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Possible functional significance of spigot placement on the spinnerets of spiders

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Abstract. This paper discusses the possible functional significance of the locations of the spigots of different types of silk gland on the different spinnerets of spiders. Deductions are based on recognition that some types of line are initiated by being attached to the dragline, that there is an anterior-posterior asymmetry in how such lines can be initiated, and that spigot location also affects the possibility of attaching lines to the substrate. Possible explanations are given for several morphological details, including the anterior location of the dragline, piriform and cribellum spigots, planar arrays of piriform and cribellum spigots, and posterior location of aciniform spigots. I argue that piriform gland products are not used to attach egg sac lines to each other, that sticky wrapping lines are initiated in theridiids and pholcids by attaching them to draglines and that lines from both aciniform and cylindriform glands are laid along with liquid that renders them sticky. The possible role of phylogenetic inertia in determining spigot locations is discussed. Further work is needed to determine whether termination of lines and accessibility of spigots for cleaning also influence their positions.

Keywords: Silk, silk gland, phylogenetics inertia

Spinneret morphology provides many useful taxonomic characters in spiders, and the distributions and forms of the spigots of different silk glands have been described for many species (summaries in Coddington 1989; Platnick et al. 1991; Agnarsson 2004; Griswold et al. 2005). Surprisingly however, there has been little discussion of the possible functional significance of the locations of spigots on spinnerets. Perhaps the most striking exception is the onchyroceratid *Ochyrocera cachote* Hormiga, Álvarez-Padilla & Benjamin 2007, which builds small domed sheet webs containing sectors with large numbers of precisely parallel lines (Hormiga et al. (2007). The posterior lateral spinnerets of *O. chachote* have an unusual row of tightly spaced aciniform spigots, and the similarity between the length of this row and the number of spigots with the width of the arrays of parallel lines and the numbers of parallel lines in the swaths (about 20) leave little doubt that each swath is produced during a single pass of the spider's spinnerets (Hormiga et al. 2007). Similar arrays of many parallel lines also occur in the webs of another *Ochyrocera* species in Costa Rica (G. Barrantes & W. Eberhard unpubl. results). A second case in which the possible functional significance of spigot positions on spinnerets has been discussed is the tight physical association between the spigots of the aggregate and the flagelliform glands in araneoid orb weavers, allowing the spider to coat the flagelliform line with sticky material from the aggregate gland as the line emerges from its spigot (Coddington 1987; Blackledge et al. 2009).

The present note combines direct observations and video recordings (30 frames/s) of the behavior of mature females of large araneoid species, data from the extensive literature on spinneret morphology, and data from the much less extensive literatures on how different types of lines are initiated and on their morphology (especially in the SEM) to propose possible functional explanations for the positions of a number of types of spigots in spiders. I argue that the sites of different spigots relative to each other influence the spider's ability to initiate and to coordinate the production of different types of lines, and that selection on these abilities may explain why particular spigots are located at particular sites. The arguments are not all complete, and the aim is to initiate discussions rather than to provide exhaustive, final answers.

General considerations regarding how lines are initiated and fastened.—Spigot placement probably affects how a spider can initiate lines. As is well known, spiders cannot eject silk lines, but must have them pulled from their bodies (Witt et al. 1968; Foelix 1996). Three different mechanisms have been proposed for line initiation. The best known, ‘‘direct contact’’ initiation technique occurs when the spider presses its spinnerets against a substrate and then pulls away (e.g., Kullmann 1975). If the spinnerets are held in appropriate positions, if the spigots are at appropriate sites on the spinnerets to bring their tips into contact the substrate, and if there is liquid silk at the tips of the spigots (they are ‘‘wet’’) (presumably due to abdominal pressure – Wilson 1962a), then this liquid will adhere to the substrate and the spider can initiate a new line when it pulls its spinnerets away. Similarly, lines could be initiated by direct contact between different spinnerets, with or without another line between them (see below).

A second way of initiating lines, ‘‘dragline initiation’’, was observed when *Nephila clavipes* (Linnaeus 1767) and *Argiope argentata* (Fabricius 1775) wrapped prey. For instance, when a large female *N. clavipes* begins to wrap a prey, the lines in the swath of wrapping lines (presumably from her aciniform gland spigots) are attached to her dragline (Fig. 1). The spider wraps the prey by snagging the wrapping lines with her legs IV and pulling out more silk by extending them toward the prey to press the wrapping lines against it. A second context in which dragline initiation occurs in a variety of species is initiation of airborne lines, when the distal ends of airborne lines are attached to the spider's dragline as it descends (Eberhard 1987) (in this case, the glandular origins of the lines are unknown). Initiation of these wrapping and airborne lines presumably occurs when the spider applies the ‘‘wet’’ tips of the spigots that produce these lines to a dragline while the dragline is being pulled as the spider moves.

