spread widely; they sometimes appeared to move relative to each other in successive frames of the video, both at moments when she made attachments (Fig. 9*d*) and between apparent attachments. In no case did the spider hold her drag line with one leg IV while walking or while apparently making an attachment, as is typical in araneoids, uloborids and deinopoids (Eberhard 2020). In some cases, however, one tarsus IV appeared to hold the line to which an attachment was being made at the moment when the spider dabbed her spinnerets nearby (Fig. 9*d*). In many other cases (at least near the retreat), no legs were near the site where an apparent attachment was made. The spinnerets often protruded posteriorly when attachments of non-sticky lines were made (Fig. 9*d*). In several excursions, the spider moved only 1–3 body lengths from the mouth of her retreat and then immediately returned (perhaps building non-sticky runway lines).

The spider used type II behavior (Eberhard 1988) to comb cribellum silk from the cribellum: both legs IV moved simultaneously anteriorly and posteriorly, with the tarsus of the combing leg IV (which presumably brushed posteriorly across the cribellum – this detail was not resolved) resting on the tarsus of the other leg IV (Fig. 9*a*). In at least some sequences the spinnerets protruded posteriorly and were spread apart in both lateral (Fig. 9*e*) and ventral views (Fig. 9*a*) at the moment when the combing legs reached their maximum rearward extension. Both legs III were bent and extended ventrally, and were immobile (possibly holding a line or lines) while legs IV combed (Figs. 9*c*,*e*). In a few favorable viewing angles, glints from the lines showed that each leg III held a different non-sticky line during combing (Fig. 9*e*). At least sometimes one leg I may have held the same line being held by the ipsilateral leg III (Fig. 9*e*). The frequency of combing movements appeared to be approximately 10–15/s, but the movements were too rapid for me to determine their frequency precisely.

The spider periodically paused during combing behavior to apparently attach the cribellum line. Legs IV ceased combing and separated, and one or both reached ventrally and posteriorly to apparently grasp the line that was being held by one leg III (Fig. 9b). The spider raised (and slightly twisted) her abdomen laterally, bringing her spinnerets approximately

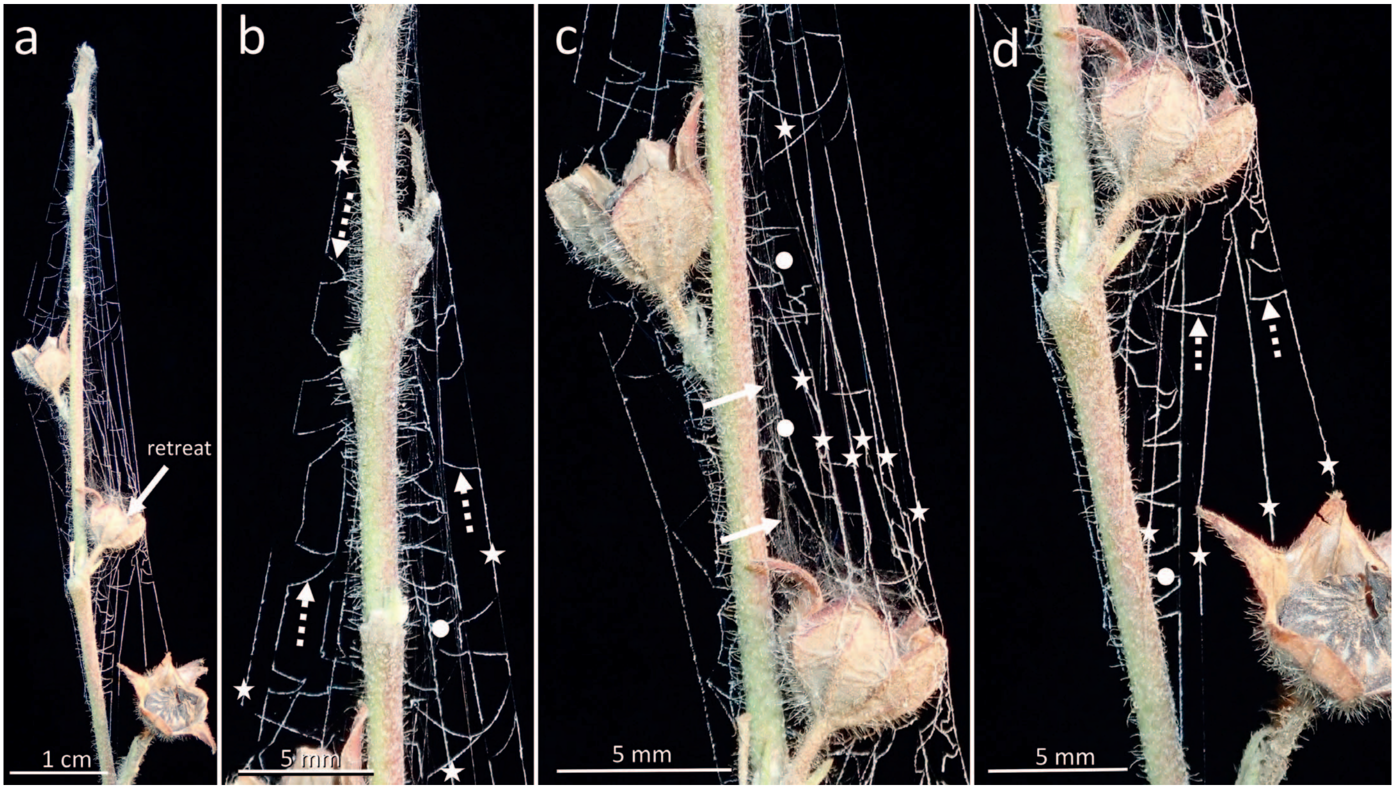

Figure 6.—This web built on a *Sida* sp. plant in captivity was unusual in not being at the tip of the branch; also atypically, it extended farther distally than basally from the retreat (*a*). Closeup views of different portions (*b–d*) show that it had an unusually large number of single sticky lines (stars) compared with ladders (dots), and also how single sticky lines sometimes merged with silk ladders (dotted arrows in *b* and *d*). There were few if any short cribellum lines on the schizocarp retreat (contrast with Fig. 5*c*), but a few possible runway lines extended distally (solid arrows in *c*)

to the level of the tips of her tarsi III, perhaps touching the line held by one leg III just posterior to point held by the tarsus (Fig. 9*b*) where it remained for approximately 0.1–0.2 s (upper dashed lines in Fig. 9*b*). Some other apparent attachments of the cribellum line were far from any legs, however. In no case did any leg appear to grasp a line posterior to the point where the attachment was made; this detail contrasts with several uloborids in which both legs IV consistently grasped the radius to which the cribellum line was being attached, one on either side of the attachment point (Eberhard 1972, 1982). On average, apparent attachments occurred every 9.0 ± 1.9s ($n = 23$, in 3 cribellum lines). In no case did the spider raise her leg IV as if to push the cribellum line onto a non-sticky line, as occurred in ladder construction by the eresids *Stegodyphus* spp. (Hingston 1923; Eberhard 1988). Combing resumed on average 0.63 ± 0.13s (maximum 0.9s, $n = 8$) following each attachment, after the abdomen had moved back to approximately its former position. Often legs IV exchanged combing and support roles following an attachment. The spider's anterior legs tapped rapidly anteriorly for a few tenths of a second after each attachment, and her body eased forward slightly and then became immobile again as she combed.

