

Hub construction by *Leucauge mariana* (Araneae, Araneidae)

William G. Eberhard

Smithsonian Tropical Research Institute

and

Escuela de Biología,
Universidad de Costa Rica,
Ciudad Universitaria, Costa Rica

Summary

Leucauge mariana (Keyserling) holds a central point in its web with inner leg III during hub construction and probably uses this as a point of reference around which it produces a spiral pattern of lines. The sequence of movements of the outer legs is more or less rigid, and differs from those of some other araneids and perhaps from that of a uloborid. The hub line is usually initiated while the spider moves upwards in inclined webs. Hub loops are spaced farther apart in the lower sectors of inclined webs and in the outer part of the hub. The number of hub loops is positively correlated with the number of radii in the web.

Introduction

The radii of nearly all orb webs are connected by a spiral, non-sticky line in the area where they converge (Fig. 1). This spiral probably reinforces the connections between radii, serves as a platform on which the spider can rest, and perhaps also improves the transmission of vibrations between radii. In most araneoid orb-weavers the hub spiral is completed during or immediately following radius construction; the centre of the hub is removed later, after the sticky spiral has been finished (Eberhard, 1982). This paper concerns the original construction of the hub loops immediately following radius construction. To my knowledge there are no detailed published descriptions of hub construction in any orb-weaving spider apart from the general accounts given in Eberhard (1972, 1982), even though construction behaviour is a promising source of information regarding the controversial taxonomic relationships among major groups of orb-weaving spiders (Eberhard, 1982; Coddington, in press).

Methods

All observations were of mature female *Leucauge mariana* (Keyserling) and their webs, collected near San Antonio de Escazu, Costa Rica. Leg movements were studied using frame by frame analyses of videotapes (30 frames s^{-1}) and direct observations. In the field, adult female *L. mariana* webs are usually somewhat inclined; in 66 webs the angle from the horizontal varied from 8 to 83° (mean $39.9 \pm 12.9^\circ$). Since hub designs seemed to vary with web inclination, measurements were made from photographs of webs in wire hoops in which inclination could be controlled. The hoops had handles which allowed them to be positioned at an angle of either 0° or 45° with the horizontal (Eberhard, in prep. a). Webs were photographed after the spiders had been removed from their webs following initiation of sticky spiral

construction, and after the webs had been coated with talcum powder. Distances between points where hub loops crossed radii were measured on the radius that ran most nearly directly up, the radius most nearly directly down, and the two radii most nearly perpendicular to these (Fig. 2). In 0° webs "up" and "down" were arbitrarily designated as corresponding to the radii running most nearly parallel to the handle of the wire hoop. The number of loops of hub spiral in each photographed web was estimated by averaging the numbers crossing the up, down, right and left radii. Average measurements are followed by standard deviations. Tests of significance are Mann-Whitney U-tests unless otherwise specified.

Results

Sequence of leg movements

The outer (o) legs (those on the side of the spider away from the web's centre — Fig. 3) moved in a fixed or nearly fixed sequence. At the moment of attachment (Fig. 3a) legs oI and oII held R1 while oIII and oIV held R0. First leg oI and then leg oIII advanced one radius each (to R2 and R1 respectively — Fig. 3b). Leg oIII always gripped R1 closer to the centre of the web than did leg oII (Fig. 3b). In 13 of 17 cases leg oI clearly moved before leg oIII, in 2 they appeared to move simultaneously, and in 2 leg oIII moved first.