This dragline initiation technique is only feasible if the spigots of different glands are aligned on the spinnerets in

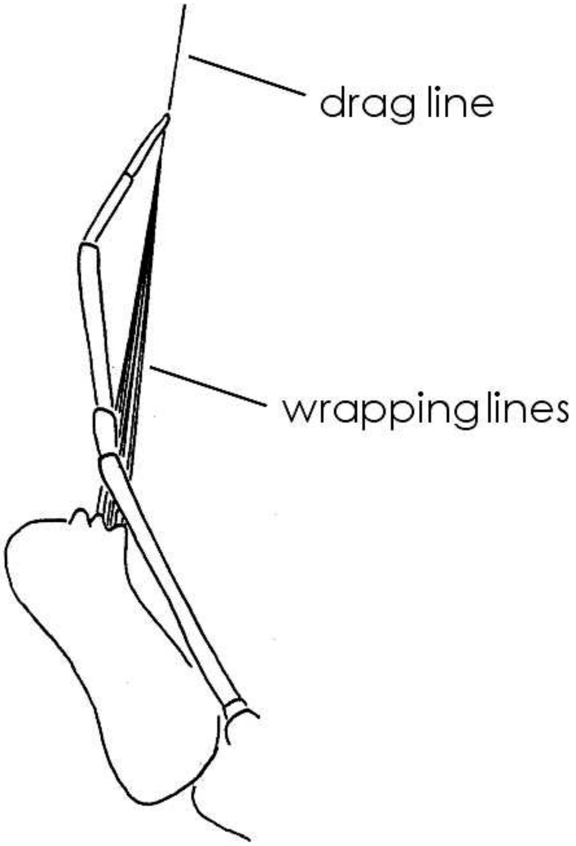

Figure 1.—A swath of aciniform lines is attached to the dragline of a mature female *Nephila clavipes* as she descends, just before she initiates prey wrapping (drawn from a video recording).

certain ways. Spiders almost always move forward rather than backward while spinning draglines, so lines from spigots on the "downstream", posterior median and posterior lateral spinnerets (e.g., the aciniform spigots in araneoids) can be initiated using lines from spigots on the "upstream", anterior lateral spinnerets (e.g, dragline or major ampullate spigots). Movements of more posterior spinnerets in an anterior direction, and manipulations of lines with the legs can relax these constraints somewhat (see description of *Nephila* behavior below). The short lengths of most spinnerets, however, suggest the general rule that spigots that are located farther posterior on the spider's body (more downstream) can initiate lines by touching their tips to lines from more anterior (upstream) spigots, but not vice versa.

A final possible mechanism for initiating lines, "clapping initiation", involves spreading movements of the spinnerets with respect to each other (Blackwell cited in McCook 1889; Nielsen 1931; Eberhard 1987). For example, the spider could clap or rub pairs of spinnerets together, and then pull them apart. The spider could then either pull further silk with its legs, or use friction with the air to elongate the short lines between the spinnerets. Although there are reports that spinnerets are spread widely when some lines (e.g., airborne lines) are being initiated (Blackwell in McCook 1889; Eberhard 1987), I know of no confirmed demonstration of clapping initiation.

One further aspect of "upstream – downstream" locations concerns the use of one type of silk to fasten lines of another type of silk to the substrate or to other lines. The spigots of the fastening silk need to be either at the same level or downstream of the spigots that produce the lines that are being fastened.

Possible functional significance of spigot placements.—The placements of spigots on the spinnerets could alter the feasibility of all three possible types of initiation, and their observed positions may possibly be explained in terms of functional consequences. I will discuss possible functions according to the probable glandular origin of the lines.

Ampullate gland spigots: As far as I know, the only technique that has been observed in dragline initiation (which is relatively rarely observed in the many species that produce draglines more or less continuously) is direct contact (e.g., Kullmann 1975 on an unspecified species; W. Eberhard unpubl. results on *Micrathena duodecimspinosa* (O. Pickard-Cambridge 1890) when they initiate the dragline after finishing construction of the sticky spiral). The rather basal position of the major ampullate spigots on the anterior lateral spinnerets of many species (Coddington 1989) (Fig. 2) probably obliges the spider to either spread these spinnerets widely, or to insert the substrate (e.g., another line, the spider's tarsus) deep between them. I know of no direct observations, however, of this detail. Kullmann (1975) noted that dragline initiation can occur by contact even when the spider is anesthetized.

Aciniform gland spigots: As noted above, initiation of aciniform wrapping lines in araneoids apparently occurs using the dragline initiation technique (Fig. 1). The downstream placement of the aciniform spigots (on the posterior median and lateral spinnerets) (Fig. 2) in araneomorph spiders in general (Griswold et al. 2005) with respect to the major ampullate spigots may function to allow initiation of aciniform wrapping lines by attachment to draglines. The downstream placement of aciniform spigots in mygalomorph spiders and presumably on the common ancestor of all spiders must have a different explanation, however, as these spiders lack dragline silk (Palmer et al. 1982; Palmer 1985; Blackledge et al. 2009). The arrangements of the aciniform spigots of some mygalomorphs in a line along the long axis of the long posterior lateral spinneret (Peters 1967) is apparently an ancient trait (Vollrath & Selden 2007). Similar linear arrays of aciniform spigots also occur in other groups with long posterior lateral spinnerets, such as agelenids and hersiliids (Peters 1967). They probably facilitate both the production of sheets of fine lines, rather than of cables of lines, and the placement of these swaths of lines using movements of the highly mobile spinnerets (Fig. 3). Sheets rather than cables are useful to these spiders, which line their retreats with sheets of silk, build sheet webs to capture prey and wrap their prey in wide bands of silk (Coyle 1986; Barrantes & Eberhard 2007).

