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BEHAVIORAL CHARACTERS FOR THE HIGHER CLASSIFICATION OF ORB-WEAVING SPIDERS

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A number of studies have shown that behavior patterns can be useful taxonomic characters (see review by Mayr, 1958; also Evans, 1966; Crane, 1975; Michener et al., 1978; Eickwort and Sakagami, 1979; Greene, 1979). The webs and web-building behavior of orb-weaving spiders are complex, apparently stereotyped characters, and as such offer promise of being useful in indicating taxonomic affinities. As Levi (1978*a*, 1978*b*) has noted, however, this promise has not been fulfilled. The gross, relatively superficial web characters such as the presence or absence of stabilimenta, or open versus closed hubs which have been studied to date have not proved to be useful indicators of subfamilial relations. Webs are directly involved in orb weavers' interactions with a number of aspects of their environments (particularly prey), and relatively minor changes in environmental factors could result in selection for changes in web form. Levi argues (echoing Darwin, 1859) that at least some aspects of web design might thus be expected to be evolutionarily non-conservative and of little use in indicating higher taxonomic relationships.

This does not, however, eliminate the possibility that webs and web-building behavior may be useful as taxonomic characters. It is possible that some details of web design with apparently low functional significance may be more conservative than other more obviously functional characters. I have the impression that many web characters are not scattered randomly among the webs of araneoid species, and that their patterns of occurrence will be of at least some use in systematics, particularly at generic and tribal levels. The analysis necessary to

substantiate this has yet to be performed, although Risch (1977) has made a promising start by finding that two congeneric species' webs were more similar to each other in a number of details than to those of two species from other genera.

It is also possible that some details of construction behavior are employed by spiders in unchanged form to construct a variety of different web forms, and that these behaviors are thus slow to evolve even while the webs themselves change rapidly. This paper describes several such behaviors and shows that they are conservative enough to characterize the classical subfamily and family groupings which have been based on adult morphology and can thus be used to indicate relationships between them, a topic on which there is currently substantial disagreement (e.g., Lehtinen, 1967, 1975; Levi, 1978*a*, 1980; Robinson and Robinson, 1978, 1980; Opell, 1979).

Obviously the more characters used in constructing a system of relationships the greater the likelihood of the results being correct. A great deal is known about the morphology of orb weavers, but no comprehensive surveys of characters are yet available (but see Levi, 1980), so they cannot yet be included. This paper is meant to provide useful data for later syntheses, not to give the final word on the classification of orb weavers.

Choice of Characters

When one has collected data on a previously untried character or set of characters, the first step in their analysis is to compare their distribution with previous taxonomic schemes based on other characters. If the new characters are function-

ally independent of the older ones—as would appear to be the case here since the morphology of male and female genitalia, eye positions and structures, cheliceral morphology, cephalothorax form and other morphological characters used by other workers would seem to have little functional relation to the details of leg movements and thread manipulation during web construction and attack and courtship behavior—then there are several possible results. If the previous schemes are all incorrect, the distribution of the new characters will not be in accord with any of them, and the new characters can be used to construct a new set of relationships. If, on the other hand, the previous schemes are at least approximately correct, then the degree to which the new characters “fit” will depend on the rates of evolution of these characters. Those which have evolved very slowly will be uniform over many different groups, those which have evolved relatively rapidly will vary even within given taxa, and still others will more or less match the taxonomic scheme. Since some of the behavioral characters examined in this study do have distributions similar to the classical groupings of Simon (1892) based on adult morphology, this scheme is probably at least approximately correct.

There were other characters which were constant in all the groups studied (e.g., starting sticky spiral from the edge rather than the center or any other part of the web), and others which varied within given subfamilies (e.g., pulling motions of legs IV on sticky spiral as it was produced). These behaviors are not included here since the basic objective of the study was, after testing the classical scheme, to attempt to use the behavioral characters to indicate relationships between subfamilies and families. Thus only those characters which appear to be constant or nearly constant within subfamilies or families and which also differ between them are discussed. Detailed descriptions of these characters, the different states which they assume, their functional indepen-

dence, and the most probable directions of transformation are given in Appendix 1.

MATERIALS AND METHODS

Specimens of spiders are deposited in the Museum of Comparative Zoology, Cambridge, Mass. 02138. The specimen numbers mentioned in the text and appendices refer to numbered labels included in individual spiders' vials. At present it is unfortunately impossible to identify many (most?) orb-weaving spiders at the species level, and most specimens are given only generic names. This situation does not seem likely to change radically in the near future, and it thus seemed wise to proceed with the presentation of the data in this paper rather than wait for more complete identifications. Unless otherwise noted all references to subfamilial and tribal groupings are based on the monumental work of Simon (1892). The uloborid names follow Opell (1979).

The techniques of observation and their limitations are described in the Appendices. As might be anticipated, many details of web-building behavior are extremely stereotyped within a given species (see Appendix 1). This uniformity makes web-building behavior an attractive set of characters to study because relatively brief observations suffice to characterize a species.

RESULTS AND DISCUSSION

Observations of at least 148 species in at least 55 genera are presented in Appendices 2 and 3 and summarized in Table 1. The data are arranged according to the groupings of Simon (1892). Both substantial concordance within subfamily and family groups with respect to a number of characters and clear differences between subfamilies and families are evident. These patterns constitute confirmation of the classical groupings. The one distinction which is not confirmed is that between Tetragnathinae and Metinae, as there were no consistent differences between species of these two groups.

TABLE 1. Summary of data in Appendices 2 and 3 and Robinson and Robinson, 1980. The data are relatively scarce for some characters for Theridiosomatidae and Anapidae and their characterization here is tentative. Parentheses indicate character states thought to be secondarily derived within the group; in all cases fewer than 10% of the species observed for that group have the presumed secondary state, and the species involved have all been classified without question on morphological grounds in the taxa in which they are placed here. Further justifications for considering these as convergences rather than synapomorphies are given in the text and Appendices 2 and 3. The numbers of the character states refer to designations in Appendix 1 and the text.

Group	Behavior									
	A	B	C	D	E	F	G	H	I	J
Araneinae	2 (4, "3")	1	1	2 (1, 3)	1	1 (3, 4)	2 & 3 (1)	1 (3)	3 & 1†	2 (1)
Tetragnathinae-										
Metinae	1 (2)	1	1	1 (3)	1	1	2 (1, 3)	1 (3)	2	?1††
Nephilinae	3	1	1	1 & 2	1	2	1	1	1	1
Theridiosomatidae-										
Anapidae	1 & 4	1	1	1 & 3	1	1	4 & 5	2 & 3	1 & 2	?
Uloboridae	2	2	2	1 & 2	2 (1)†††	4	1	1	2	?

† Gasteracanthae, Micratheneae, Mastophoreae, Cyrtarachneae, and Celaenidae only.

†† Pers. observ. of *Leucauge* sp. near *venusta* and *Tetragnatha* sp. (#0-19-1); TR also absent in *Tetragnatha* spp. and *Pachygnatha* spp.—see Bristowe, 1958

††† *Hyptiotes* spp. which spin reduced, presumably derived orbs (e.g., Marples and Marples, 1937; Comstock, 1940).

Relationship between Uloboridae and Araneoid Orb Weavers

There has been a long unresolved controversy concerning the possibility that orb web construction, which is known in six different spider families, evolved more than once (see Kaston, 1964, and Kullmann, 1972, for the most recent summaries). There is general agreement that the five araneoid orb-weaving families (Araneidae, Theridiosomatidae, Anapidae, Mysmenidae, and Symphytognathidae sensu Forster and Platnick, 1977) all evolved from a single ancestor, but their relationship to the sixth family, Uloboridae, is disputed. Some authors have thought that the lack of clear synapomorphies shared by Uloboridae and other, non-orb-weaving taxa plus the similarities between the designs of the webs and the web-building behavior of uloborids and araneoids are so great as to make a common derivation inescapable (e.g., Petrunkevitch, 1926; Wiehle, 1928; Lehtinen, 1967; Opell, 1979; Levi, 1980b; see also Brignoli, 1979). But in other, more widely used schemes (e.g., Simon, 1892) uloborids are widely separated from ara-

neoids on the basis of their possession of a pair of structures (cribellum and calamistrum) involved in the production of one type of sticky silk. The presence or absence of these structures has recently been shown, however, to be unreliable as an indicator of higher-level relationships in several other spider groups (e.g., Lehtinen, 1967; Forster, 1970; Kullmann and Zimmermann, 1976).

The distributions of behavior patterns in Table 1 support the idea that Araneidae is more closely related to Theridiosomatidae and Anapidae than to Uloboridae (fragmentary data on Mysmenidae and Symphytognathidae will be presented elsewhere; they suggest close ties between these families and Anapidae). They do not permit one to decide whether or not all four groups evolved from a common orb-weaving ancestor, but they suggest that they did not. In order to decide between a single or a dual origin of orb webs, one must compare the orb weavers' behavior with comparable behavior of non-orb-weaving araneoid groups such as theridiids (possible sister groups of araneoid orb weavers) and non-orb-weaving cribellates such as Dictynidae (possible sister groups

