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Web forms and the phylogeny of theridiid spiders (Araneae: Theridiidae): chaos from order

Abstract We trace the evolution of the web designs of spiders in the large family Theridiidae using two recent, largely concordant phylogenies that are based on morphology and molecules. We use previous information on the webs of 88 species and new data on the web designs of 78 additional theridiid species (representing nearly half of the theridiid genera), and 12 other species in related families. Two strong, surprising patterns emerged: substantial within-taxon diversity; and frequent convergence in different taxa. These patterns are unusual: these web traits converged more frequently than the morphological traits of this same family, than the web traits in the related orb-weaving families Araneidae and Nephilidae, and than behavioural traits in general. The effects of intraspecific behavioural ‘imprecision’ on the appearance of new traits offer a possible explanation for this unusual evolutionary plasticity of theridiid web designs.

Key words behavioural evolution, cobwebs, behavioural imprecision hypothesis

Introduction

One of the payoffs from determining phylogenetic relationships is that they provide opportunities to understand otherwise puzzling distributions of traits within a group. Two recently published phylogenies of theridiid spiders, one based on morphology and to a lesser extent on behaviour (Agnarsson, 2004, 2005, 2006) and the other on molecules (Arnedo *et al.*, 2004), offer such an opportunity. The two types of data yielded largely similar trees, suggesting that they represent close approximations to the evolutionary history of this family. Theridiidae is one of the largest families of spiders, with over 2300 described species distributed world-wide in 98 genera (Platnick, 2008) (many other species await description). Theridiid webs have a variety of designs (e.g. Nielsen, 1931; Benjamin & Zschokke, 2002, 2003; Agnarsson, 2004). To date the scattered distribution of several different web designs among different taxa has seemed paradoxical. Is this because the similarities in apparently isolated taxonomic groups are due to common descent that was masked by incorrect taxonomic grouping? Or is it that the web forms of theridiids are indeed very plastic and subject to frequent convergence? The new phylogenies offer a chance to answer these questions.

This analysis also brings further light to bear on the controversy concerning the relative usefulness of behavioural traits in studies of phylogeny (Wenzel, 1992; de Quieroz & Wimberger, 1993; Foster & Endler, 1999; Kuntner *et al.*, 2008).

The unusual patterns found in this study provide insight regarding the possible evolutionary origins of behavioural divergence. In particular, they offer a chance to evaluate the ‘imprecision’ hypothesis, which holds that greater non-adaptive intraspecific and intraindividual variance in behaviour facilitates more rapid evolutionary divergence (Eberhard, 1990a).

In this paper we summarise current knowledge of theridiid web forms, using the published literature and observations of 78 additional, previously unstudied species. We estimate the plasticity of theridiid webs by optimising web characters on a phylogeny, and compare the level of homoplasy in theridiid web characters with characters of morphology in theridiids, with behaviour and web characters in orb weaving spiders, and data from other behavioural studies.

Methods

Webs were photographed in the field unless otherwise noted. All were coated with cornstarch or talcum powder to make their lines more visible unless noted otherwise. Scale measurements were made holding a ruler near the web, and are only approximate. Voucher specimens of species followed by numbers are deposited in the Museum of Comparative Zoology, Cambridge MA. Vouchers of the others will be placed in the US National Museum, Washington, DC. We opted to present many photographs, rather than relying on sketches or word descriptions, because the traits we used (Appendix 1) are to some extent

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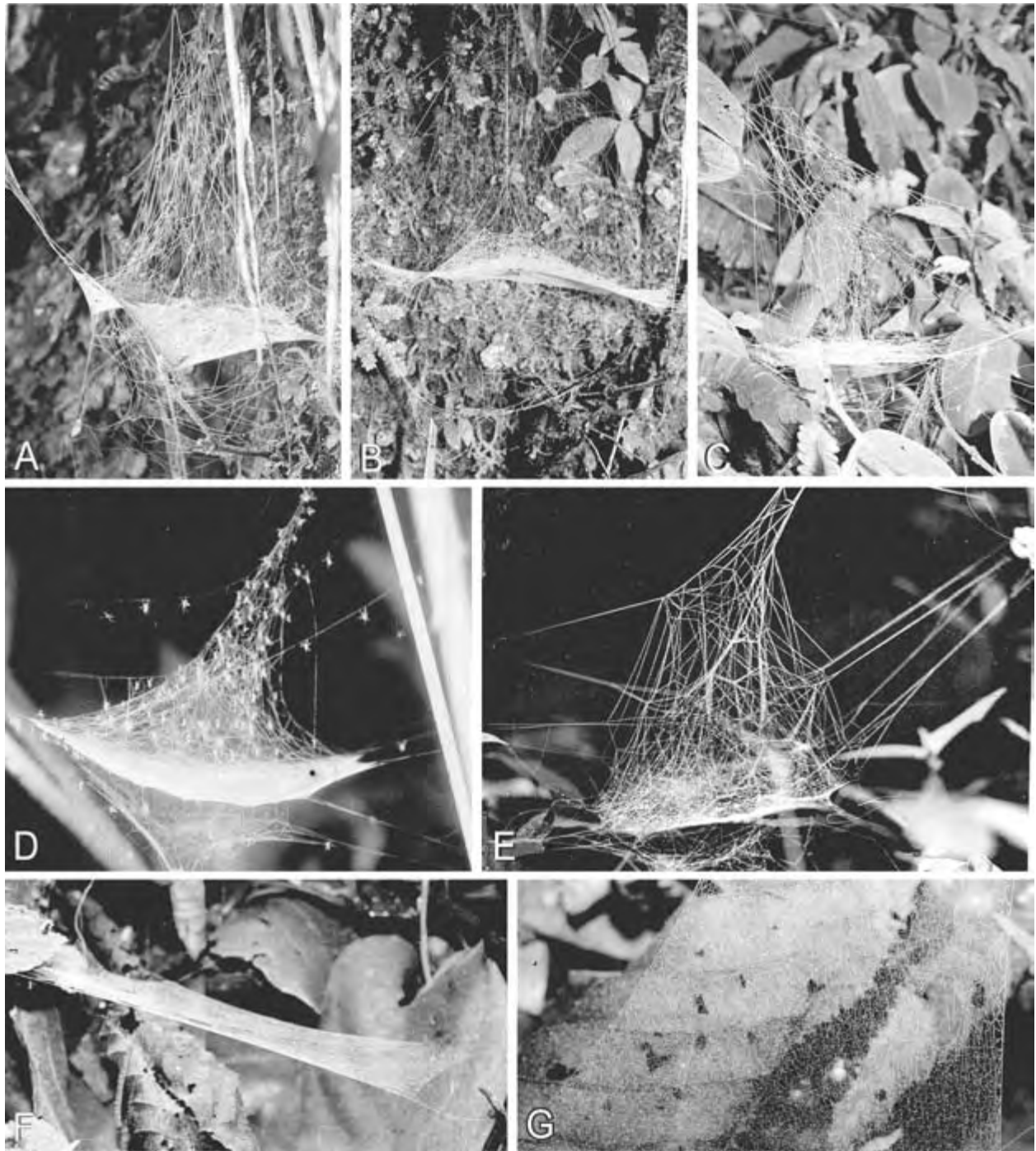


Figure 1 Linyphiidae (all unknown genus except E). A and B #3255. Lateral views; C #3634. Lateral view; D #2315. Lateral view. A swarm of small nematoceros flies rested on the web; E *Dubiaranea* sp. Lateral view; F and G #3248. Lateral (F) and dorsal (G) views. Approximate widths of photos (cm): A 15; B 15.7; C unknown; D 14; E 29; F 19.6; G not known.

qualitative rather than quantitative; we also expect that future studies of theridiid webs may discover further traits that can be discerned in photographs. Multiple webs are included for some species to illustrate intraspecific variation. Notes on the webs, when available, are included in the captions. We did not include the observations of *Coelosoma blandum* reported by Benjamin and Zschokke (2003), as the spider was apparently misidentified (S. Benjamin pers. comm.).

We analysed as ‘webs’ only those structures of silk lines that apparently function in one way or another in prey capture. We have thus not included webs that are apparently specialised for egg sacs (e.g. in *Ariamnes*, *Faiditus*, *Rhomphaea* – see figs. 95E, 98C, 101F in Agnarsson, 2004). Egg sacs (which are frequently associated with theridiids in museum specimens and in field guides) and the webs associated with them (which are in some cases elaborate, as for example the adhesive tangle

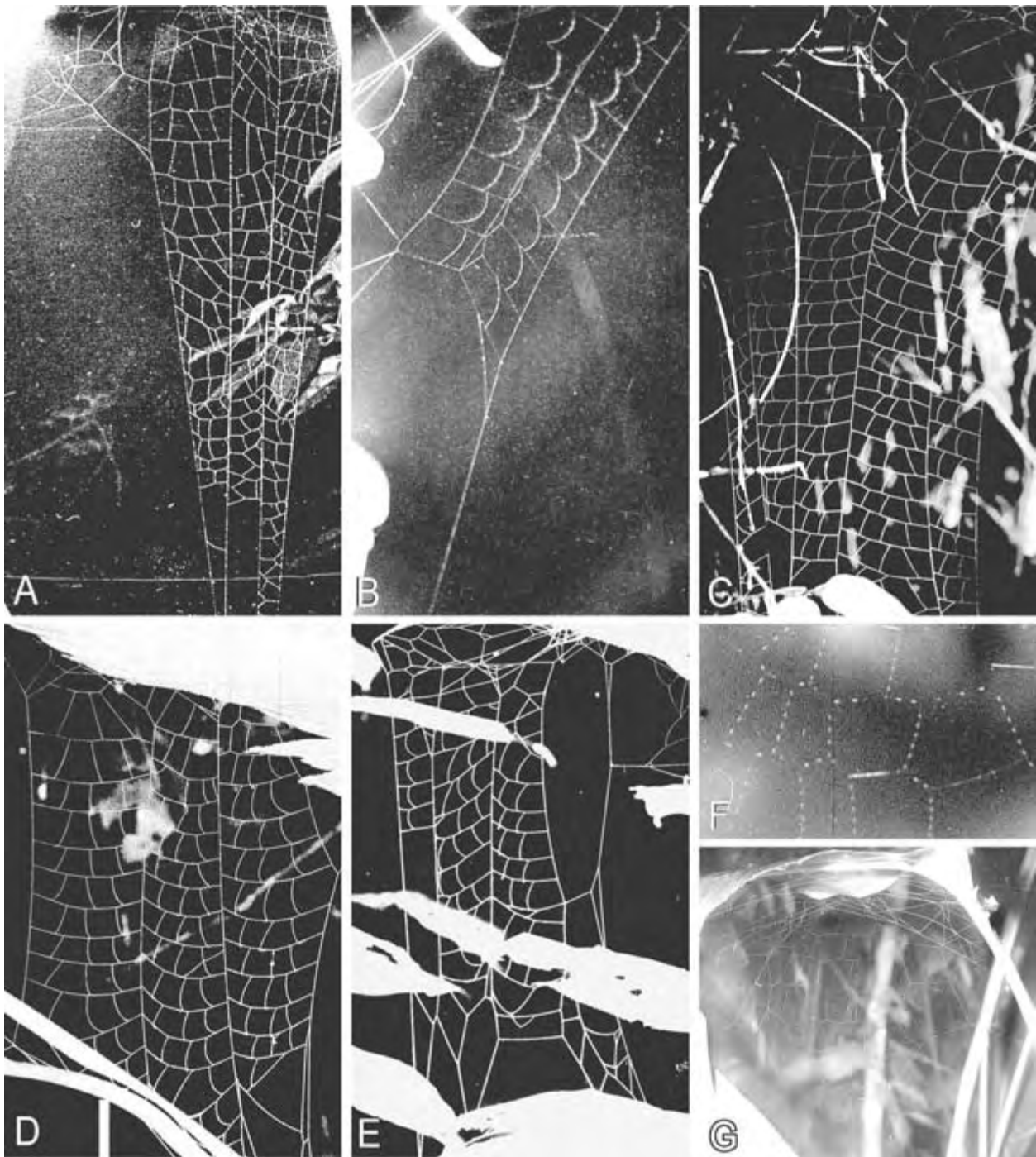


Figure 2 Synotaxidae. *Synotaxus*. A *Synotaxus* sp. juv #649b; B juv. #918.; C *S. monoceros*; D *S. turbinatus* #1012; E *S. turbinatus* #1026; F *S. turbinatus* #2342 without white powder, showing the dots of sticky material on the zig-zag vertical lines; G, lateral view of same web as F with white powder. Approximate widths of photos (cm): A 18.4; B unknown; C unknown; D unknown; E; F 10.8; G 31.4.

around the egg sac of *Steatoda bimaculata* – Nielsen, 1931), will undoubtedly provide further characters. We have included photographs of species identified only to genus level (those not fitting the description of any described species, and thus probably representing undescribed species) and assumed that these species are different from any of the named species in literature accounts or that we studied. The convention we followed with names was *Theridion* nr. XXX is surely (within taxonomic

error) not species XXX; “*Theridion* c.f. XXX” might be species “XXX”.

The character descriptions and comments in Appendix 1 discuss many aspects of the distinctions and terms we used, but several terms need to be defined here. We use the word ‘tangle’ to designate three-dimensional networks of interconnected lines (both sticky and non-sticky) in which we could not perceive clear patterns in the connections. We use the

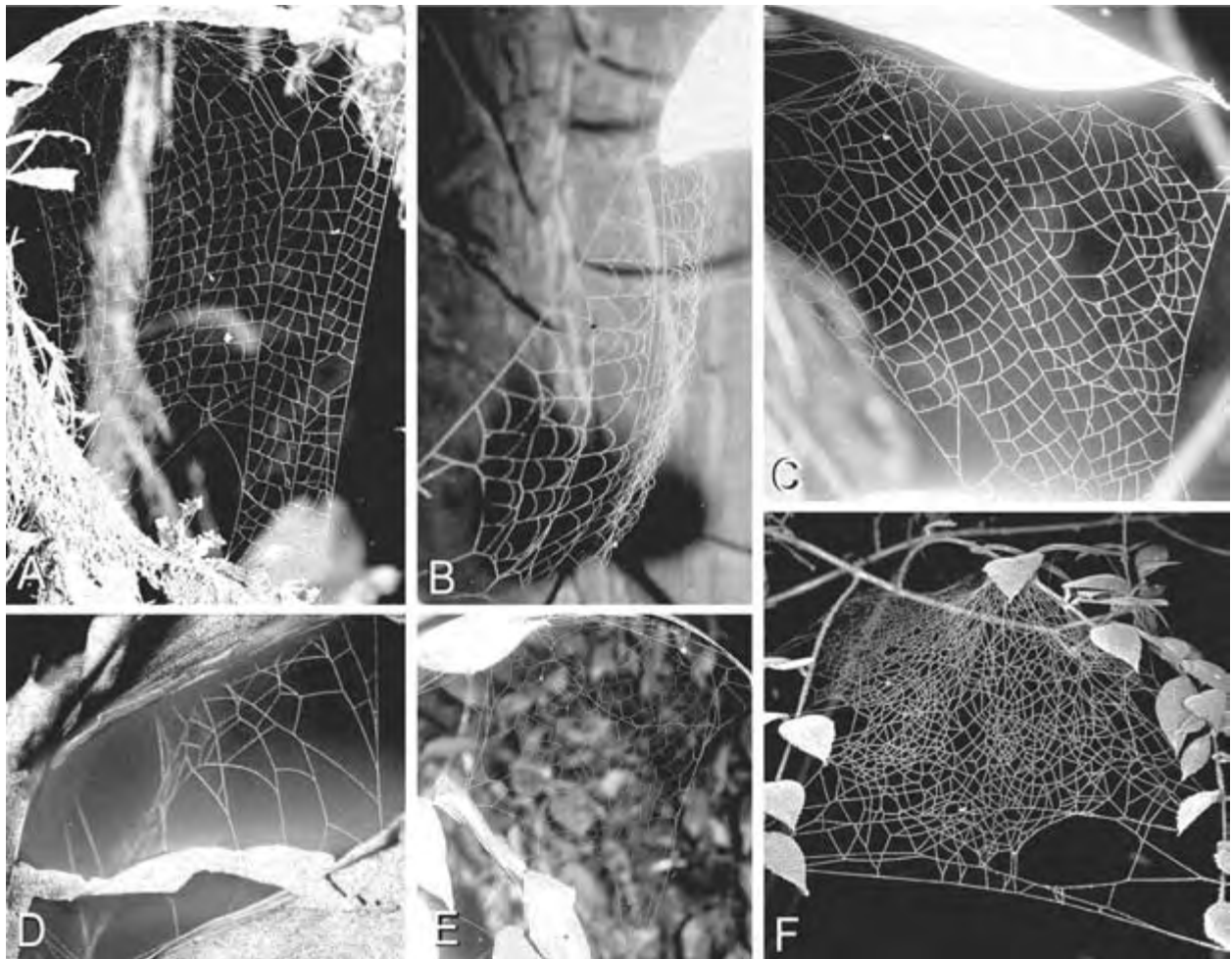


Figure 3 Synotaxidae. *Synotaxus*. A *Synotaxus* juvenile #1109. Lateral view; B–C *S. ecuadorensis* #2341. Lateral views (B is nearly parallel to the plane of the web); D *S. ecuadorensis* #2337. Lateral view of web with spots of glue; E. *S. ecuadorensis* #2683. The spider rested on the underside of the central leaf, surrounded by a sparsely meshed bell-shaped wall; F *Chileotaxus sans* (photo by J. A. Coddington). Approximate widths of photos (cm): A 16; B unknown; C 26; D 14.4; E 15; F unknown.

word ‘mesh’ to refer to the spaces between adjacent lines (open mesh, closed mesh, regular mesh shape, irregular mesh shape). We thus attempt to avoid the possible confusion that can result from previous use of ‘mesh’ (e.g. Eberhard, 1972) to designate what we are calling ‘tangle’. We used the term ‘glue’ rather than the more common phrase ‘viscid silk’ to refer to the sticky liquid that occurs in small, approximately spherical balls on lines. ‘Glue’ makes no suppositions regarding chemical composition (which has not been determined, and which varies (Barrantes & Weng, 2006)). Also, the glue is not fibrous, and thus does not conform to at least some common interpretations of the word ‘silk’. We used ‘balls’ of glue to refer to individual masses, and do not imply thereby that the masses were perfectly spherical. The phrase ‘sticky line’ refers to any line bearing balls of glue, while ‘dry lines’ lacked balls of glue visible to the naked eye. We use the word ‘retreat’ to refer to any modification of the web or nearby objects made by the spider where it rests during the time when not engaged in other activities.

