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FUNCTION AND PHYLOGENY OF SPIDER WEBS¹

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INTRODUCTION

A general discussion of the designs and functions of the silk structures spiders use to capture prey has not been attempted since the book of Witt et al (319). Knowledge has increased so greatly in the intervening years that complete coverage is now impossible in a review article. I have cited primarily more recent and general publications. Related aspects of web biology not emphasized here are reviewed in papers on particular taxonomic groups (260), general feeding ecology (233), choice of websites (131, 232, 234), inter- and intra-specific competition (and the lack of it) (273, 275, 314), ecophysiology (192), web removal (20), sexual behavior (139, 238), vibration transmission in webs (175), neurobiology (3), attack behavior (237, 279), communication (320), energetics of web-building (227), timing of web construction (229), cues used for orientation during web construction (80, 308), structure and composition of web lines (224, 290), physical properties of silk (109, 322), and silk glands (138).

Due to the numbers of papers on orb webs, orbs are emphasized over non-orbs. The imbalance in research is strong (the ratio in the reference section is about 2:1 orb:non-orb, despite the fact that the ratio in numbers of species must be closer to 1:2 (H. W. Levi, personal communication). At least partially repairing this imbalance is a pressing need.

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IS WEB DESIGN A USEFUL TAXONOMIC CHARACTER?

Some animal constructs are useful in distinguishing closely related species (117), and it is not unusual to read that orb design is a genus- or species-specific character (17, 96, 186, 210, 235, 261, 301, 318). It is indeed true that in a local fauna species of orbweavers can often be determined from their webs (11, 96, 261).

The impression of species-specificity may usually, however, be the product of lack of information; knowing the characteristics of relatively distantly related local species, but not those of many close relatives, will give one a false impression that all are distinctive. Given the long-standing (226) and repeated documentation of substantial *intraspecific* variation in at least gross web characters such as numbers of radii, spiral loops, spacing between loops, angle of web plane with vertical, web area, top-bottom asymmetry, and stabilimenta (61, 83, 85, 159, 226, 235, 267, 299), Levi's prediction (153) that species-specificity will be uncommon seems likely to be correct. Limited comparisons of 2-4 congeners in two araneid genera have shown statistical differences in some web characters (174, 235, 295, 296, 300).

Perhaps instead orb designs will prove to be useful characters at higher taxonomic levels. Although descriptions of small numbers of species have been made with this in mind (153, on *Argiope*, *Cyclosa*; 32, 235, 295, 299, on *Araneus*), this possibility has not yet been carefully tested. The degree of both *intraspecific* variation and *interspecific* uniformity in different web characters of numerous congeneric species will have to be determined to decide which web characters can be usefully compared. Coddington's work on theridiosomatids (29) is a step in this direction, though specific mention is made of webs of an average of only 2.5 ± 1.3 species/genus in the 8 web-building genera. Subsequent information has already made it necessary to substantially expand the range of webs made by one theridiosomatid genus (85). Attempts to characterize a "genus web" for *Araneus* (32, 235) do not fit the webs of some species in this large genus (97, 110). In several araneoid and uloborid genera, at least some apparently basic web characters are definitely *not* constant within the genus (*Eustala*—64, 68, 75; *Araneus*—32, 97, 110, 199, 235, 271, 291; *Alpaida*—76, 157; *Tetragnatha*—76, 155, 199, 265, 268; *Wixia*—76, 276; *Wendilgarda*—29, 85; *Uloborus*—61, 163, 166; *Philonella*—8a, 163). Some suprageneric groupings (e.g., Cycloseae of Simon, the Synotaxidae of Forster et al) also do not reflect similarities of web design (181, 98).

It may well be that in some other groups some aspects of orb design are indeed genus-specific. For instance, all known *Cyrtophora* "orbs" are fine-meshed, nonsticky, radially organized horizontal sheets with lines converging

on a hub which are hung in a mesh (161, on *cicatrosa*, *cylindroides*, and *monulfi*; 141, on *citricola*; 160, on *moluccensis*; 269, on *exanthematica* and *unicolor*; W. G. Eberhard, unpublished, on *nympha*). Orb characters may even link genera (e.g., *Cyrtophora* with *Mecynogea*, *Nephila* with *Nephilengys* and *Herennia*, *Argiope* with *Gea*). The modified orb of *Deinopus* may characterize the entire family (31). Web characteristics may eventually be found that will characterize even the genera mentioned above as lacking characteristic designs, or that will justify intrageneric groupings. The data and analyses necessary to demonstrate such usefulness have not yet been assembled, however.

Just as in orbs, non-orb webs also show both clear divergences within groups and dramatic convergences between groups. The related and primitive *Austrochilus*, and *Progradungula* have quite different webs (99, 112, 259), and several genera close to *Progradungula* have secondarily lost their webs (99). Web designs vary widely within the theridiid genera *Achaearanea* (e.g. 30, 52, 62, 167, 173, 269) and (to a lesser extent) *Latrodectus* (147, 282, 284) as well as the amaurobiid genus *Titanoeca* (134, 283) (*Achaearanea* may be polyphyletic, however—98). There may be species-specific differences in the designs of *Diguetia* sheet webs (200) and *Latrodectus* tangle and gumfoot webs (282, 284). On the other hand, intraspecific variation occurs in such basic aspects of web design as the presence or absence of a sheet, and presence or absence of a mesh above the sheet in the theridiid *Anelosimus jucundus* (194), and the presence or absence of sticky “gum foot” lines near the substrate in *Latrodectus geometricus* and *Theridion purcelli* (147).

Convergent evolution of horizontal aerial sheets with a mesh above and/or below is common; this design occurs in such widely separated groups as Linyphiidae (e.g. 269), Theridiidae (52, 62, 142, 162, 269, 282, 284), Cyatholipidae (115), Diguettidae (200), Pholcidae (57, 86, 162), Araneidae (269), and Uloboridae (166). Tightly woven, approximately horizontal sheets that are associated with the substrate and with a retreat, often in the form of a funnel which is positioned at one edge, also occur in a wide range of families. In some, such as Austrochilidae (99), Psechridae (240), Oxyopidae (114, 179), Amaurobiidae (111), Stiphidiidae (54, 100), the spiders run on the underside of the sheet. In others, such as Dipluridae (40), Tenggellidae (252), Hahniidae (215, 269), Agelenidae (269), Lycosidae (132), and Pisauridae (188), the spider runs on the top of the sheet (some hahniids and oxyopids move about on both sides—135, 215). Shear (261) gives similar examples of convergence. Judging by the fact that the primitive sister groups of araneomorphs (hypochilids and austrochilids) move under their sheets, the tendency to run on top of the sheet is derived rather than primitive, as has been supposed by many previous authors (e.g. 134). Such evolutionary flexibility and rampant convergence suggest that attempts to use generalized

webforms such as these as taxonomic characters (e.g. 178) must be treated with caution (36).