After legs oI and oIII had moved, leg oIV advanced to R1, and then leg oII moved from R1 to R2 (Fig. 3c). In some cases leg oIV arrived at R1 before oII released its hold on R1; in others it was not clear whether oIV arrived before oII moved on. When oIII and oIV were in place on R1, they sometimes pulled the radius

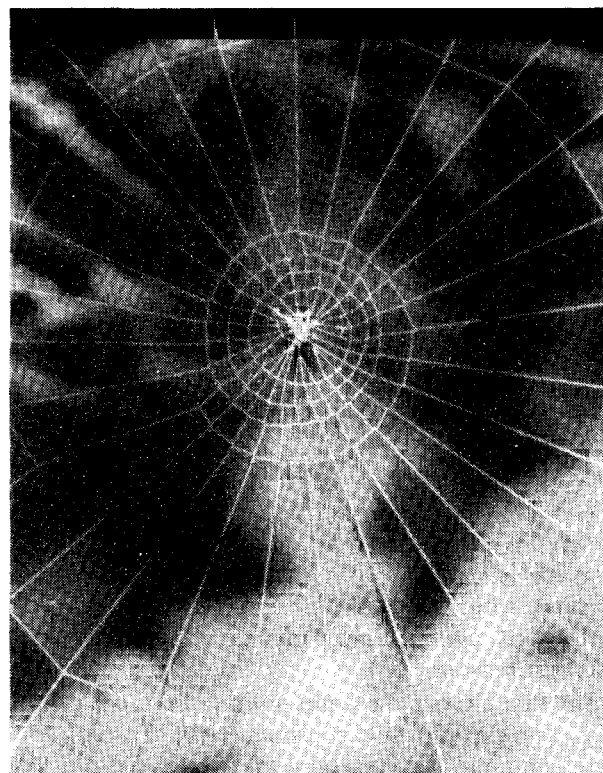


Fig. 1: The hub of the web of a mature female *Leucauge mariana* in the field.

towards the spider's spinnerets as the attachment was made (Fig. 3a, d).

Leg *oi* moved most quickly, and often took less than one frame of the videotape (0.033 s) to move from one radius to the next. Other legs usually moved more slowly, generally taking two to three frames or more to arrive at the next radius after releasing their hold.

During most of the process of hub construction the tarsus of leg *iii* was held immobile, touching a central point in the accumulation of loose silk where the radii converged in the centre of the hub. Sometimes the tarsus was lifted and then replaced immediately at the spot it had been holding or nearby, but spiders often laid 360° or more of hub loop before I was able to see that leg *iii* was shifted. At the start of hub construction the tarsus of *iii* was ventral to the spider's cephalothorax, but by the end leg *iii* was nearly completely extended, as its tip remained at the hub centre. When hub construction ended, leg *iii* stepped away, usually without any sign of being entangled. Occasionally, however, it snapped free after a quick tug. Since any line held by the tarsus of this leg would have been twisted around the tarsal claw during the course of hub construction, it seems that despite the appearance of tension, leg *iii* does not seize any lines while it is held at the centre of the hub.

The positions and movements of the other inner legs were variable. They did not move every time an attachment was made as did the outer legs, but approximately every 2-4 attachments. Early in hub

construction *ii* and *iii* held radii beyond the outer edge of the hub, and *ii* consistently "followed" (in a positional sense) *iii* (Eberhard, 1972), seizing the radius outside the point where *iii* held it just before *iii* was advanced. As the hub grew, the points where *iii* grasped radii came to be closer and closer to the outer hub loop, and during the last loop or so it held lines within the outer margin of the hub. Leg *ii* continued to grasp radii beyond the edge of the hub and to advance just before *iii* did, but often seized a different radius from that held by *iii*; often it grasped the radius immediately beyond the one held by *iii*. Probably this variability was a result of the form of the grasping movement of leg *ii*, in which the leg was extended past the point to be gripped and then moved laterally and inwards towards the spider. The leg intercepted the radius during this movement.

Initiation

In 55 webs built at 45°, the hub spiral was initiated while the spider moved upwards in the web in 41 cases (e.g. Fig. 2), while it moved downwards in 8, and started laterally at the top or bottom (12:00 or 6:00) in 6 ($p < 0.001$ comparing upwards vs. downwards with Chi-Squared test). Initiation tended to occur in the upper half of the hub of 45° webs; 39 of 54 hub spirals started between 9:00 and 3:00, and 15 between 4:00 and 8:00 (expected values 31.5 and 22.5 with Chi-Squared, $p < 0.05$).

