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Orb web construction plasticity in the spider family Uloboridae (Araneae)

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Abstract. Orb webs constructed by members of the spider family Uloboridae are characterized by the presence of cribellate thread on frame lines and cribellate thread placed on radii to form zig-zag patterns in a web's perimeter. Both features are added before more typical, fully circular capture spiral production begins. Zig-zags give the impression that a spider is filling in the gaps between a web's outermost spiral and frame line, although they are constructed before capture spiral turns begin. We examine these traits in orb webs of six species (*Philoponella vicina* (O. Pickard-Cambridge, 1899), *Siratoba referens* (Muma & Gertsch, 1964), *Uloborus glomosus* (Walckenaer, 1841), *Uloborus trilineatus* Keyserling, 1883, *Waitkera waitakerensis* (Chamberlin, 1946), and *Zosis geniculata* (Olivier, 1789). In four species, the distance between the outermost capture spiral and frame line was correlated with the length of cribellate thread on a radius. A web's capture area increased as the area encompassed by zig-zags was added to that encompassed by the outermost fully circular cribellate spiral thread and again when cribellate thread on frame lines was included. When constructed in frames of the same size, webs of *S. referens* and *U. glomosus* were less symmetrical and contained more capture thread switchbacks per spiral turn and per web area than did horizontal orb webs of *Leucauge venusta* (Walckenaer, 1841) (family Tetragnathidae). Features in the perimeter of uloborid webs may adapt these small spiders to irregular spaces within vegetation by allowing them to cover larger portions of their webs with sticky lines.

Keywords: Web traits, cribellate capture spiral, web symmetry, prey capture area

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Of the 22 features that are typical of horizontal orb webs constructed by members of the spider family Uloboridae (Eberhard & Opell 2022), two striking and easily identified traits occur at a web's perimeter. After a temporary spiral has been constructed, a spider often deposits cribellate thread on some radii to form a zig-zag pattern, and also places cribellate thread on some frame lines (traits 8 and 7, respectively, in Eberhard & Opell 2022) before adding regularly spaced capture spiral turns (Figs. 1a, b). Zig-zags are added when a spider carries a cribellate thread as she moves outward on a radius from the temporary spiral, attaches the thread before reaching the frame line, returns to the temporary spiral, and attaches the cribellate thread to this radius a second time before progressing to the next radius (Fig. 2). These zig-zags are more common where longer radii extend to an anchor line. They give the impression that a spider anticipates where she will place the first complete cribellate capture spiral turn and is filling in areas where there will be larger gaps between this spiral and the frame line. There are no quantitative analyses of the sites in orb webs where zig-zags occur or the effect that these features and cribellate thread on frame lines have on the area of a web that contains cribellate thread and has the potential to retain prey.

In this study, we examined the orb webs of six uloborid species (Table 1), which represent five of the eight genera known to exhibit one or both of these features (Eberhard & Opell 2022). Our objectives were to determine where zig-zags appear in orb webs and the contribution of zig-zags and cribellate thread on frame lines to a web's capture area. For this comparison, we measured web photos of six species whose webs had more than three zig-zags to allow the comparison of radii with and without zig-zags. As this involved characterizing all radii within a web, we limited this analysis to 4–6 webs per species.

We also compared the symmetries and number of capture thread switchbacks in webs that were constructed in boxes of the same sizes by two uloborid species and by *Leucauge venusta* (Walckenaer, 1841) (family Tetragnathidae), a somewhat larger spider that also constructs horizontal orb webs. We hypothesized that, as uloborid webs can be found in small spaces among vegetation, these spiders spend less time exploring a web site and begin constructing a web after establishing a less symmetrical frame line polygon than do araneoid orb weavers. A shorter exploration and frame line establishment time may also help offset the apparently greater cost of spinning cribellate threads (Lubin 1986; Opell 1998). Therefore, we predicted that the uloborid webs will be less symmetrical than those of *L. venusta* even when provided with the same space available for web construction. This study was based on larger sample sizes because these measurements were less time consuming and testing this hypothesis did not require a uloborid web to contain zig-zags.

METHODS

As is typical for uloborid orb weavers, most of the species that we studied occupy humid environments where they are found on low vegetation and the lower branches of trees (Comstock 1912; Kaston 1978; Forster & Forster 1999; Bradley 2013; Rose 2022). *Uloborus glomosus* (Walckenaer, 1841) is also found on landscaping shrubbery (Opell, unpublished observations). *Zosis geniculata* (Olivier, 1789) is a pantropical species that appears to have been introduced into the New World, where it can be found in buildings (Opell 1979). In tropical forests, *Philoponella* species often attach their webs to the support lines of other spiders (Eberhard 2020) (Opell unpublished observations). The New Zealand species *Waitkera waitakerensis* (Chamberlin, 1946) is reported as often being found in the same habitat as the tetragnathid *Nanometa purpurapunctata* (Urquhart, 1889), which builds a horizontal orb web of similar size (Forster & Forster 1999).