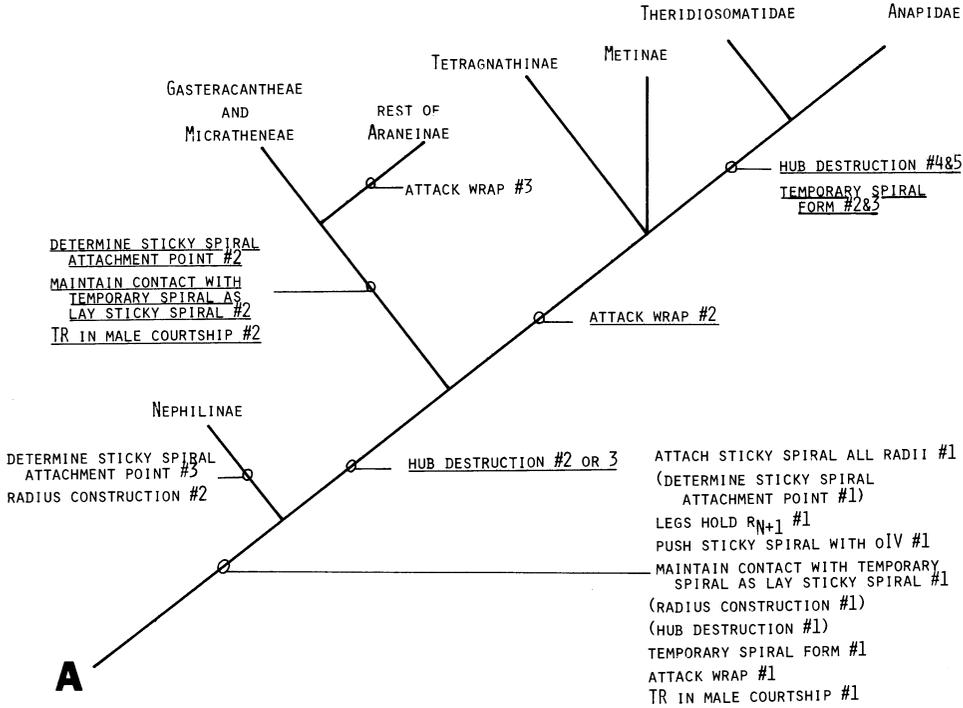
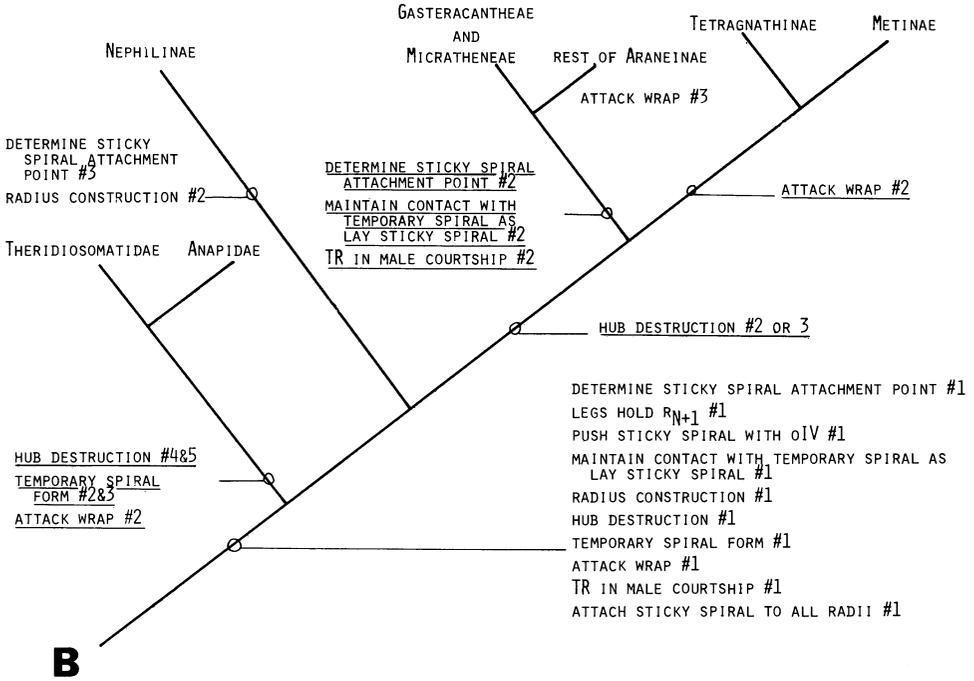


FIG. 1. Schemes of relationships between araneoid orb-weavers favored by the data in Table 1. A) Most parsimonious scheme assuming that lack of attack wrapping (I1) is primitive. B) Alternative scheme assuming that attack wrapping evolved independently in Theridiosomatidae-Anapidae. Proposed synapomorphies are underlined, autapomorphies are not. The placement of male courtship behavior is tentative since no data are available for some groups. The probable character states of the ancestral stock are given for all characters. There is less certainty for some of these than others (e.g., the character states designated as autapomorphic in A for Nephilinae could also be plesiomorphies and the alternative states synapomorphies in the line which

of Uloboridae). Since the behaviors examined here are mostly involved with orb web construction, this is not strictly possible. However some non-orb weavers do attach sticky lines to non-sticky lines, and the positions of their legs III and IV can be compared with characters B and C of the orb weavers. The following observations were made in an attempt to permit such comparisons.

The mesh-weaving araneoid *Achaearanea tepidariorum* (Theridiidae) attached a line with sticky silk to a dry line with the same movements as those of all araneoid orb-weavers (ipsilateral legs III and IV held the dry line on either side of the attachment, and the other leg IV held the sticky line), thus suggesting a closer relation of araneoid orb weavers to Theridi-

idae than to Uloboridae. The cribellate mesh-weaver *Mallos gregalis* (Dictynidae), on the other hand, did not use either of the hind legs to stretch the cribellum silk as it was attached, thus resembling the uloborids. Both legs IV seized the dry silk (probably more than one line—I could not convince myself on this point), but instead of holding one IV anterior to the other, they were both equally to the side and posterior to the spinnerets, and these were then touched closer to one leg and somewhat anterior to it. Thus this species' behavior was similar but clearly not identical to that of the uloborids. Another unidentified dictynid species was so small and moved so quickly that the details of its behavior could not be distinguished, but it seemed to behave as did *M. gregalis*.



split from Nephilinae); this uncertainty is indicated by parentheses. Species of the araneine groups Mastophoreae, Cyrtarachneae, and Celaenidae are related on morphological grounds to Gasteracanthae (Levi, 1978) and also lack attack wrapping behavior, and should thus probably be included on this basis with Gasteracanthae and Micratheneae in the diagrams. It is possible however that they lost attack wrapping secondarily as a result of specialization on moth prey (see Appendix 1). Uloborids differ from the hypothetical araneoid ancestors in six of nine characters.

The attachment behavior of another cribellate, *Tengella* sp. (Tengellidae?), was identical to that of *M. gregalis*, but still another cribellate, *Filistata hibernalis*, behaved differently. It lowered both IV's to the substrate out of contact with the web, and pulled the dry line toward its body with one leg III and held it there as the sticky line was attached.

These limited data on characters B and C support the classic dual origin hypothesis (unless one makes the unlikely assumption that theridiids or dictynids and tengellids have secondarily lost orb webs [see however Levi, 1980b]). Araneids are closer to theridiids than to uloborids and other cribellates, and uloborids are closer to dictynids and tengellids than to araneids or theridiids. The similarity between

uloborids and other cribellates is only approximate, however. An additional reason to doubt a close relationship between uloborids and theridiids is given in the discussion of directions of change in character I in Appendix 1.

It is worth noting that a convergent evolution of orb web construction in two separate lines may not be as improbable as some authors suggest, since an orb-like geometry probably has several advantages over other web designs (Witt, 1965; Langer, 1969; Eberhard, 1972; Denny, 1976).

Groups within Araneoid Orb Weavers

The data in Table 1 could be interpreted to support a number of alternative systems of relationships. If however one accepts that I1 is more primitive than I2 and

I3 and that only in well-defined conditions will a reversion occur (see Appendix 1), much of the ambiguity disappears. The system of relationships illustrated in Fig. 1a seems to be favored. It should be noted that the lack of attack wrapping (I1) in Gasteracanthae and Micratheneae, which nevertheless show three characters which may be synapomorphies with the rest of the araneines (A1, D2, and J2) necessitates an independent evolution of attack wrapping in the groups "other Araneinae" and Tetragnathinae-Metinae. Postulation of such a convergence is justified by three considerations: 1) convergence has already been documented for *post-attack* wrapping behavior in at least four groups of spiders (Eberhard, 1967; Rovner and Knost, 1974; Robinson and Lubin, 1979); 2) convergence has also occurred in *immobilization* wrapping in such diverse groups as Pholcidae, Hersiliidae, Oecobiidae, and Theridiidae (pers. observ.); and 3) the details of araneine attack wrapping seem to be consistently different (I3) from those of other araneids (I2) (see Appendix 3). The same general argument favoring independent evolution of attack wrapping could also be applied to wrapping attacks by Theridiosomatidae (still poorly documented), and this could permit a system of relationships (Fig. 1b) more in accord with other schemes of relationships that have been proposed on the basis of adult morphology and which is thus probably more likely to be correct.

It is interesting to note that the character A3 which is characteristic of Nephilinae can be performed only in webs in which the separation between radii is small compared to the span of the spider's legs, and is also energetically the least costly since the spider moves directly from one attachment to the next (see Peakall and Witt, 1976, for a preliminary discussion of the costs of movements during web construction). This suggests that the evolution of A3 behavior may have occurred at the same time as or after the development of tightly meshed webs. All of the few known nephiline webs—*Nephila madagascarensis* (Wiehle, 1931), *N. clavipes*, *N. macu-*

lata (Robinson and Robinson, 1973), *Hermannia ornatissima* (Robinson and Lubin, 1979a), and *Nephilengys malabarensis* (pers. observ.)—are indeed tightly meshed, and the *Micrathena* species (*gracilis* and #2200) which have apparently convergently evolved A3 behavior also make relatively tightly meshed webs and only use this behavior in the central portion where the mesh is smaller. Nephiline radius construction behavior (F2), with its strong emphasis on radii originating on the temporary spiral rather than at the hub may also be adapted to produce tightly meshed webs (viz. similar radius patterns in the very tightly meshed webs of *Cyrtophora* and *Mecynogea*). At least until more nephiline webs are discovered and described, one can tentatively suppose that some of the unique behavioral characters of this group represent adaptations related to spinning tightly meshed orbs.

This interpretation is contrary to the schemes of web evolution proposed by Kaston (1964) and Kullmann (1972) because it has the distinctive nephiline webs secondarily derived from more typical orbs (autapomorphic) rather than ancestral to the first typical orbs. The interpretations of Kaston and Kullmann were based on far fewer data than those available now. In addition both authors took as primitive those araneid webs that most closely resemble the webs of certain species of theridiids and linyphiids. There is a great variety of web forms however in these families, especially in Theridiidae (see for example Bristowe, 1958; also Marples, 1955a, 1955b; Kullmann, 1970; Mascord, 1970; Forster and Forster, 1973; Eberhard, 1977b, 1979; Carico, 1978; Clyne, 1979; pers. observ. of *Chryso* spp. and *Chrosiothes* sp.). These authors give no reason for assuming links to the particular species they chose (other than that the species are common temperate forms and thus better known). Their decision to consider certain araneid web characters primitive thus seems arbitrary.

In addition the web character on which both place emphasis—the presence of a mesh or "barrier" web on one or both sides

of the orb—would seem to have a number of possible functions (e.g., Hingston, 1922c; Robinson and Robinson, 1973; Lubin, 1975) and to be a good example of the non-conservative characters mentioned by Levi (1978a). The presence of barrier webs near the orbs of such diverse genera as *Metepeira* (Araneinae, Araneae—e.g., Simon, 1892), *Spilasma* (Araneinae, Araneae—pers. observ.), *Arachnura* (Araneinae, Arachnureae—Main, 1976), *Argiope* (Araneinae, Argiopeae—e.g., Lubin, 1975), *Gasteracantha* (Araneinae, Gasteracanthae—pers. observ.), *Leucauge* (Metinae—e.g., Comstock, 1948), and the uloborid genera *Philoponella* (Peters, 1953; Eberhard, 1969; Lahmann and Eberhard, 1979; Opell, 1979) and *Uloborus* (Lubin et al., unpubl.) as well as in the nephiline genera *Nephila* (Nephileae) and *Phonognatha* (Phonognatheae—Main, 1976) indicates that the presence of a mesh cannot be taken as a reliable indication that other aspects of that species' web are primitive.