The aciniform lines of both mygalomorphs and araneomorph spiders adhere at least weakly both to each other and to the substrate, and SEM and light microscope images indicate that they have small amounts of liquid associated with them when they are produced (Kullmann 1975 on ctenizid and diplurid mygalomorphs; Weng et al. 2006 on an uloborid and an araneid; W. Eberhard unpublished on the araneid *A. argentata*). This stickiness of aciniform lines helps make functional sense of some aspects of spinneret morphology. Mygalomorphs are able to glue lines together and to the

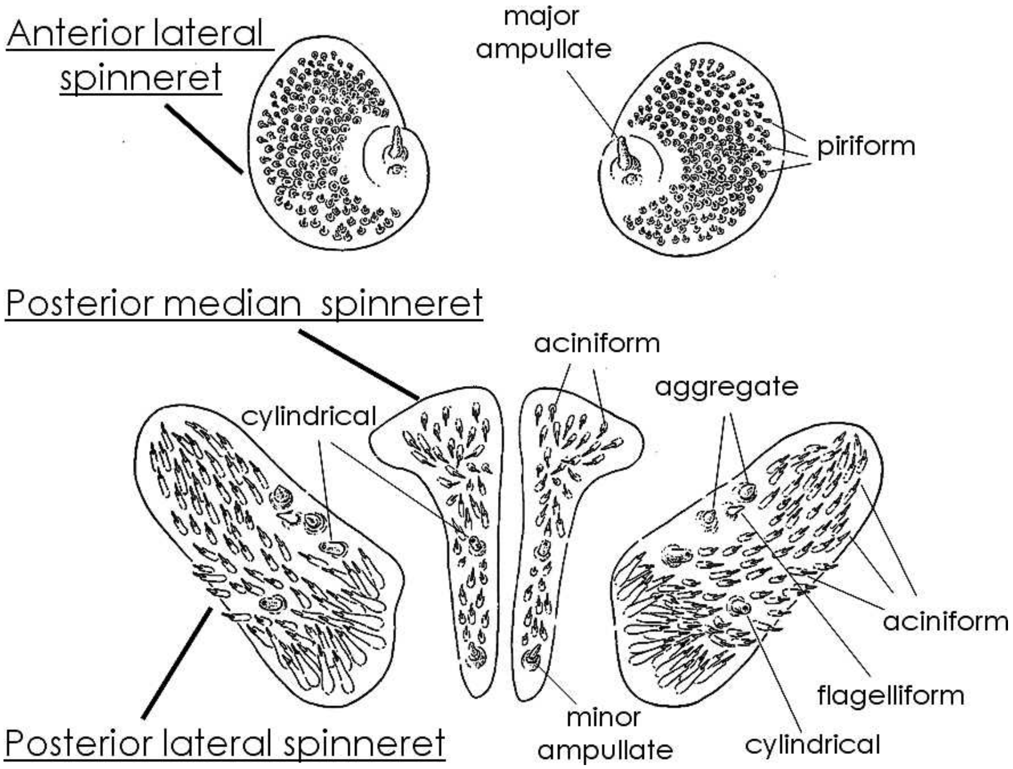

Figure 2.—Basic diagram of the locations of spigots on the spinnerets of araneoid spiders (after Coddington 1989).

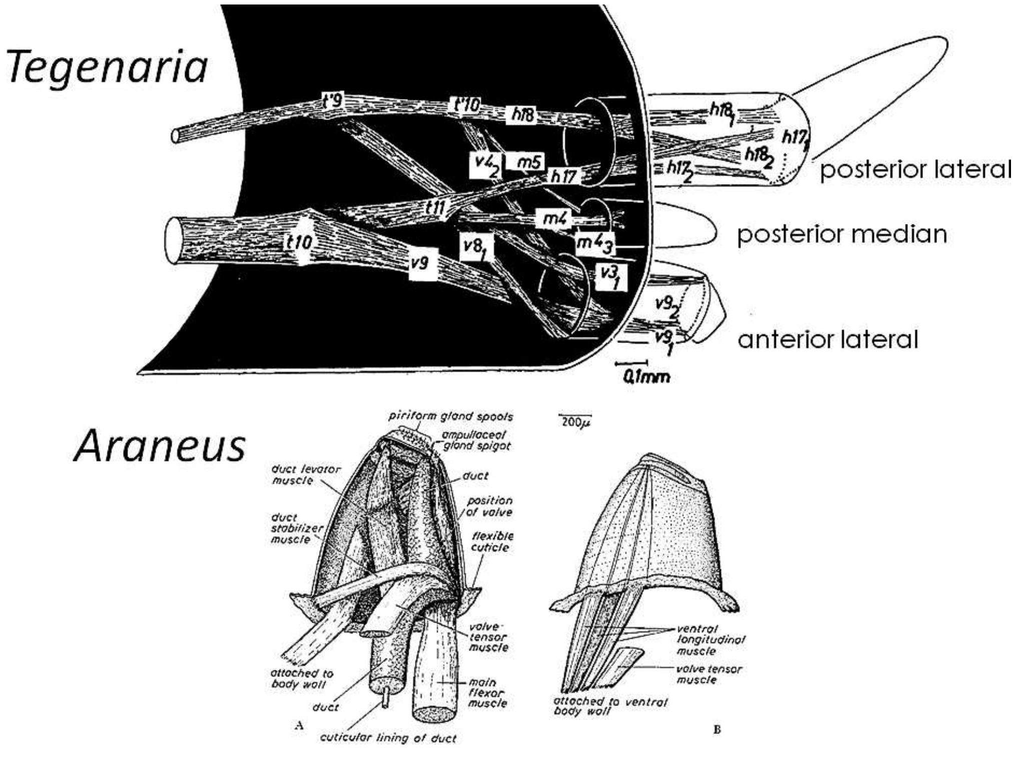

Figure 3.—The complex muscles associated with the spinnerets of an agelenid (above) and an araneid (below) indicate that these spiders are able to make diverse, finely controlled spinneret movements (above from Peters 1967; below from Wilson 1962b).

substrate, despite that fact that they lack piriform glands, whose products are used to fasten lines to other objects in araneomorph spiders (Schütt 1996; Foelix 1996; below). The aciniform spigots of araneomorphs are downstream from the piriform spigots, so their aciniform lines probably cannot be easily attached using piriform silk.