In some cases silk glands and their products rather than webs are taxonomically useful at higher levels (30). The data are still so sparse, however, that surprising discoveries are being made. For instance, drops of more or less liquid glue, thought to be confined to orb-weaving araneoids and theridiids, have been found in the webs of such diverse families as Linyphiidae (142, 178, 224), Pholcidae (9), Lycosidae (178), and Agelenidae (246). Their glandular origins and possible homologies are as yet undetermined.

Very preliminary indications suggest that chemical composition of silk is not taxonomically useful, since proportions of amino acids in ampullate gland silk show intraspecific and even intraindividual variation (323). There are substantial differences in ninhydrin reactive vs ninhydrin negative fractions of the water soluble portions of webs of one species of *Nephila* and two of *Argiope* (286, 287).

One possibly useful character that presumably results from silk chemistry is the yellow rather than the typical white color of orbs of all observed species of *Nephila* (271, on *clavata*; 26, on *senegalensis*; 2, on *edula*; 255, on *inaurata*; 162, on *clavipes*; 89 on *constricta*, *pilipes*, *turneri*; 244 on *maculata*) (it is white in the related *Nephilengys malabarensis* and *N. cruentata*—W. G. Eberhard, unpublished). In *N. clavata*, the color is present in only the webs of mature and nearly mature individuals (217). It has been claimed (46) that webs of both juvenile and adult *N. clavipes* are sometimes colorless, but this contradicts other observations (39, 41, 162, 244; W. G. Eberhard, unpublished). Yellow silk occurs in a scattered group of araneids, including *Cyclosa* sp., *Araneus expletus*, *Araneus* near *legonensis*, and *Cyrtophora nympa* (W. G. Eberhard, unpublished). The functional significance of the color is unknown, but the contrasting white color of wrapping and retreat silk in *A. expletus* suggests that the yellow color of orbs may be related to prey capture (see 48).

USE OF WEBS TO DETERMINE PHYLOGENIES

While Levi (153) argued that orbs are not useful in determining phylogenies at lower taxonomic levels, there have been a number of attempts to deduce spider phylogeny from web structure. Unfortunately, some (e.g. 10, 119, 134, 144, 325) have relied on the risky combination of only a fragmentary knowledge of webs (e.g. araneid and theridiid webs mostly restricted to temperate species), and the mistaken assumption that a web design that is structurally intermediate indicates evolutionary (historical) intermediacy.

Although details of orb structure such as barrier webs, stabilimenta, free sectors, and web reduction show repeated convergences (74, 110, 153, 195),

some details of the behavior patterns used in building orbs have apparently been more conservative. As noted by Ades (1), orb construction is actually very simple, in that the same motor patterns are repeated over and over; it is in the adjustments of these patterns to different conditions that the complexity and derived nature of orbs is manifest. Details such as leg positions and movements, sequences of lines laid and broken, patterns of sticky spiral attachments to radii, and patterns of orb repair have provided evidence for associating different families of araneoids (30, 74, 78, 84, 103), families of cribellates (81), for defining the family Uloboridae (30, 74, 84) and the subfamily Nephilinae (30, 74, 158, 198, 263–264—see also 240, 255), and for determining that the reduced webs of deinopids are derived from orbs (31).

Another potential source of evolutionary information is behavioral ontogeny (77, 87, 153, 319). It appears that when orb web designs change substantially as spiders mature, the designs of webs of older spiders are usually more derived (77).

ARE ORB WEBS MONOPHYLETIC?

The old question of the monophyly of the orb design reacquired some of its controversial heat with the realization that the cribellum and calamistrum are plesiomorphic for araneomorphs (higher spiders). Thus these characters, classically used to justify the separation of the orb weaving family Uloboridae (and its possible ally Deinopidae) far from the rest of the orb weaving families (all in Araneoidae), cannot justify this separation. Coddington (30, 33–36) has argued that uloborids and/or deinopids are the sister group for araneoids, combining characters which have not been used traditionally, such as silk gland types, valves in silk gland ducts, presence and location on spinnerets of spigots through which silk fibers emerge, and details of construction behavior, with more traditional genitalic and somatic characters. Some workers are in agreement (e.g. 154), while others are not convinced (137, 178, 298).

Classifications are currently changing rapidly (37), and there are several reasons to think that it is probably too early to draw confident conclusions about monophyly. The methodological assumption of equal weight for all characters in the cladistic analyses used is likely to be misleading (e.g. 23, 184, 258). Because of the small sample available, the most complete analysis of spigot and spinneret morphology is “*at best* a first draft” (35, emphasis in original). Few species have been checked for valves in silk gland ducts (30), so it is hard to evaluate the possibility that evidence (lack of valves in a linyphiid) that is not in accord with predictions of the monophyly hypothesis can be chalked up to secondary loss (30). Homologies of different palpal sclerites are also still uncertain (34, 53, 118). Some statements about char-

acter states in current analyses are also dubious. For instance, the supposed lack of sticky spiral localization behavior in non-uloborid and deinopid cribellates (33, 36) ignores the reports of what appear to be similar exploratory tapping in *Titanoeca* (283) and *Psechrus* (79), and the very regular spacing of sticky lines (presumably resulting from localization behavior) in webs of *Fecenia angustata* (240) and *Prograndungula carraiensis* (112). Other problems yet to be solved are mentioned in 30 and 84.

Our almost incredible ignorance of the details of spinning behavior of non-orb weavers in both araneoid and cribellate families (possible outgroups) makes deductions regarding homologies and directions of behavioral transitions still uncertain (30, 84, 261). A few general descriptions exist (14, 147, 282), but to my knowledge there are only two relatively detailed behavioral studies for all of the probably >10,000 species of spiders which build non-orb webs (H. W. Levi, personal communication) (65, 102); and one concerns the obviously derived and atypical genus *Synotaxus*!