Because lines were not generally visible, I could not consistently determine with confidence the coordination (if any) between the production of non-sticky and sticky lines. In one case, however, cribellum line production began just after the spider had apparently built two non-sticky lines, moving across and then back in a space that was approximately seven body lengths long. She began combing within 0.1 to 0.2s after she turned back from apparently attaching the second of these lines to the substrate, and the cribellum line was laid in the same general area where the two non-sticky lines appeared to have been placed. In two other cases, the initiation of combing was immediately preceded by the apparent production of a single short non-sticky line that was only about 2–3 body lengths long; in at least one of these sequences, it was possible to see that the subsequent attachments of the cribellum line appeared to be in a single line in the general area where the non-sticky line had just been laid. Thus, the non-sticky lines on which these cribellum lines were laid may have been produced immediately preceding initiation of the cribellum line. Nevertheless, some other cribellum lines were apparently attached to lines that were already present. The initiation of one short bout of combing near the retreat (8 attachments) was not immediately preceded by any movements that might have involved the deposition of long non-sticky lines in that area and was immediately followed by a return to the retreat. Another short, clearly zig-zag line (9 attachments) was preceded by placement of, at most, only a single non-sticky line. Some bouts of combing occurred while the spider hung under lines (Figs. 9*a–c*,*e*), but others occurred while she walked on the upper surface of a plant structure.

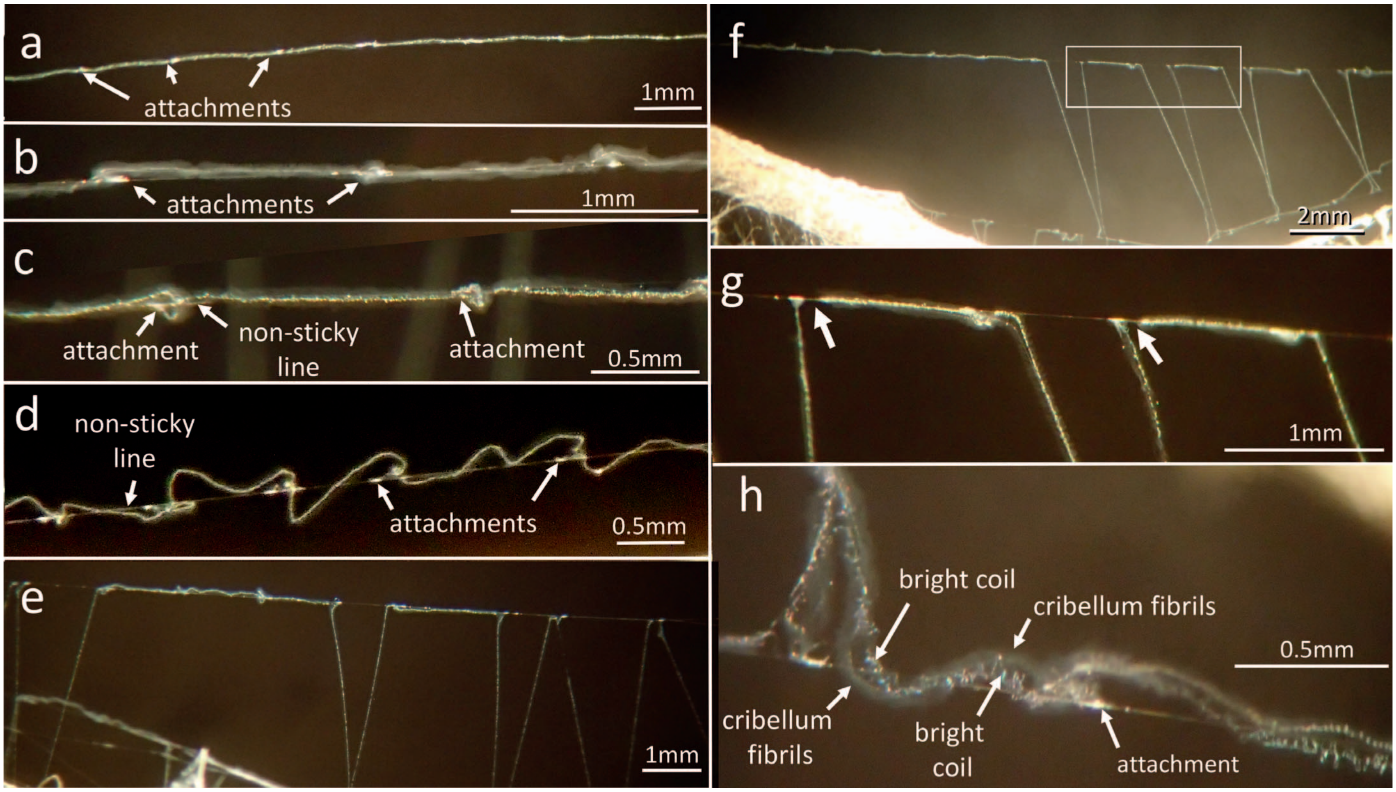

Figure 7.—Unpowdered cribellum lines seen under a dissecting microscope. The single sticky lines in (*a–d*) show increasing degrees of coiling on a non-sticky support line; small loops (*b, c*) were most common. The silk ladder in (*e*) has both sharp and blunt turnbacks; there are four attachments to the non-sticky line in the blunt turnback on the left. In (*f*), a single sticky line with small loops (left side) gave way to a zig-zag silk ladder (right side). An enlarged view (*g*) of the portion in the rectangle marked in (*f*) showed small apparent gaps in the sticky line (arrows) adjacent to attachment sites, revealing that the spider moved from left to right while building the cribellum line. In (*h*), small separations between the mat of grey cribellum fibers and the bright coil are marked with arrows near an attachment of a highly coiled cribellum line.

DISCUSSION

Webs of *Dictyna meditata*.—The overall forms of *D. meditata* webs seemed to be strongly influenced by the highly variable patterns of nearby plant structures (Fig. 2). When supports were available nearby, seemingly regardless of wherever they might be, the spider attached lines to them and the web extended in those directions. Similarly, it was possible to induce spiders to build nearly planar webs by only providing them with co-planar supporting structures (Figs. 4–6). Similar effects of supports on general web form are thought to occur in other dictynids (Bond & Opell 1997) (see also Blackledge et al. 2009 on webs in other groups that are tightly linked to the substrate). The lack of obvious, consistent organization in field webs of *D. meditata* (Fig. 2) was in general accord with the vague terms such as “irregular mesh” that have often been used to describe dictynid webs.

