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William G. Eberhard a

a Depto. de Biología, Universidad del Valle, Cali, Colombia and Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Panama Canal Zone

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The ‘inverted ladder’ orb web of Scoloderus sp. and the intermediate orb of Eustala (?) sp. Araneae: Araneidae

WILLIAM G. EBERHARD
Depto. de Biologia, Universidad del Valle, Cali, Colombia and
Smithsonian Tropical Research Institute, P.O. Box 2072,
Balboa, Panama Canal Zone

Introduction
Robinson & Robinson (1972) recently described the web of a New Guinean araneid spider which deviates remarkably from the standard orb web pattern, the lower part of the web being so greatly elongated that they named it a ‘ladder web’. Although the species has not yet been determined, it apparently belongs to the araneid subfamily Metinae. This article describes another ladder web produced by a South American Scoloderus sp. of the araneid subfamily Araneinae, which, although quite different in a number of details, represents an almost incredible convergence to the same bizarre web form. In addition, observations are presented on a third web, spun by Eustala (?) sp. (Araneinae) which appears to be an intermediate between the ladder webs and typical orbs.

Methods
Webs were photographed in the field in the following way. After the spider was carefully removed from the hub, the web was coated with cornstarch by patting a cloth bag full of the powder close to the web, thus creating a cloud of white dust which stuck to the threads. Any leaves or twigs in front of and behind the web were clipped, and then the photograph was taken using a portable flash. The length of some easily recognizable web dimension (e.g. the longest diameter of the free zone, the longest horizontal radius, etc.) was then recorded so as to permit subsequent determination of the scale of photographic prints.

Specimens of Scoloderus sp. and Eustala (?) are in the Museum of Comparative Zoology, Cambridge, Massachusetts 02138, U.S.A.

Scoloderus sp.

Web sites
All observations were made near Cali, Colombia, in an area classified by Espinal & Montenegro (1963) as dry tropical forest. Webs were not common; all were in second growth, at sites which were more or less sheltered from above. One mature female which I fed nearly nightly stayed at one site in a large Hibiscus hedge for at least 14 days before she was collected.

Construction behaviour
All webs were built at night, with starting times (three observed and two estimated from webs first seen partially completed) ranging from 8 to 11 p.m. (most observations were made before 1 a.m., and webs built after this time would
FIG. 1. Stages in web construction by Scoloderus sp. After establishing the future hub (a), the spider builds a long lateral frame thread ((b)-(d)). She first lays a line from the hub to point 1, then, as she descends this line, attaches another line to it at point 2 and continues on past the hub (b). She attaches this line at 3 (c), then climbs up it, breaks the attachment at 2, have gone unrecorded). All webs were completely destroyed by morning, without a single line marking where they had been. Parts of five web constructions were observed, including three sticky spiral constructions, three temporary spiral constructions, and two web initiations. All construction observations involved the same mature female except for one observation of sticky spiral placement; the descriptions below and the diagrams in fig. 1 represent syntheses of these observations.

Both web initiations were very similar. As soon as dusk fell, the spider strung a few more or less horizontal lines near the top of the space where the web would be, and rested nearly motionless there. Then, in periodic short bursts of activity, she extended this network laterally by walking along leaves, and made long descents, pausing at the end of the line and then climbing back up without having touched any other object. In some descents she may have
and reattaches that line at 4, then returns to the hub (d). The long lateral frame on the other side is built in the same way (e), and the rest of the radii are added as described in the text (f). Finally the temporary spiral is added, pulling the radii in the upper part of the web into positions which standardize the distances between them (g).

been paying out silk in order to establish connections to other supports, but in others this did not appear to be the case. The descents probably also served to inform the spider of the presence of any objects in the space under the lines she had already laid. One evening she laid several lines 15–20 cm above a leaf, but after encountering the leaf on repeated descents, she shifted her centre of activity to an adjacent, clear area and built her web there. Towards the end of this period of intermittent activity the spider descended all the way to a leaf below, and attached a single, almost perfectly vertical line there.

This line and the more or less horizontal lines which would be the upper frame threads were already in place when the spider finally began sustained activity and built the web. First an inverted Y was formed at the bottom of the long line (fig. 1 (a)), and next one of the long side frames was laid, along with a radius running to it (fig. 1 (b)–(d)). Then, either immediately afterward
or after one or two more radii were laid to the first long side frame, the other side frame and a radius running to it were laid in an identical manner (fig. 1 (e)).

