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SHORT COMMUNICATION

Small details in a large spider: cheliceral and spinneret behavior when *Trichonephila clavipes* (Araneae: Araneidae) cuts lines and wraps prey

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Abstract. The large size and slow movements of mature female *Trichonephila clavipes* (Linnaeus, 1767) permit observations of some seldom-studied details of behavioral processes, such as cutting and initiating silk lines, that help clarify functional morphology. Silk lines were cut after being grasped by the cheliceral fangs; but direct observation and details of cheliceral morphology showed that cutting was not accomplished mechanically, as has sometimes been assumed. Lines were probably cut by contact with an enzyme in the mouth region. Initiation of wrapping lines involved rapid, coordinated movements of the spinnerets and the abdomen that caused the spigots for these lines to brush against each other and dragline silk. The posterior lateral spinnerets were spread widely during wrapping; this behavior and the positions of spigots on the spinnerets probably serve to widen the swath of wrapping lines applied to the prey.

Keywords: Cheliceral morphology, spinneret morphology, aciniform wrapping lines, silk-degrading enzyme

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Most spiders are small and move rapidly, and it is often difficult to resolve minor behavioral details that have important consequences for understanding functional morphology. This study follows the lead of previous studies, both new and old (e.g., Hingston 1922a,b,c; Wolff & Herberstein 2017) by taking advantage of the relatively large size and slow movements of mature female nephilines to clarify a few previously poorly understood details of behavior and morphology associated with the manipulation of silk lines.

Cutting silk lines has been described in *Trichonephila* (= *Nephila*) *clavipes* (Linnaeus, 1767) and the closely related genus *Nephila* Leach, 1815 in general terms as the result of bringing lines to the mouth area (Hingston 1922a,b,c; Robinson & Robinson 1973; Eberhard 1990a); but there was no mention of the movements of the chelicerae. This study employs observations of behavior and morphology to examine three hypotheses for the mechanism used by *T. clavipes* to break silk lines: mechanical cutting with a scissors-like action of the chelicerae; mechanical cutting with a knife against a chopping-block type of action of the chelicerae; and chemical cutting with a silk-digesting enzyme.

Initiation of wrapping lines in spiders has been associated with movements of the spinnerets, but only in vague terms such as "special movements of the spinnerets" (Robinson 1975) or "wiggled its spinnerets" (Rovner & Knost 1974). In general, initiation of silk lines has seldom been carefully described, probably both because direct observation is difficult and because the physical process of producing silk lines makes initiation difficult to understand. The transformation of spider silk from a liquid in the spider's silk glands to the semi-crystal solid state of silk lines is accomplished as a result of the silk being pulled; spiders do not eject or emit the lines from their spigots (Craig 2003; Foelix 2011). Thus, the pulling mechanism when a line is initiated is not intuitively obvious: if a line has not yet emerged from a spigot, how can it be pulled? Spinneret-spinneret contact appears to play a role in the initiation of attachment disc lines (Wolff et al. 2015; Wolff & Herberstein 2017) and perhaps also balloon lines (Hingston 1922a; Coyle 1983, 1985; Eberhard 2006); but initiation of wrapping lines is still not understood.

Mature female *T. clavipes* spiders were induced to build orbs indoors and at the edge of an outdoor porch. About ten individuals were observed (sample sizes varied for different types of behavior) using a 2X headband magnifier, a Sony DCR TRV50 camera equipped with +7 closeup lenses, and an Olympus TR-4 "Tough" camera. The camera was focused tightly on a given body area (e.g., the spinnerets or the cheliceral fangs) while the spider moved. The anterior lateral (AL) spinnerets, and the posterior lateral (PL) spinnerets were easily visible in most video recordings. The shorter, posterior median (PM) spinnerets were generally not visible except when viewed at certain angles when the spider had spread her spinnerets widely.