Designs of non-orb webs are also poorly documented, though there is one character that may link uloborids to dictynids and eresids. Many dictynids and allies (e.g. *Dictyna*-39, 199; *Ixeuticus* spp.-172; *Matachia*-169 and the eresid *Stegodyphus* (79, 143, 223-4) lay "blunt zig-zag" sticky lines between more or less parallel nonsticky lines, with the sticky line running along each nonsticky line a short distance before bridging back to the other nonsticky line or, occasionally (224: Fig. 67a) to a third nonsticky line. Judging from photographs, such zig-zags do not occur in the webs of amaurobiids *Titanoeca* (283), *Amaurobius* (133), the filistatid *Filistata hibernalis* (39), or the psechrids *Psechrus* and *Fecenia* (79, 240). Similar patterns, in which a sticky line hangs free, runs along a nonsticky line, hangs free, etc. (alternate between "autonomous" and "heteronomous" in the language of 224)—occur in at least the outer portions of the orbs in at least four genera of uloborids (*Uloborus*, *Philoponella*, *Tangaroa*, *Hyptiotes*) (61, 163, 199), and in the orb-like egg sac web of *Miagrammopes* (165). In the uloborids *Polenecia* and *Miagrammopes* sticky lines are laid for long distances along nonsticky lines (165, 311), and in some *Uloborus* they sometimes run along nonsticky frame lines (61, 163). In contrast, orb weaving araneoids almost never lay sticky silk along a nonsticky line except at the attachment itself (the "sawtooth" orb of *Eustala* is an exception-75; but comparison with other *Eustala* webs indicates this is an independent convergence). This contrast holds even for webs reduced to one or a few long sticky lines (compare the araneoid *Wendilgarda galapagensis* (85) and the uloborid *Miagrammopes* (165). Until more information is available regarding the distribution of web designs and construction behavior of nonorb builders, it will be difficult to decide whether or not this and several of the proposed synapomorphies in construction behavior linking uloborids and araneids (30) are actually plesiomorphies.

Several basic aspects of the organization of orb construction behavior may be plesiomorphies that preceded the evolution of orbs. Preliminary construction of a scaffold or skeleton which is then filled in occurs in several theridiids (65, 147, 282), agelenids (51, 293), and two pholcids (9; W. G. Eberhard, unpublished study of *Modisimus* sp.) (such a pattern is not inevitable, as the theridiid *Chrosiothes* sp. gradually extends its sheet with a crocheting-type of behavior along the edge of the sheet—W. G. Eberhard, unpublished). Placement of sticky lines following rather than preceding nonsticky line construction is common (65, 102, 147; 282, on theridiids; 79, 240, on psechrids; 283, on an amaurobiid; 79, on eresids and a filistatid). Radial arrangement of nonsticky lines occurs, for instance, in the theridiid *Theridium* (102), hersiliids (312; W. G. Eberhard, unpublished), hypochilids (259), and an oecobiid (whose webs further resemble orbs in having the radial nonsticky lines run over an expanse of sticky silk which encircles the spider's resting place) (107). A process laying sticky lines starting at the edge of the web and working inward occurs in several cribellate families (79, 81). The apparently ancient ability to remember distances and directions moved is used to achieve regular spacing of both temporary and sticky spiral lines in the orbs of *Leucauge* (80).

Lamoral (147) found that species in three different theridiid genera start their webs by making a three-dimensional array of "radial" nonsticky lines converging on a retreat. They then interconnect these lines with shorter, nonradial nonsticky lines. Finally they lay sticky lines, in this case attached to the ground. The general resemblance to construction of the radii, temporary spiral, and sticky spiral of an orb is striking. Szlep (282) also noted radial lines laid in the horizontal platform of one theridiid, and regularly spaced but nonradial lines in that of another. She likened the vertical, gumfoot lines and the behavior employed in choosing sites where they will be laid to radii in an orb, and the regularly meshed platform where the spider waits to the hub of an orb. The order of construction (vertical lines interspersed with filling in the platform mesh) is appropriate for this comparison. Given the uncertainty as to whether theridiids had an orb-weaving ancestor, it is not clear whether these behavior patterns represent vestiges of ancestral orb construction behavior, convergences, or predecessors of orb construction in araneoids.

However the monophyly debate eventually turns out, the apparently primitive behavior of nephiline spiders indicates that even a monophyletic derivation of all orb weavers will require postulation of substantial convergences in basic aspects of exploration, radius and frame construction, and perhaps hub destruction behavior (84).

When one considers the rapid rate of discovery of new web forms and that at least three unrelated groups make nonorb webs which are nevertheless planar and have regularly spaced arrays of sticky lines (*Titanoeca*—283;

Fecenia–240, 255; and *Synotaxus*–65), it appears that the transition to this general webform has not been especially difficult to evolve. It is a dismaying indication of the difficulty of higher-level taxonomy to realize that even after the quantum leap forward represented by the large amounts of new data added recently and Coddington's extensive syntheses and analyses, there is so much yet to be done to obtain answers to these puzzles.

HOW ORBS FUNCTION

Effects of Web Geometry

The traditional idea is that orbs act as passive sieves in prey capture and that closer spacing of sticky lines evolved to capture smaller prey (e.g. 16, 123, 305, 317). This idea is being replaced by the realization that orbs do not act as simple filters, and that they must perform at least three different functions in prey capture: interposition of the web in the path of prey (interposition); absorption of the prey's momentum without breaking (stopping); and adhesion and/or entanglement of the prey to retain it until the spider arrives to attack (retention) (22, 42, 186, 303). The importance of the stopping and retention functions is illustrated by field observations of frequent prey escapes after hitting an orb: about 40% for *Tetragnatha elongata* (106); 61% for *T. praedonia* (326); 53% for *Metabus gravidus* (16); 17% for *Micrathena gracilis* (304); 58% for *Araneus trifolium* (205); 63% for *Argiope trifasciata* (205); about 10% for *Nephila maculata* (160) (blowflies only); 58–82% for nonadhesive sheet "orb" of *Cyrtophora moluccensis* (160) (blowflies only); and 33% in *Metepeira* colonies (301) (impacts with orbs only).

Features that improve one functional aspect of an orb can impair other functions. For instance, wider spaces between lines will result in a larger area being covered by a given volume of silk, and thus improved interposition, but will reduce stopping and retention (22, 42, 76). More closely spaced sticky lines with more or larger viscid droplets and lines with larger diameters will stop and retain prey more effectively, but make the web more visible and more easily avoided (at least during the day) (44, 46, 76). No single design is best for all prey. Those analyses of orb prey capture functions that consider only a subset of these functions (e.g. 186) can lead to unjustified conclusions ("larger webs . . . are a waste of silk"–195). Although there is a general trend for an orb to have approximately the same number of radii and sticky spiral loops (61, 76, 297, 298), some species tend to make radius-rich or radius-poor orbs. Since radii are much more effective in stopping prey (42, 76), radius-rich orbs are thought to represent adaptations for heavier, faster moving prey (42, 76).

