

Radial organisation in the web of a pisaurid, *Thaumasia* sp. (Araneae: Pisauridae)

William G. Eberhard

Smithsonian Tropical Research Institute, and
Escuela de Biología, Universidad de Costa Rica,
Ciudad Universitaria, Costa Rica

Summary

The pisaurid *Thaumasia* sp. builds a small, radially organised web on the upper surface of a leaf by repeatedly moving out from a central area and directly back. Many attachments were made to web lines, but the spiders never used their legs to locate, hold, or otherwise manipulate lines during construction, in contrast to the behaviour of most other web-weaving spiders that have been studied. Instead, they appeared to use a kinesthetic sense, movements of the abdomen, and probably also sometimes of their palps to guide construction and to locate lines to which to attach.

Introduction

The radial organisation of prey capture webs, with multiple lines converging on a central area, is a hallmark of spider orb webs, and thus a topic of central interest in discussions of the evolution of spider webs in general. Radial designs appear to have evolved independently in a number of non-orb weaving groups, in which the central area is the spider's retreat or burrow. Such webs occur in liphistiids and mygalomorphs (Coyle, 1986), hypochilids (Shear, 1969), filistatids (Comstock, 1948), the psechrid *Fecenia* (Robinson & Lubin, 1979), the amaurobiid *Titanoeca* (Szlep, 1966), some theridiids (Freisling, 1961; Szlep, 1965; Lamoral, 1968; Joerger & Eberhard, in press), and several species in the linyphiid genus *Meioneta* (G. Hormiga, pers. comm.). Yet another radial web, built by a hersiliid, has lines that converge on an otherwise unmodified resting site on a tree trunk (Williams, 1928).

The behavioural mechanisms used to produce radial patterns in non-orb web spiders are known in only a few groups. In some the spider lays a line or lines starting at the mouth of the retreat and moving away from it in a more or less straight line, and then moves more or less directly back to the retreat again; this behaviour occurs during sticky silk production in the eresid *Stegodyphus* sp., the filistatid *Kukulcania hibernalis* (Hentz), and an unidentified dictynid (Eberhard, 1987). A second technique utilised by the theridiid *Acharaeanea tessellata* (Keyserling) is to return occasionally to the retreat mouth while building other parts of the web, on each visit attaching the dragline at one of a few points and then using short pre-existing radial lines from those points to move directly into the retreat itself and then to move back out (Joerger & Eberhard, in press).

This paper describes another, independently derived non-orb with a radial organisation built by an unidentified species in the pisaurid genus *Thaumasia*. Strong radial organisation of webs has never been observed previously in Pisauridae. Many spiders in this family hunt prey without using a web (Bristowe, 1958; Murphy & Murphy, 2000; Carico, 2005), but webs have

been found in a variety of genera. Pisaurids have long been known to make “nursery webs” for their offspring (Foelix, 1996), but substantial sheet-like prey capture webs occur in *Inola* spp. (Davies, 1982), *Architis nitidopilosa* Simon (Nentwig, 1985), and *Euprosthops proximus* Lessert (Heidger, 1988) and several other African genera (Gerhardt & Kaestner, 1937 and Blandin & Célérier, 1981 in Nentwig, 1985; Dippenaar-Schoeman & Jocqué, 1997), and in immature *Pisaura mirabilis* (Clerck) (Lenler-Eriksen, 1969). The most detailed descriptions are of the webs of *A. nitidopilosa* and *P. mirabilis*. In both species a pair of more or less funnel-shaped sheets project from the ends of a short tube that is open at both ends. The spider rests in the tube, with its legs projecting laterally from each end of the tube onto the sheet. The web of *Inola amicabilis* Davies is similar in having a short horizontal tube open at both ends; in this species the lower edges of the tube are extended to form a large horizontal sheet (Davies, 1982). Immature *Pisaurina mira* (Walckenaer) build retreats resembling a reduced tubular portion of such webs, but apparently use them only for refuge rather than for prey capture (Carico, 1985). There do not appear to be any published accounts of the web building behaviour of any pisaurid. Apparently the only behavioural observation of any species of *Thaumasia* is the description of prey wrapping in Panamanian *T. uncata* F. O. P.-Cambridge (Nitzsche, 1988).

