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# Web building and prey wrapping behavior of *Aglaoctenus castaneus* (Araneae: Lycosidae: Sosippinae)

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**Abstract.** Funnel webs are common and widespread taxonomically, but little is known about how they are built or details of their structure. *Aglaoctenus castaneus* (Mello-Leitão, 1942) (Lycosidae) builds horizontal, densely meshed funnel webs of non-adhesive silk, with a tangle of lines above. Web construction behavior was unique in that the spider frequently laid swaths of lines rather than simple drag lines, both to float bands of fine lines on the breeze as bridges to distant objects and to fill in the sheet. Spiders utilized special spinneret movements to widen the swaths of lines that they laid on sheets. These movements have not been seen in web construction by other araneomorphs, but are were similar to and perhaps evolutionarily derived from those used during prey wrapping by many other species. Observations, made with a compound microscope, of the construction behavior of the agelenid *Melpomene* sp. O.P. Cambridge 1898, and of lines and attachments in sheets of these species and another funnel web spider, the zoropsid *Tengella radiata* (Kulczyński, 1909) demonstrated the possibly general nature of including obstacles in the web. This probably disadvantageous behavior may be related to constraints in selecting web sites imposed by the need for sheltered retreats, or to the spider's inability to remove preliminary lines. The observation also showed the importance of further improvements in the discriminations made between "sheet" and "brushed" webs in recent discussions of spider web evolution.

**Keywords:** Sheet web, funnel web, web evolution

The evolutionary history of prey capture webs in spiders includes complex series of acquisitions and losses (e.g., Kaston 1964; Kullmann 1972; Vollrath & Selden 2007; Bond et al. 2014). "Sheet" webs constitute one widespread class of webs with a more or less planar, horizontal dense array of lines where the spider walks and captures prey. One common and widely distributed type of sheet web built by taxonomically diverse spiders is the "funnel web", a tightly meshed, approximately horizontal sheet of generally (though not always) non-adhesive lines on top of which the spider walks, and which is connected at one edge with a tubular retreat. Some funnel webs also have a tangle of lines above the sheet. Funnel webs occur in Dipluridae (Coyle 1986; Paz 1988; Viera et al. 2007; Eberhard & Hazzi 2012), Agelenidae (Bristowe 1958), Zoropsidae (Eberhard et al. 1993), Pisauridae (Nentwig 1985; Santos 2007) and Lycosidae (Hingston 1920; Brady 1962; González et al. 2015). Funnel web construction has almost never been observed directly (see Rojas 2011; González et al. 2015). Nevertheless, dense swaths of fine lines (presumably from the aciniform glands) are said to be laid across other lines in the sheet and seldom (if ever) attached to them with piriform attachment discs in some "brushed" funnel webs (Blackledge et al. 2009). Funnel webs have probably evolved convergently in different groups, but details have yet to be resolved.

Most species in the large, monophyletic wolf spider family Lycosidae (approximately 2400 species) (Platnick 2016) are vagrant hunters and do not build any silk structure to capture prey. However, a few genera build funnel webs and recent molecular studies suggest that lycosids may be descended from web builders (e.g., Bond et al. 2014; Fernández et al. 2014). These species, which tend to have longer posterior lateral (PL) spinnerets (Yoo & Framenau 2006), are in the genera *Hippasa* Simon, 1885, *Aulonia* C.L. Koch, 1847, *Anomalosa* Roewer, 1960, *Venonia* Thorell, 1894 (the latter two are thought to be sister genera – Yoo & Framenau 2006), *Sosippus* Simon, 1888 and *Aglaoctenus* Tullgren, 1905 (the only two genera of the New World subfamily Sosippinae) (Hingston 1920; Brady 1962; Santos & Brescovit 2001; Viera et al. 2007; González et al. 2015). The funnel webs described for sosippine lycosids resemble those of Agelenidae in several respects, and fit the characterization of "brushed" sheet webs (J. A. Coddington, pers. com.): they consist of dense, extensive, approximately horizontal sheets that are connected at one edge with a tubular retreat, and often have a tangle of lines above the sheet (Santos & Brescovit 2001; Viera et al. 2007; González et al. 2015).

Both morphological and molecular traits indicate that Sosippinae is monophyletic (Santos & Brescovit 2001; Murphy et al. 2006). Conclusions from these recent analyses were contradictory, however, regarding the evolution of web construction in lycosids. One model consistently suggested a non-funnel web ancestry for the family Lycosidae, and four independent origins of funnel webs within Lycosidae. A second suggested that funnel web construction was an ancestral lycosid trait (Murphy et al. 2006), in accord with the speculation of Jocque & Alderweireld (2005) that lycosids were originally forest-dwelling web builders.

With respect to sossipine web structure, all four species in the genus *Sosippus* for which observations are available build funnel webs (Brady 1962), but with somewhat different designs. The tunnel retreats of *S. californicus* Simon, 1898 and *S. texanus* Brady, 1962 were often in cavities in the ground (Brady 1962), while those of a species in Costa Rica (presumably *S. agalenoides* Banks, 1909, the only species reported from this country) were often a meter or more above the ground, and the silk tunnels were built among the leaves and branches of weeds and shrubs (W. Eberhard, unpub. obs.). The sheet portions of the webs of *S. agalenoides* and *S. californicus* were relatively larger than those of *S. texanus* and



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*S. floridanus* Simon, 1898 (Brady 1962). The closely related, widely distributed South American sosippine genus *Aglaoctenus* includes five species (Santos & Brescovit 2001; Piacentini 2011). Santos & Brescovit (2001) characterized *Aglaoctenus* webs as "a horizontal non-adhesive sheet with width and length between 4.5 and 90 cm" connected to a tubular retreat, with "vertical barrier threads" above the sheet. Photos of the webs of both *A. castaneus* (Mello-Leitão, 1942) (Santos & Brescovit 2001) and *A. lagotis* (Holmberg, 1876) (Viera et al. 2007; González et al. 2015) conform in to this description. However, the limited descriptions of *A. yacytata* Piacentini, 2011 webs (of a mature female with eggs, and a juvenile), mention a silk tube but no sheet (Piacentini 2011).

Funnel web construction behavior is surprisingly poorly known, despite the wide taxonomic and geographic range of groups that build funnel webs and their relative abundance. Two brief studies of funnel web construction were performed in captivity. Rojas (2011) studied the early stages of web construction of the agelenid *Melpomene* sp. and González et al. (2015) observed the sosippine lycosid *A. lagotis*. One brief field study (Eberhard & Hazzi 2012) described the early stages of web construction by the diplurid *Linothele macrothelifera* Strand, 1908. All three studies were fragmentary in many respects. The diplurid's behavior was the simplest. The spider appeared to lay only one kind of silk, which consisted of a swath of lines produced while the spider moved about on the substrate near the tubular retreat; there was no preliminary skeleton of lines. On the other hand, the two araneomorph species performed two types of building behavior very early in web construction. One consisted of more or less straight, approximately radially oriented movements from near the mouth of the tunnel to the edge of the web and beyond to attach lines to the substrate and to each other, thereby producing a support or "skeleton" sheet. The second type consisted of more erratic, wandering movements across the skeleton web, during which the spider swung her abdomen repeatedly from side to side, often with her PL spinnerets spread laterally, filling in the skeleton with a sheet of fine lines. The two types of behavior alternated, and their relative durations varied. These two species also differed from the diplurid in attaching lines to each other and to the substrate with brief dabs of the tip of the abdomen that probably produced piriform attachment discs (mygalomorphs lack piriform glands). Fragmentary observations (Hingston 1920) indicated that the lycosid *Hippasa olivacea* (Thorell, 1887) also built a skeleton web of single lines, and then filled it in with swaths of finer lines. By selectively sealing individual spinnerets of *A. lagotis* with paraffin and observing close-up video recordings of spiders constructing webs, González et al. (2015) deduced that the support or skeleton lines emerged from the anterior lateral (AL) spinnerets (and may thus be major ampullate gland lines), while the fill-in lines came from the PL spinnerets (and are thus aciniform gland lines – see below). They also reported on the likely metabolic costs of web construction, in terms of reductions in the spider's immune responses.

The observations of Santos & Brescovit (2001) concerning the approximate numbers and locations of the spigots of different glands on different spinnerets in *Aglaotenus* provide an important morphological foundation for observations of spinning behavior reported here. The AL spinneret has two major ampullate gland spigots and 70-80 piriform spigots; the posterior median (PM) spinneret has 30-40 aciniform spigots; and the longer PL spinneret has 30 aciniform spigots, all on the medial-ventral surface of the elongate triangular distal segment. We thus assumed in the descriptions below that lines that emerged from the PL spinnerets were aciniform lines.

Here we report observations of *A. castaneus* webs, construction behavior and prey-wrapping, and observations of the webs and behavior of *Melpomene* sp. (Agelenidae) and *Tengella radiata* (Kulczyński, 1909) (Zoropsidae). This report has several objectives: to document some basic differences between funnel web construction behavior and the better-studied orb web construction that are important for understanding the evolution of funnel web designs; to provide a basis for future comparative studies of funnel web construction; to point out the potential usefulness of several behavioral details as taxonomic characters (see Eberhard 1982, Kuntner et al. 2008 for examples in other spiders); to document the possible evolutionary origin of one aspect of funnel web construction in prey wrapping behavior; and to provide criteria to help improve some over-simplifications made in recent discussions of the evolution of spider webs.

## METHODS

**Study area.**—We observed *A. castaneus* in the field on 21–24 August, 2013 in riparian and secondary dry forest in the Parque Natural Regional El Vínculo (3°, 50′, 23" N, 76°, 18′, 07" W; elev. 950–1100 m), a tropical dry forest zone in the Holdridgian classification (Espinal & Montenegro 1963). The reserve is contiguous with the edge of the floor of the Cauca Valley, 3 km south of the Municipio de Buga, Valle del Cauca, Colombia (elev. 1020 m).

**Field observations.**—The spiders were extremely abundant (Cabra-García et al. 2010). We measured the approximate width and length of each web with a ruler and sketched the outline of the sheet. In order to observe web construction and freshly-built webs in which patterns in lines could be more easily deciphered, we removed webs in the field in the afternoon, leaving only the mouth of the tunnel and the tunnel itself intact (the mouth of the tunnel will be termed the "retreat" hereafter). We then waited in the evening to watch spiders build (until about 23:00), and returned for further observations at 04:00 the following morning. We repeated this procedure with different webs on three days. We made recordings of a total of >60 min of the behavior of two mature females using a SONY HDR-HC9 camera equipped with and near infra-red illumination ("night shot") and a +4 closeup lens; the spider's body could fill the frame in closeup shots.

This recording method of illumination provided an unanticipated payoff. Occasionally, when the angles of view were favorable, the illumination glinted off lines that the spider was producing; we used these occasional glints to determine the positions of lines. This technique had the limitation that only those lines that were at favorable angles to the illumination were visible. In some cases, different lines "lit up" in successive frames of a recording, demonstrating that not all the lines that a spider was producing at a given moment were necessarily visible in a given frame. There were often many successive

frames in which no lines were visible, followed by one or a few frames in which many lines were visible. Given our substantial recording time, however, we were able to build up general ideas regarding some common spinning processes. Our drawings represent particular spiders at particular instants, but these moments were chosen to illustrate what were typical aspects of behavior. Similarly, our ability to see lines only occasionally and perhaps incompletely meant that we had to assume that an "attachment" occurred each time the spider brought her spinnerets into contact with other lines or a solid substrate (these presumed attachments will be called "attachments" hereafter), and that attachments involved the production of piriform discs. We were only able to confirm directly that some attachments had occurred by observing that lines adhered to previous putative attachment sites (Fig. 6a); in no case did we check for attachment discs. When the spider swung her abdomen laterally, we termed the side toward which the abdomen moved as the "leading side", and the other as the "trailing side". We also photographed 35 webs after dusting them with talcum powder. We left six powdered new webs built on the first night intact, and checked them for further additions on the following two days.

We collected samples of lines in the sheets of newly spun webs or of large repair sectors that had been built the night before for *A. castaneus, Melpomene* sp., and *T. radiata*; we pressed a plastic ring (made from the top 2–3 cm of a plastic drinking cup) against the underside of the sheet, taped the sheet to the sides of this ring, and cut it free with scissors. We took care not to include the tangle above the sheet (this control was especially strict in *T. radiata* and *Melpomene* sp.). Sections of these samples were later carefully taped to microscope slides, cut free from the rings, and viewed without a coverslip or any further treatment at ambient indoor temperature and humidity in San Jose, Costa Rica. Although the sections of the sheets survived these treatments intact, it was possible that the tensions on lines on the slide were not the same as they had been in intact webs.