None of the hypotheses explaining different orb geometries as adaptations to capture different prey (22, 76, 277) has yet been tested adequately. Tests

will not be easy, as available prey, spider size (and thus, probably, the diameters of web lines and amounts of adhesive), and spider attack behavior must be taken into account in the field where prey are free to avoid webs. Some preliminary data are in accord with predictions. The elongate, dense vertical array of sticky lines in *Scoloderus* webs apparently increases, as predicted, captures of moths, as compared with more standard orb designs of syntopic species (276) (data for other species were not given, however). Larger prey were captured by *Micranthema gracilis*, which had more radii and more tightly spaced sticky lines, than by the sympatric and similar-sized species *Leucauge venusta* (305). Comparisons of prey captured by *M. gracilis* with prey in sticky traps also suggested that this species specializes on larger prey, especially large flies (304). Comparisons of prey from five species in a tropical forest understory showed that those with denser, more radius-rich orbs (*Micrathena*, *Mangora*) captured heavier prey and prey with higher predicted impact energies than those (*Leucauge*, *Epilineutes*) with more open, radius-poor orbs (42). The species with high energy orbs were substantially larger than the others, however, so this confirmation is inconclusive. None of these studies tested the possibility that differences in microhabitats and attack behavior were responsible for differences in prey captures.

There are other suggestive but even less complete confirmations. *Tegrag-natha extensa* (199) and *T. praedonia* (271) and *Metleucauge yunohamensis* (271) make wide-meshed orbs, and *T. elongata* and *T. laboriosa* probably make similar designs typical of this genus (39). These species capture, as predicted, mainly weakly flying prey such as nematocerans and aphids (182), nematocerans (327), very small flies (106, 326), and small flies and cicadellids (152). Spider attack behavior varied with different prey, however, and some heavy prey (beetles) captured momentarily in *T. laboriosa* orbs were discarded by the spiders or allowed to escape (152). In *T. montana*, prey found in the webs (not necessarily a reliable indicator of prey attacked and consumed) were also mostly small and weakly flying dipterans (50).

The extraordinarily large variations in prey of the better studied genera *Argiope* and *Nephila* (190), which apparently have similar web designs in different species, indicate that in general apparent confirmations like those just noted should be treated with caution. For instance, in ten studies of *Argiope* (those summarized in 193 plus 1a and 177), Diptera ranged from 1.3% to 80%; Coleoptera from 0.5% to 22%; and Lepidoptera from 0.3% to 36% of the total numbers of prey. Similar variation occurred between studies of two species of *Nephila* (10–62%, 5–27%, and 0.7–24% respectively) (190, 244). In three studies of the same species (*A. aurantia*) the percent of odonates in the totals ranged from 0% to 32%. Clearly, attempts to characterize the prey taxa of at least some orb weavers are risky. The variability means that attempts to explain web design and prey capture

behavior and morphology as specializations for certain prey (e.g. 205—see also below) can also be risky. Perhaps other prey characteristics (e.g. flight speed or agility, momentum on impact) are less variable, but this remains to be tested.

Some insects take evasive action to avoid orbs they are about to encounter (16, 41, 161, 193, 206, 244), and others clearly maneuver around webs [e.g. the kleptoparasitic empidid fly *Microphor* which flies along radii and sticky spiral lines as it searches for tiny prey caught in orbs (191)]. Thus, the interposition function of at least diurnal orbs is probably influenced by their visibility. Artificially increasing an orb's visibility can cause a dramatic reduction in the frequency of prey impact (44). A web's visibility is probably influenced by diameters and densities of lines, sizes and densities of balls of adhesive on the sticky spiral, and the background of the web (41, 44, 46). The importance of background has been demonstrated (44, 46); effects of higher thread density which may increase avoidance have also been studied (41), though larger species made the more dense webs used in this study, and its thicker lines (42) were probably seen more easily by the insect. The evolutionary effects of visibility on particular design characters of orbs are as yet unstudied. The lack of obvious consistent differences between designs of orbs that are used only at night (*Acacesia*, *Metazygia*, some *Tetragnatha*, *Eustala*, *Bertrana striolata*, some *Eriophora*) as compared with orbs built in the early morning and used during the day (e.g. many *Araneus*, *Mangora*, *Leucauge*, *Metabus*, *Argiope*, *Cyclosa*, *Micrathena*, *Dolichognatha*) argues, albeit inconclusively, against the selective importance of visibility on orb geometry.

Despite the fact that arachnologists often discuss "the" mesh size of an orb (e.g. 87, 177, 186, 190, 205, 305, 319), spacing between lines in a single orb varies widely. The radii are much farther apart at the edge than near the hub; sticky spirals are usually also farther apart near the edge than near the hub (61, 183, 316); and both radii and sticky spirals in the upper portions of vertical orbs are usually farther apart than those below the hub (150, 94a, 187, 309, 319). By comparing rates of prey encounter and capture in different portions of an orb it should be possible to measure the effects of these differences. This has been attempted (94a, 187), but unfortunately only for the subset of prey (mostly very small) which the spider ignored and left in the web without attacking, and which are probably of minor biological significance (205).

Movement of the web itself, as in ray spiders (Theridiosomatidae) (e.g. 29, 266), probably aids in the capture of insects with slow, tentative flight such as some nematocerous flies, though this has not been demonstrated experimentally. It is also possible that movements of typical orbs in the wind often help overcome evasive actions by prey (47). Additional measurements of orbs in nature which are not loaded in ways that increase their displacements are needed, however, to demonstrate this.

Still another important factor which must at least sometimes influence all three prey capture functions is the web's ability to resist or evade environmental stresses such as the spider's own weight, wind, rain, and falling debris (45). Production of thinner lines when spiders were weightless in space (321), and thicker lines when weights were increased by gluing weights to spiders' abdomens (25), indicates that support of the spider's weight is an important design consideration (some, however, have failed to find correlations between spider weight and diameters of draglines—7). Adjustments in web design or placement that are apparently designed to reduce wind damage have been noted in the orb weavers *Uloborus* (60), *Argiope* (94, 161), *Tetragnatha* (152), *Metepeira* (256), and *Araneus* (122) as well as the sheet weaver *Diguetia* (200); but in others, such as *Micrathena*, wind has little if any importance (5). Amounts of web damage due to wind, rain, debris, insects, and the spider's movements in the field are reported for three species (45) (criteria for distinguishing different types of damage, an apparently difficult task, were not given, however). Webs of some species accumulated damage more rapidly than those of others in the same general habitat (45).

