# The primary webs of Uloboridae (Araneae)

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**Abstract.** "Primary" webs of uloborids have large numbers of very fine lines and usually lack sticky cribellum silk. This paper reviews their taxonomic distribution (19 species in 5 genera) and the ontogenetic stages in which primary webs are built (spiderlings newly emerged from the egg sac, older juveniles, mature males, and normal and senile females), expands the knowledge of construction behavior, and describes several previously unnoticed design details. Primary webs differ from typical uloborid orbs in several ways: large numbers of fine radial and non-radial lines; facultative hub removal and replacement; usually closely spaced temporary spiral loops; and lines beyond the frame lines. Construction of supplemental radii in primary webs is distinctive in several respects: break and reel construction; tendencies to lay successive radii either on opposite sides of the web or close together in the same sector; high frequencies of aborted trips from the hub to the frame; production of multiple lines during a single trip from the hub to the frame and back; long pauses during the production of single radii; and variation in the sequences in which radial lines are added to a given sector. Some aspects of primary web construction resemble araneoid rather than typical uloborid behavior. The relation between primary webs and the evolution of orb webs, and the mechanism that spiders use to produce abundant non-radial lines despite making only radial movements during web construction remain uncertain. We speculate that primary webs are favored when spiders are unable to afford the costs of producing cribellate silk for a typical orb.

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Web-building spiders generally rely on their webs to capture prey, and their spiderlings typically must build prey capture webs soon after they emerge from the egg sac if they are to survive. In general, the designs of the webs of newly emerged spiderlings are similar to those of conspecific adults; newly emerged individuals of orb weaving species build orb webs, sheet weaver spiderlings build sheet webs, etc. But studies of web ontogeny have revealed minor design changes in both orb weavers (LeGuelte 1966; Peters 1969; Eberhard 1975; Edmunds 1978; Higgins 2006) and in non-orb weavers (Barrantes & Madrigal-Brenes 2008; Eberhard et al. 2008; Barrantes & Eberhard 2010). The challenges faced by tiny spiderlings are often quite different from those faced by conspecific adults with respect to metabolic demands, abundances of prey that the spider can overcome and that are large enough to be nutritionally significant, predators, and abiotic environmental factors such as wind and humidity (e.g., Eberhard & Wcislo 2011; Quesada et al. 2011; Eberhard 2020). There is thus no reason to assume that the webs of a species will be uniform during ontogeny.

Ontogenetic changes in web designs have sometimes been thought to follow the so-called "biogenetic law," in which the ontogenetic sequence mimics the sequence in which designs evolved (Petrusewiczowa 1938 and Bristowe 1941, 1958 on orbs; Eberhard et al. 2008 and Barrantes & Eberhard 2010 on theridiid gumfoot webs). A recent summary of 71 traits in 47 species and groups of congeneric species showed, however, that while there is indeed a trend toward this "ontogeny recapitulates phylogeny" pattern, it is by no means universal: the juvenile trait was ancestral in only 71% of 55 orb web traits, and 75% of 16 non-orb traits (Eberhard 2020). A speculative hypothesis was offered to explain this inconsistent trend, based on possible underlying contrasts in the ecological conditions (water balances, abundances of prey of different sizes, metabolic needs) that are experienced by smaller and larger individuals.

The present paper concerns an especially dramatic ontogenetic change in uloborid web design that was discovered nearly 100 years ago in Uloborus walckenaerius Latreille, 1806 and Zosis geniculata (Olivier, 1789) (Wiehle 1927). Spiderlings newly emerged from the egg sac (Vachon's "nymph 1" instar) (Foelix 2011) build approximately horizontal, radially organized sheets that contain extremely high numbers of very fine radial lines ("supplemental radii") but no sticky spiral (Wiehle 1927; Peters 1953; Szlep 1961; Eberhard 1977, 2020). These socalled "primary webs" (Szlep 1961) resemble typical orb webs in including non-sticky hub, radii, frame, anchor, and temporary spiral lines, and they are built using the same sequence of activities used to build typical uloborid orbs (Szlep 1961; Eberhard 1977). But the spiderling then adds a dense planar mat of very fine, nearly invisible lines that are arranged both radially (Szlep 1961 on U. plumipes Lucas, 1846; Eberhard 1977 on U. diversus Marx, 1898) and non-radially (Peters 1953 on Philoponella semiplumosa (Simon, 1893)) (= variegata); Eberhard 1977 on U. diversus). Fragmentary direct observations of the behavior of U. diversus spiderlings showed that the supplemental radius construction behavior differed from typical radius construction in the orbs of the same species. When returning to the hub, the spiderling broke and reeled up each line that it had laid as it moved away from the hub, rather than leaving this line intact as occurs in typical uloborid radius construction (Eberhard 1982). This behavior resulted in the gradual accumulation of small masses of loose silk at the center of the hub. Such masses never form during

typical uloborid radius construction but are typical in many araneoids that also break and reel lines during radius construction (Eberhard 1982, 2020).

The nymph 1 instar lacks a functional cribellum (Wiehle 1927), and the dense arrays of fine lines in primary webs have classically been thought to compensate for the spiderling's resulting inability to produce sticky spiral lines (Wiehle 1927, 1931; Peters 1953, 1955; Szlep 1961). Lubin (1986) proposed that primary webs might also function to conceal the spider. The compensation hypothesis for primary webs was reinforced by two subsequent discoveries. The transition from primary webs to ordinary orbs does not depend on behavioral experience; nymph 1 spiderlings of U. plumipes kept in small tubes where they could not spin primary webs nevertheless built ordinary orbs with sticky spirals in larger containers after they had molted to the next instar and acquired a functional cribellum (Szlep 1961). And primary webs are built by some mature male uloborids, which also lack a functional cribellum (Eberhard 1977; Grismado 2004).

Nevertheless, the compensation hypothesis fails to explain why similar mats of fine lines sometimes occur in some orb webs that also contain cribellate silk, including those of some nymph 2 spiderlings of *U. plunipes* (Szlep 1961) and of "senile"mature females of *U. diversus* (Eberhard 1971). Nor does the hypothesis answer the underlying but hitherto undiscussed question of why the cribellum and calamistrum are lacking in nymph 1 uloborid spiderlings, even though these spiders depend on webs to capture their prey. We know of no evidence regarding the more general question of whether the nymph 1 spiderlings of other cribellate spiders also lack functional cribella and calamistra.

In this paper, we describe several heretofore unappreciated design details in primary webs, present new details of primary web construction behavior, explore explanations for the mechanism by which spiders produce large numbers of nonradial lines while moving in nearly exclusively radial directions, and present a tentative hypothesis regarding the possible functional significance of this web design. A further objective is to complement a general survey of web types in Uloboridae (Eberhard & Opell 2022) by documenting the species and the developmental stages in which primary webs occur.

### **METHODS**

Most webs were coated with white powder (either corn starch or talcum powder) to be observed and photographed. As previously noted by Peters (1953), many of the lines were so fine that they were otherwise invisible, even with strong illumination and a dark background. We classified the more or less circular lines that we observed away from the immediate vicinity of the hub and not at the edge of the web as temporary spiral lines rather than sticky spiral lines. Justification for this classification came from their similar orientation and spacing to temporary spiral lines in the primary webs of other species, direct observations of construction behavior that showed that the spider did not comb silk from the cribellum while building them (Szlep 1961; Eberhard 1977), and from differences in how these lines and cribellum silk lines reflected light in unpowdered finished webs (Szlep 1961). We did not examine these lines under a microscope to confirm that they did not include cribellum silk. We assumed that all webs that we

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photographed during the day were finished, and that, if the hub was intact, it would not have been subsequently replaced.