A further difference between the scheme proposed here and those of Kaston and Kullmann is my placement of *Cyrtophora* and *Mecynogea* (= *Allepeira*) as a derivative group within the Araneinae, far from the ancestral stem of the orb weavers. The objections to their choice of primitive character states apply here also. In addition, while the building behavior data are limited (these genera do not spin sticky spirals and have distinctive radius construction behavior), the existence of both F1 and F3 radius construction behavior in *Argiope anasuja*, a member of a genus closely related to *Cyrtophora* in its adult morphology (Levi, 1978), attack behavior (Robinson, 1975), and egg sac form (Simon, 1892) is in accord with a derived position for *Cyrtophora* and *Mecynogea*. Robinson and Robinson (1978) suggested placing *Argiope* near the base of the araneid line on the basis of mating behavior (mating site). Their argument is not convincing since this character seems to be non-conservative (see Appendix 3) and since, as they themselves point out, it is not possible to establish whether the more

simple type of courtship is primitive or derived. They imply that *Argiope* may be close to Nephilinae, but it is clear that the data here do not support such a grouping. Attack behavior (Robinson, 1975; Appendix 3) and the occurrence of tarsal rubbing in male courtship as well as other details of mating behavior (Robinson and Robinson, 1980) also argue for separation of the two groups and a relatively more derived position for *Argiope*.

Some authors (e.g., Kaston, 1948; Forster, 1967; Lehtinen, 1967, 1974) have placed tetragnathines in a separate family, but the data here could only support this classification if metines were also placed in this separate family and if the hitherto unquestioned araneid group Nephilinae were put in its own family. Lehtinen (1975) proposed, on the basis of the structure of genital organs, trichobothrial patterns on legs, and color patterns (no precise data were given however), that Metinae and Leucauginae be split from Tetragnathidae and combined with Nesticidae and Mimetidae in a family separate from both Araneidae and Tetragnathidae. The data here do not support this split since *Leucauge* and other metines seem identical to the tetragnathines in all the characters examined. In addition they share the construction of orb webs with Tetragnathinae but not Nesticidae and Mimetidae. One would have to postulate a secondary loss of orb webs in nesticids and mimetids to justify grouping them with the orb weavers.

SUMMARY

Some details of orb web construction and attack behavior are evolutionarily conservative and appear to be useful in defining subfamilies and families and determining relationships. Their patterns of distribution among the at least 148 species in at least 55 genera surveyed here agree in general with classical taxonomic schemes based on adult morphology. The data suggest that convergent evolution of orb webs may have occurred in two lines (uloborids and araneoids). They also indicate that several previous proposals re-

garding the evolution of orb weavers and their webs may be incorrect. Certain behaviors appear to constitute autapomorphies for Uloboridae, Nephilinae, and Araneinae, while others may be synapomorphies for Theridiosomatidae-Anapidae.

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Note added in proof: Fukumoto (1973, 1981), working with *Nephila*, *Tetragnatha*, and five species in four araneine genera (probably all species were different from those in this study) recognized some of the similarities and differences in sticky spiral construction (characters A, B, and C) which are documented here. I thank M. Stowe for kindly translating these articles from Japanese.

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APPENDIX 1.

Behavior descriptions and probable directions of change

Spiders were observed in the wild and in a large screen cage. Those building in the dark were illuminated at least periodically with a headlamp. Super 8 movies were made of several species as they spun sticky spiral (see Appendix 2) and were analyzed frame by frame. The positions of web threads were sufficiently clear in the movies to give good confidence that the drawings made from them (Figs. 2-4) are precise, and enough repetitions observed to ascertain that the behavior described is typical and highly stereotyped. In no case did I see significant variation among individuals of a single species in the behavior patterns described here except for the differences (noted in Appendix 2) between young and old individuals of some Nephilinae and two species of *Micrathena* in character A and some araneines in character D. Most observations were of mature females.

The characters are denoted by letters, and the character states by numbers (e.g., character B has two states, B1 and B2). The descriptions are organized with respect to the stage of web construction in which the behavior occurs. The probable functions of some of the behaviors are discussed elsewhere (Eberhard, 1981c).

I. Sticky Spiral Construction

All orb weavers whose behavior is known place the sticky thread on their webs after building a "scaffold" of radii, frame lines, hub, and (with some exceptions) temporary non-sticky spiral lines. They start the sticky spiral near the edge of the web and gradually work inward. Figure 1 illustrates this process, and gives the names used for the various lines

and legs used in the behavioral descriptions which follow.

A. Determination of sticky spiral attachment point

A1: Tap forward with leg iI (Fig. 2). The spider faced inward as she attached to r_N , proceeded toward the hub, and then turned to face out the next radius (r_{N+1}) and moved forward rather than sideways out to encounter the inner loop, finally turning 180° to attach again. This abrupt turning to face inward and then outward was especially dramatic as the spider laid sticky spiral near the hub. As the spider moved out r_{N+1} , iI tapped or pushed forward to contact the inner loop while oI was held in nearly the same position but was involved in gripping the radius.

A2: Tap sideways with leg oI (Fig. 3). The spider moved sideways away from the hub along r_{N+1} waving or tapping repeatedly with the outer of her front legs which was directed laterally to the side toward which she was moving (Fig. 2). Her body was thus oriented perpendicular to the radius, and her outer leg I was more or less parallel to it.

A3: Extend leg oIV backward (Fig. 4). Instead of moving inward toward the hub and then back outward, the spider moved almost directly from one attachment to the next, sidling across the web as she faced inward toward the hub. The front legs were not brought near the site where an attachment was about to be made, although oII sometimes tapped toward the inner loop several radii in advance of the current attachment site. The spider used oIV to probe for the point where r_{N+1} intersected the inner loop.

A4: No contact. The spider's body was small compared to the spaces between radii and between loops of sticky spiral. After attaching to r_N and moving inward to reach r_{N+1} , the spider faced outward as she moved away from the hub along r_{N+1} , but stopped when still several body lengths short of the inner loop and turned to attach.

B. Legs holding r_{N+1} near attachment point when attachment made

B1: oIII just inside the attachment point, oIV just outside it. As the spider neared the attachment point, leg oIII seized r_{N+1} just inside the point where the attachment was to be made. Then as the spider positioned her abdomen to make the attachment, oIV grabbed the radius just outside the attachment point (Figs. 2, 3, 4).

B2: oIV just outside the attachment point and iIV just inside it. The spider ceased combing sticky cribellum silk with her legs IV just before making the attachment, and gripped r_{N+1} on either side of the attachment point with these legs as she faced inward.

C. Push current segment with iIV just before attaching

C1: Push the line. Leg iIV was extended (Fig. 4) and/or bent ventrally (Fig. 2) just before the attachment was made; in each case the tip of the leg moved away from the spinnerets, so additional line was probably drawn out (see Eberhard, 1981c). In

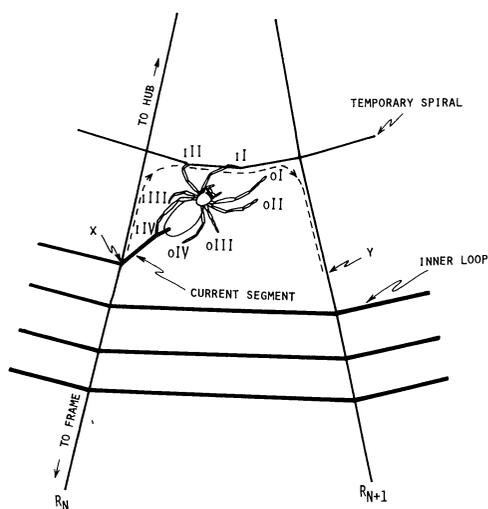


FIG. 1. Path taken by a typical araneid as it moves between one attachment of the sticky spiral and the next (sticky spiral lines shown thicker than others). The line is attached to radius r_N at point x, and then the spider moves (dotted line) to radius r_{N+1} via the outermost loop of temporary spiral. It then moves out r_{N+1} and attaches the current segment of sticky spiral (the line which it has produced as it moves) at point y. The size of the spider compared to the distances between radii and between the sticky spiral loops is relatively constant within species but varies widely between them. The legs designated as inner (i) are closer to the hub, and the outer (o) ones closer to the web's edge. When the spider doubles back (i.e., moves clockwise instead of counterclockwise in the figure), i legs become o legs and vice versa.

Nephila clavipes, *Micrathena gracilis* and *M. sex-spinosa* I was able to ascertain that the exact point where the sticky line contacted the leg was variable, and was usually on the side rather than the tip of the tarsus. It appeared that the line snagged on the stiff hairs covering the sides of the leg.

C2: Sticky line not pushed with legs. The current segment was not touched by any leg as it was attached to r_{N+1} .

D. Contact with temporary spiral as lay sticky spiral

D1: Lose contact. The spider moved beyond the outermost loop of temporary spiral and was completely out of contact with it as she attached at least some of the outermost loops of sticky spiral.

D2: Maintain contact. The spider maintained contact with the temporary spiral at all times while spinning sticky spiral. The outline of the area covered by sticky silk thus more or less reflected the outline of the outer loop of temporary spiral.

D3: No temporary spiral. There was no temporary spiral in the web.