**Observations of *A. castaneus* in captivity.**—We observed web construction by four mature females and one penultimate male in two 30 × 20 cm terraria with the bottom covered with moist earth in which a retreat had been made by inserting a finger into the earth. We observed fragments of construction behavior of all four females, and filmed two of them. A black cloth was placed behind the cage to increase the visibility of the silk lines. Repair behavior was elicited by cutting a circular hole in the sheets of three females; one repair was filmed.

We tested for prey wrapping behavior using acridid grasshoppers, noctuid moths, and calliphorid flies. Because spiders only wrapped the flies, we then staged six wrapping episodes with flies, two for each female. Attacks were staged between 19:00 and 20:30, and filmed with a SONY HD-ACHD video camera. We also observed prey capture and wrapping with three gryllid crickets during the day in the field. One mature female *Melpomene sp.* was filmed in captivity during a bout of construction behavior that followed the capture of a fly on her relatively intact sheet web.

In order to avoid the use of the less specific "it" and thus increase the clarity of behavioral descriptions, we adopted the convenient illusion (as in Spanish, French, and German) that all spiders are females, and will refer to "her legs", etc. Because of the problems in providing precise descriptions of web forms that do not correspond to common English words, and because of the history of inconsistent use of terms such as "sheet" and "funnel" in previous publications (see the discussions of Viera et al. 2007 and Blackledge et al. 2009), we use photographs and drawings extensively. We describe spinneret movements in some detail because they are useful in resolving which lines in the web resulted from which glands (González et al. 2015). Because of our reliance on glints to visualize lines, our descriptions may constitute only a partial list of the basic behavioral "vocabulary" of these spiders. In our descriptions we use the words "thick" and "thin" only with reference to the overall diameters of lines, and not to the diameters of the fibers that may or may not have comprised them. We use the category "orbicularians" (which may be paraphyletic – see Garrison et al. 2016) in only a descriptive sense, to denote araneoid and deinopoid families.

Specimens of *A. castaneus* were kindly identified by Adalberto Santos, and vouchers are deposited in the Museo de Entomología of the Universidad del Valle (MUSENUV), Cali, Colombia, and in lot "*A. castaneus* UFMG 4990" of the Universidade Federal de Minas Gerais, Brazil. Specimens of *Melpomene* sp., collected previously as part of the study of Rojas (2011), were identified by D. Ubick; specimens of *T. radiata* were also identified previously, as part of the study of Eberhard et al. 1993. Vouchers of *Melpomene sp.* and *T. radiata* are in the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica.

## RESULTS

*Aglaoctenus castaneus*

**Webs in the field.**—The >100 webs that we observed in the field resembled in general terms the previous photographs and descriptions of the webs of *A. lagotis* and *A. castaneus* (Santos & Brescovit 2001; Viera et al. 2007; González et al. 2015). Each web consisted of an approximately horizontal, densely meshed sheet that was continuous with the lower surface of a tubular retreat at one edge; most webs also had a tangle of lines above the sheet (Fig. 1). We can add several details. The spider usually rested immobile day and night at the retreat on the upper surface of the sheet, fleeing briefly into the tunnel when disturbed, only to re-emerge a few minutes later. The tunnel's diameter was consistently very large compared with the size of the spider (Fig. 1b, c). The sheets of mature adults and penultimate nymphs were near but always somewhat above the ground (usually about 10–30 cm), rather than being on its surface (Figs. 1a, b, 2a–c); a few were much higher, up to >1 m above the ground. The outer portions of a few sheets had long straight lines or very sparse sheets just below them (Fig. 2a–c). Finally, five partially destroyed, detritus-laden webs were found in which there was a female carrying an egg sac.

When we removed approximately 20 sheets of adults and penultimate nymphs in the field, we found that more than half had at least fragments of a second, evidently older sheet with abundant holes and detritus a few cm beneath it, often draped loosely on the ground or other supports. The lax nature of the older sheets and their separation from the newer sheets suggested that the old webs had been at least partially destroyed by the spider before the newer sheets were built,

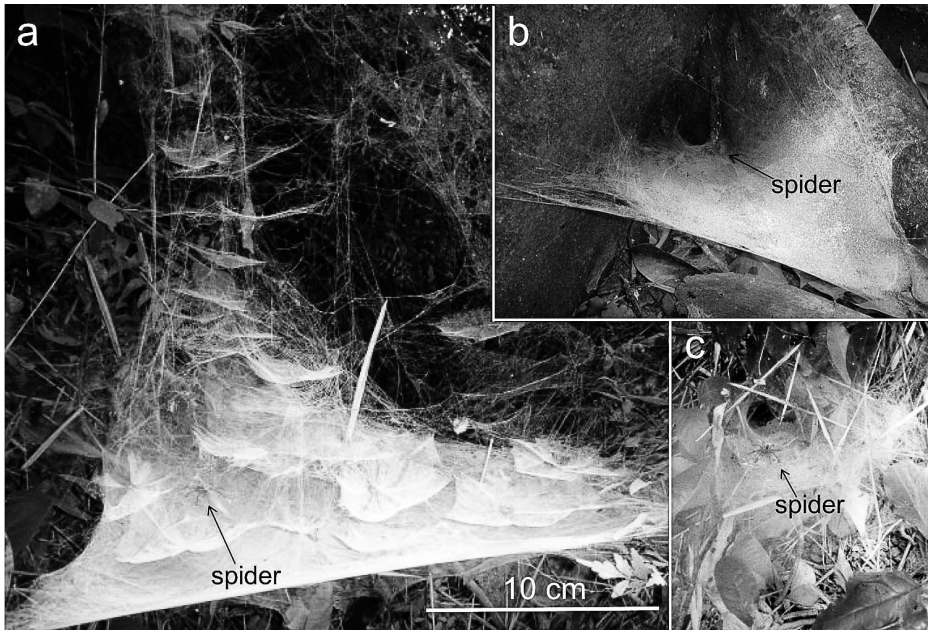



Figure 1.—Webs of *Aglaoctenus castaneus*. (a) Lateral view of the web of a mature female of *A. castaneus* with the spider (arrow) resting near the tunnel mouth on a typical, approximately horizontal sheet that was near but nevertheless above the ground. The tangle above this sheet (outlined in part by the large number (>18) of orb webs of the commensal uloborid *Philoponella* sp.) was especially high (95 cm). (b) Approximately horizontal web of a mature female at the base of a tree trunk; there were no supports available above the sheet, and the web had no tangle. The left edge of the sheet was more sparsely filled in than the rest. The spider (arrow) rested during the day in a typical position near the tunnel mouth, which was very large compared with the spider. (c) Web of a mature male, visible resting on the sheet near the retreat. This web differed from others in lacking multiple tiers.

and that spiders did not simply build a new sheet directly on top of a pre-existing sheet (though this did occur in captivity). We did not observe *A. castaneus* cutting silk lines, but it is worth noting the behavior used to cut silk lines in *A. lagotis* (M. González, pers. comm.) differed from the cutting behavior of araneoid and deinopoid spiders. The lycosid appeared to break lines mechanically, rather than chemically, by tugging and pulling on lines with her chelicerae and her entire body.

There was usually a tangle of lines above the sheet. In adult webs, the tangle often extended 30-50 cm above the sheet, and sometimes up to >2 m; tangles often had multiple orbs (up to about 20) of adults and nymphs of the apparently commensal uloborid *Philoponella* Mello-Leitão, 1917 sp. (Fig. 1a). When coated with white powder, many of the tangle lines appeared to be relatively thick; but fine, lax lines were also abundant in some tangles. Both fine and thicker lines occurred in the tangles of newly built webs, and in webs that lacked commensals, so they were likely produced by *A. castaneus*. At some sites, where there were no attachment sites available directly above the sheet, there was no tangle (Fig. 1b).

Some isolated attachment points for both the sheet and the tangle were very likely inaccessible from the retreat via walking (e.g., Fig. 1a), indicating that spiders likely used airborne bridge lines to obtain access to some web supports.

Detailed examination of lines near the edges of newly built sheets, where the densities of lines were lower and different types of lines were easier to distinguish, revealed both long, sparse, relatively straight and apparently thicker lines that were attached to supporting objects, and abundant apparently thinner lines that were often somewhat parallel or that radiated from apparent points of attachment to the thicker lines (Figs. 2b, 3c, d). These two types of line probably correspond to the skeleton and fill-in lines ("DTT" and "DDT" lines) that González et al. (2015) observed in *A. lagotis* (the thicker lines may have been cables of fine lines, however; see descriptions of behavior below).

Another apparently new detail was that sheets almost always (except perhaps for that of one mature male—see below) had several small swaths of approximately 10–20 more or less parallel, thin, lax lines that were one to a few mm above the sheet (Fig. 2a) (we will call these "tiers"). We did not discern a pattern in the locations of tiers on the sheet, other than that they seemed to span small concavities. Often the swath of lines in a tier was up to one cm wide in places, and the fine lines often converged to at least some extent at one edge (arrow in Fig. 2b). Although the PL spinnerets were relatively long (about 1.0 mm in an adult female) and could be spread so their tips were about 1.75 mm apart, some tiers were thus often substantially wider (Figs. 2b, 3c, d). Some sheets also had larger, sparse sheets above the main sheet (Fig. 4).

In a few webs, one or more dead twigs or stems protruded through the sheet (Fig. 5a, b). There were also upward bulges in some sheets (Fig. 5c) where objects such as dead leaves just below the sheet projected upward.

**Construction behavior.**—*General movements:* We observed sheet but not tangle construction behavior. Ten of the eleven spiders whose webs were destroyed in the afternoon and then rechecked made a replacement web on the following night. In

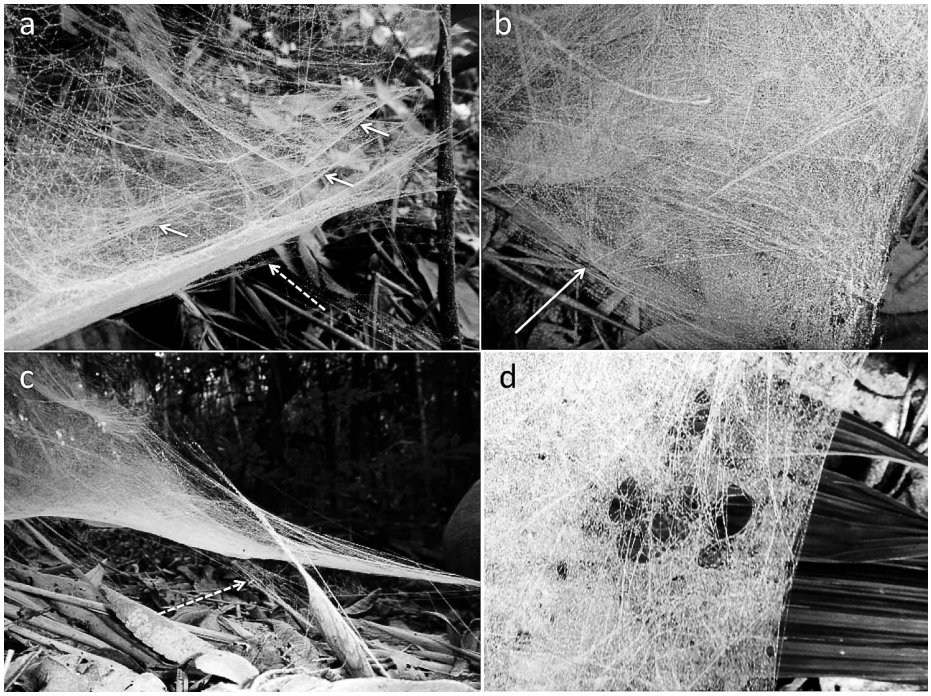



Figure 2.—Webs of *Aglaoctenus castaneus*. (a) Edge-on view of the far edge of a sheet. There is a complex array of small, sparse sheets ("tiers") of more or less parallel fine lines (solid arrows), and a possible "false start" just below the main sheet (dashed arrow). (b) Dorsal view of the far edge of the sheet. A clearly distinguished swath of widely diverging lines is attached at the edge of the sheet (arrow). (c) A larger "false start" group of lines below the outer portion of another sheet dashed arrow). (d) Holes produced in a newly built sheet where a cricket was captured.

captivity, we observed two episodes of building by two spiders in detail, from beginning to end. Construction behavior in these cases was intermittent, with bursts of activity that lasted on average 19 ± 7 min ($n = 26$), interspersed with pauses near the retreat.

