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Stabilimenta of *Philoponella vicina* (Araneae: Uloboridae) and *Gasteracantha cancriformis* (Araneae: Araneidae): Evidence Against a Prey Attractant Function

William G. Eberhard[1]

Smithsonian Tropical Research Institute, Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

ABSTRACT

Both the uloborid *Philoponella vicina* and the araneid *Gasteracantha cancriformis* spiders sometimes placed silk stabilimenta on non-orb "resting webs" that consisted of only one or a few lines. These webs completely lacked sticky silk, so their stabilimenta could not function to attract prey. Some non-orbs were built by spiders when their orb webs are damaged. These observations contradict the prey attraction camouflage hypothesis for stabilimentum function, but are compatible with the spider camouflage and web advertisement to avoid web destruction hypotheses.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: camouflage; non-orb webs; spider; stabilimentum function; uloborid; web advertisement.

Several species of orb-weaving spiders that rest at the hubs of their webs during the day sometimes incorporate bands or masses of white silk or detritus ("stabilimenta") into their orbs. While detritus stabilimenta are generally thought to function as camouflage for the spider (Eberhard 2003, Gonzaga & Vasconcellos-Neto 2005, Chou *et al.* 2005), the function of silk stabilimenta is controversial. At least five general hypotheses have been proposed to explain the function of silk stabilimenta: attract prey; physically reinforce the web; camouflage the spider from predators; advertise the web (to prevent damage from large animals by inducing them to avoid webs, or to avoid approaching close enough to prey on the spider); and shade the spider (reviewed in Herberstein *et al.* 2000, where several other hypotheses which have little or no supporting data are also mentioned). Herberstein *et al.* (2000) used a phylogenetic analysis to argue that stabilimenta have evolved independently up to nine different times in three different families. Even this number is probably an underestimate, as subsequent discoveries have documented silk stabilimenta in at least two additional genera, *Metepeira* and *Araneus* (Levi 2001, Piel 2001, Bruce *et al.* 2004); neither *Metepeira* nor *Araneus* is thought to be closely related to other genera with silk stabilimenta (Scharf & Coddington 1997).

The controversy over silk stabilimentum function is complicated by the fact that they may have different functions in different groups. Herberstein *et al.* (2000) judged that the weight of available evidence (mostly from the araneid genus *Argiope*) favors the prey attraction hypothesis. They argued that some of the controversy over functional interpretations may be due to silk stabilimenta that evolved independently in different groups having different functions. While independent derivations do not necessarily imply different functions (for stabilimenta or any other traits; Eberhard 2003), one salutory effect of this idea is to focus attention away from the genus *Argiope*, in which data on stabilimenta are abundant but contradictory, and instead onto other groups in which stabilimenta have evolved independently.

Recent studies of three distantly related groups in Araneidae, including *Araneus* and *Gasteracantha*, which make silk stabilimenta, and *Cyclosa* and its close relative *Allocyclosa bifurca* (McCook), which make silk, detritus, and egg sac stabilimenta (Tso 1998, Eberhard 2003, Bruce *et al.* 2004, Gonzaga & Vasconcellos-Neto 2005, Chou *et al.* 2005, Jaffé *et al.*, in press), concern silk stabilimenta that evolved independently from the stabilimenta of *Argiope* (though some of the silk stabilimenta of *A. bifurca* closely resemble in form those of some *Argiope*). The studies of *A. bifurca* and *G. cancriformis* L. shared the conclusion that prey attraction is an unlikely function for the silk stabilimenta (Eberhard 2003, Jaffé *et al.* in press). The present note comes to a similar conclusion, on the basis of a separate set of data from *G. cancriformis*, and from observations of a further group in which stabilimenta have evolved independently, the family Uloboridae. The conclusions are based on a clear prediction of the prey attraction hypothesis: if silk stabilimenta function to attract prey, then spiders that do not have prey capture webs should not build stabilimenta.