Lower tensions improve a web's ability to stop prey, but it is not clear whether or not they also make a web better able to withstand wind stresses. A looser web will have a smaller radius of curvature under wind pressure, thus reducing the load on the supporting framework (42, 108). It will also, however, flap more in the irregular breezes typical of natural websites (e.g. 104); the sudden accelerations and decelerations during snaps probably cause increased stresses (61, 148). Lower tensions will also give sticky spiral lines more freedom to swing, and thus to hit and stick to each other. Judging by photos of artificial wind damage to orbs (45), this last factor may be most important in nature (these webs were loaded, however, with powder before being exposed to wind). The marked intra-web differences in tensions on radii in *Nuctenea* and *Araneus* webs (58, 313) also suggest lesser importance of mechanical stability, as more nearly equal tensions would be needed to distribute stresses more evenly (148). Some behavioral details during orb construction seem designed to reduce tensions on both radii and sticky spirals (73, 78).

The relatively high tensions in the orbs of species such as *Araneus sexpunctatus* (145)), *Micrathena*, and *Cyclosa* (42) may represent compromises promoting greater weblife in exposed sites at the cost of some reduction in the ability to stop and hold prey. In contrast, *Meta meriana* builds in very sheltered sites, and its orb is under much less tension (145). The very slack, relatively exposed web of *Pasilobus* is, as predicted, often substantially damaged within only an hour of construction (245). Some orb weavers, such as *Micrathena* and *Wagneriana*, may try to get the best of both worlds by holding the web taut while waiting for prey, then relaxing it suddenly on

impact (222; W. G. Eberhard, unpublished), as do the reduced web builders *Miagrammopes* and *Hyptiotes* (165, 207).

Defense against predators is another important characteristic of orbs and associated structures like meshes, retreats, and signal lines. These structures are discussed by Edmunds & Edmunds (89) and are not reviewed here. More data are needed to test the possibility that interposition capabilities of some orbs are improved by chemical attractants (124), as appears to be the case in a the tangle webs of social dictynid (285), and single line webs of some theridiids (71, 265a).

Effects of Physical Properties of Silk

The physical properties of silk lines ultimately determine the properties of the web they form. Important properties of araneoid nonsticky (ampullate gland) silk include high tensile strength which results in increased stopping ability and high extensibility combined with low resilience, a feature that aids retention by reducing trampoline-like rebound after prey impact (109). Supercontraction of wet major ampullate gland lines (322) may increase tensions on newly laid slack lines and increase the orb's ability to survive light rain (322). The rubber-like extensibility of the sticky spiral line (flagelliform gland) probably increases prey retention by denying purchase to struggling prey (58). It is possible that the glycoproteins, amines, potassium, and inorganic phosphates in the sticky material on the sticky spiral, which sometimes constitute nearly half the weight of an orb (286, 289), may function not only to adhere to prey but in retention and/or accumulation of water in sticky balls (due to hygroscopic properties of GABamide) and prevention of bacterial degradation (254, 288).

Improved understanding of the composition and physical properties of the lines themselves will probably help to explain, in terms both of the cost to the spider (76) and the ability to capture prey, the functional significance of different orb designs. Craig's demonstration (42) of strong relations between spider size and diameters of both sticky and nonsticky lines in araneoids is an important step. Other possible examples include the stronger and more extensible frame silk of *Micrathena* and its webs, designed to capture large, fast-moving prey (42); the large and especially sticky viscid droplets of the reduced orbs of *Pasilobus* sp. (245) and, apparently, *Cyrtarachne inaequalis* (268), which probably increase retention (and whose cost may explain the reduced orbs); the low-shear radius-sticky spiral junctions in *Pasilobus* (245), and perhaps *Poecilopachys* (27) and *Wendilgarda* (85a), which may increase stopping and/or retention capacities; the sliding radius-sticky spiral connections of many araneoids (67), which probably increase a web's stopping and perhaps retention capacities; and the highly coiled lines in the sticky ball of bolas spiders (70), which increase the striking range of the spider.

ORB DESIGNS IN RELATION TO ATTACK BEHAVIOR

Orb design and the speed with which spiders attack prey may be partially complementary. Species such as *Leucauge mariana*, which have radius-poor webs presumably adapted for only short restraint (see 42, 45 on *L. globosa*), attack very rapidly (82). Spiders such as *Micrathena* and *Gasteracantha*, which make more restraining orbs, on the other hand, attack more slowly (82, 303, 304). Some other species such as *Mangora* (W. G. Eberhard, unpublished), that attack rapidly make relatively dense orbs (42, 76).

Attack behavior probably explains the consistent tendency for the hub of a vertical orb to be nearer the top than the bottom of the web (and perhaps the associated trend for the sticky and nonsticky lines below to be closer together). Spiders reach prey below the hub more rapidly than those above it (176). Right-left displacement of the hub toward one side of the orb is also probably related in many species to running times (to run to the hub from the web's edge or a retreat in order to capture prey, and/or to run to the edge or a retreat from the hub in order to escape danger) (176). In species with retreats or preferred sides toward which spiders run, the hub is consistently closer to the side where the spider hides in both vertical orbs (e.g. 94a, 110, 143, 150, 199) and horizontal orbs (e.g. 63).

Olive (205) used data on differences in prey types and attack success with different prey in *Araneus* and *Argiope* at one site to argue that distance between sticky spiral lines may also correlate with the spider's ability to overpower prey (spiders with smaller chelicerae had more densely meshed orbs to restrain more dangerous, slowly escaping prey). Given the extreme variability in prey in different studies (above), more data are needed to test this hypothesis.

HORIZONTAL ORBS

The nearly horizontal orientation of the orbs of some species and genera is puzzling because it probably substantially reduces both interposition (sticky trap captures were reduced by 70% when the trap was horizontal rather than vertical—22) and retention (numbers of a sepsid fly retained for more than five seconds (enough time for most attacks) were reduced by about 20% in horizontal orbs—82). Horizontal orientation probably also increases damage from rain and falling debris, though comparative data have not been gathered.

Possible advantages of horizontal orbs, most of which are as yet undocumented, include allowing spiders to run and attack more rapidly (82), reducing wind stress (60, 61), allowing web oscillations to sweep up slow moving insects flying horizontally (47), and providing access to particularly

favorable microhabitats where prey are common (16). Horizontal orbs may be more difficult for prey to see, at least from below, because of background problems (44, 46) from the sky.