The aciniform lines also vary substantially in diameter, in both mygalomorphs (Kullmann 1975 on a diplurid; Stern & Kullmann 1981 on a ctenizid), and araneomorphs (Kullmann 1975 on an araneid; Weng et al. 2006 on an uloborid and an araneid; W. Eberhard unpubl. results on the araneid *A. argentata*). Presumably these differences are associated with the differences in aciniform spigot diameters seen in many species (Griswold et al. 2005), but nothing appears to be known regarding the possible functional significance of these differences, or the possibility that silk composition varies in lines with different diameters. In *Uloborus* there are two kinds of cells in all aciniform glands (Kovoor 1977).

Piriform gland spigots: Small masses (‘‘attachment discs’’) of piriform gland products are used to attach draglines to the substrate or to other lines. They are apparently always initiated using the direct contact technique. Piriform lines are initiated either when the spider places a silk line against her spinnerets or presses her spinnerets against a substrate such as a leaf. Production of an attachment disc generally involves a short pause in spinning other lines, and in at least some cases the spinnerets rub rapidly against each other or against the substrate when an attachment is made (Schütt 1996; W. Eberhard unpubl. results on various araneid, nephilid, tetragnathid, and theridiid species). The looped forms of individual piriform lines in an attachment disc (e.g., Foelix 1996) probably result from these spinneret movements, but this behavior has never been studied in detail. Piriform lines are generally terminated almost immediately, when the spider pulls her abdomen away from contact with the substrate.

Use of the contact technique for initiation means that the piriform gland spigots do not need to be ‘‘downstream’’ of other spigots. In accord with this, piriform spigots consistently occur at relatively ‘‘upstream’’ sites, on the anterior lateral spinnerets (Fig. 2). Two additional details regarding the positions of piriform spigots on the anterior lateral spinnerets may be functionally important. The spigots are consistently at or near the tips rather than along the sides or at the bases of the spinnerets; and the surface on which the spigots are present is often relatively flat and tends to slope downward medially (e.g., Platnick et al. 1991; Agnarsson 2004; Griswold et al. 2005). Both the placement at the tip and the slanting flat field may serve to facilitate simultaneous contact between numerous piriform spigots and a flat substrate when the spinnerets are spread. Perhaps the different degrees of slant in different species (e.g., Griswold et al. 2005) are associated with different degrees to which the spinnerets are spread when producing attachment discs. The piriform spigots are also generally well placed to apply their products to the dragline emerging from the major ampullate spigots on these same spinnerets, thus allowing the spider to attach its dragline to the substrate. In some species the piriform spigots physically surround the major ampullate spigots (Fig. 2).

Microscopic examination of piriform attachment discs shows that they include liquid components, and also possibly more than one type of line (Kullmann 1975 and Stern & Kullmann 1981 on an oecobiid and an araneid; Schütt 1996 on a linyphiid and an araneid; Foelix 1996 on a thomisid). It is apparently not known whether different piriform spigots produce different products. Judging from the relatively uniform coating of apparent liquid on the piriform lines of the linyphiid *Drapestica socialis* (Sundevall 1833) (Schütt 1996), piriform lines in this species may emerge from their spigots with a liquid coating, rather than having liquid applied later. The description of Griswold et al. (2005: 59) ‘‘These spigots extrude the glue that attaches silken lines’’ is correct in a general sense, but does not include the thread-like products of these spigots, which are drawn from rather than ‘‘extruded’’ by these spigots.

The behavior of the spinnerets associated with the production of piriform silk was studied in video recordings of a large, slow-moving spider (an adult female *N. clavipes*) as she attached draglines to other non-sticky lines at the hub, and sticky spiral lines to radii. Spinneret behavior was highly stereotyped. In both types of attachment, the spider held the segment of the non-sticky line to which the attachment was to be made between her tarsi III and IV and placed it (using movements of these legs and of her abdomen) deep in the cleft between her anterior lateral spinnerets (the radius was approximately halfway down the length of her anterior lateral spinnerets). The radius often, though not always, passed over the tips of her posterior lateral spinnerets. Both the basal and the distal segments of her anterior lateral spinnerets were flexed medially, and the tips of the spinnerets rubbed rapidly back and forth against each other briefly, with one spinneret moving anteriorly while the other moved posteriorly. Probably contact occurred on the surfaces where the piriform spigots are located (Kuntner et al. 2008).

When attaching the dragline, each anterior lateral spinneret rubbed several times against the other (up to three complete cycles in about 0.77 s). Such movements may serve both to initiate piriform lines and to surround the dragline and the other line with piriform lines and glue; this could result in an increase in the surface area of these lines that is contacted by piriform products, presumably increasing the strength of the attachment that is formed.

When attaching the sticky spiral, the spider made only a single forward-backward rubbing movement with each spinneret (lasting about 0.06–0.09 s). Her posterior lateral spinnerets, which bear the spigots for the sticky spiral line and the glue that covers it, were flexed forward. This flexion occurred 0.03–0.06 s before the radius was brought into contact with her spinnerets and was maintained while the anterior lateral spinnerets rubbed against each other. Meanwhile her leg iIV pushed the sticky line ventrally and somewhat anteriorly, and the line appeared to make contact with the anterior lateral spinnerets during their rubbing movements. The anterior movements of the posterior lateral spinnerets, in combination with the fact that the spider pushed the new sticky line ventrally and anteriorly with one of her legs IV, thus brought the sticky line far enough forward that the piriform spigots were able to apply their silk to it during the rubbing movements. Finally the anterior lateral spinnerets spread apart and (often about 0.03 s later) the posterior lateral spinnerets spread and moved posteriorly as the spider pulled her abdomen away from the radius, leaving the finished attachment.

