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Orb web traits typical of Uloboridae (Araneae)

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Abstract. Web designs have long been used to characterize spider taxa and to deduce the relations between them; but systematic documentation of the amount of variation in webs within and between taxonomic groups is rare. This study, based on previously published observations and new observations of 15 species in the family Uloboridae, including two genera, *Octonoba* Opell, 1979 and *Siratoba* Opell, 1979, whose webs were previously undocumented, reviews the taxonomic distribution and variation in 22 orb web traits in at least 43 species in 11 genera in uloborids. These traits appear to occur in all orb-weaving genera in which reasonable samples are available, though only small samples are available for many species. Larger samples of the webs of three species of *Uloborus* Latreille, 1806, two of *Hyptiotes* Walckenaer, 1837, and one each of *Zosis* Walckenaer, 1841*, Siratoba, Octonoba, Waitkera* Opell, 1979 and *Philoponella* Mello-Leitão, 1917*,* revealed greater intra-specific consistencies in some traits than others. Hub traits were especially consistent. Variations in three traits may represent adjustments to the size of the space in which the orb is built. "Primary" webs, which combine orb and sheet-web traits, are built by spiderlings newly emerged from the egg sac and by adult males in at least five genera of orb-weaving uloborids and may be unique to this family. Preliminary comparisons between uloborid and araneoid orbs suggest that uloborid orbs may also differ from araneoid orbs in combining several other traits.

Keywords: Behavioral characters, web evolution, primary webs

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Spider webs constitute easily observed physical records of behavior, and some basic designs of webs, such as orbs, gumfoot webs, and sheets, have long been used to typify spider taxa (McCook 1889; Comstock 1912; Marples 1962; Kaston 1964; Vollrath 1988; Blackledge et al. 2009; Eberhard 2020). Orb webs offer detailed and easily analyzed records of construction behavior (Zschokke & Vollrath 1995) and have been especially well studied. Arachnologists have repeatedly mentioned the possibility that particular orb traits may be specific to particular groups (e.g., Lubin 1986; Zschokke & Vollrath 1995; Craig 2003), but few have attempted to document such comparisons with quantitative analyses of the variation within and between different groups. Instead, only a single web design has been used to characterize "the" web form of a given species, despite abundant evidence that many aspects of web designs are flexible (summaries in Herberstein & Tso 2011; Eberhard 2020). Because behavior is often more flexible than morphology, variation can be a problem when using behavioral characters to distinguish taxa (de Quiroz & Wimberger 1993). At present, the question of whether orb designs are consistent enough within species, genera, or families to be used to characterize taxonomic groups of spiders is largely unresolved (Eberhard 2020).

Two quantitative analyses of orb web traits have documented taxonomic differences most convincingly. Gregorič et al. (2010) found that some web characters in the four genera of the *Zygiella* group of araneoids showed some overlap between species, but were potentially phylogenetically informative because as they showed statistically significant shared variation among species. Some traits of the orb webs of sympatric species of *Tetragnatha* Latreille, 1804 endemic to different islands of Hawaii also differed statistically (Blackledge & Gillespie 2004). A survey of details of the behavior used to build orbs showed several qualitative differences that were shared at the level of family or subfamily in a sample of 112 species in 44 genera of araneoids and 13 species in 4 genera of uloborids (Eberhard 1982). These behaviors included the sequences of attachments made during radius and hub construction, the positions of legs at the moment that sticky spiral lines were attached to radii, and the removal or lack of removal of the center of the hub after the sticky spiral was complete. This behavioral study was somewhat typological, however. Most species were observed directly (not filmed) in the field; because of the repetitive nature of many aspects of orb construction, a given detail of behavior was observed over and over until the detail was understood. A few additional checks were performed to confirm that the spider executed the same behavior repeatedly, but larger samples of dozens or hundreds of such checks to confirm that there was never any variation were not made. Subsequent analyses of video recordings have shown that some variations were missed. For instance, *Leucauge mariana* (Taczanowski, 1881) spiders occasionally attach the sticky spiral to a radius even though they have failed to contact the inner loop with exploratory taps with inner leg I (behavior A4 instead of A1 of Eberhard 1982) (W. Eberhard unpub.). Inner loop localization behavior also varies occasionally in the araneid *Deliochus* sp. and the Australian tetragnathid *Leucauge* sp. (Kuntner et al. 2008), as do radius attachments to the frame in the nephiline *Nephila pilipes* (Fabricius, 1793) (Kuntner et al. 2008) and hub removal in the araneid *Metepeira olmec* Piel, 2001 (W. Eberhard, unpub.).

This paper concerns the orbs of the small family Uloboridae (with 290 species in 19 genera as of January 4, 2022) (World Spider Catalogue 2021). Uloborid and araneoid orb construction is similar in several respects (McCook 1889; Wiehle 1927, 1928; Marples 1962; Eberhard 1972; Lubin 1986; summary in Eberhard 2020), and the cues that guide construction behavior

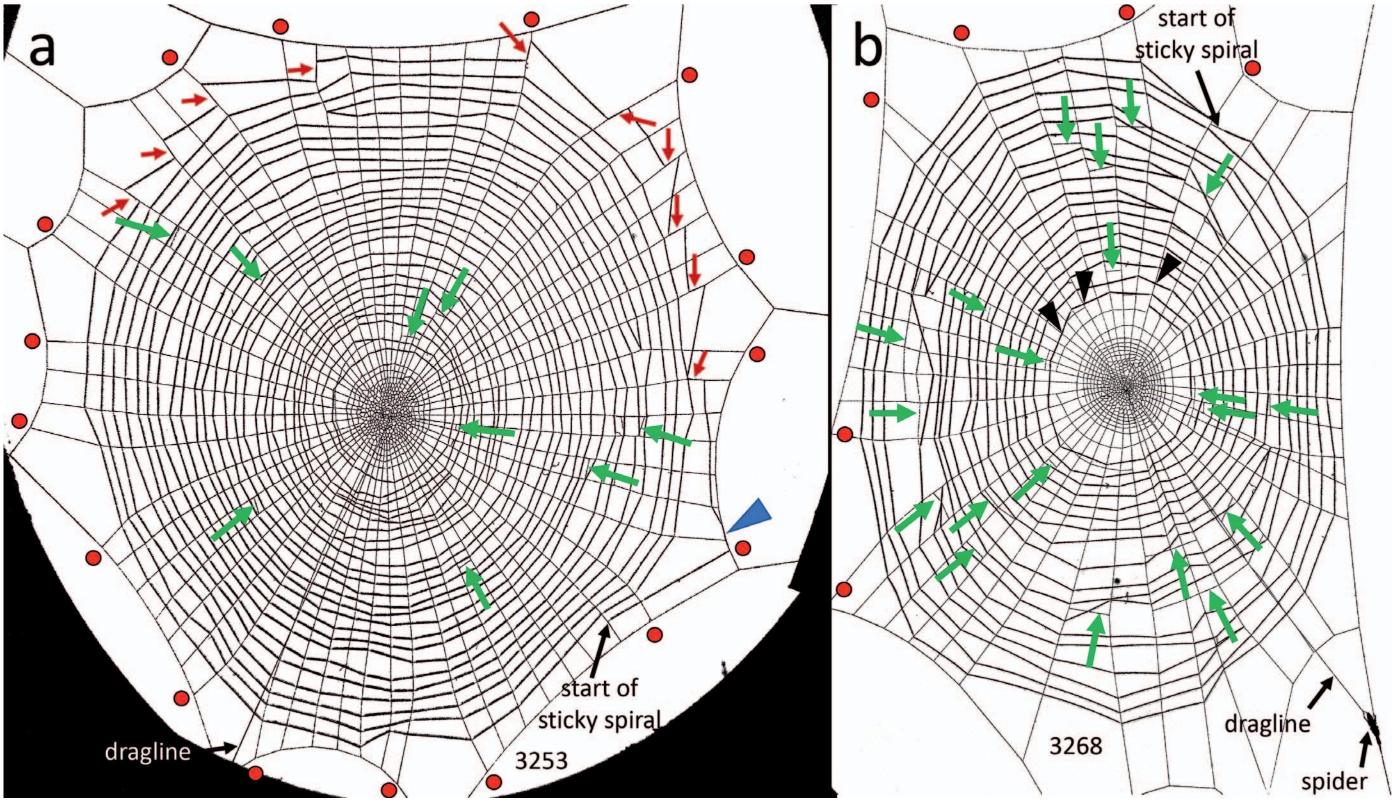

Figure 1.—Webs of adult female *Uloborus trilineatus* built in captivity illustrate several typical uloborid traits (numbered as in Tables 1, 2) (the thicker lines are sticky): lack of a hole in the center of the hub (#1); lack of a hub hole scar (#2); intact segments of temporary spiral (#5) (green arrows); sticky spiral line laid along a frame line (#7) (blue triangle in *a*); zig-zag attachments of the sticky spiral to some radii (#8) (dark red arrows in *a*); pairs of radii both of which curve toward the anchor between them (#12) (pairs of red dots); and sticky spiral segments that crossed radii near the hub without being attached to them (#9) (a few intersections are marked with black triangles in b). Intra-specific variation is illustrated in (b), which lacks the zig-zag attachments of the sticky spiral to the radii seen in *a*.

are also similar (Eberhard & Barrantes 2015). In addition, there is overlap in some traits that were previously thought to differ between the two groups. The orientation of the web plane with respect to gravity (previously said to be horizontal in uloborids, vertical in araneids) (e.g., Kaston 1964; Bond & Opell 1998), has proven to vary. Some uloborids, such as *Uaitemuri rupicola* Santos & Gonzaga, 2017 (Santos & Gonzaga 2017), *Zosis geniculata* (Olivier, 1789) (Marples 1962; Lubin 1986; Eberhard 2020) and *Philoponella tingens* (Chamberlin & Ivie, 1936) (Opell 1979; Lubin 1986; Eberhard 2020) sometimes build nearly vertical orbs. And species in several araneid genera, including *Enacrosoma* Mello-Leitão, 1932, *Eustala* Simon, 1895, *Mangora* O. Pickard-Cambridge, 1889*, Spilasma* Simon, 1897 and *Azilia* Keyserling, 1881 routinely build nearly horizontal orbs (Eberhard 2020). In addition, web inclinations vary substantially within many species in both families (Eberhard 2020). A second possible difference during construction that was mentioned by Coddington (1986) and Zschokke & Vollrath (1995; p. 535)—that "cribellates always moved the frame thread on return to the hub during frame construction; ecribellates never moved it"—is also inconsistent. The radius attachment point on the frame line was also moved outward in ecribellates such as the araneid *Scoloderus tuberculifer* (O. Pickard-Cambridge, 1889) (Eberhard 1975) and the tetragnathid *L. mariana* (Eberhard 1990, 2020).

There may also be differences between uloborid and araneoid orb web designs. Lubin (1986) and Eberhard (2020) speculated that the following details in uloborids may differ from araneids: lack of a central hole in the hub; lack of scars left from repairing hub holes; many closely spaced loops of hub spiral; double attachments of the hub spiral to each radius that pull the radii into sawtooth patterns; at least a few zig-zag patterns in the outer loops of sticky spiral where the sticky line runs for short distances along non-sticky lines (radii or frame lines); scattered intact segments of temporary spiral; and sticky spiral segments that skip over some radii without attaching to them in the inner portion of the orb (Figs. 1, 2). These impressions have not been tested, however, with systematic surveys of web designs. A further untested possible difference in uloborids is the construction of a "primary web" (Szlep 1961; Eberhard & Zschokke 2022)

The objective of the current paper is to build on previous reviews (Marples 1962; Lubin 1986) to assemble data on web designs in Uloboridae. There is at least fragmentary information on the web designs in 15 of the 19 genera (Tables 1 and 2) (nothing is known regarding the webs of *Ariston* O. Pickard-Cambridge, 1896*, Astavakra* Lehtinen, 1967*, Daramulunia* Lehtinen, 1967*,* or *Orinomana* Strand, 1934). Orb webs occur in 12 of these 15 genera (*Conifaber* Opell, 1982*, Lubinella* Opell, 1984*, Octonoba* Opell, 1979*, Philoponella* Mello-Leitão, 1917*, Purumitra* Lehtinen, 1967*, Siratoba* Opell, 1979*, Sybota*

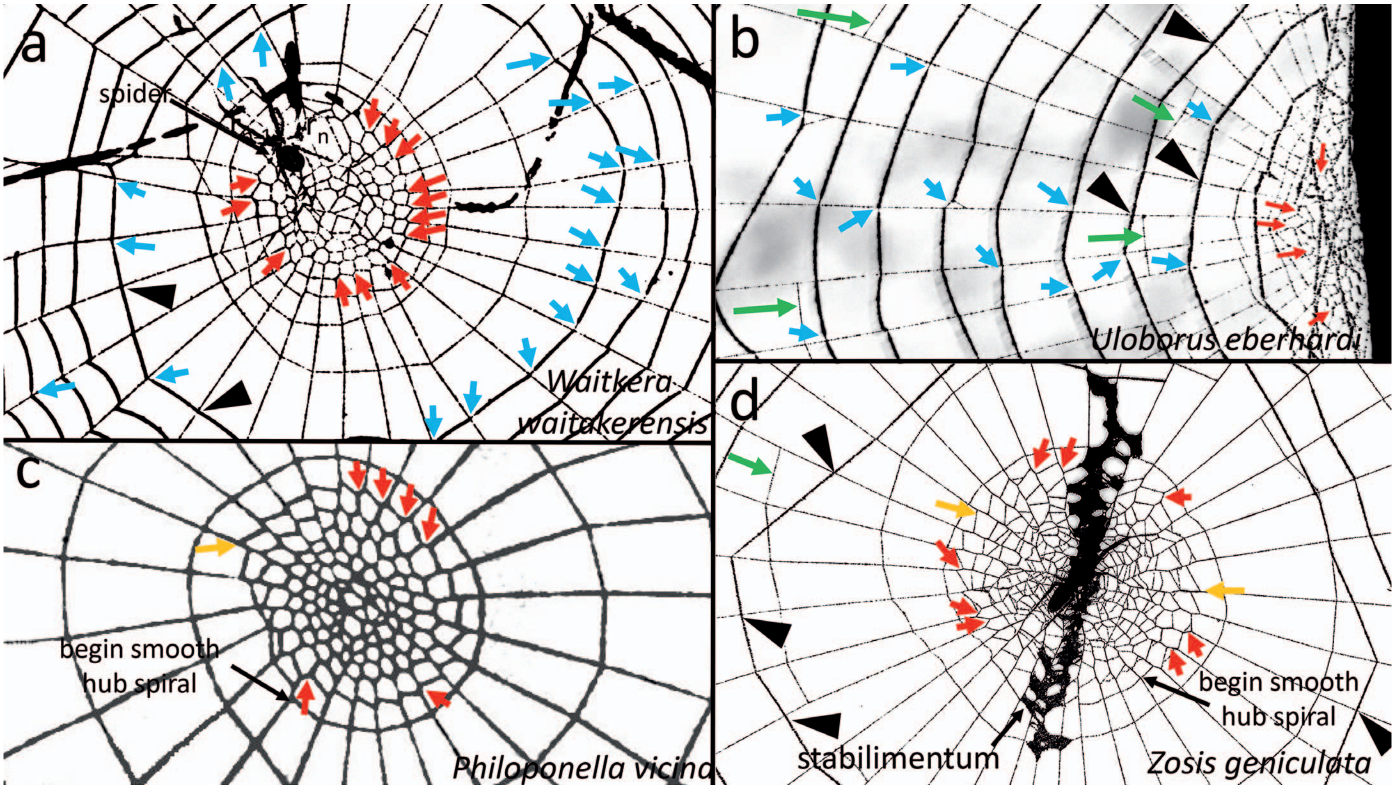

Figure 2.—These closeups of hubs of the uloborids *Waitkera waitakerensis* (a), *Uloborus eberhardi* (b), *Philoponella vicina* (c) and *Zosis geniculata* (d) illustrate several traits in Tables 1, 2. Blue arrows in *a* and *b* indicate the points where the width of the mat of cribellate fibrils in the sticky spiral "necked down," narrowing immediately following an attachment to a radius; black triangles indicate radii that lack this pattern because the sticky line skipped the radius without being attached to it. Other sites where the sticky spiral skipped over a radius without being attached to it were deduced from the lack of deflection of the sticky spiral in *a, b* and *d*. Intact segments of temporary spiral line (green arrows in *b* and *d*) were distinguished by being thinner than capture spiral lines in the photos (because of their smaller accumulations of powder). Sawtooth patterns of radii that were produced by double attachments of the hub spiral (red arrows in all four photos) occurred even in the partial hub of *U. eberhardi* that was built against a twig (*b*). The degree to which radii were deflected by the hub spiral varied greatly, even in the same web; in some junctions the hub spiral rather than the radius was deflected (orange arrows); in other junctions the radius was deflected (red arrows).

Simon, 1892, *Lehtineniana* Sherwood, 2022 (= *Tangaroa* Lehtinen 1967), *Uaitemuri* Santos & Gonzaga, 2017*, Uloborus* Latreille, 1806*, Waitkera* Opell, 1979*,* and *Zosis* Walckenaer, 1841 (Opell 1979, 1994; Lubin 1986; Peaslee & Peck 1983; Grismado 2004, 2008; Santos & Gonzaga 2017; Eberhard 2020). The other three genera (*Hyptiotes* Walckenaer, 1837*, Polenecia* Lehtinen, 1967*,* and *Miagrammopes* O. Pickard-Cambridge, 1870) build webs that are thought to be derived from orbs (Marples & Marples 1937; Opell 1982; Peters 1995; Lubin et al. 1978). Orb webs appear to be plesiomorphic for the entire family (Coddington 1990; Coddington & Levi 1991; Opell 1979, 1994). We also explore intra-specific variation in several genera, and document that some web traits appear to represent adjustments to the size of the available space in which to build the web. Finally, we make preliminary comparisons with the webs of the much larger group of orb-weaving spiders, Araneoidea.

METHODS

All new, previously unpublished data are from webs that were photographed after being coated with corn starch or talcum powder to make lines more easily visible. The numbers given for unidentified species refer to specimen labels in the collection of the Museum of Comparative Zoology at Harvard University. Because the traits discussed here concern relatively minor details that are seldom included in verbal descriptions of webs, we used only previous publications that included photographs of webs rather than using drawings or verbal descriptions; the only exceptions were verbal descriptions of the very distinctive primary webs (Szlep 1961), and the unusually detailed drawings of Wiehle (1927). The *Uloborus glomosus* (Walckenaer, 1841) webs built in captivity in Baton Rouge, LA were in plastic containers lined with black paper, including round containers from 14.0 to 16.0 cm diameter and square containers approximately 14 cm across. In contrast, the webs that this species built in captivity in Blacksburg, VA were on 30 × 22 cm or 34 × 22 cm rectangular wooden frames in larger containers.

We chose the 22 web traits listed in Tables 1 and 2 on the basis of traits mentioned in previous studies (Marples 1962; Lubin 1986) and our own preliminary impressions of uloborid web traits that may consistently differ from those of araneoids. We separated webs built in the field from those built in captivity to take into account that some traits are probably influenced by the space available to the spider in which to build. We did not include orbs that were replacement repairs

Table 1.—Traits visible in photographs of the webs of different species in the family Uloboridae (species of *Purimitra* Lehtinen, 1967 and *Lehtineniana* Sherwood, 2022 are also known to build orbs, but to our knowledge no photographs have been published). All new data are from webs photographed after being coated with white powder to make lines more visible. The numbers given for unidentified species refer to specimen labels in the collection of the Museum of Comparative Zoology at Harvard University. Numbers in parentheses indicate the sample sizes for different observations; % refers to the fraction of webs that had the trait indicated. All web design details from previously published accounts in this table were recorded from photographs rather than from the text of published accounts because these details are seldom mentioned in published texts. Therefore, the sample sizes for published studies are the numbers of published figures, rather than the sample sizes on which the authors based their accounts. "Y" = yes; "Y?" = probably yes; "N" = no; "N?" = probably no; "?" = no data are available; numbers in parentheses = number of webs in which trait was visible. See METHODS for detailed descriptions of these traits.

