ORB WEBS IN "NON-ORB WEAVING" OGRE-FACED SPIDERS (ARANEAE: DINOPIDAE): A QUESTION OF GENEALOGY

JONATHAN A. CODDINGTON[1]

[1]*Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560*

Abstract—Observations of web spinning behavior in Costa Rican *Dinopis* sp. reveal the same behaviors synapomorphic for orb weavers: specifically frame, radius, non-sticky spiral construction, and sticky spiral construction, as well as more detailed motor patterns. Dinopids are therefore highly derived orb weavers, although the behavioral data do not conclusively indicate whether they are more closely related to the uloborid or araneoid orb weavers. A cladogram of dinopids, uloborids, and araneoids is presented.

Introduction

The rare, circumtropical "ogre-faced" spiders (Dinopidae) enjoy a somewhat sinister reputation for their bizarre method of catching prey. Their webs are first of all remarkable for their distinctive form and regularity (Fig. 1), and second for the way they are used. The spider grasps the periphery of the completed web with its first three pairs of legs (Fig. 11) and lunges at pedestrian (or aerial, W. G. Eberhard, pers. comm.) prey, simultaneously expanding the web and entangling the insect (Robinson and Robinson, 1971). Dinopids do not, as is often thought, cut the web free of the substrate and fling it at the prey. The web is at all times connected to the substrate by guy lines.
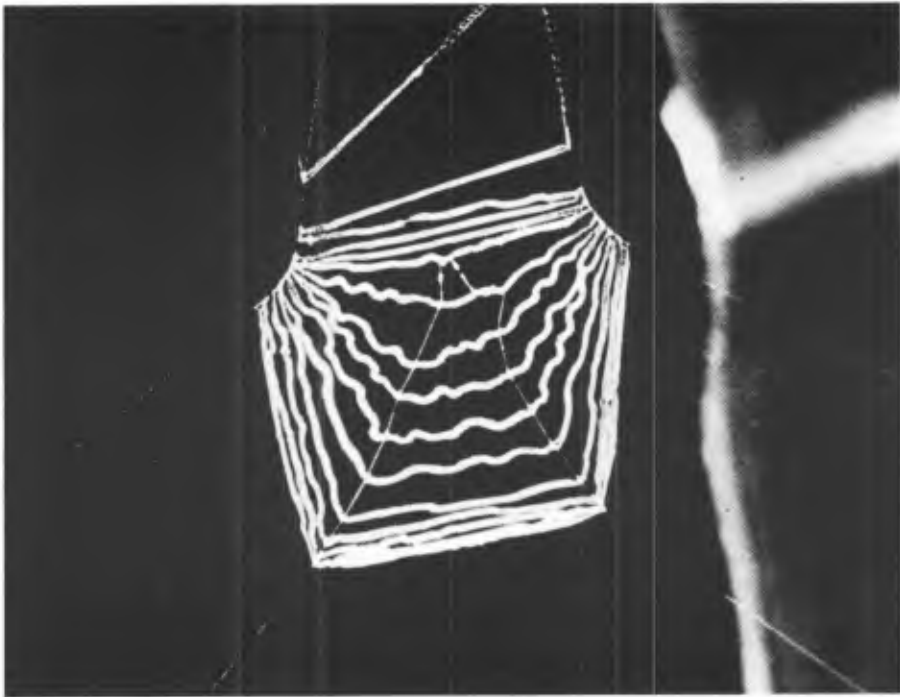

Fig. 1. The central portion of the snare of *Menneus camelus*. Photograph by M. K. Stowe.

Dinopid web building behavior has been described by various authors *(Menneus camelus:* Ackerman, 1926; *Dinopis subrufus:* Baum, 1938; Roberts, 1953; Clyne, 1967; *Dinopis spinosus:* Theuer, 1954) but past workers concentrated on sticky silk (hereafter SS) spinning rather than the spinning of the non-sticky (hereafter NS) scaffolding. The latter is equally characteristic of orb weaving spiders (Coddington, in press). Also, these authors did not present detailed descriptions of motor patterns and did not evaluate their observations in the context of the known ethology of web spinning spiders. None of the authors suggested that the impressive dinopid web might be the homolog of an orb and, indeed, the phylogenetic placement of the family has been uncertain (Levi, 1982). Here the web construction behavior of *Dinopis* sp. is compared to that of orb weaving spiders to demonstrate that dinopids do indeed spin orb webs, however highly derived.

The use of behavior to infer the phylogeny of spiders has a long history (Peckham and Peckham, 1889; Petrunkevitch, 1926; Wiehle, 1927, 1928, 1931; Robinson, 1975; Robinson and Robinson, 1980; Eberhard, 1982). In a study of 148 species in 58 genera, Eberhard (1982) showed that minute details of motor patterns used to construct orb webs are highly stereotyped and consistent across lineages of family rank. Coddington (in press) extended the analysis to include other motor patterns involved in non-sticky silk spinning, as well as the overall sequence of web construction. Although some disagreement exists over the phylogenetic implications of the data (Eberhard, 1982; Coddington, in press), workers concur that many motor patterns in web spinning are so consistent that qualitative variation occurs at the level of taxa, not individuals, and thus may be used in systematic research.

Methods and Terminology

An adult female *Dinopis* captured at the OTS Field Station Finca La Selva, Puerto Viejo, Heredia Prov., Costa Rica, was kept in captivity and web construction was observed wholly or in part 18 times. Many sequences were difficult to describe at first viewing, but transcriptions of the sequence of motor patterns became more and more similar as repeated sequences were observed. By the time 14 building sequences had been observed, descriptions were consistently similar. The spider was kept in a 3-sided wooden box (20 × 20 × 40 cm) with coarse mesh covering the fourth side. The spider fed readily (and normally, judging from observations of *D. longipes* by the Robinsons) on ants, small wasps, flies, and moths (the latter only if they were held until securely wrapped by the spider). Observations took place under very subdued illumination provided by a headlamp covered by a red filter. Before each observation interval, I destroyed any remaining major web lines so that the spider had to start afresh each time it built a web. This intervention assured that complete, comparable building sequences would be observed. In general, if an orb weaver is allowed to retain a previously built web, it may only repair that structure rather than replacing it, especially during a single activity period. In particular, the earliest stages of web construction frequently are omitted. The nocturnal *Dinopis* usually remove all traces of their web before dawn.

The spider I observed vanished after a month, apparently eaten by marauding ants, so that a specific voucher specimen, very unfortunately, is not available. A female *Dinopis* also collected from La Selva (W. G. Eberhard, viii. 1982, in Museum of Comparative Zoology) is *D. lamia* Macleay (the type species) using the key of Kraus (1956), but that key does not separate this species from the South American *D. fastigata* Simon, *D. biaculeata* Simon, or *D. rhodopthalamus* Mello-Leitão. Among neotropical *Dinopis* these species are reportedly distinctive in having only one pair of abdominal tubercles, a feature shared by the animal I studied. The species identification is therefore so uncertain that it seems wisest to refer here simply to *Dinopis* sp., while noting that the genus needs revision. Although the literature portrays dinopid web architecture as fairly uniform, thus suggesting that these observations may be valid for the genus, they should be used

with caution in any future comparative studies of *Dinopis* web construction. Eighteen observed sequences from a single animal is obviously a less than ideal basis for generalization, but the rarity of dinopid spiders, and the paucity of our knowledge about them, justifies the reporting and analysis of these observations.