We were not able to distinguish thick lines from thinner lines as they were being built; all glimpses of lines provided by glints revealed swaths rather than only one or two lines being produced, even during the early stage when long, apparently strong lines from the retreat were built (Fig. 6n); in no case was it certain that only thick lines were being produced. We suspect that many of the thicker lines in finished webs (e.g., arrow heads in Fig. 3b) consisted of cables of smaller diameter lines (perhaps including both fine aciniform gland lines and thicker ampullate gland lines).

Although spiders may have tended to lay thicker lines earlier in construction, thick lines and swaths of fine lines were often produced as part of the same process, even very early in construction (Fig. 6). In one web, the spider repeatedly ($n = 6$) laid long lines between the retreat (or lines nearby) to objects that were five or more body lengths away, where the far edge of the sheet would be. Typically, she did not attach the lines she was producing to any other lines on the trip away from the retreat, and walked on the vegetation at the far edge of the web before finally attaching one or a few times to a leaf or a twig (Fig. 6k); she then returned more or less directly to the near vicinity of the retreat apparently along the line she had just laid, again making few or no attachments along the way (Fig. 6c, d). Presumably these long lines corresponded to the long, thick lines visible at the far edges of some finished webs in the field (Fig. 3c, d).

Close-up video recordings showed that even when the spider was laying such long lines, she produced swaths of multiple lines (Fig. 6d, n, o). Some of the fine lines that were laid along with the early skeleton web lines contacted other lines in the sheet, but others billowed loose in the gentle breezes, and may have been used to float bridge lines to distant objects. The maximum distance we saw a line float was 1 m. Construction of strong support lines also sometimes occurred later, during periods when the spider was apparently filling in the spaces between thick lines with swaths of fine lines. In sum, we were unable to distinguish stages of skeleton web construction and filling-in behavior (*sensu* González et al. 2015) in terms of thick and thin lines.

We did not see enough behavior to be able to be sure whether there were any patterns in the sequences of areas of the web in which the spider worked during early sheet construction, except that she frequently returned to the mouth of the tunnel. Occasionally she paused there for a minute or more, or immediately left again to continue construction in either the same or a different sector.

*Details of spinneret and leg movements during early stages of web construction:* Early in web construction (Fig. 6a, d, f), the two PL spinnerets were often spread laterally, with each emitting a swath of fine lines (Fig. 6f). Occasional lateral views suggested that these spinnerets were also flexed dorsally, and that the AL spinnerets were flexed ventrally (Fig. 6d). In some cases it appeared that, when one or both PL spinnerets were

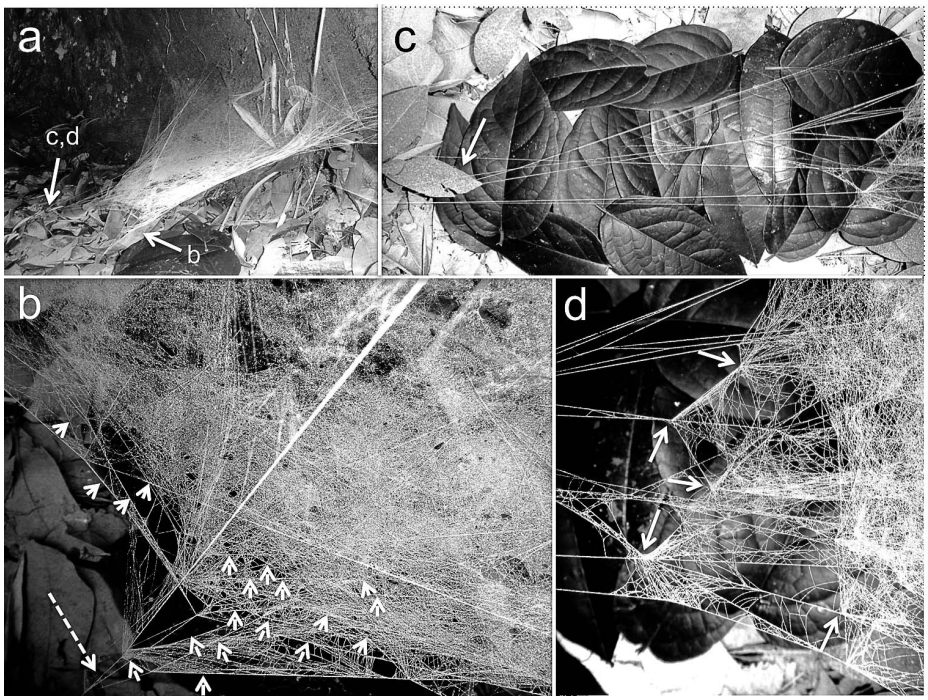



Figure 3.— Details of the far edge of a sheet, where the lines were less dense and thus more easily resolved, reveal an organization into skeleton and fill in lines. (a) View of the sheet built with its retreat against a buttress root near the ground, and almost completely lacking tangle lines. The two portions of this web illustrated in close-ups in (b)–(d) are indicated with arrows. (b) Some of the long, straight, and in at least some cases, perceptibly thicker "skeleton" lines near the edge are marked with arrowheads; (c) Several long "skeleton" anchor lines extended beyond the sheet. (d) Some of these skeleton lines shown in (c) were connected by apparently thin, loose (curved) fill-in lines; in some places, many apparent fill-in lines radiated from an attachment point (marked with arrows).

directed more posteriorly, the swath of lines condensed into what appeared to be a single line. A further complication was that the spider sometimes clapped or rubbed her PL spinnerets together repeatedly while she was walking, perhaps causing aciniform gland lines to adhere either to each other or to ampullate gland lines. In other cases, the PL spinnerets waggled medially rapidly but did not touch each other (left portion of Fig. 6b), or one waggled medially while the other was quiet; the consequences of these movements for the lines being laid were not clear.

Figure 4.—Webs of *A. castaneus* that had a sparse, "extra" sheet above the main sheet. (a) In this lateral view looking toward the tunnel mouth of a newly built web that nearly entirely lacked a tangle above, there was a sparse sheet of thin lines just above the main sheet (arrow). There was also a sector near the right edge of the sheet that was perhaps older, or less densely filled in. (b) Seen in lateral view, another web shows a more extensive tangle above, in which two "extra" sheets are visible (arrows). The right edge of the main sheet is relatively sparsely filled.

The way the spider walked along a single long line (as, for instance, when she returned toward the retreat along a long line that she had just laid early in construction) was often strikingly different from that of orb weavers, and indeed from any other published description of spider behavior that we know of. Instead of using the legs on both sides of her body to grasp the line and support her weight, the spider used mostly or exclusively the legs on only one side; the legs on the opposite side of her body were extended, and were either immobile or waved in the air below her body (Fig. 6c) (in some cases lower leg I was also used to grasp and contact the line along which she was moving). In one case, the spider began a return trip along a long line using the legs on both sides for three to four body lengths, and then shifted to holding the line with only ipsilateral legs (those on only one side of her body). In walking along the line, upper leg II (LII in Fig. 6c) followed upper I (LI in Fig. 6c), upper III followed upper II, and upper IV followed upper III (similar following behavior between adjacent ipsilateral legs is widespread in orb weavers—Hingston 1922; Eberhard 1987a). In contrast, when *A. castaneus* walked on a solid surface such as a trunk, following behavior was uncommon: even though some movements were coordinated (e.g., III did not make its next step forward until

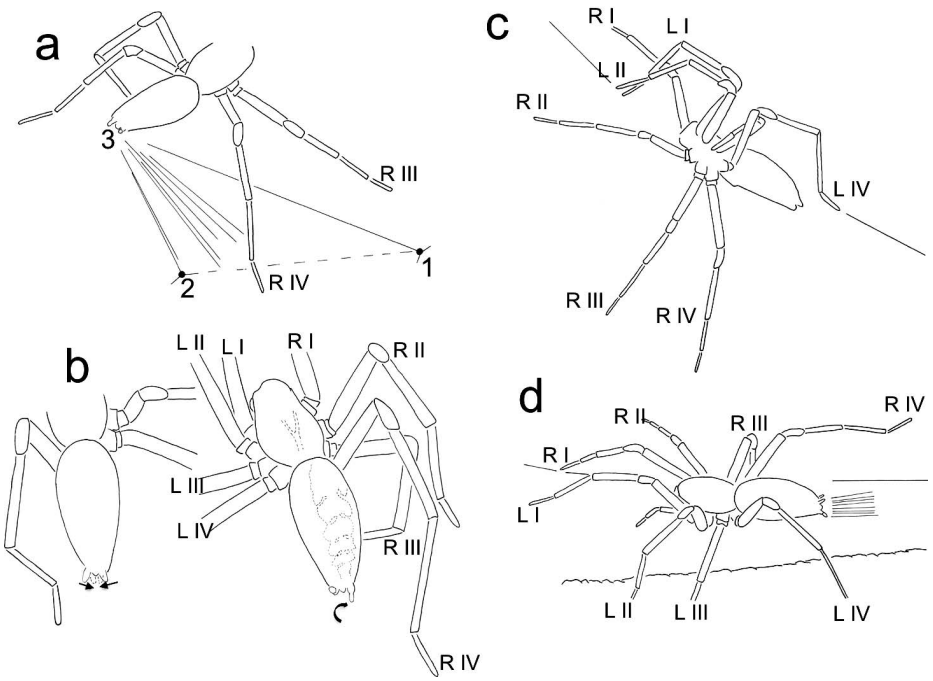
Figure 5.—Possible errors in planning. (a) This sheet had two stems (dashed arrows) protruding through it. Some sectors near the far left and the far right edge were apparently older, and had numerous small holes. (b) The lines attached to these stems sloped upward. (c) The "lumps" (arrows) in another sheet web were caused by dead leaves that projected into the plane of the sheet. The presence of obstacles such as these stems and lumps seems likely to slow the attacks of spiders; they are thus probably disadvantageous, especially in view of the webs' apparent poor abilities to retain prey.

just after ipsilateral IV had landed on the trunk), IV usually contacted the trunk far from III.

We noted two additional differences with orb weavers and their relatives. There was never any indication that spiders broke and reeled up lines along which they walked. Nor did we ever see one leg IV holding the drag line as the spider walked and allowing it to slip through her tarsal claws (Eberhard 1982; Eberhard & Barrantes 2015). Occasionally, however, one leg IV rested on her drag line (and may have held it in some cases) at the moment it was being attached to the substrate after a long trip away from the retreat (Fig. 6e); the leg remained on the line while the spider turned and then grasped the line with her ipsilateral leg II (e.g., leg II followed ipsilateral leg IV) as she began to move back toward the retreat. On some other occasions, however, leg IV clearly did not contact the line as it was being attached when the spider attached to the substrate and then turned back toward the retreat (Fig. 6h). Holding the drag line with one leg IV was more common when attaching to the substrate (5 of 12 cases in which this detail was clear) than when attaching to other silk lines (0 of 45 cases). It was not certain whether the ventral surface of tarsus IV (see Fig. 6e, g) or the tarsal claw contacted the line (e.g., whether she grasped the line).

*Attachments to other lines and to the substrate:* The process of attaching to an object like a twig or a leaf lasted on average nearly five times longer than attaching to other silk lines (the respective means ± standard deviations were 1.53 ± 0.63 s, $n = 14$, and 0.33 ± 0.26 s, $n = 49$). They also differed in other respects. The spider rocked her abdomen from side to side during 10 of 15 attachments to the substrate (Fig. 6i), but in only 1 of 44 attachments to silk lines. In 10 of 18 attachments to the substrate, the spider immediately turned back toward the direction from which she had come, while no turn backs of this sort occurred in 43 attachments to silk lines.

