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A COMPARISON OF CAPTURE THREAD AND ARCHITECTURAL FEATURES OF DEINOPOID AND ARANEOID ORB-WEBS

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ABSTRACT. Orb-webs constructed by the superfamilies Deinopoidea and Araneoidea share a common architecture, but differ in both their orientation and the type of capture thread that they contain. This study uses transformational analyses to determine which web features these clades share and which features are unique to the Araneoidea and may be associated with changes in web orientation and capture thread composition. It examines relationships among spider weight, the cross sectional area of capture thread axial fibers, and features of orb-web architecture in four species of the Family Uloboridae that construct horizontal orb-webs containing cribellar thread and four araneoid species that construct vertical webs containing adhesive capture thread. In both groups, spider weight was positively related to web area and the number of radii in a web were positively related to the number of spirals. In uloborids, weight was negatively related to the number of spirals per web area and axial fiber cross sectional area was positively related to the number of radii per capture spiral turn. In araneoids, spider weight was positively related to axial fiber cross sectional area. The number of radii per capture spiral turn was greater in uloborid webs, and the weight-specific axial fiber cross sectional area was greater in araneoid webs. Many of the features that distinguish araneoid orb-webs appear to equip them to absorb the greater forces of prey strike that are associated with a vertical orb-web orientation.

Orb-weaving spiders that produce cribellar capture threads and belong to the superfamily Deinopoidea and those that produce adhesive capture threads and belong to the superfamily Araneoidea share a common web architecture by virtue of their common ancestry (Coddington 1986a,b, 1990a,b; Coddington & Levi 1991). The transition from dry, cribellate orb-webs to viscous, adhesive orb-webs is associated with an increase in species diversity (Bond & Opell pers. obs.) and with changes in web orientation and capture thread composition that have the potential to alter orb-web architecture and performance. This study uses phylogenetic techniques to determine which web features are shared by both deinopoid and araneoid orb-weavers and which features are unique to each clade and may thus reflect differences in the operational dynamics of their webs. It examines associations among spider weight, the cross sectional area of capture thread axial fibers, and orb-web architectural features. These relationships provide a better understanding of factors that have constrained the design and dynamics of spider orb-webs and changes that have been associated with the evolution of araneoid orb-weavers.

Deinopoid and araneoid orb-weaving spiders are distinguished by differences in web orientation and in the material that covers the axial fibers of their prey capture threads. The horizontal orientation of orb-webs spun by members of the Deinopoidea is plesiomorphic for the Orbiculariae, whereas the vertical orientation of orb-webs constructed by the Araneoidea is a synapomorphy of this clade (Bond & Opell pers. obs.). As a result of their vertical orientation, araneoid orb-webs tend to intercept faster flying insects and, therefore, are often required to absorb greater forces of impact than are cribellate orb-webs (Craig 1987a; Eberhard 1989). Thousands of fine cribellar fibrils surround the axial fibers of cribellar capture threads produced by the Deinopoidea (Eberhard 1988; Eberhard & Pereira 1993; Opell 1990, 1993, 1994a-c, 1995, 1996; Peters 1983, 1984, 1986, 1992), whereas a chemically complex viscous solution that coalesces into droplets surrounds the homologous axial fibers of adhesive capture threads produced by orb-weaving Araneoidea (Peters

1995; Tillinghast et al. 1993; Townley et al. 1991; Vollrath 1992; Vollrath et al. 1990; Vollrath & Tillinghast 1991). Each of the droplets of adhesive thread draws in a length of axial fiber that can be played out when tension on the thread increases (Vollrath & Edmonds 1989). This windlass increases the extensibility of adhesive threads (Köhler & Vollrath 1995) and, thereby, helps maintain web tension and probably reduces capture thread tangling under windy conditions.

Differences in architecture can affect orb-web performance. For example, among araneoid spiders, orb-webs that have a large number of radii relative to the number of spiral turns they contain (radius-rich webs) more effectively stop heavier or faster flying prey than do radius-poor webs (Craig 1987b; Eberhard 1986). Some of these differences are associated with differences in spider weight. In araneoid orb-weavers, spider weight is directly related to the diameter of the axial fibers within a capture thread (Craig 1987a) and in uloborid orb-weavers, spider weight is directly related to web area and web stickiness (Opell 1996).