As described previously for *T. clavipes* (Robinson et al. 1969; Robinson & Mirick 1971) and the closely related *N. pilipes* (Fabricius, 1793) (Hingston 1922c; Robinson & Robinson 1973), spiders repeatedly broke both sticky and non-sticky web lines in the process of removing bulky prey packages from the web before carrying them to the hub, and also during orb construction and when they removed detritus from the web (Eberhard 1990b; 2020). In some cases, it was clear that just before the spider began to break lines when removing a prey, a clear liquid appeared at her mouth. During the period when she was cutting lines, her mouth area repeatedly became apparently dry and then somewhat wet again. Some lines were cut at moments in which none of this liquid was visible in this area (though limitations on visibility ruled out certainty on this score). In sum, liquid did sometimes appear on the spider's mouthparts just before cutting began; it may have been present in all cases, but this was not certain.

The spider cut lines by seizing them with the tarsus of a palp or a leg (usually leg II or III) and pulling them to her mouth area. Judging by the direction of the pulls, lines were probably hooked by the tarsal claw, but I could not resolve this detail. The spider generally opened one fang and seized the approaching line by closing the fang. The line was generally held nearer the base than the tip of the fang. Some apparent attempts to cut failed after the line was clearly grasped by the chelicera, and not infrequently a line was released and then grasped again one or more times before it was cut. Both sticky and non-sticky lines parted quickly and smoothly when they were cut; and there was never any sign of "sawing" or "tugging" on the line as if the spider were mechanically severing it with her chelicerae. Rather, the cut ends simply sprang apart when the line was brought to the mouth area. These smooth cuts involved lines that made a wide variety of different angles with the chelicerae; there were no signs that spiders attempted to align the lines in any particular orientation with respect to their chelicerae before cutting them.

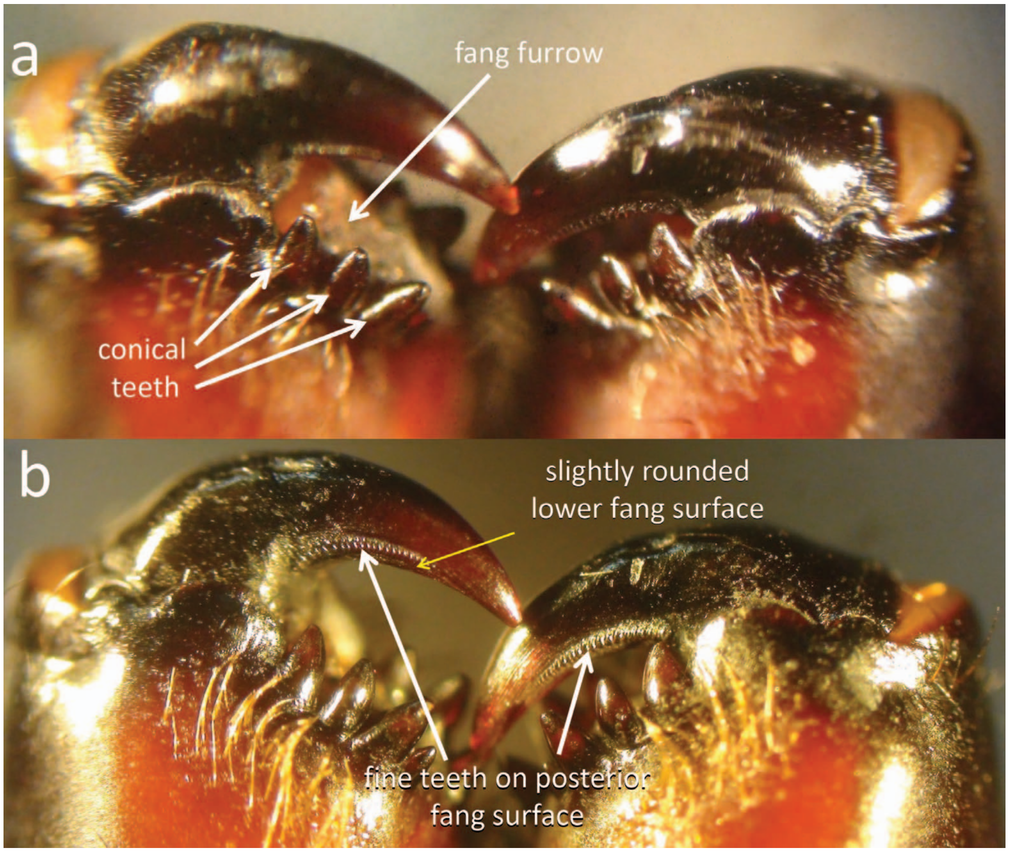

Figure 1.—The chelicerae of a mature female *Trichonephila clavipes* in posterior views from slightly different angles. The large conical teeth along the posterior margin of the fang furrow and flat-bottomed furrow are visible in the more ventral view (a). In the more posterior view (b), the serrate area on the rear surface of the fang and the slightly rounded inner surface of the fang are visible.