Nevertheless, the sticky lines that *D. meditata* added to webs in captivity, as well as the webs that they built from scratch in captivity and the webs photographed the day after the first rain showed several clear, highly repeated patterns: new cribellum lines were often laid in zig-zag ladder patterns, either between adjacent, approximately parallel non-sticky lines or between a single non-sticky line and a plant stem; and they were also often laid on a single non-sticky line, usually with a small loop near each point of attachment. New cribellum lines also almost certainly tended to be added to the outer edges of the existing structure, rather than to its interior.

Undoubtedly the greater geometric regularity of lines observed in lab as opposed to field webs was largely due to lax lines in the field swinging into contact with the substrate or other lines in the wind, quickly reducing their geometric regularity. The impacts of prey and detritus, and other disturbances and the tendency to simply add more lines to a web rather than remove damaged lines may also have obscured geometrically regular patterns.

It is not clear why *D. meditata* built lax sticky lines. Although lower tensions on sticky lines would be expected to give them greater abilities to both stop and retain prey, the function of laying lines that are so quickly modified under field conditions, losing both their regular spacing and their low tension when they adhere to other lines, is unclear. I know of similarly lax sticky lines in four other, distantly related non-orb groups: the eresid *Stegodyphus pacificus* Pocock, 1900 (Hingston 1923); synotaxids in the genus *Synotaxus* Simon, 1895 (Eberhard 1977, 1995; Eberhard et al. 2008); the zoropsid *Tengella radiata* (Kulczyński, 1909) (Eberhard et al. 1993), and pholcids in the genus *Belisana* Thorell, 1898 (Deeleman-Reinhold 1986; Huber 2005). The webs of all these groups except the eresid differed, however, in being built at sites deep in tropical forests (B. Huber pers. comm. for *Belisana*) where winds were often nearly imperceptible.

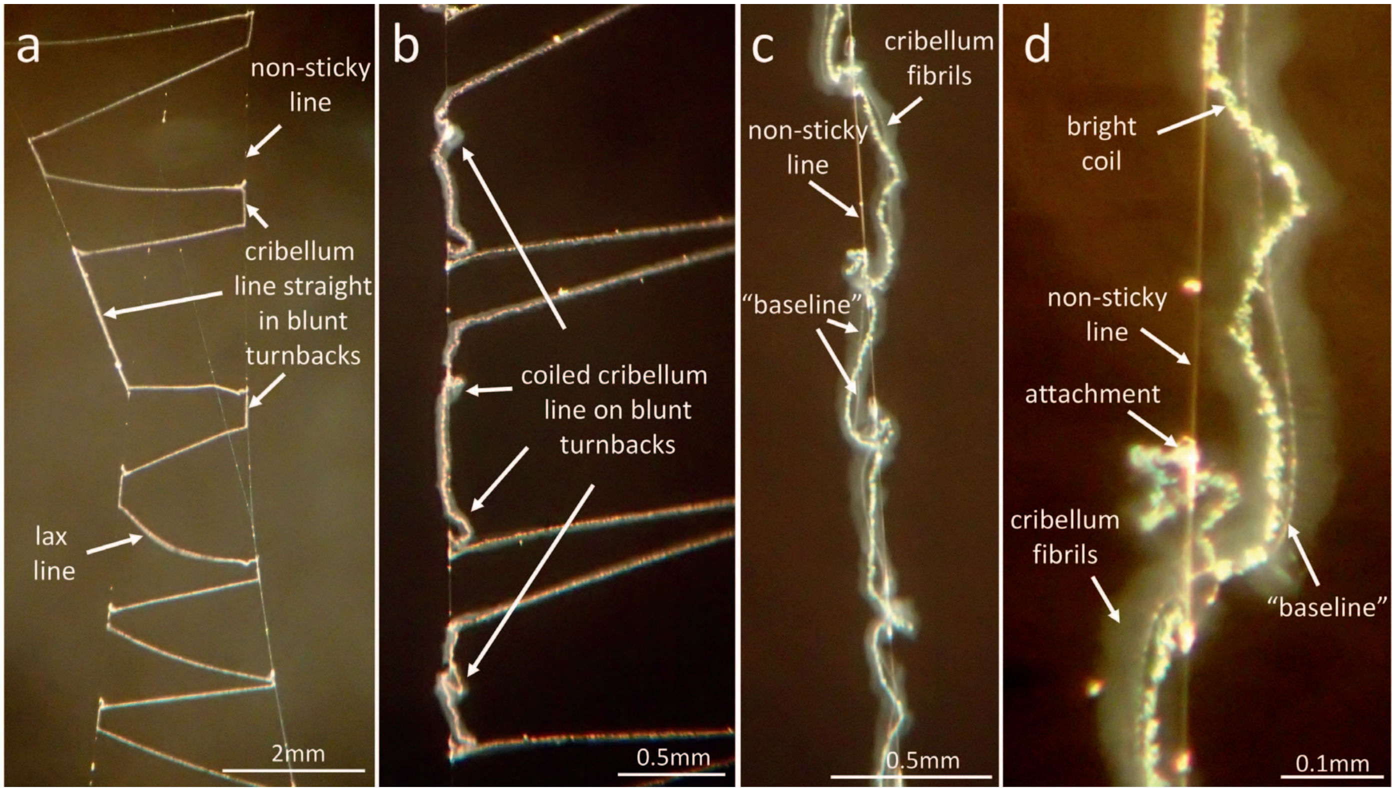

Figure 8.—Unpowdered sticky and non-sticky lines seen under a dissecting microscope. The cribellum line (brighter) in (*a*) zig-zagged between two non-sticky lines, forming a silk ladder. One lax "rung" hung in a curve and moved in gentle air currents. Most turnbacks in this ladder were blunt, and the sticky line was straight rather than coiled where it ran along the non-sticky line. The sticky line in (*b*) was slightly coiled in the portion where it ran along the non-sticky line in the blunt turnbacks in this ladder. In (*c*) and (*d*), an unusually highly coiled cribellum line that formed part of a single sticky line allows visualization of its components: a dense mat of cribellum fibrils; a "baseline"; a presumed piriform attachment to the non-sticky line; a bright, apparently coiled internal line; and the non-sticky support line. The outline of the mat of cribellum fibrils is only very slightly sculptured.

The webs of *D. meditata* do not fit easily into any of the categories used in recent studies of web evolution (Table 1). They were rarely planar and were usually distinctly three-dimensional (Fig. 2), so they are not appropriately called "sheets". Parts of the web were always in close contact with the substrate, but other parts were more or less aerial, so neither "aerial" nor "substrate" is entirely appropriate. The forms of their aerial portions varied widely, so "stereotyped" is clearly inappropriate. They were not truly irregular either, because both aerial and substrate-associated portions had clear geometric organizations (especially when newly built); thus "cob-web" is also not appropriate, either in the sense of a three-dimensional tangle of non-sticky lines, or in the sense of such a tangle that includes lines bearing adhesive near their attachments to the substrate (gumfoot lines) (Blackledge et al. 2009). The most directly applicable study (Blackledge et al. 2009), *Dictyna* webs were characterized as "irregular ground sheet webs"; none of these three descriptors is appropriate for *D. meditata* webs.