Spiders in six uloborid genera build silk stabilimenta (Lubin 1986, Opell 1987, Herberstein *et al.* 2000), but there are few published data on stabilimentum function in this family. The most convincing comparative test was made by Marples (1969). He compared an exceptional species of *Uloborus*, *U. gibbosus* Koch, in which no stabilimenta are made, with other uloborids, including *U. plumipes* Lucas, and *Zosis* (=*Uloborus*) *geniculatus* (Olivier) in which stabilimenta are common. Spiders of the species with stabilimenta consistently rested at the hubs of their webs during the day (as is in general also true for araneids that make stabilimenta; Herberstein *et al.* 2000), while *U. gibbosus* usually rested at the edges of their orbs where they were very cryptic, and dropped readily to the ground if disturbed while they were on the web (Marples did not give sample sizes, however). The list of *Uloborus* that both rest at the hub and generally make stabilimenta can be extended to include

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[1] Corresponding author; e-mail: archisepsis@biologia.ucr.ac.cr

U. diversus (Eberhard 1973) and *U. glomosus* (Opell & Eberhard 1983, Cushing & Opell 1989). Marples argued that the unusual combination in *U. gibbosus* of lack of stabilimentum and resting off the web supports the camouflage hypothesis, because only in spiders resting at the hub of the web during the day would selection favor adding devices to protect them from visually orienting predators.

A second, experimental study of an uloborid came to different conclusions. The central portion of an orb with the strongly UV-reflecting stabilimentum silk of *Octonoba sybotides* was more attractive to *Drosophila* sp. flies than the central portions of orbs without stabilimentum silk (Watanabe 1999). The deduction that prey attraction is a possible function of the stabilimentum in this species is difficult to judge, however, because the flies were in an experimental situation from which they may well have been trying to escape (UV light is used by some insects as a guide toward the sky when they are attempting to escape danger); the fraction of potential prey in the wild that are attempting to escape danger is unknown. In addition, many other species are captured by these and other uloborid spiders, so the relative importance of the behavior of this species of *Drosophila* for the spiders in nature is uncertain (most orb-weavers are generally highly generalist predators; Eberhard 1990). An additional line of evidence apparently supporting the prey attraction hypothesis for *O. sybotides* was that spiders on webs in the field that had stabilimenta were observed feeding more often than those on webs lacking stabilimenta (Watanabe 1999). These data are also inconclusive, however, because there was no control for the possible effects of differences in site quality and spider nutrition, factors known to be important in other stabilimentum-building species of orb weavers (Blackledge 1998).

Regarding the uloborid genus *Philoponella*, silk stabilimenta have been observed on and near hubs of the orbs of several species (Lahmann & Eberhard 1979, Lubin 1986, Opell 1987), and also on lines below their webs (Opell 1987). Otherwise nothing seems to be known regarding their possible function.

A previous study of silk stabilimenta on the webs of the araneid *G. cancriformis*, which occur mostly on the long frames and anchor lines (Peters 1953, Marples 1969, Muma 1971, Jaffé *et al.*, in press), confirmed one prediction of the web advertisement hypothesis, failed to confirm one prediction of the prey attraction hypothesis, and noted that the presence of stabilimenta on moulting webs, which lack sticky spirals, contradicts the prey attractant hypothesis (Jaffé *et al.*, in press). Marples (1969) also noted silk stabilimenta on webs that were not "complete," but it is not clear from his description whether these webs did or did not have sticky lines and were capable of trapping prey.

METHODS

Mature females and penultimate and ante-penultimate nymphs of the uloborid *Philloponella vicina* O. Pickard-Cambridge were observed in the field between 1000 h and 1400 h on five different days near San Antonio de Escazú, San Jose Province, Costa Rica (1300–1600 m asl). Care was taken to search at different sites to avoid observing the same individual more than once. Spider sizes were estimated by comparing spiders on their webs in the field with collections of individuals of different apparent instars that had been placed in a vial and positioned so they were pressed against the glass wall with cotton. A small amount of cornstarch was dusted on some sites where spiders were likely to occur (especially above *Tengella radiata* webs), to make webs visible. Additional observations were made of mature females released onto hoops with silk lines indoors.

Mature and penultimate females of *G. cancriformis* were studied on four days in January 2006 near Parrita, Puntarenas Province, Costa Rica (10 m asl). Orbs were destroyed experimentally between 1300 h and 1600 h by cutting all but two radii near the frame lines with a scissors, leaving the frame lines intact. Orbs were then revisited 1–2 h later to observe the spider's response. Means are reported ± 1 SD.