One non-sticky line was cut even though the spider did not grasp it with her chelicerae. This was an "incidental" line that was near her mouth, in the groove between her two chelicerae and more or less parallel to the long axes of the basal segments of her chelicerae. The spider was cutting other lines, and did not respond overtly to this line, but it broke when it came into the vicinity of her mouth (perhaps incidentally). The spider did not seize the line with her chelicerae at any time.

Additional indications that the chelicerae did not mechanically cut lines come from their morphology, which is inappropriate for either a "scissors" or a "blade against a chopping block" mechanical cutting function (Fig. 1). The distal surface of the basal cheliceral segment does not have any sharp-edged planar surface that could act in opposition to the fang like the blade of a scissors. Instead, it has a row of three heavy, conical teeth just anterior to the fang furrow (which is flat-bottomed rather than curved), and three similar teeth along its posterior edge (Fig. 1a). The interior surface of the fang is not sharp, but nearly flat with rounded edges, and bulges slightly (Fig. 1b). It has a row of small serrations on its posterior surface. The fang thus has no sharp edges that could act as a blade closing against the basal cheliceral segment, either as a scissors or as in the chopping block hypothesis.

When wrapping prey at the capture site in the web or at the hub, spiders initiated wrapping lines in at least three different ways, in all cases after they had bitten the prey and its struggles had subsided (Robinson et al. 1969; Robinson & Mirick 1971; Robinson & Robinson 1973). Often the initial wrapping lines were attached to the spider's dragline (Barrantes & Eberhard 2007) and emerged as she descended slightly further after grasping the prey with her chelicerae, drawing out additional dragline silk (Fig. 2a). The second technique began with making a dragline attachment to the web or to the prey; when the tip of the spider's abdomen pulled away from this attachment, a swath of wrapping lines, apparently also attached at the dragline attachment, emerged from her spinnerets along with the dragline.

The third technique was performed repeatedly by one individual. The spider began by climbing a step or two backward up her dragline (toward the hub) while holding the prey in her chelicerae; this backward movement caused her dragline to go slack, and then she turned 180° to begin wrapping. The wrapping lines were initiated by rubbing her spinnerets rapidly against each other for up to a second or more. In some cases, both AL and PL spinnerets rubbed briefly against each other and then spread apart laterally. These movements evidently caused small lengths of wrapping silk to be pulled out, as a small white mass formed between her spread PL spinnerets. This mass adhered to her dragline when the spider then began pulling dragline and wrapping silk from her spinnerets with her legs IV and applying it to the prey (Figs. 2b,c). A swath of wrapping lines was attached to the dragline, and all three pairs of her spinnerets were spread widely as the swath was pulled by legs IV (Fig. 2c). In some cases, the spider paused during wrapping, rubbed her spinnerets against each other, and then spread them and resumed wrapping. The density of lines in the swath increased immediately following each such pause, so these rubbing and spreading movements resulted in production of additional lines, presumably from additional spigots.

All three hypotheses for how lines are cut are compatible with the grasping movements of the chelicerae that were typically associated with cutting a line. Three types of evidence argue against the two