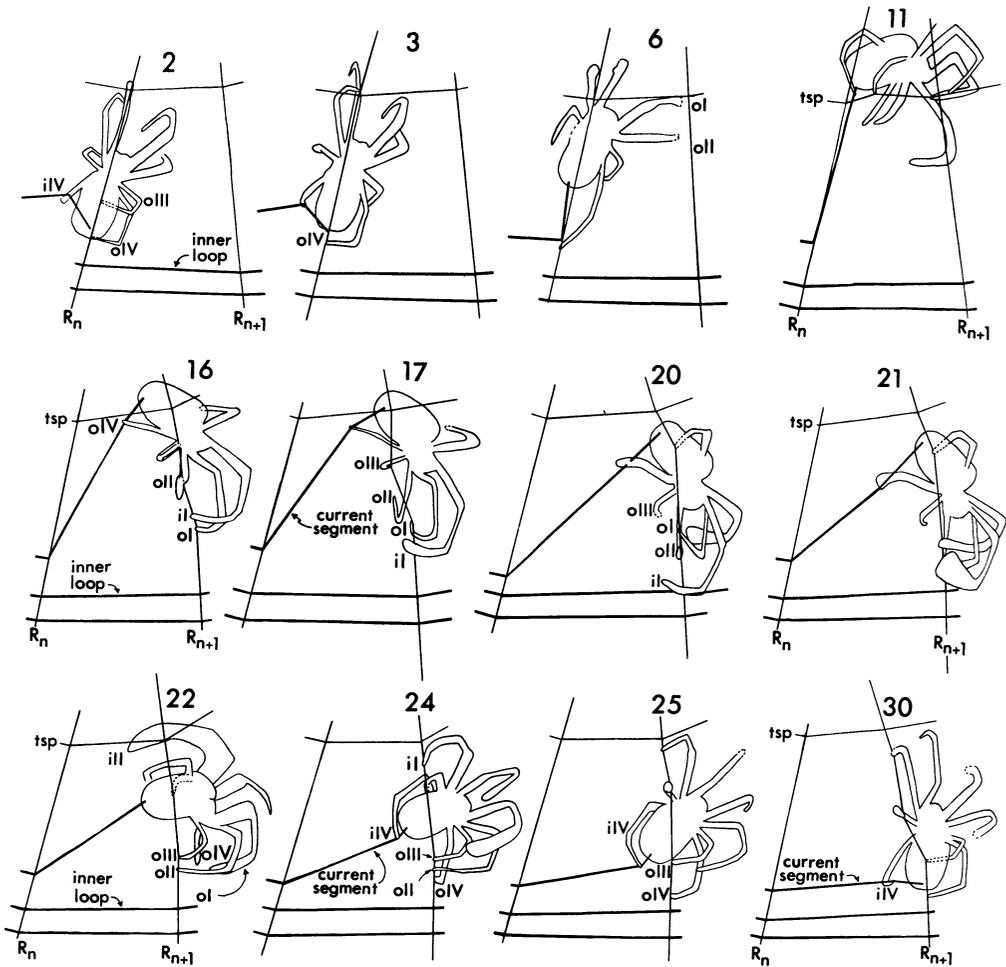


FIG. 2. A1 determination of sticky spiral attachment point behavior, illustrated from films of *Leucauge* sp. (#1556) taken looking down at the spider as it moved counterclockwise on a horizontal web. Conventions are as described for Figure 3. Body: faced inward as attachment was made to R_N (2) and as the spider moved inward along R_{N+1} (3, 6); then turned to face more or less along the temporary spiral (11), and then away from the hub as the spider moved out R_{N+1} (16–21); finally it turned 180° briskly (22) just after leg iI touched the inner loop and stayed in this position as the attachment was made. Leg iI: held R_N as the attachment was made; after variable behavior while the spider moved in and across the temporary spiral, it was extended forward and was bent ventrally at the mt-tibia joint as the spider moved out R_{N+1} (16, 17) until it made contact with the inner loop (20), then swung back to seize R_{N+1} (24) as the spider turned to make the attachment. Legs oI and oII: held nothing while the attachment was made (2); waved and contacted R_{N+1} as the spider moved inward toward the hub and across the temporary spiral bridge, then moved along R_{N+1} in a “hand-over-hand” pattern (e.g., 17, 20); as soon as leg iI touched the inner loop, leg oI swung to the side as the spider began its 180° turn (21, 22), but leg oII retained its hold on R_{N+1} until oIII and oIV had seized this thread (24), and then it also swung to the side (25). Leg oIV: held R_N just beyond the attachment point as the attachment was made (2); retained its hold on R_N as the spider moved inward (3, 6), then seized the current loop of sticky spiral (16), pulled it once (17), then held it as the spider moved out R_{N+1} , finally releasing its hold (22) and moving to seize R_{N+1} just outside the point where oII was holding it (24); it maintained this hold until the attachment was made. Leg iIV: after releasing the sticky spiral line (generally “plucking” it with a snap—3), moved irregularly until oIV released its hold on the current segment (24) and, just before the attachment was made, pulled out more silk by extending with a straightening at the femur-patella-tibia joints (30).

E. Attach sticky spiral to each radius crossed

E1: Attach to each one. The spider attached the sticky line to each radius she crossed as she moved around the web. Apparent exceptions occurred only on webs in which all radii were not in the same plane and the spider did not "encounter" all radii which crossed her path.

E2: Skip some radii. The spider crossed some radii as she laid sticky spiral without attaching to them. This behavior, which can be deduced from finished webs, was especially common near the hub.

II. Radius Construction

F. Order of thread placement

F1: One trip from hub—one radius laid (Fig. 5). Starting from the hub, the spider moved to the edge of the web along a pre-existing radius, paying out a new line as she went. She attached this line to the frame, but then immediately broke it and rolled it up as she returned to the hub, laying a replacement line behind her as she went. Usually radius construction was uninterrupted by hub construction, and the hub loops were laid only late in the radius construction stage or after it was finished.

F2: One trip from hub—two radii attached at two points on the frame (Fig. 6). Starting either at the hub as she laid hub loops or at some point away from the hub as she spun the temporary spiral, the spider moved to the edge of the web, paying out a new line as she went. She attached this line to the frame, then moved farther along the frame and attached it again; finally she used the line laid on the way out for support as she returned to the hub, laying a second new radius as she went. On arriving at the point of origin she resumed laying hub or temporary spiral line. Thus in contrast to the preceding case, hub loop construction was an integral part of radius construction.

F3: One trip from the hub—two radii attached at a single point on the frame (Fig. 7). *Cyrtophora* webs have no sticky spiral, but they do have very tightly spaced radii. These were laid two at a time along with hub and "temporary spiral" lines, but differed from F2 behavior in being attached to the frame only once instead of twice, and to the hub or temporary spiral at two points rather than one. This type of behavior could be deduced from inspection of finished webs since it results in characteristic "V" shaped intersections of radii with frame threads.

F4: One trip from the hub—one double radius (Fig. 8). Interrupting hub construction, the spider walked from the hub along a pre-existing radius and attached the line she laid behind her to the frame, then returned to the hub along this line, laying another behind which was attached to this one when the spider resumed hub construction and which effectively doubled the new radius.

III. Hub Destruction and Replacement

G1: Hub left intact. The spider left the hub of the web intact after finishing the sticky spiral.

G2: Hub center removed. The spider moved to the hub and apparently ingested the threads in the very center, and left this hole in the finished web.

G3: Hub center removed and replaced. After making a hole at the center of the hub the spider laid additional lines which more or less "sewed up" the hole she had created.

G4: Entire hub removed. The spider destroyed the entire hub rather than just the inner part, and either reattached the radii directly to each other or made new hub loops which were attached to the radii outside the points where they had been joined previously.

G5: No hub. There was no localized area where radial lines converged, and no lines were broken after completion of the sticky spiral.

IV. Temporary Spiral Form

H1: Spiral. As the name indicates, the non-adhesive line spun just after radius construction and which joined the radii together away from the hub approximated a spiral, at least near the hub.

H2: Circle. The temporary spiral consisted of a single circle, or, in the case of *Epeirotypus* (?) sp. (#2170), two circles, one inside the other.

H3: No temporary spiral. No temporary spiral was spun.

V. Attack Behavior

I1: Attack all prey by biting. Spiders attacked prey by biting, and only wrapped them, if at all, after a bite had been administered.

I2: Attack wrap with rotation in the web. Spiders attacked at least some prey by wrapping before biting. The wrapping behavior often included rotating the prey while it was still attached to the web (usually to a radius) so that it spun "rotisserie-fashion" (or "bobbin-fashion" in Robinson, 1969) and the turning movement of the prey itself appeared to pull wrapping silk from the spider's spinnerets. When the prey was very large the spider ran around and over it rather than spinning it.

I3: Attack wrap without rotation in the web. Spiders attacked at least some prey by pulling silk from their spinnerets with legs IV and laying it onto the prey before administering a bite. The prey was not spun rotisserie-fashion while it was still attached to the web, but was sometimes rotated slowly while being wrapped after it had been cut free from the web.

I4: Attack wrap with rotation unspecified. Most accounts of attack wrapping in the literature do not specify whether the prey was rotated while in the web or not. Species for which only this type of information is available are assigned to this category. This is thus not a distinct character state, but rather is equivalent to "either 2 or 3."

It should be noted that attack behavior varies with the identity of the prey (e.g., Robinson, 1969) and is thus more difficult to characterize than web-building behavior. Failure to observe a given type of attack may signify that the spider is incapable of that