We categorized the developmental stages in which spiders built primary webs as follows: "nymph 1" (first instar outside the egg sac); "juvenile" (a later instar spiderling whose orbs contained cribellum silk); "mature male" (with fully formed genitalia); "normal female" (mature females seen on orb webs in nature); and "senile female" (older females in captivity that had previously built typical orbs). Some adult females with unknown histories were classified as senile on the basis of similarities in the designs of their webs to those of *U. diversus* females that were known to be of advanced age (Eberhard 1971). Radial lines laid prior to temporary spiral construction are termed "typical radii" (with no intention to imply that other radial lines are somehow atypical); fine radial lines laid after the temporary spiral was complete are termed "supplemental radii".

The paths of nymph 1 spiderlings of U. plumipes as they built three primary webs were recorded using the automated technique described by Benjamin & Zschokke (2002). The setting in which these recordings were made was free of air movements and strong stimuli such as light or vibrations, so we assume that the pauses in the spiders' behavior were not due to disturbances. In these recordings, only the position of the spider's body was recorded; the positions of the legs and of the silk lines could not be discerned. Based on these recordings, we made a recording for analysis that showed the spider's movements in which each frame represented 0.33 seconds; periods of immobility lasting longer than 20 seconds were truncated, but a clock superimposed on the images showed the exact time elapsed. We termed every period of immobility that lasted at least 3 frames (>1 s) a "pause". For simplicity, we describe the path in which the spider left the hub moving radially and then returned also moving in a radial direction as "placement of a single radius". We distinguished three types of radii in these recordings: typical radii (built prior to temporary spiral construction); the "early" supplemental radii (the first 30-45 radii laid immediately following temporary spiral construction); and the "late" supplemental radii (the last approximately 45 supplemental radii laid before construction ended on the first night).

The reader should keep in mind the limitations resulting from our inability to see the web lines in the recordings. Multiple lines were probably laid during some trips away from the hub; perhaps the spiders spread their spinnerets as they moved, but our automated recordings did not register this detail (Eberhard 1977).

The values associated with behavioral variables were not distributed normally, and some had two widely separated peaks, so we emphasized distributions rather than central values in making comparisons, and employed simple, non-parametric statistical tests (using the program PAST) (Hammer et al. 2001).

The species identities of spiderlings in captivity were determined by the identity of the female that had produced the egg sac from which the spiderling emerged. Immature individuals were identified in the field as *U. trilineatus* Keyserling, 1883 on the basis of their web designs, their posture at the hub (Opell & Eberhard 1984), their coloration, and because only adults of this species of *Uloborus* were found

at the same site. One nymph 1 spiderling was identified as *P. vicina* (O. Pickard-Cambridge, 1899) in the field because it was in the same three-dimensional tangle as several mature female *P. vicina*.

### RESULTS

Figures 1-5 illustrate traits of primary webs built by different ontogenetic stages: nymph 1 spiderlings of Z. geniculata (Fig. 1), U. sp. nr. eberhardi (Fig. 2), U. trilineatus (Figs. 4e-i), and P. vicina (Fig. 5d); mature males of Z. peruana (Keyserling, 1881) (Figs. 3b-d), U. trilineatus (Fig. 4c) and P. tingens (Chamberlin & Ivie, 1936) (Fig. 3a); "senile" females of U. glomosus (Walckenaer, 1841) (Figs. 5a-c), U. trilineatus (Figs. 5f, g), and P. vicina (Figs. 4a, b); and older juveniles of U. trilineatus (Figs. 5d, e). Nymph 1 spiderlings of Z. geniculata and U. sp. nr. eberhardi did not build webs the first day after they emerged from the egg sac, as reported by Szlep (1961) for U. plumipes, but spent 2–7 days clustered near the sac before they dispersed and built their first webs. Table 1 shows that primary webs or at least primary web traits occur in five uloborid genera in five different life stages, and summarizes the distribution of the following design details of these webs.

Hub removal and replacement.—The structure of the hubs of some primary webs of nymph 1 Z. geniculata and U. sp. nr. eberhardi indicated that the hub center had been removed and then replaced (Figs. 1e, f, 2a, b): masses of non-radial lines were present just beyond the hub (Fig. 1f), apparently representing accumulations of cut lines; fine lines were lacking in the hub proper (Figs. 1e, f); and the hub was attached to the surrounding mat of fine lines by only a few lines that crossed a small open space (Fig. 1e). Similar patterns occurred in the web of a nymph 1 U. sp. nr. eberhardi (Figs. 2a, b), a senile female U. glomosus (Fig. 5c), a juvenile U. trilineatus (Figs. 5d, e), and in 10 of 10 webs of nymph 1 U. trilineatus (Figs. 4e, g*i*). In contrast, the hub apparently had not been removed and replaced, and many lines from the mat of fine lines converged at the very center of the hub in the primary webs of other nymph 1 spiderlings of Z. geniculata (Figs. 1a-d, g) and U. sp. nr. eberhardi (Fig. 2c), of senile female U. glomosus (Fig. 5a) and U. trilineatus (Figs. 5f, g), and of a mature male U. trilineatus (Fig. 4d). The hub was only partially removed in the web of one nymph 1 U. trilineatus.

Abundant non-radial fine lines.—Many fine lines in the dense mat were not radially oriented. In some webs, many fine lines converged on points other than the hub (Figs. 5a, b, d); in other webs, many fine lines were approximately parallel, with non-radial orientations (Fig. 2a); in still other webs many fine non-radial lines showed no consistent orientation (Figs. 1a, 2a). Fine non-radial lines were usually combined with fine radial lines ("supplemental radii"), but the web of a "normal" female *Conifaber parvus* Opell, 1982 may have lacked supplemental radii: only a few, probably typical radii, were attached to the frame lines (Lubin et al. 1982), and the dense mat of fine lines may have consisted entirely of non-radial lines (individual lines could not be resolved in the photo, however).

We tested the strength with which non-radial lines were attached to other web lines by pulling on individual lines in relatively open areas (where individual lines could be distinguished) of lightly powdered webs of two nymph 1 U.

trilineatus. We attempted to avoid radii and temporary spiral lines by choosing lines with orientations that were neither radial nor perpendicular to radial. We used a fine insect pin with a hooked tip to pull the line gently downward at a relatively small but variable angle with vertical, and observed the lines being pulled under a dissecting microscope. In only 2 of 26 lines was there any slippage at the junctions that the line being pulled made with the adjacent web lines on either side of the hook; in all other lines, and in 9 of 10 fine radial lines that were tested, both junctions remained intact until the line being pulled broke. These tests did not precisely standardize the rates of pulling, the directions of pulling, or the segment lengths of line being pulled, nor did they discriminate between lines laid earlier or later in the construction process. Nevertheless, they were sufficient to show that non-radial lines often adhere to the lines that they cross in the web.

**Fine lines beyond the frames.**—Some of the fine, non-radial lines in the mat extended beyond the frame lines in webs of nymph 1 spiderling *U*. sp. nr. *eberhardi* (Fig. 2*a*); this pattern also occurred in nymph 1 *U. diversus* (Eberhard 1977) and in a nymph 1 *U. plumipes* whose web building behavior we recorded.

**Spacing of temporary spiral loops.**—Temporary spiral lines were present in the primary webs of all species in which this detail could checked, though individual lines could not be resolved in the especially dense mats of a mature male *Uloborus* sp. #1015 (Eberhard 1977) or a mature female *Conifaber parvus* (Lubin et al. 1982). In some webs, the temporary spiral lines were visible only as higher concentrations of fine lines (or perhaps only higher concentrations of powder) (Figs. 1b, 3a); in others the temporary spiral lines themselves could be distinguished in areas where the fine lines were less dense (Figs. 1b–d, 2b, c, 4a). The spaces between temporary spiral loops were relatively large in some webs, on the order of those in a typical orb of *U. diversus* (Eberhard 1972) (Figs. 1b–d, 3a, 5a, f). In others, the spacing was relatively close (Figs. 2 b, c, 3d).

