Eberhard, W. G. 1987. Web-building behavior of anapid, symphytognathid and mysmenid spiders (Araneae). J. Arachnol., 14:339-356.

WEB-BUİLDING BEHAVIOR OF ANAPID, SYMPHYTOGNATHID AND MYSMENID SPIDERS (ARANEAE)

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ABSTRACT

The web building behavior of species of *Anapis* and *Anapisona* (Anapidae), *Patu* (Symphytognathidae), and *Maymena* and *Mysmena* (Mysmenidae) is homologous with orb construction of other araneoids. Possible behavioral synapomorphies linking these three families, and linking Anapidae with Mysmenidae are proposed.

INTRODUCTION

The families Anapidae and Mysmenidae were recently separated from the family Symphytognathidae (Forster and Platnick 1977) on the basis of morphological differences. These authors speculated that web building behavior would provide "some of the best clues" to resolve the present difficulties in understanding the relationships between these and other families formerly grouped in Symphytognathidae. Recent work with other orb-weaving spiders has shown that some details of web building behavior are indeed useful in indicating relationships (Eberhard 1982, Coddington 1986a and b, in prep.), and this paper is an attempt to use direct observations of building behavior by six species and indirect evidence from finished webs of at least seven others as indicators of the relationships between these three families. The observations, which are generally in agreement with the fragmentary notes of previous authors, are also compared with those of orb-weavers in the families Araneidae and Theridiosomatidae.

Anapid webs and behavior are better known than those of the other two families. Horizontal orb webs are built by species in the genera *Anapis*, *Anapisona* (Platnick and Shadab 1978, Eberhard 1981, Coddington 1986a), *Chasmocephalon* (Forster 1959, Coddington 1986a), *Conoculus* (Shinkai and Takano 1984), *Risdonius* (Hickman 1938), and probably *Pseudanapis* (Forster and Forster 1973). In the first three genera there are one or a few radii above the plane of the orb, and a few sticky lines are attached to them. Several details of the construction behavior of *Anapis* and *Anapisona* are given in Eberhard 1981 and 1982, and Coddington (1986a) noted that both horizontal and non-horizontal radii of *Chasmocephalon shantzii* Gertsch are laid before the sticky line is produced. Some anapids' webs have "supplementary" radii that differ from the other radii both in being thinner (Hickman 1938) and in the angles they make with sticky lines (e.g., Coddington 1986a), but the construction behavior associated with these lines has not been carefully described.

In Symphytognathidae at least four species of *Patu* plus an unidentified Puerto Rican genus are known to construct fine-meshed horizontal orbs (Marples 1955, Forster 1959, Forster and Platnick 1977, Coddington 1986a), while *Symphytognatha globosa* Hickman makes a "web . . . of a few irregular threads in a more or less horizontal plane . . . the web seems to be made on the under-surface of the stones . . . The threads do not appear to be adhesive." (V. V. Hickman in Forster and Platnick 1977). There are no direct observations of the spiders' building behavior.

In Mysmenidae Marples (1955) noted that the webs of *Mysmena* (=*Tamesesia*) *rotunda* Marples and *M. acuminata* Marples consist "of a set of threads radiating in all directions from a centre . . . The space between the radials is filled with threads of a sticky silk, so fine that the droplets can only be seen under the microscope . . . the general impression is of an orb web in three dimensions." Photographs of webs of *M. jobi* (Kraus) (Shinkai 1977), *M. guttata* Bishop and Crosby and *M.* sp. in Coddington 1986a conform to this description. The web of *Maymena ambita* (Barrows) however resembles the orbs of anapids (Coddington 1986a). Marples (1955) observed that when *M. acuminata* spins sticky lines "the spider keeps going quickly out along different radials. Apparently it attaches a thread to a radial and carries the other end to the centre and out along another radial to attach it there. The web is built from the periphery inwards." Coddington (1986a) also found that radial and frame lines were laid before sticky lines in *M.* sp., and that in the center of *M. guttata* webs some radii ended on other radii rather than all ending at the central point or system of lines (hub).

MATERIALS AND METHODS

The spiders of this study are all minute, the smallest, *Mysmena* sp., being less than 0.5mm long at maturity. The lines they spin are thus normally invisible to the naked eye except under unusually favorable light conditions. It was nevertheless possible to acquire a relatively detailed picture of web construction by combining several techniques. Paths of moving spiders were followed closely and used as indicators of the positions of lines already in place. A strong headlamp was used to observe lines at favorable angles to the light. Those angles between lines that are indicative of tensions on the lines were watched especially closely to deduce whether the spider broke certain lines as it moved (see Eberhard 1981 for a description of this technique). The entire set of lines which a spider had laid was made visible periodically by breathing gently on the web. Due to the very humid microhabitats in which the webs were built (tropical rain forest leaf litter), this caused tiny drops of water to condense on all the lines, thus making the entire web easily visible (this technique was discovered independently by J. Carico in humid forests in New Zealand). The drops soon evaporated, leaving the web undamaged. The spider was generally disturbed briefly by being blown on, but in all but one case it resumed building, sometimes so soon afterward that the droplets were still on the lines, allowing for still more detailed observations.

I assumed, based on studies of larger and more easily observed species (e.g., Jacobi-Kleeman 1953, Eberhard 1982) that many details of web construction are highly stereotyped; thus when I succeeded in seeing a given detail of behavior clearly, I assumed that similar behaviors were executed in homologous situations which were less easily observed.

Finally, both partially built and finished webs were collected on microscope slides and examined with a compound microscope. It was found that when the edges of the slide were wetted just before the slide was pressed against the web, the positions of web lines were usually only slightly distorted by the process of collection.

Some of the species mentioned here are identified only to genus due to present incomplete taxonomic knowledge of the groups. Voucher specimens are deposited in the Museum of Comparative Zoology, Cambridge, Mass. 02138 U.S.A. The numbers and letters after names refer to labels in the vials with the specimens. Webs were photographed after being lightly coated with cornstarch or talcum powder.

The behavior reported here was compared to that of other orb weavers with respect to characteristics useful in the characterization of families and subfamilies (Eberhard 1982). The italicized letters and numbers (*A1*, *B2*, etc.) used below designate character states used in that study.

There is some inconsistency in the literature regarding terms that designate radii made before and after sticky spiral construction. Szlep (1961) used the terms "ordinary" and "additional"; Eberhard (1977) spoke of "original" and "supplementary" radii, and Coddington (1986a) termed them "structural" and "accessory" radii. Although the lines may have evolved independently in Uloboridae and the araneoids, they are geometrically and probably functionally analogous, so it seems desirable to standardize terminology. Some previous terms have imprecise or misleading connotations: ordinary and original imply character transformations which have not been established; and radii which are not "structural" are by implication not part of the structure. An additional problem is that some obvious alternative names (primary, secondary) have already been used to distinguish different radii of the first type that are laid at different stages of radius construction (e.g., LeGuelte 1966). I thus propose that radii laid before sticky spiral construction commences be called "elementary" radii, and those after the sticky spiral is complete "supplementary" radii. These terms are used in the descriptions that follow.

Throughout this paper "sticky" lines are those which have small balls of liquid distributed along their lengths, and "non-sticky" lines are those which lack such balls.

RESULTS

Anapidae.—Webs: The webs of the individuals whose building behavior was observed, *Anapisona simoni* Gertsch (No. 2166), *Anapis calima* Platnick and Shadab (SJ1-39-A1), and *Anapis* sp. (SJ1-69-K), shared several characteristics. They were horizontal orbs with one or a few non-sticky lines running upward from the hub and variable numbers of sticky lines attached to these lines (Figs. 1-3). In the web of *Anapis calima* only about 10-20 elementary radii were

Fig. 1—Web of *Anapis anchicaya* Platnick and Shadab with a single non-sticky line above the hub that has no sticky lines attached to it. Photograph is 7.4 cm wide.

fastened together at the hub, and the supplementary radii were either attached to the elementary radii or ended on sticky lines near the hub (Fig. 4).