We dusted webs with cornstarch before photographing them to enhance the contrast of their threads (Fig. 1a). Care was taken to ensure that a web's plane was parallel to the camera's film plane in both field and lab photographs. This was confirmed by all parts of the web plane being sharply focused. A sketch of each *W. waitkerensis* web was made before photographing this web in the field and the distance between web landmarks was measured and recorded to serve as a scale when taking measurements from the photographic prints. In the laboratory, three species constructed webs in plastic

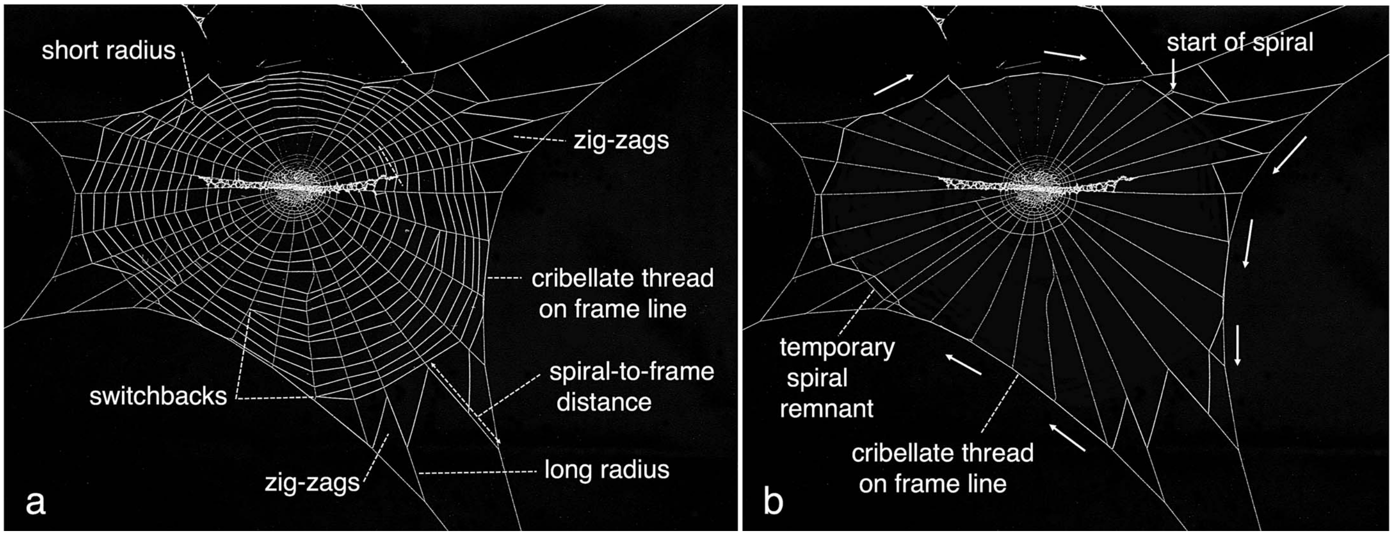

Figure 1.—*Siratoba referens* orb web. (a) Web features identified. (b) Digitally edited image showing only cribellate thread added during the spider's first excursion around the web perimeter. Arrows show the direction of cribellate thread deposition. In some regions of the web the cribellate thread is visible as a zig-zag or as a spiral sector. In other regions, such as the right side and bottom of the web, the cribellate thread is placed on a frame line and is not easily distinguished from this line.

cylinders with an inner diameter of 15 cm (Table 1). Three other species constructed webs in large, 12 cm deep plastic boxes whose tops were covered by a lid and bottoms by Glad Cling® polyvinyl chloride food wrap to contain a spider and block air movement. To provide web attachment structures, 4.4 mm diameter wooden dowel rods were glued to 1 cm wide supports affixed to the box's inner surfaces 6 cm from the top of the box. This provided a framework that was 22 cm wide and had a width of 30 cm in some boxes and 34 cm in other boxes. We used the 22 cm frame width as a scale when taking measurements from photographic prints of these webs.

Lab-constructed webs were spun by spiders that were collected in the field, placed in plastic cylinders or boxes whose sides were misted with distilled water to provide moisture. A few *Philoponella vicina* (O. Pickard-Cambridge, 1899), *Uloborus trilineatus* Keyserling, 1883, and *Zosis geniculata* (Olivier, 1789) were fed one or two *Drosophila* sp., but individuals of other species were not fed. Most spiders constructed webs the day after being placed in cylinders or boxes and the remainder constructed webs within three days. Therefore, we believe that the nutritional condition of these spiders prior to constructing webs was similar to that of spiders of these species that constructed webs in the field.