		1. Lack hub hole	2. Lack repair of hub hole	3. Double att. HS to radii	4. Radii sawtooth in hub	5. Intact temp. spiral	6. St. sp. beyond frame	7. St. sp. along frame	8. St. sp. zig-zag on radius
Conifaber guarani Grismado, 2004 (field)	Grismado 2004	?[1,2]	?[1,2]	Y[3] (1)	?[1,2]	Y (1)	N (1)	Y (1)	Y (1)
Conifaber parvus Opell, 1982 (field)	Lubin et al. 1982	?[4]	?[4]	?	N?[4] (1)	?[5]	-[6]	-[6]	-[6]
Conifaber yasi Grismado, 2004 (field)	Grismado 2008	?[1]	?	?	?[1]	?[1]	?[1]	?[1]	Y (1)
Hyptiotes affinis Bösenberg & Strand, 1906 (field)	Shinkai & Takano 1984	?[7]	?[7]	?[7]	?[7]	N (1)	N (1)	N (1)	Y (1)
Hyptiotes cavatus (Hentz, 1847)	Opell 1982; Comstock 1967; Witt et al. 1968; this study	No hub[7]	No hub[7]	No hub[7]	Y?[7] 40% (5)	N[7] 0% (32)	N 0% (32)	Y 6% (32)	Y 100% (32)
Hyptiotes gertschi Chamberlin & Ivie, 1935 (45 field, 10 captivity)	this study	?[7]	?[7]	?[7]	?[7]	N[7] 63% (55)	N 0% (55)	Y[8] 29% (52)	Y 100% (55)
Hyptiotes paradoxus (C. L. Koch, 1834) (field?)	Marples & Marples 1937	Y?[7] (1)	Y?[7] (1)	Y?[7] (1)	N?[7] (1)	N[7] (1)	N (1)	N (1)	Y (1)

Table 1.—Continued.

Miagrammopes animotus Chickering, 1968 (captivity)	Opell 2001	-[9]	-[9]	-[9]	-[9]	-[9]	-[9]	-[9]	-[9]
Miagrammopes simus Chamberlin & Ivie, 1936 (field)	Lubin et al. 1978	-[9]	-[9]	-[9]	-[9]	-[9]	-[9]	-[9]	-[9]
Lubinella morobensis Opell, 1984 (field)	Lubin 1986	Y? + (1)	?	?	?	?	?	?	?
Octonoba sinensis (= *octonaria*) (Simon, 1880) (field)[10]	Peaslee & Peck 1983; this study	Y 100% (21)	Y 100% (8)	Y 100% (21)	Y 100% (21)	Y 100% (21)	Y 10% (21)	Y 30% (20)	N 100% (20)
Octonoba (*Uloborus*) *sybotides* (Bösenberg & Strand, 1906) (field)	Shinkai & Takano 1984	?	?	?	?	?	?	?	?
Octonoba (*Uloborus*) *varians* (Bösenberg & Strand, 1906) (field)	Shinkai & Takano 1984	Y? (1)	?[2]	?[2]	?[2]	?[1]	?[1]	?[1]	?[1]
Philoponella divisa Opell, 1979 (field)	Opell 1979	Y (1)	Y? (1)	Y (1)	Y (1)	N (1)	N (1)	Y?[11] (1)	N (1)
Philoponella fasciata (Mello-Leitão, 1917) (field)	Grismado 2008	?	?	?	?	?	?	?	Y (1)
Philoponella oweni (Chamberlin, 1924) (captivity)	Eberhard 2020	Y (1)	?	Y (1)	Y (1)	N (1)	Y (1)	Y (1)	Y (1)
Philoponella quadrituberculata (Thorell, 1892) (field)	Murphy & Murphy 2000	?	?	?	?	?	?	Y? (1)	Y (1)
Philoponella republicana (Simon, 1891) (field)	this study	Y 100% (5)	?	Y 100% (3)	Y 100% (3)	?[1]	N (1)	?[1]	?[1]
Philoponella semiplumosa (=	Peters 1955, this study	?	?	?	?	?	?	?	?

Table 1.—Continued.

variegata) (Simon, 1893)[12] (field)									
Philoponella tingens (Chamberlin & Ivie, 1936) (field)	Opell 1979; Eberhard 2020	Y (2)	Y? (2)	Y (2)	Y (2)	?[13]	?[13]	?[13]	?[13]
Philoponella undulata (= *Uloborus undulata)* Thorell, 1878 (field)	Lubin 1986	N(?) (1)	?	?	?	?	?	?	?
Philoponella variabilis (Keyserling, 1887) (field)	Lubin 1986	Y (1)	?	?	?[1]	N[1] (1)	N?[1] (1)	Y?[1] (1)	Y (1)
Philoponella vicina (O. Pickard-Cambridge, 1899) (field)	this study	Y 100% (19)	Y 93% (16)	Y 100% (19)	Y 100% (19)	Y 25% (16)	Y 11% (18)	Y 42% (12)	Y 38% (16)
Philoponella vicina (captivity)	this study	Y 100% (31)	Y 100% (19)	Y 100% (31)	Y 100% (31)	Y 26% (31)	Y 41% (29)	Y 66% (29)	Y 23% (31)
Philoponella vittata (Keyserling, 1881) (field)	this study	Y 100% (7)	Y 100% (3)	Y 100% (8)	Y 100% (8)	Y 29% (7)	N 0% (4)	Y 67 (3)	Y 75% (4)
Philoponella Mello-Leitão, 1917 sp. nr. *emarginata* (field)	Lubin 1986	?	?	?	?	?	?	Y? (1)	N? (1)
Philoponella sp. G (field)	Lubin 1986	Y (1)	?	?	?	?[1]	?[1]	?[1]	?[1]
Philoponella (?) sp. Sta. Ana (captivity)	this study	Y (1)	?	Y (1)	Y (1)	Y 67% (3)	Y 100% (3)	Y 67% (3)	Y 100% (3)
Polenecia producta Simon, 1873 (field)	Wiehle 1931; Peters 1995	Y (1)	Y?[14] (1)	Y (1)	Y (1)	Y (1)	-[15]	Y (1)	Y[15] (1)
Purimitra Lehtinen, 1967 sp. (field)	F. Soley unpub.	Y (1)	?	?	?	?	?	?	?
Siratoba referens (Muma & Gertsch, 1964) (field)	this study	Y (1)	?[1]	Y (1)	Y (1)	?[1]	?[1]	?[1]	Y 33% (3)
Siratoba referens (captivity)	this study	Y 100% (7)	Y 100% (3)	Y 100% (9)	Y 100% (9)	Y 30% (10)	Y 40% (10)	Y 90% (10)	Y 90% (10)

Table 1.—Continued.

Sybota Simon, 1892 sp.[16] (field)	Grismado 2001; Dmitrov et al. 2016	Y (1)	N? (1)	Y (1)	Y (1)	N?[17] (1)	N (1)	Y (1)	Y[18] 50% (2)
Uaitemuri rupicola Santos & Gonzaga, 2017 (field)	Santos & Gonzaga 2017	Y (1)	?	?	?	N? (1)	?	Y (1)	Y[19] (1)
Uloborus barbipes L. Koch, 1872 (field)	Lubin 1986	Y (1)	?	Y (1)	Y (1)	?[1]	?[1]	?[1]	?[1]
Uloborus bispiralis Opell, 1982 (field)	Lubin et al, 1982	Y (1)	?	Y? (1)	Y? (1)	?	?	?	Y (1)
Uloborus conus Opell, 1982 (field)	Lubin 1986; Lubin et al. 1982	Y (1)	?	Y (1)	Y (1)	N 100% (2)	N 100% (2)	N 100% (2)	Y[20] 50% (2)
Uloborus diversus Marx, 1898 (captivity)	Eberhard 1972, 1977, this study	Y 100% (43)	Y 100% (13)	Y 100% (42)	Y 100% (42)	Y 91% (43)	Y 51% (43)	Y 88% (43)	Y 2% (43)
Uloborus eberhardi Opell, 1981 (field)	Eberhard 2020	Y (1)	?	Y (1)	Y (1)	Y (1)	N (1)	Y (1)	Y (1)
Uloborus glomosus (Walckenaer, 1841) (captivity, 14-16 cm)	this study captivity in Baton Rouge	Y 100% (65)	Y 94% (48)	Y 97% (69)	Y 100% 66)	Y 81% (78)	Y 14% (64)	Y 72% (67)	Y[21] 39% (71)
Uloborus glomosus (captivity, (30x22 or 34x22cm)	this study, captivity in Blacksburg	Y 100% (20)	Y 100% (17)	Y 100% (28)	Y 100% (28)	Y 100% (27)	Y 32% (28)	Y 74% (28)	Y 96% (28)
Uloborus glomosus (field)	Comstock 1967; this study, Baton Rouge	Y 100% (6)	Y 100% (4)	Y 100% (4)	Y 100% (4)	Y 50% (6)	Y 33% (6)	Y 67% (6)	Y 100% (5)
Uloborus plumipes Lucas, 1846 (captivity)	Wiehle 1928; Szlep 1961	Y[22] (1)	Y?[22] (1)	Y[22] (1)	Y[22] (1)	Y (1)	N (1)	?[1] (1)	?[1] (1)
Uloborus trilineatus Keyserling, 1883 (captivity)	this study	Y 100% (72)	Y 100% (72)	Y 100% (73)	Y 100% (73)	Y 97% (73)	Y 5% (73)	Y 43% (73)	Y 47% (73)
Uloborus trilineatus (field)	Coddington 1986; Lubin 1986; this study	Y 100% (6)	Y 100% (4)	Y 100% (6)	Y 100% (6)	Y 83% (6)	N 0% (6)	Y 33% (6)	Y 17% (6)

Table 1.—Continued.

Uloborus walckenaerius Latreille, 1806 (captivity)	Wiehle 1927; Szlep 1961; Zschokke & Vollrath 1995	Y?[23] (1)	?	Y (1)	?[23]	?	?	?	?
Uloborus Latreille, 1806 sp. J (field)	Lubin 1986	?[1] (1)	?	?	?[1]	Y (1)	N (1)	Y (1)	Y (1)
Uloborus sp. MB (field)	Lubin 1986	Y (1)	?	Y (1)	Y (1)	Y (1)	Y (1)	N (1)	Y (1)
Uloborus sp. nr. *eberhardi* (captivity)	this study	Y 100% (5)	Y 100% (4)	Y 100% (5)	Y 100% (5)	Y 100% (5)	Y 100% (5)	Y 100% (5)	Y 20% (5)
Uloborus sp. #242 (field)	Eberhard 1986	Y (1)	Y? (1)	Y (1)	Y (1)	Y (1)	N (1)	N (1)	N (1)
Uloborus sp. #2072 (field)	Lubin et al. 1982	Y (1)	Y? (1)	Y (1)	Y (1)	Y (1)	N[1] (1)	Y (1)	N (1)
Uloborus sp. (#1015) (field)	Eberhard 1977	Y (1)	Y?[24] (1)	Y (1)	Y (1)	?	?	?	?
Uloborus sp. South Africa (field)	Griswold et al. 2005	Y? (1)	?	?	?[1]	Y (1)	N (1)	?	Y (1)
Waitkera waitakerensis (Chamberlain, 1946) (field)	Opell 1999, this study	Y 100% (26)	Y 88%[25] (24)	Y 100% (27)	Y 100% (27)	Y 23% (27)	Y 26% (27)	Y 68%[26] (25)	Y 50% (26)
Zosis geniculata (Olivier, 1789) (captivity, 14 cm diam)	Eberhard & Barrantes 2015; this study	Y 100% (55)	?	Y 98% (51)	Y 98% (44)	Y[27] 31% (43)	Y 37% (43)	Y[28] 86% (43)	Y 7% (43)
Zosis geniculata (captivity, 50 cm diam)	Wiehle 1927; Eberhard & Barrantes 2015; this study	Y 100% (45)	?	Y 100% (42)	Y 100% (40)	Y[27] 73% (37)	Y 26% (35)	Y[28] 33% (36)	Y[29] 18% (38)
Zosis peruana (Keyserling, 1881) (field)	This study	Y 100% (5)	Y 100% (1)	Y 100% (5)	Y 100% (4)	Y 80% (5)	N 100% (5)	Y 40% (5)	Y 60% (5)

Table 1.—Continued.

[1] Photo provides only an incomplete view of the web or web too damaged to ascertain traits.
[2] Hub lines could not be deciphered because the hub was covered with a stabilimentum.
[3] The outer 2–3 hub loops have single attachments to radii, but a tiny portion of the inner part of the hub, which is otherwise obscured by a silk stabilimentum, has two loops of sawtooth hub spiral visible. The webs of recently emerged spiderlings are unknown.
[4] Inner hub loops could not be deciphered in the photograph; the outer loops did not have sawtooth patterns in the radii; there are other, "V" lines, that are vaguely similar to those of *W. waitakerensis*.
[5] Possible intact temporary spiral lines were not easily distinguished from lines in cone below the orb.
[6] No sticky spiral was visible in the web.
[7] The homologies of some lines attached to radii near the apex of the triangle web are uncertain. In the drawing by Marples and Marples (1937) of a *H. paradoxus* in the process of construction, there are 4 closely-spaced loops near the apex that they called "scaffolding" (temporary spiral) that were later removed by the spider (no details of this process were mentioned). The loops' tight spacing and their position near the apex suggest, however, a homology with the hub spiral rather than the temporary spiral. The outermost loop forms a weak sawtooth pattern in this drawing, suggesting double attachments to each radius, and thus the hub spiral. In direct observations of construction of one *H. cavatus* web (W. Eberhard, unpub.) there were two rather than four loops near the apex. The outer of these loops was attached doubly to one radius (also seen in one photo of a finished web of this species, and in the inner loop in another); as in *H. paradoxus*, the spiral line rather than the radius had a sawtooth form, at least when the web was finished. This suggestion of homology with hub rather than temporary spiral loops is not in accord, however, with the order of building in the two species (Marples & Marples 1937; W. Eberhard unpub.): the two loops were not made during radius construction (as are hub loops in other uloborids) but after radius construction was complete (as in the temporary spiral construction in other uloborids). A further detail that differs in both species from both hub and temporary spiral construction was that the spider returned to the apex of the web after making each loop. In sharp contrast with these observations, McCook's eight different figures illustrating the construction and webs of this same species, *H. cavatus,* show no sign of either hub or temporary spiral lines. He clearly watched the spiders carefully, but surely got some details wrong (he missed the fact that the spider breaks and reels the line so that its body forms a bridge between the two broken ends). Photos of finished webs of both *H. cavatus* and *H. gertschi* include small, slack lines near the apex (Fig. 20), suggesting McCook did miss details of lines near the apex. One new, subtle behavioral detail in *H. cavatus* (W. Eberhard, unpub.) that involved these loops does not homologize obviously with either hub or temporary spirals: after completing the sticky spiral, while the spider was returning to the apex of the triangular web, it broke the lowermost radius just on the "apex" side of the inner of the two spiral loops (it broke the line between the apex of the triangle and the inner loop of the hub/temporary spiral). The result was that the tension on the web lowered; and it also meant that the lowest radius in the finished web actually included a segment of the former inner loop of the hub/temporary spiral; the outer loop of hub/tsp remained intact in my sketch of these events. Neither hub or temporary spiral lines nor radii are broken following sticky spiral construction in other uloborids. Our entries for traits #1–4 in the species of *Hyptiotes* in the table are based on the assumption that loops near the apex corresponded to hub spiral lines. We emphasize that this homology is tentative, and that further observations are needed.
[8] Segments of sticky spiral on the frame line were short.
[9] Web was not organized as an orb.
[10] Free-ranging spiders were in a greenhouse.
[11] The sticky lines on frame lines may be due to damage after the web was complete.
[12] Spider was identified in the publication as *P. vicina*, but a handwritten note added by H. Peters to a reprint copy 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 identified by B. Opell as *P. variegatus* (see Fig. 16 of the present paper), and differs from the planar orb webs of specimens identified by B. Opell as *P. vicina.*
[13] The web is too damaged to ascertain this trait.
[14] The web is a highly modified orb, with the hub against a twig, so it was not possible to see lines where the center of the hub would be, or to even know whether such lines exist.
[15] All sticky lines were laid on non-sticky lines.
[16] It is not clear whether one or two species are represented. Different traits were visible in photographs in the two publications, so most sample sizes were only one.
[17] The extraneous non-sticky lines appear not to be temporary spiral lines; only one segment of sticky spiral probably skipped radii in the inner two loops of sticky spiral.
[18] The several small zig-zags near the edge might possibly have been produced by distortion of the web, though the positions of other nearby lines suggest not.
[19] Egg sac webs also had sticky lines that zig-zagged on radially oriented lines.
[20] Sticky lines ran for short distances along radii both in the orb and in the cone below.
[21] In two photos perhaps taken in the field (Comstock 1967) there are no zig-zags in the sticky spiral; but zig-zags were frequent and sometimes very common in webs in captivity (Fig. 5); and they also occurred on radial lines associated with egg sacs (Eberhard 2020).
[22] This characterization is based on the drawing of Wiehle 1928, which is detailed and clearly depicts sawtooth patterns.
[23] There are two small holes in hub in the photo of Wiehle 1927, and the larger is not at the center of the hub, thus suggesting damage rather than hub removal by the spider. This damage presumably reduced the tensions on radii, so the sawtoothed pattern might be an artifact caused by the damage.
[24] The center of the hub of a primary web of a mature male had clearly not been removed.
[25] While there was clearly no sign of a scar in these hubs, at least five others had patterns very similar to scars, so there is uncertainty in this trait.
[26] Numbers of webs with sticky lines along frame lines may be underestimated due to lack of consistent differences in the thickness of sticky and non-sticky lines in the photographs.
[27] The difference between spiders in large and small containers is significant, $Chi^2 = 14.6$, $p < 0.001$.
[28] The difference between spiders in large and small containers is significant, $Chi^2 = 23.0$, $p < 0.001$.
[29] In contrast with *U. glomosus* (footnote 22), no zig-zags occurred in sticky lines in egg sac webs ($N = 5$) (Eberhard 2020).

Table 2.—All literature references are the same as in Table 1. All previously unpublished data are from webs photographed after being coated with white powder to make lines more visible. The numbers given for unidentified species refer to specimen labels in the collection of the Museum of Comparative Zoology at Harvard University. Numbers in parentheses indicate the sample sizes for different observations; % refers to the fraction of webs that had the trait indicated. All of the web design details from previously published accounts in this table were recorded from photographs rather than from the text of published accounts, because these details are seldom mentioned in published texts. Therefore, the sample sizes for published studies are the numbers of published figures, rather than the sample sizes on which the authors based their accounts. For trait #12, the results of statistical tests of the hypothesis that "BOTH" was more common than expected by chance (assuming a 1/9 ratio – see text) are indicated as follows: * = $p<0.05$; ** = $p<0.01$; *** = $p<<0.0001$. The letters for trait #17 (primary webs) indicate the following: N1 = nymph 1 recently emerged from egg sac; J = older nymph; M = mature male; F = normal adult female; S = senile adult female. When more than one developmental stage built primary webs and information is available for the different stages, traits #18 to #22 of the webs are listed separately for each stage in this same order. Mean ratio of number of loops of sticky spiral/number of radii and mean numbers of loops and radii are followed by ± one standard deviation when sample >2 webs. "Y" = yes; "Y?" = probably yes; "N" = no; "N?" = probably no; "?" = no data are available; numbers in parentheses = number of webs in which trait was visible. See METHODS for detailed descriptions of these traits.