Web features such as these have been examined principally among the Araneoidea (e.g., Craig 1987a,b; Eberhard 1986; Risch 1977; Witt et al. 1968) using correlation or regression techniques. Since these studies were done, transformational analysis has become the accepted method of analyzing relationships of features in a phylogenetic context (Harvey & Pagel 1991). Therefore, I use this comparative method to examine relationships among spider weight, the cross sectional areas of capture thread axial fibers, and features of web architecture. This analysis found five significant relationships. Two relationships are shared by both deinopoid and araneoid clades and are hypothesized to be synapomorphies of the Orbiculariae. Two relationships are unique to the Deinopoidea and one relationship is unique to the Araneoidea. Changes in these three relationships are hypothesized to be associated with the origin of araneoid orb-weavers.

METHODS

Species studied.—Ten species of web-spinning spiders were studied. Their phylogenetic relationship is shown in Fig. 1. Data for the five araneoid species are taken from the studies of Craig (1987a,b). To these I added data for five species of the family Uloboridae. These species were selected to represent the family's diversity by including representatives of its major clades (Coddington 1990b) and included the orb-weavers, *Waitkera waitakerensis*, *Siratoba referena*, *Uloborus glomosus*, and *Octonoba sinensis* and the triangle-web species *Hyptiotes cavatus*. *Hyptiotes cavatus* was not included in the final comparison of web features, but was used to add resolution to the phylogenetic analysis that generated data used in this comparison. Voucher specimens of each species are deposited in Harvard University's Museum of Comparative Zoology.

Web measurements.—Orb-web architecture is sometimes portrayed as being highly stereotypic and species-specific. For example, Foelix (p. 128, 1996) states that "The number of radii varies little within a particular species of orb weaver, and is often characteristic of that species. . . .These numbers of radii imply that many orb weavers show a species-specific geometry in their webs. It is thus often possible to identify a certain spider solely by its characteristic web structure." However, while acknowledging that "in a local fauna species of orbweavers can often be determined from their webs", Eberhard (p. 342, 1990) documents a number of factors that contribute to intraspecific differences in orb-web architecture and cautions that: "The impression of species-specificity may usually, however, be the product of lack of information. . . . Given the long-standing and repeated documentation of substantial intraspecific variation in at least gross web characteristics such as numbers of radii, spiral loops, spacing between loops, angle of web plane with the vertical, web area, top-bottom asymmetry, and stabilimenta, Levi's prediction that species-specificity will be uncommon seems likely to be correct."

This study attempts to minimize the potential problem of intraspecific variation in uloborid web features by using species means in transformational analyses. As only one web per individual was measured, it does not address the intra-individual variability in web features that may result from differences in nutritional levels or reproductive status. However, the minimum sum of squares algorithm used by the transformational analysis minimizes the hypothesized evolutionary changes