Table 1 summarizes how often behavioral sequences or bouts were observed, and Table 2 presents brief definitions and descriptions of the terms abbreviated in the figures or used in the text (see also Eberhard, 1982, for additional descriptions of some of these motor patterns). ''Primary'' radius construction in any orb weaver refers to the construction of the initial radial lines which also serve to anchor the web to the substrate (Tilquin, 1942). Some of these (Coddington, in press) persist as ''radii'' in the finished orb. ''Secondary'' radii are those radial lines produced by frame behavior (e.g., Figs. 4, 6). ''Tertiary'' radii are those produced by radius behavior (e.g., Figs. 5, 7). *Dinopis* webs (Fig. 1) are bilaterally symmetric, but their NS and SS spirals may be either left or right-handed from the observer's point of view. Consequently remarks that can apply to either side of the web don't specify left or right (e.g., upper right radius or upper left radius) unless referring to a specific observation.

Whenever an orb weaver pauses or arrives at the hub of the web, it usually connects the lines at the hub with segments of non-sticky silk. In my experience, successive attachments of these segments usually go in one direction, thus the spider spirals about the hub, laying non-sticky spiral loops (see Eberhard, 1972, for a description of this behavior). Species vary in how many of these segments they make between the spinning of radial lines. All orb weavers I have seen interrupt their construction of radial lines to spin at least a few of these segments, but a minority of species spin no such segments whatever (W. G. Eberhard, pers. comm.). This discrepancy remains unresolved, but the hypothesis that these non-sticky line segments are homologous to those spun during unambiguous non-sticky spiral construction seems supported, and so I call the similar segments spun by *Dinopis* non-sticky spirals.

Results

The spider constructed nightly webs (sometimes 3–4 per night) spanning the top and one side of the box, slightly inclined from the vertical, thus agreeing with the orientation typical for dinopids (Robinson and Robinson, 1971, fig. 3a). The overall sequence of web construction is presented schematically in Figure 2 and detailed listings of motor patterns involved in frame, radius, NS spiral, and SS spiral construction are provided in Figures 3–11. Schematic drawings have to serve in place of photographs because the angle of view during observation precluded clear photographs. General as well as more specific descriptions of web construction, behavioral details, and comparison to other orb weavers follow.

Table 1

Number and type of behavioral acts or bouts observed. A ''bout'' is a series of similar behaviors. Thus SS spiral construction consists of several dozen SS attachment behaviors.

Overall Sequence	18
Midline Construction	10
NS Spiral Construction	18
Frame Construction	50
Radius Construction	25
SS Spiral Construction	18

A	(attach). L_{34} grip a line segment, and the spinnerets attach DL. The contralateral 4th leg may hold DL during attachment.
alt	(alternate). Legs alternate the same behavior, e.g., alt L_4 PP.
CUT	The line is brought to the chelicerae and severed, presumably enzymatically.
D, UP	(D = down). Moving relative to gravity. Usually L_{12} pull the spider along the support line, L_3 suspend it on the support line, and L_4 manipulate DL.
DL	(dragline). The NS line being spun. Subscripts indicate important line segments in temporal sequence, e.g. DL_1–DL_5 in frame behavior (Figs. 4, 6).
CR	(cut and reel). Moving by cutting and reeling in the front support line with L_{12} as DL is spun and held by L_4 behind. Often L_3 gather the slack as it is reeled in.
FL	(frame line). A web element spun during frame behavior (Fig. 4).
i,o	(inside, outside). The side of the spider nearest to (i) or furthest from (o) the hub, or, during movement, the trailing (i) or leading (o) side of the spider, e.g., iL_4.
IN, OUT	Moving to (IN) or away from (OUT) the web center. See "D" for description.
JX	(junction). Intersection of web elements, defined by an attachment point.
L	(leg). The spider's legs, numbered front to rear as L_1–L_4.
low, mid, high	Parts of a line, e.g., ML (high), ML (mid), ML (low).
ML	(midline). The first web element spun in a *Dinopis* web (Fig. 3).
NSS	(non-sticky spiral). A web element spun during non-sticky spiral construction (Fig. 8).
nx	A subscript indicating number of times a behavior is repeated.
PP	(pluck-pluck). Plucking, pushing, or pulling silk from the spinnerets, e.g. L_4 PP.
R	(radius). A radial line: upper, middle, lower, left or right, e.g., Ru, Rm, Rl.
SA	(stop-attach). Stopping or pausing, and attaching DL to another web element.
SB	(substrate). The substrate to which peripheral web elements are attached.
SPN	(spin). Moving along the support line, spinning DL. Often L_4 holds DL.
SRA	(stop-reverse-attach). Like SA, but reversing orientation on the support line before attachment.
SWB	(switchback). Reversing direction during a series of attachments.

GENERAL DESCRIPTION OF WEB CONSTRUCTION

The first act in web construction in a new site is the construction of the midline (Fig. 3a–c). Basically, the spider first attaches its dragline to the upper anchor point, then to the lower, and finally reinforces the line by doubling the midline along its length.

The second major element of web building is the construction of the first frame lines (Fig. 4a–c). The spider attaches its dragline near the middle of the midline, moving down to the substrate and laterally away from the midline before attaching its dragline a second time (Fig. 4a, steps 1–3). It then returns toward the hub via the line it has just laid, attaching the dragline spun on the return trip at least twice (Fig. 4a, step 5). When the spider reaches the midline, it continues up the midline for some distance before reversing and attaching its dragline to the upper part of the midline (Fig. 4b, step 7). The spider then moves out toward the T-shaped junction of the three major line segments it has just spun, and attaches its dragline very close to that junction (Fig. 4b–c, steps 8–10). Lastly, the spider cuts the first line segment it spun during frame behavior (Fig. 4a, DL_1), and reels up that line segment as it lays the last one behind it (Fig. 4c, step 11, DL_5).

Having completed one cycle of frame behavior on one side of the web, the spider repeats the same sequence on the other side of the web, thus producing a symmetric structure consisting of the midline and T-shaped frame lines lateral to it.

START

1° RADIUS CONSTRUCTION

NETWORK OK?

NS SPIRAL CONSTRUCTION   ?

RADIUS CONSTRUCTION

YES

RADII PLACED?   FRAME PLACED?   NO   FRAME CONSTRUCTION

NSS COMPLETE?