These activities essentially established the limits of the almost perfectly vertical web space. Subsequent radii were laid in a manner similar to that of other araneids which have been studied. There was no apparent tendency to lay the long up radii in any special order, except perhaps to lay them somewhat later than the others. The approximate directions (12.00 being upward, 6.00 downward, etc.) of the last 19 radii in one web were 9, 7.30, 4, 12.30, 3.30, 9, 12.45, 4, 8, 11.45, 11, 8, 12.30, 4.30, 8, 10.45, 1, 8, and 10.45, the spider showing a tendency to lay successive radii about 100° apart. The spider usually (always?) left along the upper of the two radii bordering the sector in which she was laying a new radius. The first radius laid to a long side frame (e.g. that in fig. 1 (d)) was always the uppermost radius ending on that frame, and the radii above it (laid using the long up radius as an exit) all ended on the upper frame threads. The spider seldom (1 of 20 times) laid additional radii between a given radius and the exit radius (i.e. radii were laid at ' final angles ' which were not subsequently subdivided). In leaving along the upper edge of the sector to be filled, in the choice of exit radii, and in laying radii at final angles, Scoloderus resembles the other araneids (Araneus, Zilla, Micrathena) whose behaviour has been studied (Witt et al., 1968; Le Guelte, 1966; Dugdale, 1969).

The spider turned slowly at the hub after she laid each radius, and during at least the last half of radius construction, connected the existing radii with hub threads as she turned. The hub line was actually continuous with the radii, and the points where some radii originated could be determined by close examination of the hub (fig. 2 (b)). After laying a radius, the spider generally continued turning at the hub in the direction she had been moving before, except in the case of long radii; after these she generally turned to move in the opposite direction. This resulted in fewer hub threads crossing the top part of the hub than the bottom (fig. 2 (b)), a pattern I believe to be found in other araneids only when the hub is near the top of the web.

The presence of little tufts of silk at the bases of radii (they were especially obvious at the bases of the long radii, but do not show in the powdered web in fig. 2) indicated that Scoloderus incorporates only the radial line laid on the way back to the hub into the finished web. Probably the spider broke the line laid on the way out and rolled it into a little ball as she moved toward the hub as do other araneids such as Araneus diadematus (Witt et al., 1968), but this could not be confirmed by direct observation.

When the last radius had been laid, the web looked like fig. 1 (f), with a gap on each side between the group of long up radii and the uppermost radius attached to the long side frame. There was no abrupt transition from radius and hub thread construction to temporary spiral construction, the spider simply gradually spiralling away from the hub. As she laid the temporary spiral, she fastened the upper radii into the strongly curved configurations they had in the finished web (figs. 1 (g), 2 (a)), thus filling the two gaps mentioned above.

In the upper part of the web the spider laid the temporary spiral from one side frame to the other in the pattern shown in fig. 1 (g), actually running the
Fig. 2. (a) Photograph of the web of *Scoloderus* sp. taken in the field; (b) detail of the hub of the same web. The arrow marks the origin of a radius; (c) detail of the part of the upper half (of another web), showing radii (vertical lines), sticky spiral (horizontal lines which sag slightly), and temporary spiral (other horizontal lines).
temporary spiral thread upward along the frame thread before turning back. This kind of attachment of temporary spiral to frame threads has not been seen in other araneids’ webs.

After a short pause when the temporary spiral was completed, the spider began laying the sticky spiral, starting from the top of the web and working downward. The major details of sticky spiral construction were similar to those of other araneids like *Araneus diadematus* (Jacobi-Kleemann, 1953), except that the spider did not destroy the temporary spiral in the upper part of the web as she laid sticky spiral, and she left a space between the loops of sticky spiral where the temporary spiral was situated (fig. 2 (c)). The spider tapped with leg I toward the last loop of sticky spiral she had laid, extending it laterally as she moved laterally along the radius; when she reached the last loop, she flexed the segment of sticky spiral she was laying with a hind leg (probably thus lengthening the segment—Eberhard, in preparation), attached the sticky spiral to the radius, and then moved on to the next radius. The spider worked quickly, averaging about two attachments per second, and was not seen to pause during the approximately 1.5 hour sticky spiral construction period.

