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# 'Rectangular orb' webs of Synotaxus (Araneae: Theridiidae)

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# 'Rectangular orb' webs of *Synotaxus* (Araneae: Theridiidae)

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## Introduction

Typical orb webs, spun by spiders in the families Araneidae and Uloboridae, consist of regular arrays of sticky threads placed on planar scaffolds of nonsticky supporting threads. The very regular thread patterns in orbs have probably resulted from selection to regularize the distribution of both the sticky lines (to maximize prey-catching efficiency) and the supporting threads (to maximize web strength and the spider's attack efficiency—see, for example, Witt, 1965, and Eberhard, 1972). Typical webs spun by spiders of the family Theridiidae, on the other hand, are three-dimensional tangles or 'space webs' with only low levels of organization. Since many theridiids also place sticky lines in their webs (e.g., Kaston, 1948, 1964; Kullmann, 1972), it would seem possible that the same selection pressures might produce geometrically regular arrangements of sticky and supporting threads in this family also. This expectation has been realized with the discovery of the webs of *Synotaxus turbinatus* and *Synotaxus* sp.; this note illustrates their webs and describes construction behaviour.

The descriptions below are based on observations of more than 20 completed *S. turbinatus* webs and about 10 construction sequences; two webs of *Synotaxus* sp. were also seen, one of which was just being finished. In addition, Dr. Yael Lubin kindly made available her notes on *S. ecuadorensis*. The webs in figs. 1 and 3 were photographed with a portable flash after being coated with cornstarch (see Eberhard, 1976 b). Specimens of the spiders have been deposited in the Museum of Comparative Zoology in Cambridge, Massachusetts 02138, U.S.A.

*Synotaxus turbinatus* and *S. ecuadorensis* were studied in secondary forest on Barro Colorado Island in the Panama Canal Zone during August 1974 and October 1975; spiders were particularly common near small streams. *Synotaxus* sp. was found in Colombia on the western slope (el. 400 m) of the western range of the Andes near the road between Cali and Buenaventura, in an area classified by Espinal & Montenegro (1963) as pluvial tropical forest.

### *Webs*

Figure 1 shows a typical *S. turbinatus* web; the webs of *Synotaxus* sp. were essentially identical. Both species' webs had the following characteristics: they were very nearly planar, and close to vertical; the sides of the webs were long, unbent nonsticky single lines, and in most there were also long straight dry vertical threads in the central part of the web; the webs were placed under relatively large leaves and there was a small mesh of threads above the top edge of the web under the leaf where the spider rested; and the straight or

FIG. 1. Newly-completed web of *Synotaxus turbinatus* (scale marker = 10 cm).

nearly-straight horizontal threads were of nonsticky silk while the vertical jagged threads were of sticky silk with several 'balls' on each segment (e.g. fig. 2).

Probably both species often build (or rebuild) their webs in the evening. *S. turbinatus* consistently built webs early in the evening, some as much as 45 minutes before darkness; sometimes but not always they tore them down some time before the next morning. In some cases it appeared that the spiders built only part of their webs in the early evening, and it is possible that other parts of the webs were added later (after rain, for instance). One web of *Synotaxus* sp. was just being finished at about 9 p.m. and the other found at the same time was untattered and apparently new. Lubin's observations of *S. ecuadorensis* (all during the day) agree with this pattern except that she found one apparently new web at 9.30 a.m.

*Construction behaviour*

When an old tattered web was already in place where the new one was to be strung, the spider's first activity was to clear the space of threads; I could not ascertain whether or not the spider ingested the old web threads. Often the frame threads from old webs (threads at edge and bottom of web) were left