STICKY SPIRAL CONSTRUCTION

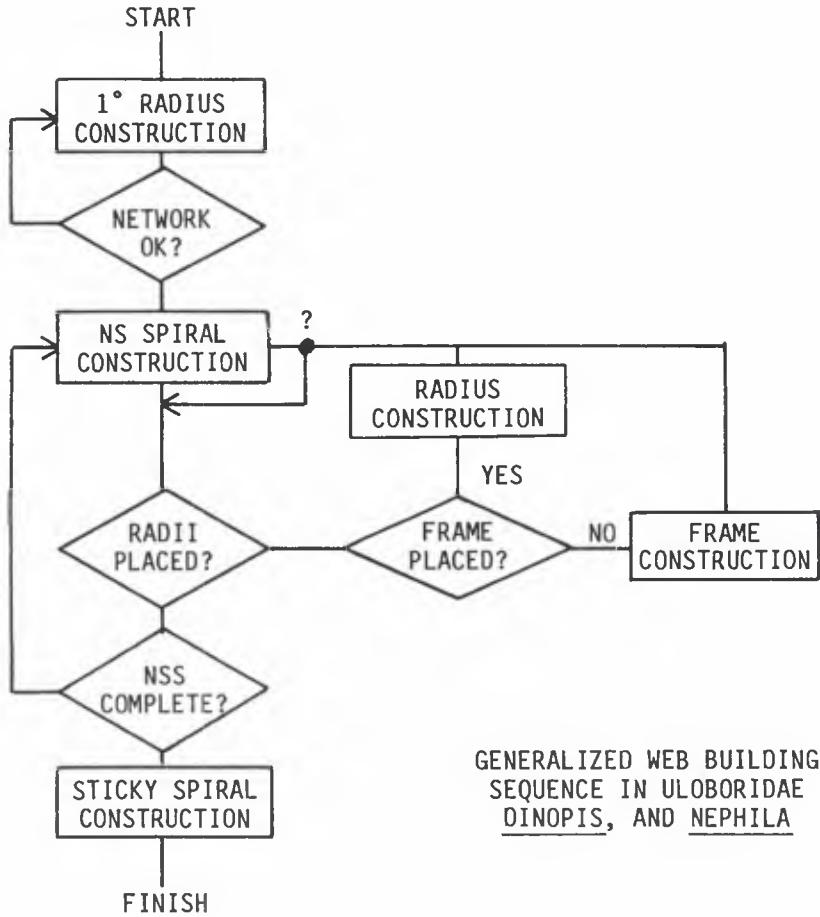GENERALIZED WEB BUILDING SEQUENCE IN ULOBORIDAE DINOPIS, AND NEPHILA

FINISH

Fig. 2. Orb web construction sequence. In *Dinopis* primary radius construction is equivalent to midline construction (cf. Fig. 3).

The third major element of web building is the comparatively simple construction of the upper radii. In effect, the spider replaces the last line segments spun on each side of the midline during the preceding two bouts of frame construction. Thus DL_5 of Figure 4c is cut out, and a new line (DL_2 of Fig. 5b) replaces it. Figure 5c illustrates the web as it appears at this stage of construction, with frame lines and upper radii complete.

The fourth major element of web building is the construction of the middle radii (Fig. 6). The spider builds its middle radii by using frame behavior (described above). The effect of this repetition of frame behavior is to add one T-shaped web element to each side of the web inside the lower web cells defined by the previous cycles of frame construction (Fig. 6c).

The fifth major element of web building is the construction of the lower radii (Fig. 7a–c). The spider again attaches its dragline to the midline near the origins of the upper and middle radial lines, exits on a middle radius, moves down the lower arm of the outer bifurcation, attaches its dragline, cuts this initial line (DL_1 of Fig. 7a), and reels the cut end up as it lays a new line to the midline (Fig. 7b, step 4, DL_2).
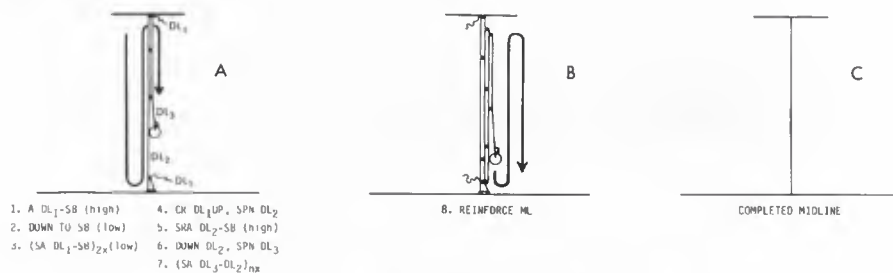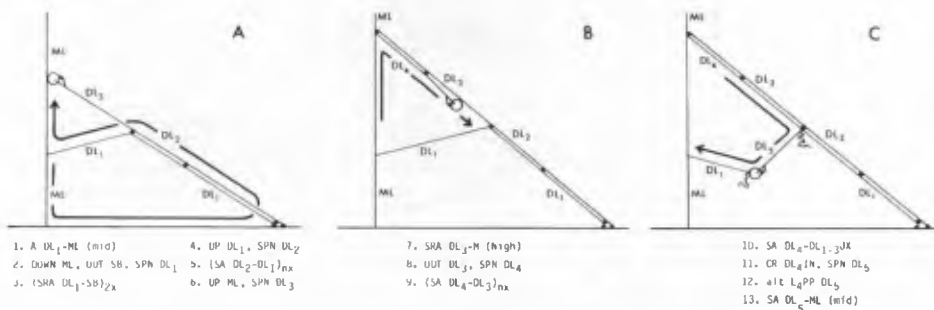
Figure 3: MIDLINE CONSTRUCTION

A

B

C

1. A DL_1-SB (high)	4. CK DL_1UP, SPN DL_2
2. DOWN TO SB (low)	5. SRA DL_2-SB (high)
3. (SA DL_1-SB)$_{2x}$(low)	6. DOWN DL_2, SPN DL_3
	7. (SA DL_3-DL_2)$_{nx}$

8. REINFORCE ML

COMPLETED MIDLINE

Figure 4: FRAME CONSTRUCTION.

A

B

C

1. A DL_1-ML (mid)	4. UP DL_1, SPN DL_2
2. DOWN ML, OUT SB, SPN DL_1	5. (SA DL_2-DL_1)$_{nx}$
3. (SRA DL_1-SB)$_{2x}$	6. UP ML, SPN DL_3

7. SRA DL_3-M (high)
8. OUT DL_3, SPN DL_4
9. (SA DL_4-DL_3)$_{nx}$

10. SA DL_4-DL_{1-3}JX
11. CR DL_4IN, SPN DL_5
12. alt L_4PP DL_5
13. SA DL_5-ML (mid)

Figs. 3, 4. See Table 2 for explanation of abbreviations in figures. The spider is represented by the circle (not to scale). The finer line from the rear of the circle represents the line being spun currently, and the angled line connecting it to the circle represents a fourth leg. The spider is always figured as moving forward, or so as to lengthen the dragline. The overall motion of the spider is as the thick arrow suggests. Black dots bridging two lines represent attachment points. Motor patterns are listed in sequence below each diagram. Squiggles represent lines after they have been cut (e.g., after cutting and reeling). In each successive figure web elements constructed previously are simplified to preserve clarity. Figs. 8–10 document particular sequences observed; the spiral may be either left or right, and the number of NS spiral or SS spiral segments also varies.

The sixth major element of web building is the cutting of the lower portion of the midline (Fig. 7c, step 8). When the spider does this, the geometry of the web changes considerably because of the loss of the anchor point (compare Figs. 7b,c).

The seventh major element of web building is the completion of the outer loops of the non-sticky spiral (Fig. 8). Up to this point, the spider has often circumnavigated the hub, laying non-sticky lines between the major behavioral sequences described above. This intermittent spiralling results in a confusion of lines at the hub, which Figures 3–7 indicate schematically. After completion of the lower radial lines, however, the spider no longer interrupts non-sticky spiral construction to lay other web elements, and thus lays a continuous line outward from the hub. As in some other orb weavers, the spider tends to switchback at the ends of the lower loops of the non-sticky spiral, but the outermost loop is a complete spiral turn.