"Mixed" webs.—Some juvenile U. trilineatus (estimated to be nymph 3 or 4) and a senile female U. glomosus built "mixed" webs in captivity that had both adhesive sticky spiral lines and mats of very fine lines that resembled those in primary webs (Figs. 5d, e). Hub replacement was confirmed with greater certainty in these webs because the lines were thicker and thus more easily distinguished; there were no fine lines among the replacement hub lines (Figs. 5c, e). Two other juvenile U. trilineatus of similar sizes that were observed in the field had, in contrast, typical orbs with sticky spiral lines but no mats of fine lines. One of these webs had an unusual peripheral detritus stabilimentum-a small string of detritus hung at edge of the orb-that was connected directly to the hub by a line, and the spider left the hub to hang among the detritus when disturbed. Similar detritus stabilimenta occur in an unidentified Australian uloborid (Eberhard 2020) and the tetragnathid Dolichognatha pentagona (Hentz, 1850) (Eberhard 1986).

**Construction behavior.**—*Path forms:* In an attempt to understand how fine non-radial lines are produced, we examined several details of the supplemental radius construction and contrasted them with the construction of typical radii. We also examined differences early and late in the



Figure 1.—Primary webs of nymph 1 Zosis geniculata spiderlings. Webs a-e were coated with powder and then jarred repeatedly to dislodge larger accumulations of powder; f and g were not powdered. Each primary web had a hub, frame lines, many radial lines, and many more non-radial lines. The photo in b is a close-up of the central portion of a, showing several loops of temporary spiral (black arrows). Other webs (c and d) illustrate substantial variation in the degree to which temporary spiral lines (black arrows) were covered by other lines. The webs in f and g (not powdered) contrasted with the others in that the spider had removed the central portion and replaced it with a new hub. The red arrows in e and f mark the edges of this hole, contrasting with the lack of a hole in the intact hub in g.

process of supplemental radius construction to document possible differences that might be related to non-radial lines.

Tracings of the paths followed by U. plumipes nymph 1 spiderlings while they built three primary webs confirmed Szlep's report (1961) that the spider first built "typical" radii, frame lines and then a temporary spiral, as is typical in uloborid orb webs (black and red lines in Fig. 6). Then, after having finished the temporary spiral, the spider added many supplemental radii (blue lines in Fig. 6). In two of the three webs, the spider also added supplemental radii on subsequent nights (the third web was damaged after the first night in an attempt to take a photograph). In all three webs, the spider's path during supplemental radius construction was usually similar to its path during typical radius construction: the spider moved in a more or less straight radial line from the hub to the frame (along a pre-existing radial line, the "exit"), then made a short lateral movement along the frame, and finally moved back to the hub in a more or less straight line (the "return"), apparently along the new radial line (Fig. 7). Similar paths occurred during construction of typical radii built earlier by the same spider, by adult U. diversus (Eberhard 1972) and U. walckenaerius (Zschokke & Vollrath 1995a, b), and by many other orb weavers (Eberhard 2020).

Small zig-zags in radially oriented paths occurred sporadically (Figs. 6b, 7a). Perhaps these movements resulted from small swinging movements as the spider moved along a line; but in no case did the spider move back and forth as if it were dangling at the end of a line below the web.

In some cases, the spider left the hub but turned back before reaching the frame (dotted arrows in Fig. 6b; lines 13, 32, 34, 39, and 40 in Fig. 7b). Such "false starts" were significantly less common among the early than late supplemental radii in each web. The intra-web differences were statistically significant in all three webs; in total, 5.9% of 169 early radii were false starts while 36.2% of 105 late radii were false starts ( $\chi^2 = 41.1$ , P =<<0.0001). Similar false starts sometimes occurred during typical radius construction in these same webs but were relatively rare (7.3% of 55 typical radii in the three nymph 1 webs). They were also rare (4.0%) in adult *P. vicina* (Eberhard 1990). False starts in primary web construction may be involved in production of non-radial lines (see the discussion).

*Pauses:* The spider usually paused at the frame line for at least 1 s during supplemental radius construction just before turning back to return to the hub (92.4% of 250 supplemental radii) (e.g., at 5 for the supplemental radius 5 in Fig. 7a). Presumably it attached the new supplemental radius to the frame during the pause. Many of these "attachment" pauses at the frame lasted only 1–2 s (58.4%); but 28.6% lasted >3s. Attachment pauses were shorter during early than during late supplemental radius construction. The fraction of the pauses at the frame that lasted 1–2 s as opposed to those lasting >3 s was significantly lower for the earliest 30 supplemental radii



Figure 2.—Primary webs of nymph 1 *Uloborus* sp. nr. *eberhardi* spiderlings. The spider removed and then replaced the hub of the web in a (enlarged in b), while the hub in the web in c was intact, with the radial lines converging where the spider rested. At least some radii in the replacement hub were bent into sawtooth forms by double attachments of the hub spiral (red arrows in b). These webs had more loops of temporary spiral (black arrows in a-c) that were relatively more closely spaced than those in the webs of nymph 1 *Zosis geniculata* spiderlings (Fig. 1). A few fine lines extended beyond the frame line in a.

than for the last 45 supplemental radii in two webs (*P* values in  $\chi^2$  Tests were  $3x10^{-5}$  and 0.02); the third web had a nonsignificant trend (*P* = 0.5) in the same direction. Attachment pauses for the typical radii in these webs also tended to be short: 23% of 56 lasted less than 1 s, and the maximum was 3.7 s; only 8% of 231 attachment pauses for supplemental radii lasted less than 1 s ( $\chi^2 = 11.9$ , *P* = 0.003), and the maximum was 21.0 s.

There were also many pauses at other sites during supplemental radius construction. The number of "pauses along a radius" during the construction of a single supplemental radius ranged from 0 to 18 (Fig. 8). This number tended to be lower during early than during late radius construction in all three webs: the fraction of early supplemental radii with 0–3 pauses was 98%, 75% and 51% in the three webs, while the same fraction during the late radii was 61%, 50% and 32% (respective *P* values in  $\chi^2$  Tests were 4x10<sup>-5</sup>, 0.03, and 0.06) (Fig. 8). Even fewer pauses occurred during typical radius construction in these same webs (Fig. 8).

The durations of the pauses along a radius during early and late supplemental radius construction were similar, although they were more often especially short (0.3 s) and less often especially long (> 6 s) while building early radii (Fig. 9) ( $\chi^2 = 14.5$ , P = <0.005, df = 2). The pauses along radii that occurred during typical radius construction were even shorter than those while building early supplemental radii (Fig.9; comparing < 1 s vs. > 1 s in these two types of radii,  $\chi^2 = 16.7$ , P < 0.0001)).

Each of the ten longest pauses was during a "false start" during late supplemental radius construction (these occurred in two webs, and ranged from 22 to 582 s). The tendency for these especially long pauses to occur during false starts was significant, as the overall frequency of false starts in the 78 late radii in these two webs was 44% ( $\chi^2 = 14.8$ , P = 0.00012). Long pauses may be involved in production of non-radial lines (see the discussion).

Angles between successive supplemental radii: The angles between successive early supplemental radii were larger than the angles between successive late supplemental radii; the difference was statistically significant in two of the three webs (Table 2). The angles between typical radii in these same webs tended to be smaller than those for supplemental radii, and resembled those for typical radii in orbs built by mature female U. diversus (Fig. 10).