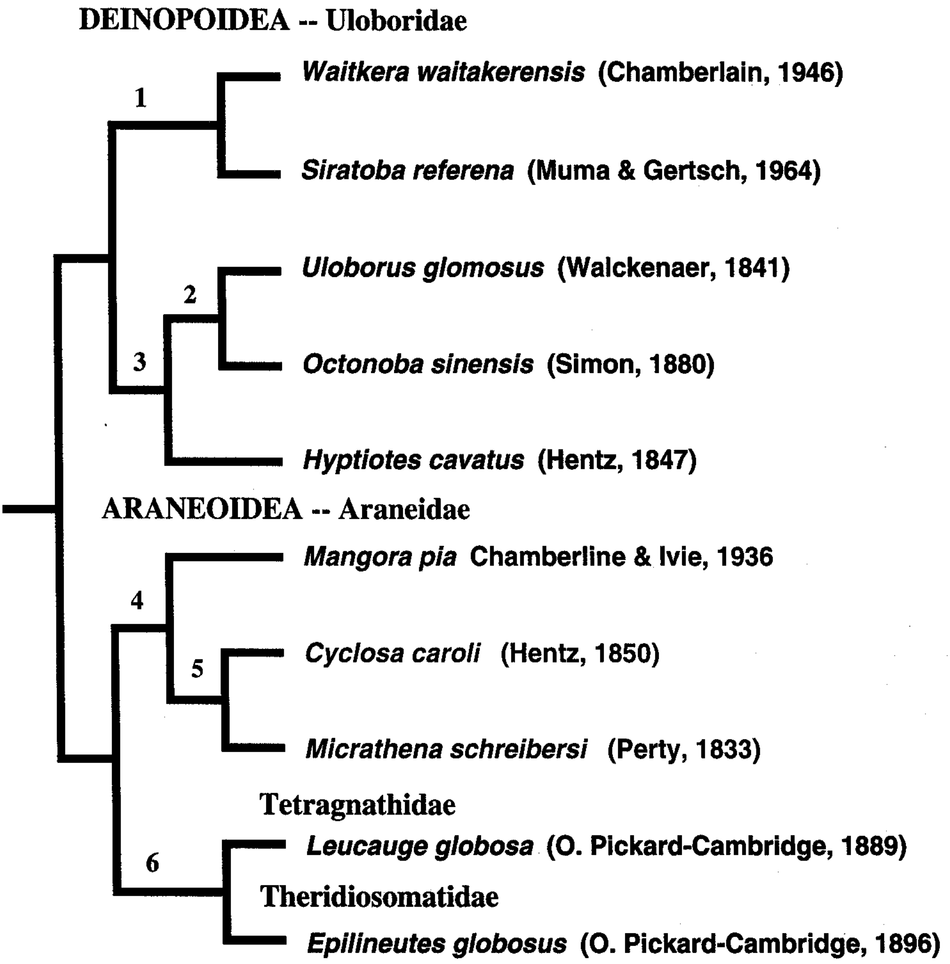

Figure 1.—Cladogram of the species included in this study (from Coddington 1990b; Coddington & Levi 1991; Levi 1985).

that are used in statistical analyses and, thereby, makes the results of these analyses conservative.

I dusted the webs produced by adult females with corn starch to make their threads more visible (Carico 1977) and photographed only webs that were not damaged. I photographed the webs of *W. waitakerensis* in the field and those of *O. sinensis* in a greenhouse. In field photographs of the other three species, it was difficult to distinguish the threads from background vegetation. Therefore, I allowed these spiders to build their webs in individual plastic boxes that contained a framework of wooden dowel rods and photographed these webs against a black background. Spiders were placed into boxes immediately after being collected and were not fed. Those that did not build a web within three days of capture were released. Boxes were housed in an environmental chamber with a 1 h dawn, 11 h light, and 1 h dusk light cycle. Temperature was maintained at 24 °C and relative humidity ranged from 80% during the night to 70% at dusk and dawn, to 60% during the day.

After photographing a spider's web, I collected and weighed to the nearest 0.00 mg the spider that produced it. Conspecific web capture has not been studied in the species that were included in this study. Therefore, there is a small possibility that some spiders whose webs were photographed may not have actually constructed the webs in which they were found.

It is possible that the boxes in which spiders constructed their webs may have affected the size of these webs. To assess this for the two orb-weaving species, I determined the mean framework diameter and the maximum capture spiral diameter for each species and compared this with the dimensions of the plastic boxes in which these spider's constructed their webs. Mean framework diameter was computed from the minimum and maximum lengths of straight lines that extended across a web's center to its outermost, non-sticky framework threads. Maximum capture spiral diameter is the length of a straight line extending across a web's center to its outermost capture thread. The dowel rods inside these boxes formed a frame with inner dimensions of 29.0 × 21.5 cm, although some spiders attached their threads to the walls of boxes and, therefore, perceived the space available for web construction as 1–2 cm greater than this. The mean web diameters for *S. referena* was 11.7 cm (n = 26, SE = 0.7) and that for *U. glomosus* was 18.7 cm (n = 29, SE = 0.5). The maximum capture spiral diameter for *S. referena* was 11.8 cm (n = 26, SE = 0.7) and for *U. glomosus* was 19.1 cm (n = 29, SE = 0.5). Thus, the mean web diameter of *S. referena* is 54% and the maximum capture spiral diameter is 54% of the minimum box dimension. For *U. glomosus* these values are 87% and 89%, respectively. Therefore, box size clearly did not restrict the size of *S. referena* webs and probably did not cause *U. glomosus* to construct smaller webs than those found in the field.

To assess the effect of box size on the triangle-webs of *H. cavatus*, I compared the length of the second radius (the top of the web being the first of four radii) in webs constructed by adult females in the field with those constructed in the laboratory. The length of this radius is highly correlated to other web parameters (Opell unpubl. data) and is, therefore, a good index of web size. The mean length of the second radius in webs constructed in the field was 11.1 cm (n = 19, SE = 0.7) and that for webs constructed in the laboratory was 14.3 cm (n = 30, SE = 0.5). The values for both populations were normally distributed (Shapiro-Wilk W-statistic $P > 0.45$) and a t-test showed that their means were different ($t = 3.928$, $P < 0.001$). This indicates that the structural spacing that *H. cavatus* typically encounters in the field limits the size of its web to a greater degree than that provided in the laboratory. Consequently, webs constructed in the laboratory may be considered to be of optimal size.

From enlarged photographic prints I counted the number of radii and spirals in each web and measured the web's area with a digitizing tablet. There are two measurements of web area that can be taken: total area, the area inscribed by a web's frame lines, and capture area, the area between a web's outermost and innermost capture spirals. I measured total web area because it seemed a better index of web size for comparisons of web architecture, whereas capture area seems more appropriate for assessing a web's prey capture potential. Craig (1987b) does not report total web area, but does give the mean radius length for each species she studied. I used these data to compute the total area of each species' web as if it were a circle.