The eighth major element of web building is the construction of the sticky spiral (Figs. 9–10). The spider begins to lay sticky silk across the lower four radii, reversing its direction of motion after attaching to the middle radii. Only in the later phases of sticky spiral construction does the spider attach sticky silk to the upper radii. As in other orb weavers, the spider cuts out segments of the non-sticky spiral as it spins the sticky spiral
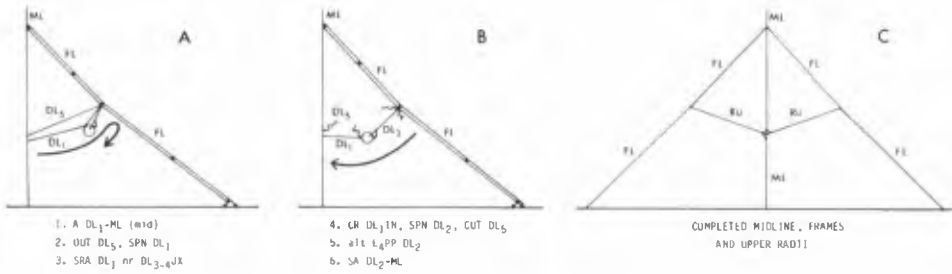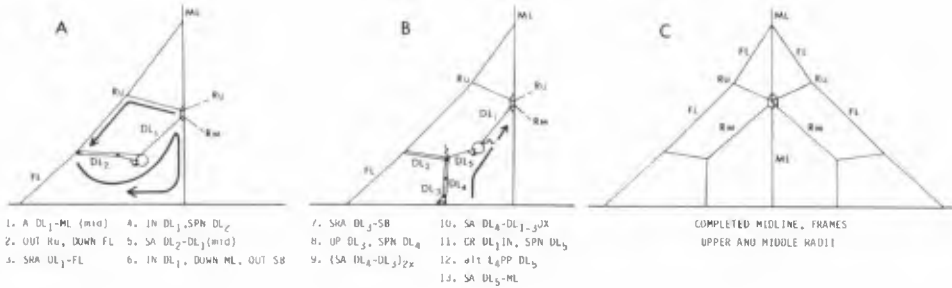
Figure 5: UPPER RADIUS CONSTRUCTION

1. A DL$_1$-ML (mid)
2. OUT DL$_5$, SPN DL$_1$
3. SRA DL$_1$ nr DL$_{3-4}$JX

4. CR DL$_1$IN, SPN DL$_2$, CUT DL$_5$
5. alt L$_4$PP DL$_2$
6. SA DL$_2$-ML

COMPLETED MIDLINE, FRAMES
AND UPPER RADII

Figure 6: MIDDLE RADIUS CONSTRUCTION

1. A DL$_1$-ML (mid)
2. OUT Ru, DOWN FL
3. SRA DL$_1$-FL

4. IN DL$_1$,SPN DL$_2$
5. SA DL$_2$-DL$_1$(mid)
6. IN DL$_1$, DOWN ML, OUT SB

7. SRA DL$_3$-SB
8. UP DL$_3$, SPN DL$_4$
9. (SA DL$_4$-DL$_3$)$_{2x}$

10. SA DL$_4$-DL$_{1-3}$JX
11. CR DL$_1$IN, SPN DL$_5$
12. alt L$_4$PP DL$_5$
13. SA DL$_5$-ML

COMPLETED MIDLINE, FRAMES
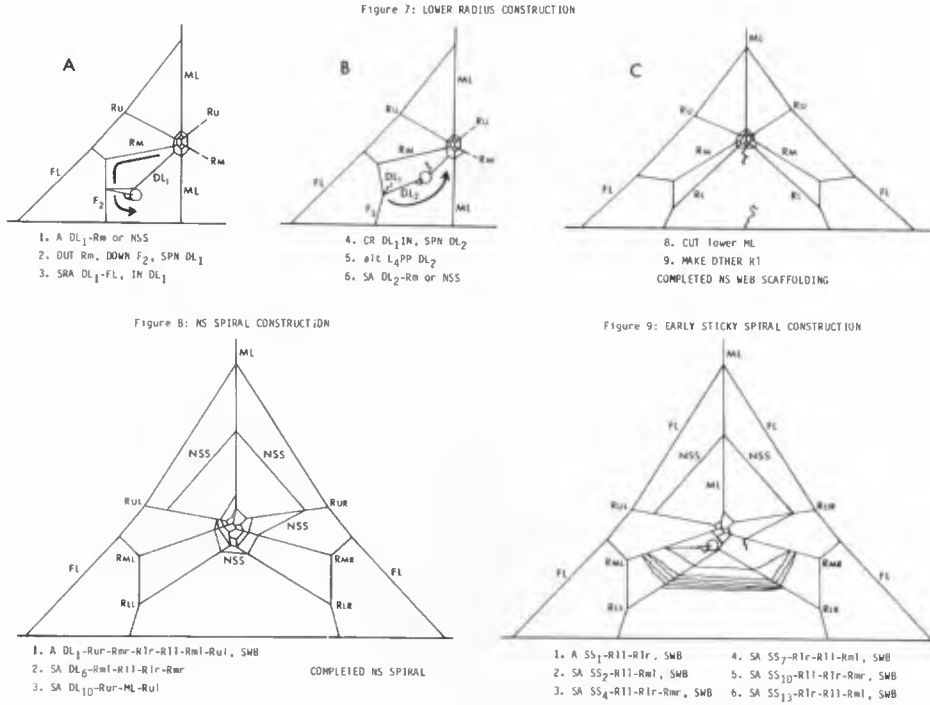UPPER AND MIDDLE RADII

Figs. 5, 6. See legend to Figures 3, 4.

inward. In *Dinopis,* however, the process of web element removal is carried much further, and even the inner ends of the lower four radii are cut (Fig. 10, steps 1,2,6,7).

COMMENTS ON SPECIFIC BEHAVIORS

Frame behavior (Figs. 4, 6) in *Dinopis* seems more similar to that observed in araneoid orb weavers than in uloborids, because it does not include the cutting of the second frame arm and its reattachment further out on the first frame arm which characterize uloborids (Eberhard, 1972; Coddington, in press). Presence of the araneoid pattern in *Dinopis* suggests that the distinctive frame behavior in uloborids is an autapomorphy of that family. Middle radius construction in *Dinopis* uses the same sequence as frame construction (compare Figs. 4, 6), and is thus an example of "secondary" frame construction (Eberhard, 1972). The sequences are extremely similar, however, so that it is simpler to say that web construction in *Dinopis* involves two instances of frame behavior (Figs. 4, 6) and two of radius behavior (Figs. 5, 7) on each side of the midline.

In its radius behavior, *Dinopis* cuts and reels DL$_1$ in (see CR, Table 2), spinning DL$_2$, as do all araneoids except *Nephila.* Uloborids do not cut and reel tertiary radii, thus some of their radii are doubled (Eberhard, 1982). In this respect, *Dinopis* is also more similar to araneoids than to uloborids.

Although of brief duration and reduced, NS spiral construction in *Dinopis* seems as stereotyped as in other orb weavers (Fig. 8; compare Eberhard, 1972, on *Uloborus*). Prolonged non-sticky spiral construction begins after lower radius construction, but throughout the construction of the NS web scaffolding the spider connects the proximal ends of radial lines with non-sticky spiral segments, so that the hub region becomes densely woven. Frequently the A DL$_1$ step of lower or middle radius construction (Figs.