	9. St. sp. skips radii	10. Silk stab.	11. Stab: Line-Circle-Disc	12. Radii curve: Both-One-Neither	13. Tert. radii	14. Sec. frame	15. Max. num loops stsp/ num radii	16. Mean num stsp loops; Mean num radii	17. P. web Life stage	18. P. web Hub repl.	19. P. web Line Beyond frame	20. P. web lines non-radial	21. P. web Space tsp	22. P. web stab.
Conifaber guarani (field)	?	Y (1)	?	?	N (1)	Y (1)	0.3 (1)	12; 40 (1)	M	?[1]	?[1]	Y	?[1]	?[1]
Conifaber parvus (field)	-[2]	Y (1)	1-0-0	?	?	?	?	-	F	Y	?[1]	Y	?[1]	Y, N
Conifaber yasi (field)	?[2]	?	-	?	?	?	?	?	?	?	?	?	?	?
Hyptiotes affinis (field)	N (1)	N (1)	-	N (1)	N (1)	N (1)	3.8 (1)	15; 4 (1)	?	-	-	-	-	-
Hyptiotes cavatus	N 0% (32)	N 0% (32)	-	-	N 0% (32)	N 0% (32)	4.0±0.9 (31)	15.8; 4.0 (31)	none	-	-	-	-	-
Hyptiotes gertschi	N 0% (55)	N 0% (55)	-	-	N 0% (55)	N 0% (55)	2.9±0.8 (1)	11.1; 4.0 (1)	?	-	-	-	-	-
Hyptiotes paradoxus (field?)	N (1)	N (1)	-	N (1)	N (1)	N (1)	2.2 (1)	9; 4 (1)	?	-	-	-	-	-
Miagrammopes animotus	-[3]	N (1)	-	-[3]	-[3]	-[3]	-[3]	-[3]	none	-	-	-	-	-
Miagrammopes simus (field)	-[3]	N (1)	-	-[3]	-[3]	-[3]	-[3]	-[3]	none	-	-	-	-	-

Table 2.—Continued.

Lubinella morobensis (field)	?	Y (1)	0-1-0	?	?	?	?	?	?	?	?	?	?	?
Octonoba sinensis (= *octonaria*) (field)[4]	Y 100% (20)	Y 90% (21)	17-2-2	33-16-10 ***	Y 57% (21)	Y 25% (20)	0.45±0.11 (19)	21.8±5.6; 49.0±6.9 (19)	N1	?	?	?	?	?
Octonoba (*Uloborus*) *sybotides* (field)	?	Y (1)	1-0-0	?	?	?	?	?	?	?	?	?	?	?
Octonoba (*Uloborus*) *varians* (field)	?[1]	Y (1)	0-1-0	?	?	?	?	?	?	?	?	?	?	?
Philoponella divisa (field)	Y? (1)	N (1)	-	1-0-0	N (1)	?	1.0 (1)	22; 22 (1)	?	?	?	?	?	?
Philoponella fasciata (field)	?	N (1)	-	?	?	?	?	?	?	?	?	?	?	?
Philoponella oweni[5] (captivity)	Y? (1)	Y (1)	1-0-0	0-1-2	N (1)	Y (1)	0.68 (1)	21; 31 (1)	?	?	?	?	?	?
Philoponella quadrituberculata (field)	?	N (1)	?	?	?	?	0.4 (1)[6]	14; 35 (1)	?	?	?	?	?	?
Philoponella republicana (field)	?[1]	N (1)	-	?	?	?	?	?	?	?	?	?	?	?
Philoponella semiplumosa (= *variegata*) (field)[7]	?	Y (1)	1[7]-0-0	?	?	?	?	?	N1	Prob[7]	?[1]	?[1]	?[1]	N
Philoponella tingens (field)	?[8]	N 0% (6)	-	1-6-2	Y 40% (5)	N (3)	0.87±0.30 (4)	22.2±6.7; 26.2±4.8 (4)	M	Y	N	Y	loose	N
Philoponella undulata (field)	?	Y 50% (2)	1-0-0	?	?	?	0.54 (1)	14; 26 (1)	?	?	?	?	?	?
Philoponella variabilis (field)	?	N (1)	-	0-1-1	N (1)	Y (1)	0.87 (1)	26; 30 (1)	?	?	?	?	?	?
Philoponella vicina (field)	Y 56% (16)	Y 71% (17)	11-0-2	?	Y 11% (9)	Y 75% (4)	0.70±0.18 (14)	16.2±4.8; 23.2±2.6 (14)	N1	?	?	?	?	?
Philoponella vicina (captivity)	Y 45% (31)	Y 93% (28)	21-2-7	21-25-22 **	Y 12% (25)	Y 20% (25)	0.63±0.18 (29)	15.7±5.2; 24.6±4.3 (29)	?	?	?	?	?	?

Table 2.—Continued.

Philoponella vittata (field)	Y 80% (5)	N 0% (6)	-	0-1-1	Y 25% (4)	Y 33% (3)	0.70±0.21 (9)	24.3±9.0; 34.6±4.8 (9)	?	?	?	?	?	?
Philoponella sp. nr. *emarginata* (field)	?[1]	N (1)	-	?	?	?	?	?	?	?	?	?	?	?
Philoponella sp. G *(field)*	Y (1)	Y 100% (2)	0-2-0	?	?	?	?	?	all sizes[9]	Y[9]	?	Y?[9]	?	N
Philoponella(?) sp. Sta Ana (captivity)	Y 100% (3)	Y 50% (2)	0-0-1	0-2-1	N (1)	Y (1)	0.56 (1)	20; 36 (1)	?	?	?	?	?	?
Polenecia producta (field)	N[10] (1)	Y[10] (1)	0-0-1	0-0-1	N (1)	N (1)	-	-	none[11] (1)					
Purimitra sp. (field)	?	Y (1)	0-1-0	?	?	?	?	?	?	?	?	?	?	?
Siratoba referens (field)	N (1)	Y 100% (6)	6-0-2	?	?	?	0.38 (2)	16; 42 (2)	?	?	?	?	?	?
Siratoba referens (captivity)	Y 62% (8)	Y 100% (10)	9-1-2	14-10-6	N (9)	N (9)	0.52±0.08 (9)	19.8±4.6; 38.1±7.7 (9)	?	?	?	?	?	?
Sybota sp.[12] (field)	Y(?)[13] (1)	N (2)	-	?	Y (1)	?	0.5 (1)	14; 28 (1)	?	?	?	?	?	?
Uaitemuri rupicola (field)	?	N (1)	-	?	?	?	0.71 (1)	10; 14 (1)	?	?	?	?	?	?
Uloborus barbipes (field)	Y (1)	N (1)	-	?	?	?	?	?	?	?	?	?	?	?
Uloborus bispiralis (field)	?	?	?	?	?	?	0.52 (1)	21; 49[1] (1)	?	?	?	?	?	?
Uloborus conus (field)	Y[14]	N (1)	-	?	?	?	0.26 (1)	9; 34 (1)	?	?	?	?	?	?
Uloborus diversus (captivity)	Y 100% (43)	Y 84% (26)	24-4-0	33-29-13 ***	Y 6% (31)	Y 42% (31)	0.63±0.10 (30)	24.5±5.5; 38.1±5.8 (30)	N1/ S[15]	Y/ N	Y/N	Y? Y	Very tight/?	N/N
Uloborus eberhardi (field)	Y (1)	N (1)	-	0-2-2	Y 50% (2)	N 0% (2)	0.96 (2)	21.5; 22.5 (2)	?	?	?	?	?	?

Table 2.—Continued.

Uloborus glomosus (captivity, 14-16 cm)	Y 99% (69)	Y 51% (55)	26-1-1	49-42-19 ***	Y 12% (48)	Y 26% (47)	0.43±0.15 (53)	15.4±5.7; 36.1±8.9 (53)	S	Y, N	N	Y	loose	Y, N
Uloborus glomosus (captivity, (30x22 or 34x22cm)	Y 100% (28)	Y 56% (27)	15-0-0	43-17-16 ***	Y 8% (26)	Y 23% (26)	0.46±0.15 (27)	14.9±4.3; 33.3±7.3 (27)						
Uloborus glomosus (field)	Y 100% (5)	Y 40% (5)	2-0-0	2-4-3	Y 14% (7)	Y 14% (7)	0.54±0.13 (5)	17.2±4.7 32.5±9.6 (5)	-	-	-	-	-	-
Uloborus plumipes (captivity)	Y (1)	N (1)	-	1-0-1	?	?	?	?	N1/ J	Y, N/Y	Y/?[1]	Y/?[1]	tight/ tight	N/N
Uloborus trilineatus (captivity)	Y 100% (79)	N (63)	-	157-16-5 ***	Y 37% (62)	Y 15% (62)	0.43±0.13 (57)	20.6±6.5; 47.2±6.6 (57)	N1/J/M/ S	Y/N/Y/N	N/Few/N/N	Y/Y/Y/Y	loose/?[6]/ loose/ loose	N/N/N/N
Uloborus trilineatus (field)		N (5)	-	13-1-1 ***	Y 20% (5)	Y 40% (5)	0.64 (5)	27.6±4.8; 43.6±3.4 (5)	?	?	?	?	?	?
Uloborus walckenaerius (captivity)	?	Y 100% (10)	10-0-0	?	?	?	0.43 (1)	16; 37 (1)	N1	N	?[1]	Y	tight	Y
Uloborus sp. J (field)	Y (1)	N (1)	-	?	N (1)	?	0.54 (1)	19; 35 (1)	?	?	?	?	?	?
Uloborus sp. MB (field)	Y (1)	Y[15] 50% (2)	1-0-0	?	?	?	0.33 (1)	7; 21 (1)	?	?	?	?	?	?
Uloborus sp. nr. *eberhardi* (captivity)	Y 100% (5)	Y 60% (5)	3-0-0	7-5-2 *	N (5)	Y 40% (5)	0.55 (5)	28.0±7.6; 51.8±4.5 (5)	N1	Y, N	some	Y	tight	N
Uloborus sp. #242 (field)	Y (1)	N (1)	-	3-0-0	N (1)	N (1)	0.51 (1)	26; 51 (1)	?	?	?	?	?	?
Uloborus sp. #2072 (field)	Y (1)	N (1)	-	?	?	?	0.77 (1)	33; 43 (1)	?	?	?	?	?	?
Uloborus sp. (#1015) (field)		N (1)	-	?	?	?	?	?	M	Y	some	Y	?[1]	N
Uloborus sp. South Africa (field)	Y? (1)	Y (1)	1-0-0	0-1-1	N (1)	N (1)	0.74 (1)	35; 47 (1)	?	?	?	?	?	?
Waitkera waitakerensis (field)	Y 75% (24)	N (27)	-	22-32-23 **	Y 4% (26)	Y 70% (27)	0.49±0.11 (25)	13.0±3.3; 26.8±4.9 (25)	?	?	?	?	?	?

Table 2.—Continued.

Zosis geniculata (captivity, 14 cm diam)	Y 100% (43)	Y 100% (52)	39-24-46	25-39-67	Y 6% (50)	Y 8% (49)	0.54±0.23 (47)	12.7±6.1; 23.2±5.1 (47)	N1	Y, N	?[1]	Y	loose	Y
Zosis geniculata (captivity, 50 cm diam)	Y 100% (37)	Y 98% (41)	24-26-39	57-31-18 ***	Y 13% (39)	Y 13% (39)	0.58±0.13 (39)	20.8±6.5; 36.0±6.9 (39)						
Zosis peruana (field)	Y 100% (5)	Y 100% (4)	1-3-0	7-3-2 *	Y 50% (4)	N (4)	0.35±0.08 (5)	15.2±6.6; 43.8±14.1 (5)	M	N	N	Y	tight	Y

[1] This detail could not be resolved in the photos.
[2] No sticky spiral was visible in the web.
[3] The web was not organized as an orb.
[4] Spiders ranged freely in a grain elevator. No web photographs were presented, but the text specifically mentions the distinctive "primary webs" described by Szlep 1961.
[5] Also builds 3-D tangles with sticky silk.
[6] Temporary spiral had been removed, and only the sticky spiral (with normal spacing) was present.
[7] 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. Spider is identified in the publication as *P. vicina*, but a handwritten note added by H. Peters to a reprint copy of the 1955 paper changed the name to *variegata*. The photo of the domed web of the species he observed (his Fig. 13) is similar to the orbs associated with specimens identified by B. Opell as *P. variegata* (see *P. semiplumosa* in Fig. 13 of the present paper) and differs from the planar orb webs of specimens identified by B. Opell as *P. vicina*.
[8] Web was too damaged to ascertain this trait.
[9] at least a few non-radial lines were visible in a mature male primary web; Lubin (1982) mentions that spiders "of all sizes", including mature females and mature males occurred on primary webs; hub replacement was documented only in two mature males.
[10] Only a tiny patch of silk where spider's leg held the web.
[11] "Instar I" of Peters (1995) lacked a cribellum and calamistrum, and remained inside the egg sac and did not build a web. "Instar II" had a functional cribellum and calimistra, and built a typical prey capture web. Thus at least early instars did not build primary webs.
[12] The extraneous non-sticky lines appear not to be temporary spiral lines; only one segment of sticky spiral probably skipped radii in the inner two loops of sticky spiral.
[13] The several small zig-zags near the edge might possibly have been produced by distortion of the web, though the positions of other nearby lines suggest not.
[14] The sticky spiral skipped some radii in the cone below the orb.
[15] Senile web patterns appeared gradually over the space of days and weeks, and were associated with females presumed to be virgins because they did not lay eggs. The web traits given here represent extreme cases. Both sticky and non-sticky lines were present in some orbs, but it is not possible to distinguish whether the spiral lines in the published photo were sticky or not.

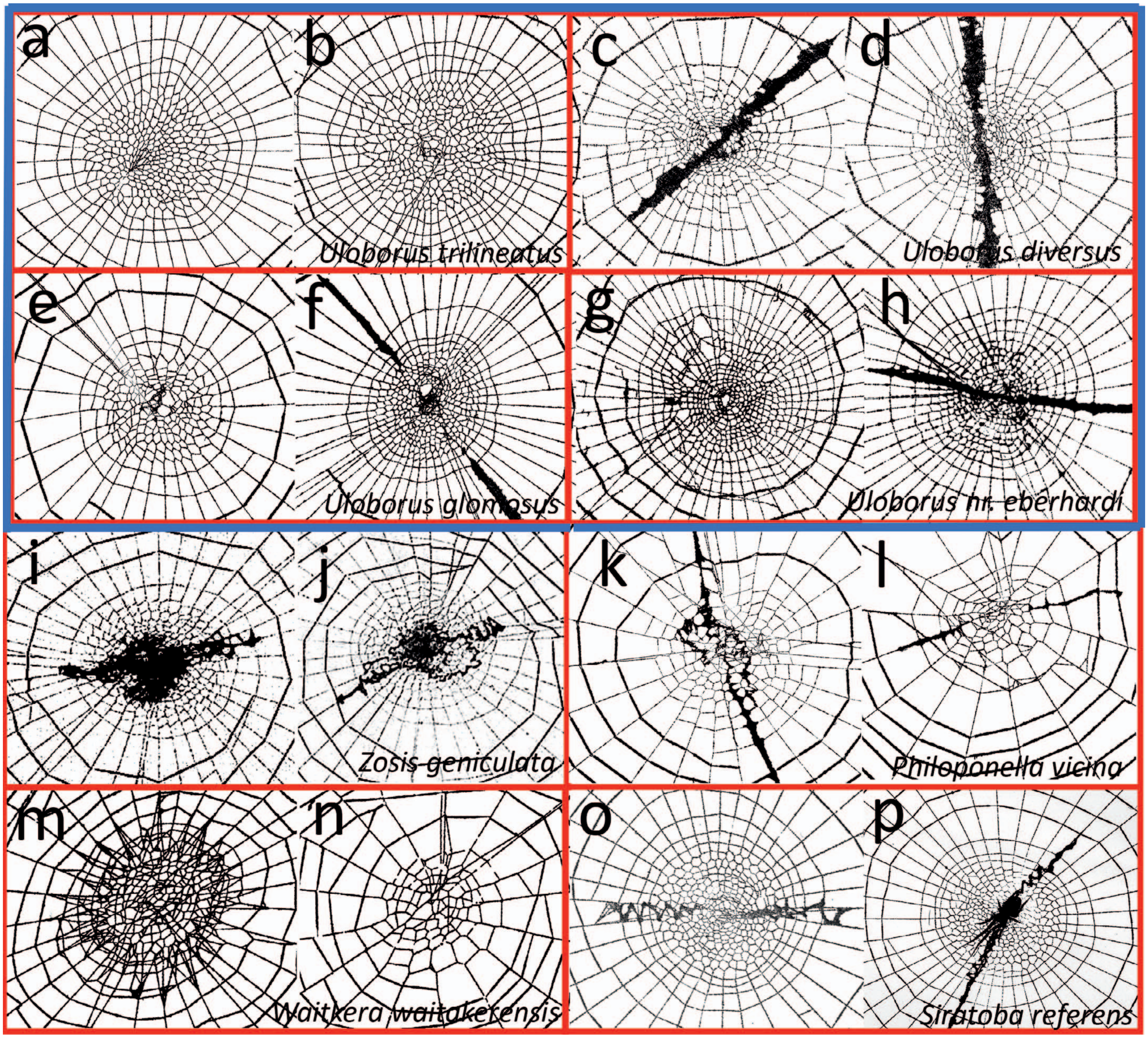

Figure 3.—This sampler shows a pair of typical hubs in each of 8 species in 4 uloborid genera, allowing side-by-side comparisons that illustrate both intra- and inter-specific uniformity and variation. The red lines enclose species, and the blue lines enclose species in the genus *Uloborus*. All of the species show hub traits #1–4 in Table 1: lack of a central hole; lack of a repair scar; double attachments of hub spiral to radii in the central portion of the hub; and sawtooth radii pulled out of line by hub spiral lines.

of previous orbs, or orbs built alongside egg sacs (Eberhard 2020). The traits of finished webs and the criteria that we used to distinguish them were the following:

1. *No central hub hole*. The central-most portion of the hub had no open space more than about 10% the diameter of the hub (e.g., Figs. 1–3); there was thus no central open space such as that in Fig. 4*d*, *f*. Small or off-center openings like those in Figs. 3*e*, *f*, *l*, 5*d*, 6*b* were not counted as central hub holes (some of these holes may have been due to damage). This trait corresponds to "hub not open" of Kuntner et al. 2008.
2. *No scar of a previous central hub hole*. Behavioral observations have shown that many araneoid orb weavers remove the lines at the center of the hub but then immediately fill in the hole with other lines; such behavior (which might function to reduce web tensions and then strengthen the web) did not occur in the few uloborids that have been observed (Eberhard 1982, 1987, 2020). We evaluated photographs of uloborid webs for whether such removal and subsequent replacement had occurred by checking for the borders of the hole that remain in the finished hub after the hole is filled in. We traced the radii inward toward the center of the hub: the border of the