Our intention in classifying web traits (Appendix 1) was to highlight possibly novel traits that may result from particu-

lar derived abilities of the spider (e.g. curl leaves for retreats rather than just use leaves that are already curled). While we attempted to code characters in a manner appropriate for phylogenetic analyses, we view our effort as only a first attempt to reduce the complexity of theridiid webs to homology hypotheses. We utilised relatively fine divisions, in contrast with previous discussions of theridiid webs such as those of Benjamin and Zschokke (2003) and Agnarsson (2004), in order to maximally call attention to informative characters. It may well be that we have over-divided some characters. In some cases, however, we essentially gave up in attempts to atomise particularly complex characters (e.g. sheet form), and instead used an ‘exemplar approach’ (e.g. Griswold *et al.*, 1998). Hopefully our shortcomings here will help focus the observations of future workers on the data necessary to refine these homology hypotheses.

The species for which we obtained web data were nearly all different from the species on which previous phylogenetic analyses were based (Agnarsson, 2004; Arnedo *et al.*, 2004). Because a novel phylogenetic analysis including web characters is premature due to the lack of overlap between



Figure 4 *Synotaxus*. A *S. turbinatus* #3638. Lateral view.; B *S. turbinatus* #3646. Lateral view; C *S. longicaudatus* #3561. The spider was near the underside of the leaf at the top, surrounded by a bell-shaped retreat. The irregular form of the 'frame' line at the bottom did not appear to be due to damage; D *S. turbinatus* #3638; E *S. turbinatus* #3645. Lateral view of nearly perfectly planar web. Approximate widths of photos (cm): A unknown; B 18.9; C 26; D 28.5; E 36.

species in the different data matrices, several problems were posed for exploring the phylogenetic distribution of web characters. The lack of overlap meant that it was not possible to simply lay our web data directly onto the phylogeny derived from previous studies. In addition, the taxon overlap of the molecular and morphological matrices themselves is incomplete, and the phylogenetic hypotheses generated from the two data sets, while broadly similar, differ in many details. Therefore we attempted to trace the evolution of web characters by optimising them on a non-quantitative, manually constructed 'best guess' phylogenetic hypothesis. This hypothesis is based on current morphological and molecular phylogenetic knowledge, but also includes several genera for which we have web data but that have not been included in the previous quantitative phylogenetic analyses. Such genera were arbitrarily placed on the phylogeny basally within the subfamily to which they are thought to belong (see Agnarsson, 2004), unless additional evidence such as taxonomical hypotheses/species groups suggested by the works of Levi (Levi, 1953a, b, 1954a,

b, c, d, 1955a, b, c, 1956, 1957a, b, c, 1958, 1959a, b, c, 1960, 1961, 1962a, b, 1963a, b, c, d, e, f, 1964a, b, c, d, e, f, 1966, 1967a, b, c, 1968, 1969, 1972; Levi & Levi, 1962), an explicit phylogenetic hypothesis, or preliminary phylogenetic data, suggested a 'more precise' placement within the subfamily.

Web data were scored in the following three ways (for raw data on all species see Appendix 2, which is available as 'Supplementary data' on Cambridge Journals Online: http://www.journals.cup.org/abstract_S1477200008002855). When web data was available for a species previously placed phylogenetically, these were scored directly for that species. When this was not the case (the majority of the species) codings for all species of a single genus were combined into a single 'dummy' taxon, where each character was scored for all states occurring in the different species in this taxon (hence polymorphic when more than one state occurred). Scoring the dummy taxa as polymorphic represents the minimal number of steps required to explain intrageneric variation in webs (and thus may have led to underestimates of the numbers of



Figure 5 Nesticidae A *Gaucelmus calidus*. Dorso-lateral view of web built in captivity in a humid container. Nearly the entire length of each of the long lines to the substrate below was covered with large sticky balls (which shrank appreciably when the container was opened and allowed to dry out). Similar long, more-or-less vertical sticky lines present in webs in the field were more clustered. The lines in the small tangle just above the long sticky lines were not sticky. Approximate width of photo (cm): A 20.

transitions). When a congener lacking web data was present in the phylogeny the generic dummy taxa simply replaced it, to minimise the manual introduction of branches. However, when this was not the case, the dummy taxon formed a new branch in the phylogeny and was placed as explained above.

This approach makes assumptions whose violation may alter our results, so these assumptions must be kept in mind. First, we must assume that the placement of the dummy taxa is reasonable (at least approximately ‘correct’ at the level of the subfamily) and that minor changes in their placement will not alter our results. As discussed below we have reasons to believe that this holds true. Second, the dummy taxa carry an implicit assumption of genus monophyly, an assumption that for some genera we suspect is false. For instance, *Theridion*, *Achaearanea*, and *Chryso* probably represent polyphyletic ‘wastebasket’ genera (Agnarsson, 2004). The seriousness of the violation of this assumption for our conclusions is difficult to evaluate. However, as discussed below, morphologically plausible taxon transfers between genera are not likely to greatly reduce the number of web character transitions we observed. Rather, they will just move the changes to different branches. Third, it should be noted that our comparisons of relative frequency of homoplasy in web characters versus morphological characters (see discussion) are probably somewhat

biased upward. Agnarsson’s (2004) parsimony analysis minimised homoplasy in the morphological characters, whereas the web characters are merely mapped on this phylogeny. We are assuming that the phylogeny is a reasonable approximation to the ‘true’ phylogeny (see assumption one), and that inclusion of web characters in a ‘total evidence’ quantitative phylogenetic analysis would yield results similar to Figs 46–47.

Three consistency indices (CI) were calculated for each trait: that generated by Winclada, which does not take into account the additional steps required by polymorphism in terminal clades (both true intraspecific polymorphism and the ‘polymorphism’ in the dummy taxa stemming from intrageneric differences); a ‘total CI’ that took these steps into account, either conservatively, assuming that only one additional step would be needed for each intrageneric ‘polymorphism’ (the preferred CI values), or by counting all polymorphism as extra steps.

Results

Table 1 (available as ‘Supplementary data’ on Cambridge Journals Online: http://www.journals.cup.org/abstract_S1477200008002855) summarises previously published information on web characters for 88 theridiid species. Figures 1–45 document the web designs of 78 additional species with web photographs and notes on the distribution of sticky lines in these webs. The species are arranged according to their approximate likely relationships (Figs 46–47). We have notes but no photographs for five additional species. One late juvenile *Tidarren* sp. in Santa Ana, Costa Rica (SAE10–9A) rested in a tangle above a relatively dense, bowl-shaped sheet at its bottom edge (as in *Anelosimus*). The spider rested in a retreat made of pieces of detritus. Both *Phoroncidia studo* or close (#1126) and *P. reimoseri* each had a single more-or-less horizontal sticky line. The spider rested at one end, and broke and reeled up the line as it moved toward a prey, and again broke and reeled as it returned after capturing the prey. On the way to the prey it laid a new non-sticky line, and on the way back it laid a new sticky line. When it reached the end, where it fed, the spider turned to face toward the central portion of the line, and then tightened the line by reeling up line with its hind legs. *Nesticodes rufipes* webs were typical, non-star gumfoot webs, with 10–30+ gumfoot lines more or less perpendicular to the substrate (below or to the side of the tangle). These lines were relatively short (1–2 cm), and each had closely spaced balls of glue along its entire length. There was a substantial tangle, and the spider rested at the edge, on or near the substrate. *Ameridion latrhropi* (#2191) had gumfoot lines that were sticky only near their distal tips where they were attached to the substrate. *Theridula gonygaster* had more or less vertical long sticky lines under a small tangle near the underside of a bent grass leaf where the spider rested.

Figures 47 and 48 summarise the transitions in all of the different web traits, while Figs 49–59 optimise each of the web traits on the phylogeny. The phylogenetic tree was based on

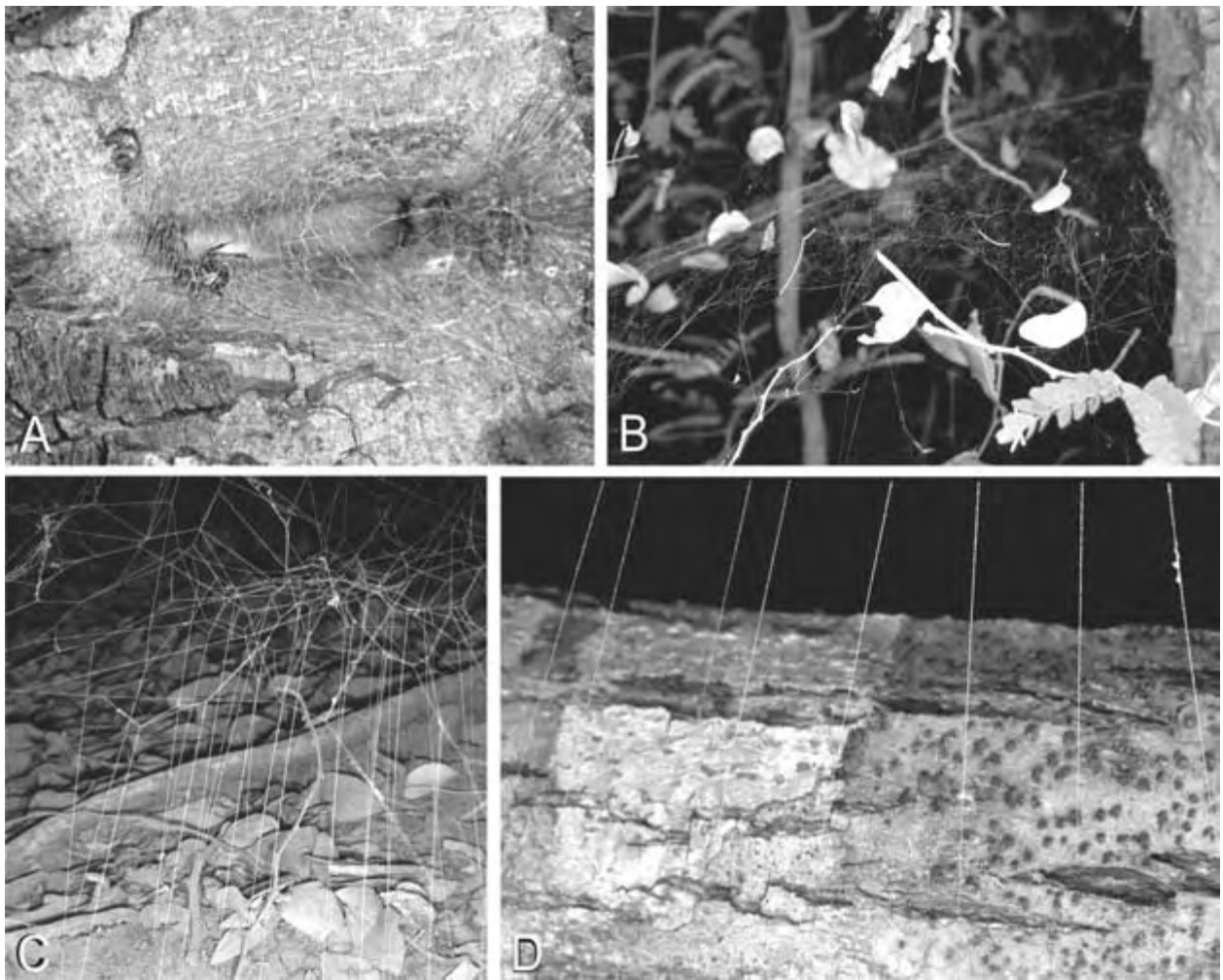


Figure 6 *Latrodectus*. A–D *L. geometricus*. A female inside silk retreat at edge of web; B, domed sheet reaching from the retreat at right (at about 150 cm) to 20–30 cm above the ground; C, gumfoot lines leading from the end of the sheet to the substrate; D, tips of gumfoot lines. Approximate width of the photos (in cm): A, 12; B, 90; C, 25; D, 10.

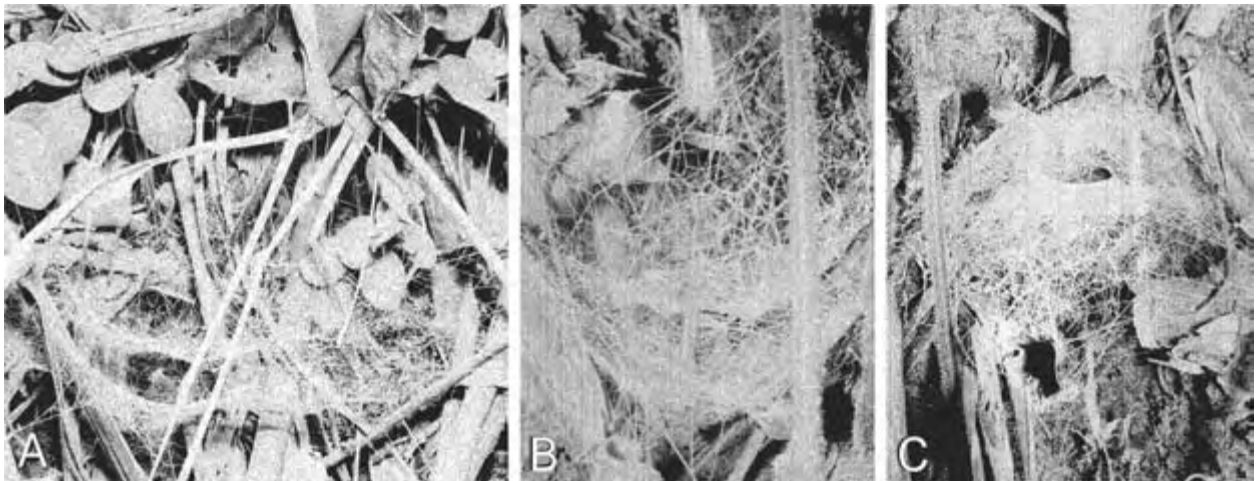


Figure 7 *Steatoda*. A. *S. moesta* #1213. The upper sheet extended into a tunnel, and the spider ran on the lower surface of this sheet; B (juvenile) #1200a sheet with tangle above, sheet below; C (juvenile) #1200b. Approximate widths of photos (cm): A 15; B 6; C not known.

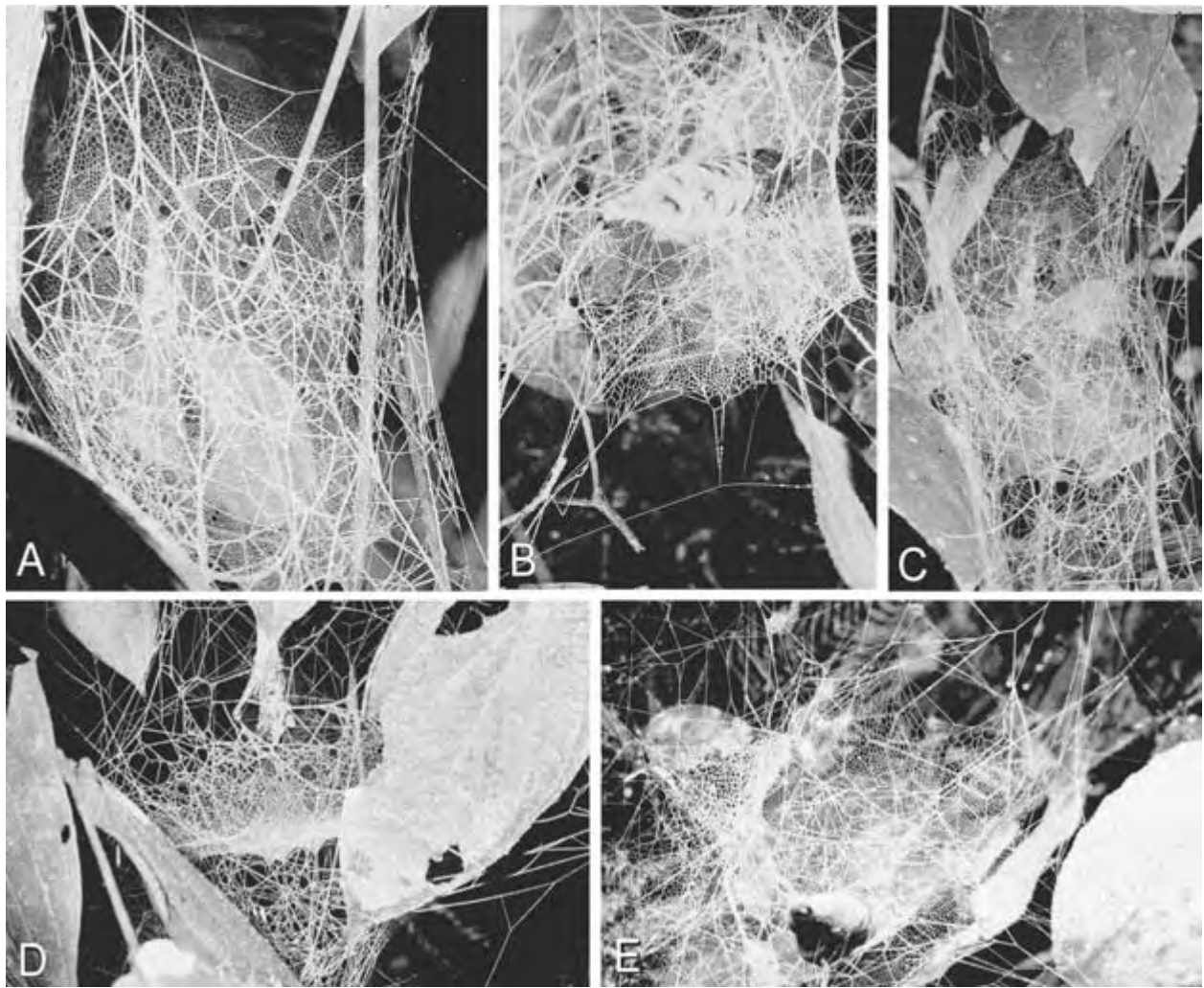


Figure 8 *Chrosiothes portalsensis*. The following observations were made on the webs in this and the next figure (Fig. 9). No sticky lines were noted in any of the webs, and each spider was in a curled leaf retreat that was suspended in the tangle above the sheet, with the opening facing downward. The sheets curved upward at their edges, and projected downward at each point where they were attached to lines running to the tangle below. The mesh sizes in the sheet were greater near the edges of the sheet. A #842. More-or-less dorsal view; B #961. More-or-less dorsal view (note leaf retreat in upper half of photo); C #842. Approximately dorsal view; D #842. Lateral view; E #957. Dorsal view (note leaf retreat near bottom of photo). Approximate widths of photos (cm): A 5.3; B 12; C 8.7; D 14.7; E 25.8.

morphology (Agnarsson, 2004) and molecules (Arnedo *et al.*, 2004) (see Methods). Tables 2 and 3 summarise the data in these figures with respect to evolutionary flexibility (Table 2) and convergence (Table 3).