Figure 7: LOWER RADIUS CONSTRUCTION

A
1. A DL_1-Rm or NSS
2. OUT Rm, DOWN F_2, SPN DL_1
3. SRA DL_1-FL, IN DL_1

B
4. CR DL_1 IN, SPN DL_2
5. alt L_4 PP DL_2
6. SA DL_2-Rm or NSS

C
8. CUT lower ML
9. MAKE OTHER R1
COMPLETED NS WEB SCAFFOLDING

Figure 8: NS SPIRAL CONSTRUCTION

1. A DL_1-Rur-Rmr-R1r-R11-Rml-Rul, SWB
2. SA DL_6-Rml-R11-R1r-Rmr
3. SA DL_{10}-Rur-ML-Rul

COMPLETED NS SPIRAL

Figure 9: EARLY STICKY SPIRAL CONSTRUCTION

1. A SS_1-R11-R1r, SWB   4. SA SS_7-R1r-R11-Rml, SWB
2. SA SS_2-R11-Rml, SWB   5. SA SS_{10}-R11-R1r-Rmr, SWB
3. SA SS_4-R11-R1r-Rmr, SWB   6. SA SS_{13}-R1r-R11-Rml, SWB

Figs. 7, 8, 9. See legend to Figures 3, 4.

4–7, step 1) attaches DL_1 to an NS spiral segment rather than to the midline. Similar events occur in uloborids and nephilines (Coddington, in press). Thus it may be valid to characterize frame and radius construction in orb weavers as embedded in a larger cycle of non-sticky spiral construction (Fig. 2). After completion of the last lower radius the spider does only non-sticky spiral construction, reversing direction at the lateral radii, until the final attachment at the upper radius. Detailed notes on NS spiral attachment sequences were only taken for six sequences, but my impression is that the other, merely observed, sequences corroborated the consistency. Usually the spider constructed two distinct pendulum arcs of NS spiral (Fig. 8). The last three attachments (Ru, ML, Ru) are always placed much further out on those lines than any preceding attachments, and those two NS spiral segments are among the few (in general the only) segments not removed during sticky spiral construction.

The sequence of SS spiral attachments is also fairly stereotyped, although I was unable to obtain completely consistent notes on the sequence, even after repeated observations. The spider does seem to switchback consistently at the second lower radius and thereafter only at the middle radius for the middle phase of sticky spiral construction (compare Fig. 1, the web of *Menneus camelus*). The later SS arcs are more widely spaced than the earlier. As sticky spiral construction proceeds, the spider cuts out virtually all NS spiral segments as well as severing the middle and lower radii. Because the order of removal depends on the order in which the spider encounters NS spiral segments, it is very difficult to tell in the later stages of sticky spiral construction whether an SS attachment is being made to a remnant of NS spiral segment or a radius.

The NS and SS spiral (Figs. 8–10) are arcs rather than complete circuits around the hub. The only complete circuit of the hub in web construction involves the last three

NS spiral attachments (Fig. 8), placed much further out on radial lines than preceding attachments. Such incomplete spirals or arcs are common in many other orb weavers (e.g., *Hyptiotes, Nephila, Herennia, Nephilengys, Eriophora,* and *Scoloderus*).

Localization of the outer SS segment prior to SS attachment in *Dinopis* is more similar to *Nephila* among the araneoids than any other orb weaver known to me. *Dinopis* taps laterally with outside legs 1 and 2 ($oL_{1,2}$, Table 2) to touch the web in advance of the current SS attachment point. *Nephila* consistently uses an oL_2 lateral tap in this behavior, whereas araneids and uloborids use an oL_1 lateral tap (the remaining araneoids use a forward tap of the inside first leg (iL_1); Eberhard, 1982). In uloborids and araneids the ratio of body to mesh size is much smaller, and oL_1 does contact the outer SS line. As in *Nephila*, *Dinopis* seems to locate the outer SS segment by a slight downward slide of oL_4 to contact the outer SS line. I am inclined to view the downward slide as convergent in *Dinopis* and *Nephila* because the spiders are convergently large in comparison to the mesh size of their webs. The lateral taps of outer legs in both taxa are interpreted as the homolog of the lateral tap localization behavior in uloborids and araneids.

As in uloborids (Eberhard, 1972), dinopids switch the calamistrum used to comb silk from the cribellum from the outside leg calamistrum to the inside leg calamistrum during the spinning of a single SS segment. Thus, just after an SS attachment is completed, the spider begins to comb silk with the outside leg calamistrum, with the outside 4th tarsus braced against the inside 4th leg. This attitude is maintained until the spider transfers from the previous radius to the next radius (to which the next SS attachment will be made), and the roles of the fourth legs are reversed, the outside leg becoming the brace, and the inside leg begins combing. No exactly equivalent behavior occurs in araneoids, probably in part because they are ecribellate.

As *Dinopis* approaches the SS attachment site, oL_2 and oL_3 alternately grip outward on the current radius, with oL_3 ultimately just proximal to the attachment point. The spider then stops combing cribellate silk, oL_4 transfers to the current radius distal to the attachment site, and the spinnerets bob up to cement the SS line to the radius. During this sequence, iL_4 is unoccupied, usually free in space and not gripping any line. In uloborids, as Eberhard (1972, 1982) demonstrated, iL_4 grips the current radius between oL_4 and oL_3, proximal to the attachment site. The uloborid current radius grip may thus be described as i,oL_4 (Eberhard, 1982), but it is also true that oL_3 is immediately proximal to that grip. Consequently the use of iL_4 in uloborid SS attachment behavior in addition to the oL_{34} grip is also probably an autapomorphy of that family. That the oL_{34} grip is used by uloborids in most other aspects of building behavior supports this inference, and oL_{34} is apparently the only grip used by any of the other orb weaving taxa during the stereotyped phases of web construction. Eberhard (1982) presented evidence that the oL_{34} grip is absent in other cribellate taxa (potential outgroups to orb weavers), and thus that the oL_{34} grip is synapomorphic for orb weaving spiders.

FEATURES UNIQUE TO *DINOPIS*

The construction of the vertical midline (Fig. 3) is apparently a behavior peculiar to *Dinopis*. Because it occurs first in the overall web building sequence, is reinforced and adjusted in tension before the following step of frame behavior, and involves attachment to substrate, midline construction is potentially homologous to primary radius construction in other orb weavers (Fig. 2). However, the specific behaviors seen in either sequence occur elsewhere in the web building process, so that the argument for homology thus far is based on sequence and not on objective features uniquely diagnostic for primary radius construction (such as a unique motor pattern or a unique stereotyped sequence). Primary radius construction in other orb weavers and dinopid midline construction are not as stereotyped as other web building behaviors. *Dinopis* prefaces frame

construction with less exploratory construction than any other orb weaver known to me.

During the construction of the upper radii (Ru, Fig. 5), on the return trip to the midline (CR DL_1 IN, SPN DL_2, Fig. 5b, step 4), the spider cuts DL_5 of the previously constructed frame line as well (cf. Fig. 4c, step 11). The upper radius lines functionally replace the secondary radii constructed during the previous instance of frame behavior. I know of no other orb weavers that cut radial lines produced during frame behavior while engaged in tertiary radius construction.

When *Dinopis* attaches lines to the substrate, it uses a double attachment behavior (e.g., Fig. 3, step 2; Fig. 4, step 3). Other orb weavers will double-attach on occasion, but *Dinopis* did so consistently.