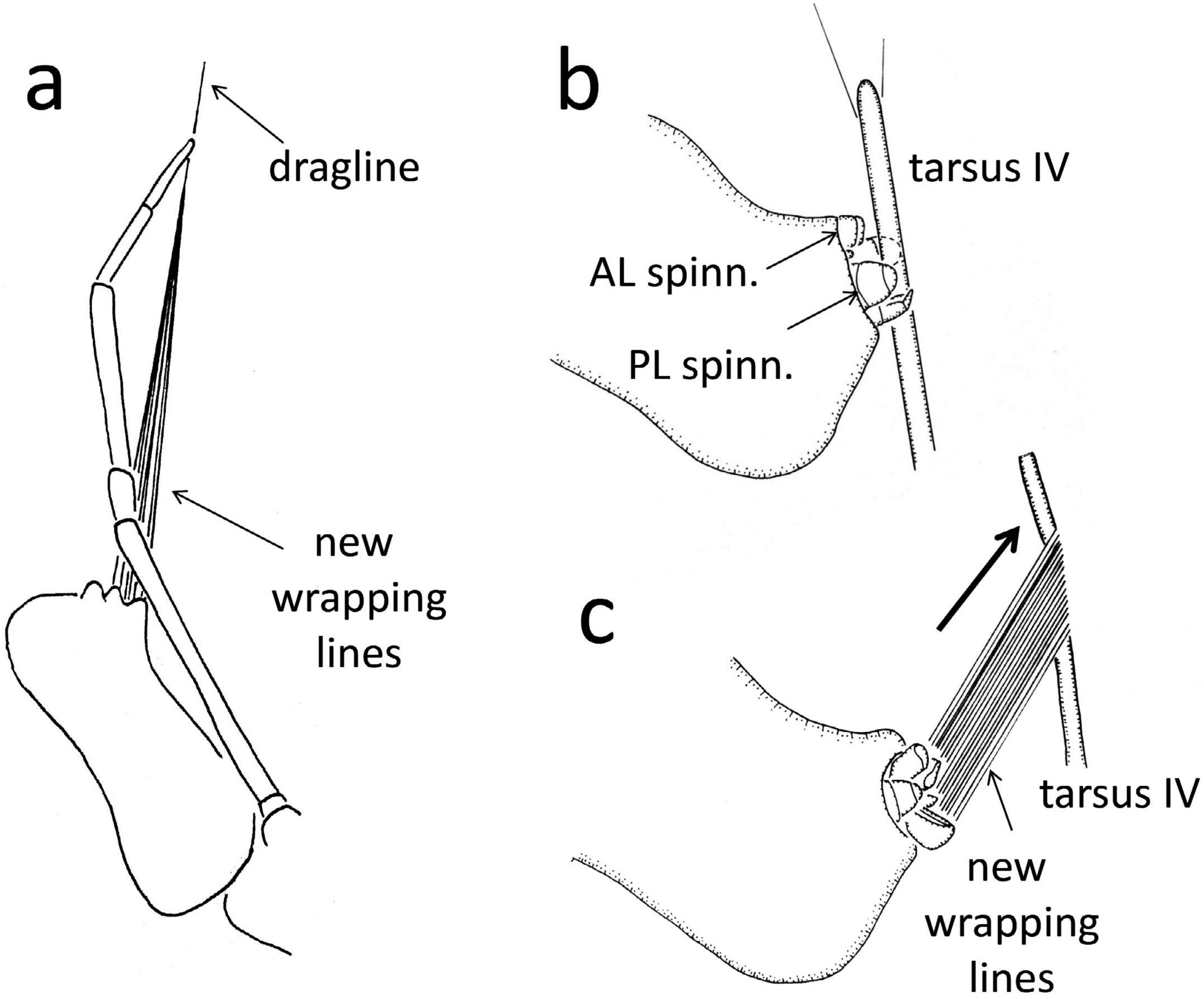

Figure 2.—Initiation of wrapping lines. (a) wrapping lines originated at attachments to the spider's dragline as it was pulled from her spinnerets as she descended slightly after having bitten the prey; (b) tarsus IV was between the spread spinnerets as it began a wrapping movement carrying the silk to the prey; (c) As tarsus IV pulled away from the abdomen in a wrapping movement, all three pairs of spinnerets were spread wide as the swath of wrapping lines emerged (the drawings are traced from video recordings).

mechanical cutting hypotheses, however. The observation of a line that broke when it came into the vicinity of the spider's mouth without being seized by her fang clearly contradicted both of these hypotheses. The second line of evidence comes from the observation that lines with a wide variety of orientations with respect to the spider were broken with no perceptible differences; under the scissors and the chopping block hypotheses, the spider would have been expected to have had difficulty cutting lines that were nearly parallel to her fangs.