RESULTS

Philloponella vicina.—Orb webs of *P. vicina* were found at sheltered sites such as overhanging stream banks and at the bases of large tree trunks in forested and second-growth habitats. This species apparently prefers to attach its webs to the webs of other spiders, such as the tangle of lines above the sheets of *T. radiata* (Fincke 1981) or the tangles of *Tidarren hemaroidalis*, but it also attaches its webs to other substrates.

Of 70 orbs in the field, 44 (62.9%) had stabilimenta. All stabilimenta on orbs were composed of one or more linear multistrand bands of white silk attached to a radius (Fig. 1A); the most common design (73.9%) was two lines on radii slanting up and down on the opposite sides of the hub, so that one was above the spider and one below. There was a space between the lines in the central portion of the hub, where the spider rested. The second most common design was a single line (15.2%), most of which (6 of 7) were on a radius above the spider.

Of a total of 110 spiders checked, 18 did not have orbs and were resting on a "resting web" consisting of 2–6 lines converging on the spider. Of these non-orbs, six had silk stabilimenta on at least one line. In the two simplest cases, the spider rested on a single broken line, with a stabilimentum line on this line just in front of and behind the spider (Fig. 1B). When disturbed, the spider immediately reeled up one of the stabilimentum lines as it moved away on this line (Fig. 1C). In three cases, the spider was near the edge of a deserted, damaged orb web; for instance, one orb had a twig lying across the hub, and the spider was beyond the edge of the orb, on lines connected to the frame lines.

These stabilimentum lines did not appear to be remnants of stabilimenta from previous orbs. They were on simple "clean" lines that did not have the remnants of previous attachments to other lines such as sticky spirals that would have been expected on remnant lines. The lack of re-use of previous stabilimentum lines in non-orb webs with stabilimenta was confirmed in two cases in which a

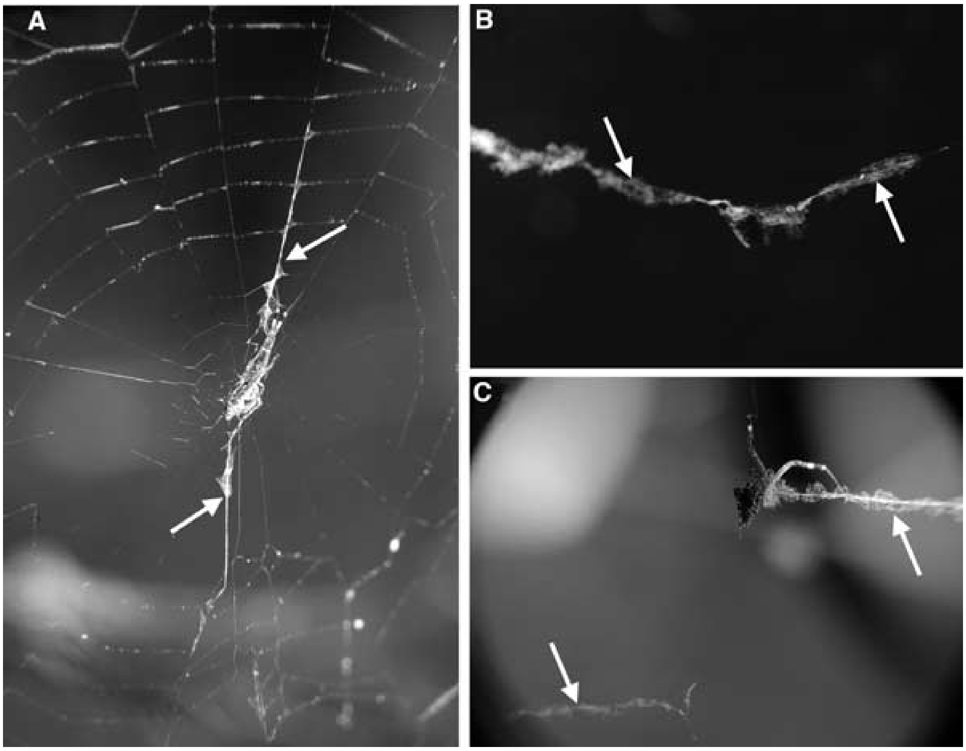

FIGURE 1. Silk stabilimenta of *P. vicina*. (A) Spider at the hub of an orb with a two-line stabilimentum; (B) non-orb stabilimentum on a single line on either side of a crouching mature female; (C) non-orb stabilimentum after the spider, in response to a disturbance, carried one stabilimentum line laterally (arrows mark stabilimentum lines).

spider built a non-orb with a silk stabilimentum the same day it was placed on an orb web in captivity; the non-orb was on new lines built nearby the previously built orb.