Supplemental radii also differed from typical radii in that they less often showed the "final angle" pattern that was the rule in the typical radii of these webs (there were only two exceptions in the typical radii of the three primary webs). In the final angles pattern, which is also the rule in typical orbs of other uloborids (Eberhard 1972, 2020; Zschokke & Vollrath 1995a, b) and in araneoid orbs (summary in Eberhard 2020), the spider gradually builds outward from previous radii into unfilled spaces, using each new radius as an exit for the next (e.g., radius 1 served as an exit when the spider built radius 18 in Fig. 7b). Supplemental radius construction differed in that



Figure 3.—Webs of mature males. The hub of the primary web of a mature male *Philoponella tingens* in *a* was replaced. The webs of mature males of *Zosis peruana* (*b*–*d*) include both a primary web (*b*; enlarged in *d*) and a resting web that lacked cribellum silk (*c*). The loops of temporary spiral were relatively widely spaced in the *P. tingens* web (white arrows in *a*). There were no clear temporary spiral lines in the overview of the *Z. peruana* web (*b*), but the closeup (*d*) reveals many, closely spaced loops (white arrows). This closeup also shows that the hub was not removed and replaced, and that the fine lines extended nearly to the center of the hub. Both the resting (*c*) and the primary web (*d*) of mature male *Z. peruana* had a prominent silk stabilimentum. Some radii were pulled into sawtooth forms by double hub spiral attachments (red arrows in *c* and *d*).

radii were often built in the space between previous supplemental radii and their exit radii. In Fig. 7 for instance, the angle formed when supplemental radius 8 was built was subsequently subdivided by radii 25 and 27; the original angle formed by 2 was later subdivided by 21 and 31. Nevertheless, re-examination of the recordings of the construction of typical radii by *U. walckenaerius* described by Zschokke & Vollrath (1995b) revealed two webs in which the spider subdivided an angle, laying one or two new radii between the exit radius and a previously built radius. Only three exceptions to the final angle rule were found in observations of 598 spaces between radii in 14 webs built by the araneid *Micrathena duodecimspinosa* (O. Pickard-Cambridge, 1890) (W. Eberhard, unpublished data).

The placements of new supplemental radii with respect to the exit radius and previous supplemental radii also showed other variations. Some paths repeated nearly exactly the path of a previous supplemental radius, presumably resulting either in the doubling or even tripling of some supplemental radii (or in their removal and replacement) (e.g., 11, 17 and 19 in Fig. 7b). This pattern did not occur in the typical radii of these three nymph 1 webs, except in two radii where one radius was apparently laid on top of a previous radius. Such doubling has never been reported in typical radius construction in uloborids (Eberhard 1972, 1990, 2020; Zschokke & Vollrath 1995a, b). Re-examination of the recordings of typical radius construction by *U. walckenaerius* (Zschokke & Vollrath 1995b) revealed, however, a few atypical radii in six of seven webs in which one to three radii may have been laid twice (it was unclear whether the spider doubled the radius or removed the previous radius) (these radii are depicted in Fig. 17 of Zschokke & Vollrath 1995b).

In some other cases, the spider reused a given exit radius but walked past a previous supplemental radius before attaching a new supplemental radius to the frame (e.g., 14 in Fig. 7*a*; 26 in Fig. 7*b*). This pattern also differs from the "final angles" pattern. Re-examination of the automated recordings of *U. walckenaerius* made by Zschokke & Vollrath (1995a, b) did not reveal any exceptions of this sort to the usual pattern.

*Exit radii used in supplemental radius construction:* Except during early stages, typical radii were seldom used as exit radii when the spider moved from the hub to the frame; for instance, supplemental radius 2 in Fig. 7b was used as an exit when the spider built supplemental radius 37. Nor were the exit radii for supplemental radii in a given sector usually clumped on any single supplemental radius; instead, the paths used in building supplemental radii were generally splayed apart (Fig. 6), indicating that the spider tended to use different supplemental radii as exits during supplemental radius construction. Nevertheless, some radii were reused as exits



Figure 4.—The "mixed" web of a senile female *Philoponella vicina* (*a*) illustrates a reduced sticky spiral and an intact, widely spaced temporary spiral (red arrows) combined with a mat of mostly non-radial fine lines; the hub (*b*) had not been removed. In contrast, the hub of the primary web in the field of a nymph 1 of this species (*c*) had been removed and replaced; the temporary spiral (arrows) was widely spaced. The hub of the web of a mature male *Uloborus trilineatus* built in captivity (*d*) was not replaced, and the fine lines only partially covered the widely spaced temporary spiral (red arrows); most of the fine lines were parallel, and few if any were radial (an anchor line at approximately 4:00 was broken). In contrast, there were many fine radial lines and a widely spaced temporary spiral (red arrows) in the webs of nymph 1 *U. trilineatus* (*e*–*i*). The hub in *g* (unpowdered) had been completely removed and replaced. Only portions of the hubs in *h* (unpowdered) and *i* had been removed. The dashed arrows in *g*–*i* indicate accumulations of silk at the edge of the hole made when the early hub was removed and then replaced. The solid arrows in *h* indicate white masses at the center of the intact remains of the first hub. The solid arrows in the closeup *g* indicate sawtooth attachments of the hub spiral to radii.

during supplemental radius construction (for instance, the same exit was used in building supplemental radii 8, 16, 23, 25 and 27 in Fig. 7*b*). Repeated use of particular radii as exits was unusual in typical radius construction in these primary webs, and also in the typical radius construction by adult female *U. walckenaerius* (Zschokke & Vollrath 1995b) and *U. diversus* (Eberhard 1972).

The temporary spiral lines in the *U. plumipes* primary webs were laid before rather than following supplemental radius construction (Szlep 1961; Fig. 6). Thus, it appears that Szlep's statement that the spiral lines were below rather than above the fine lines in the primary webs of this species was probably mistaken.

## DISCUSSION

**Taxonomic distribution of primary webs.**—Table 1 shows that primary webs are widely distributed among uloborid spiders, and that they show considerable flexibility in both their designs and in the developmental stage in which they occur. Primary webs occurred in individuals of more than one life stage in three species: in individuals of all sizes (including adult males and females) of *Philoponella* sp. G (Lubin 1986); in nymph 1 spiderlings, older juveniles, and senile females of *U. diversus*; and in nymph 1, older juvenile spiderlings, mature males, and senile females of *U. trilineatus*. Nevertheless, building primary webs in one developmental stage may not guarantee that they are built in another: mature males of *Z. geniculata* apparently do not build primary webs (Eberhard 2020) even though nymph 1 spiderlings did. The primary webs described in the present study resembled previous descriptions of the primary webs of nymph 1 spiderlings of *U. walck-enaerius*, *U. plumipes U. diversus*, and *Z. geniculata* and a mature male *Uloborus* sp. (Wiehle 1927; Szlep 1961; Eberhard 1977).

Table 1 also documents substantial evolutionary flexibility in the primary web designs of different species. The dense mat of fine lines in the web of a mature female *Conifaber* (Lubin et al. 1982) may be unique in lacking fine radial lines and in being composed exclusively of fine non-radial lines. The spacing between the loops of temporary spiral in primary webs was wide in the primary webs of nymph 1 *Z. geniculata* (Figs. 1*c, d*) and mature males of both *P. tingens* (Fig. 3*a*) and *U. trilineatus* (Fig. 4*e*); in contrast, the temporary spiral loops of nymph 1 of *U.* sp. nr. *eberhardi* (Fig. 2*b*), *U. plumipes* (Szlep



Figure 5.—Pictured here are the following: primary webs built by senile mature female *Uloborus glomosus* (a-c) (*b* is an enlarged view of the portion outlined in *a*); the "mixed web" (*d*, *e*) of a juvenile *U. trilineatus* (estimated nymph 3 or 4) (*e* is an enlarged view of *d*), and the web (*f*, *g*) of a senile female *U. trilineatus* (*g* is an enlarged view of *f*). The red arrows in *c* indicate the edge of the hole that was produced when the spider removed the hub and then replaced it; the red triangles in *e* mark the ends of lines that were broken when the hole was made; the spider apparently removed the first hub and replaced it after the web was otherwise complete. The mixed web in *d* contained both mats of very fine lines and also sticky spiral lines. The closeup view in *g* shows that the senile female *U. trilineatus* did not remove and replace the hub.