Spaces between hub loops

Two patterns were clear. First, hubs of webs spun at 45° were asymmetrical, with loops below the centre of the hub spaced farther apart than others. In 54 webs the average for the first space (*a* in Fig. 2) was 1.93 ± 0.63 mm below the centre, while those above and to the left and right sides were 1.76 ± 0.54 , 1.71 ± 0.27 , and 1.64 ± 0.22 mm respectively (below and right side differ, $p < 0.05$). In 45 of these webs that had an additional (third) loop, the average for space *b* below was 2.20 ± 0.72 , while above and to the sides *b* averaged 1.42 ± 0.48 , 1.54 ± 0.77 , and 1.37 ± 0.80 mm (all differ from below, $p < 0.001$). In 16 webs with a fourth loop, the space *c* below averaged 2.44 ± 0.61 mm, and above 1.27 ± 0.32 mm ($p < 0.001$). The difference between above and below is thus more pronounced in later loops. The average total dimensions of hubs above, below, and to the left and right sides were, respectively, 8.17 ± 1.21 , 9.64 ± 2.19 , 8.33 ± 1.29 , and 8.08 ± 1.70 mm (below again differs from all others, $p < 0.001$).

Secondly, within-web comparisons in 54 webs spun at 45° (each web was measured up to four times, once in each direction) confirmed that hub loops near the outer edge of the hub were usually spaced farther apart than those nearer the centre: *a* was less than *b* in 81 cases, greater than *b* in 77, and equal to *b* in 16 (not significant, $p > 0.5$ with Chi-Squared); *b* was less than *c* in 64, greater than *b* in 77, and equal to *b* in 16 (not significant, Chi-Squared). Similar trends occurred in 50 webs spun at 0°: *a* was less than *b* in 87, greater than *b* in 63, and

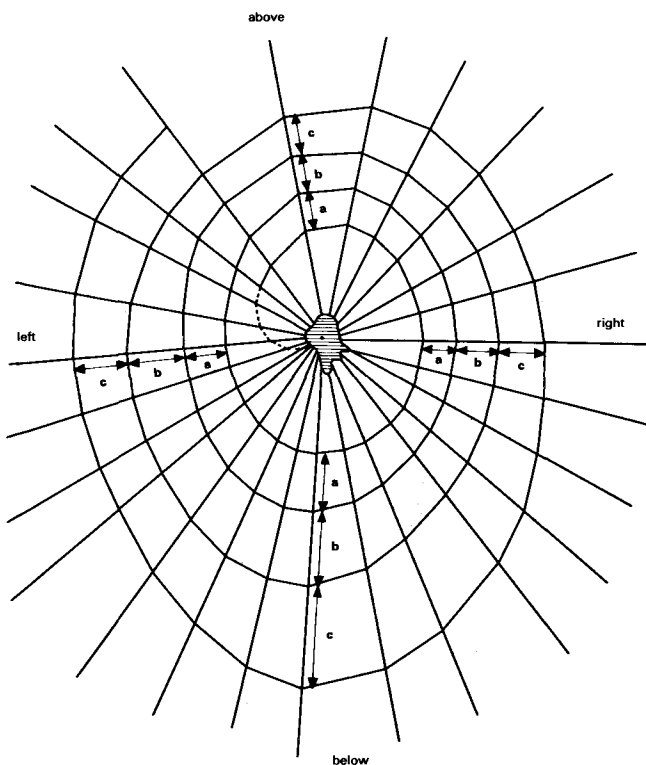


Fig. 2: Measurements made on photographs of hubs of *L. mariana* webs. The shaded portion represents the loose silk that accumulated at the centre during radius construction. The dot represents the hub centre (estimated visually in each web). The dotted lines are the first few segments of the hub spiral; the first 90° of the hub spiral was not counted in measurements involving the "first loop".

equal to b in 21 (p about 0.05 with Chi-Squared); b was less than c in 64, greater than c in 27, and equal to c in 3 ($p < 0.001$ with Chi-Squared). Thus the two spaces between the first three hub loops were often more or less equal, with the second space showing a slight tendency to be larger. The third space was generally larger than the second.