Material and methods

Observations were made on 14–17 December 2005 of immature specimens that were abundant in early second growth vegetation along an abandoned road at the edge of forest in Parque Estadual Intervales (24°16'S, 48°25'W), which forms part of a 120,000 ha protected segment of Atlantic Forest in São Paulo State in south-eastern Brazil. Specimens will be deposited in the Instituto Butantan collection in Rio de Janeiro. Although no mature spiders were collected, mature individuals of possibly an undescribed species of *Thaumasia* have been seen at other times of the year on small webs on leaves at exactly the same site (A. Santos, G. Machado, pers. comm.). One web of a mature female of a second species, *Thaumasia argenteonotata* (Simon, 1898) was photographed near Gamboa, Panama in June, 2006. This specimen will be deposited in the Museum of Comparative Zoology, Cambridge, MA.

Webs were studied in the field by coating them with cornstarch; five of these were photographed. Two webs were observed after breaking off the leaf carrying the web and taking it to a dissecting microscope. Web construction was induced by gently breaking and pulling away webs from under spiders. The spider either remained on the leaf's upper surface, or moved briefly to the underside of the leaf and then back to the top. Of 10 webs removed in this way before 09:00, seven were replaced within the next two hours. Of an additional 4 webs removed soon after 10:00 and 3 at about 17:00, none was replaced before sunset on that day. Replacement webs appeared to be smaller and to have

fewer lines. I videotaped one web replacement in its entirety, the majority of another, and portions of a third. The spider's drag line was occasionally visible in the recordings when lighting and viewing angles were favourable, allowing confirmation that attachments which were deduced from the spider's behaviour (see below) did indeed occur. Means are reported ± 1 standard deviation.

Results

Each of the 20–25 spiders found during the day and night was on a small web across an indentation on the upper surface of a leaf (Fig. 1a–c). Leaves of at least five species of plants were utilised. One web was occupied for at least two days, and then deserted on the third day, and several other apparently abandoned webs were also seen. Spiders ran extremely rapidly to attack prey, and were not dependent on their webs to capture prey. Three individuals whose webs I had removed struck at insects that passed nearby, and one of these captured the prey.

All of the approximately 10 webs that I powdered with cornstarch had the same general design, with a peripheral array of straight, radial lines that were attached to the leaf, and a central area in which the orientation of the lines was more variable (Fig. 1). In webs built across relatively narrow leaves, radial lines were absent on the narrow sides of the web (Fig. 1c). Some radial lines were longer, and originated farther

from the upper surface of the leaf than others (Fig. 1a). In five photographed webs, there were on average 39.8 ± 14.0 radial lines, of which 35.6 ± 11.5 were of the long type. The central portion of the central area formed a depression, into which the spider's body fitted as it rested on its web (Fig. 1b).

The spider's behaviour during all three web constructions that were observed was similar, in that the spider repeatedly moved from the central area to the edge of the web or beyond (in some cases to the edge of the leaf), attached its dragline, and moved back to the central area where it attached its dragline several times before moving to the edge again (Figs. 2, 3). In the web whose entire construction was filmed (Figs. 2, 3), the spider averaged 1.9 ± 3.4 (range 1–16) attachments between successive radial lines. Each time the spider attached to lines in the central area, it twisted its abdomen slightly and directed the tip ventrally. Attachments to the leaf near the edge of the web (the numbered "turnbacks" in Figs. 2 and 3) generally involved a strong ventral flexion of the abdomen that brought the spinnerets into contact with the leaf, and were always followed by the spider pivoting approximately 180° , keeping its spinnerets against or near the surface of the leaf (Fig. 4a), before moving back in the same approximate direction from which it had come. Probably the first attachment of the dragline that was made on the way back was often to the line it had laid on the way out, resulting in the "Y" junctions observed on most of the radial lines that were attached to the substrate (thick arrows in Fig. 1a). It