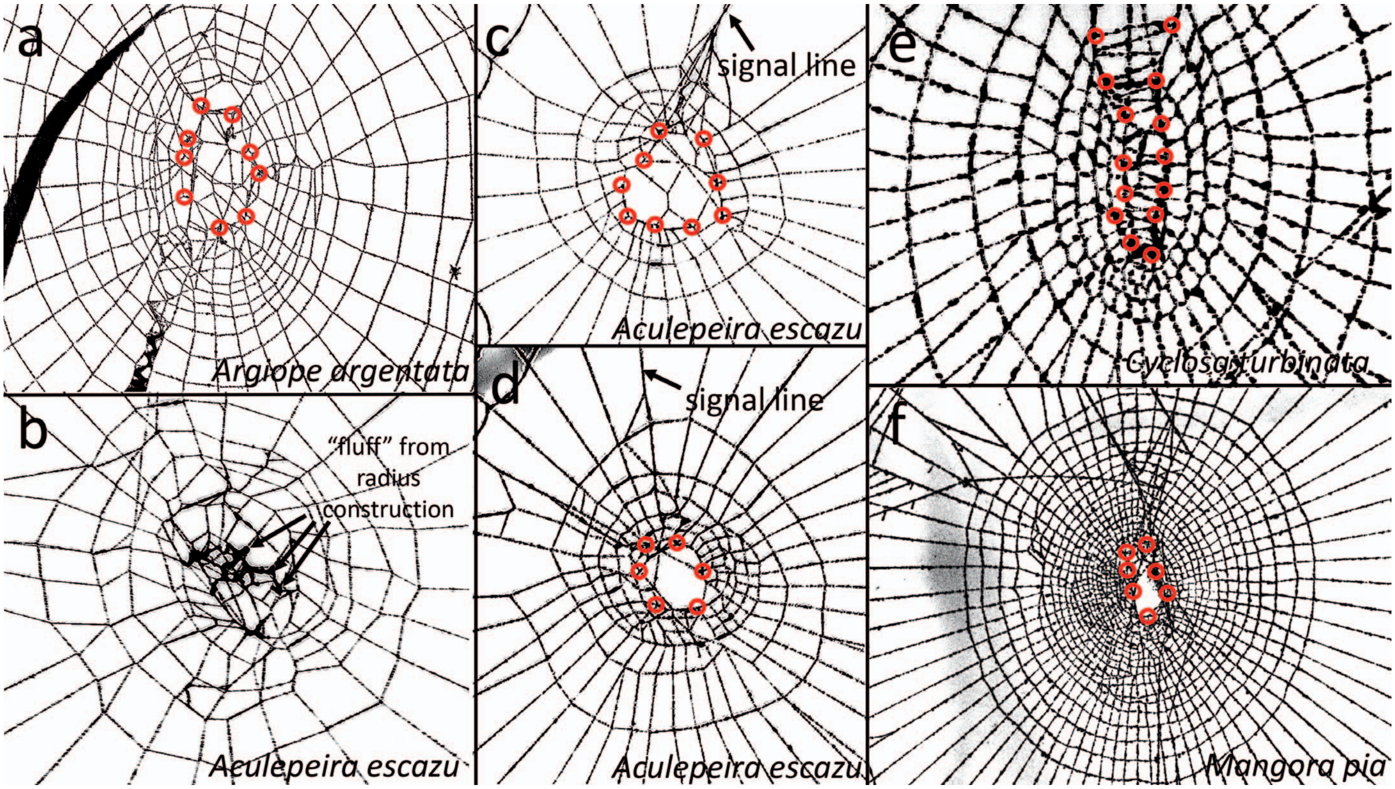

Figure 4.—Closeup views of the hubs of several species of araneids, including *Argiope argentata* (*a*), *Aculepeira escazu* (*b–d*), *Cyclosa turbinata* (*e*), and *Mangora pia* (*f*) that illustrate variations in the types of "scars" left when the spider removed the center of the hub following sticky spiral construction and then filled in the hole with additional lines (the red circles mark the margins of the hole). Fill-in lines vary in density and the degrees of organization: lack of apparent order in *a*; clear zig-zag patterns in *e*; denser in *a* and *e* and more sparse in *c* and *d*. Intra-specific variation in *A. escazu* (*b–d*) ranged from no hub removal (*b*) to removal and minimal replacement (*d*) (photos are to different scales). Most of the radii in the *C. turbinata* web (*e*) were pulled into sawtooth configurations by hub spiral attachments in the inner portion of the hub (trait #4 in Table 1); in other webs of this same species, however, radii in the hub were straight.

hole (if there was one) can be deduced using the points where the radii end (Fig. 4*a*, *c–e*). Lack of a scar was indicated when the radii could be traced all the way to the central area of the hub (e.g., Figs. 2*c*, *d*, 3), and when there was no clearly recognizable area in the hub's center that was filled with non-radial lines (Fig. 4*a*, *c*, *e*). This trait corresponds to "hub bite out absent" of Kuntner et al. (2008).

3. *Double attachments of hub spiral to radii*. The hub spiral was attached at two places to each radius that it crossed, producing a sawtooth pattern in the hub spiral line (red and orange arrows in Fig. 2).
4. *Sawtooth pattern in radii due to hub attachments*. The radii were pulled into sawtooth profiles by the double attachments of the hub spiral (red arrows in Fig. 2).
5. *Intact segments of temporary spiral*. Segments of the non-sticky temporary spiral were intact (dark green arrows in Figs. 1, 7*d*, *e*) (temporary spiral lines were distinguished from sticky spiral lines by having smaller diameters in the photos due to their carrying smaller amounts of white powder; this difference was also used to distinguish sticky lines from frame lines in traits 6 and 7).
6. *Sticky spiral lines beyond frame lines*. A portion of the sticky spiral was beyond the frame line at the outer edge of the orb (Figs. 7*e* 8*a*).
7. *Sticky spiral lines on frame lines*. Portions of the sticky spiral ran along a frame line, as in Figs. 5*b*, 7*d*, *e*, 8*a*. This pattern is probably associated with the unusual behavior seen in *U. walckenaerius* Latreille, 1806 of walking along the frame line during sticky spiral construction (Zschokke & Vollrath 1995), a behavior not seen in several araneids (we may have underestimated the frequency of this trait in *Waitkera waitakerensis* (Chamberlin, 1946) because sticky and non-sticky lines were difficult to distinguish in some photos). In no case was the sticky line coiled or looped, as in some dictynids (Eberhard 2021); it was always straight along the frame line.
8. *Zig-zag sticky spiral*. Segments of the sticky spiral ran along radii for short distances, producing a zig-zag pattern of the sticky spiral (Figs. 5*b*, *c*, 8*a*). When these patterns occurred, they were always in the outer portions of orbs. In webs in which it was possible to trace the spider's path, the spider always moved inward rather than outward along the radius as it laid a zig-zag sticky spiral. In no case was the sticky line coiled or looped – it was always straight along the radius.
9. S*ticky spiral skips radii*. Segments of the sticky spiral crossed some radii without being attached to them in the inner portion of the orb. The attachment of the sticky spiral line to a radius could be distinguished in some

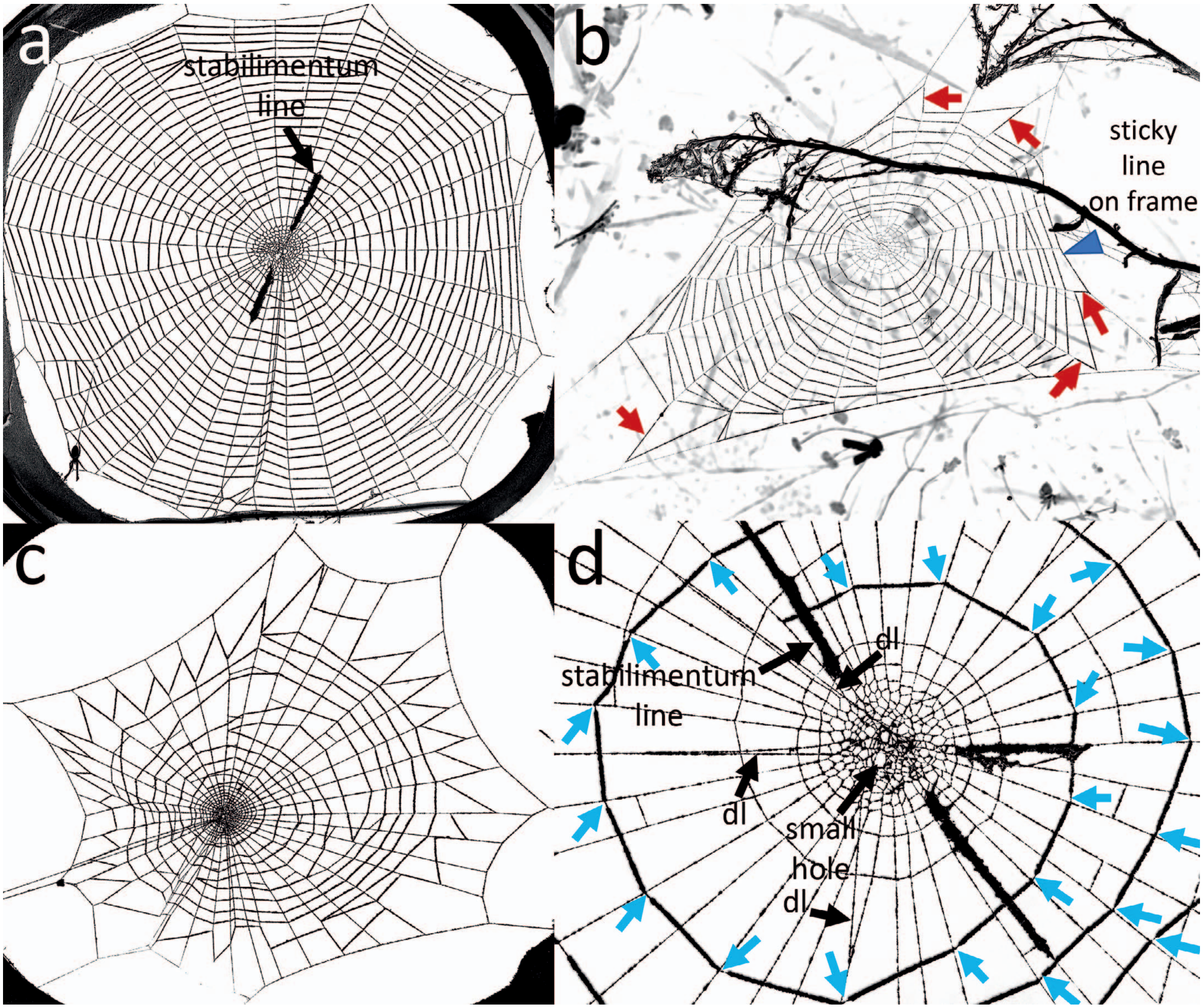

Figure 5.—Variation in *Uloborus glomosus* webs in captivity (*a, c, d*) and the field (*b*). Field webs often had one or a few sticky spiral zig-zags (dark red arrows in *b*). The large majority of webs in captivity lacked any zig-zag sticky spiral lines (*a*), but occasional webs had zig-zag sticky lines on nearly all the radii (*c*). The closeup of the hub of a web in captivity (*d*) illustrates several traits: small non-centric holes in the hub that were not counted as hub center removal (trait #1 in Table 1); smooth-sided thick stabilimentum lines (similar to that in *a*; contrast these with the serrated sides of stabilimentum lines of *U. diversus*, *Philoponella vicina* and *Siratoba referens* in Fig. 3); and drag lines ("dl") that formed "false V" patterns at the edge of the hub superficially similar to the "V" patterns in some *Waitkera waitakerensis* hubs (Fig. 3*m*). The blue arrows in *d* indicate sites where sticky spiral lines necked down just after attachments to radii; the spider thus moved in a counter-clockwise direction while building these inner loops of sticky spiral, and only attached the capture thread to some of the radii that it crossed (trait #9 in Table 2).

close-up photos by the reduction in the width of the mat of cribellate fibrils ("necking down" immediately following the attachment); lack of an attachment to a radius was indicated by a lack of necking down where the sticky line crossed the radius (Figs. 2*a*, *b*, 5*d*, 10*d*) (Peters 1995; Eberhard 2019, 2020). In photos with lower magnifications changes in the width of the sticky line could not be distinguished, and we resorted to the less reliable criterion of sticky spiral lines that passed straight over some radii with no deflection where they crossed the radii.

10. *Silk stabilimentum*. Bands or discs of highly visible white silk were present on hub lines, radii near the hub (Fig. 3*c*, *d*, *h–l*, o, *p*), or lines below the hub (Fig. 7*c*).
11. *Stabilimentum pattern*. We distinguished three stabilimentum patterns: lines along one or two radii (often two lines, usually one on either side of an uncovered, central portion of the hub where the spider rested); non-radial white lines that resembled circles or spirals that were sometimes relatively smooth but more often serrate (Fig. 9*b*); and more-or-less circular discs at the center of the hub, often of less intensely white silk (Figs. 3*i*, *j*, 8*b*). Some

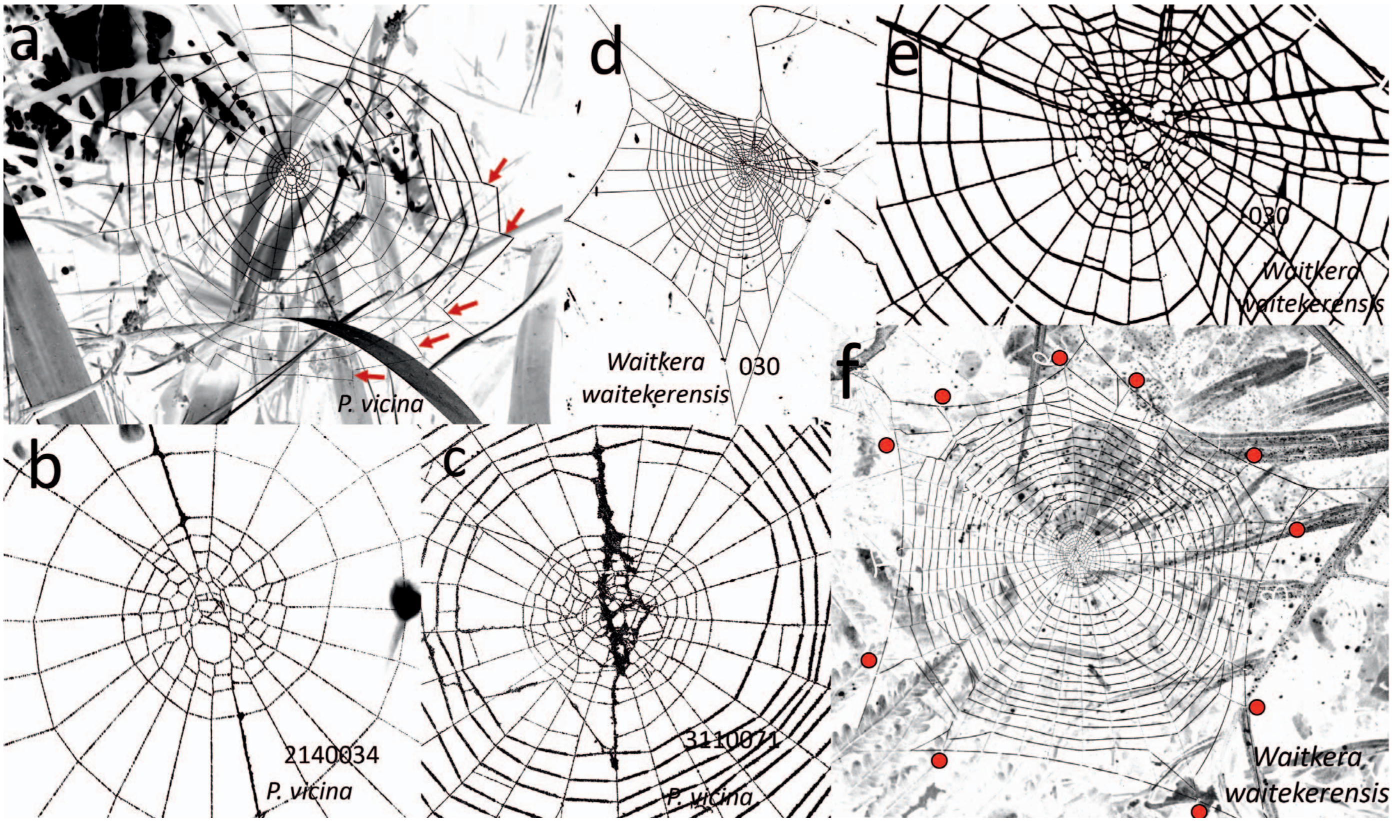

Figure 6.—These webs illustrate occasional uncertainties concerning hub removal in *Philoponella vicina* (*a*; enlarged view of hub in *b*) (zig-zag sticky spiral patterns are indicated with dark red arrows in *a*), and possible scars from filling in hub holes in *P. vicina* (*c*) and *Waitkera waitakerensis* (*d–f*). The hole in the hub in *a* and *b* was not counted as hub removal, despite its relatively large size compared with the open spaces in other *P. vicina* hubs (*c*, Fig. 3*k, l*), because it was slightly to one side of the center where lines were abundant. The lines in the central portion of the hub in *c* were arranged more irregularly than was typical in many other hubs of this species (Figs. 3*k, l*), giving the impression that the spider may have removed the center and then filled it in. The hub of one *W. waitakerensis* web (*d*; enlarged view in *e*) gives a similar impression (compare with *f*, Fig. 3*m, n*). Both webs were counted as "?"; direct observations of building behavior may be needed to verify whether the center of the hub is occasionally removed and then replaced in these species. The web in *f* illustrates how occasionally pairs of radii curved toward adjacent anchor lines (red dots) even in a species in which this pattern was rare (Table 2).

stabilimentum lines were smooth-sided, as in Fig. 5*a*, *d* of *U. glomosus*, but most had serrated outlines as in Fig. 3*c, d*, *i–l*, *o*, *p*) (see also Cushing & Opell 1990).

12. *Both radii adjacent to an anchor curved toward the anchor*. We chose three pairs of the radii that were among the longest in the web and that had an anchor line between them (regardless of the angles between them), and classified them into one of three categories: (*a*) both radii curved toward the anchor ("DOUBLE CURVE" in Fig. 11, "BOTH" in Table 2; see Figs. 1, 6*f*, 8*c*, 10*a*); (*b*) only one of two curved toward the anchor ("ONE" in Fig. 11); or (*c*) neither radius curved toward the anchor ("NEITHER" in Fig. 11). On the basis of the nine possible combinations of pairs of curved and straight radii (Fig. 11), we calculated expected values for *a, b*, and *c* as, respectively, 1/9, 4/9 and 4/9 of the total observations for each species. Because these calculations assumed equal frequencies for straight and curved radii even though straight radii were more common, they underestimated the expected frequency of pattern *a* (the trend that was being evaluated). Pairs of radii with nearby web damage or with nearby draglines were not counted, so fewer than three pairs of radii were counted in some webs. Observations of the construction behavior of *U. diversus* Marx, 1898 showed that double curves in radii are generally produced during temporary spiral construction, when especially widely separated radii were pulled toward each other. The displacements persisted when the spider subsequently removed the temporary spiral because the sticky spiral she had built continued to pull the radii toward each other (Eberhard 1972).
13. *Tertiary radii*. At least one radius originated away from the hub (Fig. 10*a*), at a junction between the temporary spiral and another radius (primary and secondary radii originate in the hub – Eberhard 2020).
14. *Secondary frames*. At least one frame line (a line to which the outer end of at least one radius was attached) spanned a corner between two other (larger) frame lines (Fig. 9*a*).
15. *Counts of maximum numbers of sticky spiral loops and numbers of radii*. We counted the maximum number of loops of sticky spiral that crossed any radius in the orb, and all radii except tertiary radii; we avoided counting draglines laid when spiders moved between the hub and the edge of the web (Fig. 1*a*, *b*).