Anapidae.—Building Behavior: Frame construction, which was observed only in *Anapisona simoni*, was similar to that of araneids and theridiosomatids (Savory 1952, pers. obs.) both with respect to the sequence of attachments made

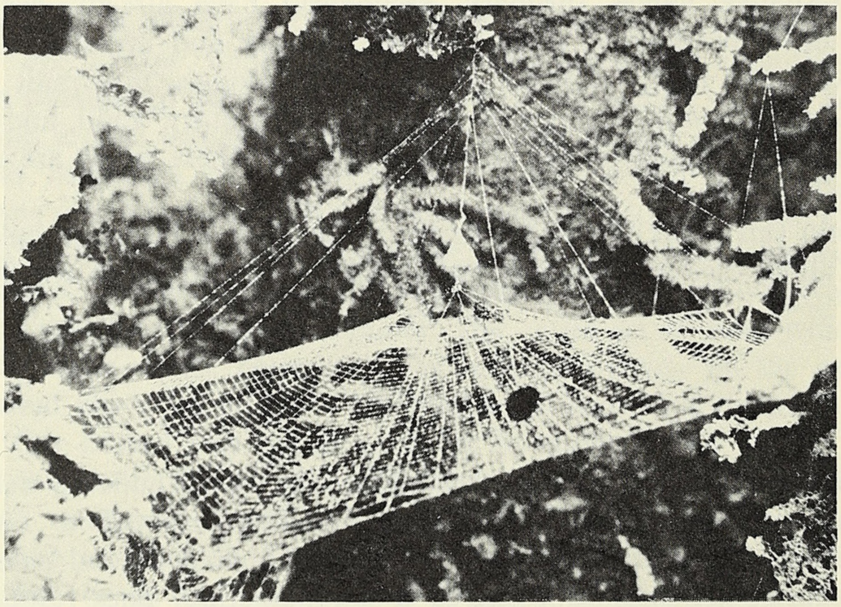

Fig. 2—Web of *Anapis heredia* Platnick and Shadab with a single non-sticky line running upward from the hub. The slanting lines attached to this line are excursions of the sticky spiral (see text). The large object just above the spider at the hub is an egg sac. Photograph is 4.7 cm wide.

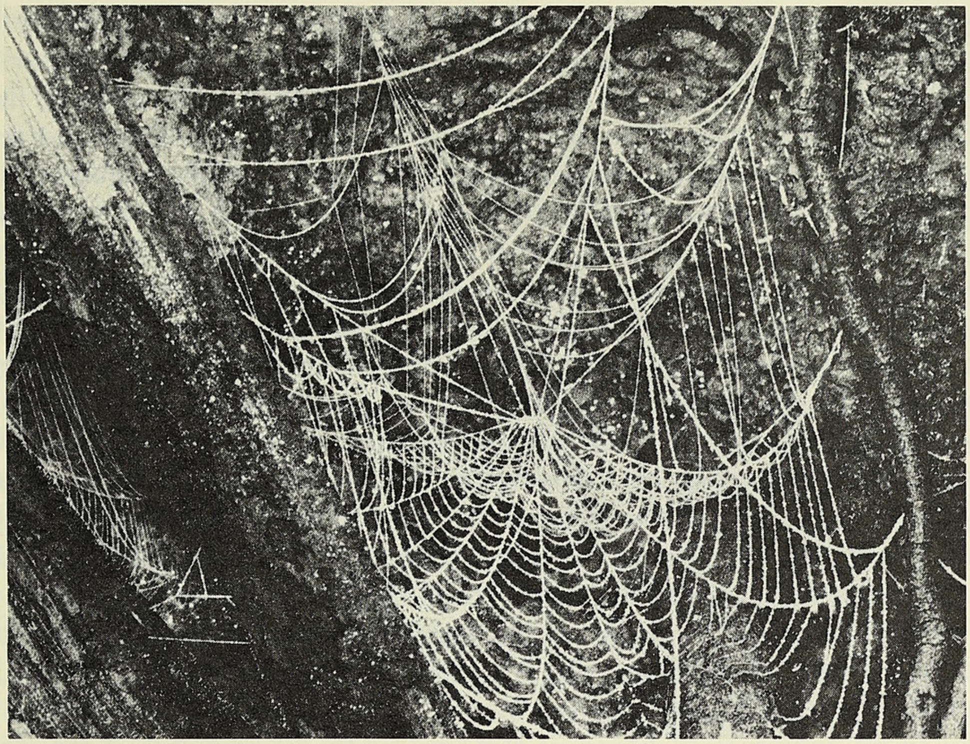

Fig. 3—Web of *Anapisona simoni* Gertsch with multiple non-sticky lines running upward from the hub. Numerous sticky lines are attached to these lines. Photograph is 15.6 cm wide.

to the radii bordering the sector that was spanned by the new frame line, and the fact that a single new radius was laid in the process of each frame construction. Construction of the rest of the elementary radii, also observed only

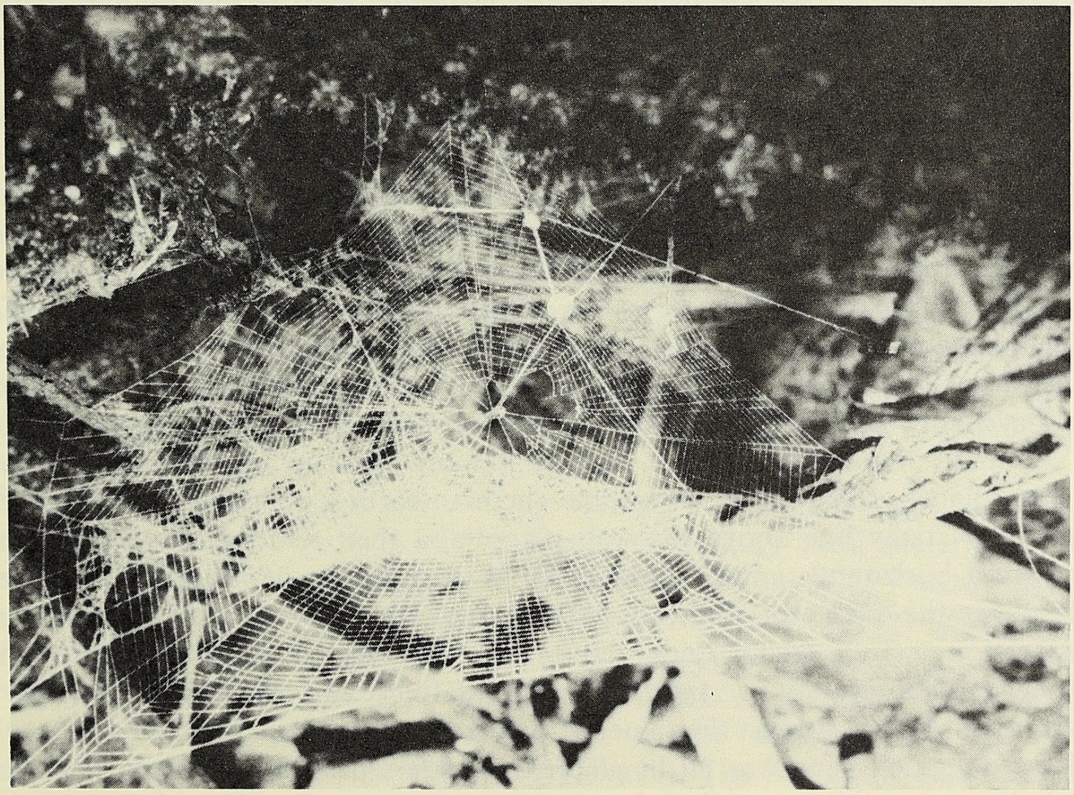

Fig. 4—Web of *Anapis calima* Platnick and Shadab. Many supplementary radii are broken near the hub. A single line runs upward from the hub to an egg sac, and pulls the hub slightly above the plane of the rest of the orb. Photograph is 10.0 cm wide.

in *A. simoni*, continued after the frames were complete, and was similar to typical araneid and theridiosomatid behavior (character state *F1* of Eberhard 1982) in that a single radius was laid for each trip away from the hub, and the line laid on the way out from the hub was apparently broken and rolled up and replaced by a new one laid on the trip back (breakage was deduced from observations of angles between web lines and from observations of a small white mass of loose silk at the center of the hub—in araneids similar masses accumulate during radius construction as a result of broken radial lines being rolled up and left there—Eberhard 1982). The construction behavior for radii out of the plane of the orb was the same in *A. simoni* as that for horizontal radii, and they were laid interspersed in the sequence of construction of horizontal radii. No hub loops were laid by this species during radius construction.