It is possible that these piriform products differ from others, because there are other data which suggest that the attachments of sticky spiral lines to radii in araneoid orbs may not be made from "typical" piriform gland products (Kullmann 1975 on differences in silk morphology in SEM images; Eberhard 1976 on differences in physical properties; Tillinghast et al. 1981 on differences in chemical properties).

Cribellum gland spigots: A second type of line that is also both initiated and then pulled by an external agent is cribellum silk; multiple fibers are pulled from the cribellum with brushing movements of the comb of setae (the calamistrum) on the spider's leg IV. There is no need for the spigots of lines that are pulled by the spider's legs to be downstream of other spigots, and the cribellum is indeed upstream of all other spigots. In addition, the spinnerets on which cribellum spigots occur (the anterior medians) have been modified to form flat plates whose angles can apparently be modified by special muscles (Peters 1967), a design that is appropriate to allow the linear calamistrum to snag lines from the entire array with a single pass.

Pseudoflagelliform gland spigots: The placement of the spigots of the pseudoflagelliform glands is also functionally logical. These glands are thought to produce the straight baselines associated with the mat of cribellum lines in the sticky spiral of uloborids. The pseudoflagelliform spigots are on the tips of the posterior lateral spinnerets (Coddington 1987), appropriately distant from the cribellum to avoid being snagged by the calamistrum (the pseudocribellar line, which is much shorter than the cribellum lines, is presumably pulled by the walking movement of the spider rather than by the combing action of the calamistrum). The sticky spiral of the uloborid *Uloborus diversus* is initiated when the spider touches her spinnerets to a radius (Eberhard 1972), so the direct contact technique may be used to initiate the pseudoflagelliform lines.

Cylindriform gland spigots: Cylindriform gland lines are used to make egg sacs. They seem to be slightly sticky when they emerge, because some lines in egg sacs are covered with liquid (Kullmann 1975 on an araneid, a mimetid and a deinopid; Stern & Kullmann 1981 on a theridiid), and they very frequently adhere at least weakly to each other, even though the spider only briefly dabs her abdomen to the egg sac during construction; the dabs are not accompanied by short pauses, as when piriform discs are produced (Kullmann 1961; Gheysens et al. 2005; Moya et al. 2010). It thus appears that piriform silk is not used to hold sticky cylindrical gland lines together; this is consistent with morphology, as the cylindrical gland spigots are downstream with respect to the piriform gland spigots (Fig. 2)

Flagelliform and aggregate gland spigots in theridiids: The upstream placement of dragline spigots probably has still another important functional consequence in theridiid spiders, which use flagelliform and aggregate gland products to wrap and subdue prey. Initiation of these wrapping lines occurs as the spider moves toward the prey (Barrantes & Eberhard 2007), and it seems very likely (though initiation has never to my knowledge been directly observed) that these wrapping lines are initiated by being attached to the emerging trail line. The downstream placement of the flagelliform and aggregate gland spigots in theridiids (on the posterior lateral spinnerets) with respect to the ampullate gland spigots (on the anterior lateral spinnerets) (Coddington 1989; Agnarsson 2004) makes dragline initiation feasible.

The silk used in the later stages of theridiid wrapping attacks tends to be dry rather than wet (Barrantes & Eberhard 2007), presumably as aciniform lines replace wet sticky lines. Initiation of these presumed aciniform lines does not involve any obvious change in the wrapping movements of the spider's legs or abdomen. The downstream position of aciniform spigots (posterior median and lateral spinnerets) with respect to major and minor ampullate spigots, and the fact that they are also downstream or parallel in position with respect to the flagelliform spigots on the basal portions of the posterior lateral spinnerets (Agnarsson 2004), also makes it feasible that the aciniform lines are initiated by being attached to either the dragline (if it is still being produced) or to the flagelliform line.

In some of the orbicularion groups that no longer spin orbs, the tightness of the physical association between the flagelliform and aggregate spigots on the posterior lateral spinnerets is less consistent (e.g., Griswold et al. 1998, Agnarsson 2004). The possible the reasons for this dissociation are not clear.

Pholcid spigots: The spinnerets of pholcids have only small numbers of spigots compared with those of araneoids (as few as 8, with a maximum of 20 – B. Huber, pers. comm.; contrast this with >1300 spigots in *Araneus diadematus* Clerck 1757– Foelix 1996), and some glands and their spigots have been difficult to homologize with those of other spiders (Kovoor 1986; Platnick et al. 1991). The enormously enlarged tip of one spigot (the spigot for gland "B" of Millot) at the tip of the anterior lateral spinneret (Platnick et al. 1991; Huber 2000) appears to produce sticky liquid that is used both in wrapping prey (Kirchner & Opderbeck 1990; Eberhard 1992), and in making the puddle of liquid that attaches lines to the substrate (Schütt 1996). This spigot lies immediately adjacent to the spigot that probably produces the dragline (major ampullate gland; gland "C" of Millot) (Kovoor 1986; Platnick et al. 1991). Pholcids resemble theridiids in rapidly initiating sticky silk production at the beginning of wrapping attacks and then later using non-viscous silk to wrap the prey (Kirchner & Opderbeck 1990; Eberhard 1992; Barrantes & Eberhard 2007). As in theridiids, there is no perceptible pause associated with initiation of sticky silk production as the spider runs to the prey and begins to wrap it. This rapid initiation of sticky wrapping silk probably occurs when spigot B material is pulled out by (or poured onto?) the dragline while the dragline is produced as the spider moves toward the prey, in much the same way that aggregate gland silk is added to flagelliform gland silk in araneids (above). In *Pholcus phalangioides* (Fuesslin 1775) the spider applies up to four lines of silk at once to the prey (Kirchner & Opderbeck 1990), so lines from at least one additional set of spigots in addition to the major ampullates must be involved, perhaps the spigots for gland A on the posterior median spinnerets (these are thought to correspond to the minor ampullate glands) (Kovoor 1986; Platnick et al. 1991). It would be feasible (though certainly not demonstrated at the moment) for the spider to use dragline initiation for these additional minor ampullate lines during the latter stages of prey wrapping by touching the A spigots on the median posterior spinnerets to the dragline after it emerges from spigots C on the anterior lateral spinnerets.