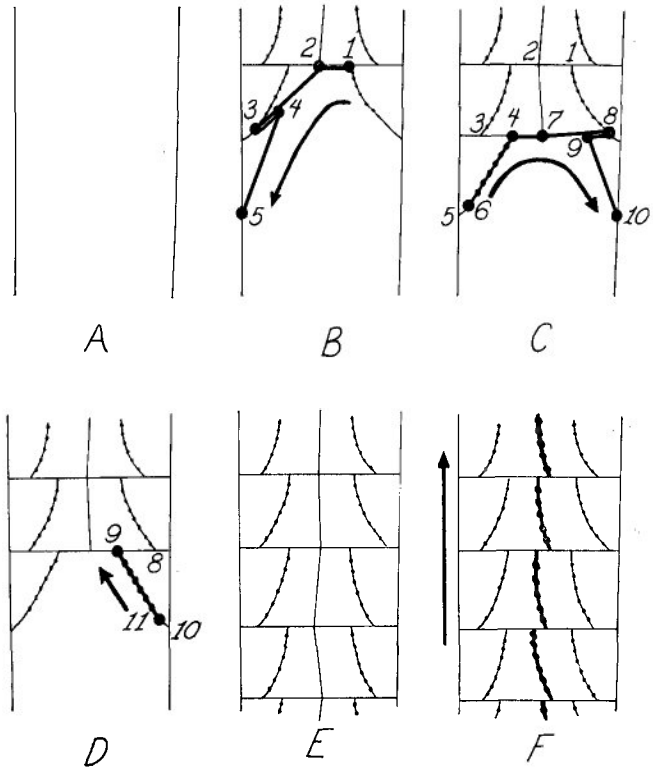


FIG. 2. Tentative order of operations by *S. turbinatus* in the construction of a ' unit web ' (large circles indicate attachment points, small ones balls of glue; the numbers refer to the order of attachments). Although, after observing approximately 10–15 constructions, I was relatively certain that the sequence shown here accurately describes the course of construction, pictures taken of partially-completed webs leave in doubt some details such as the exact position of the central nonsticky line. Despite its apparent simplicity, the building behaviour of *Synotaxus* was very difficult to decipher. (*A*) First the spider spins two vertical nonsticky frame threads. (*B*, *C* and *D*) Then moving from side to side and slowly descending, the spider places other lines with a stereotyped sequence of movements presented in these three diagrams. After attaching a nonsticky line at (1), the spider extends it to the centre line and attaches at (2), then continues this same dry line to attach it to the sticky line laid during the last cycle (3), backs up slightly to attach to the line it has just laid (4), and then continues on to the frame and down to attach at (5). Turning back in the other direction, it breaks the dry line it has just laid (6), then replaces it with a loose sticky line which is connected to the horizontal line at (4). A nonsticky line is then laid from (7) to (8) to (9) to (10) in a series analogous to the steps in *B*. Finally the dry line laid to (10) is broken at (11), and replaced by a sticky line laid to (12) (same as (9)?). (*E*) This process continues until the space between the frames is filled and the spider reaches the bottom of the web. (*F*) The spider slowly climbs up, replacing the dry central line with a zigzag loose sticky thread.

intact and reused. The first new threads laid were the long straight vertical lines which were to form the sides of the web (fig. 2 A). The spider laid these by descending at the end of a line, attaching it to the leaf or thread it encountered below, and re-ascending. Then working from the top of the web, she descended slowly, moving back and forth between the vertical lines and alternately laying sticky and nonsticky threads in the complex sequence indicated in fig. 2. During this process, a pair of zigzag vertical sticky lines, a central nonsticky line, and a series of horizontal nonsticky lines were laid.

FIG. 3. Web of *Synotaxus turbinatus* with a typical three-stranded unit web in the centre bordered with one- and two-stranded unit webs (scale marker = 5 cm).

After reaching the bottom of the web (fig. 2 E) the spider re-ascended slowly, removing the central nonsticky line laid on the downward trip, and replacing it with a sticky thread (fig. 2 F). A similar replacement of the central line with sticky thread was also observed in *Synotaxus* sp. All sticky line placements were performed by pulling a thread from the spinnerets with alternate slow strokes of legs IV. Each sticky line had on it several balls visible to the naked eye; the balls were sticky. The number of balls in a given segment of thread did not correspond to the number of strokes of the hind legs performed as it was laid.

A typical web-building cycle thus resulted in the placement of three sticky lines and their associated nonsticky scaffolding—a ' unit web '. Construction of a unit web usually lasted on the order of 10 minutes. Often spiders paused after making each unit web, but sometimes they made several units one after another. I never saw a spider pause part-way through a unit and then return to finish it.

Nearly all the web constructions and most of the finished webs I observed consisted of triplets of sticky vertical lines, but occasionally ' unit ' webs with

only one or two sticky lines were also seen (fig. 3), and in some cases the top part of a unit had three sticky lines while the bottom had fewer (fig. 1). In all cases the frame threads were closer together in the portion of the web where the number of sticky lines was reduced.

The construction behaviour for sections with less than three sticky lines was clearly related to the construction behaviour for typical unit webs. The most carefully observed case, the construction of a two-line web, is drawn and described in fig. 4. The construction of one single-line web involved placement of only nonsticky threads on the way down and the replacement of the central line with sticky silk on the upward trip, but unfortunately I had not fully understood building behaviour at the time I observed this construction, and did not decipher the details of the construction.