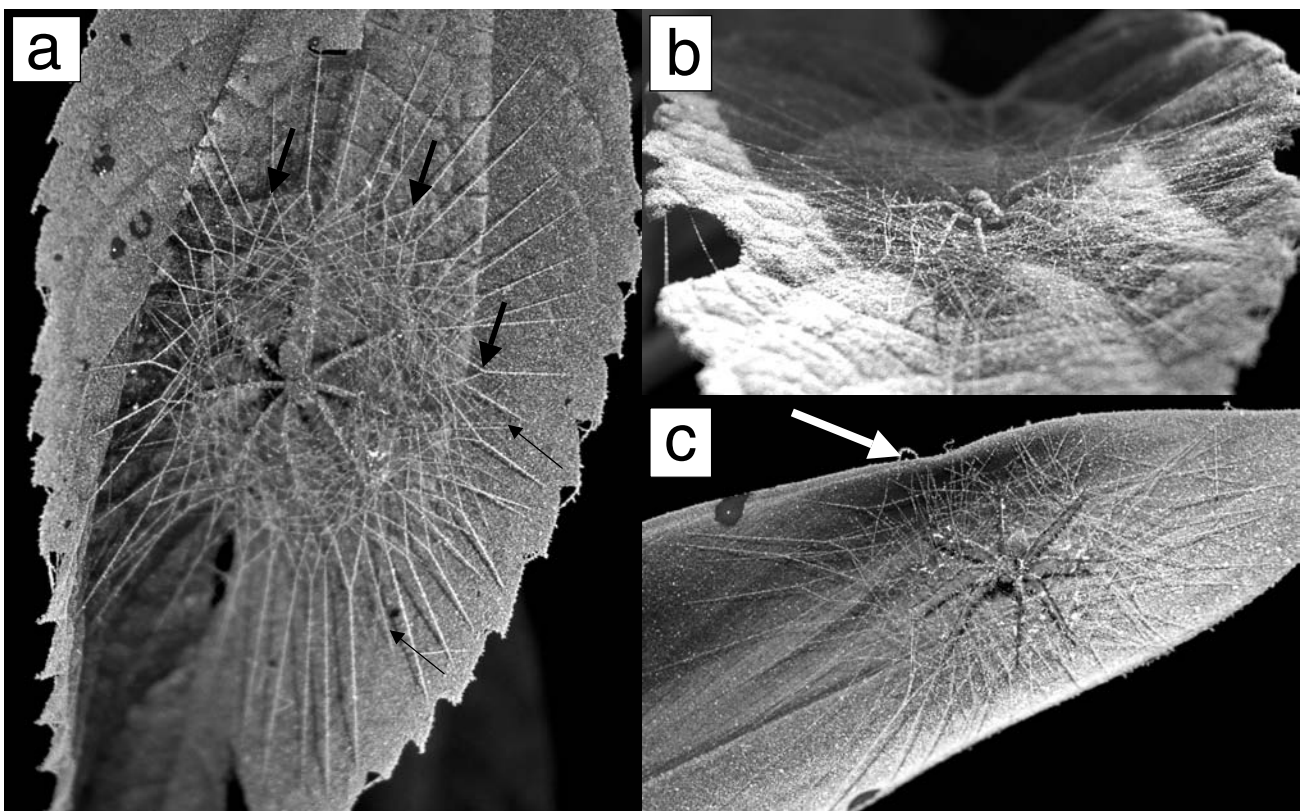


Fig. 1: Web photos. **a** Typical web on upper surface of a leaf, with spider resting with its abdomen and cephalothorax in central depression. Thick arrows indicate "Y" junctions at bases of peripheral radial lines; thin arrows indicate shorter, probably earlier radial lines; **b** Anterior view of spider, showing its cephalothorax and abdomen resting in central depression of web; **c** Web on a narrow leaf, lacking peripheral radial lines on sides nearest to leaf edges (arrow). Approximate width of leaf at level of depression where spider rests = 8 cm (a), 10 cm (b), 4 cm (c).