Number of loops

The estimated number of hub loops in 138 webs varied from 2.0 to 5.0 (mean = 3.65 ± 0.62). In 84 webs spun at 45° , there was a significant correlation between the number of hub loops and both the number of radii and the number of loops of temporary spiral (TSP) (the number of TSP loops was taken as an indication of overall web size). The correlation with the number of radii was slightly stronger ($r = 0.49$) than that with the number of temporary spiral loops ($r = 0.47$), and a multiple regression on both radii and temporary spirals improved the correlation ($r = 0.57$) (all $p < 0.001$ with critical values of r). In 54 webs spun at 0° , there was

also a correlation with the number of radii ($r = 0.32$, $p < 0.05$), but not with the number of temporary spiral loops ($r = 0.05$), and a multiple regression on both radii and number of TSP loops gave an r of only 0.32 ($0.1 > p > 0.05$). Combining the data from 45° and 0° webs gave a stronger correlation with radii ($r = 0.46$) (Fig. 4) than with TSP loops ($r = 0.27$), and no significant increase in correlation when both radii and TSP loops were included in a multiple regression ($r = 0.47$). These results suggest that the number of hub loops may be influenced by the number of radii. Similar positive correlations with numbers of radii occur in comparisons of the number of hub loops in the orbs of different species in other genera of orb-weaving spiders (Eberhard, in prep. b).

Discussion

The only other detailed analyses of leg movements during hub construction are of the uloborid *Uloborus diversus* Banks (Eberhard, 1972). The taxonomic relationship between uloborids and araneids is