Thread diameters.—The diameters of uloborid axial fibers are taken from table 2 in Opell (1996). For cribellar threads, two axial fibers were measured per web. This approach assumes that axial fiber diameter is uniform within a web and does not address the possibility that axial fiber diameter changes during the course of capture spiral production. The cribellar fibrils of these threads help hold their axial fibers apart, allowing the diameter of a single fiber to be measured under a transmission electron microscope. The total axial fiber cross sectional area of these cribellar threads was computed as the sum of the cross sectional areas of their two fibers. In contrast, even the interdroplet regions of araneoid capture threads are coated by a thin layer of viscous material. Although the water in this material evaporates under the high vacuum of an electron microscope, it leaves a thin, electron-dense residue that coats the axial fibers, making them appear as a single strand, whose individual fibers cannot be distinguished under either the scanning or transmission electron microscope (Craig 1987b; Opell unpubl. obs.). I computed the combined cross sectional areas of the axial fibers of these threads as the sum of the areas of two circles, each with a diameter of half the capture thread diameter reported by Craig (1987b). This provides a more appropriate estimate of axial fiber cross sectional area than treating the contiguous fibers as if they were a single fiber.

Statistical analysis.—The relationships among spider weight, thread diameter, and web features cannot be determined using traditional regression techniques, as the species included in this study are evolutionarily related, and their values are not strictly independent (Harvey & Pagel 1991). To minimize the effect of phylogenetic position, I employed Huey and Bennett's (1986) method for evaluating the relationships among continuous variables whose states are hypothesized to be functionally linked. This method has three steps: 1) the state of each character in a taxon's most immediate hypothetical ancestor is determined, 2) the change from this ancestral state to the state expressed by extant members is computed for each character, and 3) the relationship between these changes in character states are evaluated by Pearson correlation. If this analysis shows that changes (either positive or negative) in two characters are correlated, then their states can be considered to have coevolved. I determined ancestral values for uloborids and araneoids separately using the unrooted, minimized sum of squared changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison & Maddison 1992). Although this study compares the only uloborids that construct horizontal orb-webs and araneoids that construct vertical orb-webs, *H. cavatus* and *L. globosus* were included in determinations of ancestral values to increase the resolution of these computations.

As spider weight has the potential to affect web features, I used a one way ANOVA to determine if weight differed between: 1) uloborid and araneoid species, 2) uloborids that spin horizontal webs and araneoids that spin vertical webs, 3) uloborid and araneoid species that produce horizontal webs and those that produce vertical webs. These tests showed no differences in spider weight that would compromise this study's findings (f = 0.95–1.12, P = 0.32–0.36).

RESULTS

Values and their normality.—Because all values or their natural logs are normally distributed, parametric statistics were used in their analysis. Tables 1 and 2 give values for uloborid and araneoid species and Table 3 presents the ancestral values used in transformational analyses. A Shapiro-Wilk W-statistic test of normality showed that changes in axial fiber cross sectional area, the number of radii per web area, the number of spirals per web area, and in the number of radii per spiral turn were normally distributed ($P > 0.28$) for both the four uloborid species that constructed horizontal webs and the four araneoid species that constructed vertical webs. Change in spider weight was not normally distributed ($P = 0.002$) and the normality of change in web area was questionable ($P = 0.059$). However, changes in the natural logs of these two latter values were normally distributed ($P > 0.48$) for both the four orb-weaving uloborids and the four araneoid orb-weavers that constructed horizontal orb-webs. The number of radii per spiral turn and the weight-specific cross sectional area of axial fibers (Table 5) were normally distributed (Shapiro-Wilk W-statistic $P > 0.30$) for both deinopoid and araneoid clades.

Correlation between features.—Five features were shown by Pearson correlation to be significantly correlated for at least one group of orb-weavers (Table 4). Given the small sample size for each clade of spiders and the high correlation values obtained in these analyses, I accept as significant correlations with $P < 0.10$. For both cribellate and adhesive orb-weavers spider weight and web area are positively correlated, as are the number of radii per web area and the number of spirals per web area. However, the transition from cribellate to adhesive orbs appears to have been associated with three changes: 1) the gain of a positive relationship between spider weight and capture thread cross sectional area, 2) the loss of a negative relationship between spider weight and the number of spirals per web area, and 3) the loss of a positive relationship between web cross sectional area and the number of radii per spiral turn.

Differences between uloborid and araneoid orb-webs.—Both the number of radii per spiral turn and the weight-specific cross sectional area of axial fibers differed between uloborids with horizontal orb-webs and araneoids with vertical orb-webs (Table 5). The number of radii per spiral turn was greater in uloborid orb-webs and the weight-specific axial fiber cross sectional area was greater in araneoid orb-webs.