Females of *P. vicina* build their approximately fusiform egg sacs away from their orbs, at least sometimes at more sheltered sites, and then crouch at one end of the sac for several days, apparently guarding it. Of ten females next to an egg sac, one had a single stabilimentum line on the line attached to the opposite end of the sac.

Stabilimentum construction behavior was observed once, and closely resembled that of *U. diversus* (Eberhard 1973). The spider walked slowly forward, pulling out a swath of white silk lines from her spinnerets with alternate strokes of her legs IV; periodically she dabbed her spinnerets against the radius and thus apparently attached the swath to the radius. The stabilimentum silk was a loose mat, and the lines were not under tension.

Gasteracantha cancriformis.—A total of 51 experiments were performed with 28 different spiders (maximum three experiments/spider). In 29.1 percent of the cases, the spider responded to web destruction by building at least one new line with tufts of stabilimentum silk in the area where the sticky spiral had been (Fig. 2B); when it built several lines, they more or less converged where the spider rested. On average the spider built 3.3 ± 1.0 lines (range 2–5, $N = 19$) with an average of 2.3 ± 1.3 stabilimentum tufts on them; of those lines with stabilimenta, the mean number of tufts was 4.2 ± 2.3 (range 1–11, $N = 34$). Other responses to web destruction were to build a new orb (31.3%) (in all cases with at least one tuft of stabilimentum silk), to not build anything or to make only a few lines without a stabilimentum (33.3%), or to leave (5.9%). Tufts of stabilimentum silk also occurred in one case on lines laid in damaged sectors of an orb (Fig. 2C). They were also seen during this study and during previous observations of this species at this and other sites on more than 20 non-orb resting webs that lacked sticky spiral lines such as that in Figure 2A.

The behavior involved in laying tufts of stabilimentum silk on a line laid after an orb had been experimentally destroyed was similar to that described by Marples (1969) for tufts on an orb. The spider walked slowly, pulling a band of many white lines from her spinnerets with alternate strokes of her legs IV and applying it to the line along which she was walking. Recently, laid tufts billowed in the wind (Fig. 2B).

Uloborus sp.—A mature female of an unidentified species of *Uloborus* was observed near the Central Hidroelectrica Anchicaya, Depto (Valle del Cauca, Colombia, approximately 400 m asl). When brought in from the field and placed on a wooden frame, she built two silk stabilimentum lines on a single line; she broke the line between them, and rested immobile with one stabilimentum line anterior and other posterior to her. When disturbed, she rapidly reeled up one of these and moved away.