Subsequent behavior of at least two species deviated from typical araneid behavior. In *Anapisona simoni* radius construction was followed by hub construction, but then, instead of laying a temporary spiral of non-sticky silk, the spider immediately began laying sticky spiral. For each segment of sticky line it moved all the way from the edge of the web in to the hub, then back out again (character state *H3* of Eberhard 1982). *Anapis keyserlingi* Gertsch also failed to build a temporary spiral.

Sticky spiral construction began at the edge of the planar part of the web (not verified but probably also true in *Anapis calima*, which was observed laying only the last five, innermost loops of sticky spiral), and the spider gradually worked inward as do all orb weavers. In all species the spider faced away from the hub as it moved out a radius prior to attaching (character state *A1* or *A4* of Eberhard 1982), then turned briskly 180° to attach near the innermost sticky line already in place. I could not be certain in *Anapisona simoni* and *Anapis calima* whether the spider touched the inner sticky line before turning; it apprarently did touch it in *Anapis keyserlingi* (SJ1-69-K).

Sticky lines were laid to the radii above the plane of the web during sticky spiral construction in both *Anapisona simoni* and *Anapis keyserlingi* (SJ1-69-K) and were actually continuous with the planar sticky spiral. The spider attached the sticky line to a horizontal radius, went to the hub as usual, but then climbed one of the radii above the hub rather than going back out the next horizontal radius. It walked along this radius for approximately the same distance it had walked inward toward the hub, then attached the sticky line. From here it returned to the hub, and either walked out another horizontal radius (not the one it had started from) and attached the sticky line there, thus producing an inverted "V" of sticky line above the orb, or else it went back up another radius above the web plane, attached the sticky line there to form a more or less horizontal segment of sticky line above the web plane, and then returned to the hub and went out a horizontal radius (e.g. Fig. 3). In *Anapisona simoni* sticky lines were laid above the plane of the orb only during the early part of sticky spiral construction, so all sticky lines above the orb were attached near the orb's periphery. Photographs of *Anapis heredia* Platnick and Shadab webs (Fig. 2, Coddington, 1986a) suggest the same is true for that species.

When the sticky line was all in place, the spiders performed several behaviors which have not been described in any other orb-weavers. *Anapis calima* laid another series of radial lines (supplementary radii). Each line was laid by walking out a pre-existing radius, moving along the frame, attaching the drag-line to the frame, and then returning to the hub and apparently attaching the line there or near there. One *Anapis keyserlingi* Gertsch (No. 2166) made only a single supplementary radius; one *Anapisona simoni* did not make any (Fig. 3) while another, figured in Coddington (1986a), made only a few. There was a clear tendency to place consecutive supplementary radii on nearly opposite sides of the hub. No obvious hub lines were laid during the intervals between trips to lay new supplementary radii. The total number of supplementary radii in one web of *Anapis calima* was about 48.

The path traced by the spider as it returned to the hub during supplementary radius construction indicated that the radial line laid on the trip away from the hub was broken near the frame and was replaced with another as the spider moved back to the hub. The spider descended far below the web plane, and climbed nearly directly upward as it arrived at the hub. The placement of supplementary radii resulted in a characteristic radius-sticky spiral pattern in finished webs in which the sticky spiral changed direction whenever it crossed an elementary radius, but crossed supplementary radii without deviating (Figs. 1, 2 11). No supplementary radii were laid out of the plane of the orb.

Finally, in all species (except perhaps *Anapis calima*—I was not able to observe it well enough to be certain) the spider performed another unique behavior somewhat similar to hub destruction by theridiosomatids (character state *G4* of Eberhard 1982). Starting at the hub, the spider moved a few steps out an elementary radius, turned 180° to face toward the hub, and broke the radius. The spider evidently attached its drag-line near the outermost broken end and then payed out a length of silk, as the sticky spirals attached to that radius moved away from the hub. The spider returned to the hub as it slackened the radius or just afterward, reeling up the inner broken end of the radius and replacing it with the drag-line which it then attached at the hub. Since at least some supplementary radii were broken at or near the inner edge of the sticky spiral in finished webs (see Figs. 9 and 11), these lines were probably also broken during the loosening process, but I was unable to resolve this detail. Coddington (pers. comm.) found this to be the case in *heredia* and *Anapisona simoni.* Consecutive loosening operations tended to occur on more or less opposite sides of the web. Loosening operations on radii above the orb, which caused the orb to become less conical and more nearly planar, were interspersed with those on the others.

The loosening process continued until most or all of the elementary radii were lengthened; one *Anapisona simoni* did not loosen all of the radii, and microscopic inspection of two *Anapis keyserlingi* webs (SJ1-69-H, SJ1-69-K) showed that 15 of 18 and 11 of 11 elementary radii had been broken near the hub and presumably loosened.

Finally the spider finished the web by laying two or three tight hub loops connecting the new inner ends of the planar elementary radii (determined by direct observation in *Anapisona simoni*; in the other two species I was not certain that lines were laid as the spider turned slowly at the hub, but microscopic examination of two finished *Anapis keyserlingi* webs (No. 2166, SJ1-69-K) revealed two to three hub loops—Fig. 5). As it turned while making the hub, the spider removed the mass of rolled-up lines at the center of the hub and apparently ingested it (the white speck disappeared). The hub spiral caused sharp deflections of the radii where it was attached to them (Fig. 5), indicating that the hub line was relatively tight. Finally the spider assumed its waiting position at the hub. In none of the species observed did it flex the web, and when disturbed it climbed one of the radii above the orb. In contrast to many theridiosomatids, the spiders did not destroy any of their webs as they moved.

Symphytognathidae.—Webs: The web of the only symphytognathid observed, *Patu* sp. (No. 2194), was identical to the description of anapid webs with supplementary radii above except there were no lines above the plane of the orb.

Symphytognathidae.—Building Behavior: The presence of a white speck at the center of the hub in the web of *Patu* sp. after radius construction ended suggested that radius construction behavior was similar to that described above (character state *F1* of Eberhard 1982). After spinning about five loops of temporary spiral which spiralled outward from near the hub (character state *H1* of Eberhard 1982) the spider began spinning sticky spiral, starting from the edge and working inward. It faced away from the hub as it moved out each radius preparatory to attaching (apparently *A1* of Eberhard 1982), then turned 180° to attach. It did not maintain contact with the temporary spiral as it laid sticky spiral (*D1* of Eberhard 1982). When the sticky spiral was finished, the spider immediately began laying supplementary radii as described above except that it did not "sag" as dramatically below the orb plane as it returned to the hub. I was thus not certain whether the new supplementary radial lines were broken and rolled up as the spider moved back to the bub, but the white speck of loose silk at the hub did seem to grow. Finally the spider loosened the elementary radii as described above for anapids, and then turned slowly about three times at the hub and the white speck at the center disappeared (probably *G4* of Eberhard 1982).

Mysmenidae.—Webs: Two web forms were observed in this family. The webs of *Mysmena* sp. or spp. (Nos. 1034, 1122, 1173, 1174, 1175, 1188, 1366, 1679, and 2195) were similar to the *Mysmena* webs described and figured by Marples (1955) and Coddington (1986a). They consisted of about 20-30 non-sticky lines radiating in three dimensions from a central area or hub, with many sticky lines attached to them (Fig. 6). Some of the radii were attached directly to a support (leaf, twig, etc.), but most ended on short frame lines which were in turn attached to supports. Only two to four radii were attached to a single frame line. Microscopic examinations of webs were complicated by the webs' three dimensional structure, but in two cases (SJ1-69-M and SJ1-C) a clear hub was found. In both cases many radial lines did not extend all the way to the hub but terminated on other radial lines. Not all of the radial lines near the hub of the web of SJ1-69-M were of equal thickness.