DISCUSSION

Common web features.—Two architectural relationships appear to be plesiomorphic for

Table 1.—Features of the webs and threads of five species of Uloboridae. Mean ± 2 standard errors, sample size. Weights are those of individuals whose web features were measured. *Although many webs constructed by these two species are essentially horizontal, some are constructed at angles of up to about 45°.

	Waitkera waitakerensis	*Siratoba referena*	*Uloborus glomosus*	*Octonoba sinensis*	*Hyptiotes cavatus*
Web orientation	horizontal	horizontal*	horizontal	horizontal*	vertical
Weight (mg)	7.84 ± 0.70 $n = 32$	3.93 ± 0.44 $n = 26$	7.16 ± 0.76 $n = 29$	12.16 ± 1.58 $n = 24$	8.41 ± 1.22 $n = 30$
Axial fiber:					
diameter (nm)	236 ± 44 $n = 6$	292 ± 70 $n = 5$	307 ± 46 $n = 5$	340 ± 30 $n = 17$	419 ± 22 $n = 17$
cross sectional area × 2 (μm^2)	0.09 ± 0.04 $n = 6$	0.14 ± 0.06 $n = 5$	0.15 ± 0.04 $n = 5$	0.19 ± 0.04 $n = 17$	0.28 ± 0.02 $n = 15$
weight-specific area (μm^2/mg × 10^{-3})	19 ± 28 $n = 6$	31 ± 13 $n = 3$	21 ± 6 $n = 5$	15 ± 4 $n = 16$	40 ± 6 $n = 15$
web area (cm^2)	177 ± 28 $n = 32$	109 ± 26 $n = 26$	289 ± 32 $n = 29$	642 ± 100 $n = 24$	155 ± 16 $n = 30$
Radii:					
length	4.0 ± 0.4 $n = 25$	3.0 ± 0.5 $n = 23$	6.3 ± 0.5 $n = 27$	8.8 ± 0.8 $n = 24$	— —
number	27 ± 2 $n = 32$	35 ± 2 $n = 26$	34 ± 2 $n = 29$	50 ± 2 $n = 24$	4 ± 0 $n = 30$
number/area	0.17 ± 0.02 $n = 32$	0.42 ± 0.08 $n = 26$	0.12 ± 0.02 $n = 29$	0.9 ± 0.02 $n = 24$	0.33 ± 0.02 $n = 30$
Capture thread spirals:					
number	12 ± 2 $n = 32$	14 ± 2 $n = 26$	13 ± 2 $n = 29$	17 ± 2 $n = 24$	16 ± 2 $n = 30$
number/area	0.07 ± 0.00 $n = 32$	0.15 ± 0.02 $n = 26$	0.5 ± 0.00 $n = 29$	0.3 ± 0.00 $n = 24$	0.11 ± 0.02 $n = 30$
radii/spiral turn	2.37 ± 0.14 $n = 32$	2.64 ± 0.20 $n = 26$	2.77 ± 0.22 $n = 29$	2.98 ± 0.24 $n = 24$	0.12 ± 0.02 $n = 30$

orb-weaving spiders by virtue of their presence in both deinopoid and araneoid orb-weavers. Both clades exhibit a positive relationships between spider weight and web area and between the number of radii per web area and the number of spirals per web area (Table 4).

The positive relationship between spider weight and web area in both clades shows that this relationship plays an important role in the foraging dynamics of orb-weaving spiders. As spider weight is directly related to metabolic rate (Anderson & Prestwich 1982) and as web size is directly related to prey capture (Brown 1981), this relationship indicates that an orb-web's ability to capture prey tends to scale to a spider's metabolic needs. However, it is important to note that other factors may also affect web performance. These include prey availability in the microhabitat where a web is placed (Riechert & Cady 1983; Wise & Barata 1983; Craig et al. 1994), web and spider visibility to insects (Craig 1988, 1990; Craig & Bernard 1990; Craig & Ebert 1994; Craig & Freeman 1991), web orientation (Chacón & Eberhard 1980; Eberhard 1989), the ability of a web to absorb the force of an insect strike, web stickiness (Craig 1987b; Eberhard 1986, 1989), spider response time (Eberhard 1989), and the presence of other orb-weaving species (Spiller 1984).

An interspecific comparison of uloborid species (Opell 1996) showed a direct relationship between spider weight and web area, but

Table 2.—Features of the webs and threads of five araneoid species, as given by Craig (1987a, b). Mean ± 2 standard errors, sample size. *No variance was provided, as indices were computed from species means.