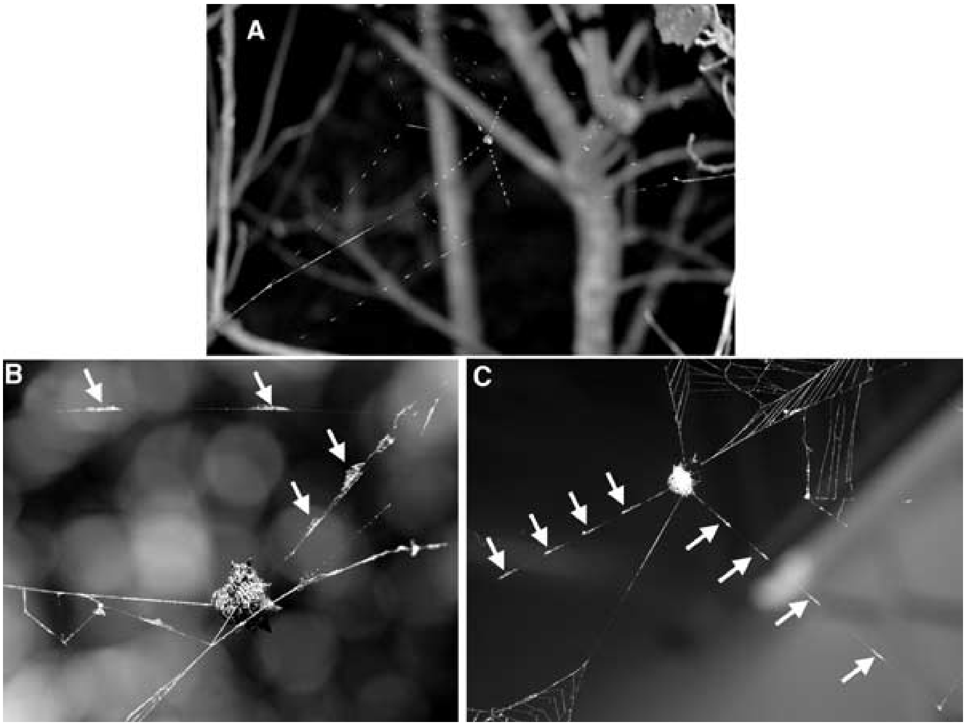

FIGURE 2. Non-orb silk stabilimenta of *G. cancriformis* (A) non-orb resting web that lacks sticky spiral lines but has abundant stabilimentum tufts; (B) lines made when the entire sticky spiral was experimentally destroyed (note the loose stabilimentum lines in the two tufts above and to the right of the spider streaming in the breeze); (C) lines laid in destroyed sectors of an orb (arrows mark tufts of stabilimentum silk in B and C).

DISCUSSION

These observations are relatively simple, but they represent powerful evidence against the prey attractant hypothesis, if one makes the apparently reasonable assumption that these fairly common non-orb stabilimenta are not simply non-adaptive mistakes by the spiders (see Herberstein *et al.* 2000 for arguments favoring this assumption), and the additional parsimonious assumption that the function of a stabilimentum when it is added to one type of web (resting web) is the same as when it is added to another (orb web). This is because these non-orb webs completely lacked sticky lines, and were thus unable to capture prey, even if they were attracted. The hypothesis that the orb web stabilimenta function to attract prey in these species could be rescued if the functions of orb and non-orb stabilimenta of a given species are different (Herberstein *et al.* 2000). There are no data, however, to support this idea, and the non-orb stabilimenta for all three species discussed here are at least superficially very similar if not identical in form to those on orbs; in *P. vicina* and *G. cancriformis* the behavior used to produce them is also apparently identical to stabilimentum construction on orbs. Similar arguments suggest that the stabilimenta on moulting webs of *G. cancriformis* also do not function to attract prey (Jaffé *et al.*, in press).

These observations of stabilimenta on non-orb webs also have implications for several other hypotheses. The web-reinforcement hypothesis is not supported in either the uloborids or *G. cancriformis*, because the webs on which they occurred were simple, to the point of consisting of only two lines converging on the spider, that did not need to absorb stresses such as those associated with prey impact, and thus had no apparent need of reinforcement. In addition, the lines of stabilimentum silk were loose (Figs. 1C and 2B), and not positioned to absorb stress on the web lines. The sun-shade function is extremely unlikely for *P. vicina*. Their webs are usually built in relatively shady, sheltered sites, and they are more or less horizontal, with the stabilimentum lines on either side of the spider rather than above it. They are thus almost completely incapable of shading the spider from direct sunlight. Most stabilimentum tufts of *G. cancriformis* were also incapable of shading the spider (*e.g.*, Fig. 2A). The web advertisement hypothesis also seems inappropriate for the stabilimenta on both orbs and non-orbs of *P. vicina,* because both were built in small, protected spaces such as in the midst of the tangle of strong lines above the sheet webs of *T. radiata* (which are in turn built in sheltered sites). Animals such as birds, lizards, or large flying insects are unlikely to be able to even move through such areas. The web advertisement hypothesis is feasible, in contrast, for the non-orb stabilimenta of *G. cancriformis*, which were built on much longer lines at relatively exposed sites (see also Jaffé *et al.*, in press).

By elimination, the non-orb stabilimenta of *P. vicina* most likely function as camouflage from predators. The close physical association of these stabilimenta with the spiders as they rested on their webs is in accord with this conclusion. If one accepts the parsimony assumption noted above, that non-orb stabilimenta have the same function as orb stabilimenta in this species, the implication is that the silk stabilimenta on orbs of this species probably also function as camouflage. The implications for *G. cancriformis* are less definitive. Again by elimination, their silk stabilimenta could function as web advertisement, or as camouflage.

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