Discussion

Homoplasy and intrageneric divergence

Figures 46–59 reveal two general patterns in the evolution of theridiid webs: striking evolutionary flexibility (Table 2); and rampant convergence (Table 3). For instance, an especially striking example of intrageneric divergence occurs in *Chrosiothes*. The webs of *Chrosiothes tonala* consist of only a few non-sticky lines that do not function as a trap, and which the

spider uses as bridges from which it attempts to drop onto columns of foraging termites. The web of *C. nr. portalsensis*, in contrast, is an elaborate trap composed of a dense, horizontal sheet with an extremely regular mesh that is at the lower edge of an extensive tangle (Figs 8, 9). Still another, apparently undescribed species of *Chrosiothes* also builds a reduced web, but it is a trap – a typical spintharine H-web (J. Coddington, pers. comm.). Two especially striking examples of convergence are the very strong, dense sheets covering gumfoot webs built in cracks or other sheltered sites by *Achaearanea* sp. nr. *porteri* #3609 (Figs 42, 43) and *Theridion melanurum* (Nielsen 1931); and the horizontal sheets of *Chrosiothes* sp. nr. *portalsensis* (Fig. 8) and *Achaearanea* sp. nr. *porteri* #3693, 3694 (Fig. 43 A–H), which share details such as upward directed ‘lips’ at the edges of the sheet, and downward projecting ‘pimples’ attached to lines running to the tangle below. It is

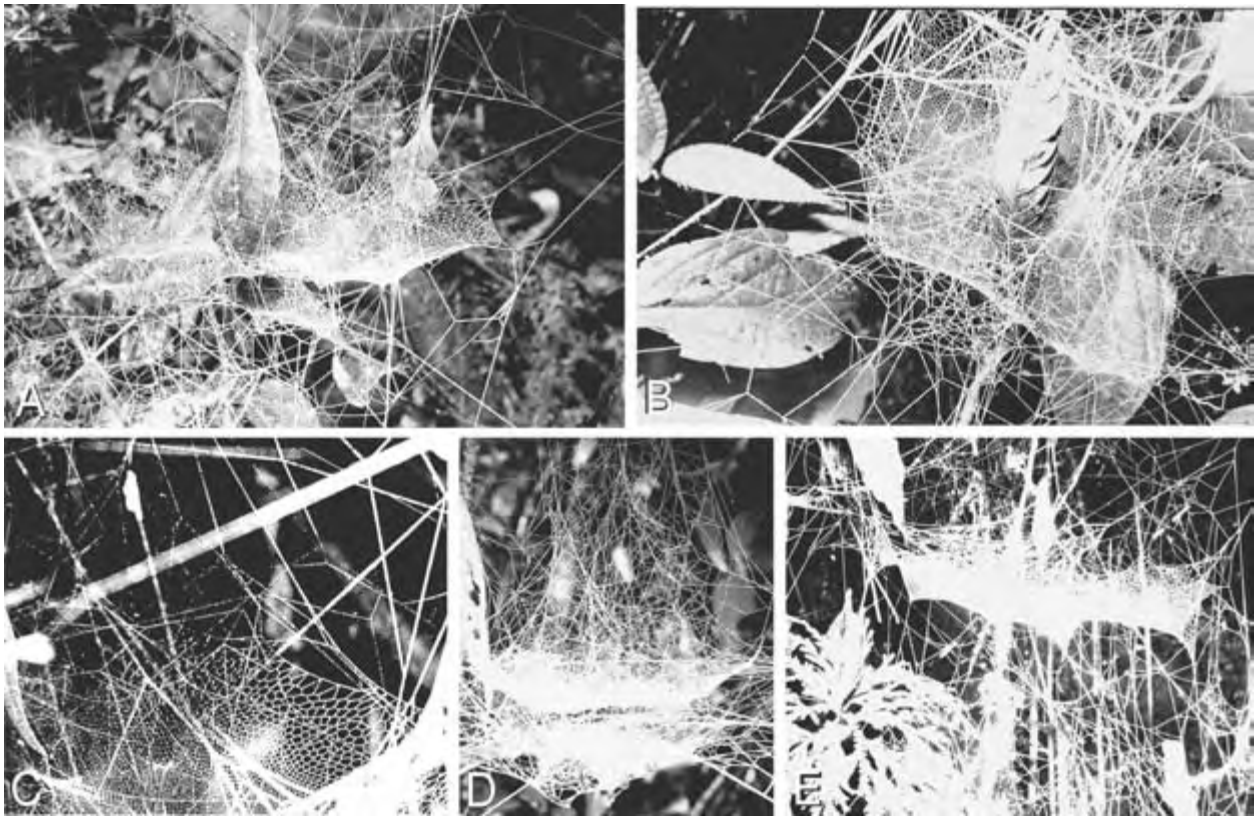


Figure 9 *Chrosiothes portalensis*. A #957. More-or-less lateral view; B #961. More-or-less dorsal view; C #958. Dorsal view of edge of sheet; D #960. Lateral view showing intact sheet above partially damaged (older?) sheet; E #958. Lateral view. Approximate widths of photos (cm): A 22.8; B 15.6; C 10.6; D 12.6; E 22.8.

interesting to note still further convergences on these same details in the distantly related *Diguettia albolineata* (Diguettidae) (Eberhard, 1967) and in *Mecynogea* and relatives (Araneidae) (Levi, 1997). The many alternative designs of aerial sheet webs in Linyphiidae (e.g. Fig. 1) and Pholcidae (Eberhard, 1992) show that these convergences are not due to mechanical constraints. Another striking recently discovered higher-level convergence with theridiid webs are the gumfoot webs of several species in the distantly related families Anapidae (Kropf, 1990) and Pholcidae (Japyassú & Macagnan, 2004).

The high frequency of homoplasy and intrageneric diversity in theridiid web characters can be illustrated quantitatively in several ways. The values of the consistency index (CI values, the minimum number of steps in a character/observed number of steps, conservatively counting multiple intrageneric polymorphisms as a single step) included for the web traits of this study were lower than the CI values of morphological traits for theridiids (Agnarsson, 2004); means were 0.299 ± 0.174 for webs, as compared with 0.467 ± 0.327 for female genitalia (13 traits), 0.569 ± 0.345 for male genitalia (82 traits), 0.588 ± 0.351 for spinnerets (22 traits), and 0.540 ± 0.343 for other body structures. Of 22 web traits, 5 had CI values ≤ 0.14 , while only 15 of 242 morphological traits had values this low ($\chi^2 = 7.3$, $df = 1$, $P < 0.0068$). These CI values for theridiid webs are also much lower than those of orb web characters, in which the mean was $0.634 + 0.262$ (see Kuntner, 2005, 2006).

Another indication of plasticity is that of the 22 web traits we distinguished, 14 varied intraspecifically (in 31 of the 165 theridiid species we analysed) (Table 2A); none of 223 morphological traits varied intraspecifically in the 53 theridiid species analysed by Agnarsson (2004) ($\chi^2 = 143$, $df = 1$, $P < 0.0001$), and only 2 of the 21 orb web characters varied intraspecifically in the analyses of Kuntner (2005, 2006) ($\chi^2 = 8.41$, $df = 1$, $P = 0.0037$), in 3 of the 32 species he analysed.

Still another indication of these same patterns can be seen by comparing the proportion of changes occurring on internal nodes, versus in terminal taxa, in the summary cladograms for web traits (Figs 46–47) and those for morphology and behaviour (Figs 103 and 104 of Agnarsson, 2004). Of the web character transitions in Figs 46–47, only approximately 25% occurred at internal nodes. A more realistic calculation, in which dummy taxa (which contain ‘false’ autapomorphies as they represent more than one taxon) were excluded, still gave only 59%. In contrast 92% of morphological and behavioural transitions were internal in the study of Agnarsson (2004). This indicates that change in web characters is more rapid than in morphological characters. It may seem that this comparison exaggerates the difference, as morphological phylogenetic studies typically exclude autapomorphic characters (characters changing only in a single terminal taxon). However, Agnarsson (2004) explicitly aimed to include such characters due to their potential use in future studies, and furthermore all our web

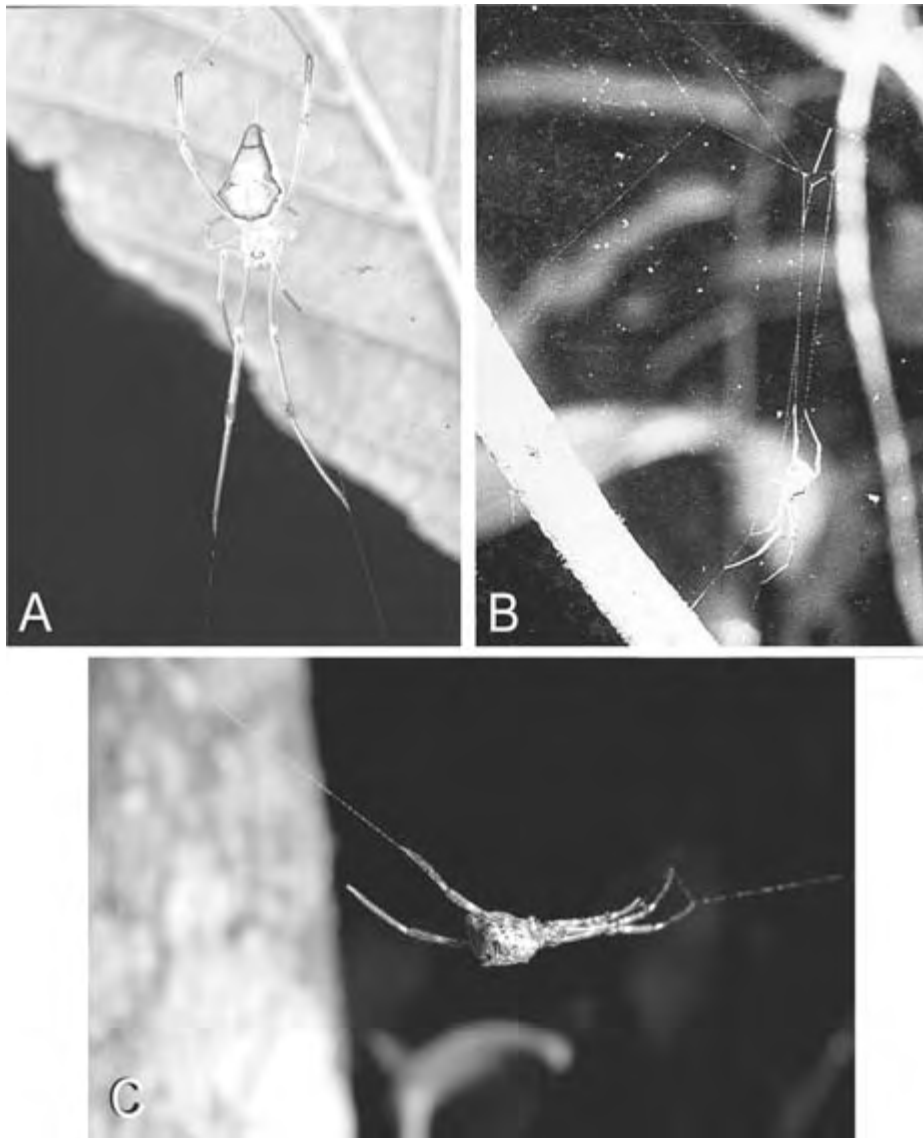


Figure 10 *Episinus* and *Spintharus*. A *Spintharus flavidus*, Photo: M. Stowe; B *Episinus cognatus* #878. The bottom tip of the line held by the spider's right leg I was sticky; C *Episinus* sp. Approximate widths of photos (cm): A 5; B not known; C 6.

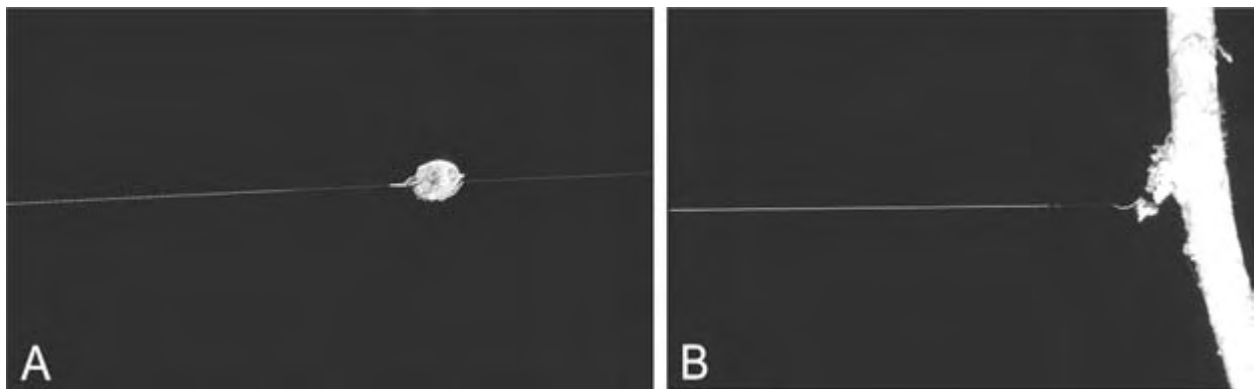


Figure 11 *Phoroncidia*. A P. sp. nov. (Chile). The single line was sticky only in the portion in front of the spider, starting about 1 cm away from it; B sp. nov. (Madagascar) the single line was sticky along its entire length, except the portion closest to the spider. Approximate widths of photos (cm): A 8; B 10.



Figure 12 *Kochiura* and *Selkirkiella*. A *Kochiura attrita*, no sticky silk was noted; B *Selkirkiella luisi*, no sticky silk was noted. Approximate widths of photos (cm): A 10; B 8.

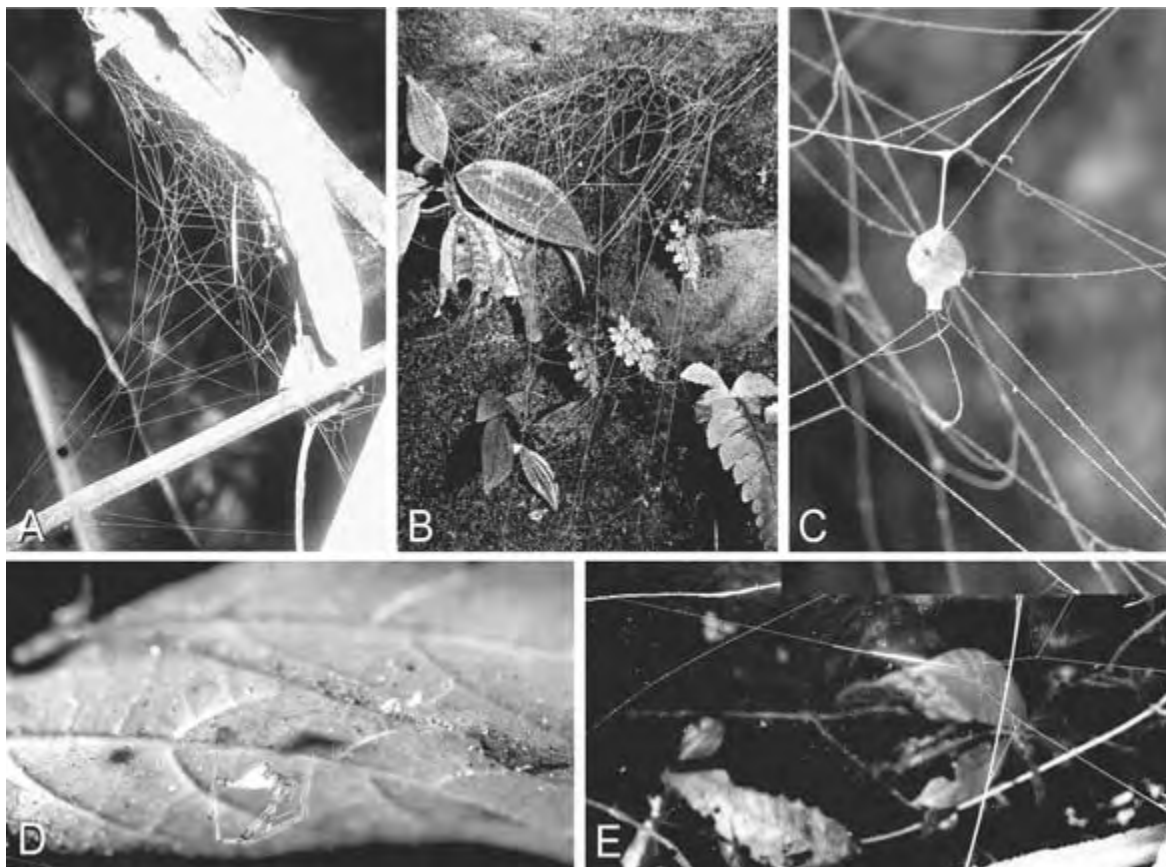


Figure 13 Argyrodoxinae. A *Ariamnes attenuatus* #2335 (egg sac web); B *Ariamnes juvenile* #3626; C *Argyrodes elevatus* (egg sac web), the egg sac was suspended in an irregular tangle of non-sticky lines attached to the barrier web of a *Nephila clavipes*; D *Rhomphaea draca*, a simple non-sticky tangle; E *A. attenuatus* #1764 ('thicker line' in upper centre is the spider). Approximate widths of photos (cm): A not known; B not known; C 2.5; D 9; E not known.