In some *Tetragnatha*, *Metabus*, and *Conoculus* (267), which build just above water surfaces, and perhaps also in the tiny anapids, symphytognathids and mysmenids that build in leaf litter (30, 78), horizontal orientation may enable spiders to build in sites particularly rich in prey (see 16 for documentation in *Metabus*). In many other groups, however (e.g. *Leucauge*, *Uloborus*), horizontal orbs are built at sites where vertical webs could be built.

The rapid attack hypothesis (82) is unlikely to explain the sometimes nearly horizontal orbs in short-legged, slow-attackers like *Gasteracantha cancriformis* (180). Further studies are needed with unloaded webs to determine whether web oscillations are biologically significant (above). In sum, no single explanation accounts for why horizontal orbs prevail in many genera.

ORBS AS SELECTIVE TRAPS, AND ARTIFICIAL ORBS

Direct observations of prey striking webs consistently show that some types of insects are more reliably captured than others (e.g. 152, 160, 185, 186, 205, 304). Experiments comparing the prey captured by spiders with the prey captured in nearby sticky traps especially designed to mimic orbs (5, 21, 262, 303, 304) consistently show that spiders' biases are different from those of traps. For instance, in a species-by-species comparison, in which unusual care was taken to equalize time, site, visibility, and orientation of traps and webs (not duplicated in any other published study), only 23% of the mean squared variation in numbers of individuals of different species of spider prey was explained by trap captures (21). Data from other studies also suggest differences in both identity (164) and (in linyphiid sheet webs) size distributions of insects (130). There are a number of possible reasons why spider web and sticky trap captures differ, including differences in airflow, visibility, microhabitat, ability to stop and retain prey, and the spider's speed of response and selective attacks on different prey (21, 164, 244, 294, 303).

Unfortunately this lesson of differential selectivity has not been understood by several workers in the burgeoning field of web-spider ecology, who have attempted to measure habitat quality by counting numbers of prey "available" to orb weavers using various kinds of sticky traps. From the point of view of a given spider, however, any potential prey which it cannot capture and eat (because the prey avoids or escapes from the web, because it tastes bad, etc.) is not available, and that prey is irrelevant with respect to habitat quality for that spider; the prey is "available" only in the evolutionary sense that future changes in the spider or its web might enable it to capture this prey. Some studies interpret all trap captures as "available" prey with no corrections (12,

186, 190, 220, 229, 250, 251, 272, 274, 275, 301), while others (106, 113) include some correction factors but omit others (effect of time of day on both spiders and prey, visibility of trap, differences between prey species in ability to escape orbs, rejection of prey by spiders). Some authors (e.g. 275) then ask themselves why their trap data are not in accord with prey consumption! An obvious improvement would be to estimate the numbers of available prey by counting numbers of prey consumed by the spiders themselves in different habitats (21).

DO DIFFERENCES IN ORB DESIGNS RESULT FROM “FINE TUNING” TO DIFFERENT PREY?

As just noted, orbs are to some degree selective traps. It is relatively clear that extreme variants on orb design, such as the asterisk web of *Wixia ectypa* or the ladder webs of *Scoloderus* and *Tylorida*, function to capture particular subsets of prey (walking insects and flying lepidopterans, respectively) (277). How far can this type of reasoning be extended? Is it probable, as is often argued (22, 42, 76, 93, 305) that different overall orb designs represent adaptations to different general sets of prey? There are several more or less direct kinds of evidence suggesting that at least the differences in details of orb designs probably do not represent fine tuning to specific subsets of prey:

1. Prey diversity within species and web types is generally very high (summary in 193; also 1a, 8a, 123, 127, 152, 177, 182, 240, 262, 302, 304 on 9 different genera). Orbweavers clearly tend to be general predators.

2. There is much intraspecific variation in web architecture related to factors other than prey type. These include: (a) amount or shape of available space (1, 97, 140, 149, 219, 239) (similar effects apparently occur in the theridiids *Coleosoma* and *Anelosimus*—49, 194 and the amaurobiid *Titanoeca*—283), (b) presence of conspecifics nearby (17, 105, 146) (may also influence space available), (c) lack of previous experience at a website (205), (d) presence or absence of water immediately below the orb (85, 267), (e) spider leg length (307), (f) amount of silk available in glands (83, 230), (g) time of day (perhaps also related to silk gland reserves?) (16, 228), (h) previous starvation (319) (also may affect silk reserves), (i) having ingested the previous day's orb (8) (also perhaps related to silk gland reserves), (j) presence of previously spun lines (105), (k) early experience prior to web-building (15, 18) and (l) weather (122, 253). Many of these factors seem unlikely to correlate with available prey or the spider's ability to capture them (no data are available, however). If one particular design was appropriate to trap the prey a spider could expect to capture, it would not seem sensible for the spider to change the designs of successive orbs.

3. Ontogenetic change in web design, with younger spiders usually mak-

ing less derived designs than older spiders (above), is not predicted in this context since fine tuning to different prey would not be likely to produce this pattern.

4. Retention capacities of an orb are extremely variable, even for a given species of prey. For instance, the coefficient of variation for retention times for 236 sepsid flies in vertical webs of adult *Metazygia* sp. was 110% (82) (A similarly large variation (c.v. = 91%) occurred in retention times of 218 sepsids in horizontal orbs of mature female *Leucauge mariana*—W. G. Eberhard, unpublished). Variation was so great that there was no statistical difference between retention in fresh orbs and that in “used” orbs, which had many segments of sticky spiral broken, or stuck to others or to radii (82). Large variations in retention time are apparently typical of both orbs and nonorbs (278).

5. Some studies suggest that websites are more important than web designs in determining which prey are captured (203, 231, 315). Wise & Barata (315) summarize other studies which also point, though less directly, to a lack of effect of web design on the sizes and kinds of prey captured by syntopic spiders. The prey of two araneids with different orb designs became more similar when the seasonal movement of one brought it into the subhabitat of the other (205). Riechert & Luczak (234) argue that (with exceptions like ladder webs) web structure plays little or no role in determining which prey taxa will be captured.

The data from all these studies share certain limitations. Different species undoubtedly built in different subhabitats, and their attack behaviors were probably not equally effective against different prey; these possible biases seem likely, however, to produce differences rather than similarities in prey capture data. Comparisons were only at high taxonomic levels (usually order), and by size categories (usually 1 mm). Similar numbers of prey in different families or orders obviously do not necessarily indicate the same species of prey were captured. As Wise & Barata (315) note, infrequent visits to some webs could have failed to document differences in smaller prey which were consumed rapidly. One study (203) used only data from prey remains left in webs rather than the prey actually fed upon by spiders.