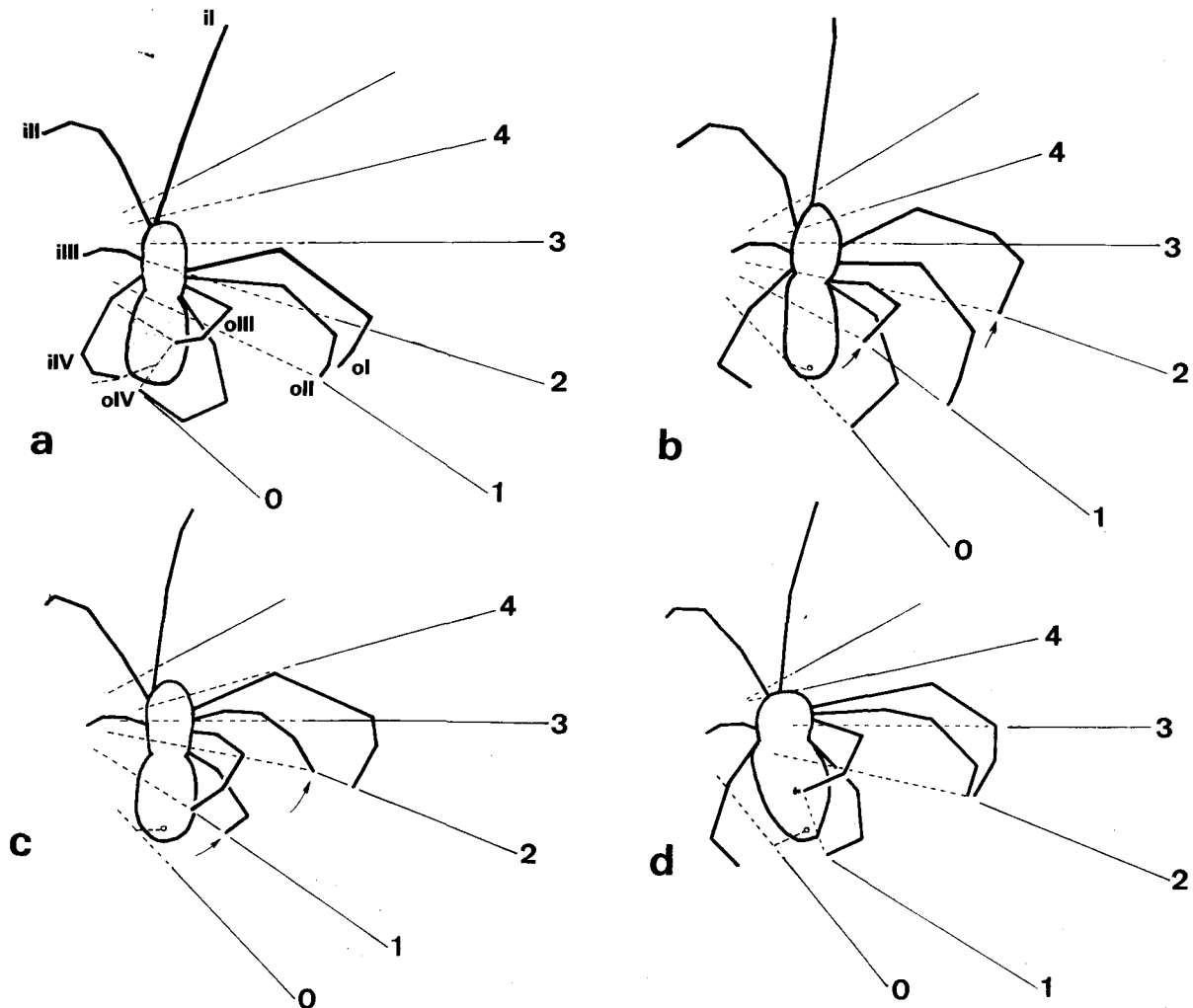


Fig. 3: Diagrammatic representation of video images of a mature female *L. mariana* building a hub. Legs on the side of the spider nearest the centre are labelled i ("inside"), those on the other side o ("outside"). The radius to which the spider had just attached the hub line is R_0 , the next one to which it would attach is R_1 . After the spider attached the hub line to R_0 (a), legs oI and then $oIII$ each advanced one radius (b). Then oIV and oII advanced one radius each (c), and the next attachment was made to R_1 (d). Starting with frame a on the tape, frames b, c and d were, respectively, 7, 10 and 12 frames later (30 frames per second). Dotted lines indicate estimated positions of lines not visible in the video images. Leg iIV was not visible in c, and was evidently being moved below the plane of focus from one radius to another.