The spider nearly always bent the tip of her abdomen at least somewhat ventrally when making an attachment (e.g.,




~~Fig.~~ 6, a–d.—Schematic drawings from video images of spiders and portions of lines that glinted in the same frame (or the one immediately preceding or following it) during the early stages of sheet construction (note: drawings include only a fraction of the lengths of the lines, and probably only a subset of the lines that were present). Presumably all "attachments" (dots) were made with piriform silk, but this was not verified. The drawings represent particular cases illustrating patterns which were repeated, but they do not stem from quantitative analyses.(a) The glints on lines seen emerging from the spider's spinnerets illustrate how selective attachments of different lines at different sites can widen the swath of lines that is laid. This spider made attachments to other silk lines at points 1, 2 and 3, in that order. When she made the attachment at 3, some lines stretched directly to the immediately preceding attachment point (2), others stretched directly to the preceding attachment point (1), and still others were apparently attached to the line (or lines) between attachment sites 1 and 2 (dotted line). The spider clapped her posterior lateral spinnerets together four times between making the attachments at points 1 and 2; perhaps the intermediate attachments were produced during these clapping movements. As was typical with other attachments to silk lines, in each of the three attachments the leading posterior lateral spinneret (on the left side at point 3) was extended posteriorly and applied directly to the surface, while the trailing posterior lateral spinneret was directed dorsally and held out of contact. (b) At the moment she made an attachment to other silk lines (drawing on the right), the spider bent her leading leg III (RIII) ventrally to hold the line to which the attachment was being made, and raised the trailing (left) posterior lateral spinneret; she bent her abdomen ventrally and laterally, and rotated it on its longitudinal axis toward this leg (curved arrow at rear of abdomen; note also the position of the markings on the dorsum of her abdomen). Some of these details were executed consistently in other attachments to silk (raise trailing spinneret, lower abdomen), while others were sometimes omitted (twist abdomen, grasp with leg III). Just 3 s before making this attachment, the spider had clapped her posterior lateral spinnerets together (arrows and dotted lines in the drawing at the left). (c) This spider used only her left legs to grasp and walk along a long line while returning to her retreat; legs RII, RIII, and RIV were held extended and nearly immobile below her inclined body, and leg RI waved dorsally toward the line, but only occasionally touched it. The line along which she walked was intact, but was only visible beyond her legs II and IV. (d) In returning toward the retreat after laying a long line to a distant edge of the web early in construction, the spider used her left legs to walk along the upper surface of the branch on which she had walked outward, while her right legs walked along the line(s) she had just laid. Her posterior lateral spinnerets were directed more or less dorsally, while her anterior lateral spinnerets were directed more nearly ventrally, as she produced a swath of approximately parallel new lines.

Fig. 6a, e, g, 7c). In some cases, the spider moved to the far side of an object to which she was attaching an early line; this behavior also occurs in orb weaving spiders (Eberhard 1990), and probably results in stronger attachments. In some lateral views of a spider making an attachment to the substrate, it was clear that the AL spinnerets pressed against the substrate and moved actively as they did so, presumably depositing piriform lines. In at least some cases the PL spinnerets also pressed against the substrate (Fig. 6g), but there were exceptions (Fig. 6k). We could not observe piriform attachments directly, but because the piriform spigots are located on the AL spinnerets (Santos & Breskovit 2001), it is unlikely for topological reasons that the aciniform lines from the PL spinnerets were fastened to the substrate with piriform silk during these attachments. Presumably piriform lines attached major or minor ampullate gland lines that were being produced, while the aciniform lines adhered to the substrate (and to other lines – see below) due to their own stickiness soon after emerging from the spigots. In a few cases, the ventral surface of at least one PL spinneret (where the aciniform spigots are located) appeared to be pressed against the substrate (Fig. 6a, b, g).

One clear (and unusual) ventral view of the spider's abdomen while she was making an early attachment in a skeleton web revealed that she clapped her AL spinnerets

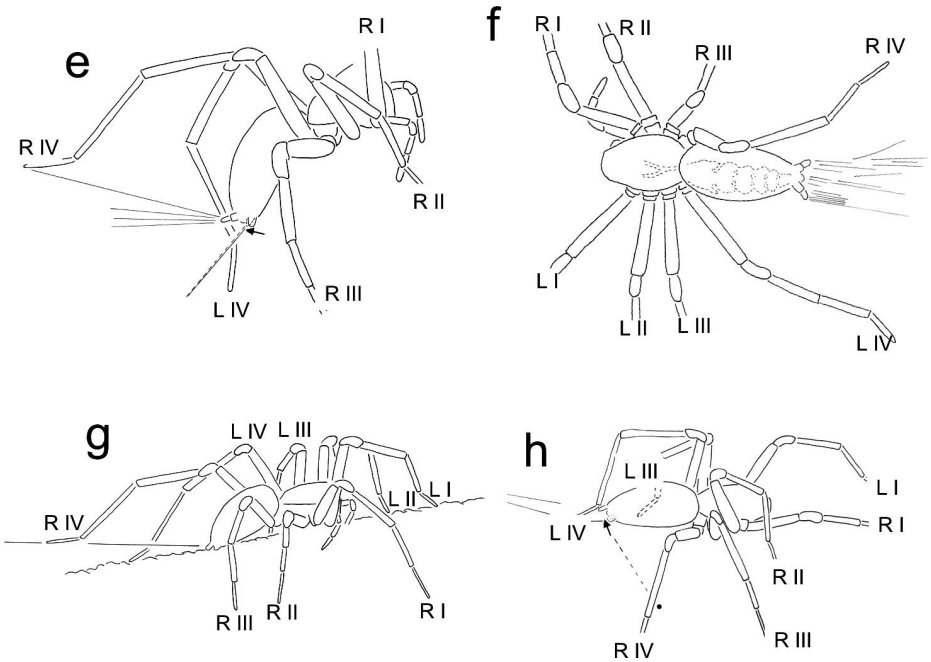



Figure 6, e–h.—(e) Just before attaching to a line, this spider moved her anterior lateral spinnerets ventrally, to apparently pinch this line and then lift it dorsally (dotted lines). One leg (RIV) rested on one or a few of the newly spun lines, but other lines radiated in other directions; no leg III grasped the line to which she was attaching. (f) While walking, the spider spread her posterior lateral spinnerets wide laterally, and produced a wide swath of approximately parallel lines. (g) In making an attachment to a branch, the spider lowered the tip of her abdomen and both her anterior lateral and her posterior lateral spinnerets to contact it. At the moment the attachment was made, the tarsus (or tarsal claw?) of leg RIV rested on the line(s) she was attaching. (h) At the moment she made an attachment to other silk lines, this spider bent her leading leg III (LIII) ventrally to hold a line (apparently the one to which she was making the attachment); the position of the tarsus of this leg is uncertain, as it was not visible. Her left leg IV may have rested on this same line. At the same time, her trailing anterior lateral spinneret moved dorsally (small arrow), probably grasping this line against the other anterior lateral spinneret and bringing it dorsally against her other spinnerets. The attachment immediately preceding this one was at the point indicated by the black dot.

together two or three times just before making an attachment to other silk lines (Fig. 6l). Lateral and dorsal views of spiders revealed similar lateral "clapping" movements of PL spinnerets (Fig. 6b), and dorso-ventral opening and closing movements of the AL and PL spinnerets (Fig. 6e, j) just before and just after attachments to other silk lines, as well as at other times while the spider was building the sheet. These movements might cause aciniform lines to adhere to or to be separated from each other near attachment sites, but we were not able to perceive any pattern of when they occurred. In two cases, it was clear that when the spider flexed her AL spinnerets ventrally, they seized the line to which the spider was going to attach between them, and that they then raised it dorsally toward the other spinnerets; this behavior to our knowledge has never been seen in any other species (Fig. 6e).

When attaching to other silk lines, the spider often (19 of 29 attachments) tilted and rotated her abdomen perceptibly on its long axis toward the leading side (Figs. 6b, 7c). This movement raised the base of the dorsally directed, trailing PL spinneret away from the attachment point, and may have pressed the spigots on the leading side PL spinneret against the lines to which she was attaching.

When making an attachment to other lines, the spider often bent her leading leg III to contact the line to which the attachment was being made anterior to her spinnerets (25 of 43 cases); in four of these cases, the ipsilateral leg IV appeared to also contact this line posterior to her spinnerets. The contact with tarsus III was generally about 3-4 PL spinneret lengths anterior to the spinnerets. The line to which an attachment was being made never glinted, however, so we could not determine whether the ventral surface of the tarsus III or its claw contacted the line. The spider lowered her abdomen toward the line and apparently lifted it toward her spinnerets simultaneously with her leg III (Fig. 6a, b). In contrast, when the spider attached to the silk sheet, leg III made no move to grasp any line near the spinnerets (Fig. 7c).

Usually, when we were able to determine the positions of the lines that emerged from the spinnerets at the moment an attachment was made to other web lines, it was clear that not all of the lines were attached: the positions of lines following attachments also occasionally confirmed that only some but not other lines that the spider was producing were attached at a given point (Fig. 6a), with different lines in a swath of lines that emerged from the spider's spinnerets just before the next attachment coming from radically different directions (Fig. 6a). Confirming this deduction, the trailing PL spinneret was always ($n = 19$ attachments) directed nearly dorsally, while the leading PL spinneret was oriented nearly directly posteriorly (Fig. 6a, b). The spider sometimes raised the trailing spinneret just as the abdomen was being lowered to make the

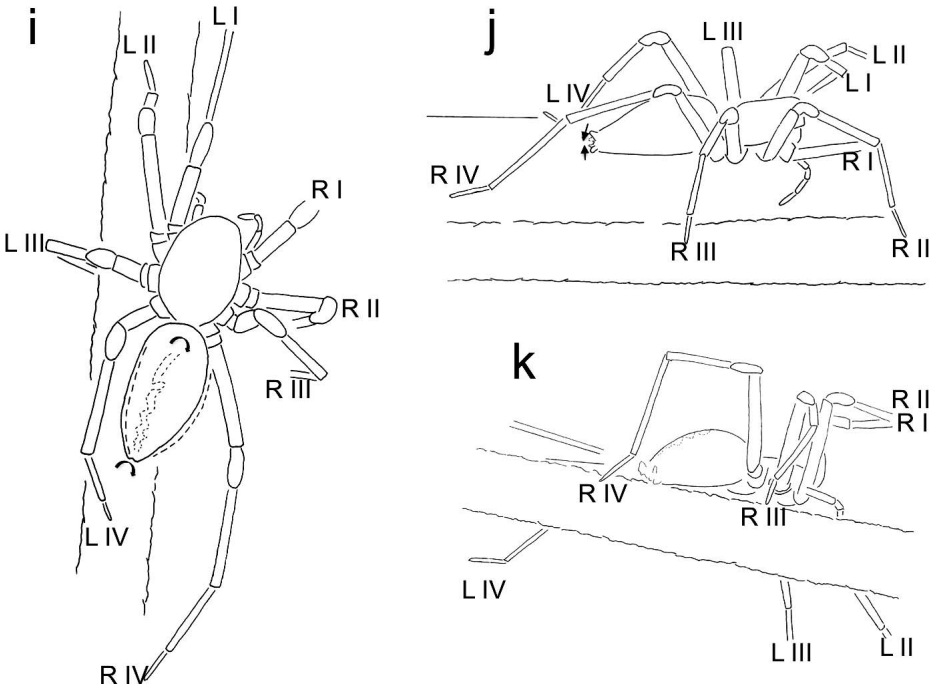



Figure 6, i–k.—(i) The amplitude of the side-to-side rocking movements of the abdomen is illustrated in this spider attaching to a branch (dotted lines were 0.12 s after the solid lines; curved arrows indicate direction of movements). (j) This spider appeared to clap her posterior lateral spinnerets against her anterior lateral spinnerets (small arrows; dotted lines indicate positions 0.09 s later). (k) The spider contacted the branch with her anterior lateral but not with either of her posterior lateral spinnerets as she made an attachment. Her abdomen was tilted on its longitudinal axis, away from the viewer.

attachment. This raised position kept the aciniform lines being produced by the trailing spinneret from the vicinity of the surface (or lines) to which other lines were being attached.

This deduction that aciniform lines from the trailing PL spinneret were not attached was also confirmed directly in a few cases when favorable lighting and viewing angles showed that the multiple lines from the raised PL spinnerets were not attached to the substrate when the AL spinneret contacted the substrate (Fig. 6a, e). Another confirmation came from the fact that, in some other cases, lines apparently emerging from the trailing PL spinneret went lax immediately after an attachment was made and the spider turned toward that trailing side.

In contrast to their relative immobility while the spider walked under a line early in construction and on solid surfaces, the palps made rapid "treading" or bicycling movement while the spider walked on a portion of partially complete sheet.

*Later in construction:* One individual was filmed for a total of about 30 min during bursts of activity while she made repeated attachments while moving on a sheet that was already partially complete (and also occasionally extended the sheet's edges slightly). Consecutive attachments to the sheet thus usually occurred every one to two seconds; they tended to be approximately one body length apart (Fig. 7), but we did not measure the distances precisely. The temporal pattern of the spider's movements was relatively consistent. After the short pause of about 0.1 s to make an attachment, she moved quickly forward and somewhat laterally, away from the side on which she had just attached (Fig. 7b); after pausing motionless for several tenths of a second (Fig. 7b), she moved forward again and swung her abdomen laterally to make the next attachment (Fig. 7c). The significance of this abrupt stop-and-go pattern of movement is not clear.