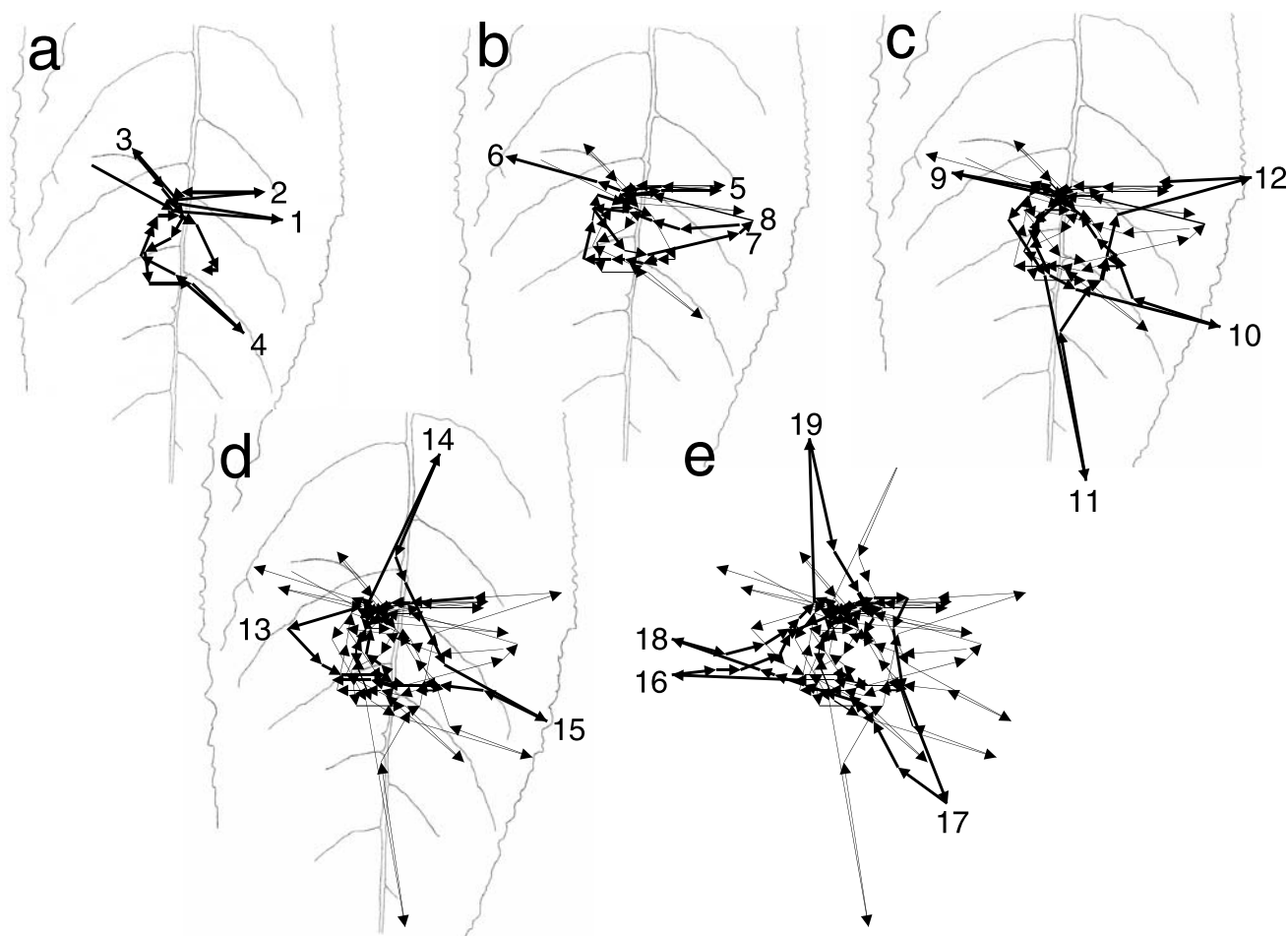


Fig. 2: Approximate locations and sequence of points of attachment (arrowheads) made during successive stages of one nearly entire web construction sequence that was videotaped (attachment points were deduced from abdomen movements). Turnbacks (which produced the peripheral radial lines — see Fig. 1) are numbered in the order they were produced. Lines connecting the most recent attachments are drawn thicker than the others (spider was briefly out of focus between turnbacks 6 and 7).

appeared that the spider tended to lay successive radial lines in approximately opposite sectors of the web (the mean angle between successive “turnbacks” in the web in Fig. 2 was $107 \pm 49^\circ$, and 12 of 18 were $>90^\circ$) but there was substantial variation (range 1–178°). Excursions later in construction involved attachments of radial lines farther from the central area (Fig. 3). The spider occasionally paused during construction for up to about 30 s. The rate of attachments while the spider was active was nearly one every 2 s (mean time between attachments in the web in Fig. 3 was 2.2 ± 1.2 s). Web construction took only a few min; the total active time to build the web in Fig. 3 was 4.82 min.

Several details of the spider’s movements were discerned. None of the spider’s legs showed any sign of tapping or otherwise attempting to locate lines that had already been laid. All legs stepped slowly and directly, and were kept in their normal spread positions rather than being flexed ventrally to manipulate lines (Fig. 4). Legs IV never came close to the spinnerets. Thus the many attachments of the drag line to other lines were made without using the legs to hold lines for the spinnerets to touch, as occurs in most other web-building spiders (see Discussion). Lines may have been located instead by the twisting ventral movement made

by the tip of its abdomen each time the dragline was attached.