Each web we measured was constructed by a different adult female spider. Photographic prints were scanned and measurements were taken from these digital images using Image J (Image_J 2006) and Onde Rulers (OndeSoft®, Beijing, China). We determined web symmetry by dividing the length of a web's shortest radius by the length of its longest radius, with the unlikely case of a fully symmetrical web having a value of 1.0. Although similar in principle to the approach used in another study of uloborid webs (Eberhard & Barrantes 2015), this index differed because we did not

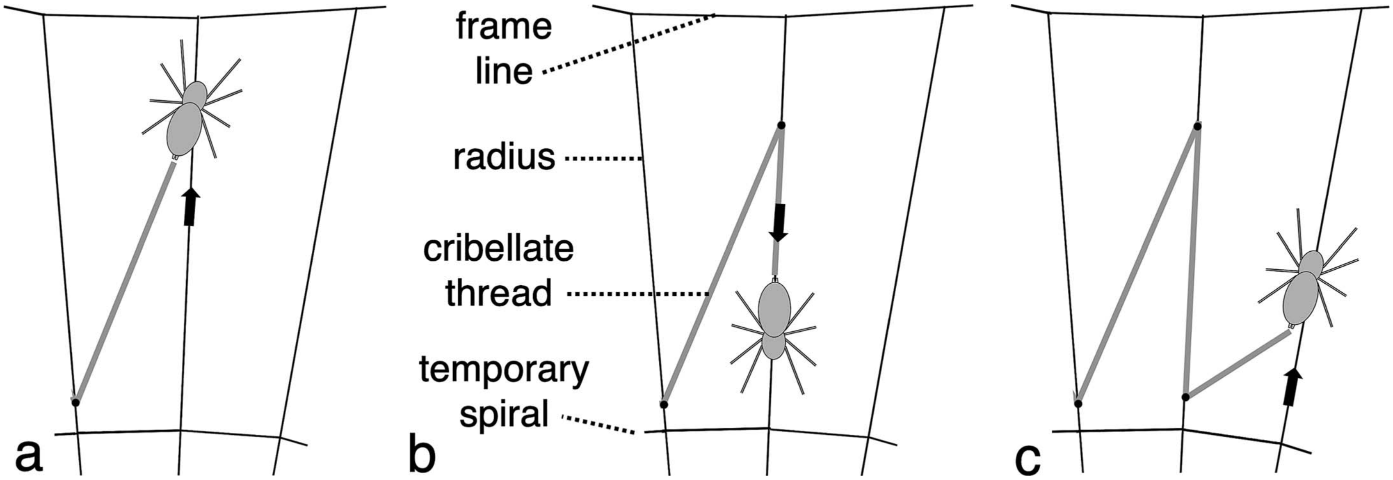

Figure 2.—Construction of a zig-zag line segment. (a) When placing a cribellate thread on a radius to form a zig-zag pattern, a uloborid carries a cribellate thread that she has attached to the previously encountered radius as she moves outward on the next radius. (b) She attaches this thread to the radius and then proceeds back toward the temporary spiral. (c) She attaches the cribellate thread to this radius a second time near the temporary spiral before moving to the next radius.

Table 1.—Species whose webs were characterized, their collecting localities, whether they were constructed in the field or lab, and, if lab constructed, the dimensions of attachment surfaces.

Species	Locality	Web constructed in
Philoponella vicina (O. Pickard-Cambridge, 1899)	Costa Rica, San José Province	lab, 15 cm diameter cylinder
Siratoba referens (Muma & Gertsch, 1964)	U.S.A., Arizona, Cochise Co.	lab, 30 or 34 × 22 cm frame
Uloborus glomosus (Walckenaer, 1841)	U.S.A., Virginia, Montgomery Co.	lab, 30 or 34 × 22 cm frame
Uloborus trilineatus (Keyserling, 1883)	Costa Rica, San José Province	lab, 15 cm diameter cylinder
Waitkera waitakerensis (Chamberlin, 1946)	New Zealand, Northland Region	field
Zosis geniculata (Olivier, 1789)	Costa Rica, San José Province	lab, 15 cm diameter cylinder
Leucauge venusta (Walckenaer, 1841)	U.S.A., Virginia, Montgomery Co.	lab, 30 or 34 × 22 cm frame

require the web's shortest and longest radii to be opposite one another. That is, our index of symmetry attempted to account for non-axial web symmetry in these horizontal webs. We determined the number of switchbacks per spiral turn by counting all switchbacks present in a web and dividing this by the maximum number of spiral turns present on a web radius. We believe that this is an appropriate index because it disassociates the number of switchbacks from the index of web symmetry.

In each analysis, the number of webs per species that we measured was guided by the effort required to take each type of measurement. We compared the zig-zag features for six species, choosing 4–6 web photos per species that clearly showed all radii and had more than three zig-zags. Thus, this study was not intended to evaluate the commonness of zig-zag patterns in these species' webs, as this information is provided elsewhere (Eberhard & Opell 2022). We considered capture spiral production to have commenced when a spider began depositing cribellate thread, but refer to the first fully circular cribellate capture spiral turn as the "outermost spiral." This allowed us to identify three capture areas of successively greater sizes, as shown in Fig. 4a: 1. The area enclosed by a web's innermost and outermost capture spirals, 2. The area enclosed by the innermost capture spiral and zig-zags or the outermost capture spiral in regions of the web where no zig-zags were present, and 3. The area enclosed by the innermost capture spiral and the outermost cribellate thread (whether this was an outermost capture spiral, a zig-zag, or cribellate thread on a frame line).