Clues to the possible functional significance of the web designs of *D. meditata* come from the prey that they captured. Many prey were relatively tiny insects such as chalcidoid wasps, psocopterans and thrips. The webs also apparently tended to capture flying rather than walking prey: worker ants were very uncommon, and the juveniles of several groups that were represented by winged adults (thrips, psocopterans, homopterans) were entirely absent. Jackson (1977) also documented a trend toward flying rather than walking prey in dictynids. The implication is that the function of the repeated patterns of sticky lines may be to capture flying prey. The fact that many sticky lines were attached directly to the twigs themselves suggests that the webs may be designed to capture flying prey that were very near the plant, perhaps in the process of landing on it. If insects in these groups tend to land on the tips of protruding branches (I know of no data on this point), this might explain the spiders' preference for building webs at the tips of plants.

The *D. meditata* trend toward especially small hymenopteran prey contrasts with some previous observations of dictynid prey. Bristowe (1958) noted that the prey (apparently of *Dictyna arundinacea* (Linnaeus, 1758)) were "often much larger than the spider herself". Jackson (1977) found that Diptera (presumably all adults) were overwhelmingly dominant in the webs of eleven solitary *Dictyna* Sundevall, 1833 and two solitary species of *Mallos* O. Pickard-Cambridge, 1902 (93.2% of 526 prey). These prey were also relatively large; nearly half (48.5%) were equal to or larger than the size of the spider. Further data on what types of prey are available at the sites where different species build their webs are needed.

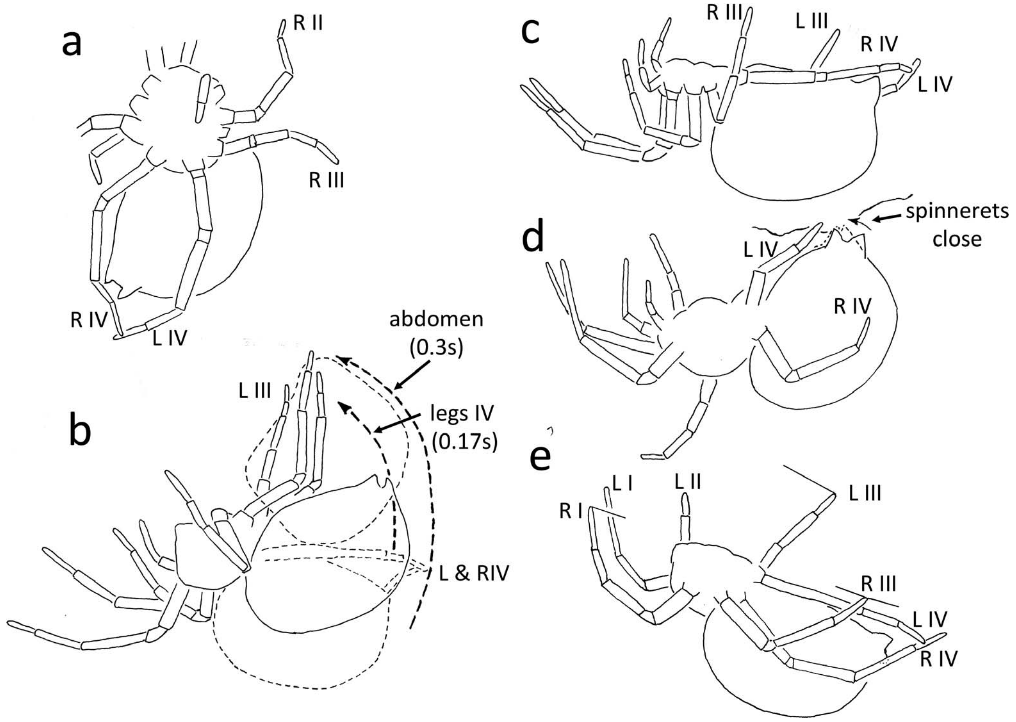

Figure 9.—Schematic drawings (traced from video images) of construction of sticky lines (*a–c, e*) and non-sticky lines (*d*) (legs whose positions were not clear in the video images are omitted). (*a*) Right leg IV combs cribellum silk and left leg IV supports the tarsus of right leg IV; the two legs are in their rearmost positions, at the end of a combing movement. The right and left spinnerets protrude posteriorly and are spread apart (see also *e*). (*b*) Following the end of a combing movement (lower dashed lines) the spider apparently attached the cribellum line. Legs IV were raised in the space of 0.17s (solid lines); the abdomen was slower, taking 0.3s to be raised to make the attachment (upper dashed lines). (*c*) The two legs III were flexed ventrally and immobile while legs IV combed out cribellum silk; the spinnerets protruded posteriorly at the end of the rearward combing stroke. (*d*) In the process of attaching a non-sticky line to a mass of silk from a previous web that was held by one tarsus IV, the spider's spinnerets closed in the space of 0.03s (dotted lines). (*e*) The two immobile legs III held different lines that glinted in the light from the camera while cribellum silk was being combed out by legs IV; these legs are in their rearmost positions, at the end of a combing movement, and the spinnerets are protruded posteriorly.

Construction behavior of *Dictyna meditata*.—In accord with other studies of both orb and non-orb weaving species (summary in Eberhard 2020), there were patterns in lower-level behavioral details of *D. meditata* behavior, such as how different legs grasp and manipulate lines. The sketchy observations reported here revealed the following: legs III may hold non-sticky line or lines to which cribellum lines will be attached while the cribellum line is being combed from the cribellum; cribellum silk attachments may be sited immediately posterior to the site grasped by tarsus III; cribellum silk is attached to non-sticky lines with piriform attachments rather than being simply laid onto non-sticky lines (as in *Stegodyphus* – see below); the non-sticky lines to which cribellum lines will be attached may be initiated immediately preceding construction of the cribellum line; the drag line is not held with one leg IV during non-sticky line construction, as in orb webs and some non-orbs (below); the spinnerets are spread and closed repeatedly during construction of non-sticky lines, and may serve as short-distance tactile organs to locate lines to which to attach (again in contrast with the behavior of araneoids – Eberhard 2020); construction is repeatedly interrupted briefly when the spider returns to her retreat, as is common in non-orb weavers (Eberhard 2020); the spinnerets are protruded posteriorly and spread with each combing movement, as also seen in *Mallos hesperius* (Eberhard 2019) (the only other dictynid whose behavior has been observed) as well as in some other cribellates (Peters 1984; Grannemann et al. 2019); and the tip of the tarsus of the combing leg IV rested on the tarsus of the supporting leg IV, as in *Mallos hesperius* (Eberhard 2019). Further observations with improved visibility of lines are needed to test most of these ideas. It is also important to note that my nearly exclusive emphasis on the sticky lines of *D. meditata* may have left further patterns in non-sticky line construction behavior unnoticed.