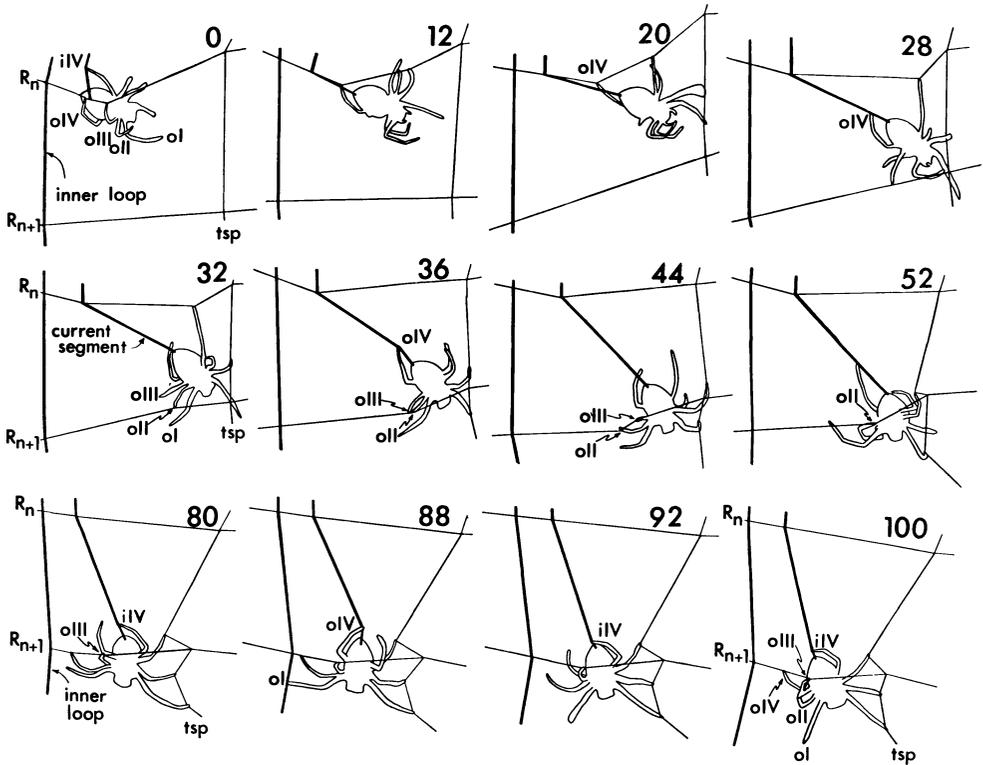


FIG. 3. Determination of sticky spiral attachment point behavior of type A2, illustrated from films (18 fps) of *Alpaida rhodomelas* (Tacz.) (#1757) taken looking at the ventral side of the spider as it moved downward near the edge of a nearly vertical web. Numbers indicate the number of frames since the last attachment of the sticky spiral (represented by thicker lines) occurred. The positions of some of the legs (especially legs III) were often unclear when they crossed the body, and are not drawn in some figures; in some cases notes taken in the field were used to arrive at the descriptions of both leg and thread positions. When legs moved rapidly they were blurred in the film, and this is indicated in the figures by thickening of their outlines (e.g., leg iII in frame 20). The movements of different parts of the body are most conveniently described separately; only movements of the legs which seem to move in consistent patterns and were important in the extraction and placement of the sticky thread are described (other legs seemed to be mainly involved in supporting the spider in the web). Body: faced inward as the attachment was made to r_N (0), and as the spider moved inward along r_N (12, 20); then it turned to face more or less along the temporary spiral (28, 32) and maintained this position as r_{N+1} was reeled in (44–88); finally it turned 90° (just starting in 100) to face inward again while the attachment was made to R_{N+1} . Leg oI: was held in the air near R_N while the attachment was made (0–12), then moved variably as the spider walked inward along R_N and along the temporary spiral (20–28); just after oII contacted R_{N+1} oI was extended laterally parallel to R_{N+1} (32) and tapped several times until it touched the inner loop of sticky spiral (88); then it was brought back and held in front of the spider and remained relatively quiet and out of contact with threads as the attachment was made. Leg oII: was held near R_N as the attachment was made and as the spider turned inward (12, 20); after irregular movements it contacted R_{N+1} and moved out this line and then reeled it in using a “hand-over-hand” motion in conjunction with oIII, each leg releasing the line just after the other grasped it, and then extending laterally to grab it again and flex ventrally so the leg tip was brought close to the spider’s body just as the other leg released its hold and reached out laterally for the next grip (various stages illustrated in 32–52). Just after leg oI touched the inner loop (88), oII ceased the hand-over-hand movement and swung anteriorly while the spider turned to make the attachment. Leg oIII: held R_N just inside the attachment point as the attachment was made (0), then moved irregularly until it began moving “hand-over-hand” with oII along R_{N+1} ; when oI contacted the inner loop (88) it maintained its grip on R_{N+1} as the spider turned to make the attachment. Leg oIV: held R_N just beyond the attachment point while the attachment was made (0), then moved along R_N (12, 20) before beginning to pull out sticky spiral line (e.g., 32, 36) as the spider moved toward the next attachment point. At first oIV pulled silk by itself, later in alternation with iIV (e.g., 80,

kind of behavior, but it may also mean only that the appropriate stimuli were not present to elicit that behavior. Only extensive observations can distinguish between these possibilities, and the data for species of some groups (particularly theridiosomatids and anapids) are as yet extremely fragmentary.

VI. Male Courtship Behavior

Robinson and Robinson (1980) noted three clear groupings of character states associated with mating site and courtship mode (direct contact vs. thread vibration). Unfortunately these patterns seem to have little to do with the taxonomic relationships of the species involved since species which are usually placed in one small, distinct group (Argiopeae—the genera *Argiope* and *Gea*—see Levi, 1968, and also Robinson and Robinson, 1980, for evidence that these genera are indeed closely related) fall in all three of their major categories. One characteristic, however, may be useful and is included here. Nearly all the observations of this character were made by Robinson and Robinson, and species are classified according to their criteria.

J. Tarsal Rubbing by Males

J1: Without tarsal rubbing. Males did not perform tarsal rubbing (TR) movements while courting females.

J2: With tarsal rubbing. Courting males rubbed their legs together with a motion similar to that made when cleaning their legs by rubbing them together.

Functional Independence of Characters

The characters B2, C2, E2, and F4 consistently occurred only together (in Uloboridae), and it is reasonable to ask if these are independent of each other and of the fact that all uloborids spin cribellate sticky silk. I have argued elsewhere (Eberhard, 1976) that the relatively non-extendible nature of cribellate sticky silk may indeed be functionally related to E2, and believe it is not unreasonable to suppose that it is also related to C2 (see functional interpretation of C1 in Eberhard, 1981c). There is however no obvious relation between any of these characters and B2 and F4.

The only other completely consistent combination was B1, C1, and E1 (in Araneoidea). Again E1 and C1 may be functionally associated with the very extendible nature of araneoid orb weavers' sticky silk and their ability to make "pulley" connections to radii (nevertheless, some groups do not seem able to make such connections—see Eberhard, 1976). There are no other obviously necessary relationships.

Character A3 and perhaps also A4 are necessarily associated with the relationship between web mesh size and spider body size: A3 would be impossible in relatively widely meshed webs (see text) and A4 would seem less likely though not impossible in webs with very small meshes. These web characteristics are however independent of the other character states.

Probable Directions of Change in Character States

A. The probable primitive nature of A1 with respect to A2 is suggested by the exceptional behavior of *Tetragnatha* sp. (#2043) and *Chrysometa* species (#'s 1824, 0–6) which all perform A1 behavior near the edges of their webs, but switch to A2 near the hubs (Appendix 2). One could consider that A2 in these species is either a remnant of an ancestral behavior which has been lost in all other observed Tetragnathinae-Metinae (i.e., a symplesiomorphy) or a new, derived behavior which evolved from A1 in both groups (i.e., either a synapomorphy or a convergence). The morphological differences between *Tetragnatha* and *Chrysometa* are so great that they have been placed in different subfamilies, so synapomorphy appears to be ruled out, and the second hypothesis thus requires convergence. Nevertheless it seems more likely than symplesiomorphy when one examines the details of the spiders' behavior. This is because A2 seems to be just a modification of A1 in which the last part of the behavioral sequence is omitted, and it is "derived from" A1 in the course of the construction of each web as is illustrated in Fig. 9. A selective advantage for A2 over A1, which could explain why the proposed convergence occurred, is easy to imagine since the turning back and forth which is characteristic of A1 must be wasteful of energy, especially near the hub where the spider can easily use the closely spaced radii to move more directly from one attachment to the next. It is interesting that *Chrysometa* is considered by some (Levi, 1978a) to be near to the ancestral stock of araneids on morphological grounds. The exceptional A2 behavior of spider #2173 (undescribed genus) (all other metines and tetragnathines performed A1) may represent the culmination of this process.

A modification of A2 similar to but not the same as A3 is present in some *Micrathena* (Appendix 2). The non-identity suggests a convergence with A3 behavior in Nephilinae and thus leaves the derivation of A3 in the latter group in doubt. Again energetic efficiency could explain the convergence.

A4 seems closest to A1 since both involve the same orientation of the spider's body along the radius. A4,

←

88). Finally, as the spider began to turn to attach, oIV seized R_{N+1} close to the point oII had been holding (100) and maintained this hold until the attachment was made. Leg iIV: stretched the sticky spiral line just as it was attached to R_N (0) and then helped support the spider as it moved inward along R_N and along the temporary spiral (20–32); then it began pulling out sticky spiral line (e.g., 52–80), at first alternating with oIV and later with consecutive pulls by itself until the last pull ended in the stretching of the line (100) as it was attached to R_{N+1} .

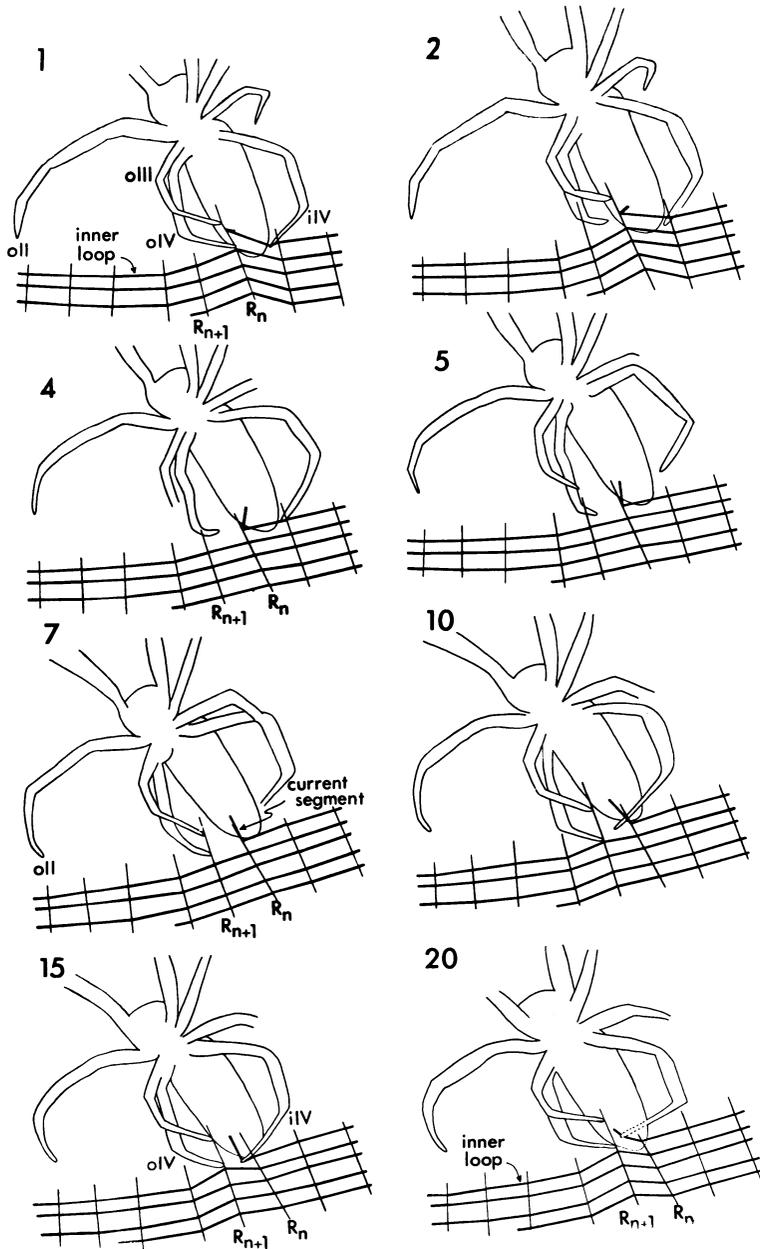


FIG. 4. A3 determination of sticky spiral attachment point behavior, illustrated from films of *Nephila clavipes* taken looking at the ventral side of a mature female spider as she moved clockwise near the bottom edge of a more or less vertical orb. Conventions are as in Figure 3. Body: faced inward the entire time, moving only slightly sideways from one attachment to the next. Leg oIV: held R_N just outside the attachment point (1); then it followed oIII to grip R_{N+1} , moving laterally until the lateral surface of the tarsus contacted the radius; it was then extended so that the tarsus slid along the radius until its dorsal surface contacted the inner loop of sticky spiral (10) (or the outer loop of temporary spiral—apparently no distinction was made between the two); it then grabbed the radius near the junction and pulled it toward the spinnerets (15) as the attachment was made just inside this point. There was some variation in the amount the tarsus oIV actually slid along R_{N+1} before contacting a spiral. Leg oIII: held R_N just inside the attachment point (1),

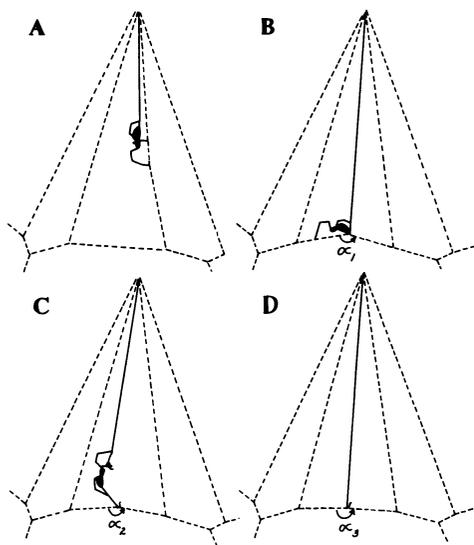


FIG. 5. F1 radius construction behavior; new lines are solid. The spider moves to a frame line along a preexisting radius, laying a new line behind it (a). This line is attached to the frame (b), and as the spider moves back toward the hub it breaks this new line and rolls it up with the pedipalps (c), laying another new line behind it. This line is fastened at the hub (d), and the spider usually proceeds to lay another radius without making any hub loop attachments.