Although we refer to each of these three areas as "capture areas", it is important to note that capture spiral spacing within the area enclosed by the innermost and outermost spiral turns was usually smaller than the space between cribellate threads within zig-zag regions. We did not measure this latter spacing because cribellate threads in zig-zag regions were not at right angles with radii and it was difficult to do consistently. However, it seems clear that both the prey interception and retention potentials of the zig-zag areas are less than that of the area occupied by typical complete spiral turns. The spacing between the outermost, capture spirals and frame lines on which cribellate thread has been placed was usually similar to that of typical, complete capture spirals.

We determined web symmetry and the number of capture spiral switchbacks in 24 *Siratoba referens* (Muma & Gertsch, 1964) webs, 29 *Uloborus glomosus* webs, and 14 *L. venusta* webs, which were constructed in the laboratory as described above. The frames within these enclosures provided more open area than typically occupied by these species' webs in nature, an important consideration because limited space is known to limit the size of orb webs (Eberhard & Barrantes 2015; Eberhard 2020). *Leucauge venusta* adult females have a mean mass of 25.9 mg, as compared to 4.4 mg for *S. referens* and 9.4 mg for *U. glomosus* (Opell 1999; Opell & Bond 2001. Therefore, we expected *L. venusta* to build larger webs. An index of how a spider might have perceived the available space within which to construct a web is the ratio of the area within a web's frame line polygon divided by the horizontal area within an enclosure's dowel rod framework, with larger values indicating a more confining space. For *L. venusta*, *S. referens*, and *U. glomosus* these values were 0.26 ± 0.02, 0.15 ± 0.02, and 0.16 ± 0.01, respectively. Although *S. referens*, and *U. glomosus* ratios were each less than the *L. venusta* ratio (Wilcoxon $P = 0.0007$ and 0.0003, respectively), we do not believe that the sizes of any of these species' webs were constrained because each occupied only 15 – 26% of the available area.

We assembled and analyzed data with SAS JMP (SAS Institute, Cary, NC, https://www.jmp.com/en_us/software/data-analysis-software.html). Most web features measured were not normally distributed for the species being compared, as indicated by Shapiro-Wilk tests $P < 0.05$, and were, therefore, compared with nonparametric Wilcoxon (W) statistical tests. The symmetries of *S. referens*, *U. glomosus*, and *L. venusta* webs were normally distributed and were compared with parametric statistical tests.

We examined the relationship between the distance separating the outermost typical capture spiral and frame line and the length of cribellate thread deposited on this radius to form a zig-zag separately in each species using a standard least square, restricted maximum likelihood repeated measures regression tests with individual spider webs designated as the random variable. Only radii on which cribellate thread were deposited were included in these analyses. This avoided including a large number of radii with cribellate thread lengths of zero. The P and R^2 values of each test are provided in plots of these data. We also used repeated measures tests to examine associations between web symmetry and both the number of switchbacks and the number of zig-zags in webs.

To clearly distinguish sample sizes, figures indicate both the number of individuals per species that were included and, in analyses involving radii, the total number of radii measured for all individuals of a species. Error bars in figures and statistical summaries are ± 1 standard error. Voucher specimens are deposited in Harvard University's Museum of Comparative Zoology, the Smithsonian National Museum of Natural History, and the New Zealand Arthropod Collection, Manaaki Whenua-Landcare.

RESULTS

Presence and length of zig-zags.—The number of web radii differed considerably among uloborid species, as did the percent of radii on which cribellate thread had been placed to form zig-zags. The total number of radii with and without cribellate thread and the mean and standard error percent radii with cribellate thread,