Comparing *Dictyna meditata* webs with those of other dictynids.—The cribellum lines of *D. meditata* differed strikingly from those of *Dictyna* sp. (Eberhard & Pereira 1993), which compound microscope and TEM images showed to lack both baselines (axial lines) and bright coils (reserve warp lines) accompanying the mat of cribellum fibrils. Baselines are lacking in clear photos of highly coiled cribellum lines of *D. calcarata* Banks, 1904 that showed bright coils and a mat of cribellum fibrils, where they should have been visible (Eberhard, in prep.); bright coils were not visible in cribellum lines laid on an egg sac in *M. hesperius* (Eberhard 2019). In contrast, *D. meditata* cribellum lines resembled those of *Mallos hesperius* (Eberhard 2019) and *D. bellans* (Eberhard 2021) in having bright coils, and perhaps also in including baselines (no baselines were noted in *M. hesperius,* but all of

Table 2.—Additions to the recent summary of dictynid web forms (Eberhard 2019) from observations of *D. meditata* (this study) and *D. bellans* (Eberhard 2021) ("*" are traits not included in Eberhard 2019).

Species	Retreat	Radial array	Ladder (zig-zags sharp/blunt)	Planar web	Aerial catching	Webs at tips of plants	Runway	*Twig ladders	*Sticky line in the blunt portion of zig-zags is straight or coiled	*Long n-s lines with crib silk
D. meditata	Y	N	Y (mostly blunt)	N[a]	Y	Y	A few	Y	Straight[b]	Y (small loops)
D. bellans	Y	Slightly	Y (both)	Y[c]	N	N	Y	N	Straight	Y (coiled)

[a] planarity can be imposed by the substrate
[b] occasionally with very small loops
[c] planar nature of webs due to their being appressed to planar substrates

the cribellum lines observed in this species were straight rather than coiled, so baselines would have been difficult to distinguish if they were present; a possible baseline in *D. bellans* is visible (though unlabeled) in the lower portion of fig. 1c of Eberhard 2021). This surprising morphological diversity, which presumably has functional consequences (e.g., Grannemann et al. 2019), requires further study.

The webs of *D. meditata* in the field resembled published photos of the aerial webs of several other dictynids, including *Emblyna annulipes* (Blackwall, 1846) (Bradley 2013), *Mallos niveus* (Jackson 1978), *M.* spp. (Bond & Opell 1997), *M. pallidus* (Eberhard 2019), *Dictyna volucripes* Keyserling, 1881 and *E. sublata* (Comstock 1967), and *Dictyna* sp. (Emerton 1902), in being usually built near the tips of the stems of small weedy plants, and in usually being three-dimensional arrays of both sticky and non-sticky lines. They also resembled the webs of these other species in having little if any overall consistent form or geometric pattern, and (at least in the case of *M. niveus*) in varying substantially intra-specifically in form in accord with available attachment sites (Jackson 1978).

Several of the subunits seen in *D. meditata* webs have also been noted in other dictynid webs (Table 2; Eberhard 2019). The known dictynid subunits include the following: silk ladders (several genera); twig ladders attached on one side to the substrate (only in *D. meditata*); runways of non-sticky lines (several genera); tubular retreats of non-sticky silk (perhaps all species); tiny zig-zags of sticky line at the web's edge very near the substrate (only in *D. bellans*); cribellum lines on single, slightly elevated non-sticky lines (in two genera) (in *D. meditata* they usually have a tiny loop near each attachment point, while in *D. bellans* and perhaps *Mallos pallidus* they form loose coils); and non-sticky spanning lines built across an indentation in the planar substrate on which the catching web is built (*Mallos hesperius, Emblyna* sp.). The leaf webs of *Emblyna* sp. and *Mallos hesperius* differed from those of *D. meditata* in never having coils of cribellum silk on non-sticky lines.

Categorizing non-orb cribellate webs and tracing their evolution.—The observations of *D. meditata* webs described above illustrate how the categories of web form that have been employed in recent studies of spider web evolution (e.g., Blackledge et al. 2009; Dmitrov et al. 2011; Bond et al. 2014; Garrison et al. 2016; Fernández et al. 2018a,b; Coddington et al. 2019) can lead to serious mis-representations. The characterization of *Dictyna* webs as "irregular ground sheet webs" (Blackledge et al. 2009) was inappropriate for *D. meditata* webs (and, for that matter, for the webs of other dictynids such as *D. bellans, Mallos niveus, M. hesperius*, or *Emblyna* sp.) (Jackson 1978; Eberhard 2019, 2021). The webs of *D. meditata* do not fit cleanly in any of the categories in this or any other recent web evolution study (Table 1).

This failure of these widely used categories supports previous suggestions that alternative types of categories may be needed (see Blackledge et al. 2009, Eberhard & Hazzi 2013, and Eberhard 2020 for discussions of problems with the "sheet" and "brushed sheet" categories). The modular nature of *D. meditata* webs, along with the possible patterns in the lower-level behavioral details of this species, suggest the outlines of an alternative approach. In what follows, I will argue that a focus on the modules or subunits that make up a web, on the behavior patterns that are employed to produce these modules, and on the patterns (or lack of patterns) in the sites in webs where these subunits are added (Table 3) may be more useful in attempts to trace the evolution of non-orb spider webs than the traditional focus on the entire web.

Modular units of web organization as categories: Both direct observations of web construction behavior and comparative analyses of web designs indicate that the construction behavior of both orb and non-orb spiders is organized into semi-independent, modular units (Eberhard 2018, 2020). This suggests that modular units similar to those seen in *D. meditata* webs might be useful categories for analyzing other non-orb cribellate webs (Table 3), and perhaps also the non-orbs of ecribellate spiders.

The "irregular" webs of many dictynids show little perceptible organization at an overall level, but nevertheless have clear regularities at lower levels (Table 2, Eberhard 2021). Other families may also have similar lower-level patterns that are combined with a lack of patterns in overall web forms. If apparently irregular and long-lived non-orb webs in other families are built piecemeal using consistent behavioral subunits like those of *D. meditata*, then previous reports of a lack of organization may be misleading. A clear example of the difficulty of perceiving organization occurs in the eresid *Stegodyphus pacificus*. Despite careful behavioral observations that documented that this species built stereotyped ladders of zig-zag sticky silk and that, when these were combined they formed "… a kind of open net" (Hingston 1923, p. 199), the web photo (Plate IX) of Hingston (1923) in this study shows no discernable sign of zig-zag organization in the abundant cribellum lines in the nearly planar sheet adjacent to the spider's retreat alongside a twig. Lopardo et al. (2004, figs. 10–12) give another clear example, in which clear early patterns in the placement of cribellum lines of the austrochilid *Thaida* *peculiaris* Karsch, 1880 were obscured by later additions to a web.

I suggest that instead of relying on the overall forms of field webs, it might be more informative in studies of web evolution to emphasize three other aspects: (1) identification of the design modules; (2) descriptions of the construction behavior that produces them; and (3) discovery of the patterns (if any) with which the modules are added to the web. The filistatid *Kukulcania hibernalis* (Hentz, 1842) offers an example of these types of regularity at the level of the additions themselves (they consisted of radial non-sticky lines laid moving away from the central retreat, and highly coiled masses of cribellum silk near their tips laid while moving back toward the retreat), and also in the locations where modules were added (they were laid over several nights in a relatively uniform pattern around the central retreat) (Eberhard 2020).