	Mangora pia	*Cyclosa caroli*	*Micrathena schreibersi*	*Leucauge globosa*	*Epilineutes globosus*
Web orientation	vertical	vertical	vertical	horizontal	vertical
Weight (mg)	21.2	5.3	146	2.7	0.8
Axial fibers of capture thread:					
diameter (nm)	1900	1038	3040	760	350
cross sectional area (μm^2)	1.42	0.42	3.63	0.23	0.05
weight-specific area (μm^2/mg × 10^{-3})	67	79	25	85	63
Web area (cm^2)	216 ± 0.7 $n = 42$	150 ± 0.5 $n = 22$	347 ± 1.9 $n = 16$	125 ± 0.7 $n = 16$	61 ± 1.7 $n = 33$
Radius length (cm)	8.3 ± 0.68 $n = 42$	6.9 ± 0.56 $n = 22$	10.5 ± 1.10 $n = 16$	6.3 ± 0.66 $n = 16$	4.4 ± 1.14 $n = 33$
Radii/web area	0.24*	0.32 ± 0.06 $n = 22$	0.13 ± 0.02 $n = 16$	0.15 ± 0.02 $n = 16$	0.06*
Capture spirals/web area	0.25*	0.30 ± 0.20 $n = 10$	0.09 ± 0.02 $n = 9$	0.18 ± 0.04 $n = 8$	0.10*
Radii/spiral turn	2.20*	1.10*	1.40*	0.83*	0.11*

studies of araneoids lead to contradictory conclusions. The latter situation may be explained by the fact that these studies are a mix of intraspecific and interspecific comparisons and that the results of interspecific studies were not analyzed in a phylogenetic context. Risch (1977) measured the weights and spiral areas (area encompassed by the web's inner- and outer-most spiral turn) of juveniles and adult females of four araneid species. His data do not show a strong relationship between these variables, although the species he studied were more similar in weight than the araneoid species included in the current study. Several intraspecific comparisons of the size of adult female araneoids and the size of their webs show that larger or heavier spiders tend to construct larger webs (Eberhard 1988; Witt et al. 1968), one found no such association in two species (Brown 1981), and another found that adding weights to adults reduced the length of thread in their webs (Christensen et al. 1962). These studies and those of the effect of silk supply, and, by implication, spider nutrition, on web size (Eberhard 1988) demonstrate that web size is plastic and document some of the proximate factors that influence this parameter. Phylogenetic comparisons, like those presented in this study, provide a complementary perspective by documenting ultimate factors that influence orb-web architecture.

Table 3.—Ancestral values used in transformational analyses. The position of these six nodes is given in Figure 1.

	Node 1	Node 2	Node 3	Node 4	Node 5	Node 6
Weight (mg)	7.83	9.76	9.96	33.4	61.6	6.9
Total area of axial fibers (μm^2)	0.21	0.21	0.29	1.29	1.78	0.31
Web area (cm^2)	160	396	248	208	235	120
Radius length (cm)	4.3	7.0	—	7.7	8.4	5.7
Radii/area	0.28	0.15	0.24	0.22	0.22	0.14
Spirals/area	0.11	0.06	0.09	0.14	0.18	0.14
Radii/spiral	2.23	2.38	1.40	1.68	1.39	0.96

Table 4.—Comparison of the relationships found among four cribellate orb-weaving species and four adhesive orb-weaving species using Pearson correlation. Significant values ($P < 0.10$) are indicated by an asterisk (*).

	Horizontal, cribellate orb-webs	Vertical, adhesive orb-webs
Change in L_n weight and in L_n web area	$r = 0.94$* $P = 0.056$*	$r = 0.96$* $P = 0.038$*
Change in radii per web area and in spirals per web area	$r = 0.99$* $P = 0.007$*	$r = 0.91$* $P = 0.092$*
Change in L_n weight and in spirals per web area	$r = -0.92$* $P = 0.078$*	$r = -0.75$ $P = 0.254$
Change in axial fiber cross sectional area and in radii per spiral turn	$r = 1.00$* $P = 0.001$*	$r = 0.37$ $P = 0.634$
Change in L_n weight and in L_n axial fiber cross sectional area	$r = 0.16$ $P = 0.844$	$r = 0.94$* $P = 0.062$*

The positive relationship between the number of radii per web area and the number of spirals per web area factors out web area and, therefore, reflects a positive relationship between the number of radii and the number of spirals in a web. This relationship has been noted by Eberhard (1972, 1986), who concluded that, although there are exceptions, the number of radii and spiral turns "are about equal". Although the current study is based on only nine orb-weaving species, it suggests that orb-webs tend to have more radii than spirals. The webs of the nine orb-weaving species studied had a mean radii per spiral turn ratio of 1.88. However, this study included four species of the family Uloboridae, a group that Eberhard (1986) considers to have a greater than typical number of radii. When these uloborid species are excluded, the mean ratio drops to 1.23 radii per spiral turn. Among araneoids, the number of radii decrease as spiders develop (Risch 1977; Wiehle 1927; Witt et al. 1968). This may indicate that larger araneoid species tend to have fewer radii in their webs than do smaller species. However, as only one very large araneoid species was included in the current study, size alone cannot account for the lower radii per spiral turn ratio in araneoid webs (Table 5).