Figure 14 *Anelosimus*. A *A. studiosus* (Ecuador), subsocial web (single mature female with offspring); B *A. eximius* (Ecuador), social web (multiple adults); C *A. tosum*, subsocial web; D *A. guacamayos*, social web; E *A. eximius*, social web. None of the webs had noticeable sticky silk. In all of them, numerous inhabitants rested under live leaves or dead leaves suspended in the web. Approximate widths of photos (cm): A 35; B 80; C 60; D 85; E 120.

characters are potentially informative (not autapomorphic), as at least two states of each character occur in at least two taxa.

Behavioural characters in general do not tend to show greater levels of homoplasy than morphological traits in other groups (deQuieroz & Wimberger, 1993; Foster & Endler, 1999; Kuntner *et al.*, 2008). In 22 groups, including insects, arachnids, shrimp and vertebrates, the mean CI values for behavioural and morphological characters were, respectively,

0.84 ± 0.14 and 0.84 ± 0.12 (deQuieroz & Wimberger, 1993). This mean CI (representing a total of 128 behavioural traits in these 22 taxa) was significantly higher than the corresponding mean CI value for the 22 web traits of theridiids in this study (0.50 ± 0.31 , calculated as they did by excluding polymorphisms in terminal taxa from consideration; traits 6, 15, and 22 were excluded as they were constant or autapomorphic) ($t = -4.41$, $df = 25$, $P < 0.001$). Only three of the CI values for



Figure 15 *Anelosimus*. A A. *eximius* (solitary female); B A. *may*; C A. *eximius*, sheet; D A. *eximius*, tangle above sheet; E A. *eximius*, with prey; F A. *studiosus* #572; G A. *studiosus* (Florida). Approximate widths of photos (cm): A 10; B 35; C 14; D not known; E 8; F 8; G not known.

theridiid web traits were as high as the lowest value compiled by deQuieroz and Wimberger (1993).

One possibility raised by these results is that theridiid web traits reflect lower-level phylogenetic relations, for instance at the intrageneric level. Recent hypotheses for the phylogeny of *Anelosimus* (Agnarsson, 2006; Agnarsson *et al.*, 2007) and *Latrodectus* (Garb *et al.*, 2003) allowed us to test the possibility

that homoplasy in webs would be reduced if analyses were carried out at lower taxonomic levels. Many characters were invariable or uninformative within *Anelosimus*, but among those that did vary ($N = 4$), homoplasy was still rampant (mean $CI = 0.34$, minimum steps including the polymorphies).

The genus *Latrodectus* offers a second chance for an intrageneric analysis. Benjamin and Zschokke (2003)



Figure 16 *Anelosimus pacificus*. A a ventral view of tangle web with tiny, barely perceptible balls of glue among living leaves of a *Ficus* tree. Spider is visible crouching under leaf in lower portion of web. Approximate width of photo 11 cm.

implied that web design in this genus is uniform (they refer to ‘the *Latrodectus*-type web’), but in fact webs in this genus are quite variable with respect to the presence/absence of sticky lines, the sites where sticky lines occur, and the presence and forms of sheet-like structures (Table 1, which is available as ‘Supplementary data’ on Cambridge Journals Online: http://www.journals.cup.org/abstract_S1477200008002855). The recent study of Garb *et al.* (2003) provides a partially resolved molecular phylogeny. Analysis of the eight variable, non-autapomorphic web characters on this tree also showed considerable, though somewhat reduced homoplasy (mean CI = 0.59). However, most of the variation represented polymorphisms; only two of the changes were synapomorphic (domed sheet for *L. bishopi* plus *L. varians*, and lack of sheet for *L. mactans* plus *L. indistinctus*). In summary, the preliminary analyses possible at the moment show that web characters also show extensive, though possibly somewhat reduced, homoplasy at the intrageneric level.

The patterns of high diversity and common homoplasy are particularly striking in light of our present degree of ignorance of the webs of most theridiids. Ignorance is likely to result in underestimates rather than overestimates of both homoplasy and intrageneric differences. In fact, the increase in knowledge resulting from this study may explain why the CI values reported here for webs are lower than those for the four web characters analysed in Agnarsson (2004) (mean = 0.560 ± 0.350). One trait was the same in both studies (snare vs. non-snare web); the CI value in this study was 0.20, while it was 1.00 in the previous study.

There is still another reason to suspect that we have underestimated convergences. We did not determine some character states for all species. For instance, due to limitations of photographs and the lack of additional observations, we were only able to check for a radial array of lines

from the mouth of the retreat (character 13–1) for some species; we also suspect literature accounts were incomplete. Incomplete scoring of this sort will lead to underestimates of homoplasy.

It is also interesting to compare the different web traits in this study among themselves. Five were especially inconsistent: presence/absence of sticky silk (#1; CI = 0.06); snare with or without sheet (#11; CI = 0.07); gumfoot lines with glue at tip (#3; CI = 0.14) or away from tip (#4; CI = 0.11); and how spider altered resting site (#18; CI = 0.08). All five traits show both intrageneric and intraspecific variation (Table 2). Other highly homoplastic traits included site where the spider rests (#17; CI = 0.19); whether or not the resting site was altered by the spider (#19; CI = 0.26); and form of the sheet (#12; CI = 0.37).

Given the apparently minor behavioural modifications needed to produce transitions in traits such as whether and how resting sites were altered (traits #18, 19), and the site where spider rests (#17), the great plasticity in these traits is not surprising. On the other hand, transitions in some of the other especially homoplasious traits would seem to require substantial behavioural reorganisation such as snares with and without sheets (#11), and the form of the sheet (#12). The high homoplasy in the inclusion of sticky silk in the web (#1) is also surprising, but for a different reason. Sticky silk per se need not be acquired and lost, as it is consistently used by theridiids for wrapping prey (Agnarsson, 2004; Barrantes & Eberhard, 2007). But the presence or absence of sticky lines would presumably have a large influence on the abilities of different web designs to capture prey, and thus be likely to affect the function of multiple web characters. Similarly, the distribution of sticky material along lines (#11, CI = 0.17) probably has a large impact on the web’s ability to retain prey (lines with sparsely spaced small balls of glue, as in the synotaxids *Synotaxus* spp. and in *Theridion hispidum* and *T. nr. melanostictum*, are only barely adhesive, and presumably function only with weak-flying and perhaps long-legged prey such as some nematocerous flies). Again, this would seem likely to affect the functionality of multiple web characters.

Homoplasy and selective advantages

Some convergences in web traits are presumably related to similar selection pressures in different evolutionary lines. For example, several convergences in Table 3 that are related to the site where the spider rests during the day and its position there seem likely to be the result of selection to avoid being preyed upon by visually orienting predators. Many of these represent traits that have also evolved convergently in other non-theridiid web building spiders: use of small pieces of detritus to construct an inverted cone or cup in which the spider rests (convergent with the araneid *Spilasma artifer* – Eberhard, 1986); use of a curled dry leaf into which the spider’s body just fits and that is suspended in the web (convergent with the araneid *Phonognatha* spp. – McKeown, 1952; Hormiga



Figure 17 *Meotipa*, *Wamba* and *Theridula*. A *Meotipa* nr. *pulcherrima* #3678. Lateral view. No sticky lines were noted. The spider was under the leaf where the mesh of the tangle was smaller; B *Theridula* sp. nov. #3673. Lateral view (without powder). Many lines were sticky along their entire length. The spider rested on the underside of the leaf, where the mesh of the tangle was especially small; C *Wamba* sp. #2862. Lateral view. Most if not all long and medium long lines were sticky along their entire length. The spider was in a retreat under the leaf at the top.; D *Theridula* sp. nov. #3673. Lateral view of the same web in B (coated), with white powder; E *Theridula* sp. nov. #3695. Lateral view. All or nearly all lines were sticky. The spider rested on the underside of the large leaf at the top. Approximate widths of photos (cm): A 23.4; B not known; C 17.6; D 18; E 24.

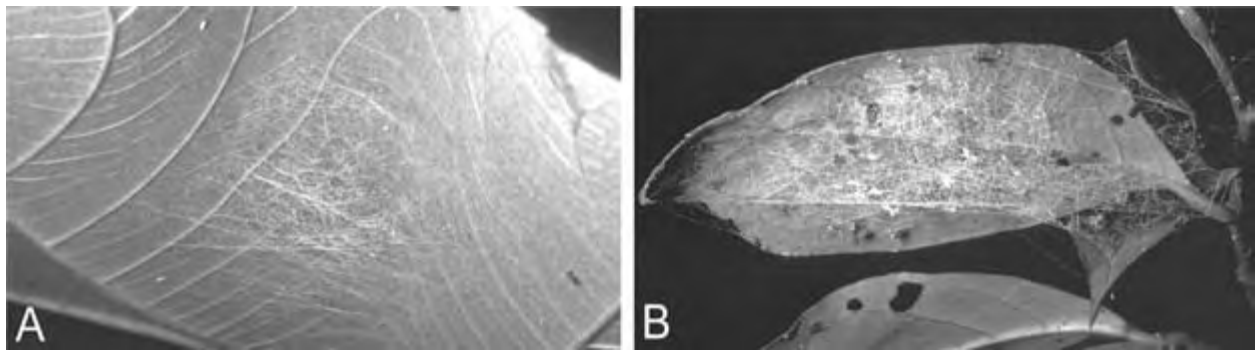


Figure 18 *Cephalobares*. A–B *Cephalobares* sp. nov. flat sheets on the undersides of leaves (photos by J. A. Coddington). Widths of photos not known.

et al., 1995; Kuntner *et al.*, 2008); and curling living leaves to form a conical retreat (convergent with *Araneus expletus*) (Eberhard, 2008) (this trait may also be associated with changes in defensive behaviour: when *Theridion evexum* is disturbed in its curled leaf retreat, it crawls into the closed end of the cone instead of dropping to the ground as many other theridiids do (Barrantes and Weng, pers. comm.)). Further traits not discussed here, involving adoption of cryptic resting postures in species lacking retreats, are also convergent with many araneids and uloborids. The variety and ubiquity of such theridiid defence structures testify to apparently strong and widespread selection to defend against visually orienting predators. The secondary loss of a modified retreat in the cave spider *Theridion bergi* (Xavier *et al.*, 1995) and the green colour of the synotaxids *Synotaxus* spp., which closely mimics the leaves where they rest, offer further support for the hypothesis of defence against visual predators.

This conclusion contrasts with the argument of Blackledge *et al.* (2003) that the tangles of theridiid webs represent an effective defence against an especially important group of predators, the visually orienting sphecids wasps. Their argument is based on prey lists of sphecids, in which theridiids are under-represented with respect to orb weavers. The causal relation with tangle webs is not clear, however. Tangle webs do not serve to defend against another group of similar-sized hymenopteran enemies that attack spiders in their webs. The polysphinctine ichneumonids (Gauld *et al.* 1998), parasitise typical orb weavers (e.g. *Argiope*, *Alloccyclosa*, *Cyclosa*, *Plesiometra*, *Leucauge* – Nielsen, 1923; Eberhard, 2000a; W. Eberhard and B. Huber, in prep.), a nephilid with a sparse tangle (*Nephila*) (Fincke *et al.*, 1990), an araneid that rests in a dense tangle web (*Manogea* sp.) (W. Eberhard unpub.), several theridiids in which the spider rests in a tangle web, including *Achaearanea* (= *Theridion*) *lunata*, *Theridion melanurum* (= *denticulatum*) (Nielsen, 1931), *Keijia* (= *Theridion*) *tincta* (Bristowe 1958), *Anelosimus* spp (J.-L. Weng unpub.; W. Eberhard unpub.; Agnarsson, 2005, 2006; Agnarsson & Kuntner, 2005; Agnarsson & Zhang, 2006), and also linyphiids (Gauld *et al.*, 1998). The contrast between the wealth of theridiid defensive structures and the near absence of such modifications in the sheet webs of linyphiids (both

with and without tangles) (e.g. Nielsen, 1931; Comstock, 1967), and of cyatholipids (Griswold, 2001) is clear, and is puzzling.

The ancestral web of Theridiidae

What is the ancestral theridiid web form? Answering this question is difficult because current phylogenies do not agree on the most immediate outgroups for Theridiidae. Morphological analyses consistently suggest that Nesticidae is sister to Theridiidae, and that these two together are sister to Cyatholipoidea (including Synotaxidae) (Griswold *et al.*, 1998; Agnarsson, 2003, 2004). Details of prey attack behaviour (leg movements and wrapping silk), which are not included in these analyses, favour the same associations (Barrantes & Eberhard, 2007). In contrast, the limited available molecular evidence suggests that the sister group of Theridiidae contains Synotaxidae and a combination of sheet and orb weaving families (Arnedo *et al.*, 2004). The traits of synotaxid webs provide little help in understanding ancestral theridiid webs. The resting site of synotaxids apparently varies. In *Synotaxus* spp. the spider rests against a leaf at the top of the web with a small approximately cylindrical or slightly conical ‘tangle’ around the spider (Eberhard, 1995; Agnarsson, 2003, 2004), while in *Pahoroides whangerei* it apparently rests on the underside of the domed sheet (Griswold *et al.*, 1998). No known synotaxid web design is shared with any theridiid: a rectangular orb web as in *Synotaxus* spp.; a domed sheet with a sparse tangle as in *Pahoroides whangerei* (Griswold *et al.*, 1998); or a simple domed sheet as in *Chileotaxus sans* (Fig. 3F; Agnarsson, 2003). The webs of other synotaxid genera are as yet only poorly described: ‘a sheet, which may be irregular or an inverted bowl’ (Griswold *et al.*, 1998 on *Mangua* and *Runga*; Forster *et al.*, 1990 on *Meringa*).

The webs of nesticids, on the other hand, resemble the webs of some theridiids. Agnarsson (2004) argued, on the basis of outgroup comparisons with the nesticids *Nesticus celulanus* (Bristowe, 1958) and *Eidmanella pallida* (Coddington, 1986), which have gumfoot lines that fork one or more times near their tips, that gumfoot webs are probably ancestral for

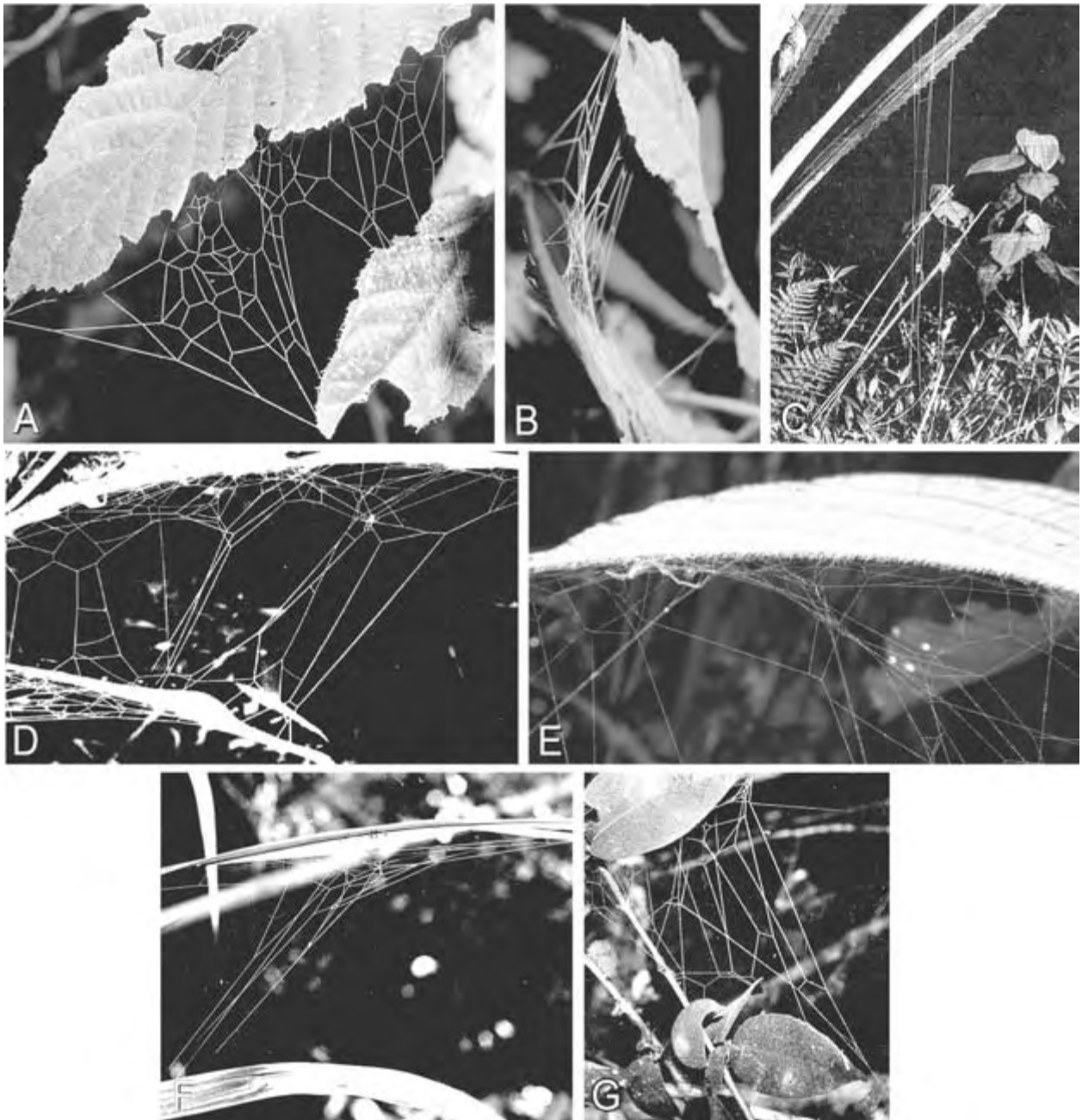


Figure 19 *Chrysso*. A–B *C. volcanensis* #3252. All or nearly all lines were sticky (A lateral view, B dorsal view). The web was nearly planar, and nearly perfectly vertical. The spider rested at the top under the leaf; C *C. ecuadorensis* #703. Each of the long, nearly vertical lines was sticky along its entire length except for about 20 cm at the bottom. The spider rested at the top, against the underside of the leaf; D *C. sulcata* #1416 (lateral view). All lines were sticky except short lines in the tangle near the underside of the leaf where the spider rested with its smooth, white, teardrop shaped egg sac. Other nearby webs varied substantially in form, but all had long lines covered with sticky balls along most or all of their length; E *C. sp. nov. nr. volcanensis* (Ecuador); F *C. nr. vexabilis* #150. Lateral view. Photo was taken after web had been jarred to remove cornstarch from non-sticky portions of lines; nearly all lines were sticky along most or all of their length (note short non-sticky stretch near tip of lowest line). The spider rested along with its egg sac against the underside of the upper leaf; G *C. vallensis* #2154. Dorso-lateral view. All lines were sticky along their entire length except short lines in the tangle just under the leaf where the spider rested. There were further sticky lines projecting from near the far side of the leaf that are more-or-less hidden from view. The web of another individual had all long sticky lines attached to the same leaf as the tangle, and its entire web was thus very close to the plane of the leaf. The spider rested against underside of leaf, with spiderlings. Approximate widths of photos (cm): A 9.5; B not known; C 56; D 15.3; E; F 20.2; G 8.1.