which presumably involves a memory of distances moved inward and outward along radii, might seem to be a very specialized character, but in fact a similar kinesthetic sense has been noted in two groups of spiders unrelated to orb weavers (Görner, 1966; Seyfarth and Barth, 1972). In addition, modifications of the experiments of Hingston (1927) show that some orb weavers which ordinarily perform A1 or A2 also appear to have the ability to sense and remember these distances (Eberhard, unpubl.); and A4 seems to have evolved convergently in the araneinine

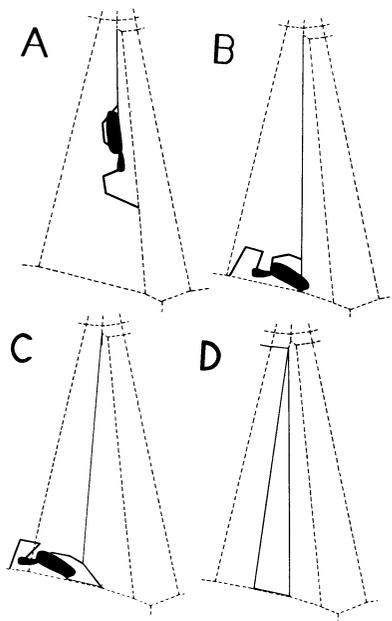


FIG. 6. F2 radius construction; new lines are solid. The spider interrupts hub loop construction (or in other cases, temporary spiral construction) to move to the frame along a preexisting radius, laying a new line behind it which it holds with one leg IV (a). This line is attached to the frame (b), and then the spider moves farther along the frame and attaches it again, maintaining its hold on the first new line with leg IV (c). Finally it returns to the hub, laying a second line behind it. As it moves it slides legs III along the first new line, and when they encounter the junction between this line and the hub or temporary spiral loop, the spider attaches the newer radius to the other and resumes hub construction (d). This description is the same as that of Hingston (1922) of *N. maculata* behavior in all details except his claim that when the first new line is attached to the frame one of the legs IV holds the radius which the spider walked along from hub to frame.

then moved to grab R_{N+1} (7) and held this radius and pulled it toward the spinnerets as the attachment was made. Leg iIV: stretched the current segment as it was attached to R_N (1), then was inactive until stretching the next current segment (15, 20) before its attachment to R_{N+1} . Leg oII: moved infrequently and was apparently used mainly for support by mature females. Immature individuals, however, directed it retro-laterally and tapped toward the inner loop of sticky spiral before most but not all attachments. Contact with the inner loop was made several radii in advance of the one where the attachment was about to be made. The leg usually tapped until it hit the inner loop; seemingly in contrast with leg oIV, it seemed to distinguish sticky spiral from non-sticky lines such as radii and temporary spiral. The movements typical of immature *N. clavipes* were also executed by mature females of *N. maculata* and *Herennia ornatissima*, and an immature *Nephilengys malabarensis* (mature individuals of this last species were not observed).

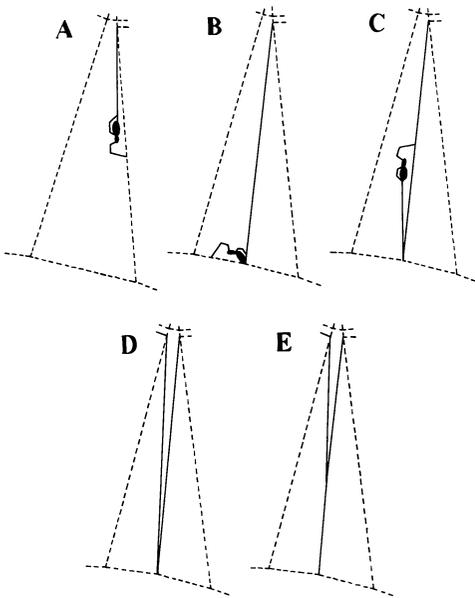


FIG. 7. F3 radius construction; new lines are solid. The spider interrupts hub loop (or temporary spiral) construction to move to the frame along a pre-existing radius, laying a new line behind it (a). It attaches this line to the frame (b) and then moves back to the hub along the new line, laying a second line as it goes (c). This line is then attached to the other radius bounding the sector where the new lines are laid, and the spider resumes hub loop (or temporary spiral) construction (d). Some radii laid this way were attached to each other part way along their length (e) by *Mecynogea* sp. (#1040).

genus *Cyrtarachne* which spins reduced orbs. Thus the relationship of A4 to the other character states is not clear.

B, C, D, E. There is no a priori way to distinguish primitive from derived states in these characters.

G, H, J. On the basis of simplicity, G1, H2, and J1 might seem primitive with respect to alternative states. In each case however these simpler states are only omissions of given behaviors, and would thus be easy to derive from other states. Thus there is no a priori certainty of direction of evolution in these characters.

F. F1 might seem derived with respect to the other states since it involves the complex behavior of breaking and rolling up one line while laying another behind rather than simply walking under an unbroken line. Essentially identical behavior is known, however in non-orb-weaving species such as *Phoroncidia pukeiwa* (= *Ulesanis pukeiwa*) (Marples, 1955a), *P. studo* (Eberhard, 1981a), *Argyrodes attenuatus* (Eberhard, 1979), *Synotaxus turbinatus* and two *Chryso* species (pers. observ.) (all in the araneoid family Theridiidae). Indeed it is not far

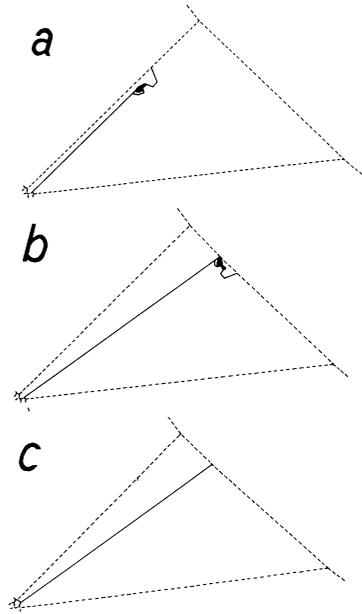


FIG. 8. F4 radius construction; new lines are solid. The spider interrupts hub loop construction to move to a frame line along a pre-existing radius, laying a new line behind it. This line is then attached to the frame (b), and the spider lays a second line as it returns to the hub. This line is attached to the first, thus doubling it, and the spider resumes hub loop construction (from Eberhard, 1972). The first radii laid (during frame thread construction) were exceptional: they entailed little or no hub thread construction, and after the frames were complete or nearly so, the spider removed the accumulation of threads in the center of the web and proceeded to begin "normal" radius construction as illustrated here.

from the behavior used by spiders of many families to ascend their safety lines after dropping from some support above. Thus there is no clear a priori way to distinguish primitive from derived. Arguments supporting the probable derivation of F3 from F1 are given in the text.

I. It seems likely that I1 is primitive with respect to I2 and I3. This is because attack wrapping is a complex behavior generally associated with web building, and lack of this behavior is widespread and is typical of groups which are undoubtedly primitive with respect to the groups discussed here in many characters including web building (Robinson, 1975; also Eberhard, 1967; Rovner and Knost, 1974; Robinson and Lubin, 1979). Due to the demonstrated advantages of attack wrapping in subduing large, powerful prey (data summarized in Robinson, 1975) it is also unlikely that once acquired it will be lost. The only possible exceptions would be in cases in

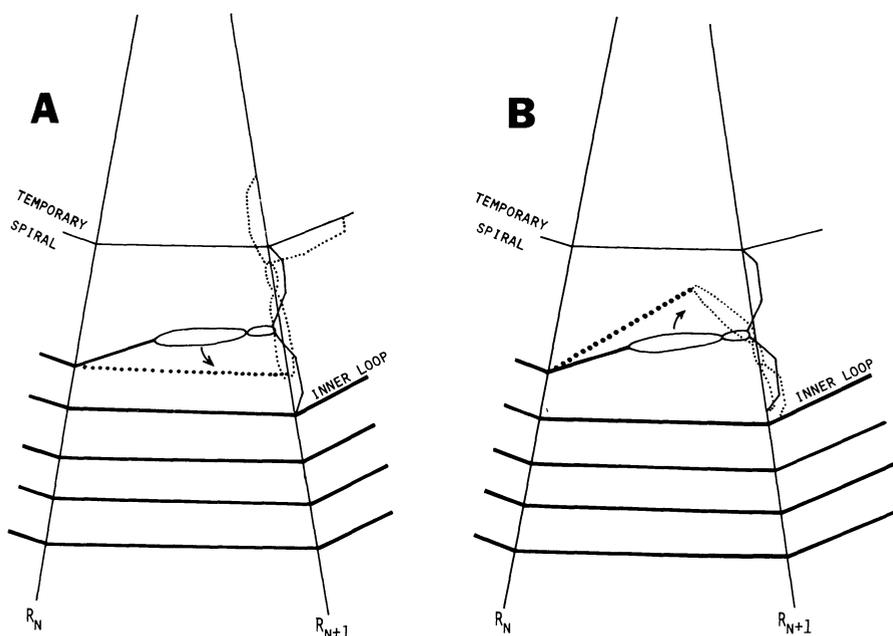


FIG. 9. A diagrammatic representation (horizontal web seen from above) of the transitional A1–A2 determination of sticky spiral attachment point behavior of *Tetragnatha* sp. (#2043). Only legs I are shown. Leg I was extended along R_{N+1} prior to grabbing it (solid drawings). If, as in A, it contacted the inner loop before grabbing the radius, the spider immediately swung to face inward and attached the current segment of sticky spiral (dotted lines), performing an A2 sequence of behavior. If it grabbed the radius before contacting the inner loop (B), it turned instead to face out R_{N+1} and used iI to locate the inner loop (dotted lines in B), performing an A1 sequence. Occasionally the spider began to swing its body to face outward before it had finished extending iI, and arrested this movement when that leg contacted the inner loop (A2 “tinged” with A1). Thus A2 appeared to be derived from A1 in that it consisted of a part of normal A1 behavior, and vestigial A1 movements were sometimes included in an A2 sequence. A1 was performed consistently near the edge of the web, and was gradually replaced by A2 as the spider moved inward.

which most or all of the spider’s prey were relatively harmless (e.g., non-stinging or non-biting) and/or either extremely efficient or extremely inefficient in escaping from the web. A possible example of the former are the bolas spiders and their kin which appear to specialize on moths (McKeown, 1952; Clyne, 1973; Robinson and Robinson, 1975; Eberhard, 1977); none of these spiders attack wraps (but it is not clear if this represents a secondary loss—see caption to Fig. 1 of the text). An example of the latter type are theridiosomatids which only occasionally attack wrap and which seem to capture mostly small nematoceros flies (J. Coddington, pers. comm.; pers. observ.).