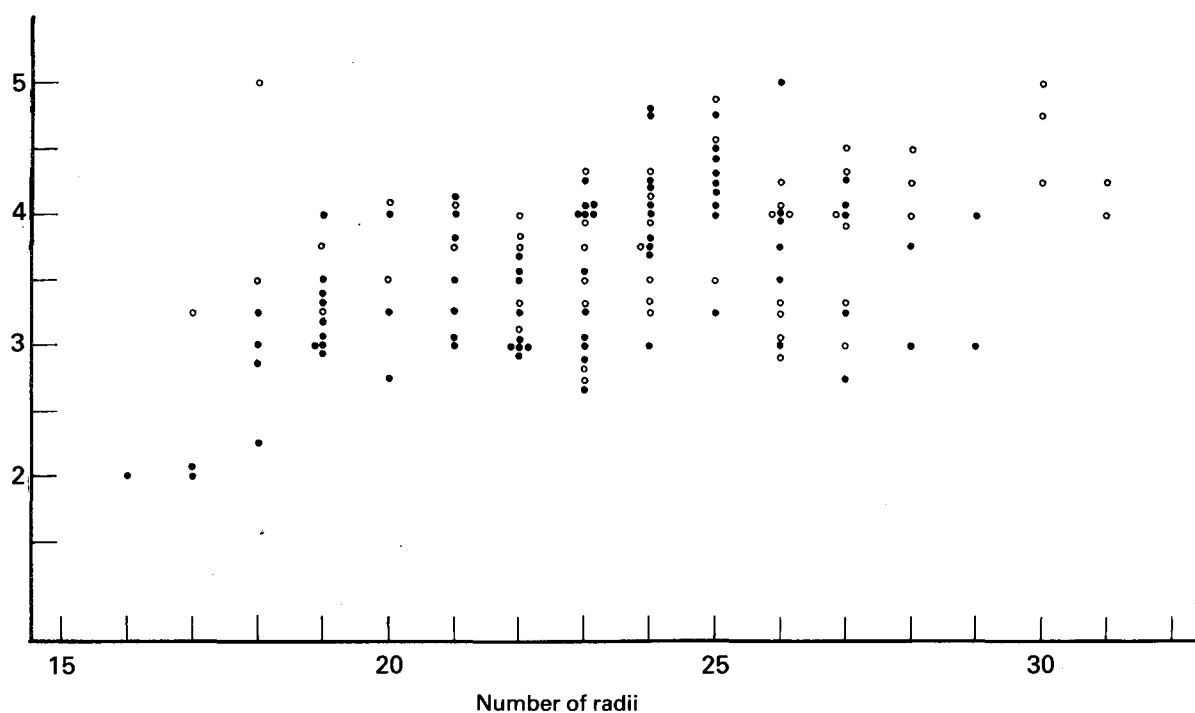


Fig. 4: Relationship between average number of hub loops and number of radii in 138 webs of mature female *L. mariana* (open circles = horizontal webs, solid circles = webs built at 45° with horizontal).

controversial (e.g. Coddington, in press), and since other aspects of web construction behaviour have furnished useful characters, comparisons with *L. mariana* as well as with previously unpublished observations of the araneids *Nephila clavipes* (L.) and *Argiope argentata* (Fabr.) are of interest. Both *N. clavipes* and *A. argentata* are large and move slowly, and their behaviour was deciphered without using videotapes.

Table 1 shows the similarities and differences between the four species. The order of movements of legs is different in each group. The araneids are relatively similar except that *L. mariana* moves oI first and *A. argentata* moves this leg last in the sequence between attachments. It is possible that the sequence reported for *U. diversus* (Eberhard, 1972) is incorrect; the movements were rapid, legs II and IV are relatively short, and no cine-films or videotapes were made. The differences in the way *N. clavipes* uses leg oI (Table 1) may be related to this species' small mesh size compared with its body size; it may be difficult or

impossible for the spider to make fine manoeuvres with this leg so close to its body. *L. mariana* differs from the other species in holding iIII more or less immobile at the centre of the hub. However, as all of the other species frequently interrupt hub construction to move away from the hub to lay radii, they cannot possibly hold iIII at one site on the hub. This is not the only reason why leg iIII is not held in the hub centre; the hub of *A. argentata* is so large that iIII cannot reach to the centre of the hub while the final hub loops are laid. The data in Table 1 do not in themselves clarify the taxonomic relations between these species, but further data on other species may yield useful insights.