Pholcids use small pools of what is probably this same adhesive silk from spigot B, combined with other lines (presumably from other, smaller wide-mouthed spigots on the anterior lateral spinnerets), to fasten lines to each other and to the substrate (Kirchner 1986; Schütt 1996) (e.g., the typical function of piriform glands). The positions of the B spigots at the tips of the anterior lateral spinnerets are also appropriate for this function. It seems likely that the wrapping function for these glands in pholcids was derived from the attachment function, and indeed B glands have chemical characteristics reminiscent of piriform glands (Kovoor 1986; Platnick et al. 1991). If this derivation is correct, the position of the piriform spigots adjacent to the major ampullate gland spigots may have represented a preadaptation for the subsequent use of this sticky silk for wrapping prey. Presumably one piriform spigot became oversized as the gland product became more liquid, possibly in association with its use in prey wrapping.

Fine airborne lines: The glandular origins of very fine bridge or balloon lines are not known, but the arguments made here suggests that their spigots are located downstream of the dragline spigots, and perhaps upstream of the spigots of the thicker lines that the spider apparently attaches to these fine lines while the fine lines are being produced (Eberhard 1987). Direct observations of the spinnerets of the tetragnathid *Leucauge mariana* (Taczanowski 1881) suggested that the fine airborne lines originate on the posterior median or posterior lateral spinnerets (Eberhard 1987).

DISCUSSION

Implications.—The data above show that the consistent sites at which the spigots of different glands are placed on different spinnerets have functionally reasonable "upstream-downstream" explanations. It is also possible, however, that these explanations for spigot placement are simply an example of historical constraint. It makes functional sense, for instance, that the major ampullate spigots are not downstream of others, due to their possibly central role in initiating lines from other glands. But the major ampullate spigots apparently evolved only once (Griswold et al. 2005), and the lack of variation of major ampullate spigot placement across spiders indicates that their placements in different species probably represents (at least in some senses) only a single evolutionary event. This skepticism regarding the functional interpretations proposed here must be tempered, however, by the fact that the "upstream-downstream" arguments can explain not only why these and other spigots are located where they are in the first place (clearly, spigots are not randomly scattered over the spinnerets); they can also explain why they have not moved subsequently. The possibility of evolutionary flexibility in spigot placement is demonstrated by the fact that aciniform gland spigots were apparently regained twice independently after having been lost from the posterior median spinneret in *Pimoa* (Hormiga 1994). Additional predictions derived from the arguments presented here could offer further tests. For instance, there should be a correlation between the positions and movements of the anterior lateral spinnerets when attachments are made and the site and slant of the planar field on which the piriform spigots are located.

It is also important to note that the kinds of functional arguments made here cannot yet explain some spigot placements and thus also represent possible areas of future research. I do not understand, for instance, how the calamistrum on the spider's leg IV can snag lines from the paracribellar spigots on the posterior median spinnerets of a species like *Filistata insidiatrix* (Forsskål 1775). In this species the paracribellar lines are highly curled and presumably pulled out by the brushing action of the calamistrum (Griswold et al. 2005), but the posterior median spinnerets are shorter than the anterior lateral spinnerets, thus apparently making it difficult for the calamistrum to pull lines from the paraflagelliform spigots (Griswold et al. 2005) (perhaps the spider can protrude the posterior median spinnerets?). The functional significance of the substantial differences in the forms of the calamistra of different species has also, to my knowledge, never been discussed or related to the differences in the form of the cribellum.

Many other smaller morphological details are still mysterious, such as the "T" shaped array of piriform spigots on the anterior lateral spinnerets of *Mecynogea lemniscata* (Walckenaer 1842) and *Cyrtophora citricola* (Forsskål 1775) (Coddington 1987), the nearly complete loss of piriform spigots in immature but not adult *Eriauchenius* (=*Archaea*) *workmani* O. Pickard-Cambridge 1881 (Griswold et al. 2005), and the loss and subsequent independent recovery of aciniform spigots on the posterior median spinnerets of some species of *Pimoa* (Hormiga 1994). It is not clear why there is variability in the tightness of the physical association between the flagelliform and aggregate spigots in some orbicularions that have lost orb webs (e.g., Agnarsson 2004). The function of the "small gland" spigots on the anterior lateral spinnerets of pholcids (Kovoor 1986), which were presumed by Platnick et al. (1991) and in the discussion above to represent piriform spigots that are used to fasten lines to the substrate and other lines, needs to be confirmed. The origin of the screw lines (Kirchner & Opderbeck 1990) in pholcid webs is apparently unknown.