It should be noted that acceptance of the ideas that attack wrapping in araneids is derived and that once acquired it will not be lost except in the cases just described requires that one consider the evolutionary origin of attack wrapping in the non-orb-weaving

araneoid family Theridiidae to be independent of that in Araneidae (unless, as noted in the text, one accepts the improbable loss of orb webs in theridiids). This is not unreasonable since theridiid attack wrapping at least often involves the use of a type of silk (from the aggregate gland) which is never used in this way by araneids (this gland’s product constitutes the sticky spiral), and because prey wrapping seems to have evolved independently in a number of spiders (see text). It is interesting to note in this connection that the different combs on legs IV used in wrapping in Theridiidae and Uloboridae argue for a separate origin of wrapping behavior in these families (the combs are on different segments and formed by modifications of different structures—see Opell, 1979; pers. comm.) (see Eberhard, 1979, for evidence that such combs do indeed function in wrapping behavior).

APPENDIX 2. *Continued.*

Spider	Source	Specimen	Behavior									
			A	B	C	D	E	F	G	H		
<i>C. conica</i>	Marples and Marples, 1937		2 (p)	1 ^b							2	1
<i>C. caroli</i> (Hertz)	film WGE	911, 1470 ^f	2	1	1	2	1	1	1 ^{ode}	3	1	1
<i>C. insulana</i> (Costa)	film WGE	2065 ^f	2	1	1	2	1	1	1 ^{ode}	3	1	1
<i>C. spp.</i> (at least 5 spp.)	film WGE	0-10, 977	2	1	1	2	1	1	1	3	3	1
		1832	2	1	1	2	1	1	1 ^{ode}	3	3	1
		1867	2	1	1	2	1	1	1 ^{ode}	3	3	1
		1892	2				1	1				
		1917						1 ^{ode}				
		1961 ^f	2	1	1	2	1	1	1 ^{ode}	3	1	1
		1095	2				1	1				
		888								3	3	
		2226	2	1	1	2	1	1	1 ^{ode}	2	1	1
<i>Salassina crassicauda</i> (K)												
<i>S. spp.</i>												
Mangoreae												
<i>Spilasma artifer</i> Simon		1437 ^f	2	1	1		1	1	1 ^{ode}	1	1	1
<i>Mangora melanocephala</i>		535	2	1	1		1 ^h	1		3	1	1
<i>M. spp.</i> (2 spp.)		1569, 1641 ^f	2 ^h			2				3	1	1
		2182	2 ^h	1 ^b						3	1	1
<i>Larinia directa</i>		833	2	1	1	2	1	1	1 ^c	3	1	1
<i>Acacesia hamata</i>		771, 1821	2 ^g	1	1		1	1	1 ^{ee}	2, 3	1	1
<i>Cyrtophora nympha</i> Simon		E129							3 ¹		1	1
<i>C. citricola</i>									3 ^m			
<i>Mecynogea</i> sp.	Kullmann, 1971	1038, 1040 ^f							3 ⁿ		1	1
<i>Eustala fuscovittata</i>		352	2	1 ^b	1	2	1	1	1	3	1	1
<i>E. spp.</i> (at least 3 spp.)		546	2				1	1	1	1	1	1
		1076	2		1		1	1	1	3	1	1
		1243	2				1	1	1		1	1
		1477	2			2	1	1	1		1	1
		1590	2				1	1	1		1	1
		1841	2	1	1	1, 2	1	1	1 ^{ode}	3	1	1
		2131	2	1	1	1	1	1	1 ^{ee}	2	1	1
Bertraneae												
<i>Bertrana</i> (?) sp.		1669	2				1	1				
Araneae												
<i>Araneus bogotensis</i>		1883	2	1	1	2	1	1	1 ^c	1	1	1

APPENDIX 2. *Continued.*

Spider	Source	Specimen	Behavior								
			A	B	C	D	E	F	G	H	
<i>A. diadematus</i>	Jacobi-Kleemann, 1953;		2	1	1	2	1	1	1 ^d	3	1
<i>A. sp.</i>	Witt et al., 1968	2144 ^f	2	1	1	2	1	1	1	3	1
<i>Araneus</i> (?) sp.		1700 ^f	2	1	1	1	1	1	1 ^c	3	1
(?) near <i>Araneus</i>		1902	2 ^k	1	1	2	1	1	1	3	1
<i>Verrucosa undecimvariolata</i> (O.P.-C.)		1722	2	1	1	2	1	1	1 ^c	1	1
<i>V. arenata</i>		2196	2	1	1	2	1	1	1 ^{cd}	1	1
<i>Wagneriana tauricornis</i>		019	2	1	1	2	1	1	1 ^{ce}	2	1
<i>W. sp. or spp.</i>		463 ^r	2	1	1	2	1	1	1	2	1
		574		1	1				1 ^c	2	
		1377	2	1	1	2	1	1	1 ^c	2	1
		1387	2	1	1	2	1	1	1 ^c	2	1
		Moz-1	2	1	1	2	1	1	1	2	1
		2204	2	1	1	2	1	1	1 ^{cd}	2	1
<i>Paravixia sp.</i>		805	2	1	1	2	1	1	1 ^c	2	1
<i>Scoloderus tuberculifer</i>		641	2	1	1				1		1
<i>Alpaida leucogramma</i>		1757	2	1	1	2	1	1	1 ^d	3	1
<i>A. rhodomela</i> (Tacz.)	film WGE	989	2	1	1	2	1	1	1 ^{cd}	3	
<i>A. tuonabo</i>		869	2	1	1	1	1	1	1 ^d	2	
<i>A. spp. (at least 3 spp.)</i>		840		1	1	2	1	1	1 ^c	2	
		1377	2	1	1				1		1
		1587	2	1	1				1		1
		2189	2	1	1	2	1	1	1 ^{cd}	3	1
		Chen5	2	1	1	1	1	1	1 ^d	3	1
<i>Eriophora edax</i>		696, 1836	2	1	1	2	1	1	1 ^{cd}	3	1
<i>E. spp. (2 spp.)</i>		WS29-32	2	1	1	2	1	1	1	2	1
		1945	2	1	1				1	3	1
<i>Metepeira sp.</i>		1313	2	1	1	2	1	1	1 ^c	3	1
<i>Metazygia gregalis</i>		769, 807, 1251, 1720	2	1	1	1, 2	1	1	1 ^{cd}	3	1
<i>M. pallidula</i>		1142	2	1	1				1		1
<i>M. witfeldae</i> (McC.)		1330	2	1	1	1, 2	1	1	1 ^d	2	1
<i>M. sp. or spp.</i>		1386	2	1	1	2	1	1	1 ^c	3	1
		1865	2	1	1	2	1	1	1 ^c	2	1
<i>M. (?) sp.</i>		1279	2	1	1				1		1
<i>Neoscona nautica</i> ¹			2	1	1				1 ^c	2	1

APPENDIX 2. Continued.

Spider	Source	Specimen	Behavior							
			A	B	C	D	E	F	G	H
<i>N. spp.</i> (3 spp.)		1514, 1573 2054 ^f 1947 ^f	2	1 ^b	1	1, 2	1	1 ^{cd}	3	1
<i>Wixia ectypa</i> ^o	Stowe, 1978		2	1 ^b	1	2	1	1 ^{de}	3	1
Gasteracanthaeae								4	1 (p)	3
<i>Gasteracantha cancriformis</i>	Peters, 1954; pers. observ.	274 ^f	2	1	1	2	1	1 ^{cde}	3	1
<i>G. minax</i> ^p	Clyne, 1975		2				1			
<i>G. theisi</i>	Robinson and Robinson, 1975		2							
<i>G. sp.</i>		2036 ^f	2	1	1	2	1	1 ^{cde}	3	1
Microtheneae										
<i>Microthenea horrida</i>		877, 1281	2 ^s	1	1	2	1		2	1
<i>M. sexspinosa</i> (Hahn)	film WGE	1681	2 ^s	1	1		1	1 ^e	2	1
<i>M. triangularis</i> (?)	film WGE	1660 ^f	2	1 ^b	1	2	1	1 ^c	2	1
<i>M. schreibersi</i>		2160		1	1	2	1	1 ^{cd}	2	1
<i>M. gracilis</i>	Peters, 1954; pers. observ.	2114 ^f	2 ^s	1	1	2	1	1 ^{cde}	2	1
<i>M. spp.</i> (at least 3 spp.)		1563	2	1 ^b	1	2	1	1 ^{de}	2	1
		1877	2	1	1	2	1		2	1
		MicraD	2	1 ^b	1	2	1	1 ^c	2	1
		2200	2 ^s	1	1	2	1	1 ^c	2	1
<i>Pronous sp.</i>		1051, 023-1	2 ^s	1	1	2	1	1 ^{ce}	2	1
Enacrosomeae										
<i>Enacrosoma anomala</i>		616, WS-105, 1811, 2197	2	1 ^b	1	2	1		3	1
Cyrtarachneae										
<i>Cyrtarachne sp.</i> ^o		1994 ^f	4	1	1	3	1	1 ^{cde}	1	3
<i>Poecilopachys australasia</i> ^o	Clyne, 1973		4 ^r				1			
Hypognatheae										
<i>Hypophthalmia sp.</i>		1586	2 ^s		1 (p)	2	1		1	1

APPENDIX 2. *Continued.*

Spider	Source	Specimen	Behavior								
			A	B	C	D	E	F	G	H	
Theridiosomatidae											
<i>Theridiosoma radiosum</i>		018-4	1 ^a	1 ^b	1	1	1	1	1 ^{ede}	4	2
<i>T. spp.</i> (4 spp.)		021-4	1 ^a , 4		1	1	1	1	1 ^{ce}	4	2
		984	4		1	1	1	1		4	2
		2184	1 ^a , 4		1	3	1	1	1 ^{ede}	4	3
		2205	1 ^a		1	3	1	1	1 ^{ede}	4	3
<i>Ogalinius sp.</i> or spp.		1543, 1569	4		3	3	1	1		5	3
		0-16d	4		1	3	1	1		5	3
<i>O. (?) sp.</i>		1292	4		3	3				5	3
<i>Epeirotypus spp.</i> (at least 4 spp.)		1233	1 ^a		1				1 ^c		2
		1566, 1600	1 ^a , 4 ^t		1	1	1	1		4 ^h	2
		1860 ^f	1 ^a , 4 ^t	1 ^b	1	1	1	1			2
		0-7, 982, 1863	1	1 ^b	1	1	1	1	1 ^{ede}	4	2
		2170 ^f	1 ^a	1 ^b	1	1	1	1		4	2
Anapidae											
<i>Anapis calima</i> Platnick		1084	1 ^a						1 ^c	4 ^u	
<i>A. heredia</i> Platnick		1293, 1309	1 ^a						1 ^v	4 ^u	3
<i>A. sp.</i>		SJ1-69-K, 2166	1 ^a	1 ^b	1	3	1	1	1 ^c	4 ^u	3
<i>Anapisona simoni</i> Gertsch		1002, 1004	1 ^a , 4 ^t			3	1	1		4 ^u	3
Uloboridae											
<i>Uloborus diversus</i> Marx	Eberhard, 1972	018-1	2 ^w	2	2	2	2	2	4	1	1
<i>U. glomosus</i>	film WGE	0-1	2 ^w	2	2	2	2	2 ^m	4		1
<i>U. trilineatus</i> Keyserling	Lubin et al., unpubl.	1452	2 ^w						4		1
<i>U. conus</i>		1770						2 ^m			
<i>U. spp.</i> (at least 4 spp.)		991						2 ^m			
		2073						2 ^m			
Philoponella divisa											
<i>P. vicina</i>	Opell, 1979	2164	2 ^w	2 ^x	2	1	1	1	4		1
<i>P. tingena</i>		021-1	2	2	2	1	1	1	4		1
<i>P. vittata</i>	film WGE	1813 ^f	2 ^w		1	1	1	1	4		1
<i>P. (?) sp.</i>		2072						2 ^m			