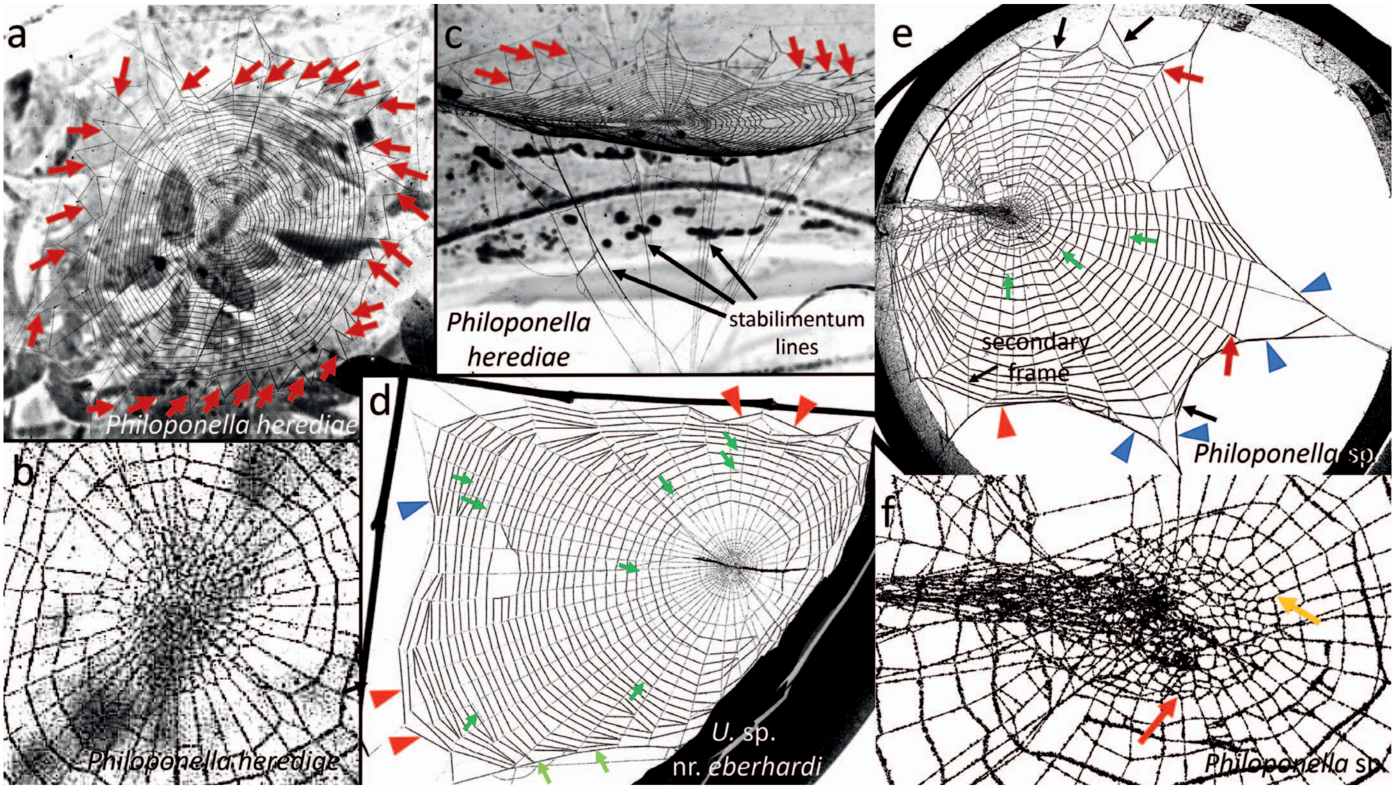

Figure 7.—The webs of mature females of *Philoponella herediae* in the field (*a–c*), *Uloborus* sp. nr. *eberhardi* in captivity (*d*), and *P.* sp. "Sta. Ana" in captivity (*e, f*). The sticky spiral of the *P. herediae* web was extreme in forming zig-zags on nearly all of the radii (dark red arrows in *a* and *c*); the web was also unusual in having long stabilimentum lines below the web (seen in the lateral view in *c*). The hub of the web of *P.* sp. Santa Ana (*e, f*) was unique in having a swath of many lines leading to the edge of the web where the spider rested (contrast with *U.* sp. nr. *eberhardi* in *d* in which the hub is also close to supports, but there is no swath of lines). Illustrations of characters in Tables 1, 2 are indicated as follows: red triangles indicate sticky spiral lines beyond the frame; dark green arrows indicate intact segments of the temporary spiral; dark red arrows indicate zig-zag sticky spiral lines; blue triangles indicate sticky spiral laid on frame lines; the red arrow indicates a sawtooth pattern in a radius caused by a double hub spiral attachment; and the orange arrow indicates a sawtooth hub spiral.

16. *Ratio of maximum number of loops to number of radii*. We calculated the ratio of sticky spiral loops to radii. This value probably has important functional consequences, because, at least in araneoids, radii are more important in stopping prey, while sticky spiral lines are more important in restraining them after they have been stopped (Craig 1987; Sensenig et al. 2012; Eberhard 2020). The ratio may give an approximate indication of the relative specialization of orbs for stopping as opposed to retaining prey (see Discussion).
17. *Primary webs*. We classified the life stages that built primary webs (see Eberhard & Zschokke 2022) as: "nymph 1" (first instar outside the egg sac); "juvenile" (a later instar spiderling that produced cribellate silk); mature male; "normal female" (mature females seen on webs in nature); and "senile female" (older females in captivity that had previously built typical orbs). We classified some females with unknown histories 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).
18. *Primary web hub replaced*. We used the criteria in Eberhard & Zschokke (2022) to deduce whether hub replacement had occurred.
19. *Fine lines beyond the frames in primary webs*. Lines in the mat of fine, non-radial lines extended beyond the frame lines (see Eberhard & Zschokke 2022).
20. *Many non-radial fine lines in primary webs*. Many fine lines in the dense mat were not radially oriented (Eberhard & Zschokke 2022).
21. *Relative spacing of temporary spiral in primary webs*. We classified the spaces between loops into two categories: "loose" and "tight" (see Eberhard & Zschokke 2022)
22. *Silk stabilimentum in primary webs*. Mats of silk formed white bands on or near the hub. Small accumulations of white silk at the very center of a hub were not counted as a stabilimentum, as these were probably accumulations of loose lines produced during the construction of radial lines (Eberhard 2020; Eberhard & Zschokke 2022).

Some traits were not decipherable in some webs, due to web damage, omission of portions of the web from the photo, lack of resolution in the photo, or because stabilimentum silk covered portions of the hub. Therefore, sample numbers for different traits varied even for the same set of webs. A web was included for surveys of traits 5–8 and 12–14 if it was possible to check at least half of the web for that trait in the photo; the frequencies of these traits may thus be somewhat underesti-

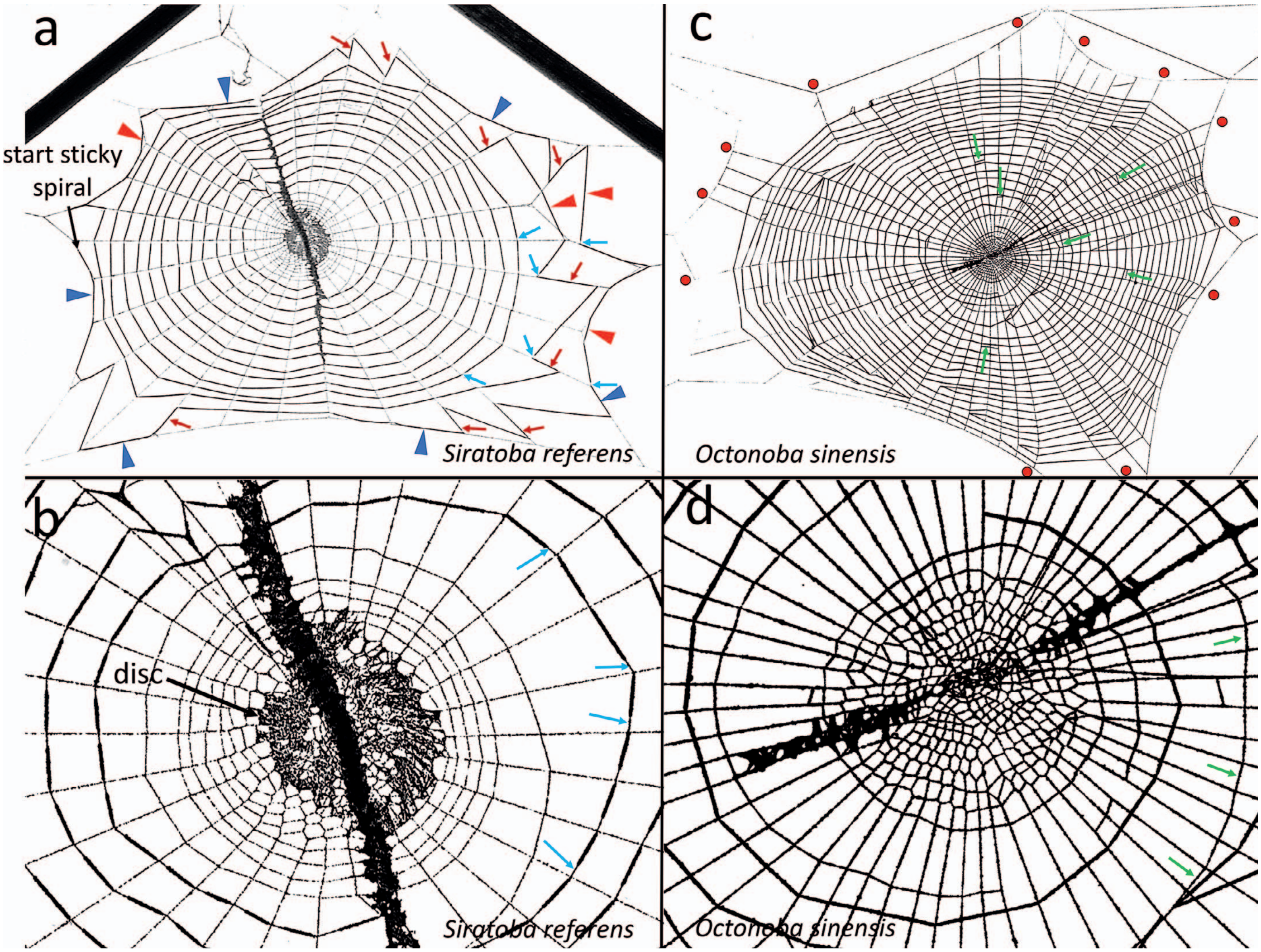

Figure 8.—Orb webs built in captivity by species in two genera whose webs have not been illustrated previously, *Siratoba referens* (*a, b*) and *Octonoba sinensis* (*c, d*), illustrate several traits in Tables 1, 2: linear stabilimenta (both species); disc stabilimentum (*b*); zig-zag sticky spiral lines (dark red arrows in *a*); sticky lines on frame lines (blue triangles in *a*); sticky lines beyond frame lines (red triangles in *a*); pairs of radii curving toward the anchor line between them (red dots in *c*); sites where the sticky spiral necked down following an attachment to a radius or a frame line (a few especially clear examples are indicated with blue arrows in *a* and *b*); and intact segments of temporary spiral (green arrows in *c*). The *S. referens* web was unusual in having abundant sticky lines on frame lines. The *O. sinensis* orb typified webs of this species in differing from those of many other genera by having many pairs of radii that curved toward anchors.

mated. All tests of statistical significance were two-tailed Chi^2 Tests, with $P < 0.05$ considered significant.

We did not include one additional trait that Lubin (1986) mentioned as possibly typical of uloborid orbs, switchbacks in the sticky spiral. Switchbacks are very widespread in both uloborid and araneoid orbs and are thought to represent adjustments of the sticky spiral to asymmetries of the web's overall form, often imposed by the size and shape of the space in which the orb is built (Wiehle 1927; Eberhard 1969). We also did not include "signal lines" or "free sectors" containing signal lines. We were unable to distinguish signal lines from draglines produced by spiders when they moved from the hub to the edge of the web. To our knowledge, the only uloborid genus with free sectors that lack sticky spiral lines and with a signal line is *Uaitemuri* (Santos & Gonzaga 2017) (a convergence with some araneid genera such as *Zygiella* F.O. Pickard-Cambridge, 1902 and related genera (Gregorič et al. 2010) and *Aculepeira* Chamberlin & Ivie, 1942 (Eberhard 2020)).

Our classification of traits contrasts with those of Peters (1987) and Lubin (1986) in that we distinguished two different categories of sticky lines laid along non-sticky lines, the sticky lines on frame lines (trait #7), and sticky lines on radii (trait #8); both of these were the "heteronomous" sticky lines of Peters (as opposed to his "autonomous" self-supporting sticky lines). We made these distinctions because we believe that the likelihood of finding biologically meaningful homologies is increased by using the details of the process that the spider uses to build her web, and by including the information that is likely available to her. In the process of building a segment of sticky line attached to non-sticky lines, a spider makes two decisions: which non-sticky line to use for the first attachment

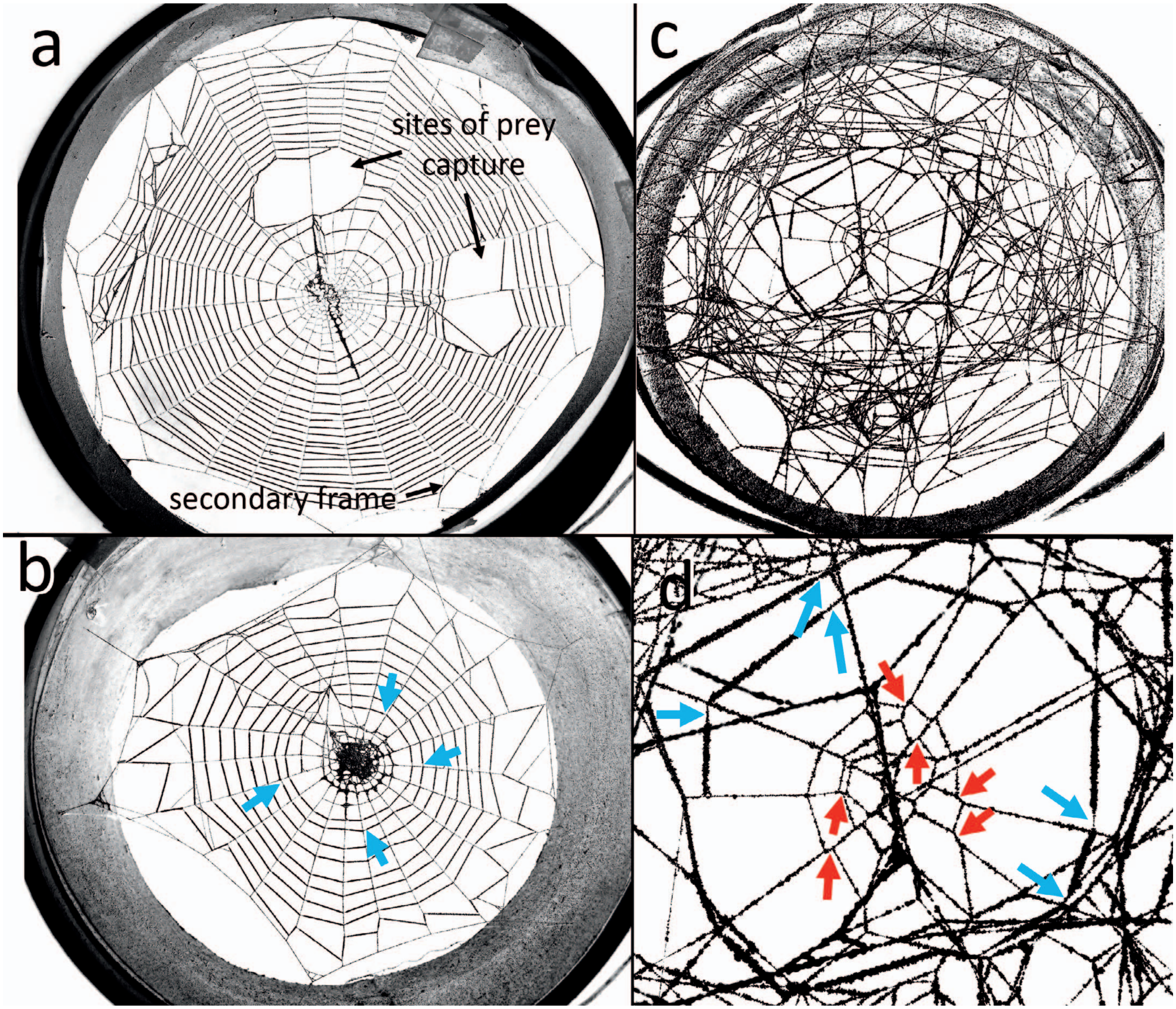

Figure 9.—Three webs illustrate major intra-specific differences in *Philoponella vicina* webs: two typical orbs (*a, b*); and a 3-D tangle of sticky and non-sticky lines (*c, d*). Although zig-zag sticky spiral lines were uncommon in this species (Table 1), occasional webs had zig-zags on nearly every radius (*b*). Spiders confined in constrained spaces (and sometimes in the field) built three-dimensional tangles (*c, d*) that included both sticky and non-sticky lines. Even the small hub in such a tangle had double attachments of the hub spiral to the radii (red arrows in *d*); some other tangle webs had sticky and non-sticky lines but lacked a hub. At least some of the sticky lines in the tangle also followed a spiral path and necked down just following each attachment to a non-sticky line (blue arrows in *d*; see also *b*) (the web in *d* had been jarred gently to reduce the amount of powder on the non-sticky lines, which thus appear especially thin).

(a radius or a frame line); and which non-sticky line to use for the second attachment (the same line as the first, or a different non-sticky line) (a different radius, or a different frame). This gives four combinations of two decisions: radius to different radius (the typical attachments of sticky spiral segments in orbs); radius to same radius (the zig-zag sticky spiral) (trait #8); frame to same frame (sticky line laid along a frame) (trait #7); and frame to different frame (sticky line beyond the frame) (trait #6). Similar distinctions were made in discussing attachments of sticky lines in the webs of dictynid spiders (Eberhard 2021). There is good reason to suppose that orb weavers, as well as *Hyptiotes* and *Polenecia*, are able to distinguish radii from frame lines: by their orientation with respect to the hub (the ability to return directly to the hub or retreat during web construction is an apparently widespread trait among both orb weavers and non-orb weavers – Eberhard 2020); and by the tensions on the lines (frame lines in orbs are under more tension – Denny 1976; Wirth & Barth 1992).

We characterized samples of five or more webs as “larger”, and samples with fewer webs as “smaller”. All individuals of the species with larger samples in Tables 1 and 2 were adult

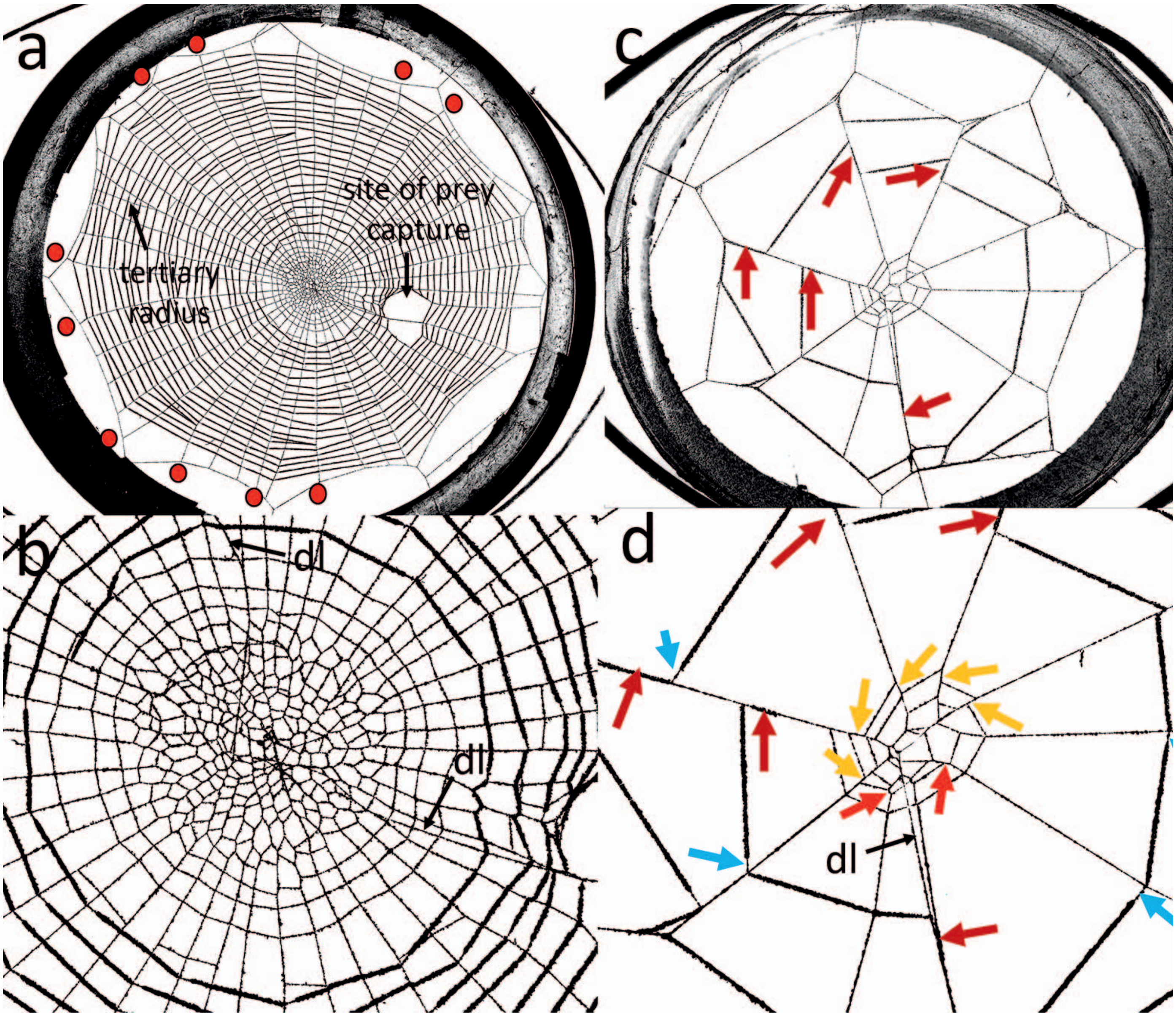

Figure 10.—Two webs illustrate major variations between typical (*a, b*) and highly reduced (*c, d*) *Uloborus trilineatus* webs. The hub of the reduced web (*d*) resembles typical hubs (*b*) in having double attachments of the hub spiral to radii; but the majority of these double attachments failed to pull the radii into perceptible sawtooth configurations (orange arrows in *d*) rather than deflecting the radii (red arrows in *d*). Zig-zag patterns in sticky spiral lines were unusual in typical orbs (*a*), but occurred on several radii in the reduced web (dark red arrows in *c* and *d*) (red dots in *a* indicate pairs of radii that both curved toward an adjacent anchor line; "dl" = dragline laid when the spider left the hub; blue arrows in *d* indicate necking down of the sticky spiral following attachments to radii).

females that were observed at the following sites: near Newport (Giles County), VA for *Hyptiotes cavatus* (Hentz, 1847); near North Bend, WA for *H. gertschi* (Chamberlin & Ivie, 1935); Davis, CA, USA for *U. diversus*; Baton Rouge, LA, and Blacksburg, VA, USA for *U. glomosus*; Blacksburg, VA for *Octonoba sinensis* (Simon, 1880); near Portal, AZ for *Siratoba referens* (Muma & Gertsch, 1964); near Tarcoles, Puntarenas Province, Costa Rica for *Z. geniculata*; near San Antonio de Escazu, San José Province, Costa Rica, el 1300m for *U. trilineatus* Keyserling, 1883 and *P. vicina* (O. Pickard-Cambridge, 1899); south of San Antonio de Escazu at 1400–1500m for *U.* sp. nr. *eberhardi* Opell, 1981; near Santa Ana, San José Province, Costa Rica at about 900m for *P.* sp. "Santa Ana"; and near Karekare, Piha, and Whangarei, New Zealand for *W. waitakerensis*.