The spider made nearly all attachments (185 of 189) to one side rather than directly behind her as she walked. Sometimes she zig-zagged, making consecutive attachments to opposite sides (Fig. 7), but there was no consistent tendency to alternate (52.9% of 174 consecutive attachments were to alternate sides). Two patterns were evident. When the spider's overall path was curved rather than straight, she tended to attach to the side away from which she was moving; thus, if, for instance, her overall path curved gradually to the right, she consistently attached to the left. When she was near the edge of the sheet, she grasped the lines to which she attached with her leading leg III (Fig. 6b). In contrast, when she was in the middle portion of the sheet, she never grasped lines with leg III (Fig. 7). In many cases, her leading leg III was not even in the vicinity of her spinnerets when the attachment was made. This difference implies that spiders sensed their general locations on the sheets.

*Other details of web construction:* We found two mature males alone on funnel webs (and another on a web with a mature female). When we removed the sheets and tangles of the solitary males and then checked the sites the following day, one had left but the other was alone on a new web. A mature

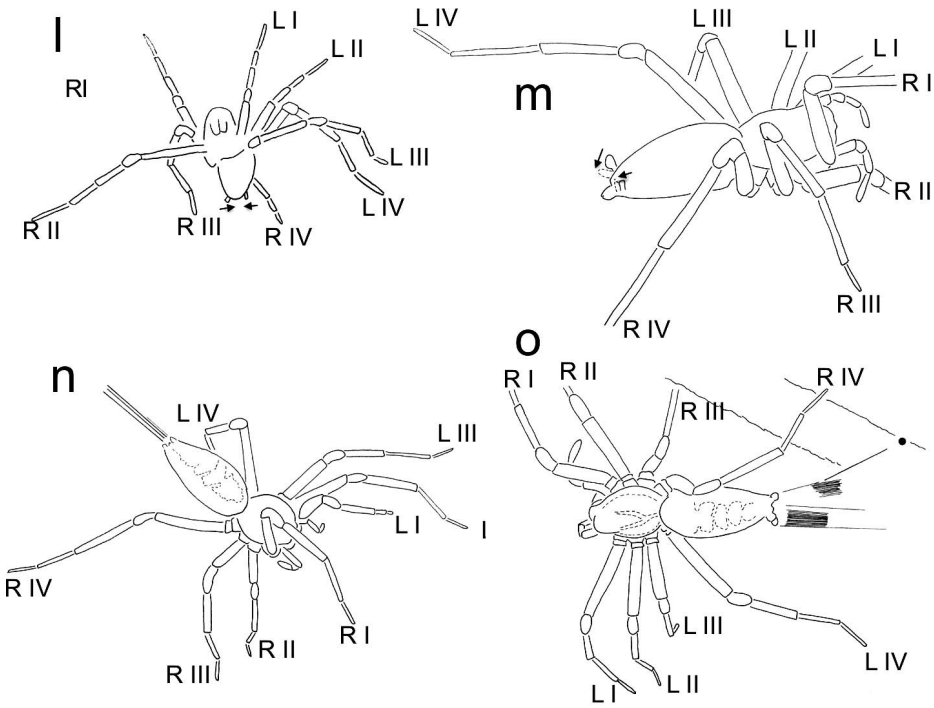



Figure 6, l–o.—(l) A ventral view of the abdomen shows how the anterior lateral spinnerets clapped together (small arrows) just before the spider made an attachment. (m) This drawing illustrates the maximum "gape" that was seen between the anterior lateral and posterior lateral spinnerets; the small arrows and dotted line indicate the positions of the posterior lateral spinnerets just 0.15 s later. (n) This drawing illustrates one limitation of the "glint" technique. A misleadingly low number of lines were visible when this spider was returning to her retreat after having laid a long line. She had not made any attachments on the way back; her posterior lateral spinnerets were directed rearward rather than being spread, and only four lines were visible. Slightly previous to this frame of the recording only two lines were visible; but when she finally made an attachment about 3 s later, her posterior lateral spinnerets were spread apart, and each could be seen to be producing a substantial swath of lines along nearly its entire length. (o) In this case, it was not clear how the swaths of lines from the two, spread posterior lateral spinnerets could be so wide (there were more lines emerging from each than are shown in the drawing). The spider had just attached at the point on the branch marked with a black dot, and at least one line that seemed to originate on her right spinneret was directed toward this point. The swath of fine lines from the left spinneret appeared to run toward the point where the penultimate attachment was made, at least three body lengths farther to the right. But it was unclear where the lines in the swath emerging from her right spinneret were attached.

male also built a sheet and tunnel in captivity. Thus, mature males build webs, at least under certain circumstances.

Sheets appeared to be constructed as units, rather than growing slowly by accretion as do the webs of some spiders, such as the austrochilids *Thaida* Karsch, 1880 and *Austrochilus* Gertsch & Zapfe, 1955 (Lopardo et al. 2004) and the filistatid *Kukulcania hibernalis* (Hentz, 1842) (W. Eberhard pers. obs.). None of six replacement webs that were powdered the morning after they were built (after they had been destroyed the previous day) showed subsequent expansions of the sheet on the following two nights, even though the spiders remained on them. One of these spiders added lines to the middle of the sheet, however, on the second night. The spiders probably added subsequently to the tangles above the sheets. The tangles of ten webs that had been destroyed the preceding afternoon were all skimpy, but some of these grew taller on subsequent days.

Observations in both the field and captivity suggested that the spiders did not excavate retreats, and that their tunnels were built in previously formed cavities. Some of these were well-protected and secure, such as cracks in thick bark and cavities in tree trunks. Many others in the leaf litter, however, were amongst loose objects and not well-protected, and the spiders could be collected relatively easily.

**Prey capture behavior.**—Running speed is probably important for *A. castaneus* in prey capture. Three small crickets (body length about one third to one half that of the mature female spiders) that hopped (probably frightened by our approach) onto the sheets and tangles in the field were temporarily retained. At first the insects were immobile; but when they began to move they showed little sign of being entangled, and moved across the sheet with no apparent difficulty. These movements elicited very rapid attacks by the spider, but one cricket nevertheless hopped off the edge of the sheet before the spider arrived. The sheet was relatively fragile, and several holes were left in the sheet at a site where one cricket was captured (Fig. 2d).

These crickets as well as the flies observed in captivity were first bitten, and then, after they were relatively immobile, wrapped using behavior very similar to that of used by *T. radiata* and *Melpomene* sp. to spread a swath of aciniform lines onto the prey (for details, see Barrantes & Eberhard

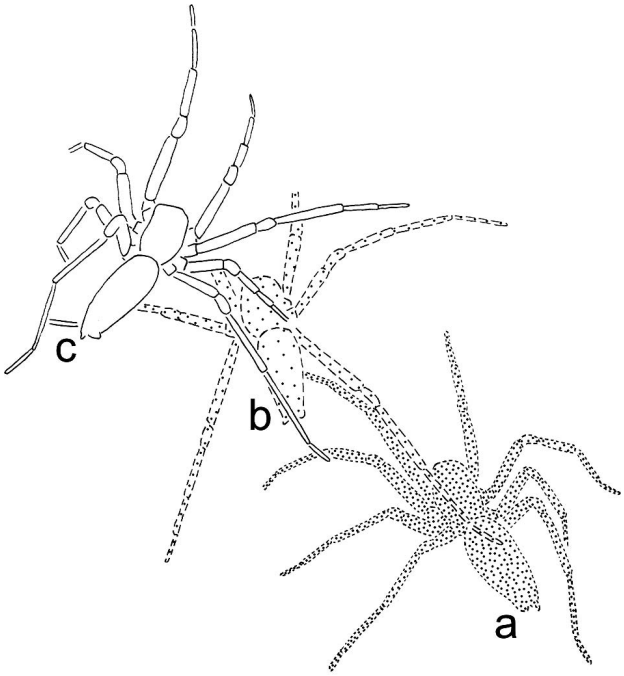



Figure 7.—A schematic view of a typical sequence of movements between two attachments late in sheet construction, when the spider was walking over a sheet and performing presumed sheet filling-in behavior (glints were very uncommon, so the detailed positions of the sheet lines and of the lines that were being produced by the spider were not verified directly; a few legs have also been omitted for clarity). After attaching to the sheet with a sweeping movement of her leading posterior lateral spinneret at position *a* (darker stippling, dotted lines), the spider moved forward and laterally to position *b* (elapsed time 0.43 s), where she remained immobile for 0.43 s (moderate stippling, dashed lines); then she moved farther forward and laterally, and bent her abdomen laterally to make the next attachment at position *c* (elapsed time 0.5 s, no stippling, solid lines). Spiders nearly always paused this way between attachments. The spinneret positions were asymmetrical during attachments, as in earlier stages (e.g., Fig. 6a), but leg III was not bent ventrally to press upward on the lines to which the attachment was made, as occurred in earlier attachments (Fig 6a, b); such a position would have been impossible, because the dense sheet prevented leg III from reaching under it.

2007). The spider began by attaching a swath of wrapping silk to the sheet and then turning slowly in place, laying a swath of fine silk lines from her PL spinnerets. She kept her spinnerets close to the sheet as she turned, and periodically attached the swath of lines to the sheet, thus causing lines to press against the prey. Just as when making attachments to other silk lines during construction, the spider often spread the swath by raising her trailing PL spinneret while she attached wrapping lines to the sheet, and thus avoided attaching the lines from the raised spinneret to the sheet. The spider's legs never touched wrapping lines. The mean duration of each wrapping sequence for the flies was 30 ± 10s, and the mean total duration was 59 ± 5s.

**Lines in the sheet under the compound microscope.**—The apparent diameters of lines and their orientations varied widely (Fig. 8). The thinnest lines were barely visible at 400x.

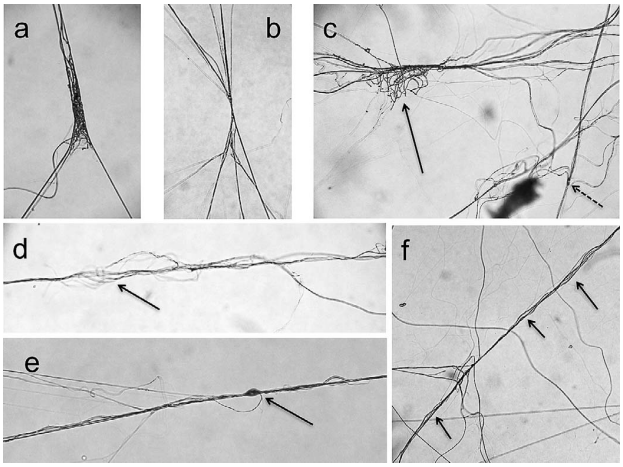



Figure 8.—Different configurations of lines from a newly-built sheet of an *Aglaoctenus castaneus* seen under a compound microscope. (a) A "large" attachment between relatively thick lines. (b) A small attachment that links multiple fine and medium fine lines for a short distance. (c) A large attachment (solid arrow) that brought multiple lines together at the attachment point and also had putative piriform lines splayed apart, apparently on the sheet, and also a small attachment of fine lines (dashed arrow). (d) a thick line that unraveled to reveal that it was composed of many thinner ones. (e) a small droplet of liquid (arrow). (f) a thick line that unraveled in places (arrows) to reveal its multi-strand composition.

We were not able to measure line diameters with confidence because "thick" lines could not be distinguished from compound cables of thinner lines (Fig. 8c). Finer resolution (e.g., SEM photos) will be needed to provide confident measurements of diameters.

As expected from behavioral observations (and despite the "brushed sheet" categorization of *A. castaneus* webs), there were numerous apparent piriform attachments in the sheet. They varied greatly in size. The largest attachments (Fig. 8a) joined relatively thick lines (or cables of lines?), and resembled those of other spiders such as the araneid *Cyrtophora citricola* (Forsskål, 1775) (e.g., Kullmann et al. 1975; Peters 1993). In contrast, the smallest (about $0.1/mm^2$) were barely perceptible thickenings along short segments of thinner lines (Fig. 8b, e). Still others were intermediate in size (Fig. 8c). In one sample sector of 340 $mm^2$, there were 9 large, 11 medium, and 14 small attachments. In rare cases, there were small droplets associated with piriform attachments (Fig. 8d); these also varied in size. No other droplets were seen at any other sites, suggesting the tentative conclusion that the droplets were material from the piriform gland.