The cloud of fine, slack sticky lines was attached to the radii in the space between the hub and the frames. These lines were so numerous and dense that it was not possible to discern any pattern in their arrangement. Microscopic examination showed that these sticky lines were thinner than the radial lines.

The webs of *Mysmena* sp. or spp. (Nos. 1608, 1687, 1689, SJ1-69-N, and SJ1-69-G) were different, being anapid-like horizontal orbs with a superstructure above. The building behavior of *Maymena* will thus be described separately below.

***Mysmena*.—Building Behavior:** Frame construction, which followed "exploratory" behavior, marked the discernable beginning of web construction, and was identical to that seen in most araneoids (above). Observations of changes in radius-frame angles during frame construction indicated that the radial line laid on the trip away from the hub was broken near the new frame and replaced as the spider returned to the hub. Subsequent elementary radii were also laid with typical araneid behavior (*F1* of Eberhard 1982). The formation of a white speck

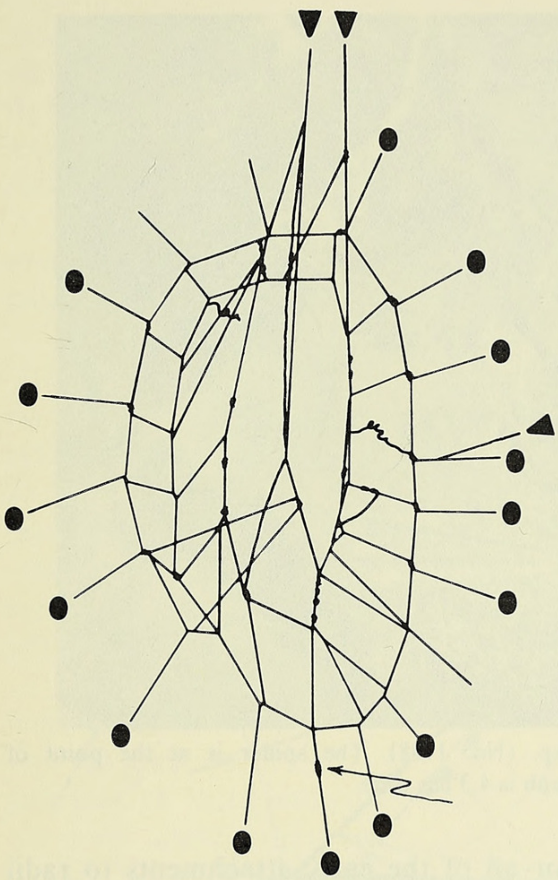

Fig. 5—Drawing of the hub of a finished web of *Anapis keyserlingi* Gertsch as seen on a slide under a compound microscope. Those lines marked with black dots had apparently been broken and repaired during web construction, since near the innermost edge of the sticky spiral each one had a mass of material (like that indicated by the arrow) which was probably pyriform silk used to attach lines together. The three lines marked with triangles were probably above the plane of the web; sticky lines were not attached to them in the central area of the web.

at the hub during radius and frame construction supported this conclusion, and microscopic examination of two webs collected at the end of this stage also revealed a tangled mass of lines at the hub which apparently corresponded to this white speck. No hub lines were laid during radius construction (direct observations were confirmed by microscopic examinations of the two unfinished webs). The spider "loosened" a few radii, moving a few body lengths away from the hub and then turning back and returning to the hub as do some other araneids (Eberhard 1981). The first radii were not concentrated in a single plane; I could not discern any pattern in the order in which radii were added. Coddington (1986a) also saw *Mysmena* build radii and frame lines before starting the sticky spiral.

After all or nearly all of the radii and frames had been laid, the spider began laying sticky lines without first making a temporary spiral (*H3* of Eberhard 1982). Coddington (1986a) also noted the absence of a temporary spiral in a *Mysmena* web. The spider moved quickly to the end or near the end of a radius, attached a sticky line there, then went quickly back to the hub and out another radius to attach again (Fig. 7). As it moved out a radius it faced away from the hub, but I was not sure if it made contact with the innermost sticky line already attached there (*A1* or *A4* of Eberhard 1982). Coddington (1986a) thought some attachments were made without contacting the inner loop. One spider which moved more slowly clearly paused just before each attachment to make several quick pulling movements with alternate strokes of legs IV (Eberhard 1981 gives evidence that such movements in other species result in more sticky line being pulled from the spinnerets). This same spider "pushed" the new sticky line away from its body with one leg IV just before the attachment was made (*C1* of

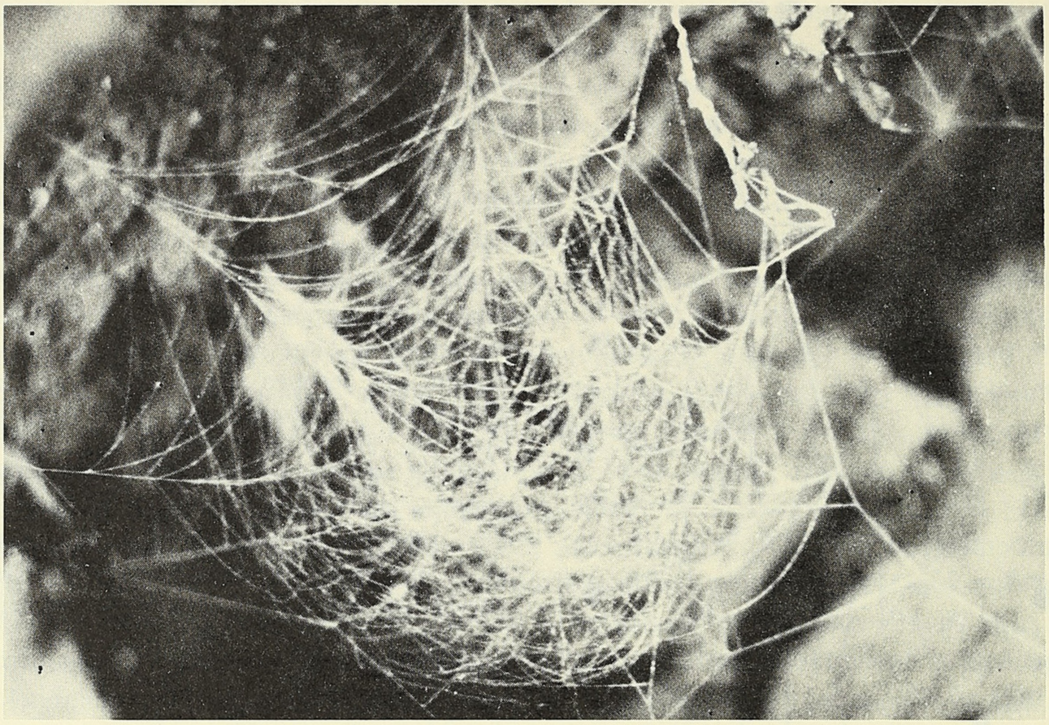

Fig. 6—"Three dimensional orb" of *Mysmena* sp. (No. 1188). The spider is at the point of convergence of lines in the center of the web. Photograph is 4.3 cm wide.

Eberhard 1982). Two spiders made most or all of the early attachments to radii above the hub.

Each successive sticky line was attached to the hub side of the point where the previous innermost sticky spiral segment was attached. The distances between successive attachments varied, the largest being more than twice the smallest.

The spider probably slid one tarsal claw along the radius as it moved out from the hub since the tiny water drops which were sometimes present on the radius were removed when the spider passed, and a single apparently larger drop was left just inside the point where the sticky line was attached to the radius.