1961; Fig. 6), and *U. diversus* (Eberhard 1977) were relatively close together. Although mature female *C. parvus* were consistently found on primary webs in the field (Lubin et al. 1982; W. Eberhard unpub.), the webs of mature female *C. guarani* Grismado, 2004 and *C. yasi* Grismado, 2004 were typical orbs (Grismado 2004, 2008).

There was substantial intra-specific variation in primary web design, even within the same developmental stage. Some primary webs of nymph 1 Z. geniculata had intact hubs (Figs. 1a-d, g), but the original hub had been removed and replaced in others (Figs. 1e, f); the primary webs of nymph 1 of U. sp. nr. eberhardi also had both intact and replaced hubs (Fig. 2); and published photographs of the webs of nymphs 1 and 2 of U. plumipes indicate that hub replacement also occurs in some primary webs but not in others (Szlep 1961). Hub replacement also occurred in ten of ten nymph 1 U. trilineatus webs but not in mature males of the same species. Mature male Z. peruana sometimes built and sometimes did not build primary webs (Figs. 3b-d).

Primary webs will probably be found in additional uloborid species as further observations accumulate, especially for the early, nymph 1 stages that arachnologists have typically neglected. Primary webs are apparently absent, however, at least in nymph 1 spiderlings, in the uloborid genera *Hyptiotes* Walckenaer, 1837 (Opell 1982), *Polenecia* Lehtinen (Peters 1995), and *Miagrammopes* O. Pickard-Cambridge, 1870 (Opell

2001), as previous authors checked for them and failed to find them. These genera have all secondarily lost orb webs, so this absence of primary webs may also be derived.

**Construction behavior and phylogenetic affinities.** By patching together direct observations of the construction behavior of nymph 1 spiderlings of *U diversus* (Eberhard 1977) and *U. plumipes* (Szlep 1961), the automated recordings of *U. plumipes* nymph 1 spiderlings (Figs. 6, 7), and deductions from structural details of webs, and by then assuming that the behavior that is revealed is representative of other ontogenetic stages and other orb-weaving uloborid taxa, we have tentatively compared primary web construction behavior with typical uloborid orb construction behavior, and also with araneoid behavior. The most extensive comparisons are summarized in Table 3 and discussed below.

Supplemental radius construction behavior differs sharply from that of typical uloborid radii: break and reel behavior occurs as the spider returns to the hub; the angles between successive radii are larger; the angles between new radii and their exit radii are more often subsequently filled with further radii; the spider pauses more often and for longer during construction of a radius; false starts are more common; and multiple rather than single compound lines may be at least sometimes produced with each trip away from the hub. In addition, early supplemental radius construction differs to Table 1.—Species and developmental stages of uloborid spiders that build primary webs with different designs. All previously unpublished data are from webs photographed after being coated with white powder to make lines more easily visible. Specimen numbers refer to labels in the collection of the Museum of Comparative Zoology at Harvard University. All web design details from previously published accounts were recorded from photographs; text descriptions in published accounts were not used unless otherwise noted. Developmental stages are as follows: N1 = nymph 1 recently emerged from egg sac; J = spiderling of a later instar; M = mature male; F = normal adult female; S = senile adult female.

Species	Reference	Devel. stage	Many fine radial lines	Hub removed and replaced	Fine lines beyond the frame	Many fine non-radial lines	Stabilimentum	Spacing of temporary spiral
Conifaber guarani (field)	Grismado 2004	М	Y	? <sup>a</sup>	? <sup>a</sup>	Y	2ª	? <sup>a</sup>
Conifaber parvus (field)	Lubin et al. 1982	F	$N?^{b}$	Y	? <sup>a</sup>	Y	Y and N	? <sup>a</sup>
Octonoba sinensis (= octonaria) (field)	Peaslee & Peck 1983	N1	Y <sup>c</sup>	?	?	?	?	?
Philoponella semiplumosa (= variegata) <sup>d</sup> (field)	Peters 1955	N1	Ŷ	prob. <sup>e</sup>	?a	? <sup>a</sup>	N	? <sup>a</sup>
Philoponella tingens (field)	this study	М	Υ	Y	Ν	Υ	Ν	wide
Philoponella vicina (field)	this study	N1	Υ	Υ	Ν	Υ	Ν	wide
Philoponella sp. G (field)	Lubin 1986	J	$\mathbf{Y}^{\mathrm{f}}$	?	? <sup>a</sup>	?	?	?
		$\mathbf{M}^{\mathrm{f}}$	Y	Y	? <sup>a</sup>	$\mathbf{Y}^{\mathrm{f}}$	Ν	? <sup>a</sup>
Uloborus diversus (captivity)	Eberhard 1971, 1977,	N1	Y	Ν	Y	Υ	Ν	very close
	this study	J	Y		?	Υ	?	?
	5	$S^{g}$	Y	Ν	Ν	Υ	Ν	? <sup>g</sup>
Uloborus glomosus (captivity)	this study	S	Y	Y and N	Ν	Y	Y and N	wide
Uloborus plumipes (captivity)	Szlep 1961, this study	N1	Y	Y and N	Y	$\mathbf{Y}^{h}$	Ν	close
	1	J	Y	Y	? <sup>a</sup>	$?^{a}$	Ν	close
Uloborus trilineatus (captivity)	this study	N1	Y	Y	Ν	Y	Ν	wide
		J	Y	Ν	Few	Y	Ν	? <sup>i</sup>
		Μ	Y	Y	Ν	Υ	Ν	wide
		S	Y	Ν	Ν	Y	Ν	wide
Uloborus walckenaerius (captivity)	Szlep 1961	N1	Y	Ν	$?^{a}$	$\mathbf{Y}^{\mathbf{h}}$	Y	close
Uloborus sp. nr. Eberhardi (captivity)	this study	N1	Y	Y and N	some	Υ	Ν	close
Uloborus sp. (#1015) (field)	Eberhard 1977	Μ	Y	Y	Y?	Y	Ν	? <sup>a</sup>
Zosis geniculata (captivity)	this study	N1	Υ	Y and N	? <sup>a</sup>	Y	Y	wide
Zosis peruana (field)	this study	М	Y	Ν	Ν	Y	Y	close

<sup>a</sup> This detail could not be resolved in the photos.

<sup>b</sup> The mat was too dense to allow resolution of individual lines; only very few radii (probably typical radii) were attached to the frame.

<sup>c</sup> From a verbal note by Peaslee & Peck 1983 rather than a photograph; spiders were free-ranging in a grain elevator

<sup>d</sup> Spider is identified in the publication as *P. vicina*, but a handwritten note added by H. Peters to a reprint of the 1955 paper changed the name to *variegatus*. The photo of the domed web of the species he observed (his Fig. 13) is similar to the orbs associated with specimens from Central America identified by B. Opell as *P. variegatus* and differs from the planar orb webs of specimens identified by B. Opell as *P. vicina*.

<sup>e</sup> There is apparently a relatively open space around the spider at the hub, suggesting hub replacement, but lack of resolution in the photo precludes complete certainty.