Other studies give contradictory results, with the degree of difference in prey correlating with the degree of difference in web design (186, 201, 202; 42 for larger faster prey). In all of these studies, however, differences in prey could result from differences between species in microhabitat. In sum, a modified version of the conclusion of Riechert & Luczak (234) seems most appropriate: Differences in habitats where webs of different designs can be (are) built are probably responsible for some differences in prey captured; web design may also strongly influence prey capture, but critical data (which could come from web and spider transfer experiments combined with observations

of attack and rejection behavior to take into account the possible role of microhabitat and active choice by the spider) are still lacking.

6. Attack and feeding behavior on given prey also varies intraspecifically. Most of the *Nephila clavipes* at one site ignored some types of prey in their webs which were captured at another site (123). Even the same individual may attack a given insect more or less rapidly as a result of previous experience (189, 234, 294), the availability of prey (50), or hunger (234). Digestive enzyme concentrations can change with feeding experience (189), and the amount of food extracted from a prey can vary with the size of the spider (214, 295) and hunger (295). Thus, payoffs from captures of identical prey may vary.

7. Prey captured often vary considerably in different geographic areas (123, 127), seasons (127, 177, 205), years (126), and nearby subhabitats (e.g. 16, 22, 24, 106, 177, 183, 200, 219, 244, 303, 315).

The evolutionary consequence of this multiply compounded variability is that selection on details of orb design in terms of prey captured must be weak in many species, because the effects of the details of design must only be perceptible, in terms of prey consumed, in very large samples. It seems likely that species in some groups (e.g. *Argiope*, *Nephila*) will prove to be extreme generalists, while others (for example, species of *Tetragnatha*, *Metileucauge*) will be more specialized (in this case, on light, weak, or slow moving prey). A prediction is that the webs of species limited to habitats where certain kinds of prey predominate will often be designed to deal effectively with those types of prey. Weak selection on details of web design makes it unclear whether or not minor details (e.g. differences in sticky spiral spacing near switch-back points in *Uloborus*—59; numbers of loops of hub spiral; larger spaces between loops of temporary spiral in the outer portion of the web 80, 309; and reduced distances between sticky spiral lines rather than switchbacks on shorted radii in *Micrathena* webs (222) are adaptive in terms of prey capture.

EFFECT OF SPIDER SIZE ON WEB FUNCTION

Webs of smaller spiders, which are probably generally made with lines of smaller diameters (42) and probably with smaller amounts of adhesive (208, 214), seem to have reduced abilities to capture larger prey. Webs of smaller *Nephila* were less able to stop and retain prey for more than three seconds (13). Isolated portions of webs of immature *Metazygia* retained sepsid flies for shorter times in experimental trials than did those of adults (82). Small *Metazygia gregalis* captured much smaller prey than large individuals of the same species in webs at the same site at the same height above the ground and the same angle with the wind (21).

Several other field studies also give evidence of smaller prey for smaller

individuals (12, 42, 101, 130, 177, 214, 274, 305), though the possibility that differences in microhabitats were responsible for prey differences was not eliminated. The probable importance of spider size suggests that the results of comparative studies of prey capture in webs in which spider size was not taken into account (e.g. the mix of species of very different sizes in 249) should be treated with caution.

STABILIMENTA

A taxonomically diverse set of orb weavers add silk and/or detritus "decorations" called stabilimenta to their orbs. The following hypotheses purport to explain their function, but lack general applicability for the reasons given:

1. Web advertisement (warning off large animals such as birds which might fly through and damage the web—90, 95, 125). But many stabilimentum builders make webs in sheltered sites where birds or other large animals seldom if ever pass—e.g. *Uloborus* spp. deep in *Stegodyphus* colonies and pack rat nests (6, 60); *Lubinella* in tree buttresses and under rocky overhangs (163); *Conifaber* under prop roots of palms (166); *Argiope* in tall grass (88).

2. Prey attraction (48, 95). But stabilimenta are nearly always placed outside the trapping zone where sticky lines are present (e.g. 88, on *Gasteracantha*, *Argiope*; 156, 196, on *Salassina*; 271, on *Zilla*; 63, 163, on *Uloborus*; 163, 211, on *Philoponella*; 196, on *Micrathena*; 133, 199, 271, 324, on *Cyclosa*; 2, 243, on *Nephila*; 120, on *Araneus*). Stabilimenta are also often made, sometimes even more consistently and/or with more silk, on rudimentary or moulting webs which are neither designed nor used for prey capture (243, 264, on *Nephila*; 88, 95, 241, on *Argiope*; 88, 91, 92, 170, on *Gasteracantha*; W. G. Eberhard unpublished, on *Uloborus*).

3. Camouflage (hide spider or its outline) (63, 88). However the stabilimenta of some *Gasteracantha* and *Isoxya* are mostly on long frame and anchor lines which are up to 0.5 m from the hub where the gaudily colored and spiny spider rests (88, 180); the white dots in webs of *Salassina crassipinna* contrast rather than blend with the spider's black or red color (162, 196).

4. Strengthening the web (241, 243). But stabilimentum silk is generally laid as unstressed, curly lines in a cottony mass, often in such a way as to preclude strengthening the web (88, 170, on *Gasteracantha*; 211, on *Philoponella*; 63, on *Uloborus*). In addition, not a single species among the many nocturnal orb weavers is known to build a stabilimentum (63, 88).

The substantial amounts of intraspecific variation in form and frequency of occurrence, typical of stabilimenta in both araneoids (88, 95, 170, 236, 247) and uloborids (63, 168, 221), are not easily explained by any but the camouflage hypothesis (95).

Some authors have argued that stabilimenta have no function and are the

products of “stress” (197) or are nonfunctional vestiges (196). The common association of stabilimenta with cryptic postures in which the spider aligns its body with the stabilimentum during the day but not at night (63, 88), their strict association with daytime webs, and the repeated convergent evolution of stabilimenta argue against these interpretations. I agree with Edmunds that most stabilimenta probably function as camouflage (in some cases possibly including outline enlargement), and some as web advertisement.

NEWLY DISCOVERED WEB FORMS

The number of known variations on both orbs and other basic web types has grown dramatically in the last 20 years. Webs show an overall pattern of exuberant diversity and frequent convergence in both orb-weaving families and others.

Many but certainly not all of the araneoid species with highly modified orb designs are of relatively small body size. Craig (43) argues that modified designs correlated evolutionarily with changes in insect sizes. Web reduction and/or loss is frequent and is often associated with increased access to prey (19, 195). In at least some cases web reduction is accompanied by substantial changes in spider morphology (212, 216).