Another possible example of a behavioral subunit is the construction of zig-zag cribellum lines (Table 3). Zig-zag cribellum lines occur on the sparse sheets of non-sticky lines in the austrochilids *Thaida peculiaris* (Lopardo et al. 2004; Griswold et al. 2005) and *Hickmania troglodytes* (Higgins & Petterd, 1883) (Ramírez & Michalik 2019), and (less certainly – data are limited to a few photos of recently built lines) the psechrid *Psechrus* sp. (Eberhard 1988). The psechrid *Fecenia* sp. (probably *F. protensa* Thorell, 1891 – see Eberhard 2020) also built zig-zag patterns of cribellum lines, but at a larger scale (the zig-zag arcs crossed multiple non-sticky lines) (Zschokke & Vollrath 1995). The spider added the arcs to the web in a patterned sequence, working gradually inward from the outer portion to fill one side of the web, and then built and filled the other side the same way. Observations of the titanoecid *Nurscia* (= *Titanoeca*) *albomaculata* (Lucas, 1846) (Szlep 1966) also suggested zig-zag patterns of cribellum lines. These zig-zag patterns differ from the additional, lower-level zig-zag patterns of individual lines within the cribellum lines of the filistatid *Kukulcania hibernalis* that results from complex behavior of the spinnerets (Grannemann et al. 2019). It is worth noting that zig-zag patterns are not universal. The zoropsid *Tengella radiata* placed linear cribellum lines near the edges of sheets, and on lines near the mouth of the retreat when attachment sites for sheets were not available (Eberhard 2020, unpub.). Spiders in two other groups that lack sticky lines also did not tend to follow zig-zag patterns when building sheets: the diplurid *Linothele macrothelifera* Strand, 1908 (Eberhard & Hazzi 2013) and the lycosid *Aglaoctenus castaneus* (Mello-Leitão, 1942) (Eberhard & Hazzi 2017).

Ladders are zig-zags in which the cribellum line is laid between two more or less parallel non-sticky lines, rather than on a sheet. Silk ladders are also widely distributed in cribellate spiders, and thus may also be very ancient. In addition to the five dictynid genera in Table 2, web photographs suggest that they also occur in other families: the phyxelidid *Xevioso orthomeles* Griswold, 1990; the desids *Matachia* sp. and *Badumna longinqua* (L. Koch, 1867) (Griswold et al. 2005); possibly the titanoecid *Goeldia* sp. (Griswold et al. 2005); the eresids *Stegodyphus pacificus* (Hingston 1923) and *S. sarasinorum* Karsch, 1892, (Eberhard 1988); the stiphidiids *Neoramia* spp. (Marples 1959); and the gradungulids *Progradungula carraiensis* Forster & Gray, 1979 (Gray 1983) and *P. otwayensis* Milledge, 1997 (Ramírez & Michalik 2019) (Table 3). If one supposes that behavior that involves more precise control of which lines were attached to which other lines is more derived (as seems likely, at least in general – Eberhard 2020), ladders may be presumed to have evolved from zig-zag cribellum lines that were deposited on more extensive arrays of non-sticky lines; they may have subsequently evolved to be attached only to a single pair of parallel non-sticky lines.

Sharp vs. blunt zig-zags constitute another possible, though less certain modular difference. Zig-zags were consistently sharp in *Thaida* (Lopardo et al. 2004) and *Badumna longinqua* (Griswold et al. 2005), and consistently blunt in *Callobius bennetti* (Blackwall, 1846) (=*Amaurobius sylvestris*) (Emerton 1902), *Matachia* Dalmas, 1917 (Desidae) and *Progradungula* Forster & Gray, 1979 (Gray 1983; Ramírez & Michalik 2019). These data come from very small samples, however, and both sharp and blunt forms occurred in *Stegodyphus* (Eberhard 1988) as well as several dictynids, including *D. foliacea* (Hentz, 1850) (Comstock 1967), *D. volucripes* (Emerton 1902; Comstock 1967; Blackledge & Wenzel 2001), *D. meditata*, *Mallos hesperius* (Eberhard 2019) *Emblyna annulipes* (Blackwall, 1846)(Bradley 2013) and *E.* sp. (Eberhard 2019). Further observations are needed.

Modules in construction behavior: Details of the behavior that spiders use to construct silk ladders may also show patterns that can help elucidate evolutionary history. The evidence to date is too fragmentary to establish convincing patterns but can serve to illustrate the kinds of behavior that could eventually prove useful. Ladder construction by both the eresid *Stegodyphus pacificus* (Hingston 1923) and the gradungulid *Progradungula otwayensis* (Ramírez & Michalik 2019) shared some behavioral details and not others with *D. meditata*. In all three species, the spider first built the non-sticky lines that were roughly parallel to each other; in both *S. pacificus* and *P. otwayensis* these lines were connected with other lines (Ramírez & Michalik 2019 proposed that these "bridge" lines serve to hold the rails more nearly parallel to each other in *P. otwayensis*; the two vertical "non-sticky" rail lines of this species were unique in including cribellum silk that was not combed from the cribellum with the calamistrum, and were thus somewhat adhesive). The eresid differed from the other two species in that the spider attaches the cribellum line by lifting the cribellum line "... up with a hind leg and attaches it to one of the[main] lines" [e.g., without a piriform attachment disc] (Hingston 1923); most attachments of cribellum silk in the congeneric species *S. sarasinorum* were similar, although the spider occasionally also dabbed its spinnerets directly against the non-sticky line (Eberhard 1988). Cribellum silk is also sometimes laid onto other lines with one or both legs IV without attachment discs in the filistatids *Kukulcania hibernalis* (Eberhard 1988, 2020) and *Misionella mendensis* (Mello-Leitão, 1920) (Lopardo & Ramírez 2007).

The pattern of cribellum line zig-zags was highly stereotyped in *P. otwayensis*, and is presumably a derived feature unique to *Progradungula* capture webs: the spider initiated the sticky line of the ladder by moving downward, making a long diagonal between the two rail lines, followed by an "X" at the bottom, and then moving upward, making a series of "rungs" with blunt zig-zags that were each attached twice to the rail line. The first of each pair of attachments was immediately

Table 3.—Preliminary list (limited by the sparse knowledge of non-orb construction behavior) of the patterns in lines in webs (I) and of the behavioral details (II) that are employed during non-orb web construction that might be used to classify types of web construction. Example spider taxa are given for each behavioral category. It remains to be determined whether similarities are due to homologies or to convergences. Four additional behavioral uniformities that are shared by many of these groups are not included here: sticky lines are laid only after non-sticky lines have been laid; building is divided into repeated episodes of different types of behavior; spiders repeatedly interrupt construction to return to a resting place (e.g., a retreat); and sticky lines are added from the periphery of the web moving inward (see Table 5.1 of Eberhard 2021).