We distinguished intermediate-sized immatures of *P. vicina* from those of *U. trilineatus* in the field at the San Antonio site by the brush of longer setae on tibia I of *U. trilineatus*. The species identities of newly emerged spiderlings were determined on the basis of the identities of the mature females that laid the eggs in captivity. Species identifications were made by B. Opell (*H. cavatus, H. gertschi, U. trilineatus, P. vicina, P.* sp. Santa Ana, *Z. geniculata, S. referens, O. sinensis*). Others were identified on the basis of Opell (1980) (*U.* sp. nr. *eberhardi*)

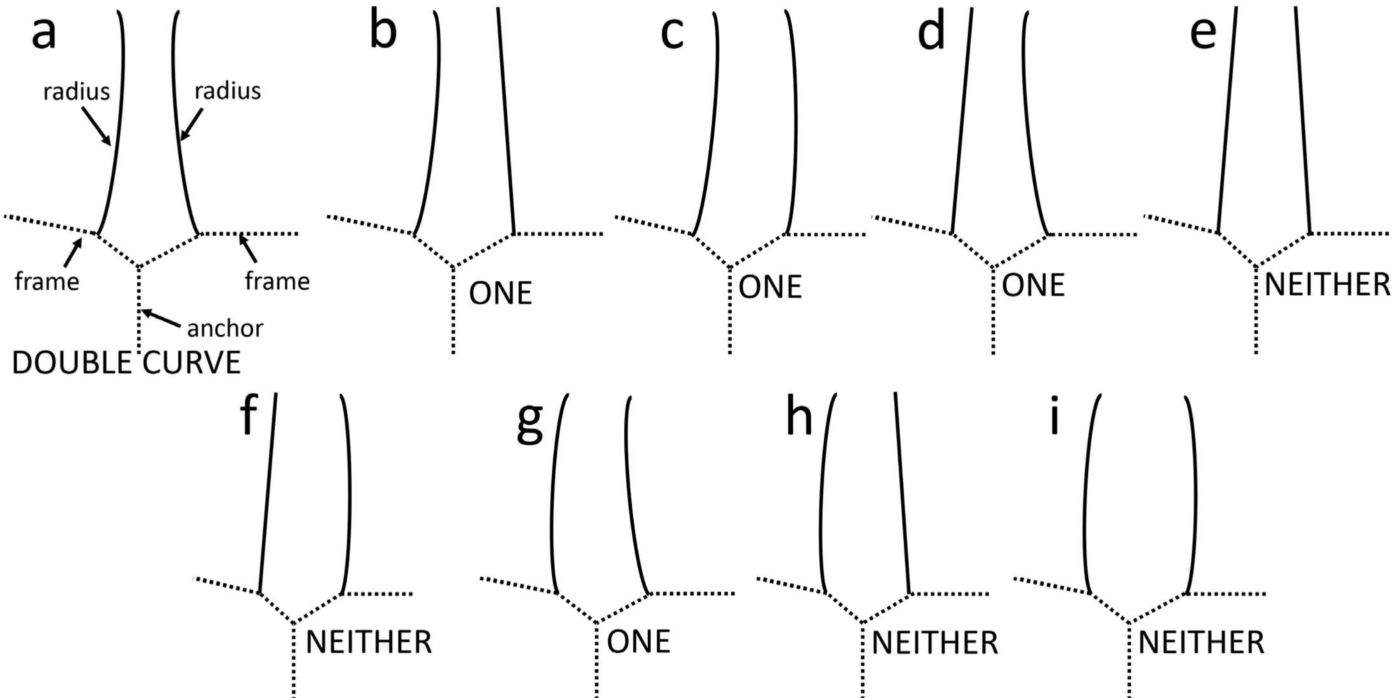

Figure 11.—Schematic representations of the nine possible combinations of curved and straight radii adjacent to an anchor line. In several species, the combination in which both radii curve toward the anchor (*a*) (trait #12 in Table 2), was more common than expected by chance (see Figs. 1, 6*f*, 8*c*, and 9*a*).

(which is not *eberhardi*) and Muma & Gertsch (1964) (*U. diversus, U. glomosus*). Voucher specimens are deposited in the Museum of Comparative Zoology, Cambridge MA (specimen numbers refer to labels in their vials), the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica, the Smithsonian National Museum of Natural History, and the New Zealand Arthropod Collection, Manaaki Whenua-Landcare.

Because the use of orb web traits as taxonomic characters in Uloboridae is still in the early stage of deciding which characters may be useful, and because web photos contain a great deal of information that includes both the traits that we discuss here and others that future workers may find useful, we present a photo of the web of each species that we observed for which no previously published web photos are available.

RESULTS

Orb webs.—The taxonomic distributions of 22 different orb web traits in at least 43 and perhaps as many as 50 uloborid species are reviewed in Tables 1 and 2 and summarized by genus in Tables 3 and 4. Taking into account the limitations in sample sizes (see Discussion), all of these web traits appear to occur at least occasionally in all orb-weaving genera of Uloboridae for which there is sufficient information. There is, however, considerable variation between species in the consistency with which different traits are present. The traits associated with the hub (#1–4) and skipping radii near the hub (#9) were the most consistent, both within the species with larger samples of webs, and among different species (see Fig. 3 for a visual summary of hub designs). Uloborid orbs were also consistently "radius-rich", with larger numbers of radii than the maximum number of sticky spiral loops (Fig. 12*a*). The frequencies of other traits that typically occurred farther from the hub varied from rare (2% for zig-zag sticky spiral lines) to nearly always present (91% for intact segments of temporary spiral) (both these extremes were in *U. diversus*).

Orbs of *Z. geniculata* built in smaller containers (14.8 cm compared with 50 cm in diameter), were more likely to have segments of sticky spiral beyond a frame line, and sticky spiral lines that ran along a frame line; and they were less likely to have intact segments of temporary spiral or double curved radii ($P < 0.001$ with Chi^2 Tests for each of these variables). Similar trends occurred in *U. trilineatus*: webs built in smaller containers (14.8 cm in diameter; $n = 12$) were more likely than those in larger containers (35 cm in diameter; $n = 67$) to have a sticky line on a frame line (50% vs. 28%) and were also less likely to have zig-zag sticky lines (8% vs. 51%) ($P = 0.06$ and 0.009 respectively with Chi^2 Tests). A similar trend occurred in zig-zag sticky spiral lines of *U. glomosus*: zig-zag patterns of sticky spiral were more common in webs built in larger spaces (Table 1; $P << 0.0001$). All of these trends probably represent adaptive adjustments to the space available in which to build the web (see Discussion). Occasional webs were striking exceptions, however. For instance, even though zig-zag sticky spiral patterns were not common in the *P. vicina* or the *U. glomosus* webs built in relatively small containers, some webs of both species in such containers nevertheless had a large number of zig-zags (Figs. 5*c*, 9*b*).

Assuming that curved and straight radii were equally common and that curves toward and away from anchors were also equally common, all eight species with larger samples showed a significant tendency toward double curves ($P < 0.05$ with Chi^2 Tests) ($P << 0.0001$ in five of the eight).

Table 3.—Summary of data on the web traits in Table 1 for the uloborid genera that are known to build orb webs or modified orbs (*Hyptiotes* and *Polenecia*). Y= the webs of at least some individuals of some species in the genus have this trait; N? = trait not found but trait is known to very intra-specifically and the sample was very small, so absence is not certain; ? = no evidence available one way or another due to lack of photos or lack of clarity in photos; - = not applicable; HS = hub spiral; Y in trait #12 indicates there was a statistically significant trend for both radii to curve toward the adjacent anchor in at least one species in the genus.

Genus	1. Lack hub hole	2. Lack scar	3. Double attach HS to radii	4. Zig-zag radii	5. Temp. spiral intact	6. St. sp. beyond frame	7. St. sp. along frame	8. St. sp. zig-zag	9. St. sp. skip radii	10. Silk stab	11. Line-circle-disc stab.	12. Radii curve toward anchor
Larger samples												
Hyptiotes[a] Walckenaer, 1837	-	-	-	-	Y	N	Y	Y	N	N	-	-
Philoponella Mello-Leitão, 1917	Y	Y?	Y	Y	Y	Y	Y	Y	Y	Y	Y-Y-Y	Y
Siratoba Opell, 1979	Y	?	Y	Y	?	?	?	Y	N?	Y	Y-Y-Y	Y
Uloborus Latreille, 1806	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y-Y-N	Y
Waitkera Opell, 1979	Y	Y	Y	Y	Y	Y	Y	Y	Y	N	-	Y
Zosis Walckenaer, 1841	Y	?	Y	Y	Y	Y	Y	Y	Y	Y	Y-Y-Y	Y
Smaller samples												
Conifaber Opell, 1982	Y	?	?	?	Y	Y	N?	Y	?	Y	Y-N-Y	?
Lubinella Opell, 1984	Y	?	?	?	?	?	?	?	?	Y	N-Y-N	?
Polenecia Lehtinen, 1967	Y	?	?	Y	Y	N	Y	Y	-	Y	N-N-Y	-
Purumitra Lehtinen, 1967	?	?	?	?	?	N	Y	Y	-	Y	N-Y-N	?
Sybota Simon, 1892	Y	?	?	Y	N?	N?	Y	Y	N?	N	-	?
Uaitemuri Santos & Gonzaga, 2017	Y	?	?	Y	N?	?	Y	Y	?	N	-	?

Because the assumption in these tests that straight and curved radii were equally common probably underestimates the frequency of straight radii, these tests were conservative. One species, *U. trilineatus*, showed a much stronger trend than all of the other species ($P << 0.0001$). Perhaps longer radii are more likely to be curved, as double curved radii were significantly more common in webs of *Z. geniculata* that were built in larger containers ($P << 0.0001$); *U. glomosus* showed a similar, but statistically non-significant trend ($P = 0.14$).

One further trait was not included in Tables 1 and 2 because of sampling difficulties (see Discussion): "replacement repairs" (Eberhard 2020), in which the spider builds a new orb that replaces a portion of a previous web but leaves a substantial portion of the previous web intact. Replacement repairs are clear in published web photos for several uloborids, including *U. walckenaerius* (Wiehle 1927), *U. diversus* (Eberhard 2020), *P. undulata* (Lubin 1986), *P. divisa* (Opell 1979), and *Z. geniculata* (Eberhard 2020); we have also seen them in *Z. peruana* (Keyserling, 1881)*, U. glomosus, U. trilineatus, P. vicina, P. tingens, O. sinensis, W. waitakerensis*, and (probably) *S. referens*.

The orbs of one *Zosis* and five *Philoponella* species that have not been documented previously are illustrated in Fig. 13.

Primary webs.—Table 2 characterizes the features of "primary webs", which were initially described for nymph 1 uloborid spiderlings (Wiehle 1927; Szlep 1961). They are discussed in detail by Eberhard & Zschokke (2022), which describes: 1. Primary webs built by nymph 1 spiderlings of *Z. geniculata*, *U. trilineatus*, *U.* sp. nr. *eberhardi,* and *P. vicina*; 2. Primary webs built by mature males of *Z. peruana, U. trilineatus* and *P. tingens*; 3. Variations in hub center removal of primary webs; 4. Ontogenetic stages in which primary webs are built; 5. The temporary spiral spacing; and 6. "Mixed" webs that include both typical orb and primary web traits.

DISCUSSION

Distribution of web traits in Uloboridae.—Of the traits summarized in Tables 3 and 4, those that occurred most consistently in uloborid orbs were the lack of a hub hole (#1), the double hub spiral attachments to radii (#3), and hub spirals that pulled radii into sawtooth patterns (#4). Relatively high numbers of radii compared with the maximum number of loops of sticky spiral (#16) were also consistent (the only exceptions were the derived webs of *Hyptiotes*). Primary webs may be a unique uloborid trait, but the taxonomic coverage for this character was much less complete. It is possible that the paucity of reports of primary webs is an artifact of the often small sizes of these webs and the short time span during a spider's life during which they are built. The unfortunate

Table 4.—Summary of data on the web traits in Table 2 for the uloborid genera that are known to build orb webs or modified orbs (*Hyptiotes* and *Polenecia*). Y= the webs of at least some individuals of some species in the genus have this trait; N? = trait not found but trait is known to very intra-specifically and the sample was very small, so absence is not certain; ? = no evidence available one way or another due to lack of photos or lack of clarity in photos; - = not applicable; HS = hub spiral. The numbers for trait #16 represent means for the species with larger samples. When more than one developmental stage built primary webs and information is available for the different stages, traits #18 to #22 of the webs are listed separately for each stage in the same order as in #17 (N1 = nymph 1; J = later instar spiderling; M = mature male; F = normal web of adult female; S = senile adult female).

Genus	13. Tert. radii	14. Sec. frame	16. Number st.sp./ number radii	17. Primary web	18. Hub replace primary web	19. fine lines bey. frames in primary web	20. fine lines non-rad. primary web	21. tsp. spacing primary web	22. stabil. primary web
Larger samples									
Octonoba	Y	Y	0.4	N1	?	?	?	?	?
Philoponella	Y	Y	0.4-0.9	N1/M	Y?/Y	?/N	?/Y	?/L	N/N
Siratoba	N	N	0.4	?	?	?	?	?	?
Uloborus	Y	Y	0.4-0.6	N1/J/M/S	Y&N/Y/N/N	Y/Y/Y/N	Y/Y/Y/Y	T&L/T&L/?/L	Y&N/?/?/?
Waitkera	Y	Y	0.5	?	?	?	?	?	?
Zosis	Y	Y	0.4-0.6	N1/M	Y&N/N	?/N	Y/Y	L/T	Y/Y
Smaller samples									
Conifaber	N	Y	0.3	M/F	?/Y	?/?	?/Y	?/?	?/Y&N
Hyptiotes	N	N	2.2-3.9	none	-	-	-	-	-
Lubinella	?	?	?	?	?	?	?	?	?
Polenecia	N	N	-	none	-	-	-	-	-
Purumitra	?	?	?	?	?	?	?	?	?
Sybota	Y	?	0.5	?	?	?	?	?	?
Uaitemuri	?	?	0.7	?	?	?	?	?	?

tendency of arachnologists to limit their behavioral observations to adults is probably also a major factor (Eberhard 2020).

Primary webs.—In at least two species, primary webs occurred in multiple life stages (nymph 1 spiderlings, mixed webs of older juveniles and senile females of *U. diversus*; juvenile spiderlings, mature males and senile females of *U. trilineatus*). There is evolutionary flexibility in primary webs; for instance, primary webs are typical of mature female *C. parvus* Opell, 1982 in the field, but not females of *C. yasi* Grismado, 2004 (Grismado 2008); mature males of *Z. peruana* sometimes do, and sometimes do not build primary webs. Their presence in one stage did not guarantee that they occur in another: mature males of *Z. geniculata* apparently do not build primary webs (Eberhard 2020; Eberhard & Zschokke 2022) even though nymph 1 spiderlings do. We presume that primary webs will be found in additional species as more observations are made. Primary webs are apparently absent, however, in at least nymph 1 spiderlings of the uloborid genera *Hyptiotes* (Opell 1982), *Polenecia* (Peters 1995), and *Miagrammopes* (Opell 2001), as previous authors checked and failed to find them. These absences may be secondary, as these genera have all secondarily lost orb webs.

Limitations of the data.—Several limitations of the data may affect conclusions that can be drawn regarding the distribution of these web traits. The sample size in many previous studies was only a single photograph; in addition, many photographs were of webs that were partly damaged, or included only the central portion of the web. These limitations were more severe for the traits such as #5 – 8 that typically occur in the periphery of a web, and whose presence is known to be erratic in species with larger samples (Table 1, Fig. 5*a–c*). In species and traits for which these sampling limitations were more severe, an indication of absence ("N" in Tables 1 and 2) is less certain; definitive proof that a trait never occurs is of course extremely difficult. In contrast, however, any "Y" in Tables 1 and 2 indicates that, despite possible sample size limitations, the trait does occur in that species. This consideration justifies inclusion of studies with very small sample sizes in Tables 1 and 2.

A second important limitation that could also artificially increase the number of "N's" in the tables is that we only included typical orb webs; we omitted both egg sac webs (e.g., Eberhard 2020 on *Z. geniculata*), and orbs with modified designs built in very small spaces (Figs. 9c and 10c,d) (Eberhard & Barrantes 2015). At present, there are very few data on these other types of webs. Further observations could be important in understanding web evolution, because web construction traits are known to have been shuffled module-like between different behavioral contexts during evolution (Eberhard 2018, 2020). For example, zig-zag sticky lines also occur in the egg sac webs of *U. glomosus* (W. Eberhard, unpub.). Thus, our omission of egg sac webs may have resulted in underestimates of the ability to make zig-zag sticky lines in some uloborids. In general, more data on egg sac webs would be of interest.

The reader should note also that we have probably underestimated intra-specific variation in some species, both because of the uniformity of the size and shape of cages in which we observed species in captivity, and because a few of the webs that we observed may have been built by the same individual.