Thirdly, the morphology of the chelicerae of *T. clavipes* is incompatible with either of the mechanical hypotheses. The scissors hypothesis is clearly contradicted by the lack of any blade-like structure on the distal portion of the basal segment on either the anterior or posterior margin of the fang furrow. Both margins have instead three large, widely spaced conical teeth, an inappropriate design to act as a scissors blade working against the fang to shear fine cylindrical lines. Similarly, the chopping block hypothesis is contradicted by the lack of any sharp-edged ridge on either the fang or the basal segment. Instead, the fang has rounded lateral edges and a slightly rounded internal surface. The rounded nature of the surface is especially clear in the basal portion, where lines tended to be grasped when they were being cut. Nor is there any ridge that might act as a blade on the floor of the fang furrow, which is quite flat. A variation on the mechanical chopping block hypothesis that could be compatible with the lack of sharp ridges is that the chelicerae clamp and compress lines and thus weaken them, and enable the spider to then break lines by physically tugging on them. Direct observations clearly contradicted this idea: there were no signs of such tugs; lines just "fell apart" without being perceptibly pulled or stressed.

By elimination, the chemical cutting hypothesis is the most likely of the three examined here; the observation that a droplet of liquid formed at the spider's mouth just before she began to cut lines supports this hypothesis. The nature of that liquid remains to be determined. Because non-sticky (ampullate gland) draglines were cut, the chemical cutting hypothesis predicts that the droplet contains special silk-degrading enzymes like those found in the araneid *Argiope argentata* (Fabricius, 1775) (Tillinghast & Kavanagh 1977), rather than only more general protease enzymes such as trypsin in digestive fluid that are unable to break dragline silk (Tillinghast 1984).

The movements of the spinnerets that were associated with the initiation of wrapping lines presumably caused newly produced and somewhat adhesive wrapping silk at the tips of the spigots to rub against other spigots and the dragline. This would cause the lines that formed to adhere there and to be pulled out when the spider drew out more dragline by moving or by pulling lines with her legs IV. The fact that newly formed aciniform lines appear to be adhesive in the araneid *A. argentata* (Robinson & Olazarri 1971) and the uloborid *Philoponella vicina* (O. Pickard-Cambridge, 1899) (Eberhard et al. 2006) is in accord with this hypothesis. The position of the aciniform spigots on the ventro-medial surfaces of the mobile PL spinnerets (Kuntner et al. 2008), where they may touch each other when the spinnerets move medially, is also compatible with this idea (it should be kept in mind, however, that the everted spinneret positions usually illustrated in taxonomic papers cloud the question of whether the spinnerets can contact each other, because the eversion presumably accentuates the distances between them). The elongate shape of this patch of aciniform spigots along the length of the PL spinnerets in nephilines (Kuntner et al. 2008) as well as other groups (Coddington 1989) may function to produce a wider swath of silk when the spinnerets are spread during prey wrapping.

These observations of wrapping silk initiation, along with the similar rubbing of AL spinnerets against each other that occurs when attachment discs are initiated (Wolff et al. 2015; Wolff & Herberstein 2017), may explain why the distributions of piriform and aciniform spigots are strongly clustered on the spinnerets. Because the two types of spigots occur in particular areas on different spinnerets and not mixed together, the spider is able to control which type of silk line is initiated by controlling which spinnerets are rubbed against each other. If the spigots were mixed together, movements of this sort would not selectively initiate the lines from a given gland.

Many spinneret designs, often figured in taxonomic papers, are still functional mysteries in other spiders. Spigot design and placement varies dramatically, as illustrated, for example, by the multiple, accordion-like folds in the walls of cribellum spigots (Opell 2013), the enlarged, elongate piriform spigots in prodidomids (Platnick 1990; Platnick & Baehr 2006), the deep longitudinal grooves on some spigot bases in *Scopoides naturalisticum* (Chamberlin, 1924) (Platnick 1990), and the splayed arrangements of piriform spigots in *Herpyllus ecclesiasticus* Hentz, 1832 (Platnick 1990). Presumably, future studies will help make adaptive sense of this diversity. The mace-like set of spigots on the AL spinnerets of the eresid *Seothyra henscheli* Dippenaar-Schoeman, 1991 and the spider's stabbing movements with its abdomen provide a dramatic example of such a functional explanation: they produce lines that tie sand grains together to reinforce the walls of tunnels in loose sand (Peters 1992).

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