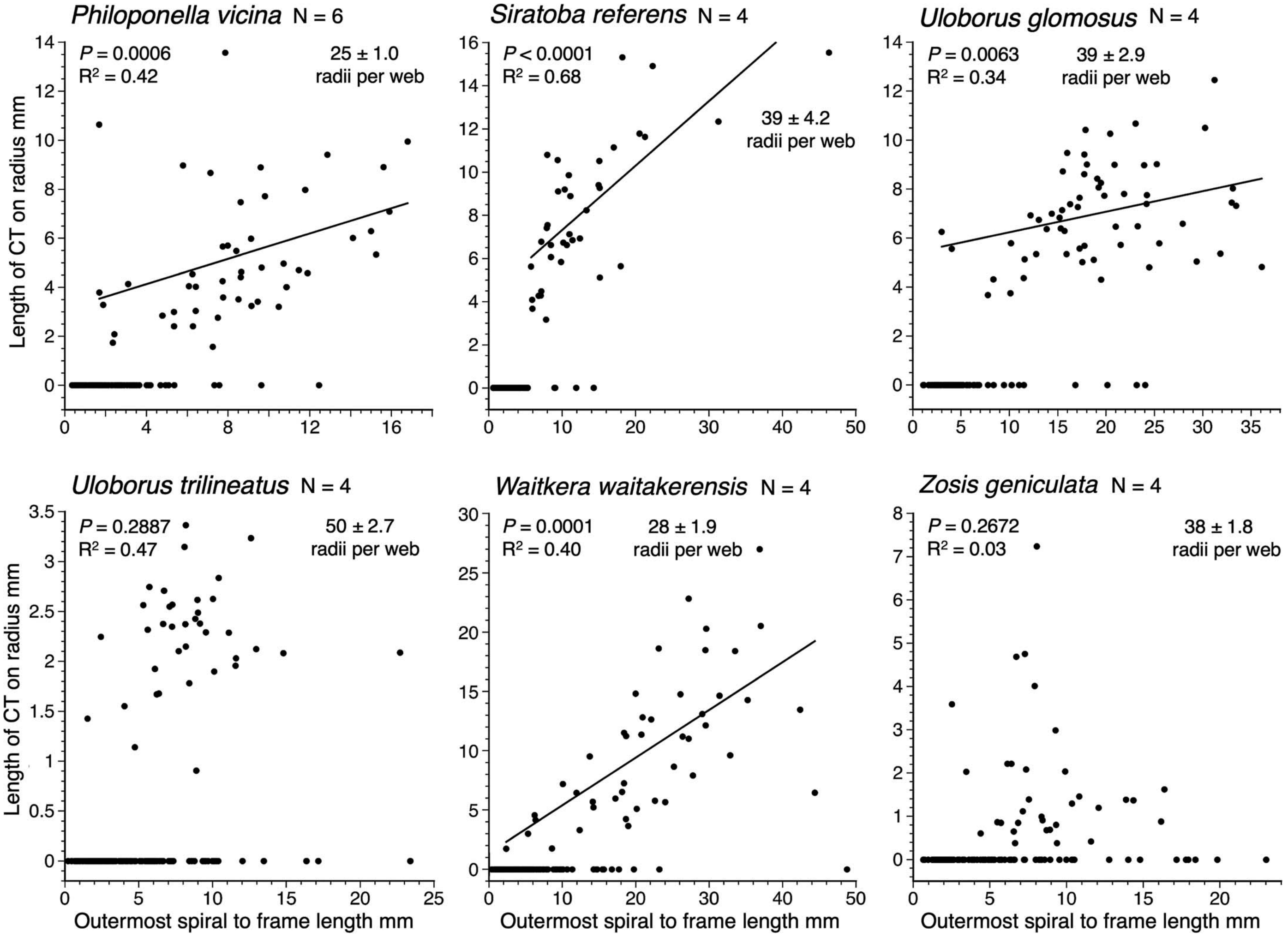

Figure 3.—Relationships between the distance along a radius that separates the outermost typical capture spiral from the frame line and the length of cribellate thread (CT) placed on a radius. P and R^2 values are provided for the repeated measures test of each species, which are based on only radii with cribellate threads and exclude radii with cribellate thread lengths of zero. A regression line derived from all webs combined is provided for each species that had a significant association. The number of webs that were measured for each species is indicated along with the mean and ± 1 standard error of the total number of radii per web.

respectively, were: *P. vicina* 47, 100, 34 ± 12%; *S. referens* 37, 117, 24 ± 3%; *U. glomosus* 58, 98, 38 ± 7%; *U. trilineatus* 37, 164, 18 ± 2%; *W. waitakerensis* 39, 74, 35 ± 5%; *Z. geniculata* 33, 120, 22 ± 16%. In all species, the distance between the outermost capture spiral and frame line was greater for radii with zig-zags than for radii without zig-zags (W $P < 0.0001$) (Fig. 3). When radii on which no cribellate thread was deposited were excluded, repeated measures tests showed that in four of the six species, the length of cribellate thread on radii was related to the distance between the outermost capture spiral and frame line (Fig. 3). The regression lines in these plots are based on radii with cribellate silk and are for all individuals combined.

In three of the six species, there appears to be a spiral to frame distance threshold beyond which cribellate thread is more likely to be deposited (Fig. 3). This is most pronounced in *S. referens*, where all but 3 of 40 radii with spiral to frame distances of 6 mm or greater had cribellate thread. This transition was less pronounced but still evident in *P. vicina* and *U. glomosus*, where the threshold appeared to be in the range of 4 mm and 12 mm, respectively.