Our focus on the traits of finished webs may have obscured the behavioral origins or the functional significance of some

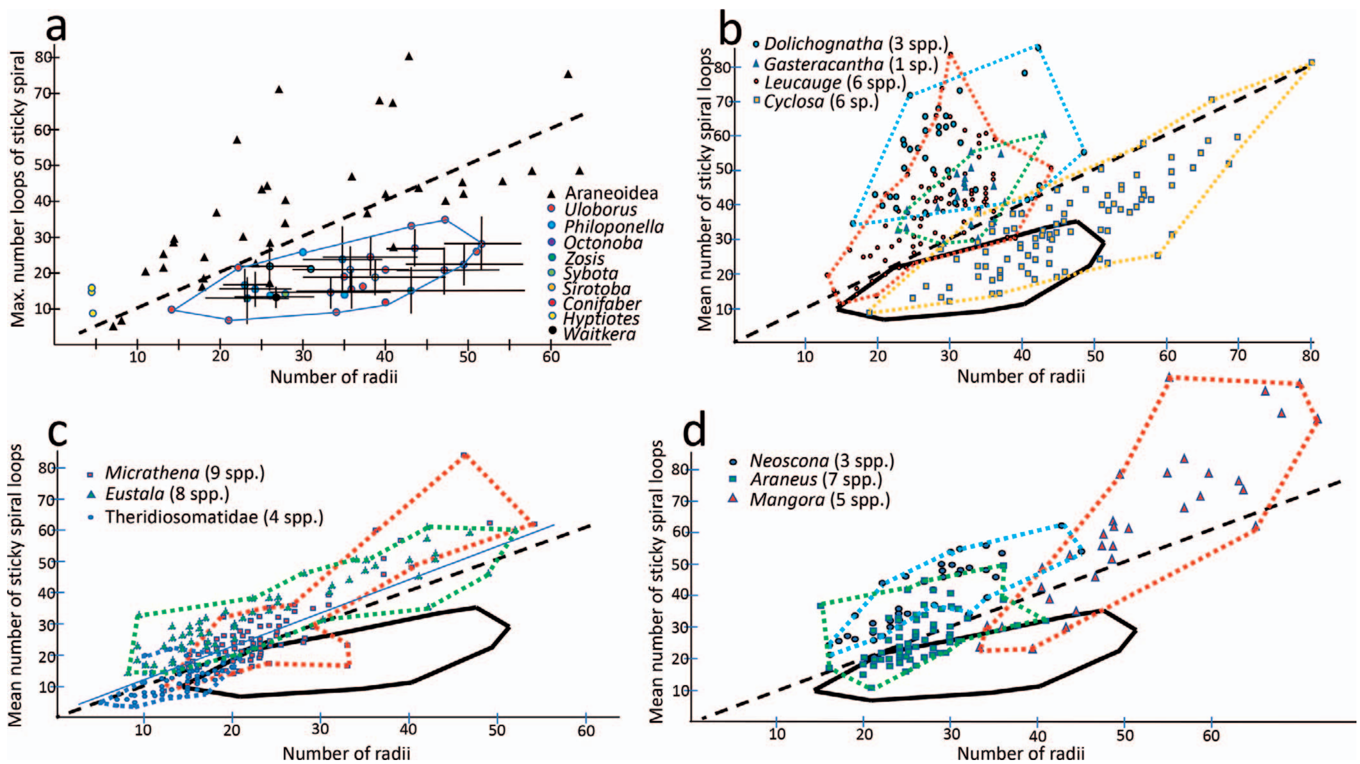

Figure 12.—These graphs illustrate differences in orb designs between uloborids and several groups of araneoids (the dashed black line in each graph provides the reference of equal numbers of radii and sticky spiral loops). Graph *a* compares the data from different uloborid genera (colored circles) in Tables 1, 2 with a variety of araneoids (black triangles) that were included in a previously published figure (Eberhard 2020) that was designed to illustrate extremes in radius-rich and sticky spiral-rich orb designs. The thin black lines through the dots for the uloborid species with larger samples represent one standard deviation to either side of the dot. The limits of uloborid designs are indicated with the thin blue line. Graphs *b–d* compare the range of variation in uloborid webs (solid black lines) with those of genera and families of araneoids (colored symbols and dotted lines) for which we happen to have series of web photographs. In general, uloborid orbs are more radius-rich compared with many araneoid orb-weaver taxa (black triangles). The graphs also suggest that different araneoid groups tend to have orbs with different degrees of radius-richness, but it must be emphasized that these graphs are only preliminary. They are intended only to illustrate the general relation of uloborid traits, and not the true limits of variation in the araneoid groups. Much larger, more systematic data sets will be needed to obtain more definitive conclusions.

traits. For instance, removal of the central portion of the hub (trait 1) may function in araneoid spiders to remove the loose silk that accumulates there during radius construction, due to their use of break and reel behavior to build radii (Eberhard 1982). As far as we know, the few uloborids whose building behavior has been observed directly all fail to perform break and reel behavior during the construction of the large majority of the radii (break and reel behavior during the construction of the earliest radii results in a small accumulation of silk, and this is removed early in radius construction when the "proto-hub" is built – Eberhard 2020); thus loose silk does not accumulate in the hub. Trait 1 could thus be interpreted to represent a lack of break and reel behavior during radius construction.

Finally, as discussed in footnote 7 of Table 1, two homologies in *Hyptiotes* (Fig. 14), double attachments of the hub spiral to radii (#3) and intact segments of temporary spiral (#5), are tentative. The question of whether these non-sticky spiral lines near the hub are homologous to hub or to temporary spiral lines is not resolved. Homology in this genus with respect to the production of double attachments *per se* seems more certain, however.

Variation and possible functions.— Intra-specific variations were larger in some traits than others in the webs of the species for which larger samples were available (*U. diversus*, *U. globosus*, *U. trilineata, H. cavatus, H. gertschi, P. vicina, S. referens, W. waitakerensis,* and *Z. geniculata*). The typical orbs of mature females were intra-specifically uniform with respect to hub traits (#1–4 in Tables 1, 2). Exceptions occurred only in webs built in very restricted spaces (Fig. 10c, d). The strong similarity in traits 3 and 4 in Table 1 intimates that the function of double attachments of the hub spiral to radii (trait 3) may be to enable hub lines to adjust tensions in the hub by increasing the tensions on more slack radii (trait 4).

In contrast, most traits in other portions of the webs were less consistent. Some intra-specific variations appear to be linked to the size of the space in which the web was built. The frequency of zig-zag patterns of sticky spiral in both *U. glomosus* and *U. trilineatus* was greater in webs that were built in larger spaces (Table 1). In both *Z. geniculata* and *U. trilineatus,* orbs built in smaller containers were more likely to have segments of sticky spiral beyond a frame line, and to have sticky spiral lines that ran along a frame line. Both of these patterns may represent adaptive adjustments that bring sticky silk supplies into better agreement with the space

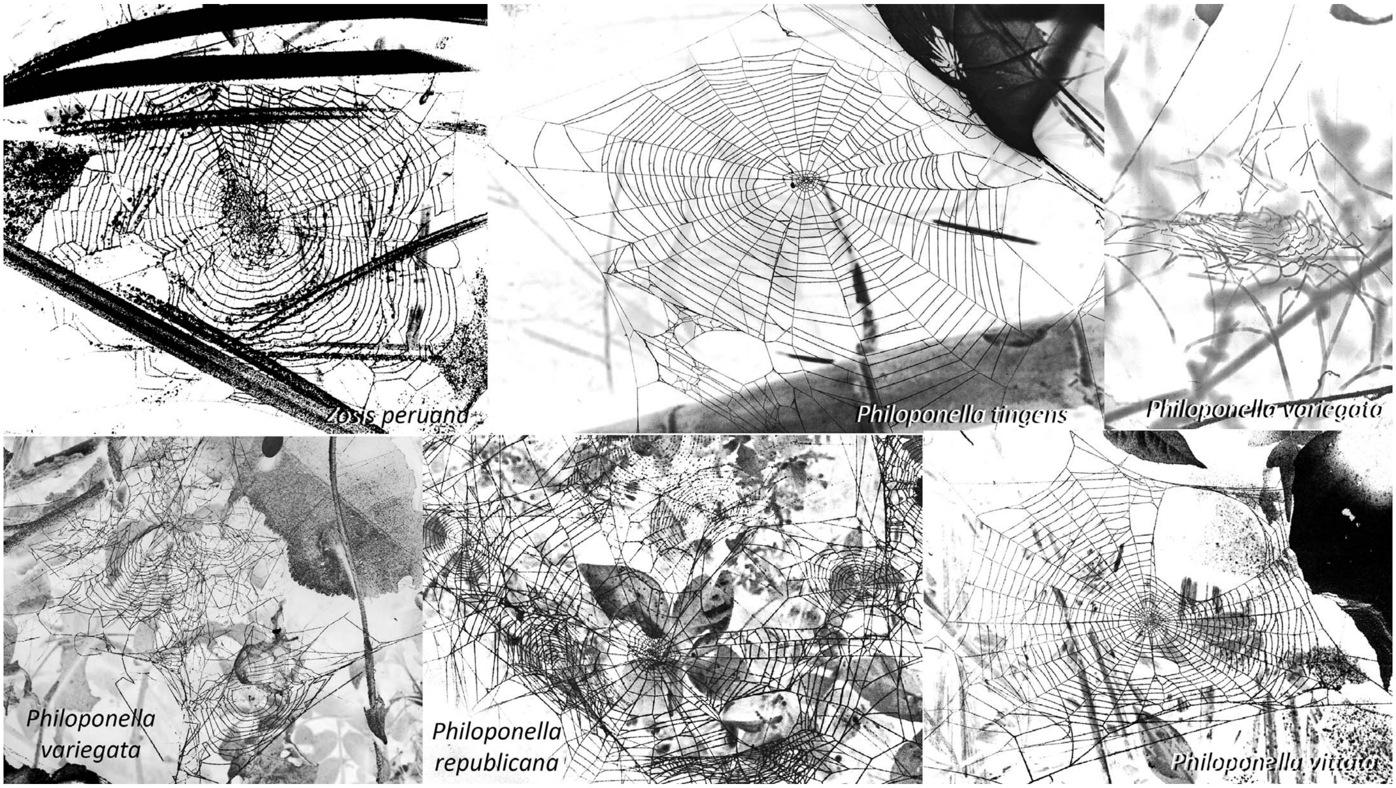

Figure 13.—Photos of webs in the field of species in this study whose webs have not been previously documented in their entirety: *Zosis peruana* (*a*) (#1555); *Philoponella tingens* (*b*) (#1167); *P. semiplumosa* (lateral view in *c* (#1327), perpendicular to web plane in *d*) (#1326); *P. republicana* (*e*) (#1021); and *P. vittata* (*f*) (#1403).

available to the spider in which to build its orb. The zig-zag patterns near the orb's edge could serve to fill in space on the web for which the spider does not have sufficient sticky spiral silk. The higher frequency of sticky lines on and beyond frame lines in smaller containers could function to increase the area covered with sticky lines when space constraints oblige the spider to build an orb that is smaller than that which it could have covered with the sticky silk available in its silk glands.

These interpretations involve adjustments to possible incompatibilities between silk supplies and the space occupied by a web; such adjustments have been noted previously in *Z. geniculata,* which sometimes builds large orbs in which the spider needs a second day to finish filling with sticky spirals (Eberhard & Barrantes 2015; Eberhard 2020). Increased spaces between the sticky spiral loops just before construction ended on the first night and reduced spaces between loops built at nearly the same sites on the second night suggest that on the first night the spiders ran out of sticky silk part way through sticky spiral construction. Supplies of sticky silk probably also influence the web size and sticky spiral spacing in orbs built by araneoids (Eberhard 1988, 2020).

A second trait for which a likely function can be suggested concerns the pairs of radii that curved toward anchor lines. The double curve pattern that occurred in all seven orb-weaving uloborid species with larger samples probably functions to reduce the sizes of relatively open spaces in the array of radii. As was noted previously for *U. diversus* (Eberhard 1972), curves in the radii probably originate during temporary spiral construction in portions of the orb where the spaces between radii are especially large. As such over-sized spaces often occur where there is an anchor line, the association of curved radii with anchors that we documented probably functions to allow the curved radii to fill in over-sized spaces. It is unclear, however, why some uloborid species showed a much stronger pattern of this sort than others.

Variation and phylogeny.—The variations just described raise questions regarding the usefulness of behavioral characters to justify taxonomic groupings. Many aspects of behavior are highly flexible, and orb webs are no exception (summaries Herberstein & Tso 2011; Eberhard 2020). One might decide that such gross intra-specific differences as those in Figs. 9 and 10, for instance, show that web design is too flexible to provide useful taxonomic characters. These deviant forms were not typical, however, and were associated with the uncommon condition in captivity of restricted space in which to build.

It seems reasonable to use the "typical" form of orb webs to characterize a species, just as "typical" morphologies are generally used in taxonomic studies of morphology. After all, one would not pretend to typify the morphology of the leg a species on the basis of an individual that had suffered damage to this leg in an early moult that caused the leg to grow into an unusual form. We believe, for instance, that it is appropriate to characterize the webs of *H. gertschi* (and probably those of the entire genus *Hyptiotes*) as having four radii, even though one web (Fig. 14*f*) among a total of 55 webs photographed in this species (and 89 in the genus) had only three. In typifying a species, the range of traits that *typically* occur is more useful than a summary of all of the traits that the species is *capable* of

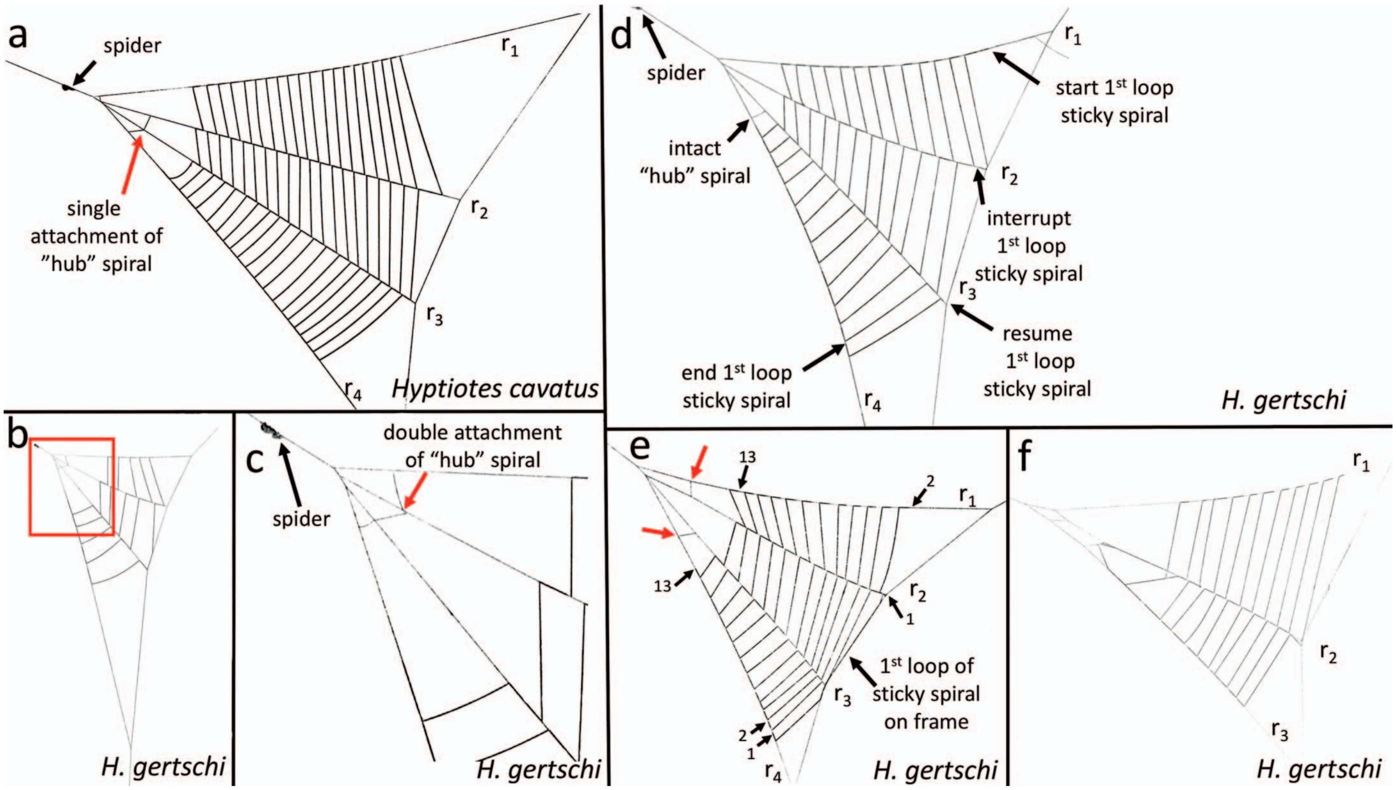

Figure 14.—Webs of *Hyptiotes cavatus* (*a*) and the previously undocumented species *H. gertschi* (*b–f*) illustrate three traits that may be homologous with traits that characterize orb-weaving uloborids: zig–zag attachments of the sticky spiral to radii (*a–f*); double attachments of the hub spiral to radii (*c*) (this is a closeup view of the sector outlined in *b*); and sticky lines laid along frame lines (*e*) (in all figures the sticky lines with cribellate silk are darker than the non-sticky lines; the red arrows indicate intact "hub spiral") (see footnote 7 in Table 1 for a discussion of this homology). In some webs, the attachment of the intact "hub spiral" to the radius was double (*c*), while in others (*a*), it was single. Two previously unrecorded exceptions among *Hyptiotes* webs are also illustrated in *e* and *f*. Analysis of *H. gertschi* web photos (W. Eberhard unpub.) suggested that the process of sticky spiral construction was usually the same as that described previously for *H. paradoxus* (Marples & Marples 1937) and *H. cavatus* (McCook 1889). There were exceptions, however, and some exceptional traits resembled those of orb-weaving uloborids in Table 1. The first loop differed from the typical sequence of attachments in ten of 55 *H. gertschi* webs, as illustrated in the web shown in *e*: the first sticky loop began on r_2 (indicated with "1" on r_2) rather than on r_1 (a similar variation sometimes occurs in *H. paradoxus* – S. Zschokke pers. comm.), and the sticky line was laid on the frame line between r_2 and r_3 (trait #7) (in some cases the sticky line was slightly beyond the frame) (trait #6). The second loop of this web was typical, however, in being initiated on r_1 ("2" on r_1). In eight webs (one is shown in *d*), sticky spiral production was apparently suspended temporarily when the spider encountered the frame line at the end of r_2, and then resumed when the spider moved onward to r_3 where it began again (the beginning and end of loops 2 and 13 are labelled in *e*) (similar variations also occur in *H. paradoxus* – S. Zschokke pers. comm.). An even more exceptional web is shown in *f*: it is the only web of any species of *Hyptiotes* ever observed that had three instead of four radii.

manifesting. In this sense, the multiple similarities in Fig. 3 indicate that several aspects of typical hub structure may be quite uniform among species in the genus *Uloborus,* even including species like *U. eberhardi* in which a twig runs through the hub (Fig. 2b). Further analyses will be needed to determine the degree of species- and genus-specificity.

We realize that determining the "typical" web form under natural conditions is not always simple. For instance, the consistent, substantial ontogenetic changes in web designs such as those in the araneids *Zygiella x-notata* (Clerck, 1757) (LeGuelte 1966) and *Trichonephila clavipes* (Linnaeus, 1767) (Fig. 15) make it necessary to include multiple designs as "typical". The same problems, of course, occur in morphology; the difference is not in kind, but in degree. The usual (though surely not always the best) solution in studies of ontogenenic changes in spider morphology and behavior has been to completely ignore all stages except mature adults (the "adultophilia" of Eberhard 2020). Given current uncertainty regarding the phylogenetic relations among uloborid genera (Coddington 1990; Santos & Gonzaga 2017) and the fact that additional studies of uloborid molecular traits are currently under way (A. Santos, pers. comm.), it seems premature to attempt to discuss the possible evolutionary histories of the traits examined here within Uloboridae. Similarly, current uncertainties regarding the mono- or polyphyly of orb webs (Bond et al. 2014; Fernández et al. 2014, 2018; Dimitrov et al. 2016; Coddington et al. 2019; Kallal et al. 2020) make speculation regarding the history of these traits in the ancestors of uloborids and orb weaving araneoids premature.