As the spider neared the hub, she started to destroy the temporary spiral she encountered, and continued in this way until finishing the sticky spiral. Then she went to the hub, turned to face upward and jerked the web several times (presumably to ascertain if any prey had been caught during sticky spiral construction), and then assumed her waiting posture, facing down with her legs drawn relatively close to her body, tightening the web slightly. The spider did not eat out the centre of the hub and then replace it as do many other araneids (Witt *et al.*, 1968; personal observation).

**Fig. 3.** Web of very young *Scoloderus* sp. (a) Entire web; (b) detail of central part of web.
Fig. 4. Web of an intermediate-aged instar of *Scoloderus* sp. (a) Entire web; (b) detail of hub area; (c) detail of upper part of web, showing intact temporary spiral (compare with fig. 2 (c)).
**Webs of immatures**

The webs of immature *Scoloderus* sp. (figs. 3 and 4)†, as seems to be common in the family Araneidae (e.g. Witt et al., 1968), were more generalized in form than those of the adults. The webs of the youngest spiders found (fig. 3) lacked several of the adult features—the top half of the web was scarcely larger than the bottom, the temporary spiral was completely removed, there were no large gaps between radii in the upper half of the web, and the radii were only slightly bent. They were similar to adult webs in being very nearly vertical, in having closely spaced sticky spiral which was especially closely spaced in the bottom half of the web, and in the general form of the hub and free zone. In general, except for the hub and the free zone, they were reminiscent of the webs of adult *Acaecesia hemata* (Eberhard, in preparation). Webs of slightly older (probably the next instar) *Scoloderus* sp. nymphs were intermediate in many respects (fig. 4). They were more elongated vertically, had several loops of temporary spiral left intact in the upper part, had gaps in the sticky spiral where the temporary spiral lines were, and the radii were bent. However, there were no large angles between radii in the upper half, and, at least in the web in fig. 4, several (6) radii split off from other radii rather than originating in the hub; in another web of a nymph of the same size, however, there were no such ‘tertiary’ radii.

**Response to rain**

One evening a spider was just finishing her web at 11.50 when a moderately hard rain began to fall. Within 10 min she had completely destroyed and presumably ingested the web, and was resting on a single line near where the top frame threads had been.

**Attack behaviour**

I observed six attacks on prey collected nearby (four flies, a grasshopper, and a leafhopper) which varied from about one-fifth to nine-tenths the size of the spider. In all cases the attack was made by biting rather than wrapping, although the prey was subsequently spun slowly and wrapped after being bitten for 30 sec or more. After freeing the prey from the web, the spider carried it in her jaws to the hub where she wrapped it again briefly, and then fastened the bundle to the hub. One additional prey, a chrysomelid beetle (Alticinae) was rejected; the spider went to the beetle (which was above the hub), then walked around it to approach it from above, held it carefully as she cut it free, and dropped it clear of the web.

Two variations in attack behaviour were seen. Twice (attacks on the grasshopper, the largest prey, and on a trypetid fly) the spider moved around the prey so as to attack it from above as it did when cutting the chrysomelid free. The function of this behaviour is probably to safeguard the spider from injury caused by struggling prey falling on to it. The other variation was seen in two of the six cases (attacks on the grasshopper and the cicadellid which

† These webs were found and photographed in the field, and since it is often difficult to identify immature spiders, some doubt might be cast as to the identity of their makers. However, this *Scoloderus* sp. is apparently unique among araneids in the Cali area in both its body form and its position on its web, and there is little doubt in my mind that the spiders responsible for the webs in figs. 2–4 are all of the same species.
was also relatively large) and involved the spider leaving the prey after biting and wrapping it, descending to the bottom of the web and laying a line there which apparently strengthened and/or tightened an anchor thread, and then returning to the capture site to continue wrapping the prey. A similar behaviour has been seen in *Micrathena* sp. (Y. Lubin, personal communication).

**Eustala (?) sp.**

*Web site and design*

The web in fig. 5 is that of an immature *Eustala (?)* photographed at about 9 p.m. on 20.iv.1973 on the Pacific coast of Colombia about 40 km south of Buenaventura in a zone classified by Espinal and Montenegro (1963) as ‘very humid tropical forest’. It was built in second growth near a settlement, and the spider rested facing down at the hub.