In addition, the spider may have also used exploratory movements of its pedipalps. The pedipalps tapped ventrally and laterally nearly continually in all taped sequences in which they were visible.

Two webs observed under a dissecting microscope had many large attachment discs that connected single lines (presumably each composed of multiple filaments). Some lines were lax, and these were kinky; none of the lines had balls of liquid on them.

A single web of *T. argenteonotata* was observed on the upper surface of a leaf near Gamboa, Panama in June 2006 (Fig. 5). No observations were made of behaviour, other than that the spider rested on the central depression in the web with its legs spread, as in *Thaumasia* sp.

Discussion

The most striking aspects of the webs of *Thaumasia* sp. are the highly regular array of radial peripheral lines (Fig. 1), and the simple behavioural mechanism by which this design was produced (move from the central area to the edge, back to the central area, and out again) (Fig. 3). A second, more subtle pattern was a depressed

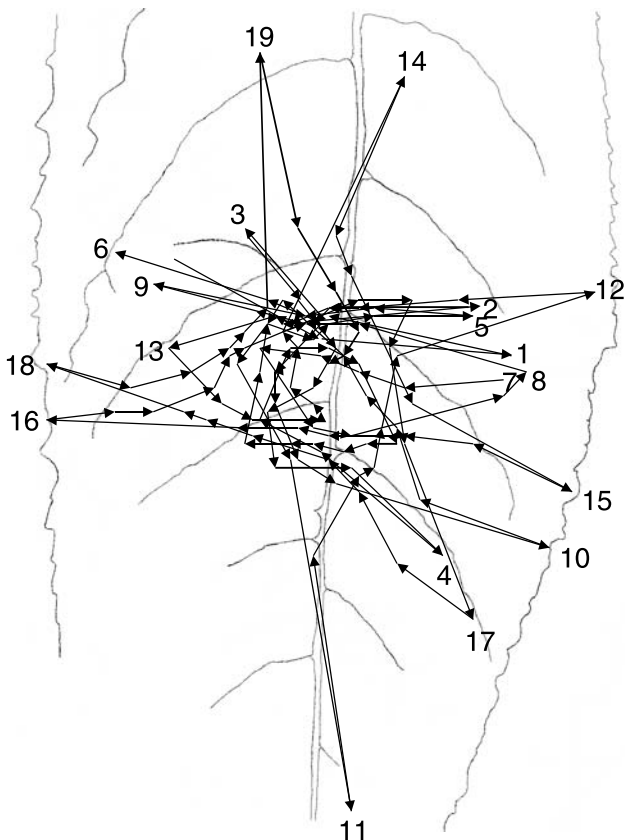


Fig. 3: Entire sequence of lines laid in web shown in Fig. 2. Sites of attachment were determined with respect to landmarks on the leaf, and are not exact. Insofar as I correctly noted all attachments, the lines approximate to the silk lines produced by the spider.

area in the central portion of the web (Fig. 1b), where attachments were seldom made and lines were not laid (Figs. 2, 3). The radial design did not function to provide the spider with physical access to different parts of its web, as it does in orb weavers (Witt, 1965), because the spiders never walked along single lines. Presumably the major function of the web is to extend the spider's sense of touch, though spiders without webs were also able to detect and successfully attack prey.

The webs of *Thaumasia* sp. resemble those of *T. argenteonotata*, *P. mirabilis* and *A. nitidopilosa* in having a sheet-like extension around the central resting place of the spider. The webs of *Thaumasia* sp. are simpler than those of the last two species in being close to two-dimensional, and not having a tube within which the spider rests. The radial design of *Thaumasia* sp. webs is much clearer than either the weak radial trend in *P. mirabilis* webs (see Fig. 1 of Lenler-Eriksen, 1969), or the complete lack of any clear radial tendency in those of *T. argenteonotata*, *P. mira* (Carico, 1985) or *A. nitidopilosa* (W. Eberhard, unpublished) (the possibility of radial organisation cannot be judged from the published figures of *Inola* (Davies, 1982), or *Chiasmopes* (Dippenaar-Schoeman & Jocqué, 1997)).