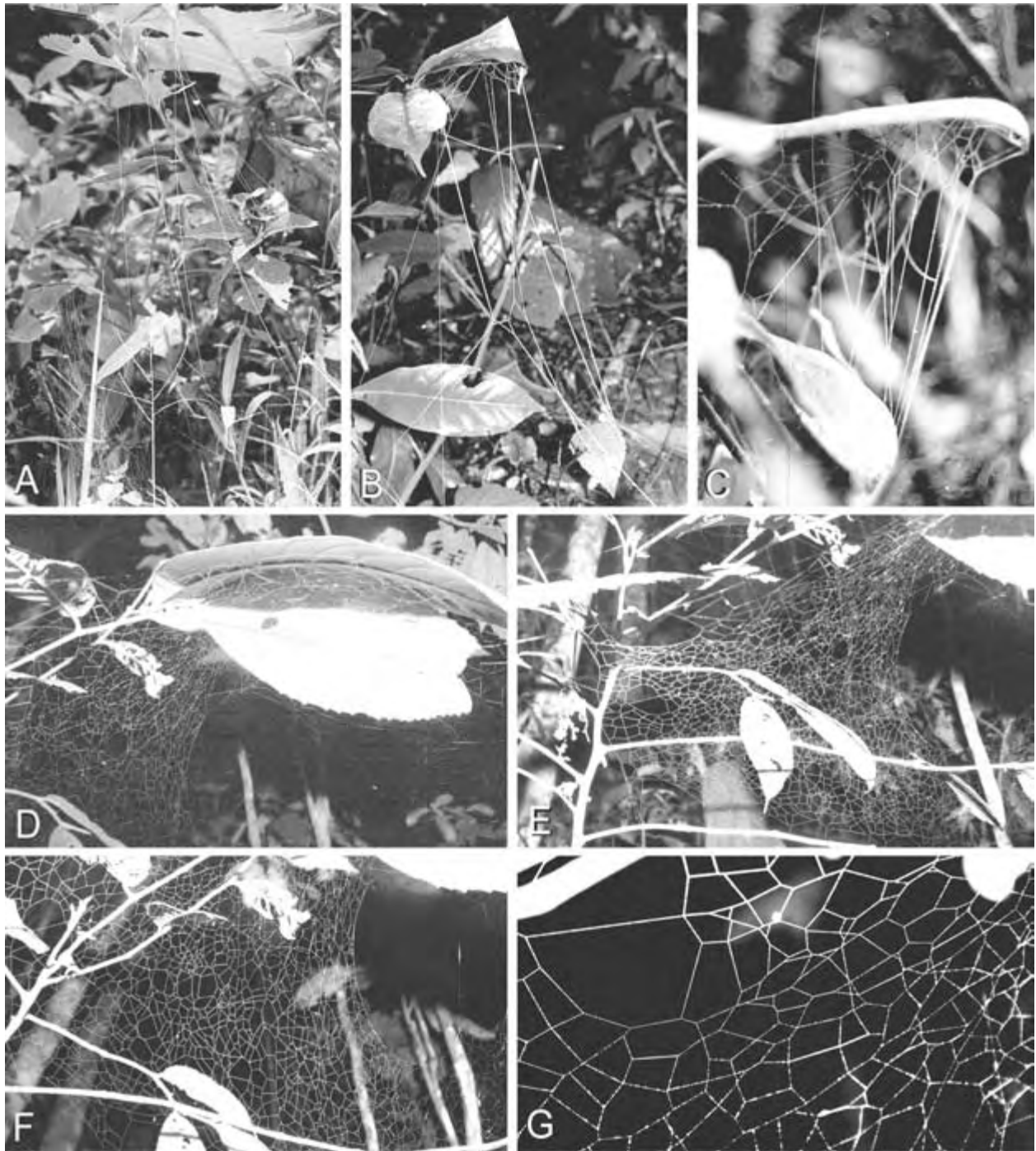


Figure 20 *Chrysso* and *Theridion*. A *Theridion evexum* #FN21–103. Lateral view. All long lines were sticky along most or all of their length; B *T. evexum* #FN21–105. Lateral view. All long lines were sticky along most or all of their length. Spider rested in the curled leaf at the top; C *C. nigriceps* #250. The spider rested under leaf at top with cluster of spiderlings; D–G *C. nr. nigriceps*. Nearly all lines were sticky. Approximate widths of photos (cm): A 16.7; B 23.6; C 13.1; D about 25 cm; E about 20cm; F about 10cm; G about 3 cm.

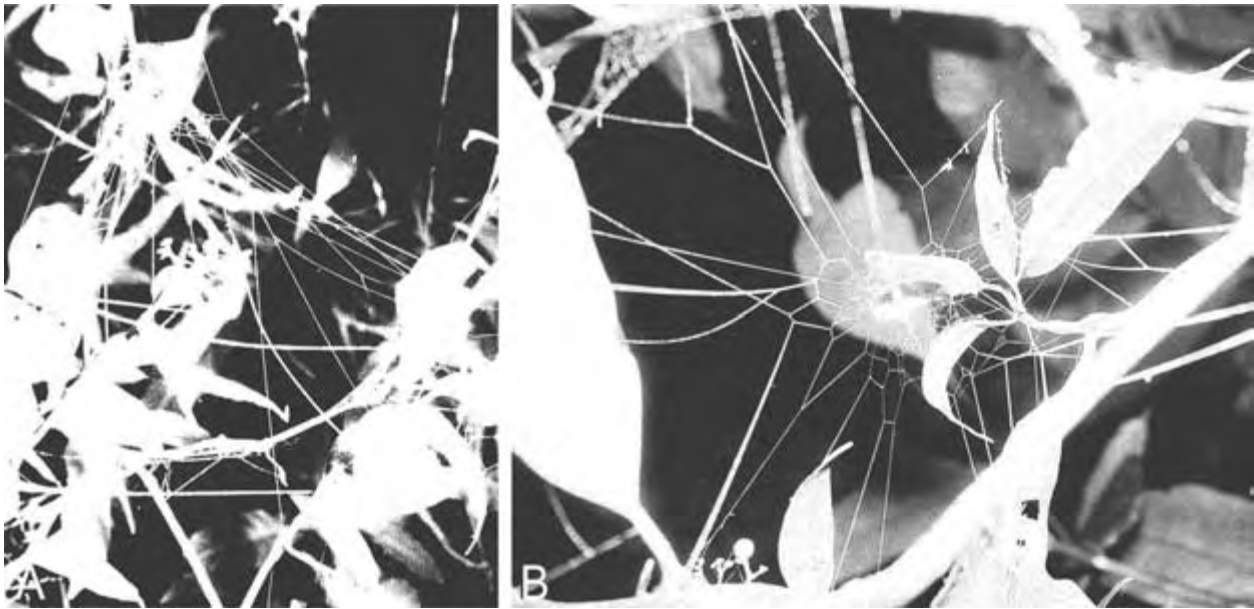


Figure 21 *Chryso*. A–B *C. diplostycha* #1220. Lateral (A) and ventral (B) views of the same web. All or nearly all lines were sticky along most or all of their length. Approximate widths of photos (cm): A 18; B 12.

theridiids. Our discovery of the web of the nesticid *Gaucelmus calidus* weakens this conclusion (although, as we will explain, we still believe it is the most likely). The *G. calidus* web (Fig. 5) has long sticky lines, most of which are nearly vertical, and attached directly to the substrate below. But the distribution of sticky balls is clearly not that seen in the gumfoot webs of other nesticids. Nearly the entire length of each of the long vertical lines was covered with glue balls, and some of these lines even lacked balls at the tip (and thus had the mirror image of the distribution of glue in typical theridiid gumfoot lines). Only a small minority of the long sticky lines were forked near their bottom ends, and young spiders did not make more forked lines (J.-L. Weng, pers. comm.), as might be expected if this trait is ancestral (Eberhard 1990a). There is a very small tangle of non-sticky lines above, where the spider rests against the underside of a sheltering rock. The web of this species is thus quite similar to those of some *Chryso* (Figs. 19C, F, G), *Wamba* sp. (Fig. 17C), *Theridion evexum* (Fig. 27E), *T. nigroannulatum* (Avilés *et al.*, 2006), *Theridula* (Fig. 17B), and that of the araneid *Eustala* sp. which makes simple webs of planar lines that are sticky along most of their length and radiate from a live leaf retreat (I. Agnarsson, unpub.). Forks near the lower ends of the sticky lines also occur in the adhesive lines of the theridiid *Neottiura* sp. (Fig. 31), although these lines were not vertical, but rather nearly parallel to the surface of a leaf and were sometimes covered only at their distal portions with sticky balls. Nevertheless, both morphological and molecular data (Agnarsson, 2004; Arnedo *et al.*, 2004) suggest that these theridiid genera (*Chryso*, *Theridion*, *Theridula*, and *Neottiura*) nest deeply within Theridiidae, arguing in favour of convergent origins of these aspects of their

webs with the webs of the nesticid *G. calidus*. In summary, several types of webs are now known in Nesticidae, and different nesticid webs resemble the webs of different groups of theridiids. The presence of a gumfoot web in an anapid and several pholcids (Kropf, 1990; Japyassú & Mecagnan, 2004), families that are thought to be only distantly related to theridiids or to each other, gives further reason to suppose that convergences on webs with sticky tips where the lines are attached to the substrate have occurred. The web of the anapid differs from all known theridiid gumfoot webs in having a tiny, nearly planar tangle where the spider rests, and multiple attachments of the gumfoot lines to the substrate (giving the impression that these lines do not function by breaking away from the substrate, as occurs in at least some theridiid and pholcid gumfoot webs – e.g. Bristowe, 1958; Japyassú & Macagnan, 2004).

Another possible source of clues for determining the derivation of web traits are ontogenetic changes, because juvenile spiders tend to make less derived web forms than those of adults (Eberhard, 1990a). Four traits in this study showed ontogenetic changes. Mature *Latrodectus* and *Steatoda* spiders consistently make a retreat at the edge of the web rather than in the tangle, while young juveniles of *L. tridecimguttatus* make a retreat in the tangle (Szlep, 1965). The retreats of these juveniles are made only of silk, while those of older individuals include detritus. This implies that the common ancestor of the latrodectines and some other theridiids made retreats in the midst of the mesh, and that the retreats in protected cavities or retreats built at the edges of the webs and with detritus were derived independently in latrodectines, and in some *Theridion*, such as *T. bergi* (Xavier *et al.*, 1995).

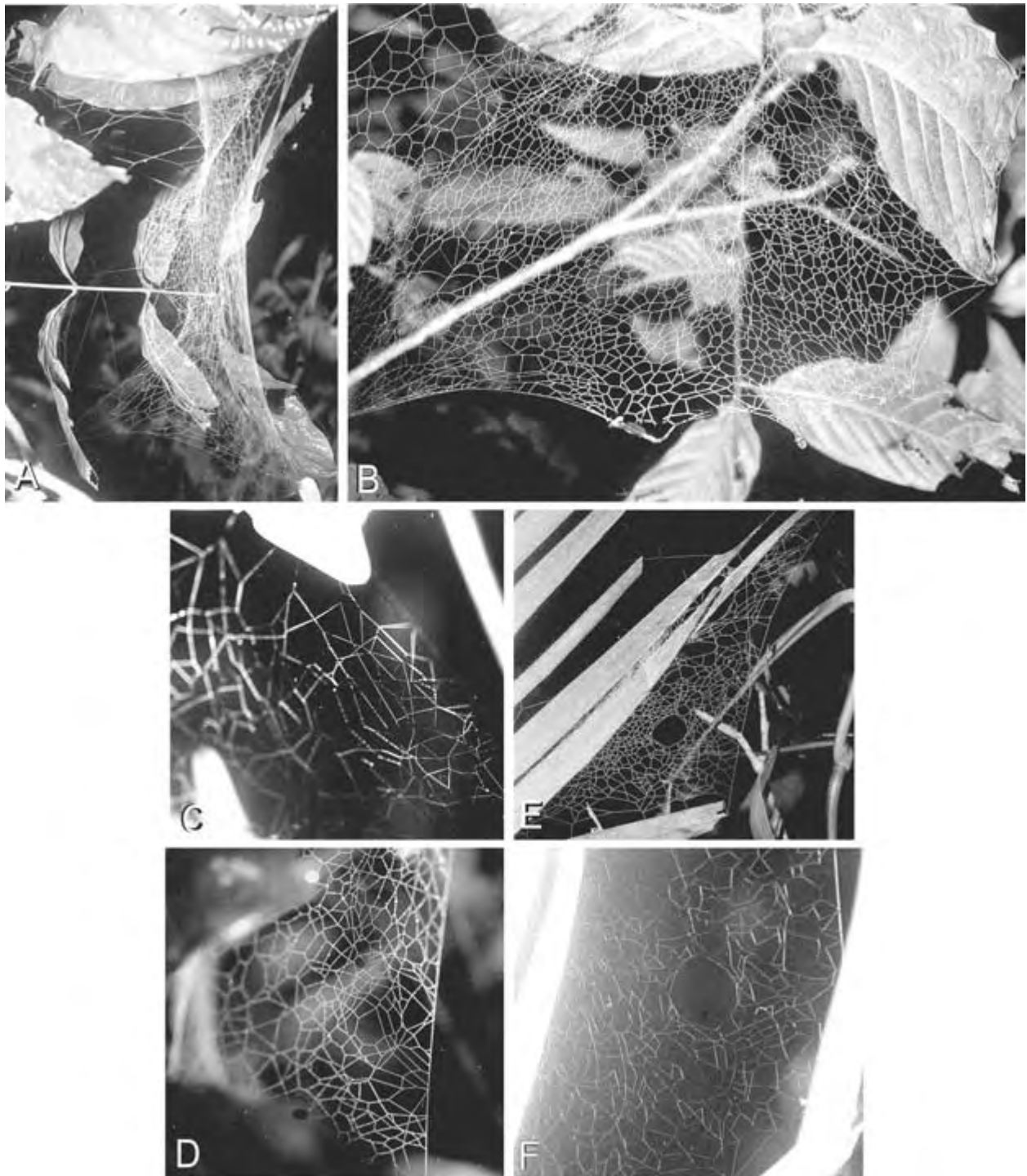


Figure 22 *Chryso*. A–D *C. cf. cambridgei* #2887 Lateral (A) and dorsal (B) views. The spider rested with many spiderlings when the sheet curved upward; C–D Close-ups of the same area of the sheet without (C) and with (D) white powder, showing that only a fraction of the lines in the sheet were sticky; E *C. cf. cambridgei* #3373. The spider rested near a prey on which many spiderlings were apparently feeding. Nearly planar web with a circular hole in which many but not all lines were sticky; F *C. cambridgei* #3372. Close-up of one of three more-or-less circular holes in a nearly planar web without powder; the lines that are brighter were sticky. Spider was under a leaf at the left edge. Approximate widths of photos (cm): A 22.3; B 17.4; C not known; D not known; E 25.3; F 13.3.