As *Dinopis* nears the midline to attach any of the six radial lines (Figs. 4-7), it pauses and lengthens the radii by pulling additional silk from the spinnerets with alternate L_4 pulls (e.g., Fig. 6, steps 12, 13). Other orb weavers (Eberhard, 1981; Coddington, in press) lengthen radial lines with alternate L_4 pulls, but the behavior is usually performed after the line is constructed (and thus requires cutting the line), and not as an integral part of the initial construction of the line. Anapids, mysmenids, and probably symphytognathids do pull or pluck with alternate fourth legs to lengthen the accessory radii that characterize their webs as the accessory radii are being constructed (Eberhard, 1981) but these taxa do not lengthen secondary or tertiary radii as does *Dinopis*.

Between the construction of the first and second lower radii, the spider cuts the lower end of the midline (Fig. 7c, step 8). Other orb weavers modify their webs (especially the hub) by cutting out lines, but except for the biting out of the protohub in uloborids (Eberhard, 1972; Coddington, in press), such modification takes place after the end of SS spiral construction.

During SS spiral construction, *Dinopis* cuts the inner ends of the lower and middle radii (Fig. 10, steps 1, 2, 6, 7). The structural integrity of the completed web thus depends primarily on the SS lines connecting the severed radial line segments. Cribellate sticky silk is much more extensible than the dry silk used to construct the NS scaffolding (Eberhard, 1972), and *Dinopis* does produce unusually extensible SS lines. The cutting of the NS scaffolding undoubtedly enables the tremendous expansion in web area (10x?) which accompanies the spider's attack behavior (Robinson and Robinson, 1971).

At least in the enclosure provided, *Dinopis* used only a part of the container as substrate for the web; thus the container was apparently of adequate size to allow construction of typical webs. The web contains few elements exceeding the spider's leg span (midline, both initial frame lines), but the space they enclose seems easily spanned by the spider's legs. Thus during web building the spider does not move whole body lengths along a few or single lines isolated in space as do most orb weavers, but instead bobbed and turned to position legs and spinnerets within the small area the web covered. Duration of some characteristic motor patterns (oL_1 lateral tap, SRA, Table 2) was thus brief, and the behaviors slightly aberrant. The same difficulties are encountered in other spiders which are large for the size of mesh they spin (e.g., *Nephila*).

Discussion

To what extent the behaviors seen in this *Dinopis* species are typical of the family is unknown, but one may predict that all dinopids use closely similar behaviors. As mentioned, previous authors studying other species have not reported the behavior in detail. Weak corroboration of that prediction is provided by the very similar web architecture of other dinopid species *(Menneus camelus:* Ackerman, 1926, pl. 23, fig. 8; *M. unifasciatus:* Austin and Blest, 1979, fig. 3; *D. subrufus:* Baum, 1938, fig. 4, Austin and Blest, 1979, figs. 1-2; *D. spinosus:* Theuer, 1954, figs. 3-6). All, for example, seem to construct webs with 6 radial lines, of which at least the lower two have been cut (cf. Fig. 11). Theuer in particular figured a recognizable NS spiral in *D. spinosus* (1954,

fig. 4), but neither he nor any of the other authors explained how the spider gains the initial substrate attachment points for the web. This study would predict that all dinopids will obtain attachment points by behavioral sequences similar to midline or frame construction. However, if an animal consistently reuses the same web site, NS silk lines may accumulate at the periphery, and the spider may use these as "substrate" rather than non-silk supports. In such a case the geometry characteristic of frame construction is difficult to differentiate from the pattern of residual silk lines (e.g., Theuer, 1954, fig 3; Ackerman, 1926, figs. 4–8). Critical tests of the prediction require close observation of a spider's movements as it constructs a web in a pristine site.

The evidence for orb weaver monophyly, and especially the orb web as primitive for the entire superfamily Araneoidea (including the families Araneidae, Tetragnathidae, Metidae, Linyphiidae, Nesticidae, Theridiidae, Anapidae, Mysmenidae, Theridiosomatidae, and Symphytognathidae), is presented in detail in Coddington (in press). Depending to some extent on data coding, at least eight behavioral features and one morphological feature are synapomorphic for orb weavers as a group (Fig. 12, characters 17–25). Dinopids share these features, and thus are orb weavers. Consequently three orb weaving lineages are now known: Dinopidae, Uloboridae, and Araneoidea. Uloboridae is monophyletic by two behavioral features (Fig. 12: 1, 2) and many morphological features. Araneoidea is also a monophyletic group on both behavioral and morphological grounds (Fig 12: 11–16.). Those morphological features as well as additional morphological features that probably are synapomorphic for all orb weavers but whose condition in dinopids is unknown are discussed in Coddington (in press).

Three-taxon statements have only three possible solutions (excluding hypotheses about literal ancestor-descendant relationships, all of which are subsumed by the three possible cladograms). Resolution of the cladistic relationships of dinopids, araneoids, and uloborids is still uncertain, mostly because only three orb weaving taxa coordinate at this hierarchical level have been identified to date. In other words, the outgroup to orb weaving spiders is unknown, and therefore the polarity of some characters remains ambiguous. Several morphological features link dinopids and uloborids (Fig. 12: 8, 10; cf. also Coddington, in press). On the other hand, dinopid radius behavior contrasts with uloborids (cf. above), and is essentially identical to that of araneoids (Fig. 12: 4 versus 6). Presence of an outside leg lateral tap in SS localization behavior in dinopids confirms that it is primitive relative to the inside first leg forward tap that characterizes metids, tetragnathids, theridiosomatids, anapids, mysmenids, and symphytognathids (Coddington, in press).
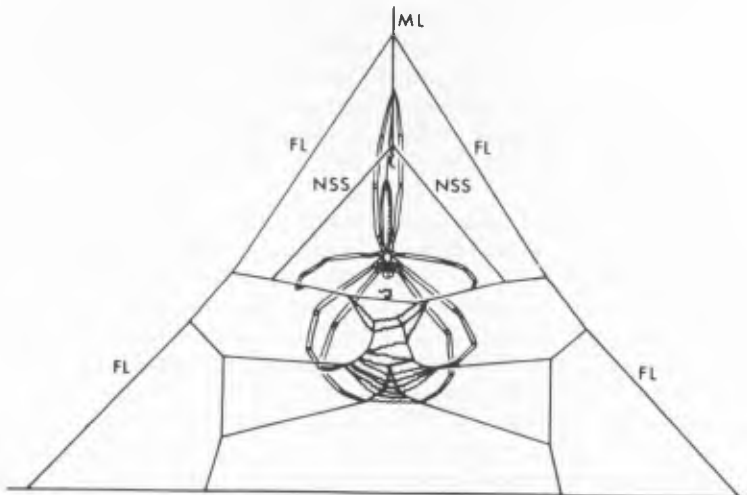
One of the uloborid-dinopid synapomorphies concerns cribellate silk handling (Fig. 12: 10), and thus cannot be assessed in araneoids because they are ecribellate. Other cribellate spiders do not have "puffed" cribellate silk, however, and thus the simplest hypothesis (1 gain) is that the feature is synapomorphic for Dinopoidea rather than synapomorphic for all orb weavers and secondarily lost in araneoids (1 gain, 1 loss). Peters (1984) discussed the puffed appearance of uloborid silk in detail, but did not investigate dinopid silk. A similar feature is the dinopid-uloborid character of switching calamistra during the spinning of an SS segment (see above). The condition of that character is, however, unknown in other cribellate taxa. The behavioral evidence suggests that dinopids are either the sister taxon of uloborids (Fig. 12: 9) or of araneoids (Fig. 12: 6), but no evidence suggests that uloborids are the sister group of araneoids. One of the three possible solutions can thus be eliminated, and morphological evidence favors only the former hypothesis. W. G. Eberhard (in litt.) has also suggested that the unusually long post-attack prey wrapping behavior typical of dinopids and uloborids may also be synapomorphic, but good quantitative data are lacking.