Contrasts with araneoid orbs.—We have shown that the traits in Tables 1 and 2 occur throughout orb-weaving uloborids. Do these traits distinguish uloborid orbs from those of araneoids? Definitive empirical tests will require surveys of araneoid webs that include many genera and

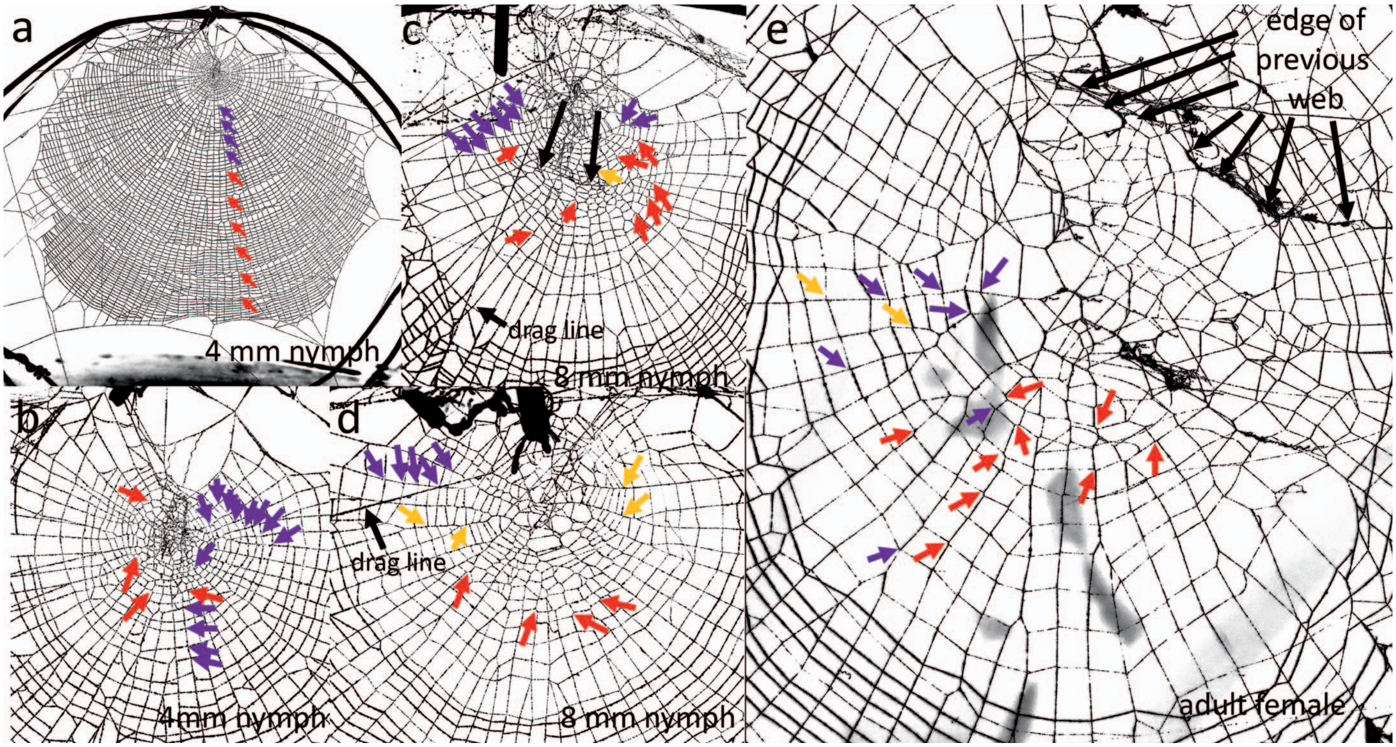

Figure 15.—Ontogenetic variation in the hubs of *Trichonephila clavipes* is illustrated by the hub of a small, 4 mm long nymph (cephalothorax + abdomen) (*a, b*), the hubs of intermediate, 8 mm long spiderlings (*c* and *d*), and the hub of an adult female (*e*); the edge of an apparent replacement repair in *e* is marked with black arrows. These hubs differed from uloborid hubs in several respects. Single attachments of the hub spiral to radii prevailed in the outer portion and the sides of the small nymph's web (purple arrows in *b*), while both single and double attachments that pulled the radii into sawtooth patterns were more common in the lower portion and nearer the center (a few of the latter are indicated with red arrows in *b*). The hubs of intermediate nymphs (*c, d*) were similar in these respects, but the lines in the central area were less dense and less orderly (*d*), and some double attachments of hub spiral lines failed to pull the radius into a sawtooth pattern (orange arrows in *c* and *d*). Both the relative density and the orderliness of the lines were further reduced in the central portion of the adult's the hub (*e*), where there were both single (purple arrows) and double attachments (orange and red arrows), and where sawtooth patterns of radii (red arrows) were less pronounced. As is common in the adults of this species (Eberhard 2020), this web was a replacement repair of a previous orb (each night the spider replaces about half of its web); the new hub was at the edge of the previous orb (black arrows). All of the *T. clavipes* hubs resembled those of uloborids in lacking a central hole, and in not having any "scar" or sign of repair of a hole in the center. A further ontogenetic change visible in the web of the early nymph (*a*) was that the attachments of the temporary spiral to radii were double in the outer portions of the orb (red arrows), as in adults (e.g., Hesselberg & Vollrath 2012), but were single near the hub (purple arrows). These photographs were made after removing the sparse tangles of lines on either side of the web, in order to obtain clearer images of the hubs.

additional families, large samples of at least some species, and reliable phylogenies to distinguish derived from ancestral traits. This is a challenging task, especially in view of the intra-specific variation in some araneoid web traits, such as the hubs of *Aculepeira escazu* Levi, 1991 (Fig. 4) and *T. clavipes* (Fig. 15). This paper is not the place to make final, sweeping conclusions regarding uloborid-araneoid differences. We will, however, risk a few preliminary comments. We will discuss uloborid and araneoid traits in what we perceive to be decreasing order of the likelihood of clear differences, based largely on our impressions of the consistencies of different traits.

The trait that seems most likely to be unique to uloborids is the primary web. Although data in uloborids are as yet sparse, primary webs or at least traits of primary web traits occur in five genera and in five different life stages (Table 2). Nothing similar to primary webs has ever been reported, to our knowledge, in any araneoid orb weaver. Nor, to our knowledge, has any other non-orb weaving cribellate spider been reported to make primary-type webs (though admittedly very little is known of the webs of early immature stages). The zoropsid *Tengella radiata* (Kulczynski, 1909) did not include cribellate lines in the sheet and the tangle above it until the 7th instar, but no alternative, compensatory web design was noted (Barrantes & Madrigal-Brenes 2008). Therefore, primary webs may be a synapomorphy of uloborids.

Turning to typical orb webs, a lack of removal of the center of the hub (traits #1 and 2) is one of the most certain differences between uloborids and araneoids (excepting nephilines, *Cyrtophora* Simon, 1864 and related genera, and *Phonognatha* Simon, 1894 – see below) because this trait has been surveyed in araneoids previously (Eberhard 1982, Kuntner et al. 2008). Hub center removal did not occur in any uloborid web (Table 1) (admittedly the data are less extensive, because this trait could only be discerned in clear closeup photos of the hub) (see Fig. 6). In addition, the direct observations of construction behavior in two uloborid species demonstrated a lack of hub removal (character G1 in

Eberhard 1982). In contrast, direct observations of the construction behavior of numerous araneoids indicated that, with the exception of four species of Nephilinae, *Cyrtophora* and related genera, and *Phonognatha melania* (L Koch, 1871) (Kallal & Hormiga 2018), removal of the center of the hub was close to universal (characters G2–G4). It occurred in 111 of the 119 species in 7 araneoid families that were observed for this trait (Eberhard 1982, 1987), and in at least 4 of the 8 exceptions the hub was either built against a solid object so that its center could not be removed (*Tetragnatha* sp. #2304, *Spilasma artifex* Simon, 1895), or the web was highly reduced (*Ocrepeira* (= *Wixia*) *ectypa* (Walckenaer, 1841), *Cyrtarachne* sp. #1994). Nevertheless, araneid species that normally remove and replace the center of the hub occasionally leave the hub intact in finished orbs (Fig. 4*b*) (similar variation also occurs in *M. olmec* – W. Eberhard unpub.).

Further data from analyses of araneid web photos (Fig. 4) also suggest that this uloborid-araneoid difference in hub removal is relatively complete. The hubs of some araneids such as *Mangora* and *Cyclosa* Menge, 1866 resemble uloborid hubs in having many, very tightly spaced loops of hub spiral (e.g., Nielsen 1932, Comstock 1967) (Fig. 4), but they either have a small central filled-in area combined with a small hole, as in *Mangora pia* Chamberlin & Ivie, 1936 (Fig. 4f), a small area filled in with more organized sawtooth lines as in *Cyclosa turbinata* (Walckenaer, 1841) (Fig. 4e), or a larger, more disorganized filled-in area as in *Argiope argentata* (Fabricius, 1775) (Fig 4a; Eberhard 1981) (see also Comstock (1967) on *Araneus bicentenarius* (McCook, 1888) (= *gigas*) and *Mangora gibberosa* (Hentz, 1847)). As noted above, nephilines are an exception, and resemble uloborids in lacking hub removal (Eberhard 1982) (Fig. 15). But their hubs differ from uloborids in that the hub spiral and the radii in the hub are not consistently bent into sawtooth forms by double attachments of the hub loops to radii (traits #3 and 4), a difference that is especially clear in adult webs (Fig. 15e).

With respect to traits #7 (sticky spiral laid on a frame line) and #8 (sticky line laid on a radius, forming a zig-zag pattern), possible uloborid-araneoid differences are difficult to evaluate; most published web photographs were taken in the field, and both patterns can be produced by damage to an orb. For instance, when an object supporting a frame line moves it causes the frame to sag briefly, sticky spiral lines sometimes adhere to the frame line (Eberhard 2020); prey or other objects that strike an orb can also displace sticky lines and cause them to adhere to radii. The most reliable data for these traits come from photos taken immediately after the web was built in the field, from webs built in captivity, or from direct observations of spiders building. Although some published web photos (Comstock 1967; Witt et al. 1968) were taken in captivity, the provenance of many others is uncertain. In addition, as is clear from Table 1, intra-specific variation in some species makes it necessary to have substantial samples to evaluate both of these traits. We judge tentatively, given these limitations, that both traits may be relatively distinctive in uloborids. To the best of our knowledge, the only webs of an araneoid in which sticky lines are routinely laid on frame lines and the sticky spiral forms zig-zag patterns on the radii are the highly derived "sawtooth" webs of *Eustala* sp. (Eberhard 1985; fig. 3.10 in Eberhard 2020).

Two other hub traits, double attachments of the hub spiral to radii (trait #3) and higher tensions on hub spiral lines than on radii that cause the double attachments pull the radii into sawtooth patterns (trait #4), were also very consistent in uloborid hubs, especially in more central portions of the hub. Previous behavioral observations of araneoid construction behavior did not include this detail, so we can only compare uloborids with photos of araneoid webs. A few araneid and tetragnathid species have double radius-hub spiral attachments and sawtooth radii (Figs. 4*e*, 15*b–e*; Eberhard 2020), but single radius-hub spiral attachments and straight radii within the hub are apparently more common (Fig. 4) (Eberhard 2020). Further data on araneoids are needed. Another relatively consistent uloborid trait was silk stabilimenta (trait #10); but stabilimenta are widespread in Araneidae, where they have arisen repeatedly (Scharff & Coddington 1997; Herberstein et al. 2000; Eberhard 2020). Stabilimenta seem not to occur in other araneoid families, however, unless nephilines are counted as a separate family (as has often been done – e.g., Kuntner et al. 2008; Garrison et al. 2016).

Some of the traits in Tables 1 and 2 that were less consistent in uloborids also occur in araneoids. These include the presence of short segments of intact temporary spiral lines in finished orbs (#5), sticky spiral lines beyond frame lines (#6), and sticky spiral lines that skip radii (#9). Fragments of intact temporary spiral are visible in photos of orbs of *Z. x-notata* (Witt et al. 1968), *C. turbinata*, and *Micrathena duodecimspinosa* (O. Pickard-Cambridge, 1890) (W. Eberhard, unpub.); but these intact temporary spiral segments seem to differ from those of uloborids (Figs. 1–3) in being less common in a given web, and limited to the innermost portions of orbs. Some *Z. x-notata* webs have sticky spiral lines beyond frame lines (Witt et al. 1968). Some segments of sticky spiral apparently cross radii without being attached to them in the inner portions of orbs of *C. turbinata* and possibly *Allocyclosa bifurca* (McCook, 1887) (Eberhard 2020, unpub.). Further data will be needed to establish the taxonomic distributions of these traits.

The positive relationship between the number of radii and the number of loops of sticky spiral is well-known in araneoids (see Emerit 1968; Tyshchenko 1986; Craig 1987; fig. 4.12 of Eberhard 2020). The orbs of the uloborids described here (Fig. 12*b–d*), and also of *U. walckenaerius* and *Zosis hurcana*(?) (Tyshchenko 1986; this species name does not appear in the World Spider Catalogue) were relatively radius-rich compared with those of araneoids (among which there may be genus-level differences, although the data are clearly only preliminary) (see the caption of Fig. 12). Tyshchenko (1986) saw no relation between the numbers of radii and of sticky spiral loops in the two uloborid species that he studied, but further data on other species show that the relationship does exist in other uloborids (Fig. 12).

Because in araneoids radii are more important in absorbing the momentum of prey and stopping them, while sticky spiral lines are more important in holding prey once they have been stopped (Sensenig et al. 2012), the uloborid orbs might appear to be more specialized for stopping prey than araneoid orbs. The functional significance of the relative numbers of radii and sticky spiral loops (trait #16) is less clear, however, in this family. There are no studies of the prey stopping power of uloborid webs as there are of araneoid webs (Sensenig et al. 2012). However, values of the stiffness (Young's modulus) of the radial lines and capture thread axial lines in orbs (Blackledge & Hayashi 2006; Sensenig et al. 2011) permit a comparison of the prey stopping power of the two types of lines. To compare uloborids with araneoids, we selected five small araneoid species that were near the size of the two uloborid species for which thread stiffness has been determined, *Hyptiotes cavatus* 8.1 mg and *Uloborus diversus* 6.8 mg (inferred from the similarly sized *U. glomosus*). The araneoids were the tetragnathids *Leucauge venusta* (Walckenaer, 1841) 26 mg, *Tetragnatha versicolor* Walckenaer, 1841 32 mg, and the araneids *Cyclosa conica* (Pallas, 1772) 10 mg, *Eustala* sp. 25 mg, *Mangora gibberosa* 8 mg (Opell 1996; Sensenig et al. 2011).

Young's modulus is a useful index for comparisons because it describes the energy required to extend a thread during its elastic phase, which corresponds to a thread's energy-absorbing performance during a prey strike. Reported as GPa (millinewtons / μm^2) Young's modulus takes into account differences in the diameters of the threads. At 10.7 GPa, *H. cavatus* has the stiffest radial threads, while the stiffness of *U. diversus* radii (7.8 GPa) falls within the range of the araneoids: *L. venusta* (5.6 GPa), *T. versicolor* (5.2 GPa), *C. conica* (6.4 GPa), *E.* sp. (8.2 GPa), and *M. gibberosa* (5.5 GPa). In contrast, the stiffness values of *H. cavatus* and *U. glomosus* cribellate thread axial lines (7.04 GPa and 1.05 GPa, respectively) were on the order of 100 times greater than those of the sticky spiral lines in the araneoids: *L. venusta* (0.058 GPa), *T. versicolor* (0.036 GPa), *C. conica* (0.022 GPa), *E.* sp (0.040 GPa), and *M. gibberosa* (0.053 GPa). The difference between radial and sticky spiral lines of the same species, expressed as the Young's modulus of radial lines/the Young's modulus of sticky spiral axial lines, is much less pronounced in the uloborids (the ratio ranges from 1.5 to 7.4) than in the araneoids (the ratio ranges from 97 to 291). In sum, it appears that the sticky spiral lines in uloborid orbs make a greater contribution to the web's ability to stop prey when compared with the radial lines, than in araneids, where the dominant role of radial lines has been documented previously (Sensenig et al. 2012). The relatively low numbers of sticky spiral loops in uloborid orbs may be related to the greater stiffness of their axial lines or to the relatively higher cost, in terms of both time and energy, of producing sticky lines in uloborids (Zschokke & Vollrath 1995; Bond & Opell 1998).

Another web trait that may be unique to a few uloborids has a puzzling distribution. Multiple "V" shaped non-sticky lines occurred, sometimes in large numbers, at the edges of the hubs of *W. waitakerensis* webs (Fig. 3m; Opell 1999; Eberhard 2020); they were also present in a web of *C. guarani* Grismado, 2004 (Grismado 2004). They were absent, however, in several webs of *C. parvus* (Lubin et al. 1982), and did not occur in any of the webs of other uloborid species (or to our knowledge in those of any araneoids). It is not known whether the "V" lines were built during radius construction or afterward.

Additional traits, which have less complete documentation from direct observations of construction behavior (reviewed in Eberhard 2020), suggest that there may be further behavioral traits that are unique to uloborids: production of a small, circular "protohub" early in radius construction that is subsequently removed; strict order in the construction of frame lines, with each new frame being built adjacent to the preceding one; and consistent use of the leading radius as the exit radius during radius construction. Direct observations of construction behavior are only available in a few species of *Uloborus* and *Philoponella* (Eberhard 1972, 1982, 1990, 2020), so it is too early to judge whether these details reliably distinguish uloborids from araneoids.

A final possible difference between uloborids and most araneoids concerns "replacement repairs" (Eberhard 2020). This behavior may be a tactic used by spiders that build in relatively sheltered sites or that have relatively indestructible webs; building replacement repairs enables the spider to have a greater amount of silk present in her web than the amount that she is capable of producing in a single day (Eberhard 2020). Replacement repairs seem to be widespread in orb weaving uloborids, and a tendency in uloborids to build in sheltered rather than exposed sites could make replacement repairs especially advantageous. In contrast, we know of only one group of orb-weaving araneoids, the nephilines (*Trichonephila* and *Herennia* Thorell, 1877), in which replacement repairs are routinely encountered in the webs of adults (references in Eberhard 2020) (replacement repairs are apparently absent, however, in the webs of early instar spiderling *T. clavipes* – Nentwig & Spiegel 1986; Higgins 2006; W. Eberhard unpub.). Replacement repairs also also occur, but only very rarely, in the tetragnathid *L. mariana* and the araneids *Cytophora citricola* (Kullmann 1958)*, M. duodecimspinosa* and *M.* sp. nr. *lucasi* (Keyserling, 1864) (Eberhard 2020). They seem to be completely absent in other araneoid species for which we have more extensive collections of web photos in the field, including the theridiosomatid *Epeirotypus brevipes* O. Pickard-Cambridge, 1894, the anapid *Anapisona simoni* Gertsch, 1941 and the araneids *A. bifurca, Argiope trifasciata* Thorell, 1873*, Araneus expletus* (O. Pickard-Cambridge, 1889), *A. marmoreus*, *Cyclosa conica*, *C. turbinata*, *M. olmec,* and *Micrathena gracilis* (Walckenaer, 1805). This trait is difficult to study in the field, however, because the degree to which a web is sheltered, and even whether or not rain fell the night before, may sometimes spell the difference between encountering or not encountering replacement repairs (*T. clavipes* adults, however, routinely make replacement repairs even when no rain has fallen) (Fig. 15*e*; Higgins 2006; Eberhard 2020). Replacement repairs occur in the pseudo-orbs of the psechrid *Fenecia cylindrata* Thorell, 1895 (Eberhard 2020), the stiphidiid *Neolana pallida* Foster & Wilton, 1973 (B.D. Opell, unpublished) and in other non-orb weavers (Eberhard 2020), intimating that replacement repairs may be ancestral.

In sum, incomplete data indicate that one uloborid orb web trait, primary webs, is probably unique to orb-weaving uloborids. The combination of a lack of a central hub hole and the presence of double attachments of numerous loops of tightly-spaced hub spiral to radii that produce sawtooth patterns in both threads may also be unique to uloborids. Several other traits that are widespread but less consistent in uloborid orbs also appear to be unusual in araneoid orbs, and further details of construction behavior may also differ, but data are less complete. It seems likely that all uloborid orb webs can be distinguished from araneoid orbs using combinations of the traits discussed here.

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