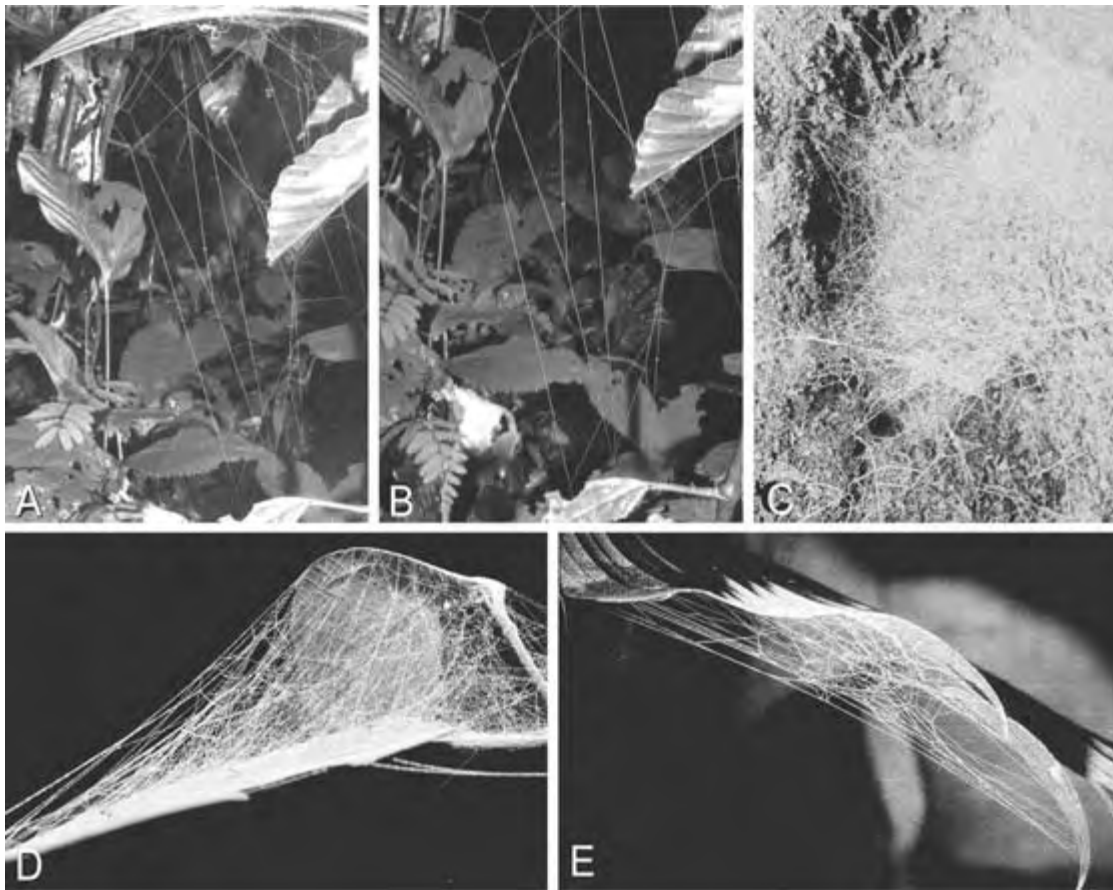


Figure 23 *Helvibis* and *Keijia*. A–B *Helvibis* nr. *thorelli*, long lines were sticky along most of their lengths; C *Keijia* sp. #1192. There were no sticky lines, at least in the outer two-thirds of the web. The spider rested with its egg sac; D *Keijia* nr. *tincta* #1267. Approximately lateral view. There was a small sheet between leaves, and a retreat at the base of a leaf with a few pieces of detritus on its sides; E *Keijia* sp. n. #2331. Lateral view. Lines on the edge of the web were almost all either completely covered with glue, or with apparent globs of glue as if they had been rained on. The spider was under the leaf, holding an egg sac on one leg IV. Approximate widths of photos (cm): A 8; B 6; C 3.1; D 10; E 15.7.

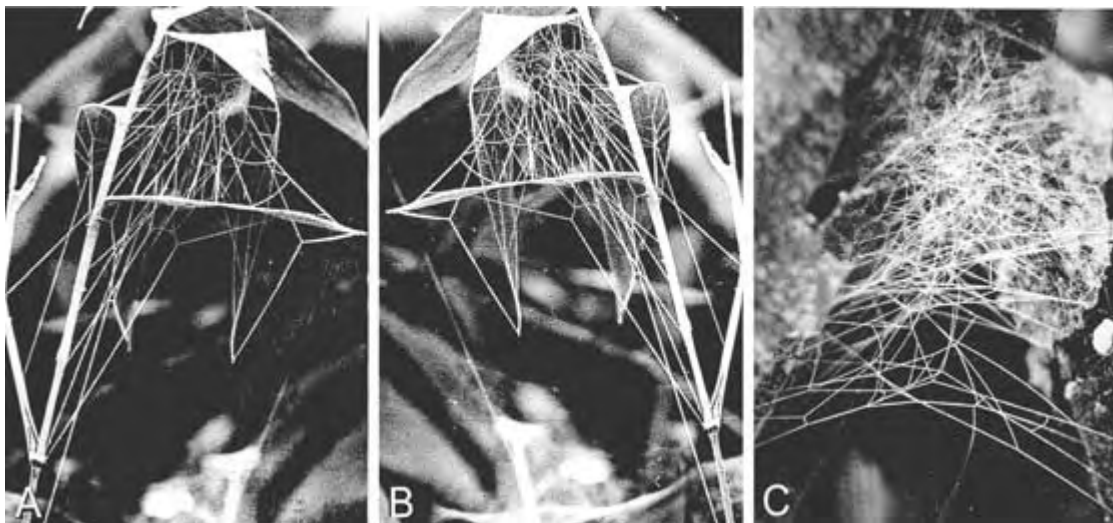


Figure 24 *Ameridion*. A–B A. sp. 1 #157. Lateral views of the same web. The tips of some of the longer lines to the leaf below were sticky. The spider rested under the top leaf; C A. sp. 2 #409. Approximately lateral view of web between branches. None of the lines to the substrate which were tested by scraping off the powder were sticky, but not all lines were tested. The spider rested with her egg sac attached to her spinnerets. Approximate widths of photos (cm): A 7.8; B 7.8; C 8.9.

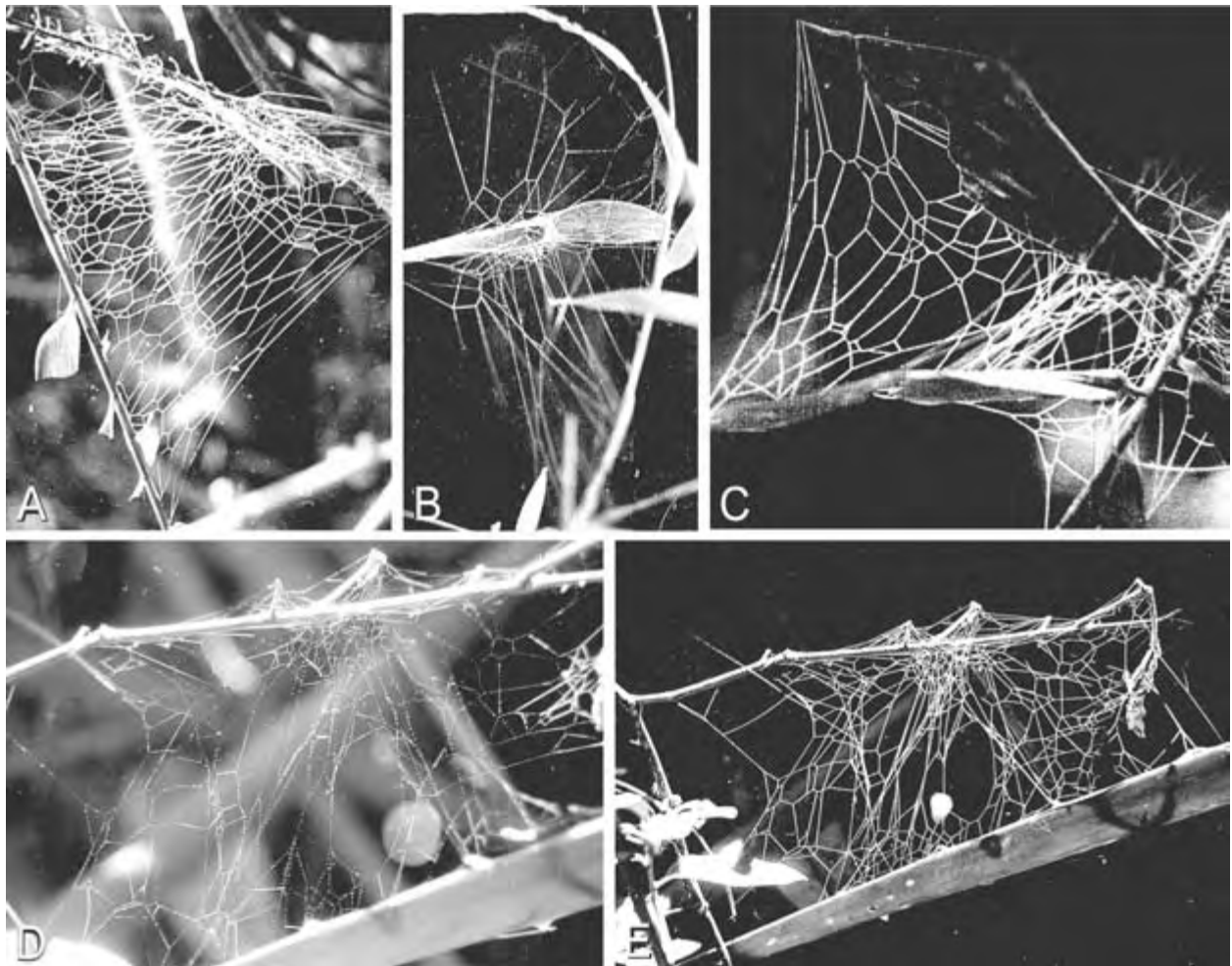


Figure 25 *Theridion hispidum*. A #41. Lateral view. Most of the longer lines were planar, with dots of stickiness; B #268. Ventral view. Most long lines have relatively evenly spaced sticky balls. Spider in curled leaf with egg sac; C #204. Lateral view. All long lines with drops every several mm, and in some places planar; D–E #294. Lateral views of the same web without (D) and with (E) white powder; the lines with sticky material (bright dots in D) were nearly planar. Approximate widths of photos (cm): A 21.3; B 6.5; C 17.7; D 19.7; E 27.9.

A second ontogenetic change occurs in *Theridion melanurum*. After making typical gumfoot webs early in the summer in Denmark, they later build webs with a thick, cylindrical sheet around the entire web (which still has gumfoot lines, at least in webs in Tyrol) when the female has an egg sac (Nielsen, 1931). The possible coordination between having an egg sac and having this presumably derived wall around the web supports the hypothesis that this strong sheet, and those of *A. apex* (Fig. 35) and *A. nr. porteri* #3609 (Fig. 42 G, H) are derived, and function as protection. A third case of ontogenetic changes occurs in *Achaearanea lunata*, in which juveniles make typical gumfoot webs with extensive tangles, while adult females omit the gumfoot lines (Nielsen, 1931). This transition is in accord with the idea that the gumfoot web is more plesiomorphic than a web lacking sticky lines, at least within this genus. Finally juvenile *Enoplognatha ovata* apparently do not make a retreat by fastening together leaves, as do penultimate

and mature adults (Nielsen, 1931), again suggesting that ancestral forms did not build modified retreats. All of these conclusions from ontogeny are in accord with our analyses (Figs 46–47).

Egg sacs and their webs

We focused on prey capture webs and their retreats, and have not attempted to compile information on egg sac structure, or on the structures that spiders build specifically to shelter egg sacs. It is clear that egg sac webs are sometimes complex, and distinct from prey capture webs (Agnarsson, 2004). It is possible that egg sac webs may have had important evolutionary relationships with prey capture webs. Thus *Anelosimus vittatus* folds a leaf and spins a delicate web over herself and her eggs that is provided with abundant globules of glue as in its prey capture web (Nielsen, 1931). In contrast, *Steatoda*

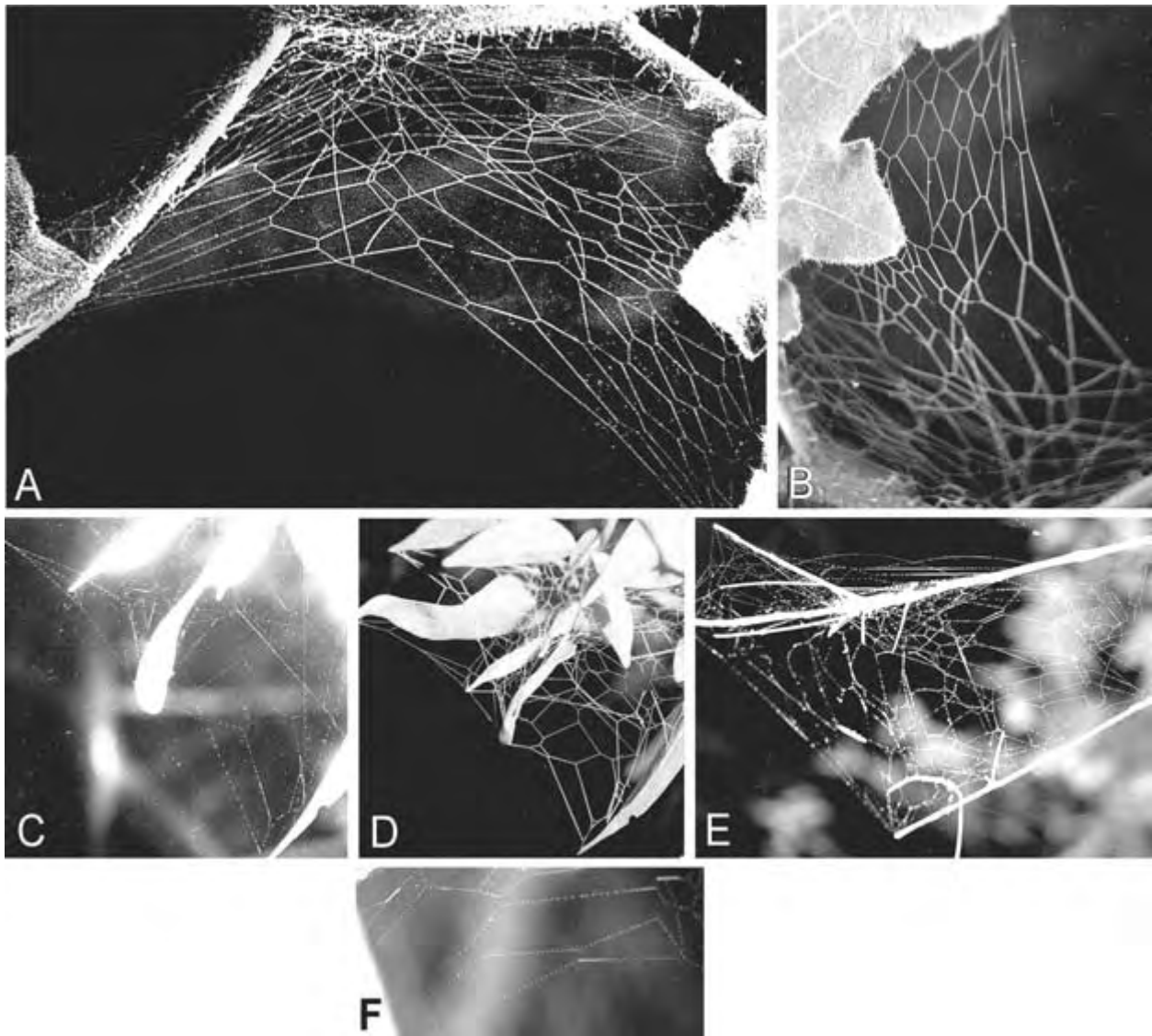


Figure 26 *Theridion*. A–B *T. hispidum* #295. Approximately lateral views. Long lines that had dots of stickiness were connected by short lines lacking stickiness (as in F). The spider rested in the tangle near the branch; C–D *T. hispidum* #673. Lateral views of the same web without (C) and with (D) white powder, showing (in C) the spots of glue on some but not all lines. The spider rested under a leaf; E *T. melanosticum* #3736. Lateral view (without powder). Some sticky were apparently fresh, with regularly spaced small balls of sticky material, while others were apparently older, with less even spacing. This web was relatively planar, probably because it was between two straight branches; other nearby webs were less planar; F *T. melanosticum* #3737. Close-up of long lines with dots of sticky material that were connected by short lines non-sticky lines (without powder). Approximate widths of photos (cm): A 24.4; B not known; C 4.5; D 6.4; E 14; F 6.8.

bipunctata has a dense sticky tangle around the egg sac, in this case with single isolated droplets rather than the closely spaced droplets of glue as in their prey capture webs (Nielsen, 1931). *Latrodectus geometricus* also places sticky lines around its egg sacs (G. Barrantes, pers. comm.). The use of sticky silk could be derived from its use in prey capture webs, or vice versa, and further study is needed to elucidate possible relations. Egg sacs themselves are also diverse (Agnarsson, 2004 on *Theridion*, *Faitidus*, *Selkirkiella* and *Synotaxus*), and are useful in distinguishing species in some theridiids (e.g. Abalos

& Baez, 1966 on *Latrodectus* and Exline & Levi, 1962 on argyrodines).