Trait	Genus	Family	References
I. Patterns in webs			
Sticky lines zig-zag on a sheet of non-sticky lines	*Diplothyron*[a]	Linyphiidae	W. Eberhard, unpub.
	Thaida, Hickmania[b,c]	Austrochilidae	Lopardo et al; 2004; Griswold et al. 2005; Ramírez & Michalik 2019
	Psechrus[b,d]	Psechridae	Eberhard 1988; Zschokke & Vollrath 1995
Sticky lines are straight on a sheet (or a reduced sheet) of non-sticky lines	*Tengella*	Zoropsidae	W. Eberhard, unpub.
Sticky lines zig-zag between pairs of approximately parallel non-sticky lines) (silk ladders)	*Dictyna, Emblyna, Mallos*	Dictynidae	Eberhard 2018, 2019; this paper
	Progradungula[e]	Gradungulidae	Gray 1983; Ramírez & Michalik 2019
	Stegodyphus[f]	Eresidae	Hingston 1923; Eberhard 1988
	Neoramia (= *Ixeuticus*) *charybdis* (Hogg, 1910)[b]	Stiphidiidae[c]	Marples 1959
	Matachia, Badumna	Desidae	Griswold et al. 2005
	Xevioso[b]	Phyxelididae	Griswold et al. 2005
	Goeldia[b]	Titanoecidae	Griswold et al. 2005
Cribellum lines that are laid along non-sticky lines are straight (S), slightly curled (SC), or highly coiled (HC)	*Matachia* (S)[g]	Desidae	Griswold et al. 2005
	Badumna (S)[g]	Desidae	Griswold et al. 2005
	Progradungula (SC)[e,h]	Gradungulidae	Ramírez & Michalik 2019
	Stegodyphus (SC)	Eresidae	Eberhard 1988
	Dictyna meditata (SC)	Dictynidae	This study
	Kukulcania, Filistata (HC)[i]	Filistatidae	Grannemann et al. 2019
	Dictyna bellans (HC)	Dictynidae	Eberhard 2019
Uniformly spaced sticky line forms an approximate spiral (or a sector of a spiral) centered on the spider's resting site[j]	*Oecobius*	Oecobiidae	Solano-Brenes et al. 2018
	Nurcia (= *Titanoeca*)	Titanoecidae	Szlep 1966
	? (#117)[k]	Amaurobiidae[k]	Eberhard 2021
	Fecenia	Psechridae	Robinson & Lubin 1979; Zschokke & Vollrath 1995
Sticky lines zig-zag between a non-sticky line and the substrate	*Dictyna meditata*	Dictynidae	This study
	Misionella	Filistatidae	Lopardo & Ramírez 2007
II. Behavioral details			
Spinneret movements during and between attachments serve to spread aciniform fibers that are being added to a sheet	*Linothele*	Dipluridae	Eberhard & Hazzi, 2013
	Aglaoctenus	Lycosidae	Eberhard & Hazzi 2017
Leg(s) IV lay sticky lines onto non-sticky lines to attach them there	*Kukulcania*	Filistatidae	Eberhard 1988, in press
	Misionella	Filistatidae	Lopardo & Ramírez 2007
	Stegodyphus	Eresidae	Hingston 1923; Eberhard 1988
Leg III holds the non-sticky line just anterior to the site where spinnerets contact it when attaching the cribellum line	*Kukulcania*	Filistatidae	Eberhard 1988, 2020
	Tengella[l]	Zoropsidae	Eberhard 1988
	Stegodyphus	Eresidae	Eberhard 1988
	Psechrus	Psechridae	Eberhard 1988
	Dictyna meditata[m]	Dictynidae	This study
Spider builds radial, non-sticky lines starting from a central retreat, and then lays sticky lines while returning to the retreat	*Kukulcania, Misionella*	Filistatidae	Eberhard 2020; Lopardo & Ramírez 2007
Spider executes a complex alternation of non-sticky and non-sticky lines to produce a rectangular pattern	*Synotaxus*	Synotaxidae	Eberhard 1977, 1995; Eberhard et al. 2008
Spider makes complex crochet-like extensions of a tightly meshed sheet	*Chrosiothes*	Theridiidae	Eberhard et al. 2008; Eberhard, unpublished)

[a] based on direct observations of building behavior

[b] evidence is weak, in some cases from only a single photo of a web being built

[c] zig-zags (with a few exceptions) are described clearly in *Thaida*; a similar pattern occurs in *Hickmania* (M. Ramírez pers. comm.)

[d] the zig-zag pattern was only approximate in *Psechrus*

[e] the rails included uncombed cribellum silk, and were somewhat sticky

Table 3.—Continued.

[f] differs from others in attaching the cribellum line to the non-sticky line without using piriform silk

[g] tentative characterization based on photographs that lack sufficient magnification for certainty

[h] the portions of the cribellum lines that run parallel to the rails are between lax and very lax, and have a folding structure (M. Ramírez, pers. comm., so HC might be more appropriate

[i] the acquisition of highly coiled cribellum lines late in the ontogeny of *K. hibernalis* (G. Barrantes pers. comm.) suggests that highly curled lines are derived rather than plesiomorphic

[j] in all but *Oecobius* the non-sticky lines to which sticky lines are attached have approximately radial orientations

[k] tentative identification in 1975 by H. W. Levi (family name may have changed subsequently); number refers to specimen in the Museum of Comparative Zoology, Cambridge, MA

[l] sometimes both leg III and ipsilateral leg IV held the line just anterior to the attachment site

[m] this characterization is tentative: lines were not visible; the site of tarsus III was often obscured by the spider's abdomen at the moment of attachment; and, in some cases, tarsus IV was nearby and possibly also grasped the line. It was clear, however, that no legs grasped the line posterior to the attachment site, so the difference with uloborids (see text) is certain

adjacent to the previous attachment to that rail, and the rail lines were thus coated with sticky silk. This pattern, with blunt turnbacks and rungs of the ladder converging regularly on both sides of the ladder (Ramírez & Michalik 2019), was never seen in any *D. meditata* webs, or in photos of the webs of any other species with ladders (Table 3).

It was not clear whether *S.* spp. and *P. otwayensis* shared two other construction details that may occur in *D. meditata*: construction of non-sticky support lines that immediately precedes initiation of a cribellum line laid onto the non-sticky line just produced; and use of legs III to hold the supporting "main" lines during combing. Both of these behaviors occur on the filistatid *K. hibernalis* (Eberhard 1988): the non-sticky line to which the cribellum line would be attached was laid immediately preceding the initiation of combing; and one leg III held the non-sticky line during combing. This leg III continued to hold the non-sticky line at the moment when the cribellum line was attached to it, as may also have occurred in *D. meditata,* and also in *S. sarasinorum* and the psechrid *Psechrus* sp., and the zoropsid *Tengella radiata* (in other cases tarsi III and ipsilateral IV held the line just anterior to the attachment point) (Eberhard 1988) (Table 3). In contrast, legs IV consistently grasped the non-sticky line on either side of the sticky line attachment point in seven species in four genera of Uloboridae (character B2 in Eberhard 1982).