*Tengella radiata* (Zoropsidae)

We can add a few details to the brief descriptions of the webs of *T. radiata* in Eberhard et al. (1993) and Griswold et al. (2005) that permit comparisons with *A. castaneus*. During the day, the spiders were almost always in their tunnels, and not visible. The sheet included both thin and thick lines (or cables of lines) (Fig. 9). The relative number of thick lines was higher than in *A. castaneus* (note the density of visible lines in the unpowdered web in Fig. 9b, where none of the thinner, uncoated lines are visible). Perhaps associated with this great

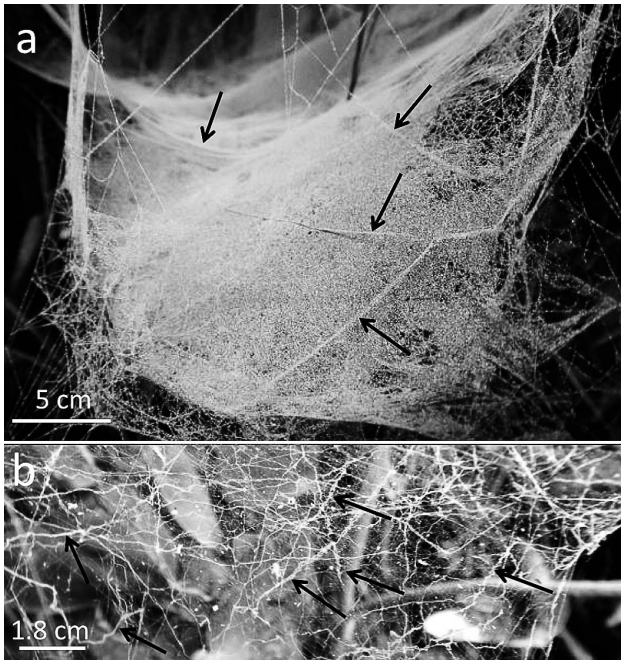



Figure 9.—(a) A portion at the edge of the sheet of a *Tengella radiata* coated with powder, seen from above and the side. The upward curve at the less densely meshed edge is visible at the left and below. Multiple tiers are absent (compare with Fig. 2a of *Aglaoctenus castaneus*, Fig. 11d of *Melpomene sp.*). The arrows indicate long, lax lines covered with cribellum silk that hung free just above the sheet. (b) A close-up view of an un-powdered sheet; arrows indicate lines of cribellum silk that were incorporated in the sheet rather than hanging above it.

density of thick lines, there were no perceptible "tiers" of fine lines like those in *A. castaneus* webs (Fig. 9). The sheet was also perceptibly tougher, and prey struggles and capture (Barrantes & Eberhard 2007) often did not result in damage to the sheet.

As in *A. castaneus*, some of the objects to which the sheets and the tangle lines above the sheets were attached would not have been accessible for a spider walking from her retreat; some anchor lines for sheets were >30 cm long. There were highly adhesive cribellum lines in the sheets and also sometimes in the tangle just above the sheet (arrows in Fig. 9a, b). The retreats were consistently associated with cavities such as holes in tree trunks, small, deep cracks in or between stones, holes in the soil, etc. that were more strongly protected than many of those which were used by *A. castaneus*. Tangle construction may resemble that of *A. castaneus* in largely occurring on days subsequent to the day of the original sheet construction (Eberhard et al. 1993). Of 73 webs of older nymphs and mature females, 24.7% had an object (usually twigs, dangling roots, or stems) that protruded through the sheet (as in Fig. 5a, b) (these webs were mostly on the steep sides of a ravine, where the frequency of such objects may have been greater than in webs built in the less cluttered spaces near the trunks of large trees). In some cases, there was a tattered, collapsed older sheet under a newer sheet, as in *A. castaneus*.

Under the compound microscope, lines in the sheets of mature females showed, if anything, a greater variety of diameters (Fig. 10) than in the sheets of *A. castaneus*. Thicker lines sometimes revealed themselves to be cables when they splayed apart into numerous thinner component lines (Fig. 10c). As with *A. castaneus*, few lines were parallel with each other.

In contrast with *A. castaneus*, all piriform attachments were associated with at least one thick or moderately thick line. As in *A. castaneus*, the piriform lines were wrapped around another line in some attachments (Fig. 10f), while in other "open" attachments in which they splayed apart rather than being wrapped around particular lines (or cables of lines) (contrast a, d, e with f in Fig. 10; Kullmann et al. 1975). Perhaps because of the greater size of *T. radiata*, it was possible to distinguish a dense array of very fine lines in some parts of the sheet that were barely perceptible at 400X. The orientations of these very fines lines varied widely; they did not tend to be parallel to each other. The presence of these fine lines (and perhaps even finer lines that could not be resolved) was suggested in many of the open attachment discs where putative piriform lines splayed apart. These had relatively thick lines which were apparently attached to the surface of the sheet (Fig. 10a, d, e). Close examination showed that in many places the putative piriform lines were apparently attached for a short distance to very fine lines in the sheet that were barely resolvable at 400x magnification (arrows in Fig. 10a, d). In these places, several piriform lines ran more or less parallel to each other, with each showing a complementary set of small zig-zags (Fig. 10a, d). In some places, it was clear that these zig-zags occurred where the piriform line intersected one of the very fine lines (arrow in Fig. 10a); in others, there was no visible fine line (but perhaps an even finer, unresolved line?). The parallel orientations of the putative piriform lines were presumably due to the AL spinneret being dragged across the sheet, producing several piriform lines simultaneously. Other piriform attachments had different forms, which included large masses of fine piriform lines joining thick lines (Fig. 10f), and small masses joining smaller lines (Fig. 10b).

A sample sector of 1.96 $mm^2$ contained 2 large attachments, 11 medium attachments (all but one were open attachment discs), 4 small, and 4 uncertain, giving a conservative estimate of 8.7/$mm^2$.

*Melpomene* sp. (Agelenidae)

The webs of *Melpomene sp.* were more similar to those of *A. castaneus* than to those of *T. radiata* in several respects. Most of the lines in the sheet were very fine; there were small tiers of fine, more or less parallel lines just above the sheet (Fig. 11d): the tubular retreats were often at the bases of plants or in the leaf litter (Fig. 11a), and were less consistently located in cavities with rigid walls; the objects to which the tangle lines above the sheets were attached were sometimes inaccessible by walking; and the tangle lines above the sheet included small accumulations of fine lines (Fig. 11b). Spiders observed building webs in captivity did not walk under lines, walking instead on top of the substrate or the sheet that they were building (Rojas 2011) (these observations were in relatively small containers, however, where there were no long lines under which the spiders could have moved). Spiders in the

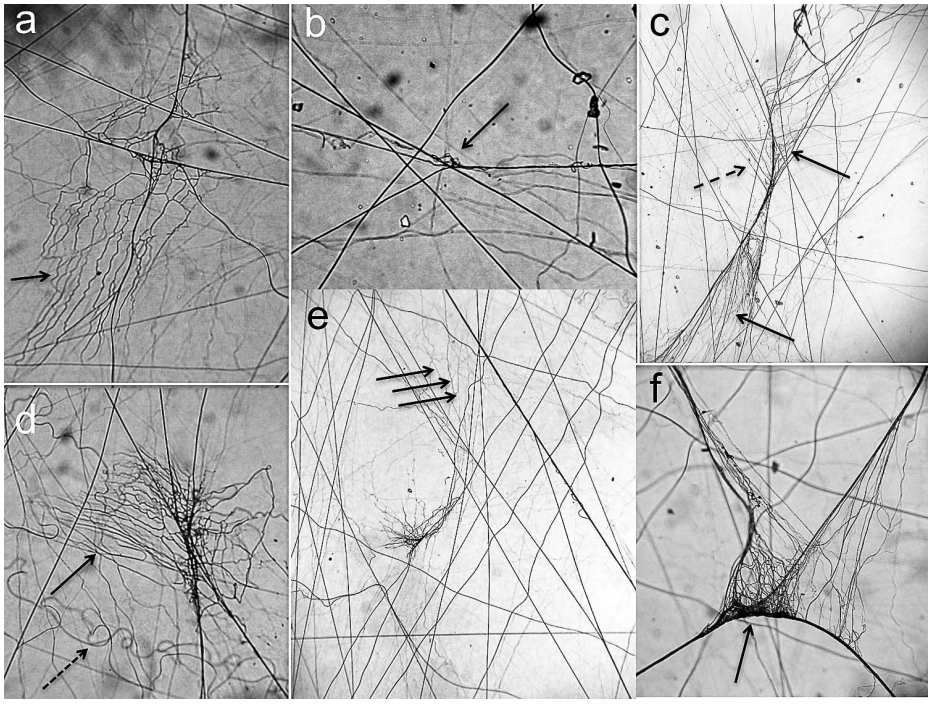



Figure 10.—Different configurations of lines from a newly-built sheet of *Tengella radiata* seen under a compound microscope. (a) A medium "open" attachment with many more or less parallel, wavy putative piriform lines. We believe these are attachments of piriform lines to a sheet. In some places (arrow) the waves in these lines are in register with each other, suggesting that they are produced by their crossing an underlying fine line in the sheet that was too thin to resolve. (b) A small attachment (arrow). (c) Two medium thick lines unravel and are revealed to consist of a large number of smaller lines (solid arrows). A swath of nearly parallel fine (aciniform?) lines is marked with the dashed arrow. (d) a large attachment "open" on the left (arrow) joins relatively thick lines. The loopy lines (dotted arrow) were part of a mat of cribellum lines that were too fine to be resolved. (e) A medium attachment, with many more-or-less parallel fine lines visible, especially in the upper portion of the photo (arrows). (f) large attachment of one thick line to another; most if not all of the putative piriform lines appear to begin or end on the thick lines.

field were generally hidden in the tunnel during the day. The sheets of *Melpomene sp*. often had one or more objects (generally twigs or pine needles) protruding through them (Fig. 11a) (87.5% of 24 webs).

Lines in one new sheet examined under the compound microscope (Fig. 12) resembled those of the other two species in the following respects: lines had a variety of diameters; sometimes a thicker line splayed apart to reveal a cable-like nature; lines showed little tendency to be parallel to each other; and there were both typical, large piriform attachments and apparent "open" attachment discs. It was not possible to determine whether the zig-zag forms of the putative piriform lines were associated with intersections of fine lines as in *T. radiata* (the much smaller size of *Melpomene sp*. made fine lines in their sheets unresolvable). Perhaps more than in the other species, most lines crossed others with no sign of an attachment (Fig. 12b) (though there were some doubtful attachments of finer lines) (Fig. 12c); again the small size of the spiders may have precluded resolution of all the lines. A sample area of 1.56 $mm^2$ had 4 large, 7 medium and 9–12 small attachments, or about 12/$mm^2$. They differed from *A. castaneus* and *T. radiata* in that their lines seemed to vary less in diameter, and (for the scale of the web) to have fewer piriform attachments.

When the spider was filling in the sheet, she walked rapidly back and forth across the web, and also returned repeatedly to the retreat, entered the tunnel and immediately turned and emerged to continue. Only occasionally did the spider appear to make piriform attachments. These occurred in or near the mouth of the tunnel, or near the edge where the sheet was attached to the wall of the container. These attachments were relatively long (the mean for 12 attachments was 0.41 s), and the spider always stopped walking; often in the tunnel, she also thrust her abdomen rearward while making an attachment.