APPENDIX 2. *Continued.*

Spider	Source	Specimen	Behavior								
			A	B	C	D	E	F	G	H	
<i>Zosis geniculatus</i> ¹			2 ^w	2	2	1	1	2 ^m	4	1	1
<i>Z. sp.</i>	2012							2 ^m			
<i>Hyphotes covatus</i>	024-1		1 ^a	2 ^h	2	2	2	1	4	4	2 ^y

^a I was not sure whether I or both of I and II were used to locate the inner loop; the spider definitely turned to face away from the hub and moved along R_{K+1} toward inner loop.
^b oIV certainly grasped R_{K+1}, but position of oIII not certain.
^c Fluff accumulated at the hub.
^d Direct observation of breakage.
^e Frame sagged as spider returned upwards toward the hub, indicating that the radius was broken.
^f Specimen number randomly selected member of species distinguished in the field at sites where I worked intensively and was confident of my ability to make such distinctions until in the inner half of the sticky spiral they never or almost never touched the inner loop with leg of, but instead used only oIV to locate the inner loop, swinging it postero-dorsally until it hit the sticky spiral, the radius, or their junction and then flexing it to hook the radial line with the tarsal claws. This behavior was thus very similar to type 3 except that the longitudinal axis of the spider's body was more nearly perpendicular to the radius than parallel to it. Presumably the similarity to type 3 behavior is due to convergence rather than common derivation. Possibly the selective advantage of this behavior is that it reduces the energy expended by the spider as it builds.
^g Probable but not certain, spider moved very rapidly or was very small.
^h Specimen identified in the field without taking a specimen (all very distinctive species).
ⁱ Could not see individual lines, but the spider was observed carefully and its movements and leg positions left little doubt that I understood its behavior.
^j Only immature specimens observed building; mature specimen was collected for identification.
^k Nearly all radii were laid with the spider moving from the hub to the frame on the "leading" radius—the radius shown *not* being used in Figure 8.
^l Detail from photograph of finished web.
^m About half of the radii were laid with the spider moving from the hub to the frame on the "leading" radius; half on "trailing" radius.
ⁿ Web modified from typical orb that comparisons with other species in the table may not be justified.
^o Identified from photograph.
^p From Fig. 5 in Robison, 1975.
^q While Clae 1973 does not describe this acral movements, it is clear from her Fig. 1 that the spider is capable of somehow sensing the distance it has travelled from the hub along a radius.
^r Tapped to side with of as in type 1 behavior but often (but not always) stopped short of making contact with the inner loop.
^s Ability to measure distance travelled out toward inner loop was deduced from modification of behavior when the spider's encounters with the inner loop were "too close" to the hub, and/or from attachments of sticky lines to radii previously devoid of sticky spiral lines were at the same distance from the hub as those to other radii.
^t After finishing sticky spiral, spider broke every or nearly every radius part way between hub and inner loop of sticky spiral, and returned to hub and relaxed the radius before attaching it there. The hub was entirely destroyed just before or as several tightly spaced hub loops were laid.
^u The radii whose construction was observed were about 50 "quaternary" radii laid after the sticky spiral, which was attached to a web of 12-16 radii, was completed. The hub destruction observed occurred after all the quaternary radii were in place.
^w Leg of swung with more than usual circular component while tapping toward inner loop.
^x It was clear that oIV held r_{K+1} just beyond the attachment point, and that oIII held it inside the attachment point, but, despite repeated observations, I could not convince myself whether oIV seized r_{K+1} just inside the attachment (between the attachment and oIII) (this seemed most probable) or whether it was held just next to r_{K+1} but out of contact with it. The disruptive coloration of the legs made observation very difficult. It was clear that oIV was not in contact with the sticky spiral as the attachment was made.
^y The web was only a segment of an orb and the two loops of temporary spiral were arcs of concentric circles. Both were left in the finished web.

APPENDIX 3. Attack behavior of at least 81 species in at least 38 genera.

Observations with no source indicated are original, and numbers refer to descriptions in Appendix 1. It should be kept in mind that "4" is not a separate category, but rather indicates ignorance of whether the character state is 2 or 3. "()" indicates that less than 6 attacks were observed, and applies only to original observations.

Spider	Attack behavior	Source
Araneidae		
Tetragnathinae		
<i>Dolichognatha</i> spp. #533	2	
#0-2	2	
Metinae		
<i>Leucauge</i> sp. near <i>venusta</i>	2	
<i>L.</i> spp. #527	2	
#526	2	
#0-21-5	2	
<i>Chrysometa</i> spp. #532	2	
#0-6	(2)	
Nephilinae		
<i>Nephila clavipes</i>	1	Robinson, 1975
<i>N. maculata</i>	1	Robinson, 1975
<i>N. constricta</i>	1	Robinson, 1975
<i>N. turneri</i>	1	Robinson, 1975
<i>Nephilengys cruentata</i>	1	Robinson, 1975
<i>Herennia ornatissima</i>	1	Robinson, 1975
Araneinae		
Argiopeae		
<i>Argiope argentata</i>	3	Robinson and Olazarri, 1971; pers. observ.
<i>A. savignyi</i>	4	Robinson, 1975
<i>A. florida</i>	4	Robinson, 1975
<i>A. aurantia</i>	3	Robinson, 1975; pers. observ.
<i>A. aemula</i>	4	Robinson, 1975
<i>A. picta</i>	4	Robinson, 1975
<i>A. ocyaloides</i>	3	Robinson and Lubin, 1979a
<i>A.</i> sp.	4	Robinson, 1975
Cycloseae		
<i>Cyclosa caroli</i>	3	
<i>C. conica</i>	3	Marples and Marples, 1937
<i>C. triquetra</i>	3	
<i>C. furcata</i> or <i>bifurcata</i>	3	
<i>Salassina</i> sp. #2226	3	
Mangoreae		
<i>Mangora melanocephala</i>	3	
<i>M.</i> sp. #1569, 1641	3	
<i>Acacesia hemata</i>	3	
<i>Cyrtophora cylindroides</i>	4	Lubin, 1973
<i>C. momulfi</i>	4	Lubin, 1973
<i>Eustala fuscovittata</i>	3	
<i>Spilasma artifer</i>	3	
Araneae		
<i>Araneus diadematus</i>	4	Peters, 1931
<i>A. marmoreus</i>	4	Robinson, 1975
<i>A. rufipalpis</i>	4	Robinson, 1975
<i>Alpaida leucogramma</i>	3	
<i>Eriophora fuliginea</i>	3	Robinson et al., 1974
<i>E. nephiloides</i>	4	Robinson, 1975
<i>E. edax</i>	3	
<i>Wagneriana</i> sp. #574	(2)	

APPENDIX 3. *Continued.*

Spider	Attack behavior	Source
<i>Metazygia gregalis</i>	3	
<i>M. sp. #0-21-2</i>	3	
<i>Metepeira labyrinthica</i>	3	
<i>M. sp. or spp. #254</i>	(2)	
#1313	3	
<i>Wixia ectypa</i>	2 ^a	Stowe, 1978
Arachnureae		
<i>Arachnura melanura</i>	3	Robinson and Lubin, 1979a
Hypognatheae		
<i>Hypophthalma sp.</i>	3	
Gasteracanthaeae		
<i>Gasteracantha cancriformis</i>	1 ^b	Muma, 1971; pers. observ.
Micratheneae		
<i>Micrathena clypeata</i>	1	Robinson, 1975
<i>M. schreibersi</i>	1	Robinson, 1975
<i>M. sexspinosa</i>	1	Robinson, 1975
Mastophoreae		
<i>Mastophora dizydeani</i>	1	
<i>Dichrostichus magnificus</i>	1	Longman, 1922
Cyrtarachneae		
<i>Poecilopachys australasia</i>	1	Clyne, 1973
<i>Pasilobus sp.</i>	1	Robinson and Robinson, 1975
Celaenieae		
<i>Celaenia excavata</i>	1	McKeown, 1952
<i>Taczanowskia sp.</i>	(1)	Eberhard, 1981b
Theridiosomatidae		
<i>Olgulnius spp. #1292</i>	(1)	
#EG2-22III76	(2)	
<i>Epeirotypus spp. #1093</i>	(1)	
#1054	(1)	
#1603	(1)	
#802	(1)	
Uloboridae		
<i>Uloborus walckenaerius</i>	2	Marples, 1962
<i>U. congregabilis</i>	2	Marples, 1962
<i>U. diversus</i>	2	Eberhard, 1967
<i>U. trilineatus</i>	2	
<i>Philoponella semiplumosa</i>	2	
<i>P. republicana</i>	(2)	
<i>P. tingena</i>	(2)	
<i>P. vittata</i>	(2)	
<i>P. oweni</i>	2	
<i>P. arizonica</i>	2	
<i>P. para</i>	(2)	
<i>P. sp. near fasciata #Moz-14</i>	2	
<i>Zosis geniculatus</i>	2	Marples, 1962, pers. observ.
<i>Hyptiotes paradoxus</i>	2	Marples, 1962
<i>Miagrammopes simus</i>	2	Lubin et al., 1978
<i>M. intempus</i>	2	Lubin et al., 1978
<i>M. sp. near unipus</i>	(2)	Lubin et al., 1978

^a Prey is wrapped on branch rather than in web, spider's web is so unusual that comparisons with orb weavers are probably not justified.

^b Robinson (1975) attributed attack wrapping to this species. Muma's account, on which Robinson based his decision, is unclear and is open to other interpretations (Muma, 1971). My own observations (20 attacks on a variety of potentially dangerous [wasps, bees] and innocuous prey suggest that this species does not attack wrap. Robinson later (Robinson and Lubin, 1979a) included *Gasteracantha* in a list of genera lacking attack wrapping.