 $^{\hat{f}}$  Individuals "of all sizes" were seen on primary webs, but additional design details were given only for juveniles and mature males. Lubin (1986) characterized primary webs as "... thin sheet of fine threads arranged in a more or less radial pattern", but the only photos were of mature male webs; her Fig. 6.6 shows a least a few non-radial lines.

<sup>g</sup> Senile web patterns appeared gradually over the space of days to weeks, and were associated with females presumed to be virgins because they did not lay eggs over this time or earlier. The web traits given here for senile females represent extreme cases. Both sticky and non-sticky lines were present in some senile female orbs, but it is not possible to distinguish whether the spiral lines in the published photo were sticky or not. <sup>h</sup> Szlep's descriptions mention only radial lines, and they were very common in her photos; nevertheless at least a few non-radial lines are visible in Figs. 1 (*U. plumipes*) and 2 (*U. walckenaerius*) of Plate III.

<sup>i</sup> Temporary spiral had been removed, and only the sticky spiral (with normal spacing) was present.

some extent from that of the last supplemental radii in the same web.

Some aspects of supplemental radius construction behavior in primary webs resemble the behavior of araneoids more than that of uloborids (Table 3). The typical radii of uloborids are built following the construction of a proto-hub, and form part of the process of hub spiral construction (summaries in Eberhard 1982, 2020). This difference has consequences for how spiders sense where to add new radii. In building typical radii, the spider probably uses the separation between legs oI and oII (the legs I and II on the side of the spider facing away from the center of the hub) to sense the presence of gaps between existing radii. These legs have stereotyped lateral positions and consistently grasp successive pairs of adjacent radii (Eberhard 1972, 1982, 2020). In contrast, direct observations of behavior showed that no hub spiral was constructed during supplemental radius construction by nymph 1 *U. diversus*, and legs oI and oII were directed anteriorly (Eberhard 1977). The spiderling's two legs I made apparently exploratory tapping or jerking movements just prior to leaving the hub to build each new supplemental radius (Eberhard 1977). Thus, the spiderling probably used the separation between its two anteriorly directed legs I (or perhaps II), rather than the separation between legs oI and



Figure 6.—The paths followed by two nymph 1 *U. plumipes* spiderlings when they built complete primary webs: the "typical" radii are black; the temporary spiral is red; and the subsequent supplemental radii are blue. Individual paths are easier to discern in web b where there are fewer lines. Nearly all typical and supplemental radius paths were relatively straight, with an "exit" from the hub, a line along the frame line, and a "return" path to the hub (labeled for one typical and one supplemental radius in b) (see also Fig. 7). There were a few small zig-zags (for example short thick arrows in a). In a few "false starts", the spider turned back and returned to the hub without reaching a frame line (dotted arrows in a and b). In some cases, the paths of several supplementary radii were nearly identical (solid arrows in b). In one web (a), the supplemental radii in some sectors (red arrows) were apparently attached to frame lines that were beyond the black frame lines to which the typical (black) radii in that sector were attached.

oII, to sense the angles between radii. Legs I are also directed anteriorly and used in an apparently similar manner in many araneoids (summary in Eberhard 2020).

A second resemblance to araneoids is that nymph 1 U. diversus spiderlings broke and reeled up the line that they had just laid from the hub to the frame as they returned to the hub during supplemental radius construction, and small masses of silk accumulated at the hub (Eberhard 1977) (our automated recording of the web building of U. plumipes spiderlings did not allow us to check for break and reel behavior). Break and reel behavior is absent in typical radius construction (after the proto-hub is built) in numerous species of uloborids, but it is typical of many araneoids (Eberhard 1982).

Still another resemblance to araneoids is the destruction and subsequent replacement of the entire hub late in web construction, which also occurs in the araneoid families Anapidae and Mysmenidae (Eberhard 1987, 2020; Lopardo et al. 2011) (but not in typical orbs in Araneidae, Tetragnathidae or Nephilidae; Kuntner et al. 2008; Eberhard 2020). Similar hub destruction and replacement occurs in the early stages of typical uloborid orb construction (Eberhard 1990), and also during web repair in uloborids (Eberhard 2020) and in the tetragnathid *Leucauge mariana* (Taczanowski, 1881) (W. Eberhard in prep.). Its use in primary uloborid webs and in anapids and mysmenids may represent reordering of a preexisting behavioral module or modules (Eberhard 2018, 2020).

The large angles between successive supplemental radii in the primary webs of *U. plumipes* resembled the large angles between successive typical radii in araneoid orbs (Eberhard 1990, 2020), in contrast to the smaller angles between successive typical radii in the same primary webs of the same nymph 1 individuals and in the orbs of adult female U. diversus (Fig. 10). This contrast is complicated, however, by an additional, fragmentary observation of a U. diversus nymph 1 spiderling: the spider made especially small angles between successive supplemental radii (Eberhard 1977), with a roughly estimated mean angle of  $28 \pm 26^{\circ}$  in 16 radii that appeared to be sequential supplemental radii that were laid during a short period in an undetermined stage in the construction of a single web.

It remains to be determined whether any of the several similarities between supplemental radius construction and araneoid behavior represent homologies inherited from a common ancestor rather than convergences, and thus represent signals of phylogenetic relations.

Several other aspects of supplemental radius construction appear to differ from all descriptions of the construction of typical radii by either uloborids or araneoids. These include the more frequent departures from the "final angles" pattern of adding radii, the longer durations of pauses both at the frame and elsewhere in the web, the greater frequencies of false starts, and the repeated use of the same radii as exits (Table 3). A further, especially dramatic difference was that a single trip during supplemental radius construction from the hub to the frame and back sometimes resulted in multiple supplemental radii being added: "when webs were powdered just after construction of supplemental radii had begun, there were several lines in each sector in which the spider had made a trip" (p. 204, Eberhard 1977).



Figure 7.—The order of the paths that a nymph 1 *U. plumipes* spider followed in the first 41 radii, during early stages of supplemental radius construction of the web shown in Fig. 6*b* (the paths of the first 14 supplemental radii are presented in *a*, and those of the first 41 in *b*). The numbers indicate the order in which the supplemental radii were built, with each number positioned at the beginning of the spider's return path to the hub; the small black square represents the spider's position at the moment represented in *a*. In some cases, the paths of several supplementary radii were nearly identical (e.g., 8 and 16; and 25 and 27 in *b*). In some cases, the spider exited from the hub several times along the same radius but returned to the hub along a different path (e.g., the exit was the same for 2, 6 and 14 in *a*, and for 5 and 15 in *b*). "False starts", in which the spider turned back on the exit radius before reaching the frame, are illustrated by radii 13, 34 and 40, in which the spider used the same exit it had used in building radius 9. Subsequent subdivision of an angle by a later radius (contrasted with the "radii at final angles" pattern of orb weavers in general) is illustrated by radius 15: it was laid in the angle that was formed when the spider built radius 5 (compare *a* and *b*) (see also radii 25 and 27, which subdivided the angle formed earlier between the exit and radius 8). The exit radii for the earliest supplemental radii in *a* were typical radii, but the exit radii for late supplemental radii were supplemental radii (e.g., 15 was the exit for radius 24). The arrow in *b* indicates a zig-zag pattern in the exit portion of radius 32 when the spider apparently moved onto an adjacent exit radius.



Figure 8.—Frequencies of pauses (other than attachments to the frame) when nymph 1 *U. plumipes* spiderlings were in the process of building typical radii and early and late supplemental radii. Typical radii had fewer pauses than supplemental radii; comparing numbers of radii with 0–3 and >3 pauses,  $\chi^2 = 11.5$ , P = 0.0007. Early supplemental radii had fewer pauses than late supplemental radii; comparing numbers of radii with 0–3 and >3 pauses,  $\chi^2 = 15.9$ , P < 0.0001.