The estimated angles between radii to which spiders made successive attachments of sticky lines were recorded in two webs. Although the data are somewhat suspect since angles were estimated rather than measured and I was not confident that all of my estimates were accurate, it appears that spiders chose radii which made angles of less than 90° more often than expected by chance. Of 243 pairs of attachments, 111 were to radii which made angles of less than 90°, and 76 were to radii which made angles of greater than 90° (56 others made angles close to 90°) (Chi Squared =6.55, $p<0.01$ assuming equal numbers of radii at less than and more than 90°. If such a tendency exists, it would explain why sticky lines are at least sometimes concentrated near the periphery of the web (Fig. 6, Coddington 1986a) since a sticky line laid from one radius to another 180° opposite would run near the hub.

One spider which was laying sticky spiral was disturbed when I blew on and apparently damaged its web. The spider remained immobile for several minutes, then laid several radial lines before returning to sticky spiral construction.

When the sticky spiral was complete, the spider loosened some of the radii near the hub (perhaps all in some cases) in the manner described above for anapids. That the radii were indeed broken and lengthened in this process was confirmed in one case by noting that a small white spot on the radius moved away from

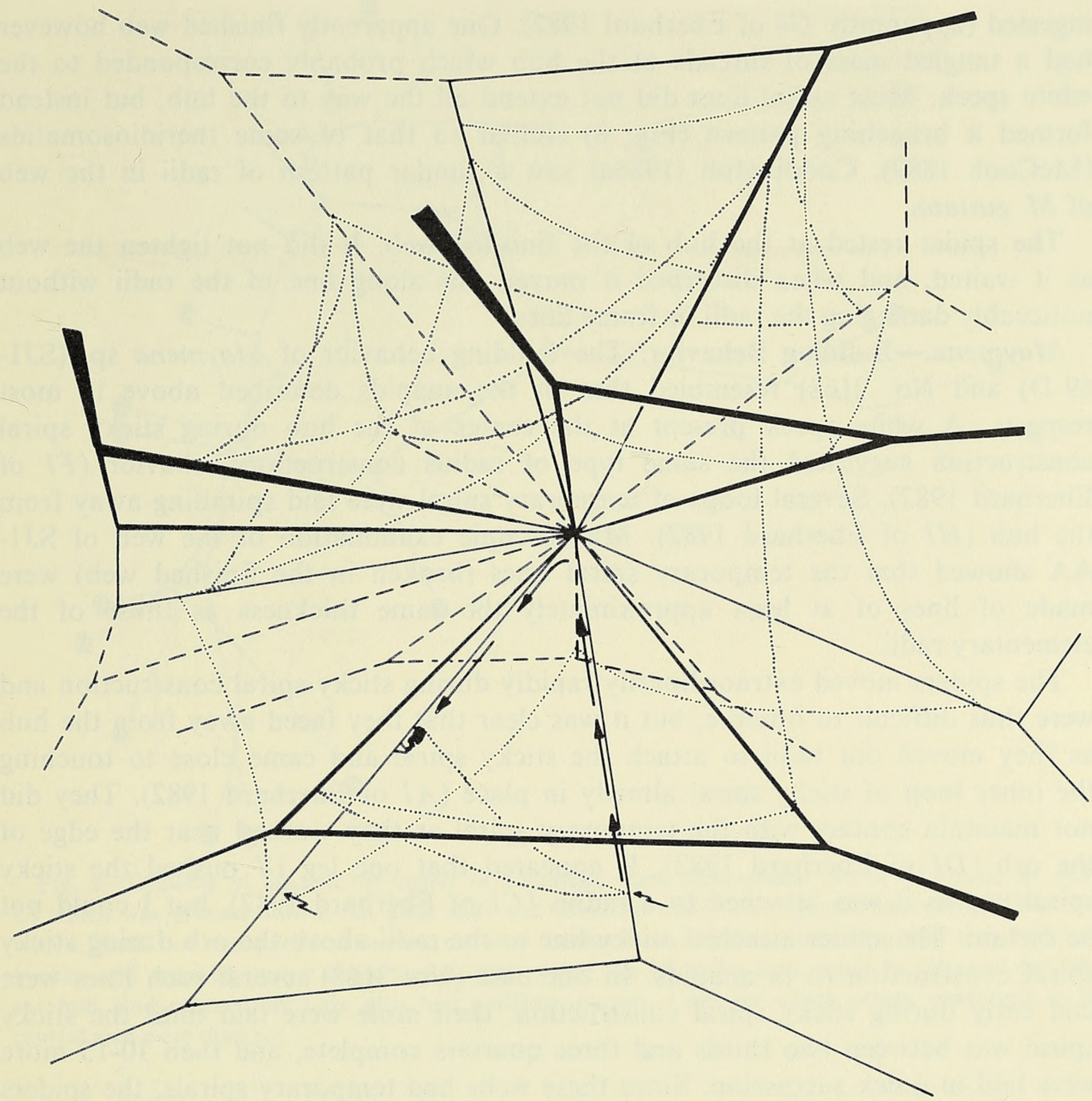

Fig. 7—Drawing of *Mysmena* sp. early in the process of sticky spiral construction. Straight lines (solid and dashed) are the non-sticky radii and frame lines. The dotted, curved lines are the sticky spiral. The spider travels all the way in to the hub and then back out (large arrows) between one attachment of the sticky spiral and the next (small arrows).

the hub as the spider moved back toward the hub. In several other cases I saw that the spider made quick alternate pulling movements with its legs IV apparently on the drag-line as it neared the hub, probably pulling additional silk as it did so. In one case the loosening behavior was at first confined to radii in the lower half of the web, and some upward-directed radii were not loosened. In finished webs that were examined microscopically, 5 of 23 radii in the web of one (SJ1-69-M) and 14 of the 19 radii which could be followed in the web of another (Fig. 8) had "pyriform masses" on them similar to those on the elementary radii of anapids and *Maymena* (below) that had been broken and lengthened.

When the loosening was completed, the spider slowly turned about 360° at the hub (3 of 3 cases), making movements which may have involved attaching the radii there together. Two completed webs on slides had a single loop of hub line (Fig. 8). As the spider turned, its anterior end was on the white speck at the center of the hub, and when it finished turning the speck was gone, presumably ingested (apparently *G4* of Eberhard 1982). One apparently finished web however had a tangled mass of threads of the hub which probably corresponded to the white speck. Most radial lines did not extend all the way to the hub, but instead formed a branching pattern (Fig. 8) similar to that of some theridiosomatids (McCook 1889). Coddington (1986a) saw a similar pattern of radii in the web of *M. guttata.*

The spider rested at the hub of the finished web. It did not tighten the web as it waited, and when disturbed it moved out along one of the radii without noticeably damaging the radii or frame lines.

***Maymena.*—Building Behavior**: The building behavior of *Maymena* sp. (SJ1-69-D) and No. 2168) resembled that of the anapids described above in most respects. A white speck present at the center of the hub during sticky spiral construction suggested the same type of radius construction behavior (*F1* of Eberhard 1982). Several loops of temporary spiral were laid spiralling away from the hub (*H1* of Eberhard 1982). Miscroscopic examination of the web of SJ1-AA showed that the temporary spiral lines (broken in the finished web) were made of lines of at least approximately the same thickness as those of the elementary radii.

The spiders moved extraordinarily rapidly during sticky spiral construction and were thus difficult to observe, but it was clear that they faced away from the hub as they moved out radii to attach the sticky spiral and came close to touching the inner loop of sticky spiral already in place (*A1* of Eberhard 1982). They did not maintain contact with the temporary spiral as they worked near the edge of the orb (*D1* of Eberhard 1982). It appeared that one leg IV pushed the sticky spiral just as it was attached to a radius (*C1* of Eberhard 1982), but I could not be certain. The spider attached sticky line to the radii above the orb during sticky spiral construction as in anapids. In one case (No. 2168) several such lines were laid early during sticky spiral construction, then none were laid until the sticky spiral was between two thirds and three quarters complete, and then 10-15 more were laid in quick succession. Since these webs had temporary spirals, the spiders must have walked to the hub on top of rather than beneath the radii, and somehow they kept the sticky spiral free of entanglement with the radius. I was not able to see how these feats were accomplished.