In all species but *P. vicina*, repeated measures tests showed that the lengths of radii with cribellate threads (CT) were greater than the lengths of radii without cribellate threads (NCT). However, in *U. glomosus* the distribution of these values resulted in the mean lengths of the two types of radii being the indistinguishable (*P. vicina* W $P < 0.2324$, CT 51.4 ± 1.1 mm, NCT 48.8 ± 0.9 mm; *S. referens* W $P < 0.0002$, CT 76.8 ±4.0 mm, NCT 59.3 ± 1.7 mm; *U. glomosus* W $P < 0.0032$, CT 87.1 ± 5.6 mm, NCT 87.3 ± 2.6 mm; *U. trilineatus* W $P < 0.0001$, CT 50.6 ± 0.8 mm, NCT 45.0 ± 0.5 mm; *W. waitakerensis* W $P < 0.0001$, CT 91.1 ± 2.8 mm, NCT 73.2 ± 2.5 mm; *Z. geniculate* W $P < 0.0266$, CT 47.3 ± 1.4 mm, NCT 43.4 ± 0.8 mm).

We did not observe a significant association between the outermost spiral to frame line distance and the length of cribellate thread on radii in *U. trilineatus* and *Z. geniculata* even though *P. vicina*, which constructed webs in the same sized rings, showed a relationship between these two variables. Adult female *U. trilineatus* and *Z. geniculata* are larger, having body lengths of up to 7.2 mm and 8.4 mm, respectively, as compared with 4.2 mm for *P. vicina* (Opell 1979). The

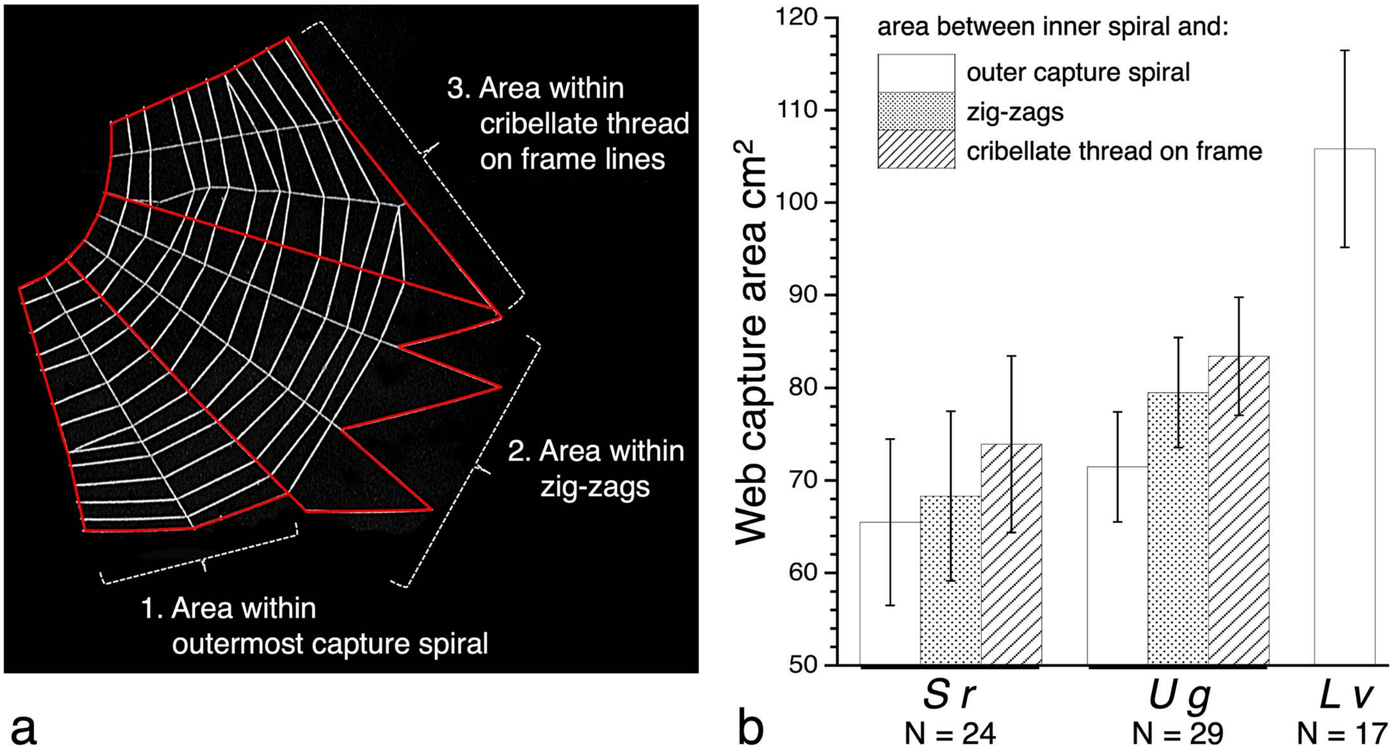

Figure 4.—Progressive increases in web capture areas. (a) Diagram of web sectors defining the capture areas of webs encompassed by: 1. The innermost capture spiral turn and the outermost complete spiral turn, 2. The innermost capture spiral and zig-zags at the web perimeter, and 3. The innermost capture spiral and outermost cribellate thread (whether this consists of zig-zags or cribellate thread on frame lines). (b) Values of these capture areas in *Siratoba referens* (Sr), *Uloborus glomosus* (Ug), and *Leucauge venusta* (Lv) webs constructed within frames of the same size. Error bars are ± 1 standard error. Numbers below each species are the number of individuals whose webs were analyzed.

smaller size of *P. vicina* would have required these spiders to take more "steps" to move outward along a radius from the outermost capture spiral and therefore, may have caused them to perceive this distance as greater. However, there were no differences in the symmetries of these three species' webs (*P. vicina* 0.66 ± 0.08; *U. trilineatus* 0.62 ± 0.03; *Z. geniculata* 0.57 ± 0.08).