Figure 9.—Durations of pauses along radii when nymph 1 *U. plumipes* spiderlings were in the process of building typical radii and early and late supplemental radii. Pauses were shorter in typical than in late supplemental radii; 53% of 75 pauses during typical radius construction were only 1 s, while the corresponding value was 30% of 522 pauses during late supplemental radius construction ( $\chi^2 = 16.7$ , *P* << 0.001). Early supplemental radii had more very short and fewer very long pauses than late supplemental radii. Pauses were differed between early and late supplemental radii when they were compared with respect to three categories of durations, (1.0 s, >1.3 and < 10 s, and > 10 s ( $\chi^2 = 14.5$ , *P* < 0.005).

**Mysteries of the fine radial and non-radial lines.**—The glandular origin of the fine supplementary radii and of other fine, non-radial lines in primary webs is uncertain. The lines must have very small diameters, as they were essentially invisible even with bright illumination and a dark background that made all the other web lines easily visible (Peters 1955; Eberhard 1977; above). This seems to rule out ampullate gland lines and suggests instead aciniform gland lines; further work will be needed to clear up this question.

Details of supplemental radius construction behavior may help clarify how the large numbers of non-radial lines of primary webs are produced. The automated recordings of U. *plumipes* give important confirmation of the earlier direct but incomplete observations of this species by Szlep (1961) and of U. *diversus* (Eberhard 1977), that *all*, rather than only a sample of the spider's movements after the temporary spiral is finished, are basically radial. Mysteriously, in spite of the radial orientations of these movements non-radial fine lines are abundant in many uloborid primary webs. Some of these non-radial lines were nearly parallel to each other, while others converged on points other than the hub (Figs. 1*a*, 4*a*, *c*–*e*, 5*a*, *b*, *d*). Some fine lines even extended beyond the frame lines (Fig. 2*a*; also Eberhard 1977).

How are such non-radial lines produced when the spider moves almost exclusively in radial directions? The answer may be related to the differences that we have documented between supplemental and typical radius construction behavior, and between the construction of early and late supplemental radii in the same web (Table 3). We speculate that at least some of these differences (perhaps especially those associated with long pauses and false starts) may occur while the spider is producing new fine non-radial lines. One possibility is that swaths of loose "balloon" lines floating in the air may be produced during the long pauses along radii: the loose ends of the lines could be carried by air movements and eventually stick to the web, producing abundant non-radial lines. An alternative hypothesis is that during pauses the spiders cut multiple fine radial lines that were already in place, and that the loose ends flew free and eventually adhered to the web. This alternative seems less likely, however, because it would result in non-radial lines that were attached at the hub, and many of the non-radial lines were far from the hub (Figs. 2, 4, 5). The adhesion of fine non-radial lines to other lines in the

Table 2.—Mean angles between successive supplemental radii in early and late stages of construction of three primary webs, frequencies of false starts in early and late radii, and numbers of pauses/radius in *U. plumipes* primary webs. Means are followed by one standard deviation; *z* values are from comparisons of early vs. late radii in the same web using Mann-Whitney Tests (\* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.0001).

	Mean angle betw. successive radii (N)			Frequ	ency of false sta	arts	Mean no. pauses/radius $\pm$ std. dev.		
	Earliest radii	Last radii	Z	Early radii	Late radii	Chi <sup>2</sup>	Early radii	Late radii	Z
Web 1 Web 2 Web 3 Total	144±30.6° (39) 144±31.2° (61) 132±35° (66) 140±33° (166)	$130 \pm 43^{\circ}$ (29) $116 \pm 48^{\circ}$ (36) $96 \pm 51^{\circ}$ (37) $112 \pm 49^{\circ}$ (102)	1.2 2.9** 3.6*** 4.4***	9.8% (41) 6.5% (62) 3.0% (66) 5.9% (169)	33% (30) 35.1% (37) 39.5% (38) 36.2% (105)	6.1* 13.4*** 23.4*** 37.1***	2.1±0.8 2.8±2.0 5.4±4.7 37.1***	3.5±2.0 4.9±3.5 6.4±4.7 4.7±3.6	3.7*** 2.7** 1.2 3.74***



Figure 10.—The angles between successive early supplemental radii in the primary web of a nymph 1 spiderling *U. plumipes* (the web shown in Fig. 7b) tended to be much larger than those between successive typical radii in this same web as well as the typical radii of three mature female *U. diversus* (data are from Fig. 7 of Eberhard (1972) depicting data from multiple webs; in the calculations reported here and in the text, we assumed that all cases that fell within a category in the graph had the median value of that category) (comparing early supplemental radii of nymph 1 *U. plumipes* with adult *U. diversus*, z = 7.8, P < 0.0001 with Mann-Whitney U Test; n = 40, 157).

web could result if newly produced lines are a least briefly adhesive (e.g., Peters & Kovoor 1991 on fine lines in linyphiid sheets).

Both of these flying lines hypotheses are complicated by the fact that at least some of the primary webs with abundant nonradial fine lines (*U. diversus, U. trilineatus, U.* sp. nr. *eberhardi, Z. geniculata*) were built in closed cages in captivity, where major air movements were precluded. While very weak air movements might be sufficient to carry fine lines, it would seem likely that such lax lines would often be curved rather than straight. Although a few of the fine non-radial lines that could be clearly distinguished in primary webs built in captivity were somewhat curved (e.g., those at the upper right in Fig. 2a of U. sp. nr. *eberhardi*), the large majority were straight (e.g., Figs. 1a, 2a, 4a, d of, respectively, Z. geniculata, U. sp. nr. *eberhardi*, P. vicina, and U. trilineatus)

An additional possible complication is that we cannot categorically confirm the existence of non-radial lines in *U. plumipes*, the species for which we have the most extensive records of radial movements by the spider. The uniform presence of non-radial lines in the mats of fine lines in the primary webs of other uloborids argues that they were also present in *U. plumipes* primary webs. Szlep's descriptions of *U. plumipes* (1961) mention only radial rather than non-radial lines, but she apparently observed only unpowdered webs, and her photos show at least a few fine non-radial lines. Our inability to see the web lines in our recordings also makes it possible (though we think unlikely) that some trips did not result in any lines being laid.

Testing the flying line hypotheses by direct observations will be challenging, because the fine lines are largely invisible, even with favorable illumination and a dark background; they only became visible when coated with powder (Peters 1955; Eberhard 1977), and the spiders ceased building when their webs were powdered (Eberhard 1977). Our hypothesis could be tested, however, by powdering a web immediately following a long pause that was associated with an early false start: this should reveal multiple non-radial fine lines that are associated with the site where the spider paused.

In sum, the mechanism by which abundant fine non-radial lines in primary webs are produced is not yet resolved. The expectation that the dense arrays of supplemental radii in primary webs are the result of the spider simply repeating typical radius construction behavior over and over is clearly wrong; supplemental radius construction clearly involves distinctive behavior patterns. Establishing the evolutionary histories of these different types of behavior may have interesting consequences for discussions of the evolutionary origins of orb webs, especially since some details of uloborid supplemental radius construction are more similar to araneoid than to typical uloborid radius construction (Table 3). Recent phylogenies based on molecular data are so divergent that it seems premature to speculate in detail regarding homologies. Different modules of construction behavior likely have different evolutionary histories.