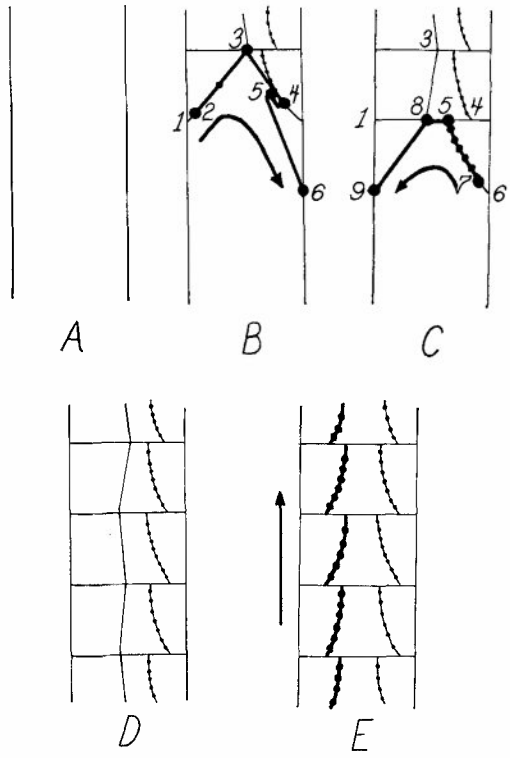


FIG. 4. Tentative order of operations in the construction of a two-stranded unit web (construction observed only once). (*A*) Vertical frame threads laid. (*B* and *C*) One complete construction cycle: Starting at one edge, the dry line just laid to (1) is broken at (2) and replaced by another dry line (often with a single sticky drop on it) which is attached at (3). The spider extends this dry line to the sticky line on the other sido (4), moves backward slightly to attach to the line just laid at (5), and then moves on down the frame to attach at (6). Turning 180°, the spider breaks the dry line just laid at (7) and replaces it with a loose sticky thread which is attached at (5). A dry line is continued from (5) to (8) and to (9). (*D*) This process continues until the spider reaches the bottom of the web. (*E*) Re-ascending slowly, the spider replaces the dry central line with a loose zigzag sticky line.

**Discussion**

The *Synotaxus* webs resemble orb webs in that they are planar, and that both the sticky and nonsticky threads are laid in very regular patterns using highly stereotyped behaviour. Probably their most remarkable difference is their complete lack of any structure resembling the hub of an orb; the webs are constructed on ' rectangular coordinates ' rather than ' polar coordinates '. All other ' pre-orb ' webs—i.e. those of *Titanoeca* (Szlep, 1966), *Sybota* (Wiehle, 1931), and *Cyrtophora* (Wiehle, 1928)—are built on polar coordinates, with hub-like structures. This basic difference suggests that the *Synotaxus* webs do not lie near the evolutionary line from which orb webs were derived, but rather represent an independent experiment in arranging sticky and nonsticky threads in a maximally effective way to trap flying prey.

Another orb-like feature is the presence of ' frame ' threads—the long straight nonsticky vertical threads. They are apparently under more tension than other threads as they are not pulled out of line at any junctions; they probably serve to support the entire web. The looser horizontal nonsticky threads probably serve to hold the array of sticky lines in place, and thus correspond at least roughly to the radii of orb webs. The tension on the sticky threads, again as in orb webs, is low, and the spider's building behaviour seems designed to produce low tensions (see Eberhard, 1976 a). In both webs lower tension on sticky threads probably increases their ability to stop and trap flying prey.

One further resemblance of *Synotaxus* webs to orbs is their apparently frequent destruction and renewal by the spiders—an unusual behaviour for theridiids but common in orb weavers. Perhaps one of the selective advantages of the high geometric regularity (and presumably high-catching efficiency) of orbs and orb-like webs is that they enable the spider to build a serviceable trap in a minimum of time; the spider can thus destroy its web during adverse conditions, and quickly rebuild it in its maximally effective form as soon as conditions improve.

It is striking that the basic differences in the organization of construction behaviour between *Synotaxus* and orb weavers are greater than the differences in the webs themselves. *Synotaxus* intersperses construction of sticky and nonsticky lines, while the orb weavers whose behaviour has been studied rigidly spin first nonsticky lines and then sticky lines (e.g. Koenig, 1951). *Synotaxus* webs are made of a number of units which are more or less equal and independent, both in time and space, while orbs are made as one single unit. These characteristics, which are both shared with *Titanoeca* (Szlep, 1966), again emphasize that the *Synotaxus* webs probably do not lie close to the evolutionary line(s) which gave rise to true orb weavers.

The reason why this particular behaviour is employed instead of other possible techniques for building the same array of threads is not clear. The sequence of steps may be slightly more efficient energetically, since the entire filling-in process (after the frames are laid) is done with only one trip down and up the web, and other methods (putting in dry silk first and then sticky silk, for example) would require several trips. One trip more or less must represent only a very minimal energy expenditure, however, and it may be that the answer is that ' it just evolved that way '—that the steps from some as yet unknown intermediate behaviour were less difficult to evolve in this direction (i.e. represented smaller modifications) than in some other.

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