Future directions.—The focus here has been on morphology, but understanding the functional significance of morphology depends on combining it with behavioral data. The behavioral capabilities of spider spinnerets, however, are as yet nearly completely unstudied. The spinnerets of many species are relatively short and thus difficult to observe, but they are segmented, and are equipped with well-developed musculature (Fig. 3), suggesting that they may be capable of substantial subtlety in their movements. The observations of *Nephila* described above document brisk, highly coordinated spinneret movements. Some mygalomorph and labidognath spiders can move at least their posterior lateral spinnerets with certain dexterity, including asymmetrically raising one and lowering the other during prey wrapping) (Barrantes & Eberhard 2007). Foelix (1996) mentions lifting, lowering, twisting and spreading movements (species not specified). Perhaps, even though the context is somewhat artificial, study of spinneret movements during forcible silking can help establish the behavioral capabilities of spinnerets. Craig (2003) stated (though with no evidence) that spinneret movements have played an important role in giving spiders great flexibility with respect to the types and character of the threads they spin.

Perhaps further study of spinneret movements will help to resolve some of these problems. Do spinnerets actually "clap" together medially to initiate airborne lines, as proposed by Blackwall (in McCook 1889), Nielsen (1931) and Eberhard (1987)? Are such claps always symmetrical (as appeared to be the case in *N. clavipes*), or is it possible for the piriform field of one anterior lateral spinneret to move medially to press on the lower interior face of the other anterior lateral spinneret and thus press on the line emerging from the major ampullate spigot? When spiders evolved to attach their draglines to other lines with piriform discs, their anterior lateral spinnerets may have already been capable of opposable movements that permitted them to "grasp" the other line to which the attachment was to be made, and thus apply piriform silk precisely to the other line. Perhaps araneomorphs evolved their relatively shorter spinnerets in association with the evolution of more types of silk glands, due to the advantage of having the spigots of different glands close to each other to facilitate coordination of production of different types of lines (B. Huber, pers. comm.).

It will be important in future work to keep in mind that the spinneret positions in taxonomic papers are somewhat unnatural, because taxonomists routinely spread the spinnerets to make the locations of different spigots easier to observe (Coddington 1989). In general, the spigots on different spinnerets are probably closer together in life than would be suggested by figures in taxonomic works. In attempting to think about "upstream – downstream" positions, it is also necessary to take into account cases in which the spider uses her leg to push a line anteriorly, as in sticky spiral production by *N. clavipes*. It will also be important to avoid typology, and keep in mind the possible consequences for spinneret use of variations in behavior; for instance, the different ways the spider grasps lines to which they are going to attach in the theridiids. *Achaearanea tesselata* (Keyserling 1884) (Jörger & Eberhard 2006) and *Tidarren sisyphoides* (Walckenaer 1842) (Madrigal-Brenes & Barrantes 2009) seem likely to affect how their spinnerets contact these lines.

Another topic that needs further work and that may provide understanding of spigot placement concerns the mechanisms that spiders use to *terminate* lines. Piriform initiation and termination is sometimes repeated literally hundreds of times very rapidly during the construction of a single orb. For instance, one mature female *M. duodecimspinosa* made 832 attachments of her hub spiral and temporary spiral to radii in the space of 428 s, or an average of 1.9 attachments/s; the time during which the spider's spinnerets were in contact with web lines (and thus the time during which piriform silk could be deposited at each attachment) was on the order of one or two tenths of a second/attachment. In other words, *M. duodecimspinosa* turns on pyriform silk production for only about a tenth of a second about twice a second, making hundreds of attachments in rapid succession. This is truly an impressive feat of coordination!

What little is known concerning termination of silk lines suggests (at least in the ampullate glands, which have long ducts) that termination generally occurs when there is a lack of liquid silk in the duct leading to the spigot, and the line breaks there as it is being pulled (Wilson 1962b; Work 1977). Presumably liquid silk then needs to be pushed to the tip of the spigot for the line to be reinitiated. It is not clear whether this termination mechanism also occurs in other glands such as the piriform and aciniform glands, which have much shorter ducts. So little is known at present that it is desirable to keep an open mind regarding whether spigot placement is also functionally related to termination.

Spigot placement could also possibly influence the spider's ability to clean its spinnerets after lines are terminated. For instance, when an adult female *N. clavipes* finishes wrapping a prey, she often "scrubs" her spinnerets together, scrapes their surfaces with the tarsus of her leg IV and then pulls the tarsus away, sometimes repeatedly.

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LITERATURE CITED

Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). Zoological Journal of the Linnaean Society 141:447–626.

Barrantes, G. & W.G. Eberhard. 2007. Evolution of prey wrapping behavior in spiders. Journal of Natural History 41:1631–1658.

Blackledge, T., N. Scharff, J.A. Coddington, T. Szuts, J.W. Wenzel, C. Hayashi & I. Agnarsson. 2009. Reconstructing web evolution and spider diversification in the molecular era. Proceedings of the National Academy of Sciences, USA 106:5229–5234.

Coddington, J.A. 1989. Spinneret silk spigot morphology: evidence for the monophyly of orbweaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. Journal of Arachnology 17:71–95.

Coyle, F.A. 1986. The role of silk in prey capture by nonaraneomorph spiders. Pp. 269–305. *In* Spiders: Webs, Behavior and Evolution. (W.A. Shear, ed.). Stanford University Press, Stanford, California.

Craig, C.L. 2003. Spiderwebs and Silk. Oxford University Press, New York.

Eberhard, W.G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). Journal of Zoology, London 166:417–465.

Eberhard, W.G. 1976. Physical properties of sticky spirals and their connections: sliding connections in orb webs. Journal of Natural History 10:481–488.

Eberhard, W.G. 1987. How spiders initiate airborne lines. Journal of Arachnology 15:1–10.

Eberhard, W.G. 1992. Notes on the ecology and behavior of *Physocyclus globosus* (Araneae, Pholcidae). Bulletin of the British Arachnological Society 9:38–42.

Foelix, R. 1996. Biology of Spiders. Second edition. Oxford University Press, New York.