Figure 10: LATE STICKY SPIRAL CONSTRUCTION
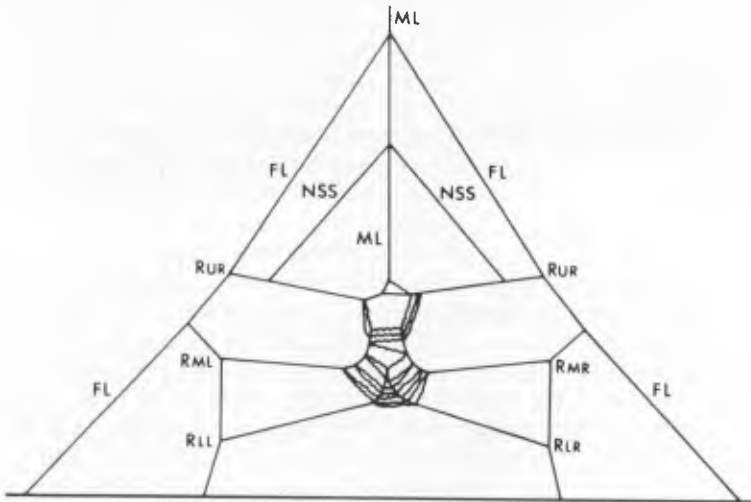
1. SA SS_{16}-Rll, CUT Rll   5. SA SS_{22}-Rmr-Rml-Rul, SWB
2. SA SS_{17}-Rlr, CUT Rlr   6. SA SS_{25}-Rml, CUT Rml
3. SA SS_{18}-Rmr, SWB, SA SS_{19}-Rml   7. SA SS_{26}-Rmr, CUT Rmr
4. SA SS_{20}-Rmr-Rur, SWB   8. SA SS_{27}-Rur

Figure 11: COMPLETED WEB

1. A DL_1-ML (high)
2. CUT ML (mid)
3. PREY READY POSTURE

Figs. 10, 11. See legend to Figures 3, 4.

1. oiL_4 GRIP IN SSC
2. ULOBORID FRAME BEHAVIOR
3. NON-CR'ED FRAME BEHAVIOR
4. NON-CR'ED RADIUS BEHAVIOR
5. CR'ED FRAME BEHAVIOR
6. CR'ED RADIUS BEHAVIOR
7. oL_4 DOWNWARD SLIDE IN SSC
8. 4th TARSAL MACROSETAE
9. CRIBELLATE SILK "PUFFED"
10. PSEUDOSERRATE PLUMOSE HAIRS
11. AGGREGATE GLANDS
12. FLAGELLIFORM GLANDS
13. SERRATE HAIRS
14. iL_4 PUSH DURING SSC
15. LATERAL EYES JUXTAPOSED
16. PARACYMBIUM ON MALE PALP
17. HUB
18. TWO DIMENSIONAL FRAME
19. STICKY SPIRAL
20. NON-STICKY SPIRAL
21. oL LATERAL TAP IN SSC
22. oL_{34} NS LINE GRIP
23. "BASIC" FRAME BEHAVIOR
24. "BASIC" RADIUS BEHAVIOR
25. SPECIALIZED SPIGOT ON POST. LATERAL SPINNERETS

DINOPIS   ULOBORIDAE   NEPHILA   OTHER ARANEOIDS
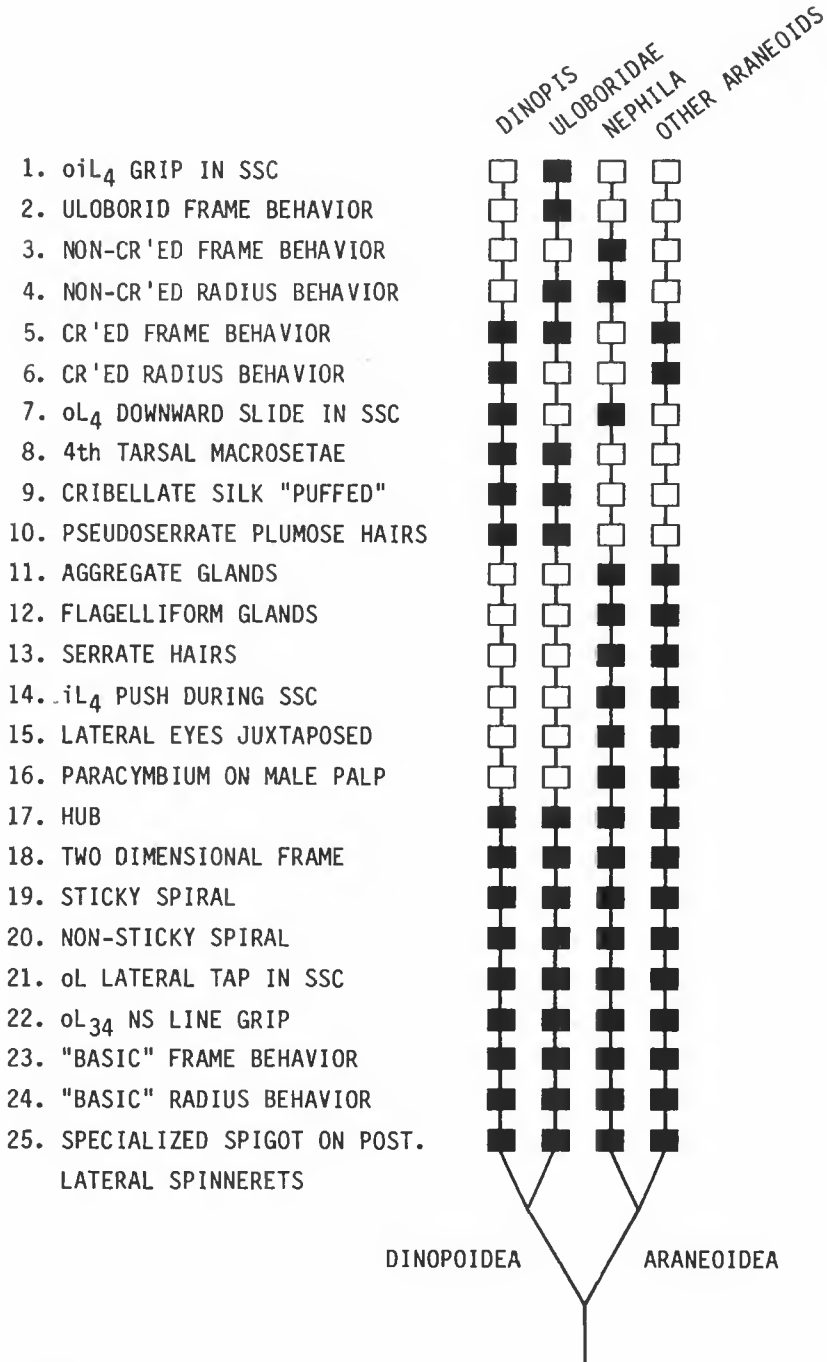
DINOPOIDEA   ARANEOIDEA

Fig. 12. Characters used to infer cladistic relationships among orb weavers and the cladogram they imply. Morphological characters (8, 10-13, 15, 16, 25) and those behavioral characters not occurring in *Dinopis* but used in the cladogram (1-4, 14) are discussed in Coddington (in press). The analysis is *NOT* meant to imply that *Nephila* is the sister group to all other araneoids. The genus is singled out here only because of its similarities to either uloborids or dinopids.