Comparing web evolution of theridiids and other orbicularians

The webs of theridiid spiders appear evolutionarily flexible when compared with those of linyphiids, araneids and nephilids. In araneids, for example, where there is a more extensive sample of the webs, the early impression was that

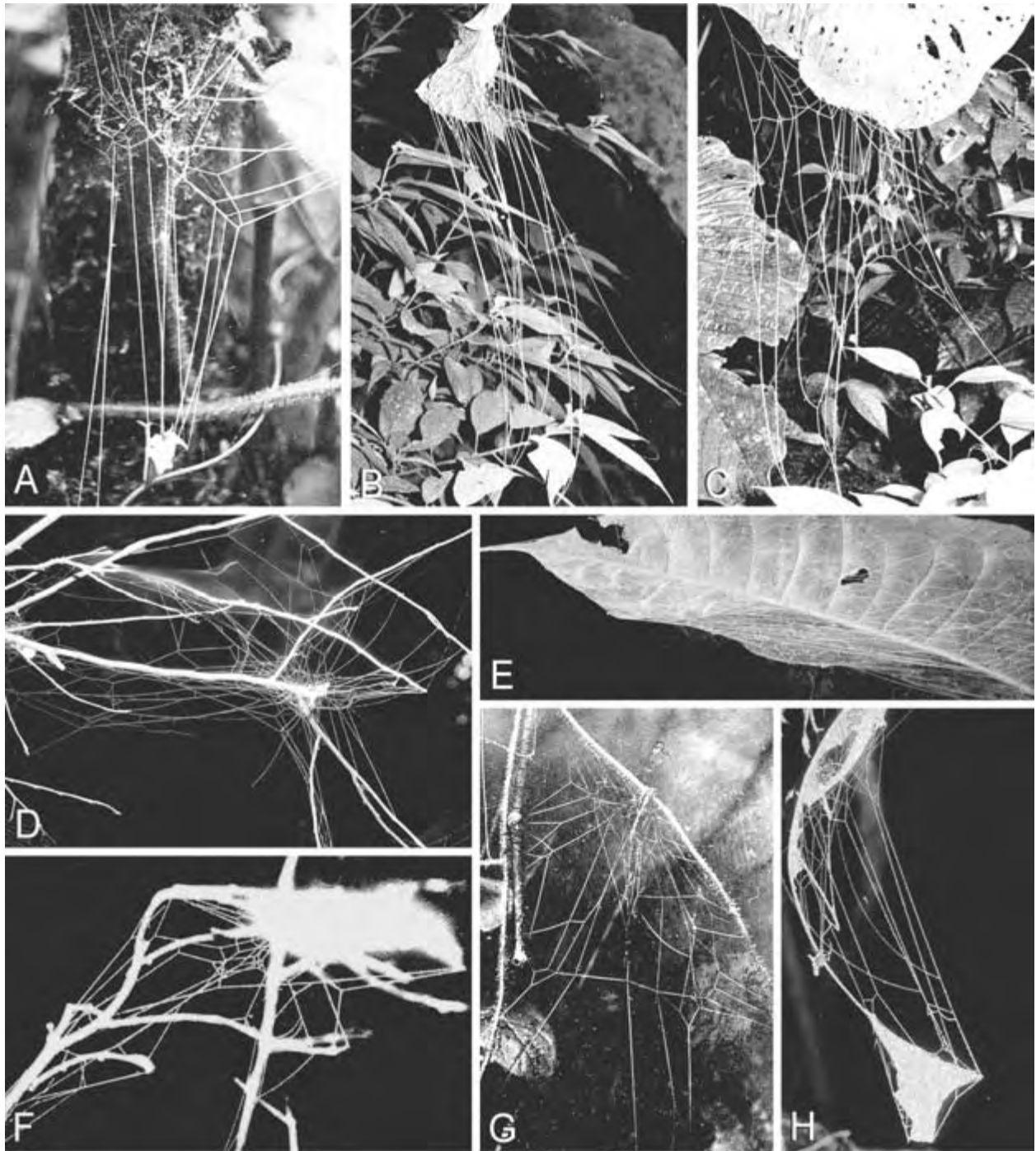


Figure 27 *Theridion*. A *T. nr. pictum* #74. Lateral view. The spider rested against the trunk; B–C *T. nr. schlingeri* #1087. Lateral and dorso-lateral views. Most but not quite all lines were sticky along their entire length. The spider was on the lower side of the leaf; D *T. nr. orlando* #1618. All lines except those very close to the retreat (against the branch) were sticky; E *T. evexum* #1219. All the long lines, but none of the others, were sticky. These lines more or less converged near where the spider rested against the leaf; F *T. nr. orlando* II #1550. All lines were sticky except the few near the spider. Some of the longer lines may not belong to this web; G *T. nr. orlando* #84. The spider rested under the node of the branch; H *T. nr. orlando* II #1450 Lateral view. All the lines were sticky except possibly a few right against the leaf at the top edge where the spider rested. Approximate widths of photos (cm): A 11.1; B 27.6; C not known; D 25; E; F 10.5; G 28.5; H 7.3.

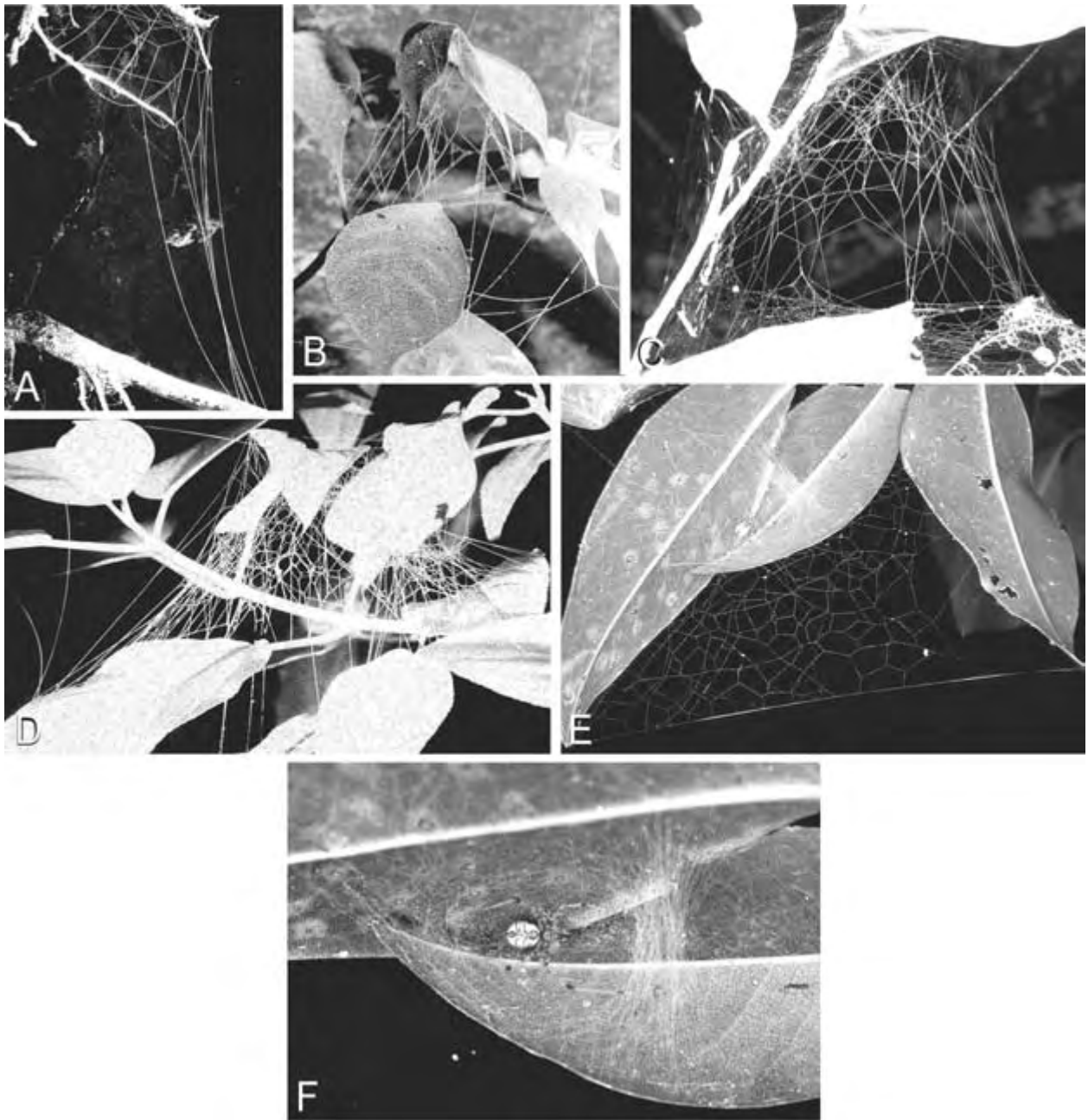


Figure 28 *Theridion*. A *T. sp. nov.?* #1268. Lateral view. All lines were sticky except short lines near the site where the spider rested on the underside of the twig near its tip; B *T. sp. juvenile*. Lateral view; C *T. sp.* (Ecuador), no detailed notes were taken; D *T. adjacens* #3264. Lateral view. The spider rested with numerous spiderlings in the retreat she had formed by curling the leaf. Only a few of the long downward directed lines were sticky; these were sticky along their entire length; E *T. sp. 2*, sticky sheet, spider rested on the underside of live leaves connected with dense array of silk lines; F *T. sp. 2*, details of resting site. Approximate widths of photos (cm): A 18; B 5.2; C not known; D 18; E not known; F not known.

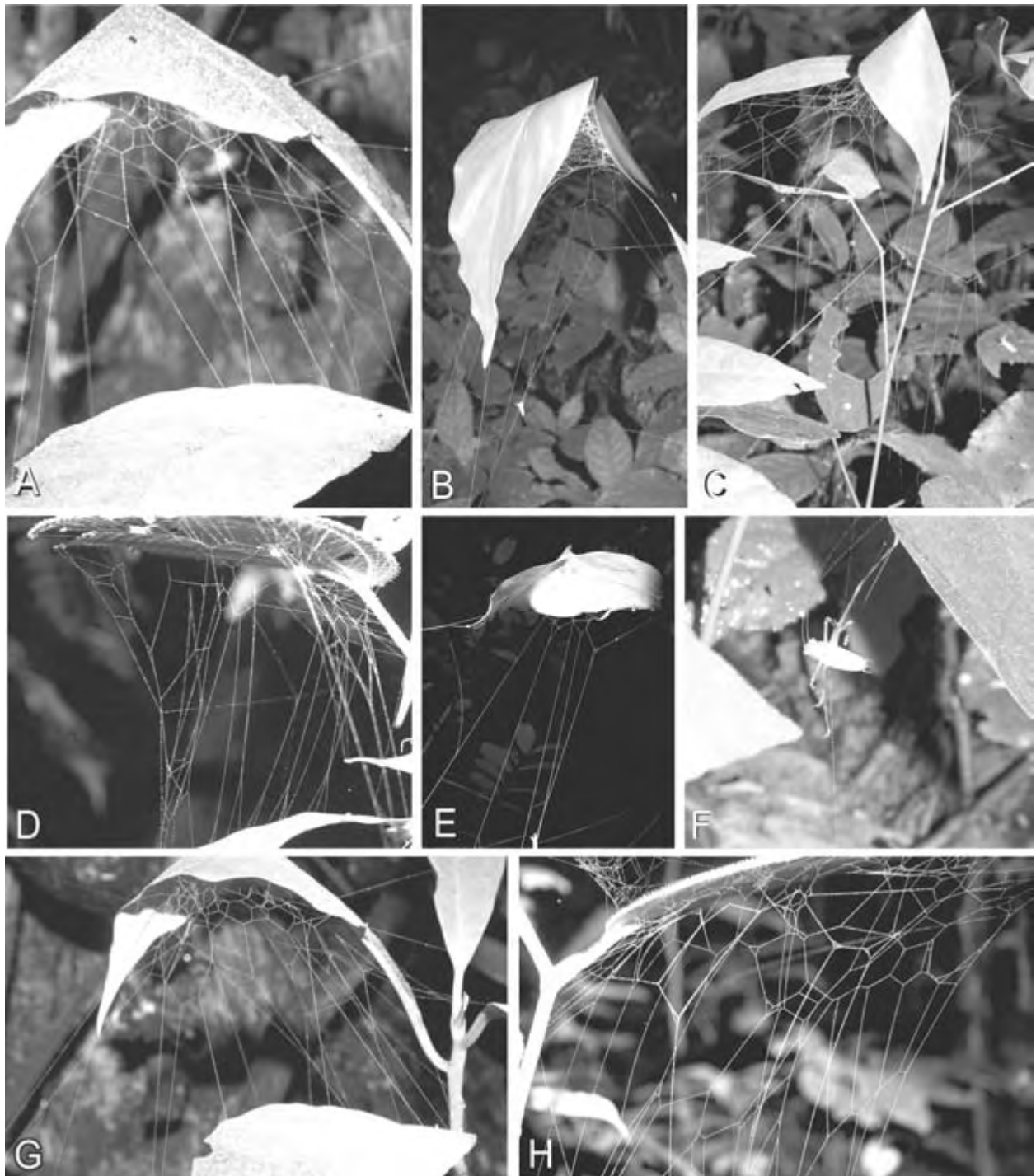


Figure 29 *Theridion* nr. *nigroannulatum*. A–H solitary webs. The spider rests on the underside of a live leaf, which is usually (A–C, E, G) folded, but sometimes not (D, H). Most of the long lines are sticky along nearly their entire length. Approximate width of the photos (in cm): A 8; B 6; C 10; D 11; E 6; F 6; G 12; H 8.

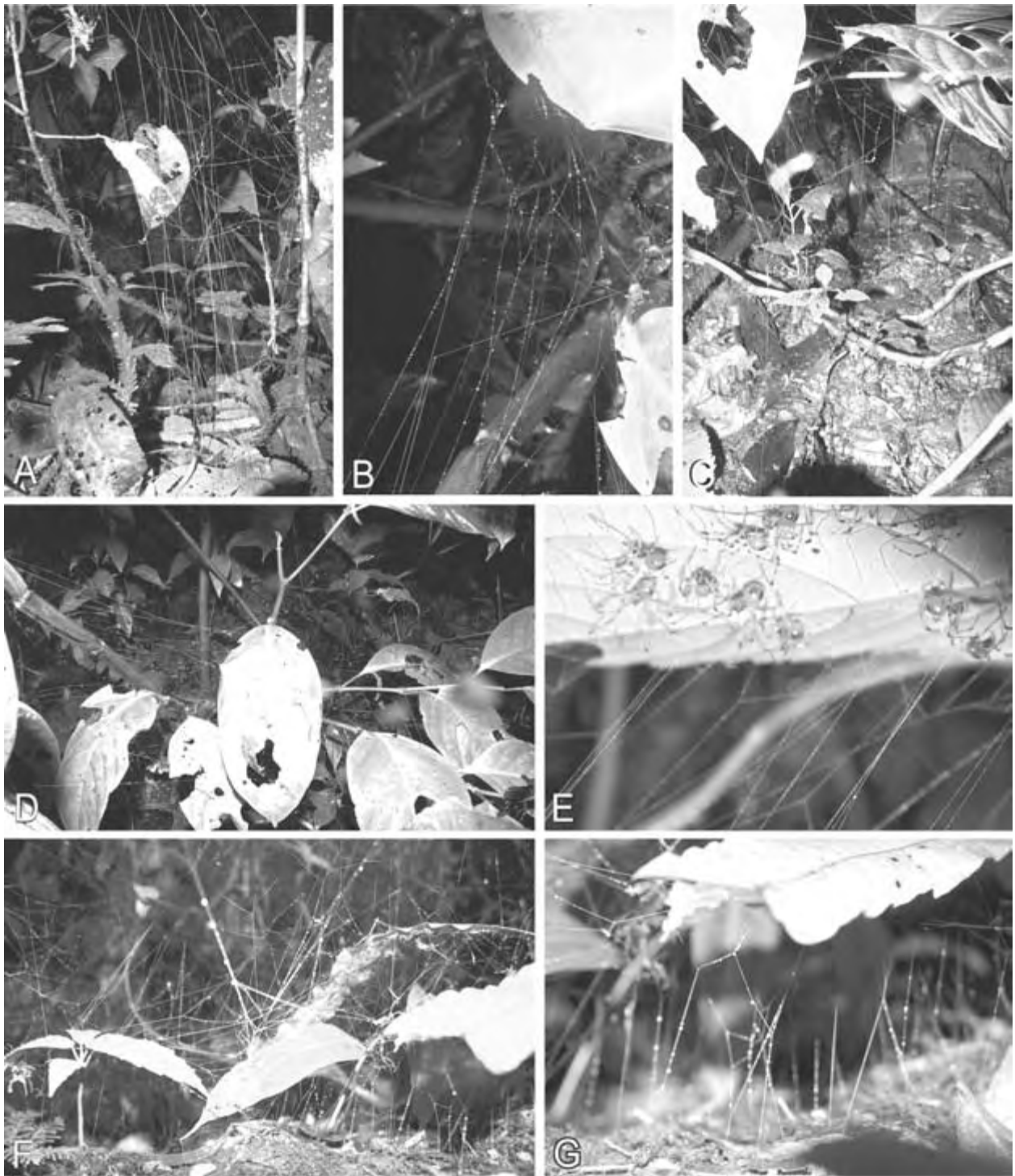


Figure 30 *Theridion* nr. *nigroannulatum*. A–G social webs. As in the solitary webs, the spiders rest on the underside of live leaves, which may or may not be folded. Arrangement of sticky silk is as in the solitary webs. Approximate width of the photos (in cm): A 10; B 7; C 10; D 30; E 15; F 40; G 15.

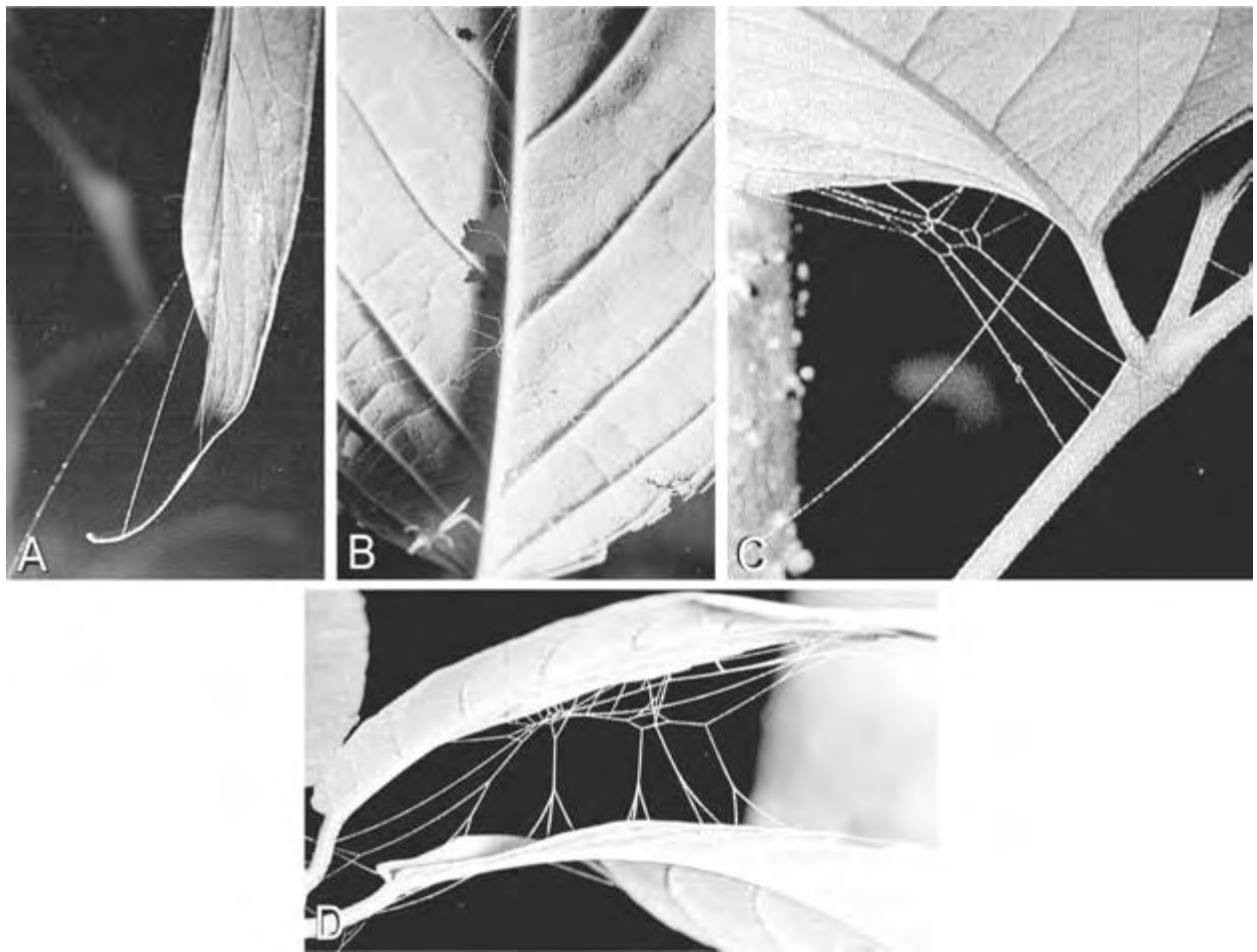


Figure 31 *Neottiura* sp. For all of these webs, the longish lines to the leaf, which more or less radiated from the site on the underside of the leaf where the spider rested, were sticky all along their length; some had one or two branches near the tip. The spiders actively flexed the webs. A #3661; B #3664; C #3671; D #3672. Some of the short lines toward the leaf above, in addition to the longer lines to the leaf below, were sticky. Approximate widths of photos (cm): A not known; B 4.1; C 6.5; D 12.

substantial intrageneric variation is much less pronounced (Eberhard, 1990a) than in theridiids. Kuntner's (2005, 2006) recent work allows a more quantitative comparison that supports this impression. Kuntner (2005, 2006) scored 24 web characters for a broad selection of orbicularians, with emphasis on Araneidae, Nephilidae and Tetragnathidae. In his analyses, orb web characters had an average CI value of 0.634 ± 0.262 , ranking with the least homoplastic morphological characters of theridiids (Agnarsson, 2004). The corresponding value in Nephilidae was 0.49 (Kuntner *et al.*, 2008). Hence, the behaviour of araneoid orb-weavers also contrasts with the high levels of homoplasy and plasticity of theridiid webs.