Differences in cribellate to adhesive orb-web.—The evolution of the Araneoidea was associated with a shift from horizontal orb-webs that contained cribellar capture threads to vertical orb-webs that contained adhesive capture threads (Bond & Opell pers. obs.). The vertical orientation of araneoid orb-webs subjects them to greater forces of prey impact than does the horizontal orientation of uloborid orb-webs (Craig 1987a; Eberhard 1989). This kinetic energy is absorbed in two major ways: some is borne by the web's radii and frame threads and some is dissipated by aerodynamic damping as the web extends and its capture threads resist movement through the air (Lin et al. 1995).

The greater weight-specific cross sectional

Table 5.—Comparison of two web features in uloborid and araneoid orb-webs. Mean ± 2 standard errors. Below the name of each index appears the results of a t-test.

	Uloborid species with horizontal orb-webs ($n = 4$)	Araneoid species with vertical orb-webs ($n = 4$)
Radii/spiral turn ($t = 3.30$, $P = 0.016$)	2.69 ± 0.26	1.20 ± 0.86
Weight-specific axial fiber cross sectional area $\mu m^2/mg \times 10^{-3}$ ($t = 3.04$, $P = 0.023$)	22 ± 7	59 ± 23

areas of araneoid axial fibers (Table 5) indicate that these adhesive capture threads are stronger than those constructed by uloborids and, thus, better adapted to transfer greater forces to the web's stronger radial threads. For the five araneoid species, there is a positive relationship (Pearson $r = 0.97$, $P = 0.007$) between the total axial fiber cross sectional area computed in this study and the capture thread tensile strength reported by Craig (1987a). As the axial fibers of cribellar and adhesive capture threads are homologous, the cross sectional area of axial fibers in cribellar thread is probably also a good index of thread tensile strength. Although the spectral properties of light reflected by cribellar and adhesive threads differ (Craig & Bernard 1990), these measurements include the non-homologous cribellar fibril and adhesive material that covers the axial fibers. Therefore, these differences do not necessarily show that the protein composition of the axial fibers of these threads differs.

Architectural differences between uloborid and araneoid orb-webs suggest that their functional dynamics also differ. Radius-rich webs, like those constructed by uloborids (Table 5), tend to be stiff and radius-poor webs, like those constructed by araneoids, tend to be more extensible (Craig 1987b). The study of Lin et al. (1995) suggests that the more extensible a web is, the more kinetic energy it is able to dissipate through aerodynamic dampening. Therefore, the greater extensibility of adhesive capture threads (Vollrath & Edmonds 1989; Köhler and Vollrath 1995) may enhance aerodynamic dampening by increasing overall web extensibility. The greater extensibility of adhesive capture thread may also serve to dissipate some force in the immediate area of a prey strike before transferring the remanding force to adjacent threads.

Additional evidence that the replacement of cribellar threads by adhesive threads changes web dynamics comes from a comparison of vertical and horizontal adhesive orb-webs. If differences between uloborid and araneoid orb-webs are associated principally with differences in web orientation, then they should also be observed when horizontal and vertical adhesive orb-webs are compared. However, Craig's (1987a) data suggest that horizontal araneoid orb-webs have fewer, not more, radii per spiral turns than vertical araneoid orb-webs. This is contrary to the difference between horizontal uloborid and vertical araneoid orb-webs observed in this study and suggests that the replacement of cribellar threads by adhesive threads may also enhance a web's ability to dissipate the force of a prey strike. It may also indicate that the radial threads of araneoid orb-webs are stronger than those of deinopoid orb-webs, either because they have greater diameters or different silk composition.