The distribution of the action pattern "cut and reel" (Table 2) represents a difficult analytical problem. Characters 5 and 6 seem to link *Dinopis* with "other araneoids" exclusive of *Nephila,* but in both features *Nephila* differs only in not cutting and reeling either frames or radii (e.g., step 11 of the sequence diagrammed in Fig. 4, and step 4 in Fig. 7, are absent in *Nephila*). Thus *Nephila* is most simply presumed to be autapomorphic in the *loss* of cutting and reeling (called "CR'ed" in characters 3, 4, 5, and 6 in Fig. 12) during these parts of web construction. Uloborids cut and reel frames but not radii. Thus uloborids do cut and reel, but they too seem to be autapomorphic in omitting that behavior during radius construction. Other, non-orb weaving spiders can cut and reel, especially when moving about on drag lines (Eberhard, pers. comm.). The mere ability to cut and reel, then, may be taken as primitive. Frame construction and radius construction, on the other hand, are synapomorphic for orb weavers (Fig. 12: 23, 24). The question is whether the presence of a probably pesiomorphic action pattern (cutting and reeling) in an apomorphic sequence (frame and radius construction) should be considered apomorphic or plesiomorphic. If one presumes that it is plesiomorphically present, then the loss of cutting and reeling in uloborid radius behavior represents one autapomorphy, and the loss of cutting and reeling in *Nephila* represents two more (one each in frame and radius behavior, assuming that *Nephila* can cut and reel in other contexts). If on the other hand one presumes that, where present in web construction, cutting and reeling is apomorphic, then the presence of cutting and reeling in *Dinopis* and araneoid radius construction argues that Dinopidae and Araneoidea are sister groups. Parsimony will always dictate that *Nephila* lost cutting and reeling, because of the araneoid synapomorphies (Fig. 12: 11–16). Characters 8–10 overrule the dinopid-araneoid relationship. The difference, then, is whether cut and reeled radius construction is primitive to orb weavers and lost in uloborids and *Nephila,* or whether it is convergently present in *Dinopis* and Araneoidea. Knowledge of how these stereotyped behavioral sequences are organized neuroethologically might settle the issue.

In sum it is simplest to interpret features 8–10 of Figure 12 as dinopoid synapomorphies, and discordant distributions of characters 4–7 according to the analysis presented above. Furthermore, although the discordant characters singly tell against the dinopid-uloborid relationship, they do not agree among themselves on either of the other possible cladistic solutions, thus implying their own homoplasy as the explanation of the discordance. However, I still consider the case for a dinopid-araneoid relationship less than decisively refuted. Decisive evidence might consist of the discovery of cut and reeled frames and radii, and an oL_1 lateral tap in sticky spiral construction in the outgroup to orb weavers (thus corroborating the autapomorphic character of uloborids and nephilines), or additional morphological evidence supporting the implications of the behavioral evidence analyzed here. The cladogram of Figure 12 most simply summarizes current knowledge, and thus at present must be the preferred phylogenetic hypothesis.

Acknowledgments

LITERATURE CITED

ACKERMAN, C. 1926. On the spider, *Menneus camelus* Pocock, which constructs a moth catching expanding snare. Ann. Natal Mus. 5: 411–422.
AUSTIN, A. D., AND A. D. BLEST. 1979. The biology of two Australian species of dinopid spider. J. Zool. 189: 145–156.

BAUM, J. 1938. On the habits of the Australian spider *Dinopis subrufus* L. Koch. Vestn. Ccsk. Zool. Spulecnosti 5: 28–33.

CLYNE, D. 1967. Note on the construction of the net and sperm-web of a cribellate spider *Dinopis subrufus* (Koch) (Arancida: Dinopidae). Aust. Zool. 14: 189–197.

CODDINGTON, J. In press. The monophyletic origin of the orb web. *In* Shear, W. A. (ed.), Spiders: Webs, behavior and evolution. Stanford Univ. Press.

EBERHARD, W. G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). J. Zool. 166: 417–465.

EBERHARD, W. G. 1981. Construction behavior and the distributions of tensions in orb webs. Bull. Brit. Arachnol. Soc. 5: 189–204.

EBERHARD, W. G. 1982. Behavioral characters for the higher classification of orb weaving spiders. Evol. 36: 1067–1095.

KRAUS, O. 1956. Eine neue Dinopidae aus El Salvador. Senck. Biol. 37: 167–170.

LEVI, H. W. 1982. Araneae. *In* Parker, S. B. (ed.), Synopsis and classification of living organisms, vol. 2. McGraw Hill, New York, pp. 77–95.

PECKHAM, G. W., AND E. G. PECKHAM. 1889. Observations on sexual selection in spiders of the family Attidae. Occ. Pap. Nat. Hist. Soc. Wisc. 1: 1–60.

PETERS, H. M. 1984. The spinning apparatus of Uloboridae in relation to the structure and construction of capture threads (Arachnida: Araneae). Zoomorph. 104: 96–104.

PETRUNKEVITCH. A. 1926. The value of instinct as a taxonomic character in spiders. Biol. Bull. 50: 427–432.

ROBERTS, N. L. 1953. The Australian netting spider, *Dinopis subrufus.* Proc. Roy. Zool. Soc. New South Wales 54: 24–33.

ROBINSON, M. H. 1975. The evolution of predatory behavior in araneid spiders. *In* Baerends, G., C. Beer, and A. Manning (eds.), Function and evolution in behavior. Clarendon Press, Oxford, pp. 292–312.

ROBINSON, M. H., AND B. ROBINSON. 1971. The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge. Amer. Midl. Nat. 85: 85–96.

ROBINSON, M. H., AND B. ROBINSON. 1980. Comparative studies of the courtship and mating behavior of tropical araneid spiders. Pac. Insects Monog. 36: 1–218.

THEUER, B. 1954. Contributions to the life history of *Dinopis spinosus.* Unpubl. MS thesis, Univ. of Florida.

TILQUIN, A. 1942. La toile géométrique des araignées. Press Universitaires, Paris.

WIEHLE, H. 1927. Beiträge sur Kenntnis des Radnetzbaues der Epeiriden, Tetragnathiden, und Uloboriden. Z. Morph. Ökol. Tiere 8: 468–537.

WIEHLE, H. 1928. Beiträge zur Biologie der Araneae, inbesondere zur Kenntnis des Radnetzbaues. Z. Morph. Ökol. Tiere 11: 115–151.

WIEHLE, H. 1931. Neue Beiträge zur Kenntnis des Fanggewebes der Spinnen aus den Familien Argiopidae, Uloboridae, und Theridiidae. Z. Morph. Ökol. Tiere 22: 349–400.