After finishing the sticky spiral, the spider paused at the hub for 10-30 seconds, then began to lay supplementary radii. The spider clearly sagged far below the plane of the orb as it returned to the hub, and thus apparently broke the line it had laid as it moved away from the hub. In one case (SJ1-69-D) it was clear that successive supplementary radii tended to be laid on nearly opposite sides of the web, and also that the spider made a series of quick, alternating pulling movements with its legs IV as it reached the hub, suggesting that additional line was being pulled from the spinnerets. Microscopic examinations of the webs of SJ1-69-D, SJ1-69-AA, and SJ1-69-G (Fig. 9) showed that the supplementary radii were much thinner than elementary radii. They could only barely be distinguished at 450X, while elementary radii were distinct even at 200X. These examinations also confirmed that only elementary radii were attached to the hub, and that the sticky spiral lines were attached only to elementary radii. No supplementary radii were laid out of the plane of the orb.

Spider No. 2168 was "distracted" by capturing and eating a series of three prey as it laid supplementary radii, and no further behavior was observed, but SJ1-69-D followed supplementary radius construction by cutting each elementary

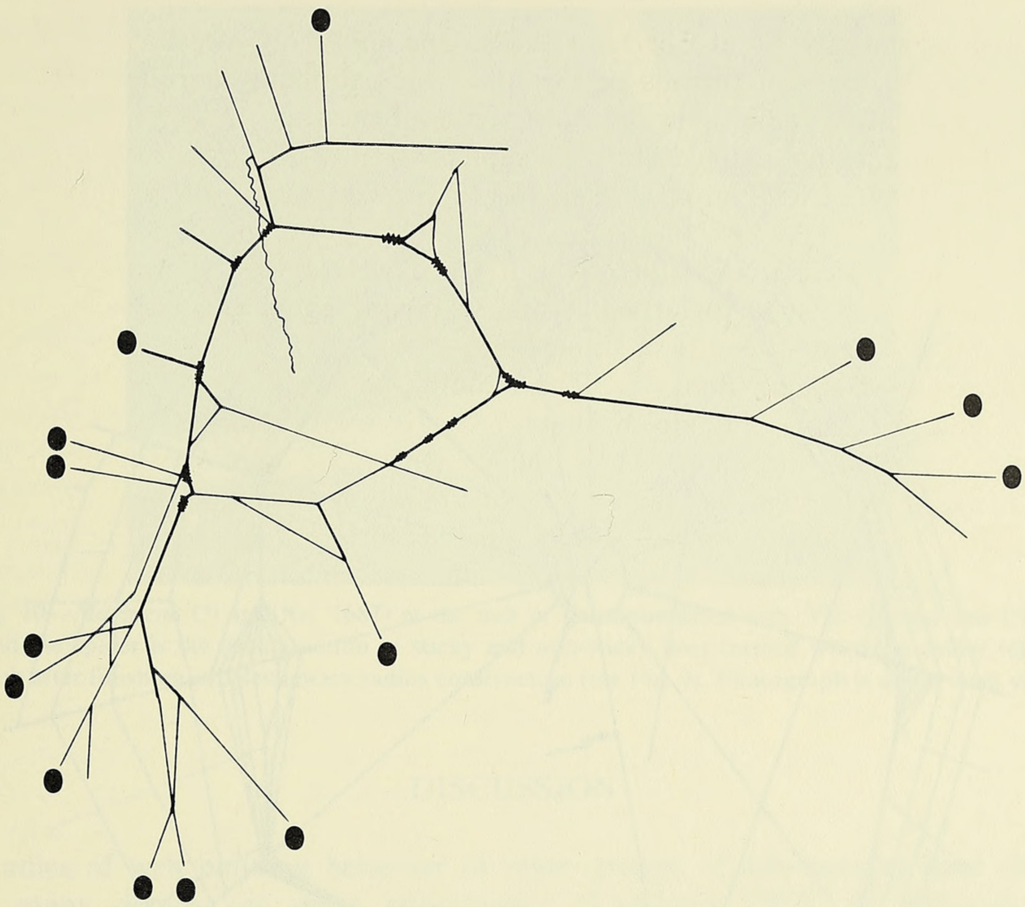

Fig. 8—Drawing of lines in the center of a finished three dimensional orb of *Mysmena* sp. (SJ1-C) which was pressed onto a flat glass slide and observed under a compound microscope. The lines with a black dot had pyriform masses on them farther from the hub, indicating that they had been broken and repaired during construction. Only 19 of the 24 radial lines could be followed far from the hub, and others may have also had pyriform masses. Lines on which others converged in the central area were thicker.

radius near the hub, lengthening it, and then reattaching it. At least some supplementary radii were also cut while elementary radii were being lengthened. I also noted pulling movements with legs IV as the spider returned to the hub during this process. The accumulation of broken supplementary radii and sticky spiral lines which had stuck together formed a "halo" of silk around the spider that was visible even in unpowdered webs (Fig. 10). Examinations of webs under the microscope confirmed both that all elementary radii were lengthened and reattached at the hub, and that all supplementary radii ended on the sticky spiral or an elementary radius and none of them reached the hub (Figs. 9, 11).

Finally the spider laid two loops of hub line around the accumulation of loose silk at the center of the hub, and in the process removed this silk (apparently *G4* of Eberhard 1982). The apparently complete web of SJ1-69-D, however, had a small mass of loose silk at the center of the hub.

Finished Webs of Other Species.—Some of the distinctive behaviors described above result in webs whose designs are also distinctive, allowing one to deduce details of building behavior from finished webs. Supplementary radii, distinguished by lack of deflection of sticky spiral lines crossing them, greater sag under the weight of cornstarch used for photography, and failure to pull frame lines to which they are attached out of straight lines, occur in the webs of the