A few modified orb designs have clear probable functions. Species in two families (Theridiosomatidae and Anapidae) have convergently evolved webs with sticky lines attached to the surfaces of streams and puddles (38, 267), presumably to capture insects in the surface film and just above it. At least three groups of species in two families (Tetragnathidae and Uloboridae) have converged on orbs with a twig running through the center (76, 233; W. G. Eberhard, unpublished observations of *Uloborus eberhardi*), presumably to hide the spider from predators. The elongate, vertical “ladder” webs (242, on a genus near *Tylorida*; 64, 276, on *Scoloderus*) probably function to capture moths.

The adaptive significance of many other variant designs is unclear. Again these include many striking convergences: the “sawtooth” orbs with radially placed sticky lines of *Polenecia* (Uloboridae) (311) and *Eustala* sp. (Araneidae) (75); the elongate webs made next to tree trunks of *Herennia ornatissima* (Tetragnathidae) (239), *Araneus atriastula* (Araneidae) (97), and *Eustala* sp. (Araneidae) (W. G. Eberhard unpublished); loss of frame lines and drastic reduction of numbers of radii and sticky spiral loops in *Tetragnatha lauta* (Tetragnathidae) (265), *Cyrtarachne* spp. (Araneidae) (268, 269) and *Olgunius* spp. (Theridiosomatidae) (29, 30); retention of temporary spirals in finished orbs in *Nephila* (Tetragnathidae) (244) and *Phonognatha* (Araneidae) (53); reduction to a few long sticky lines diverging from a central area of nonsticky line where the spider rests in some *Miagram-*

mopes (Uloboridae) (165), and some webs of *Wendilgarda galapagensis* (Theridiosomatidae) (85). Such convergences suggest that similar, as yet undetermined, selective forces have operated in widely different lineages. Other equally mysterious designs are unique to certain groups, such as the nonsticky football-shaped sheet of *Paraplectanoides* (121), and the starburst, three-dimensional orbs of *Mysmena* (30, 78).

Several altered web designs are the products of radical changes in otherwise extremely conservative behavior patterns. Radius construction in “asterisk” webs of *Wixia extypa* (276) apparently differs from that of all other araneines (74); sticky “spiral” construction in the reduced orbs of *Poecilopachys* (27) and *Pasilobus* (245) (Araneidae), and *Hyptiotes* spp. (Uloboridae) (84, 171) is repeatedly interrupted and then resumed (only occasional interruptions occur in some other orbweavers—e.g. *Uloborus*, *Nephila*, *Leucauge*—W. G. Eberhard, unpublished). Movement “backward” during the construction of sawtooth orb sticky lines in *Eustala* sp. (75), toward the last site of attachment before attaching some segments of sticky spiral, is to date unique to this species. Inclusion of some temporary spiral construction and even exploratory behavior following, rather than strictly preceding, sticky line construction in both the elongate trunk webs of *Araneus atriastula* (Araneidae) (97) and the “high land” type of web in *Wendilgarda galapagensis* (Theridiosomatidae) (85) is again a sequence unknown, as far as I know, in undisturbed construction behavior of any other orb weaver. On the other hand, some highly modified webs, such as those of *Mysmena* spp. (Mysmenidae) (30, 78) and *Deinopus* (Deinopidae) (31), conserve typical elements of orb construction.

New designs have also been discovered in groups not closely related to orb weavers: the double sheets of the pisaurids *Pisaurina* and *Architis* (151, 188); “pseudo-orbs” with either rectangular (*Synotaxus*, 65) or radial geometries (*Titanoeca*, 283, *Fecenia*, 240); an umbrella-shaped sheet and tube or inverted cone (*Stiphidion*—54, 100; *Marplesia*, 100); and gigantic aerial planar sheets containing sticky silk that are more than 1 m in diameter in *Stegodyphus* (257). Species of *Argyrodes* (*Ariamnes*) use their simple webs in a previously undocumented way—as resting places for prey and walkways along which the attacking spider can sneak up (28, 69, 270). Perhaps the most extraordinary webs are the small sticky catching ladders of the otherwise primitive araneomorphs *Progradungula* (112) and *Macrogradungula* (99), which are sprung forward to receive prey when they are flicked backward off the substrate by the front legs. Careful study of several “well-known” webs has also revealed subtle, previously unappreciated structural details: *Pholcus phalangioides* webs have loose “screw threads” and tangles of loose silk that apparently function to retain prey (136); the somewhat similar fibrillation of fibers into subunits in webs of the diplurid *Euagrus* may entangle prey (218); and there are patterns of tension differences (of uncertain function; analogous

differences aid some theridiids in finding their retreats—147) in the sheet of the linyphiid *Frontinella* (280).

Other new developments include web descriptions for previously unstudied groups (e.g. 225, on *Segestrioides*; 209, on the uloborid *Tangaroa*; 99, on austrochilids), trap construction *after* the prey has first contacted web lines in *Drymusa* (306), web construction by mature males which were previously thought incapable of web construction (66, 163, 281), lack of or reduction of webs in groups that typically build webs (56, 57, on several genera of pholcids; 4, on an agelenid; 55, on a ctenizid), and discovery of webs in genera and families previously thought to lack them (e.g. 310, on *Argyrodes*; 114, 179, on the oxyopid *Tapinillus*; 128, on the salticid *Portia* and close relatives).

Salticid webs are particularly surprising, as these spiders are relatively well-studied visial predators and have been thought to be strictly cursorial hunters. *Portia*, however, builds two types of webs, the most elaborate of which seem to function less as traps than as lookout sites for locating passing prey (especially other salticids) and perhaps also as lures for web builders of other groups (128). Salticids may be directly descended from a web-building ancestor (129). The discovery that the retreat silk of various salticids easily entangles and detains insects (116) makes it necessary to reexamine the hunting tactics of these and other cursorial spiders such as clubionids, gnaphosids, some amphinectids and anyphaenids which build similar retreats. The reverse of this, a catching web serving as a retreat (to maintain high humidity), has been documented in a linyphiid (292).

CONCLUSIONS

Knowledge of spider webs has grown rapidly in a piecemeal fashion during the last 20 years. We are especially ignorant still of the construction behavior of nonorb builders; what little we know (79, 102, 147, 282) suggests that many webs in the process of being built may be more organized than is presently suspected, since subsequent additions can obscure the original pattern. Also needed are careful experimental tests in the field and in captivity of our relatively sophisticated ideas of the advantages and disadvantages of different orb designs. Extensive quantitative surveys of orb geometry in related genera or other taxa are needed to determine whether orb design is taxonomically useful.

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