The attachments to the sheet, in contrast, were very brief. As the spider walked across the sheet, she periodically swung her abdomen somewhat laterally, and dabbed it at least slightly toward the sheet. The leading PL spinneret swept rapidly ventrally and/or laterally, apparently brushed against the sheet briefly (the precise position of the sheet was not visible in the recordings, which were taken mostly in dorsal view). In some cases, the spinneret was flexed to point nearly directly downward. The apparent duration of 17 contacts with the sheet averaged only 0.13 s; and this is probably an overestimate, as those extensions of the spinneret that lasted only 1 frame (0.03s) were not included. Frequently the spider continued walking while making a brushing movement with her PL spinneret. The trailing PL spinneret was consistently raised (or in some cases, held more or less horizontally and not

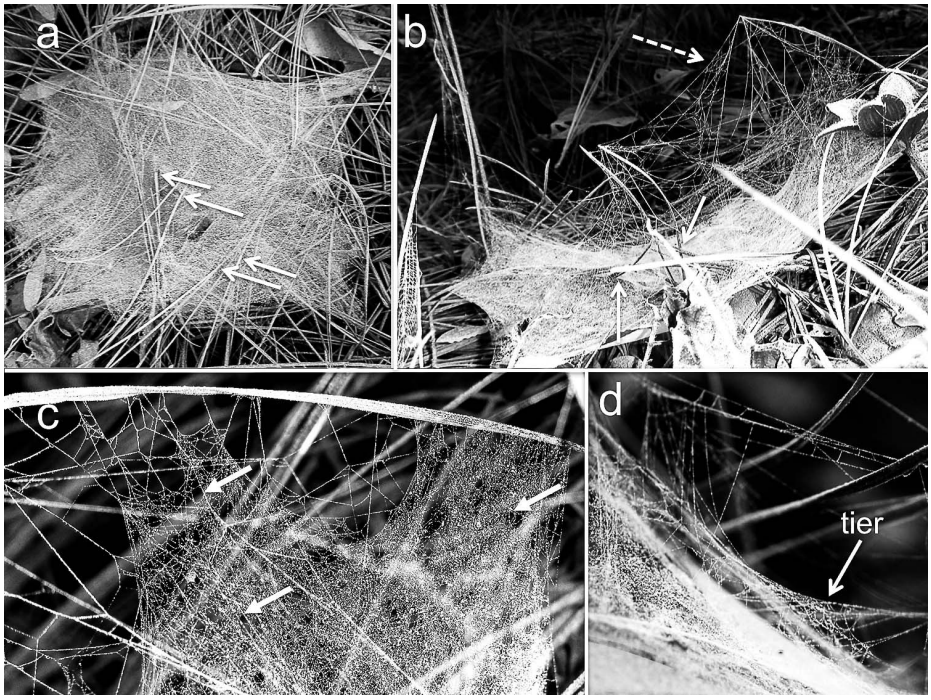



Figure 11.—A horizontal sheet web of the agelenid *Melpomene* sp. at a site where a mat of pine needles covered the ground. (a) View from above, and (b) view from the side. Solid arrows mark pine needles that project through the sheet; the dotted arrow in (b) marks a few of the many lax lines in the tangle above the sheet. (c) Close-up view at one edge of web, taken perpendicular to the sheet. Both probable skeleton lines (longer, straighter and thicker, indicated with arrows) and thinner fill-in lines are visible. (d) A small "tier" is visible just above the sheet in the lateral view.

lowered), and appeared not to touch the sheet. The low frequency of apparent piriform attachment behavior on the sheet is in accord with the low frequency of piriform masses seen under the microscope.

## DISCUSSION

**Comparisons of *A. castaneus* construction behavior with that of other species.**—*Behavior associated with laying swaths rather than simple drag lines:* It is likely that *A. castaneus* simultaneously laid both drag lines (presumably of ampullate gland silk from the AL spinnerets) and multiple fine lines (of aciniform gland silk from the PL spinnerets) at many stages of web construction. We could see that swaths of lines emerged from the PL spinnerets (e.g., Fig. 6). We were not able to observe directly that thicker lines which we suppose emerged from the AL spinnerets, as occurred in *A. lagotis* (González et al. 2015), but deduce, from the fact that the frequent attachment behavior observed could only result in piriform attachments of lines from the AL but not from the PL spinnerets, that there were indeed ampullate lines also being laid. Previous descriptions of web construction by other funnel web species, including the lycosids *Hippasa olivacea* (Hingston 1920) and *A. lagotis* (González et al. 2015), and the agelenid *Melpomene sp.* (Rojas 2011), mentioned only a single type of line being produced at a given stage of construction. Producing only a single type of line at a time is well established as the general rule for many other araneomorph web-spinning groups including, as far as we know, all orbicularians (araneoids and deinopoids) (e.g., Eberhard 1982; Vollrath 1992; Zschokke & Vollrath 1995a, b). Because the multiple lines of *A. castaneus* were only visible under favorable lighting conditions, it is possible that the lack of similar observations of swaths of lines in other lycosids is due to incomplete observations, rather than to a lack of simultaneous production of both thick and thin lines. Swaths of lines were also produced during web construction by the mygalomorph *L. macrothelifera* (Eberhard & Hazzi 2012).

Producing a swath of aciniform lines rather than a simple drag line during web construction may explain several other details. The production of swaths of lines by *A. castaneus* was associated with special asymmetrical PL spinneret movements which were used to manage these lines; this spinneret behavior is shared with both the mygalomorph *L. macrothelifera* (Eberhard & Hazzi 2011) and *Melpomene sp.* (A. Rojas, pers comm., this study), but has not been reported previously in the construction behavior of any araneomorph. Spiders routinely elevated the trailing PL spinneret at the moment they moved the abdomen laterally to make an attachment, and thus held the aciniform lines that this spinneret was producing away from the attachment. This behavior resulted in widening the swath (e.g., Fig 6a), a phenomenon which is absent in web construction behavior in many other araneomorphs. Swath widening is presumably advantageous in filling in a sheet web more rapidly and completely with aciniform lines. These movements explain how the spiders produced the paradoxi-

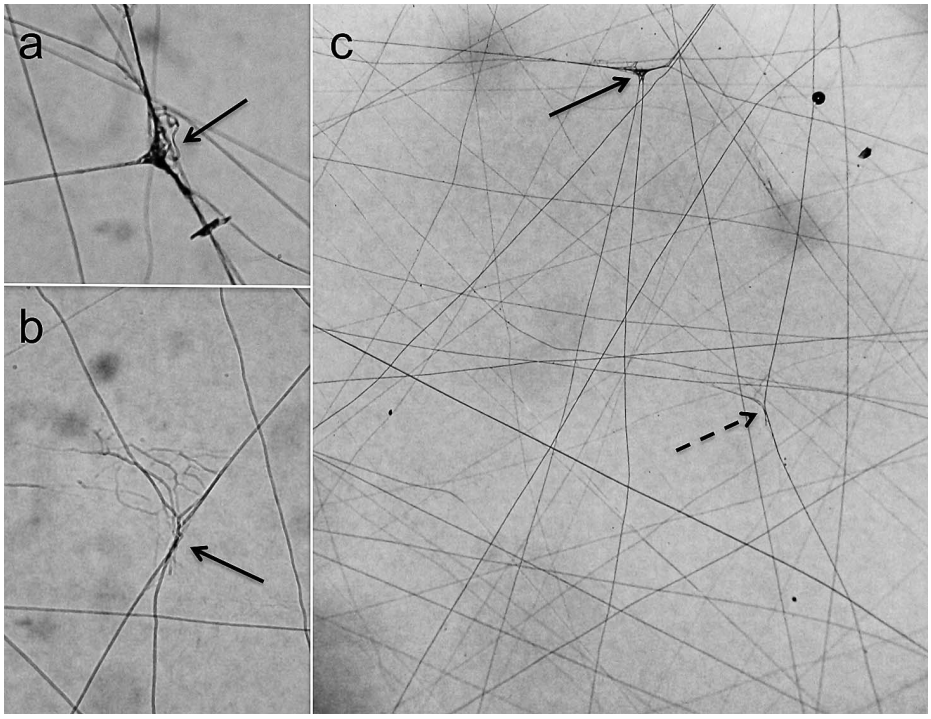



Figure 12.—Different configurations of lines from a newly-built sheet of *Melpomene* sp. seen under a compound microscope. (a) A large attachment (arrow) between two thick lines. (b) A small, possible "open" attachment between smaller lines, in which some of the putative piriform lines are spread apart. (c) A typical overview, showing how most of the lines lacked attachments where they crossed; there is one large attachment between two thick lines (solid arrow) and a small attachment (dotted arrow).

cally wide swaths of fine lines seen in photographs of finished *A. castaneus* webs (Fig. 3b, d), which reached widths of up to approximately ten times the maximum span of the spider's PL spinnerets. Swath widening during web construction behavior may have originated from prey wrapping (below).

In addition, *A. castaneus* never performed break and reel behavior, as is common in orbicularians (e.g., Marples & Marples 1937; Bradoo 1971; Eberhard 1982; Benjamin & Zschokke 2003; Eberhard & Barrantes 2015). At least in *A. lagotis*, spiders appeared unable to break lines except by physically tugging on them. Break and reel behavior may have been important in the evolution of web designs, because it allows a spider to shift the attachment sites of lines during the construction process, rather than simply accumulating lines to all the sites which she has visited during exploration and construction behavior. In addition, *A. castaneus* never slid tarsus IV along the drag line as do orbicularians (Eberhard 1982; Vollrath 1992; Zschokke & Vollrath 1995a, b), a behavior which may help the spider control the tension on her drag line. Both break and reel behavior and sliding leg IV on the drag line would seem more difficult to perform for a spider which is laying a swath of lines rather than a simple drag line.

The use of legs III and probably IV to hold the lines to which *A. castaneus* was about to attach links this species to araneomorphs (Eberhard 1982) rather than mygalomorphs, and contrasts with the behavior of the diplurid *L. macrothelifera* (Eberhard & Hazzi 2012) which never used its legs to manipulate lines. *Tengella radiata* resembled *A. castaneus* in sometimes using one leg III to hold the line to which she was making an attachment against her spinnerets (W. Eberhard, unpubl.). We speculate that using her legs to hold the line to which she is making an attachment improves the precision with which a spider can apply piriform silk, and was important in the evolution of spider webs because it improved the strength of attachments between silk lines (Wolff et al. 2015). It was not clear, however, whether *A. castaneus* actually grasped lines with her tarsal claws in these situations, as happens in orbicularians, or simply pressed lines with the ventral surface of her tarsus.

*Other behavior:* An additional behavior which appears to be unique in *A. castaneus* construction behavior, was "one-sided walking", in which only the legs on one side of the spider were used to walk along a single, long, elevated line (Fig. 6c). In our experience, all orbicularian spiders, as well as other web builders such as the pholcids *Modisimus* Simon, 1893 and *Physocyclus* Simon, 1893, use the legs on both sides of the body when walking under a line. The only other spiders we have seen performing one-sided walking were the early nymphs of a mygalomorph (probably of the ctenizid *Ummidia* Thorell, 1875 sp.) that were filmed while walking to a long-distance dispersal site (W. Eberhard, unpub.). The taxonomic distribution of one-sided walking (which we speculate may result from an inability to rotate the tarsus to grasp lines parallel to the leg's longitudinal axis – W. Eberhard, in prep.) is not known.

The order in which lines were produced during sheet construction behavior of *A. castaneus* and *A. lagotis* (González et al. 2015) included early placement of strong lines that formed the skeleton web which was attached to the substrate, and later filling in the sheet with fine lines (Fig. 3). In contrast, the diplurid *Linothele macrothelifera* added sheets of lines from the beginning, without making a preliminary skeleton (Eberhard & Hazzi 2012).

**Comparisons of *A. castaneus* webs with those of other species.**—*Obstacles in webs:* The webs of *A. castaneus* had objects protruding through the sheet, or bulges in the sheets that were produced by upwardly projecting objects just below the sheet. These barriers probably reduce the speed with which the spider can attack prey, because they would prevent direct dashes to some prey. Similar obstacles occurred in the sheet webs of *T. radiata* and *Melpomene sp.*, and are visible in photographs of the webs of the agelenids *Agelena labyrinthica* (Clerck, 1757) (Nielsen 1931) and *Agelenopsis naevia* (Walckenaer, 1841) (Kaston 1948; Comstock 1948), and the linyphiids *Erigone dentigera* O. Pickard-Cambridge, 1874 and *Microlinyphia pusilla* (Sundevall, 1830) (Kaston 1948). They may be associated with building webs close to the substrate, where there are many potentially interfering objects. Blackledge et al. (2009) mentioned that when spiders evolved webs that were raised farther above or away from the substrate, they would be less "constrained" than those whose webs make more intimate contact with the substrate. They emphasized possible constraints on the forms of webs. We propose that another advantage of elevating webs above the substrate may be reducing the numbers of obstacles in the web that impede rapid attacks on prey.

Webs with such obstacles may represent "errors" in web site selection, when the spider failed to choose a completely open space in which to build her sheet, or was unable to move or remove lines laid early in web construction when she subsequently encountered previously unperceived objects (see discussion of "break and reel" above). In our experience, such errors seem not to occur, or to be rare in aerial sheet weavers such as the theridiid *Parasteatoda tesselata* (Keyserling, 1884), the araneid *Cyrtophora citricola,* the pholcids *Modisimus guatuso* Huber, 1998 and *Physocyclus globosus* (Taczanowski, 1874), and the linyphiid *Dubiaranea* Mello-Leitão, 1943 sp., in which we have seen numerous webs (see also the web photos of e.g., Nielsen 1932; Kaston 1948; Hormiga & Eberhard in prep.); we know, however, of no quantitative studies demonstrating this aspect. Presumably these species differ either because the spiders do a better job of exploring potential web sites for obstacles prior to building their webs, or because their choices of web sites are less constrained by the presence of protected retreat sites as occurs in *A. castaneus* (and to an even greater extent in *T. radiata*) The absence of such obstacles is probably not simply a consequence of these other webs being higher above the substrate, however, but due to the abilities of these spiders to choose more open web sites. There are many possible obstructions such as twigs and leaves high above the ground, and in fact spiders can only build where there are sufficient supports to which to attach their webs. Building a more elevated web is no guarantee that such obstructions will be avoided (as implied by Blackledge et al. 2009). Thus, the existence of fewer obstructions in more aerial webs implies that these other spiders actively avoided obstructions when they chose where to build (though we know of no studies of exploration behavior in any sheet building spider). We speculate that the obstacles in *A. castaneus* webs (and those of *T. radiata* and *Melpomene sp.*) result at least in part from the lack of an ability to shift the positions of lines and their attachment sites, due to their lack of break and reel behavior. This may make it difficult for these spiders to adjust their webs to the presence of obstacles that they only discover after web construction has already begun; it may also explain the occasional apparently superfluous "anchor" lines below the sheet (Fig. 2c).