Contributions of zig-zags and cribellate thread on frame lines to web capture area.—In *S. referens* and *U. glomosus*, web capture area increased as it was expanded from the area bordered by a web's innermost and outermost capture spiral to include regions with outer borders of zig-zags and increased again to include the outermost cribellate thread, whether this was zig-zag cribellate thread or cribellate thread on frame lines (Fig. 4a). These capture areas were 5.3% and 17.7% greater, respectively in *S. referens* and 12.9% and 19.0% greater, respectively in *U. glomosus* (Fig. 4b). When these three capture areas of increasing size were normalized by dividing each individual's areas by the area between its innermost and outermost capture spirals, capture area increased progressively in both *S. referens* and *U. glomosus* (W $P < 0.0001$).

Web radii, symmetry, and switchbacks.—*Siratoba referens* and *U. glomosus* constructed smaller webs than *L. venusta* (Fig. 4b), but the number of radii in these two species' webs did not differ (W $P = 0.1340$). *Siratoba referens* webs were less symmetrical than *U. glomosus* and *L. venusta* webs (t test, two tailed $P = 0.0308$ and < 0.0001, respectively) and *U. glomosus* webs were less symmetrical than *L. venusta* webs (t test, two tailed $P = 0.0256$) (Fig. 5a).

The number of switchbacks per spiral turn did not differ between *S. referens* and *U. glomosus* (t test, two-tailed $P = 0.8237$) (Fig. 5b). Even though *S. referens* and *U. glomosus* each had fewer capture spirals than *L. venusta*, each had more switchbacks per spiral turn than *L. venusta* (W $P < 0.0001$). The number of switchbacks per area between innermost and outermost capture spiral turns did not differ between *S. referens* and *U. glomosus* (W $P = 0.2110$), but *S. referens* and *U. glomosus* each had more switchbacks per area than *L. venusta* (W $P < 0.0001$) (Fig. 5b).

Repeated measures tests show that in neither *L. venusta* nor *S. referens* was the number of switchbacks in a web related to web symmetry ($P = 0.8764$ and 0.4091, respectively). However, in *U. glomosus* this relationship was significant, showing that less symmetrical webs had more switchbacks ($P = 0.0161$, switchbacks = 14.9 − symmetry × 12.87). Repeated measures tests did not support a relationship between the number of zig-zags and web symmetry (*L. venusta* $P = 0.6770$, S. *referens* $P = 0.7476$, *U. glomosus* $P = 0.4960$).

DISCUSSION

Our study confirms that early events in uloborid orb web construction impact web features that appear subsequently. When constructed in enclosures of the same size that provided ample space, two uloborid species' webs were less symmetrical than those of the somewhat larger tetragnathid *T. elongata* and, as a consequence, contained more switchbacks per spiral turn and per capture area. As the webs of these three species' webs were horizontal, there was no apparent gravity-based web asymmetry, as there is in many araneoid orb webs (Zschokke & Nakata 2015). However, it