These observations of behavioral details are obviously only fragmentary. But other similar details of leg positions and in the order of line placement in orb weavers show consistent taxonomic patterns (Eberhard 1982; Kuntner et al. 2008), as do the positions and movements of legs III and IV while combing out cribellum silk in orb and non-orb cribellates (Eberhard 1988; Griswold et al. 2005; Ramírez & Michalik 2019). Thus, behavioral subunits like those just described may help elucidate web evolution.

Discerning patterns in "single bout" and "multiple bout" field webs: The fact that the wear and tear on webs in the field can obscure geometric patterns implies that appropriate classification of webs in the field may be easier for some kinds of webs than for others. One possibly useful criterion to evaluate the likely usefulness of classifications of field webs is the temporal pattern of their construction. Some species build their webs in a single bout of activity, and their webs are thus likely to provide more useful information on stereotyped behavioral subroutines that are employed in their construction. An incomplete list of examples includes the following: orbs and related webs in Araneoidea, Uloboridae and Deinopidae; the aerial sheet webs of Linyphiidae (Benjamin & Zschokke 2004) and Pholcidae (Eberhard 1992 on *Modisimus* Simon, 1893); various web designs in theridiids (Freisling 1961 on *Cryptachaea* (= *Theridium*) Archer, 1946; Jörger & Eberhard 2006 on *Nihonhimea* Yoshida, 2006); the substrate sheet webs of some Dipluridae (Eberhard & Hazzi 2013 on Karsch,1879), and Lycosidae (Eberhard & Hazzi 2017 on *Aglaoctenus* Tullgren, 1905); the radiating trip lines of some Pisauridae (Eberhard 2007 on *Thaumasia* Perty, 1833) and Oecobiidae (Solano-Brenes pers. comm. on *Oecobius* Lucas, 1846); and the catching ladders of Gradungulidae (Gray 1983; Ramírez & Michalik 2019 on *Progradungula*). Single bout webs that are frequently destroyed (e.g., by rain) and that are replaced daily are likely to be especially useful.

In contrast, other species extend their webs gradually in multiple bouts of "patchwork" building activity, often over the space of several nights or weeks (even, in some such as *Tengella radiata*, from one instar to the next) (Barrantes & Madrigal-Brenes 2008). Geometric patterns of lines in long-lived, multiple-bout webs are less likely to be perceived because these webs are subject to greater accumulations of damage and subsequent modifications. In some species, the sequence of sites where additions are built in the web show spatial patterns, as in the filistatid *Kukulcania hibernalis* (Eberhard 2020), and the additions themselves are also built with stereotyped subroutines (as in *K. hibernalis* and *Misionella mendensis*) (Eberhard 1988; Lopardo & Ramírez 2007). Even here the accumulation of later additions and damage in the field can obscure patterns present in earlier lines. In other groups the additions are made at sites that do not have consistent spatial patterns, as in *Dictyna meditata.* This inconsistency, along with subsequent damage, means that field webs can offer even less help in understanding underlying patterns in their designs. If the trend observed in *D. meditata* of adding sticky lines to the edges rather the more internal portions of the web occurs in other species, then the edges of multiple bout webs may offer the best chance of deciphering geometrically regular sub-units in the field (see, for instance, the apparent ladder with sharp zig-zags at the outer edge of the *Badumna longinqua* web in fig. 205C of Griswold et al. 2005); patterns may be clearest immediately after environmental damage to webs such as a rain storm.

The origin of orbs: The evolution of even the most distinctive and easily recognized of the web categories used in recent studies, the orb web, will probably be better understood by recognizing subunits of behavior. Orb web construction consists of several subroutines (radius construction, hub construction, etc.) that are guided by distinctive suites of stimuli (Eberhard & Barrantes 2015; Eberhard 2020). The cues that are used to guide orb web construction behavior, as well as the responses that spiders make to these cues, appear to have been particularly conservative over evolutionary time (Eberhard & Barrantes 2015). Understanding the evolutionary origins of orbs would likely be improved by tracing the evolution of these different subroutines and of how different cues are used. The existence of subroutines as evolutionarily discrete units in orb construction was confirmed in a study of 69 different behavioral transitions from orb construction to the construction of webs derived from orbs: numerous subroutines were found to have been repeatedly shuffled and recombined independently over evolutionary time (Eberhard 2018). It seems highly likely that at least some of these subunits had different evolutionary histories prior to the evolutionary origin of orbs per se.

One possible example of a behavioral trait employed in building orbs that probably arose prior to the origin of orbs are the patterns of building sticky lines only after non-sticky lines have been built, and of starting sticky line construction at the outer edge of the web and working inward; both are widely distributed traits among non-orb cribellate spiders (Table 3, Eberhard 2020). Similarly, radius construction, with radial lines being laid while moving away from a central area, and being laid one after the other on approximately opposite sides of the web, occurs in Oecobiidae (Solano-Brenes pers. comm.), a non-orb family that is linked to deinopid and uloborid orb weavers in some recent phylogenies (e.g., Garrison et al. 2016; Wheeler et al. 2017; Fernández et al. 2018a,b). These behavior patterns may thus also be older than orbs. The radial lines of *Oecobius concinnus* Simon, 1893 differed from those of orb weavers in being attached to the substrate at multiple points, and in not being attached to frame lines (Solano-Brenes pers. comm.), suggesting that there are further subroutines in radius construction that may have different histories. In sum, orb web construction behavior presumably did not arise all at once *de novo*, but rather from a group of ancestral behavior patterns that probably had prior evolutionary histories of their own. Understanding the history of orb web evolution will be enriched by understanding these different histories.

Furthermore, the subunits of orb as well as non-orb construction are underlain by additional, consistent "mechanical" patterns, such as which legs are utilized to perform functions like holding lines for attachments (Eberhard 1982, 2020), and the structure of attachment discs (Wolff et al. 2019); these lower level subunits may also show useful taxonomic patterns. Of special interest in this context are four behavioral traits that may represent synapomorphies of orb weavers and their descendants (Eberhard 2020): cut-and-reel behavior; construction of frame lines as part of radius construction; the "final angle" pattern of choosing where to build each new radial line; and construction of non-sticky temporary spirals working outward from the hub.

General conclusions.—The change in focus that I am suggesting for studies of web evolution entails recognizing and assembling lists of structural sub-units in webs, documenting the patterns (if any) in which spiders distribute these sub-units in their webs, describing the behavior patterns used to build these sub-units, and elucidating homologies. Table 3 presents a preliminary attempt (limited by the scarcity of observations of non-orb weavers) to enumerate the kinds of subroutines that might prove useful in Dictynidae and other families. These tasks will admittedly require additional work before evolutionary sequences can be determined. But in the end, the hard-earned data from sophisticated, powerful molecular techniques that enable construction of the phylogenies of different spider groups will be of limited usefulness in elucidating the evolution of web construction behavior until web designs are represented more accurately and completely. Even understanding the origin of orb webs themselves will require a change in emphasis, because the behavioral subunits employed to build orbs must have arisen, at some stage, from behavior patterns used to build non-orbs. In sum, a more effective use of phylogenies as tools to elucidate behavioral evolution will depend on better understanding of the behavior itself.

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