The multiple small tiers on the sheets of *A. castaneus* were probably produced when spiders laid swaths of fine lines over small concavities in their sheets. Examination of newly constructed sheets in the field showed similar multiple tiers in the agelenid *Melpomene* sp. (Fig. 11) and the diplurid *Linothele macrothelifera* (Eberhard & Hazzi 2012), but not in the zoropsid *Tengella radiata* (Fig. 9). Possibly tiers function by increasing the retention times for prey that have fallen onto the sheet, as presumably occurs with the cribellum lines included in *T. radiata* sheets.

One unexpected observation in *A. castaneus* was that the area covered by the sheet spun on the first night was not extended during the next two nights, even though additional lines were added to the surface of the sheet. The spiders in the field evidently broke and discarded old webs to replace them with new ones. In captivity, *A. lagotis* added lines to thicken but not to extend the sheet after the first night of construction (M. González, pers. comm.); in this case, however, the spiders were confined in small $10 \times 10$cm containers, so it is uncertain whether this behavior occurs in the field. Many other non-orb weaving species add to their webs gradually over the space of many days. Captive *Melpomene* sp. added tiers on successive nights and extended the attachments of the edges of their sheets upward on the sides of the container, so the upper surface of the web gradually moved upward (A. Rojas pers. comm.; W. Eberhard unpub.). Again, it is possible that this behavior was an artifact of the size of the containers in which the spiders were kept. *Aulonia albimana* (Walckenaer, 1805) also added silk to the tubular retreat and to the sheet over a period of days, and sometimes built a new sheet on top of an older one (Job 1968).

Construction of prey capture webs by mature males of *Aglaoctenus* (González et al. 2015; present study) also occurs sporadically in other families of web-building spiders, but appears not to be shared with *T. radiata* (Barrantes & Madrigal-Brenes 2008) or *Melpomene sp.* (W. Eberhard, unpub.). Mature males of the lycosid *Aulonia albimana* occasionally built silk tubes as retreats, but apparently did not build sheets (Job 1968), and thus differ from *Aglaoctenus*.

**Prey-wrapping and the evolution of web construction behavior.**—Prey wrapping in *A. castaneus* corresponds to the "post-immobilization wrapping" behavior of mygalomorphs and araneomorph species (both with and without webs); it probably serves to make the prey package more compact and manageable after the prey is subdued (Eberhard 1967; Robinson et al. 1969; Rovner & Knost 1974; Barrantes & Eberhard 2007; Hazzi 2014). The spinneret movements of *A. castaneus* during wrapping, with the trailing PL spinneret

being raised while the leading one is lowered as the spider was attaching wrapping lines to the substrate or to other lines, and the spider's use of her body rather than leg movements to pull out wrapping silk as she turned, were very similar to prey wrapping in variety of other species, including the theraphosid *Psalmopoeus reduncus* (Karsch, 1880), *Melpomene sp*. (Barrantes & Eberhard 2007), *T. radiata* (Barrantes & Eberhard 2007), and the ctenid *Phoneutria boliviensis* (F. O. Pickard-Cambridge, 1897) (Hazzi 2014). They also resembled movements during sheet construction by the diplurid *Linothele macrothelifera* (Eberhard & Hazzi 2012). This behavior probably serves to widen the swaths of lines applied to the prey (Barrantes & Eberhard 2007; Hazzi 2014). We speculate that swath widening during sheet construction in *A. castaneus* resulted from an evolutionary transfer of ancient prey wrapping behavior to the context of sheet web construction.

**"Sheet", "funnel" and "brushed" webs in evolution.**—Several recent studies of the evolution of spider web construction behavior that were based on phylogenies generated from morphological and molecular data have used the categories of "sheet" and "brushed sheet" webs in classifying web designs. Our observations reported here have important implications regarding these classifications.

As others have noted (Viera et al. 2007; Blackledge et al. 2009), many previous publications were imprecise in applying the term "sheet web" to characterize a variety of web designs. To pick just one recent example, Murphy et al. (2006) included as "sheets" many diverse structures: the tents that *Dolomedes* Latreille, 1804 spp. build around their egg sacs to protect their nymphs (Comstock 1948; Bristowe 1958); the dense silk retreat embedded in sphagnum moss of *Pirata* Sundevall, 1833 that has an open doorway from which the spider attacks passing prey (Bristowe 1958); the sparse planar arrays of sticky silk in dictynids (some on the substrate, others away from it) (e.g., Nielsen 1931; Griswold et al 2005); and the extensive sheets and silk tubes of *Aulonia albimana* (Job 1968, 1974) and sosippine lycosids. Precision in classifying web forms is obviously crucial in discussing web evolution, especially since nearly all classifications to date have been made on the basis of only the superficial appearance of the web, rather than on observations of construction behavior or the connections between lines in finished webs. Imprecision in terminology can have serious consequences for attempts to trace the phylogeny of web designs. For example, if the claims for homology among the "sheet" webs of Murphy et al. (2006) are over-ambitious, the case for considering funnel webs as ancestral for Lycosidae is weakened.

A second widely used descriptive term that is also sometimes applied loosely is "funnel web". On the basis of geometry (i.e., a tube connected with a more or less curved plane), this label would apply to webs with a more or less horizontal, planar sheet that is joined with a tubular retreat. This category would include such diverse web designs as the relatively open-meshed sheet webs with adhesive silk of the austrochilid *Thaida peculiaris* Karsch, 1880 (Lopardo et al. 2004) and the psechrids *Psechrus argentatus* (Doleschall, 1857) (Robinson & Lubin 1979) and *Psechrus* Thorell, 1878 sp. (Eberhard 1987b; Zschokke & Vollrath 1995a, b), as well as the dense sheets of fine non-adhesive lines of agelenids, lycosids and diplurids.

A welcome recent consensus appears to be emerging that different types of "sheet" and "funnel" webs need to be distinguished (see Viera et al. 2007; Blackledge et al. 2009). One step in this direction is the proposal of Blackledge et al. (2009) (which was followed subsequently in the phylogenetic studies of Fernández et al. 2014, Bond et al. 2014, and Garrison et al. 2016) to subdivide these categories. Blackledge et al. (2009) distinguished four types of sheets that they appeared to define as follows: brushed —"... brushed silk lines are not specifically and repetitively attached to structural silk threads, but rather lie upon them" and have "... no direct junctions between discreet silk threads ..." and are produced by "... numerous, identical (often aciniform) spigots operating in concert"; irregular ground —"... relatively complex three-dimensional webs that consist of multiple sheets intersecting at various angles and whose overall form tends to follow closely the contours of the substrate to which the webs are attached; irregular aerial —"... are suspended or free standing ... [and] are relatively amorphous and fill available space in the microhabitat location ..."; and stereotyped aerial —"... are architecturally stereotyped and usually taxonomically distinctive regardless of variation in microhabitat location..." (our uncertainty concerning the definitions is because the text of the "supplementary material" was not exactly parallel to the categories recognized in the figure that documented web evolution). The webs of *A. castaneus, T. radiata,* and *Melpomene* sp. are all in the "brushed" category in this classification (J. Coddington pers. comm.).

Unfortunately, placement of different species' webs in these categories has been based only on the overall appearances of webs. There were no observations of behavior; and only one short abstract on a single species (Coddington 2001) was cited concerning connections between threads in webs. The present paper is not the place to attempt a general resolution of how to define "funnel" webs or "brushed sheets". We will, however, take the preliminary step of describing some sets of shared traits, and note some problems in recognizing the "brushed sheet" category.

One species whose webs and behavior seem to fit the criteria for "brushed" is the sheet weaving diplurid *Linothele macrothelifera* (Eberhard & Hazzi 2012), based on evidence from direct observations of construction behavior, close up photos of webs, and the lack of piriform glands in the spiders. The webs of the three araneomorph species of this study, however, clearly do not fit the definition cleanly. The sheets of *A. castaneus* and *T. radiata* had numerous piriform attachments, and during web construction *A. castaneus* paused frequently to press her abdomen to the sheet, apparently making piriform attachments (though, as noted above, these probably probably attached only ampullate and not aciniform lines), rather than brushing her PL spinnerets against the web. Of the three, *Melpomene* sp. was closest to the "brushed" traits. The difficulty in classifying these species arises from the fact that the discrimination was made in quantitative terms (e.g., frequency of piriform attachments in the sheet), but no indication was provided for deciding how infrequent piriform attachments need to be for a web to qualify for inclusion in the "brushed" category.

A second problem is that the term "brushed" conjures up the image of numerous spigots operating in concert, thus leading to the expectation of many fine lines in the sheet being approximately parallel to each other. Our findings with *A. castaneus* offer only partial confirmation. In some photographs of powdered webs, there were areas with multiple, approximately parallel lines close together (e.g., Fig. 2b, 3b, d). But under the microscope, most lines in the sheets of this species, as well as those in the sheets of *T. radiata* or *Melpomene* sp., were *not* parallel to each other. The overall impression was of disorder (Figs. 8, 10, 12). Presumably the large numbers of non-parallel lines resulted largely from swath widening behavior.

As a first step toward a more natural and informative classification scheme, we point out that the webs of lycosids, agelenids, and zoropsids that are known to date share several traits: a more or less horizontal and planar sheet that is continuous with the walls of a silk tunnel within which the spider shelters; a "skeleton" of thicker lines which is built early, before the sheet is completely filled in with large numbers of very fine lines that are laid onto the skeleton (though in *A. castaneus* the two types of lines are laid simultaneously early in web construction; later behavior is dedicated, at least as far as our fragmentary observations go, more to filling in); relatively frequent piriform attachments between skeleton lines, scarcer piriform attachments involving the fine lines; some relatively parallel orientations of multiple fine lines locally in photographs of powdered webs (though not easily discerned when the sheet is examined under a microscope); highly variable orientations of lines throughout the web (which are due both to the wandering path taken by the spider while laying these lines, and to her lack of inclusion of aciniform lines from her trailing PL spinneret in attachments); and the spider's use of the upper rather than the lower surface of the sheet to move about on her web. A further shared trait is a sparse tangle of thicker lines above the sheet, though the tangle is omitted in some *Aglaoctenus* and *T. radiata* when no appropriate attachment sites are available (González et al. 2015; this paper). The zoropsid differs in also adding sticky lines to the sheet. Many of the details just listed have not been documented in published descriptions of the webs of other species, however, and some behavioral traits (such as possible one sided walking) have yet to be checked in most species. Future discoveries may reveal differences in the details of web design and construction behavior within this group that may suggest different groupings.

Our overall conclusion is that the definition of "brushed" webs is of limited utility. Some webs that were included in this category did not have some of the traits that were used to define the category, and the behavioral observations and microscopic examinations of thread connections in the sheets that would be necessary to test it are lacking in other species. This imprecision in classification raises doubts about some conclusions from some recent studies of the evolution of spider web designs (Blackledge et al. 2009; Fernández et al. 2014; Bond et al. 2014, Garrison et al. 2016). Further behavioral studies and detailed studies of webs are needed to improve the classification schemes used in phylogenetic analyses of the evolution of sheet and funnel webs.

**Limitations of this study.**—This study was brief and seriously incomplete. Even combining it with that of González et al. (2015), many basic aspects of *Aglaoctenus* web construction have not even been addressed, much less studied carefully. There is no information, for instance, on how the tangle above the sheet is built, on the cues that spiders use to guide building behavior, on the patterns (if any) in the movements during skeleton web construction or filling-in behavior, or on the possible importance of the palps (see Hingston 1920 on *Hippasa olivacea*). Surprisingly, there is still not a single thorough study of funnel web construction in any of the many taxonomic groups that build funnel webs, or of relations between variations in webs and ontogeny, microhabitat charateristics, or reproductive status.

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