Many web-building spiders use their legs to locate lines that they have already laid, and also to seize them and their drag lines and hold them close to their spinnerets while they attach the dragline to other lines (Eberhard, 1972, 1982, 1986, 1992; Coddington, 1986;

Lepoldo *et al.*, 2004). The behaviour of *Thaumasia* sp. stands in sharp contrast: the spiders did not appear to use their legs to sense the positions of lines already present, and certainly did not hold these lines with any legs while making attachments to the substrate or other lines. The behaviour with which *Thaumasia* sp. located the lines to which they attached the dragline may sometimes involve palp movements to sense previous lines, combined with a subsequent kinesthetic memory while moving to position the abdomen to make an attachment where the palp had encountered a line. A visual or kinesthetic memory was also suggested in *P. mirabilis* by the spider's lack of reliance on its dragline to move directly to its resting site (Lenler-Eriksen, 1969). In addition, the latero-ventral twisting movement of the tip of its highly mobile abdomen may also serve to locate lines to which to attach. A similar abdomen movement occurs in the distantly related *Psechrus* sp., which in addition grasps the web line to which it is attaching with its legs (Eberhard, 1987). Using the abdomen rather than the legs to locate lines to which to attach is probably typical of spiders that do not build aerial prey capture webs, as it occurs in three salticid species, a scytodid, a thomisid, and a dictynid (Eberhard, 1986: descriptions in the text of this study of the behaviour patterns for this trait (#4) are incorrect: *a* should be *c*; *b* should be *a*; and *c* should be *b*). The anyphaenid *Aysha* sp., which does not make a prey capture web, also makes very regularly spaced "sewing" movements with its

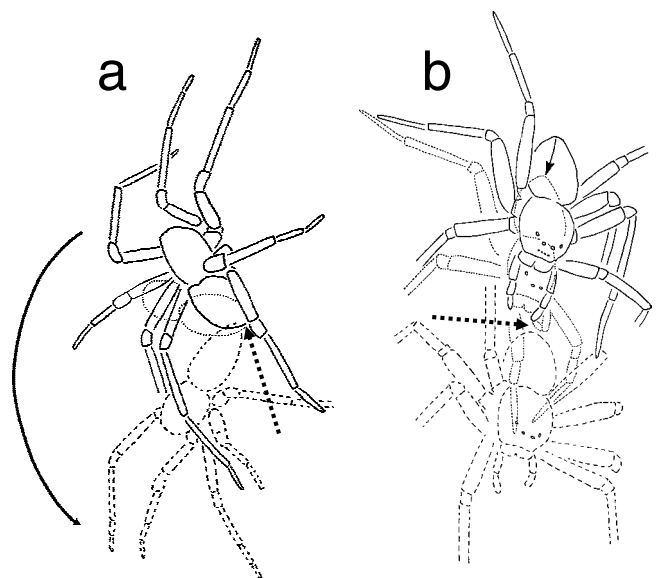


Fig. 4: Aspects of construction behaviour (traced from video images). **a** Spider attaching a peripheral radial line to the leaf (solid lines; attachment point indicated by dotted arrow) and subsequent turning movement (curved arrow and dotted and dashed outlines of spider) (position indicated by the dotted lines occurred 0.33 s after that indicated by the solid lines, and that indicated by the dashed lines followed 0.67 s later); **b** Sequence showing possible use of a palp to locate a line to which to attach the drag line. A palp was extended anteriorly (solid lines), but it retained its hold on a line (dotted arrow) while the spider moved forward (solid arrow) until it was pulled completely under the spider's body (dotted lines follow solid lines by 0.10 s); finally, 0.60 s later the spider attached its trail line very close to the site where the palp had apparently gripped the web (dashed outline of spider).



Fig. 5: Web of mature female *Thaumasia argenteonotata* on upper surface of a leaf; width of leaf at level of depression = 4.2 cm.

abdomen, without using its legs directly, when it seals up breaks in the silk that holds the edges of the folded leaf of its retreat together (W. Eberhard, unpublished).

Acknowledgements

I thank Glauco Machado for arranging my trip to Intervales, and his students Bruno Buzatti, Gustavo Requena, Thiago Del-Corso, and Thais Nazareth for numerous favours. I am grateful to Adalberto Santos for identifying the *Thaumasia* sp., Jorge Vasconcellos-Neto for the name of the anyphaenid, and Jim Carico for identifying *T. argenteonotata* and for commenting on the manuscript. Financial support came from the Smithsonian Tropical Research Institute and the Universidad de Costa Rica.

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