Gheysens, T., L. Beladjal, K. Gellynck, E. Van Nimmen, L. Van Langenhove & J. Mertens. 2005. Egg sac structures of *Zygiella x-notata* (Arachnida, Araneidae). Journal of Arachnology 33: 549–557.

Griswold, C.E., J.A. Coddington, G. Hormiga & N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). Zoological Journal of the Linnean Society 123:1–99.

Griswold, C.E., M.J. Ramirez, J.A. Coddington & N.I. Platnick. 2005. Atlas of phylogenetic data for entelegyne spiders (Araneae:

Araneomorphae: Entelegynae) with comments on their phylogeny. Proceedings of the California Academy of Sciences Series 4, 56(Supplement II):1–324.

Hormiga, G., F. Alvarez-Padilla & S.P. Benjamin. 2007. First records of extant Hispaniolan spiders of the families Mysmenidae, Symphytognathidae, and Ochyroceratidae (Araneae), including a new species of *Ochyrocera*. American Museum Novitates 3577:1–21.

Huber, B. 2000. New World pholcid spiders (Araneae: Pholcidae): a revision at generic level. Bulletin of the American Museum of Natural History 254:1–348.

Jörger, K. & W.G. Eberhard. 2006. Web construction and modification by *Achaearanea tesselata* (Araneae: Theridiidae). Journal of Arachnology 34:511–523.

Kirchner, W. 1986. Das Netz der Zitterspinne (*Pholcus phalangioides* Fuesslin) (Araneae: Pholcidae). Zoologischer Anzeiger 216: 151–169.

Kirchner, W. & M. Opderbeck. 1990. Beuteerwerb, Giftwirkung und Nahrungsaufnahme bei der Zitterspinne *Pholcus phalangioides* (Araneae, Pholcidae). Abhand Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 31/32:15–45.

Kovoor, J. 1977. L'appareil séricigène dans le genre *Uloborus* Latr. (Araneae, Uloboridae). I. Anatomie. Revue Arachnologique 1:89–102.

Kovoor, J. 1986. Affinités de quelques Pholcidae (Araneae) décelables d'aprés les caractéres de l'appareil séricigéne. Mémoires de la Société Entomologique de Belgique 33:111–118.

Kullmann, E. 1961. Der Eierkokonbau von *Cyrtophora citricola* Forskål (Araneae, Araneidae). Zoologische Jahrbuch Systematics 89:369–406.

Kullmann, E. 1975. The production and function of spider threads and spider webs. Pp. 318–378. *In* Nets in Nature and Technics. (K. Bach, B. Burkhardt, R. Graefe & R. Raccanello, eds.). Druckerei Heinrich Fink KG, Stuttgart.

Kuntner, M., J.A. Coddington & G. Hormiga. 2008. Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. Cladistics 24:147–217.

Madrigal-Brenes, R. & G. Barrantes. 2009. Construction and function of the web of *Tidarren sisyphoides* (Araneae: Theridiidae). Journal of Arachnology 37:306–311.

McCook, H.C. 1889. American Spiders and their Spinning Work. Volume 1. Published by the author, Philadelphia.

Moya, J., R. Quesada, A. Arias, G. Barrantes, W.G. Eberhard, I. Escalante, C. Esquivel, A. Rojas & E. Triana. 2010. Egg sac construction behavior of by folding dead leaves in *Pozonia nigroventris* and *Micrathena* sp. (Araneae: Araneidae). Journal of Arachnology 38:371–373.

Nielsen, E. 1931. The Biology of Spiders. Levin & Munksgaard, Copenhagen.

Palmer, J.M. 1985. The silk and silk production system of the funnel-web mygalomorph spider *Euagrus* (Araneae, Dipluridae). Journal of Morphology 186:195–207.

Palmer, J.M., F.A. Coyle & F.W. Harrison. 1982. Structure and cytochemistry of the silk glands of the mygalomorph spider *Antrodiaetus unicolor* (Araneae, Antrodiaetidae). Journal of Morphology 174:269–274.

Peters, R. 1967. Vergleichende Untersuchungen über Bau und Funktion der Spinnwarzen und Spinnwarzenmuskulatur einiger Araneen. Zoologische Beiträge NF 13:29–120.

Platnick, N.I., J.A. Coddington, R.R. Forster & C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Museum Novitates 3016: 1–73.

Schütt, K. 1996. Wie Spinnen ihre Netze befestigen. Mikrokosmos 84:274–278.

Stern, H. & E. Kullmann. 1981. Leben am seidenen Faden. Kindler Verlag, München.

Tillinghast, E.K., E.J. Kavanagh & P.H. Kolbjornsen. 1981. Carbohydrates in the webs of *Argiope* spiders. Journal of Morphology 169:141–148.

Vollrath, F. & P. Selden. 2007. The role of behavior in the evolution of spiders, silks, and webs. Annual Review of Ecology, Evolution and Systematics 38:819–846.

Weng, J.-L., G. Barrantes & W.G. Eberhard. 2006. Feeding by *Philoponella vicina* (Araneae, Uloboridae) and how uloborid spiders lost their venom glands. Canadian Journal of Zoology 84:1752–1762.

Wilson, R.S. 1962a. The control of dragline spinning in the garden spider. Quarterly Journal of Microscopical Science 104:557–571.

Wilson, R.S. 1962b. The structure of the dragline control valves in the garden spider. Quarterly Journal of Microscopical Science 103:549–555.

Witt, P.N., C. Reed & D.B. Peakall. 1968. A Spider's Web. Springer Verlag, New York.

Work, R. 1977. Mechanisms of major ampullate silk fiber formation by orb-web-spinning spiders. Transactions of the American Microscopical Society 96:170–189.

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