The lower radius-to-capture-spiral ratio of araneoid orb-webs may also contribute to the positive relationship between spider weight and axial fiber cross sectional area that characterizes vertical araneoid orb-webs (Table 4; Craig 1987a). As capture threads become a more prominent component of the vertical araneoid orb-web, they play a greater role in transferring force to the web's stiffer radial threads (Lin et al. 1995) and must be strong enough to withstand this force. However, there appears to be a limit on the amount of material that an orb-weaving spider can devote to capture thread production (Eberhard 1972, 1989; Peters 1937; Witt et al. 1968). As the total volume of adhesive capture thread in a spider's web is directly related to spider weight (Opell unpubl. obs.), axial fiber diameter may ultimately be determined by the competing requirements that a spider must produce a length of capture thread that is long enough and sticky enough to capture sufficient prey and strong enough to withstand the force of prey impact. As a spider's weight affects both its metabolic demand (Anderson & Prestwich 1982) and total thread volume, it is not surprising that the cross sectional area of araneoid axial fibers is related to spider weight.

In uloborids, the cross sectional area of capture thread axial fibers is not related to spider weight, but instead to the maximum distance that a capture thread spans in the web (Opell 1994d). This difference and the smaller weight-specific axial fiber cross sectional areas of cribellar threads suggest that different factors influence axial fibers of uloborids and araneoids. The lower forces of prey impact that uloborid webs typically experience may not require the axial fibers of their capture threads to be as strong. Additionally, as in araneoids, the volume of material that these spiders can devote to capture thread production appears to be limited (Eberhard 1972). Therefore the large amount of silk volume that uloborids must devote to the cribellar fibrils of their capture threads to achieve thread stickiness (Opell 1994b, 1996) may indirectly restrict that amount of silk that can be expended as axial fibers.

Cribellate orb-webs are characterized by a negative relationship between spider weight and the number of spirals per web area and by a positive relationship between axial fiber cross sectional area and the number of radii per spiral turn. Neither relationship is present in araneoids. The first relationship indicates that spiral spacing increases as spider size increases. Spiral spacing may be more highly constrained in uloborids because the webs that these spiders construct appear to be less well equipped than araneoid orb-webs to retain prey and because uloborids are less well equipped than araneoids to subdue intercepted prey. Not only do horizontal webs retain prey for shorter periods of time than vertical webs with threads of the same stickiness (Eberhard 1989); but, relative to the weight of the spider that produced them, cribellar capture threads are less sticky than adhesive threads (Opell unpubl. obs.). Additionally, uloborids lack poison glands and must rely entirely on silk wrapping to quiet prey and prevent their escape from the web (Lubin 1986; Opell 1979). As orb-webs trap prey more efficiently when capture spiral spacing exceeds prey diameter (Chacón & Eberhard 1980; Eberhard 1986), the more closely spaced spirals of orb-webs constructed by small uloborid species may be particularly important in equipping these webs to intercept prey that they can retain and that spiders can subdue. The greater stickiness of adhesive capture threads (Opell unpubl. obs.) may further increase the prey capture efficiency of vertical araneoid orb-webs and allow their spiral spacing more latitude to differ in ways that adapt webs to a particular habitat or prey type.

In uloborids, but not in araneoids, axial fiber cross sectional area increases as the number of radii per spiral turn increases. In view of the positive relationship between the number of radii per web area and the number of spiral turns per web area, this indicates that increased axial fiber cross sectional area adds to overall web strength by complementing an increase in the number of radii rather than by compensating for a decrease in the relative number of spiral turns. The lower extensibility of cribellar threads (Köhler & Vollrath 1995) and the stiffer, radius-rich webs of uloborids (Table 5) may help explain why the cross sectional areas of their capture threads responds to this change in web architecture and those of araneoids do not. If uloborid orb-webs have a lower ability to dissipate force through extension and aerial dampening, they may meet this challenge by becoming stronger. If the axial fibers' chemical structure is unchanged, then increased strength is gained by increased cross sectional area.

Conclusions.—Orb-webs constructed by members of the deinopoid and araneoid clades share many features, including an area that is related to spider weight. However, this study shows that there are important architectural differences between the webs that are spun by members of these sister clades. The functional implications of these differences are consistent with the observation that vertical araneoid orb-webs typically experience greater forces of prey impact than do deinopoid orb-webs. Compared to horizontal orb-webs, the vertical orb-webs of araneoids appear to have stronger capture thread axial fibers and to be better equipped to implement aerodynamic dampening by virtue of their lower radius-to-spiral ratio. The greater extensibility of adhesive capture thread may contribute in a minor way to overall web extensibility and force dissipation, but the model of orb-web dynamics developed by Lin et al. (1995) suggest that it does not play a major role. Therefore, the selective advantage of adhesive capture thread over cribellar capture thread may be due principally to the greater economy and greater stickiness of adhesive thread (Opell unpubl. data) and to its reduced ultra violet reflectance (Craig & Bernard 1990) that makes it less visible to insects and allows araneoid orb-weavers to occupy an expanded range of microhabitats (Craig et al. 1994).

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