The behavioural observations of *L. mariana* apparently provide at least a partial explanation of the cues used during hub construction. At other stages of web construction, *L. mariana* uses spirals already in place to guide its movements (Eberhard, in prep. a). The hub, being the first spiral formed in the web, cannot, however, be guided in this way. Probably leg iIII, which is held throughout hub construction at a

Behaviour	<i>U. diversus</i>	<i>L. mariana</i>	<i>N. clavipes</i>	<i>A. argentata</i>
Leg oI near attachment site?	yes	yes	no	yes
Leg oI followed by oII?	yes	yes	no	yes
Leg oI moves after each attachment?	yes	yes	no	yes
Usual order of movement of outside legs after each attachment	IV, III, II, I(?)	I, III, IV, II	III, IV, II ^a	III, IV and II (simultaneous), I
Inner III held more or less immobile at centre of hub?	no	yes	no	no
Hub construction interrupted repeatedly from early in process to lay radii?	yes	no ^b	yes	yes

Table 1: Hub construction behaviour of three araneids (each in a different subfamily) and one uloborid. Observations of *U. diversus* are from Eberhard, 1972; others are from this study. ^a occasionally IV and II are moved simultaneously. ^b In only 2 of more than 50 webs was a radius added after the spider began hub spiral construction.

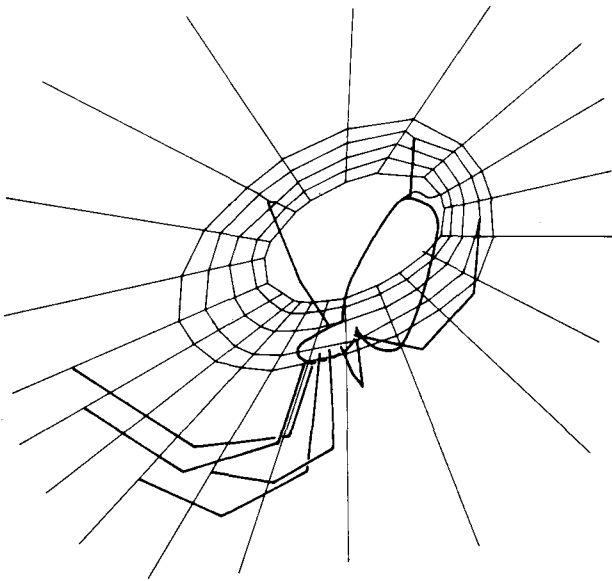


Fig. 5: Diagrammatic view of female *L. mariana* seen from above and to the side while at the hub of an inclined web. The abdomen is in the hole at the centre of the hub, legs III and IV hold hub lines and support most of the spider's weight, while legs I and II hold radii beyond the edge of the hub.

single spot in the central area of the hub where the radii converge, is used as a point of reference around which the hub is built. The spider may produce the variations in hub spacing above and below the hub in 45° webs and in inner versus outer hub loops by varying the amount by which leg iIII is extended. How this leg avoids becoming entangled as the spider turns around and around during hub construction is still a mystery.

Nomenclatural Note

The following application has been received by the International Commission on Zoological Nomenclature and has been published in *Bull.zool.Nom.* 43(4) on 11 December 1986. Comments or advice are welcomed and should be sent c/o The British Museum (Natural History), Cromwell Road, London SW7 5BD.

Possibly it makes small adjustments I failed to see, or does not grasp lines at the hub centre. The cues guiding the other species which do not hold leg iIII immobile at the centre of the hub are also unknown.

The function of the larger spaces between hub loops in the lower part of the hub is not known. Spiders nearly always rest facing downwards on inclined webs, but their legs consistently hold hub lines only in the upper portion of the hub (Fig. 5). The functional significance, if any, of initiating the hub loop in the upper part of 45° webs while moving upwards, and of increasing the spacing between hub loops in the outer part of the hub is also unknown.

Acknowledgements

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- EBERHARD, W. G. in prep. a: Web construction by *Leucauge mariana* (Araneae: Araneidae) I. The temporary spiral.
- EBERHARD, W. G. in prep. b: Correlation between number of hub loops and number of radii in orb webs.

Comments will be published in *Bull.zool.Nom.*

Case No. 2447 *Heriaeus* Simon, 1875 (Arachnida, Araneida): request for confirmation of *Thomisus hirtus* Latreille, 1819 as type species.

Editor