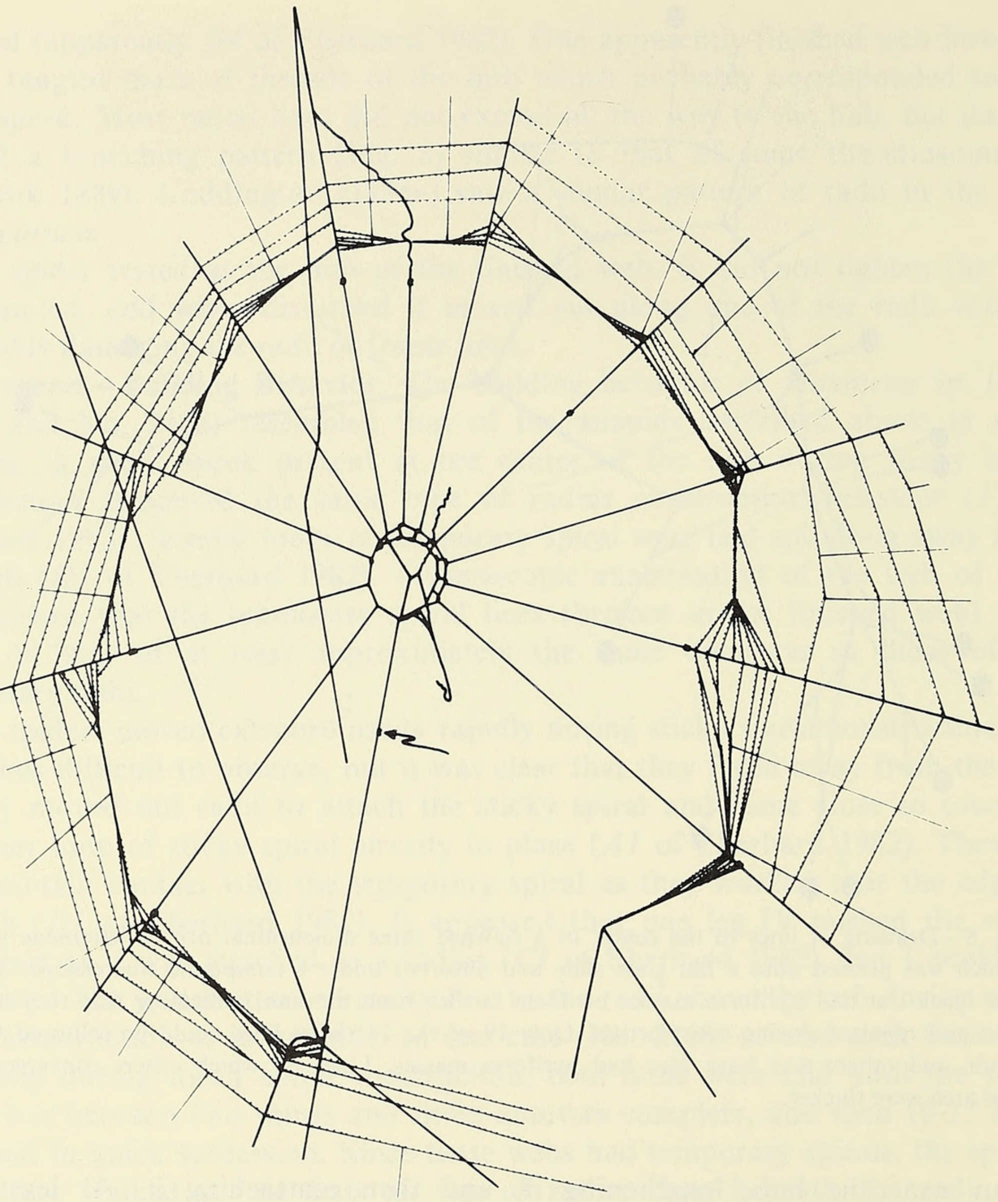

Fig. 9—Drawing of the central portion of the web of a *Maymena* sp. (No. SJ1-69-G) web that was collected on a slide and observed under a compound microscope. Thin lines with dots represent sticky lines. All elementary radii (thicker lines with larger dots) are connected to the hub, while supplementary radii (thinner lines with dots) end on sticky lines or elementary radii. The 5:00 sector of the web was evidently damaged during collection. The lines extending upward at 11:30 were probably above the plane of the orb. Pyriform masses are indicated by dark spots on the elementary radii (arrow).

anapids *Anapis anchicaya* Platnick and Shadab, *A. felidia* P. and S., *A. herediae* P. and S., the mysmenid *Maymena* sp. (No. 1687), and the symphytognathid *Patu saladito* Forster and Platnick. One web of *Anapisona hamigera* (Simon) clearly did not have supplementary radii.

When a spider which has laid supplementary radii then loosens the elementary radii, the pattern of threads near the hub is like that in Fig. 11, a pattern not seen in the web of any orb weaver which does not perform this behavior. This pattern is clear in photographs of the webs of all the species just mentioned.

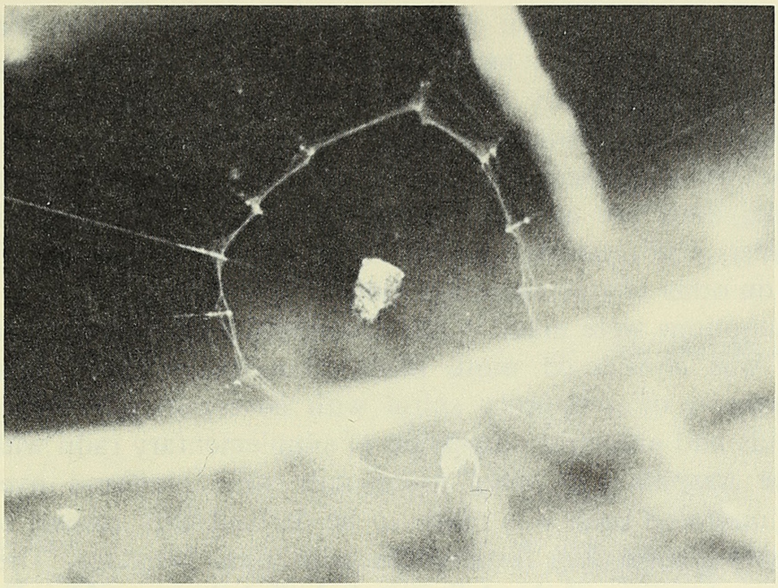

Fig. 10—*Maymena* (?) sp. (No. 1687) at the hub of its unpowdered web. The circular line ("halo") around the spider is the accumulation of sticky and non-sticky lines formed when the spider replaced the hub after finishing supplementary radius construction (see Fig. 9). Photograph is about 3 cm wide.

DISCUSSION

Studies of web building behavior of other groups of orb-weavers have shown that many details are quite conservative (Eberhard 1982), so although the numbers of species of anapids, mysmenids and symphytognathids whose webs

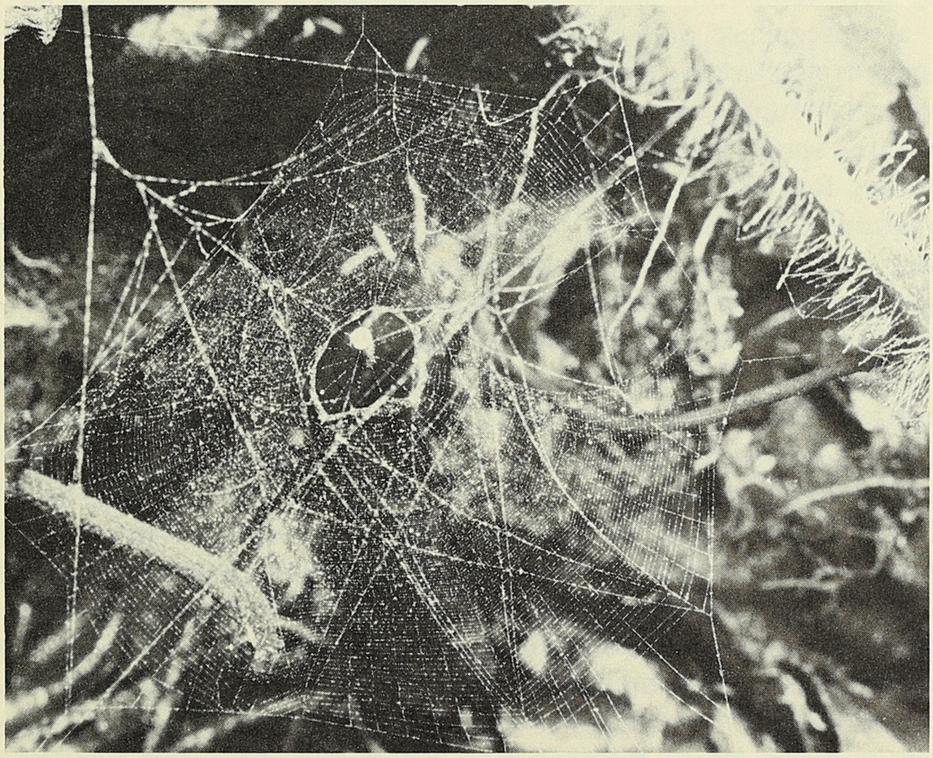

Fig. 11—Powdered web of *Maymena* (?) sp. (No. 1608). The white object above the hub is an egg sac. Supplementary radii and the "halo" of lines around the hub are visible. Photograph is 5.6 cm wide.

and building behavior have been observed is still small, the fact that they share apparently derived characters never seen in better studied groups is strong evidence that they are closely related. The data are combined with those of Eberhard (1982) and Coddington (1986a) and summarized in Fig. 12. Several synapomorphies are suggested. The term "radius" is used in Fig. 12 only for lines to which sticky lines are attached (thus excluding the "spring line" of some theridiosomatids). The relationships are in agreement with those of Coddington (1986a) based on other characters in addition to web form.