The function of primary webs: a new hypothesis.—What is the functional significance of primary webs? As noted in the introduction, they were originally thought to represent a compensation for the lack of the structures (cribellum and calamistrum) that are needed to produce cribellum silk in nymph 1 spiderlings (Wiehle 1927; Szlep 1961). Our results have confirmed, however, that some primary webs are produced by spiders that have a functional cribellum (later instar spiderlings; senile adult females); primary webs thus cannot function only as replacements for a functional cribellum. Also unresolved is the underlying question of why

Table 3.—Comparisons between the supplemental radius construction behavior used to build the supplemental radii in primary webs and the typical radii in uloborid orb webs, and between early and late stages of construction. These data are also compared with general trends in araneoids. As indicated in the footnotes, some quantitative differences were not tested statistically, but we believe they are clear. All uloborid data are from this study, Eberhard 1972, 1977, and Zschokke & Vollrath 1995a, b. Araneoid data and their published sources are summarized elsewhere (Eberhard 1990, 2020).

Behavior				
Supplemental vs typical radii	Supplemental radii	Typical radii in uloborids		
"Triangular" path (spider exits from hub on a pre-existing radial line, moves laterally along the frame, and then returns straight to hub)	Yes <sup>1</sup>	Yes <sup>1</sup>		
Break radial line and reel it up as return to the hub	Yes <sup>1</sup>	Only earliest radii (prior to proto-hub construction)		
Radial lines are continuous with the hub spiral	No <sup>1,2</sup>	Yes <sup>3</sup>		
A single trip from the hub to the frame and back sometimes results in multiple lines	Yes	No <sup>1</sup>		
The legs thought to be used to sense angles between adjacent radii during radius construction	Two legs I <sup>1,2</sup>	Legs oI and oII		
"Final angle" pattern of adding radial lines	Less common (and patterns vary more)	Nearly universal <sup>1</sup>		
Angles between successive radii	Large <sup>1</sup>	Small		
"Attachment pauses" (at frame)	Common <sup>1</sup>	Common <sup>1</sup>		
Duration of attachment pauses	Long	Short <sup>1</sup>		
Frequency of "pauses along radii" (pauses not at the frame)	More common (especially in late radii)	Rare <sup>1</sup>		
Duration pauses along radii	Long (especially in late radii)	Short <sup>1</sup>		
Frequency of false starts	High (especially in late radii)	$Low^1$		
Repeated use of same radius as an exit	Some	Rare <sup>1</sup>		
Add more radial lines after first night	Yes	No (never) <sup>1</sup>		
Early vs. late supplemental	Early	Late		
Angles between successive supplemental radii	Large	Small		
Frequency of false starts	Low	High		
Duration of pauses	Low	High		

<sup>1</sup> araneoids are similar in this respect, though no strict statistical tests are available

<sup>2</sup> exceptions occur in the last few radii in an orb in some araneoids

<sup>3</sup> Eberhard 1982

nymph 1 spiderlings of uloborids lack the very structures (calamistra and a cribellum) that are crucial for making adhesive prey traps.

We speculate that perhaps primary webs represent alternatives that are employed when the spider is unable to make the substantial investments of materials, time, and energy that are needed to produce cribellate sticky lines in an orb (Lubin 1986; Zschokke & Vollrath 1995a; Bond & Opell 1998). Orb construction involves long periods of sustained, rapid movements combing out cribellate silk with the hind legs (Zschokke & Vollrath 1995a). The switch to primary webs when females became "senile", and by apparently "weak" juveniles that failed to grow as rapidly as litter mates (Szlep 1961, W. Eberhard unpub. on U. diversus) fits this economy idea. In addition, uloborid nymph 1 spiderlings are very small (estimated on the order of 0.1 mg in U. trilineatus and U. sp. near *eberhardi*), a size at which a spider's relatively large brain (Quesada et al. 2011, 2021) may impose relatively large energy demands (Eberhard & Wcislo 2011).

Furthermore, the evolution of orb webs may have resulted in increased demands on the spider's ability to accumulate cribellate silk. When a spider begins construction of an orb, it needs to have available the entire amount sticky silk that it will need to cover the web. In contrast, many non-orb weaving cribellate species gradually add sticky silk to their webs over longer periods (Eberhard 2020). The material and energetic costs of having enough sticky silk on a given night may thus be substantially higher in orb weavers. Our observation that nymph 1 *U. plumipes* gradually add supplemental radii to the primary web over several nights fits the typical pattern of gradual additions to non-orbs. In sum, we propose that primary webs represent alternatives to both the energetic and the material demands of orbs.

**Remaining puzzles.**—The evolutionary origin of primary webs is unclear. Primary webs occur in five of the eight uloborid genera in which they have been searched for, and they are only known to be absent in three uloborid genera that build highly derived webs. Primary webs may thus be a synapomorphy of uloborids (Eberhard & Opell, 2022). qqIf our flying line hypothesis is correct, the spigots used to produce the fine lines in primary webs may be the same as those used to produce balloon and spanning lines; if so (this remains to be tested), the spigots for fine primary web lines may have been present ancestrally. To our knowledge, nothing similar to the planar, radially organized dense mat of very fine lines in primary webs has ever been seen in any araneoid orb weaver, nor for that matter in any other cribellate spider. Admittedly, astonishingly little is known of the webs of early instar spiders. In some cribellate groups, nymph 1 spiderlings appear not to produce cribellate silk. Early instar spiderlings

of the deinopid Deinopis cf. cylindracea did not make cribellate lines, but instead built a single non-sticky line that the spider held tensed and then released when a prey was nearby, causing the spider to spring forward and grasp the prey with its anterior legs (R. Periera Da Ponte et al. in prep.). Fragmentary observations suggest that similar behavior may occur in D. subrufus L. Koch (Baum 1937). Nymph 1 spiderlings of the zoropsid Tengella radiata (Kulczynski, 1909) did not include cribellate lines in the sheet or the tangle above it. Cribellate lines only appeared in the 7<sup>th</sup> instar; but no alternative, compensatory web design in earlier instars was noted (Barrantes & Madrigal-Brenes 2008). A web made by a spiderling of Oecobius concinnus Simon, 1893 that had emerged from the egg sac only a few days previously did not have visible cribellate lines (D. Solano-Brenes, pers. comm.); this web had been treated with nebulized mist that increased the visibility of cribellate lines (Solano-Brenes et al. 2018), suggesting that cribellum lines were absent. In sum, there are no reports of primary webs, or of cribellate silk in webs built by early instar spiderlings of non-orb cribellate spiders; but the data are too incomplete to draw general conclusions.

Spiders employed several apparently independent behavioral modules in different combinations during primary web construction. For instance, hub removal followed by replacement sometimes occurred and sometimes did not occur in the primary webs of nymph 1 spiderlings of U. plumipes (Szlep 1961), Z. geniculata (Fig. 1) and U. sp. nr. eberhardi (Fig. 2). A dense mat of very fine lines, similar to the mats in primary webs, occurred in the webs of mature female C. parvus (Lubin et al. 1982); in the congeneric C. guarani such mats were absent in the webs of mature females, but present in the webs of mature males (Grismado 2004). The mat of C. parvus may have lacked supplemental radii, in contrast to all other known primary webs. Mats of fine lines were combined with sticky spiral lines in "mixed" webs built by later instar spiderlings and by senile females of U. plumipes (Szlep 1961), U. diversus, U. glomosus, and U. trilineatus (Fig. 5d). Given the modular, "cut and paste" pattern of evolution of several aspects of orb construction behavior (Eberhard 2018, 2020), these behavior modules may have different evolutionary histories. For instance, the supplemental radii in the primary webs of uloborids and the supplemental radii added after sticky spiral construction by anapids and symphytognathids (Lopardo et al. 2011; Eberhard 2020) presumably evolved independently. In contrast, hub destruction and replacement in primary webs is likely homologous with hub destruction and replacement the early stages of typical orb construction that precede proto-hub construction, and the hub replacement in uloborid orb repair behavior (Eberhard 1972, 1990, 2020). More complete descriptions of the evolution of primary webs and of orbs will need to trace the evolution of these behavioral modules as separate entities.

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