![Web of Eustala (?) sp.](image)

**Fig. 5.** Web of *Eustala (?)* sp. (a) Entire web; (b) detail of hub area.

**Discussion**

There are a number of interesting points of comparison between the webs of *Scoloderus* sp., *Eustala (?)* sp., and the spider studied by the Robinsons (fig. 6). In almost all respects, the *Eustala (?)* web is more similar to that of the New Guinean species than that of *Scoloderus* sp. The most striking difference is that the long ‘ladder’ part of the *Scoloderus* web is above the hub,
Fig. 6. Diagram of the New Guinean 'ladder web' from Robinson & Robinson (1972)
while those of *Eustala* (?) and the New Guinean spider are below it. The functional significance of this difference is not clear. The nearly universal tendency of araneids which build more or less vertical orbs to make the bottom sector larger than the top (e.g. Kaston, 1948; Witt *et al.*, 1968) makes the webs of *Scoloderus* seem less probable. Some of the differences noted below may stem from this very basic difference in orientation, but as yet no direct associations are clear.

Another obvious point of comparison is the relative elongation of the webs. The New Guinean web in fig. 6 was 98 cm long and a maximum of 16 cm wide, or 6.1 times longer than wide, and the *Scoloderus* sp. web in fig. 2 was 6.9 times longer than wide (somewhat shorter webs were also seen); on the other hand, the *Eustala* (?) web in fig. 5 was only 2.7 times longer than wide.

There are also many smaller differences between the webs. The shape of the webs of both *Eustala* (?) and the New Guinean species is that of a wedge, with the two long lateral frames gradually converging, while the long side frames of *Scoloderus* sp. are parallel and nearly vertical. Associated with this is another difference: the long radii in *Scoloderus* sp. webs all make approximately 90° angles with a nearly horizontal frame thread at the top of the web, while the long radii in the other species’ webs end on the converging lateral frame threads, making very acute angles with them. As discussed in Eberhard (1972; p. 439), such acute angles with frame threads are probably structurally inferior to those which are nearly at right angles, tending to overload the frame thread on one side of the connection. The lateral frame threads in the web of *Scoloderus* sp. are only approximately as thick as the radii, while those in the New Guinean spider’s web are markedly stronger (M. Robinson, personal communication).

The ladder webs illustrate very clearly the three possible methods mentioned by Eberhard (1972; p. 450) of maintaining more or less constant spacing between radii throughout large areas of the web, a problem which is critical in webs with extremely long radii. ‘Tertiary’ radii, which originate in the outer sectors of the web and serve to fill in the holes between diverging radii, are quite common in both the New Guinea ladder web and that of *Eustala* (?) sp. The webs of *Scoloderus* sp. on the other hand have very few tertiary radii, but instead a second technique is used in which the radii are bent in such a way as to maintain relatively constant spacing over much of their length. The long radii are also bent in this way in the *Eustala* (?) sp. web, but they are nearly straight in that of the New Guinean species. And finally, both *Eustala* (?) sp. and the New Guinean spider lay longer radii closer together (i.e. with smaller angles between them at the hub). This is particularly pronounced in the New Guinean web in which the top part of the orb is almost completely reduced. In the *Scoloderus* sp. web in fig. 1 there are scarcely more radii in the top half (19) than in the bottom (17) (similar numbers were seen in other webs), but longer radii are laid at smaller angles during construction (see fig. 1 (f)).

Another difference is that the temporary spiral is left in place in the long part of the *Scoloderus* sp. web (figs. 2 (c), 4 (c)), while it is torn out during sticky spiral construction by the other species. Of all the other araneids known to build sticky orbs, only *Nephila* spp. leave the temporary spiral in place (Kaston, 1964). In *Nephila* webs the intact temporary spiral may serve to standardize the spacing between radii and tertiary radii (Eberhard, 1972). This cannot be the function in *Scoloderus* sp. webs, and another function,
related to the special problems of extremely long radii, comes to mind: since each long radius is connected to other web threads by only the relatively weak, extensible sticky spiral along most of its length, relatively inextensible temporary spiral threads would serve to distribute to other parts of the web the stress caused by (a) prey impact, or (b) loading caused by wind on prey already caught in the web, thus making it less likely that the web would break near the prey. While additional functions for the intact temporary spiral may be adduced, it seems certain that its presence is somehow associated with the special characteristics of very long radii, since the temporary spiral is actually torn out in the normal orb portion of *Scoloderus* webs and in the non-elongate orbs of young nymphs.