Several assumptions were made in constructing the cladogram. Convergent loss of characters was considered more likely than convergent origin; thus both ancestral possession of temporary spiral with covergent losses in anapids and some mysmenids and ancestral possession of supplementary radii with subsequent losses in some anapids and some mysmenids were preferred over alternative possibilities. Loosening radii was taken to be derived with respect to absence of this behavior since loosening involves an additional behavior. The decision to attribute late construction of the definitive hub and the use of leg IV to hold the radius to which the sticky spiral has just been attached away from the sticky spiral line (Eberhard 1981) to the presumptive ancestor of the non-araneid families was arbitrary, and early hub construction and not sliding leg IV could equally well be considered derived characters of araneids, unless uloborids and/ or dinopids are taken as the sister group of araneoids. As argued in Eberhard (1981), holding the radius away with leg IV is probably associated with relatively small spider size in relation to the distances between lines in the orb. I was not able to observe the mysmenids and symphytognathids in sufficient detail to ascertain whether they perform this behavior. If the relationships in Fig. 12 are correct, at least some of them probably do.

Loss of both temporary spiral and supplementary radii in *Mysmena* webs is probably a consequence of the three dimensional orb design, since it is difficult to imagine an effective three-dimensional temporary spiral, and it is probably impossible to lay supplementary radii through a dense three-dimensional array of sticky lines (the spider must move through them, however, when it captures prey). The secondary loss of supplementary radii proposed for anapids is supported by the observation of *Anapis* sp. (No. 2166) laying a single (vestigial?) supplementary radius, and the low numbers of supplementary radii in the webs of *Anapisona simoni* (Coddington 1986a) and *Anapis atuncela* Platnick and Shadab.

"Radial anastomosis" (convergence of some radii before they reach the hub) was not included in the characters used to make the cladogram even though it may be a useful taxonomic character (Coddington 1986a) because I was unable to determine whether the occasional supplementary radius terminating on an elementary radius near the hub (e.g. Fig. 7) was actually attached there or whether it fell against the elementary radius as the spider broke lines while loosening the elementary radii. It was clear that elementary radii did not "anastomize" in the orbs of any of the species studied other than *Mysmena* .

Coddington (1986a) pointed out the similarity between supplementary radii of symphytognathoids and the additional radii spun by some young uloborids (Szlep 1961, Eberhard 1977), and suggested that the possibility of homology should be considered in more detail. Supplementary radii are apparently similar to the uloborid lines in not being produced by the ampullate glands (at least they have very different diameters from those of elementary radii and hub lines). They differ however in being single lines placed on the web in radial directions rather than

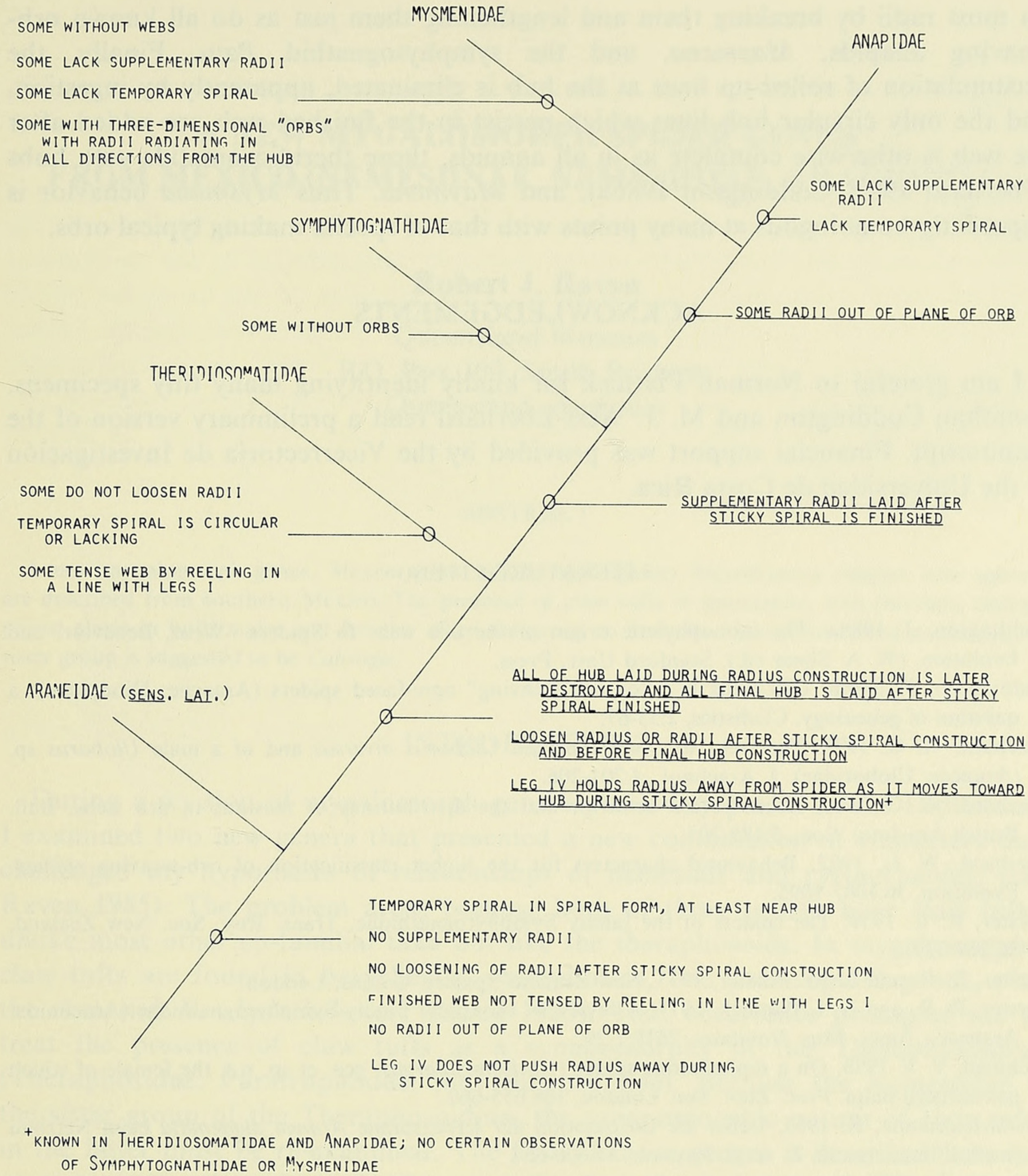

Fig. 12—Most likely system of relationships between different families based on behavioral characters (see text for assumptions made in analysis). Proposed synapomorphies are underlined.

clouds of fine fibers that often do not run radially as in uloborids (Eberhard 1977). Homology is thus unlikely.

The building behavior of *Mysmena* sp., the radial design of its web, and the orb web of the related *Maymena* clearly support the idea of Marples (1955) that *Mysmena* webs are best considered as three-dimensional orbs. Radii and frame lines are laid first, and involve behavior apparently identical to that of other araneoid orb-weavers. The tendency to lay some radii out of the plane of the orb, which also occurs in anapids and *Maymena*, is accentuated. As in all known orb-weavers, the sticky line is laid from the edge of the web moving inward so that each successive sticky spiral attachment to a radius is to the hub side of the last. As with the sticky lines of anapids and *Maymena* which are attached to radii out of the plane of the orb, all *Mysmena* sticky lines are very slack and sag under their own weight. When the sticky spiral is finished the spider lowers the tension on most radii by breaking them and lengthening them just as do all known orb-weaving anapids, *Maymena*, and the symphytognathid *Patu*. Finally, the accumulation of rolled-up lines at the hub is eliminated, apparently by ingestion, and the only circular hub lines which persist in the finished web are added after the web is otherwise complete as in all anapids, those theridiosomatids with hubs (Eberhard 1982, Coddington 1986a), and *Maymena*. Thus *Mysmena* behavior is apparently homologous at many points with that of species making typical orbs.

ACKNOWLEDGEMENTS

I am grateful to Norman Platnick for kindly identifying many tiny specimens. Jonathan Coddington and M. J. West-Eberhard read a preliminary version of the manuscript. Financial support was provided by the Vicerrectoría de Investigación of the Universidad de Costa Rica.

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Manuscript received October 1985, revised February 1986.