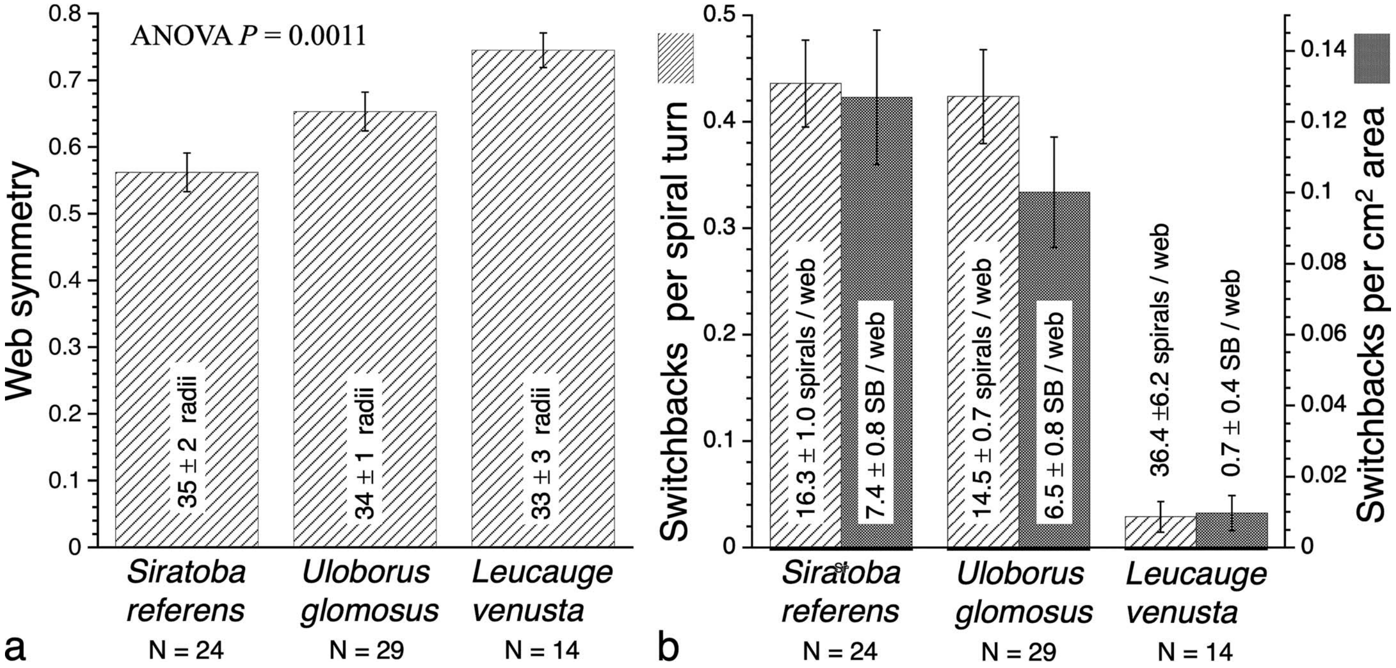

Figure 5.—Web symmetries and the relative number of switchbacks (SB) in orb webs of *Siratoba referens*, *Uloborus glomosus*, and *Leucauge venusta* when constructed within the same sized frames. (a) Web symmetries computed as the length of a web's shortest radius divided by the length of its longest radius and, within bars the total number of radii per web. Each value is mean ± 1 standard error. (b) The numbers of spiral turns (spirals) per web, switchbacks (SB) per capture spiral turn, and switchbacks per cm^2 of area between innermost and outermost capture spiral turns, as defined in Fig. 4a.

is possible that undetermined differences in their prey responses contributed to the asymmetry of the uloborid webs. Web asymmetry in uloborids may reduce the expenditure of time and energy and of major ampullate thread during exploration in the early phases of web construction. This could help offset the greater cost of spinning cribellate threads as compared to viscous capture threads (Lubin 1986; Opell 1998).

Siratoba referens exhibited the sharpest cut-off for capture spiral to frame line distance beyond which cribellate thread was deposited on radii, with only 3 of 40 radii whose distances exceeded 6 mm lacking cribellate thread. This species is distinguished by the absence of secondary frame lines in their webs (trait 14 in Eberhard & Opell 2020). Secondary frame lines bridge primary frame lines in web regions where primary frame lines extend to anchor lines and, thereby, tend to reduce distances between the outermost capture spiral and frame lines. Had secondary frame lines been present in the *S. referens* web shown in Figure 1a, they would likely have been placed between each of the pairs of long frame lines in the upper and lower right side of this photo. This would probably have resulted in each region having shorter web radii with smaller outermost capture spiral to frame line distances, making it less likely that these regions would have had zig-zags. As secondary frame lines tend to reduce the disparity in distances between a web's outermost capture spiral and frame line distances, the absence of secondary frame lines in *S. referens* may explain the more pronounced cut-off in this value at which cribellate thread is deposited in this species.

When commenting on a draft of this manuscript, William Eberhard hypothesized that a spider uses her memory of the distance traveled outward on a radius from the temporary spiral to implement a simple behavioral program that is responsible for the presence of zig-zags in uloborid webs: "If I have gone an especially long distance along a radius from the temporary spiral and still have not encountered the radius-frame attachment, I should attach the sticky line to the radius, turn around and proceed back toward the temporary spiral along the same radius, attach the sticky line to the radius a second time, and then continue on along the temporary spiral to the next radius." Thus, the outer end of a length of cribellate thread placed on a radius would represent the point at which a spider has "given up" finding a frame line. As this distance is likely measured by the number of "steps" a spider takes to reach this point, spider size probably affected the length of this cribellate strand and contributed to intra-specific differences in the lengths of cribellate thread spans along radii.

Cribellate thread zig-zags are more common in web regions where radii diverge to connect to anchor lines and thus appear associated with web asymmetry. This appears not to be the case when cribellate thread is placed on frame lines, which is similar to the addition of another capture spiral turn. Taken together, these two features suggest that uloborids have a drive to fully equip the perimeter of their webs for prey capture. This may allow these small spiders to more effectively utilize irregular spaces within vegetation by covering larger portions of their webs with cribellate lines. Uloboridae has long been considered a basal orb weaving clade (Coddington 1986; Coddington & Levi 1991; Kulkarni et al. 2021). However, we do not suggest that the presence of zig-zags and cribellate thread placed on frame lines are necessarily plesiomorphic characters of all orb weavers.

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