In *Nephila* webs, associated with the presence of temporary spiral in the finished web, there is a gap in the array of sticky spiral lines around each temporary spiral line, just as in *Scoloderus*. Two possible explanations occur to me. The first, probably least likely, is that the spiders cannot discriminate temporary from sticky spiral when they encounter it, and space the sticky spiral from it just as they would from a sticky spiral line. The second is that sticky spiral loops placed too close to temporary spiral threads would tend to touch and then stick to them; as a result of being stuck to the much less extensible temporary spiral, the sticky spiral line would lose most of its extensibility and thus much of its prey capture ability. According to this hypothesis, the spider leaves spaces around the temporary spiral threads to avoid wasting sticky spiral.

It is interesting to note that although araneids such as *Araneus* and *Zygiella* spin webs in which the free zone (the area between the outer limits of the hub and the inner loop of sticky spiral) is larger in the more extended lower part of the web (e.g. Witt *et al*., 1968) the free zone is nearly symmetrical or even larger in the smaller half of the web (fig. 4 (a)) in all of these very asymmetric webs. The significance of this is not clear.

In spite of the differences between the ladder webs, they are basically very similar to one another, and one must assume that their elongated form has the same function. Robinson & Robinson (1972) suggested that the long web 'may be a means of obtaining the maximum capture area with the minimum number of radii'. The exact meaning of this is not clear, since the number of radii could presumably be reduced or increased without necessarily changing the total area of the web. A more likely factor, which may have been implicit although not expressly stated in the Robinsons' reasoning, is that of mesh size. The ladder webs are the only orbs known in which adjacent non-sticky radial threads are essentially parallel. This allows a constant mesh size throughout a large portion of the web, something which is impossible in normal, more or less circular orbs. Perhaps, then, the two ladder webs are convergent solutions to the same selective pressure favouring webs with fixed, maximally effective mesh sizes.

Several observations of long trails of scales left by moths in *Scoloderus* sp. webs offer a further possibility. Moths trapped in orb webs tend to fall downward through the web, shedding scales as they go. It would presumably be more difficult for moths to arrive at the bottom and thus escape from long, perfectly vertical webs, and ladder webs may represent adaptations for this specific type of prey.
While the degree of confidence with which web form can be used to determine taxonomic position within the Araneidae has yet to be determined, the marked differences between the building behaviour of *Scoloderus* sp., *Eustala* (1) sp., and what little is known for other members of the Araneinae (mostly *Araneus* and *Zygiella*) suggest wide variation within the subfamily. The outstanding differences in *Scoloderus* sp.'s behaviour include (a) the inversion of the 'Y' where the hub will be built, (b) leaving over-sized angles between two pairs of radii, (c) leaving the top side of the hub relatively open by turning back after most long radius constructions, (d) not laying many more radii in the largest part of the web, (e) attaching the temporary spiral to frame threads in an unusual way, (f) leaving the temporary spiral intact in part of the finished web, and (g) not biting out the centre of the hub after finishing the sticky spiral (for these aspects of the behaviour of *Araneus*, etc., see Mayer, 1952; McCook, 1889; Kaston, 1964; Witt et al., 1968). Some of these differences ((c), (d) and (g)) are also present in the non-elongate webs of very young *Scoloderus*, while others are not ((b), (e) and (f)), suggesting a correlation between this last group of characters and elongate web form.

Summary

The South American spider *Scoloderus* sp. spins a remarkably elongated 'ladder' orb web similar to that of an as yet unidentified New Guinean spider except that it is inverted 180°, with the long part above rather than below the hub. The two webs differ in a number of details, some of which may represent alternate solutions to the special problems associated with extremely long radii. Various details of the web building behaviour of *Scoloderus* sp. differ from the behaviour of species of *Araneus* and *Zygiella*. Immature *Scoloderus* build less elongate webs which are more similar to the standard araneid orb web. *Eustala* (1) sp. spins a web similar in many respects to that of the New Guinean spider, except that it is much less elongated, and thus forms an intermediate between typical orb webs and 'ladder' webs.

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References


—. In preparation. Physical properties of sticky spirals; sliding connections in orb webs.


Inverted ladder orb web