Uloborids offer another, less well documented contrast with theridiids. Their webs are also relatively well known (reviewed in Lubin, 1986), but the family is more modest in size (about 250 species – Platnick, 2006). The overall impression is again of differences with theridiids. There are relatively wide intergeneric divergences, only occasional convergences (e.g. independent evolution of orb plus cone designs in species

of *Uloborus*, *Conifaber* and *Tangaroa*), and more modest intrageneric differences (Lubin, 1986). The data have not been quantified, however.

Some details of building behaviour per se of orb weavers, rather than of the structure of their finished webs, contrast even more strongly with the major patterns in theridiids. These behavioural details have been conserved over relatively large taxonomic groups in which the structures of finished webs vary substantially (e.g. Eberhard, 1982). For instance, Scharff and Coddington (1997) found that such web building behavioural characters had the least homoplasy of all their characters, with a remarkably high consistency index (mean $CI = 0.803 \pm 0.287$). Similarly, Hormiga *et al.* (1995) found behaviour to be quite consistent (CI of web building characters = 0.675 ± 0.318). In an analogy with human constructions, the bricks that are used to build buildings are much less diverse than the buildings themselves. The webs of orb weavers have clearly evolved more rapidly than the behaviour patterns used to construct them. Do theridiids differ from orb weavers in this respect?

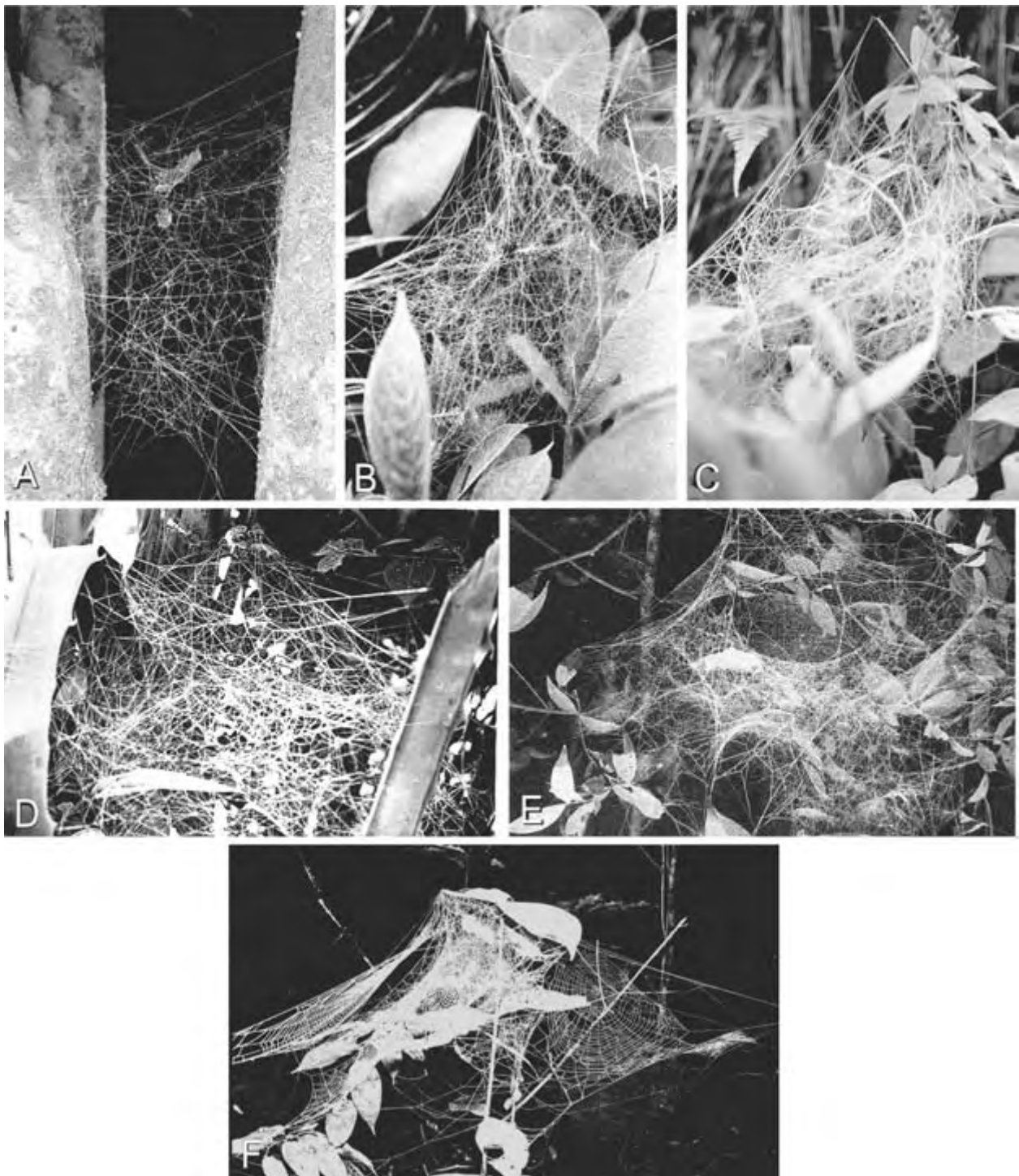


Figure 32 *Tidarren*. A *T. sp. 1* (Fannies Island, S. Africa). No sticky silk was noted; B *T. haemorrhoidale* #221. Lateral view, no sticky silk was noted; C *T. haemorrhoidale* #219. Lateral view with a *Philoponella* sp. orb attached to it. The spider's retreat was at the top of the dome-shaped sheet in the midst of the tangle; D–E *T. haemorrhoidale* #165. Lateral views with focus at different depths within the tangle. No sticky lines were noted. There was a sparse, dome-shaped sheet with a wide, irregular mesh in the tangle, sloping downward from the mouth of the curled-leaf retreat (retreat best in focus in D, connection with sheet clearest in E); F *T. haemorrhoidale* #1502. Lateral view with several (total was 12) *Philoponella* sp. orbs attached to it. No sticky lines were noted. The spider was in a curled leaf retreat suspended in the tangle with its mouth at the top of the dome-shaped sparse sheet in the tangle; G *T. haemorrhoidale* #1628. Lateral view with *Philoponella* sp. orbs attached to the tangle. Approximate widths of photos (cm): A 10; B 15.2; C 20.7; D 22.1; E 23.4; F 50.3; G 46.4.

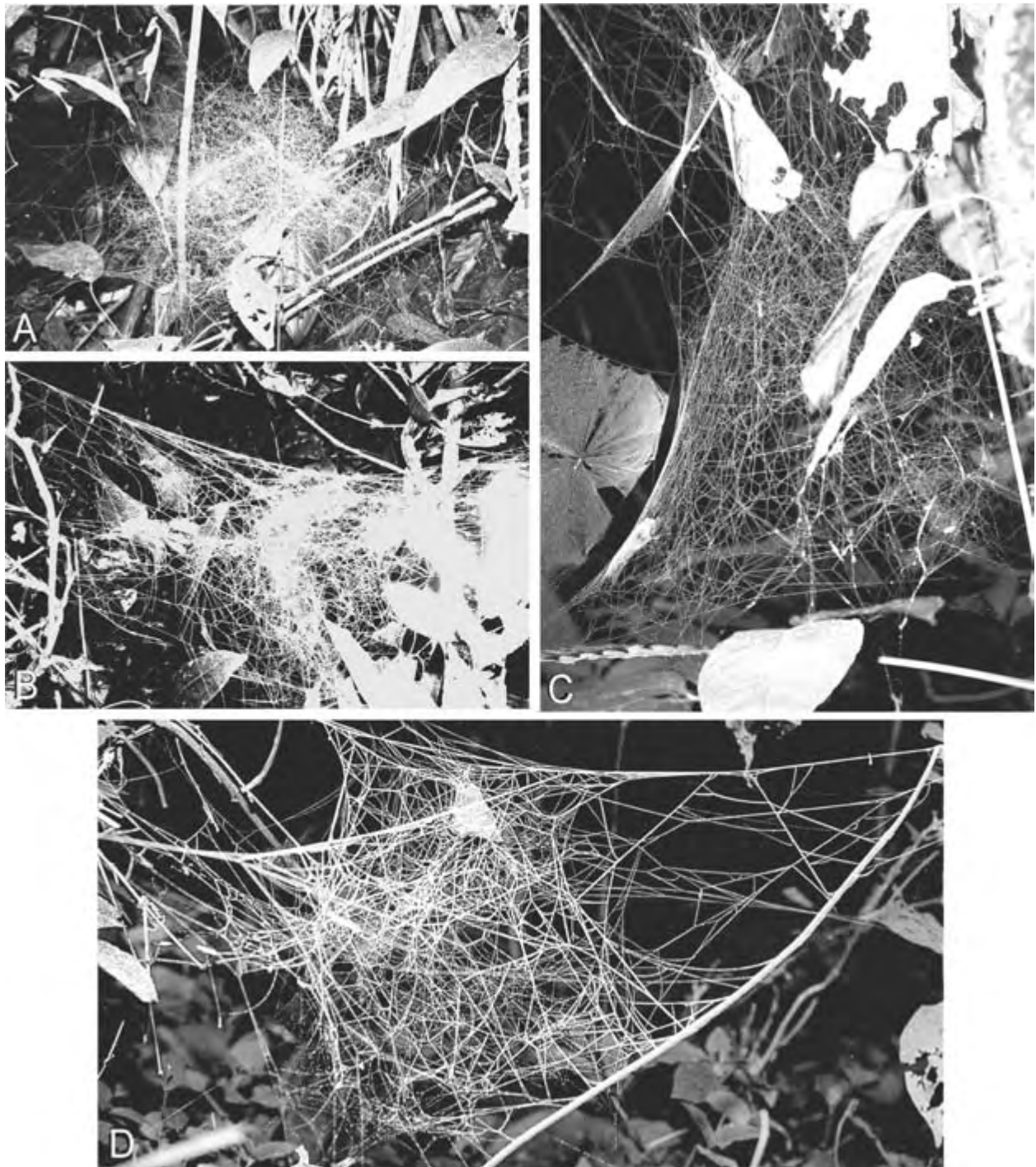


Figure 33 *Tidarren*. A *T. sp.* (juvenile) #3544. Lateral view showing the dome-shaped sheet in the midst of the tangle. B *T. sisypoides* #1373. Lateral view with uloborid webs attached to it; C *T. sisypoides*. Lateral view, curled leaf retreat located in the upper part of the web; D *T. sp.* (juvenile) #FN21 104B. Lateral view, showing sparse, cup-shaped sheet around the retreat. There were no gumfoot lines. Lines near the mouth of the curled leaf retreat were more or less radially oriented. Approximate widths of photos (cm): A 42.5; B not known; C not known; D not known.

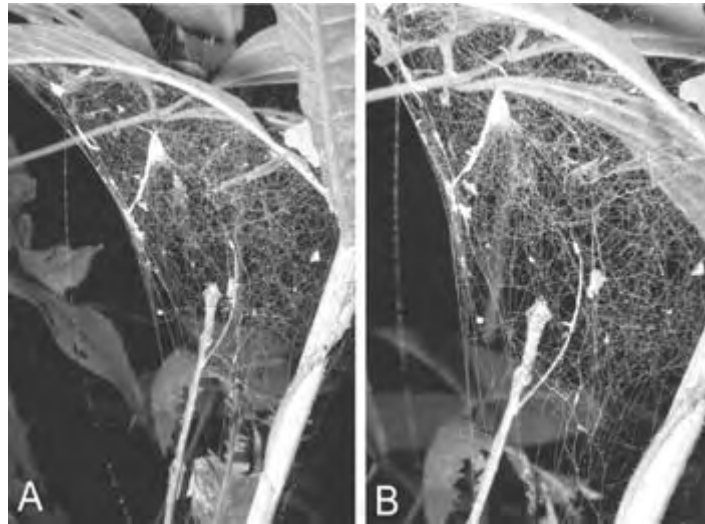


Figure 34 *Echinotheridion*. A–B *E. otlum* the silk retreat was suspended in the upper portion of the web, which was apparently not sticky. Approximate widths of photos (cm): A 10; B 8.

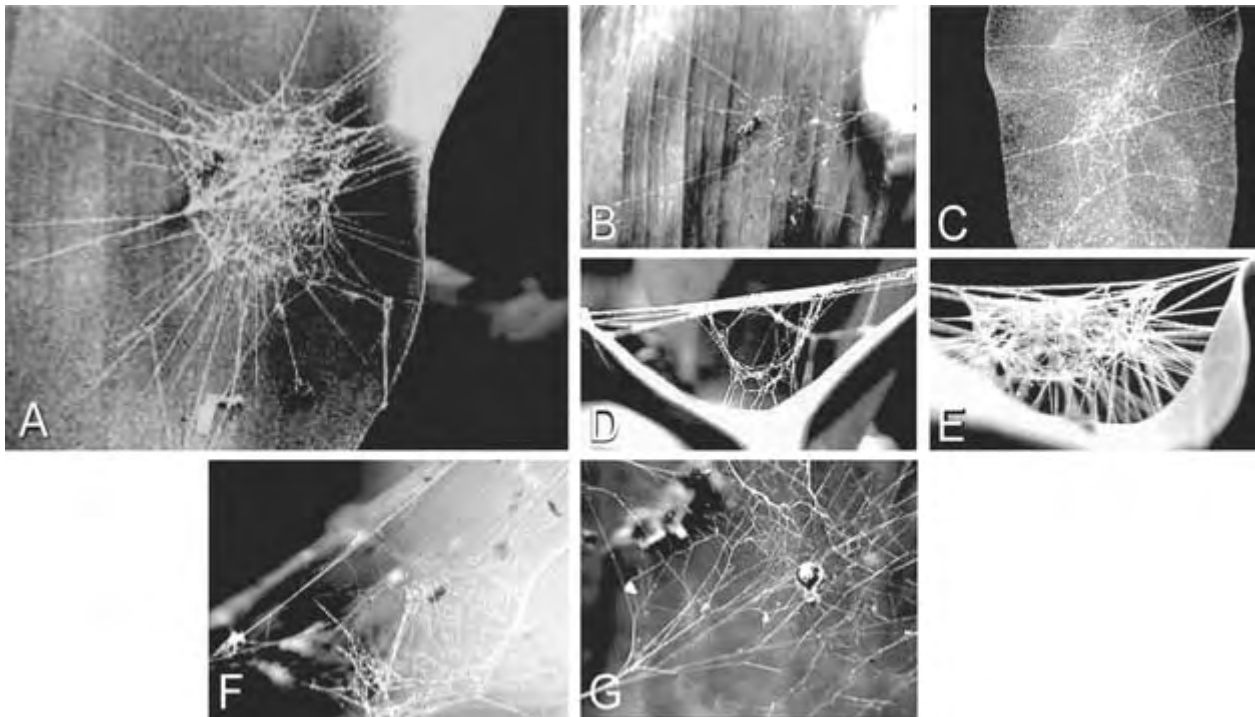


Figure 35 *Achaearanea apex*. A Dorsal view showing sheet; B Dorsal view of same web as A but without white powder, with one large mass of detritus visible; C Dorsal view of the strong lines pulling the edges of the leaf (probably causing them to curl) and the dorsal sheet attached to these lines; D Lateral view showing dorsal sheet, ventral gumfoot lines, and spider in the upper portion of the tangle between them. E Lateral view of same web as A, showing gumfoot lines attached to the lower portion of the tangle and running more or less perpendicular to the leaf surface; F Lateral view, showing dorsal sheet (visible mostly as single line), spider hanging in the midst of the tangle with more-or-less radial lines running toward lower portion of the tangle where the gumfoot lines were attached; G Close-up dorsal of spider resting in tangle (the dorsal sheet is largely out of focus). Approximate widths of photos (cm): A 6; B 5.4; C not known; D not known; E 4.2; F not known; G not known.

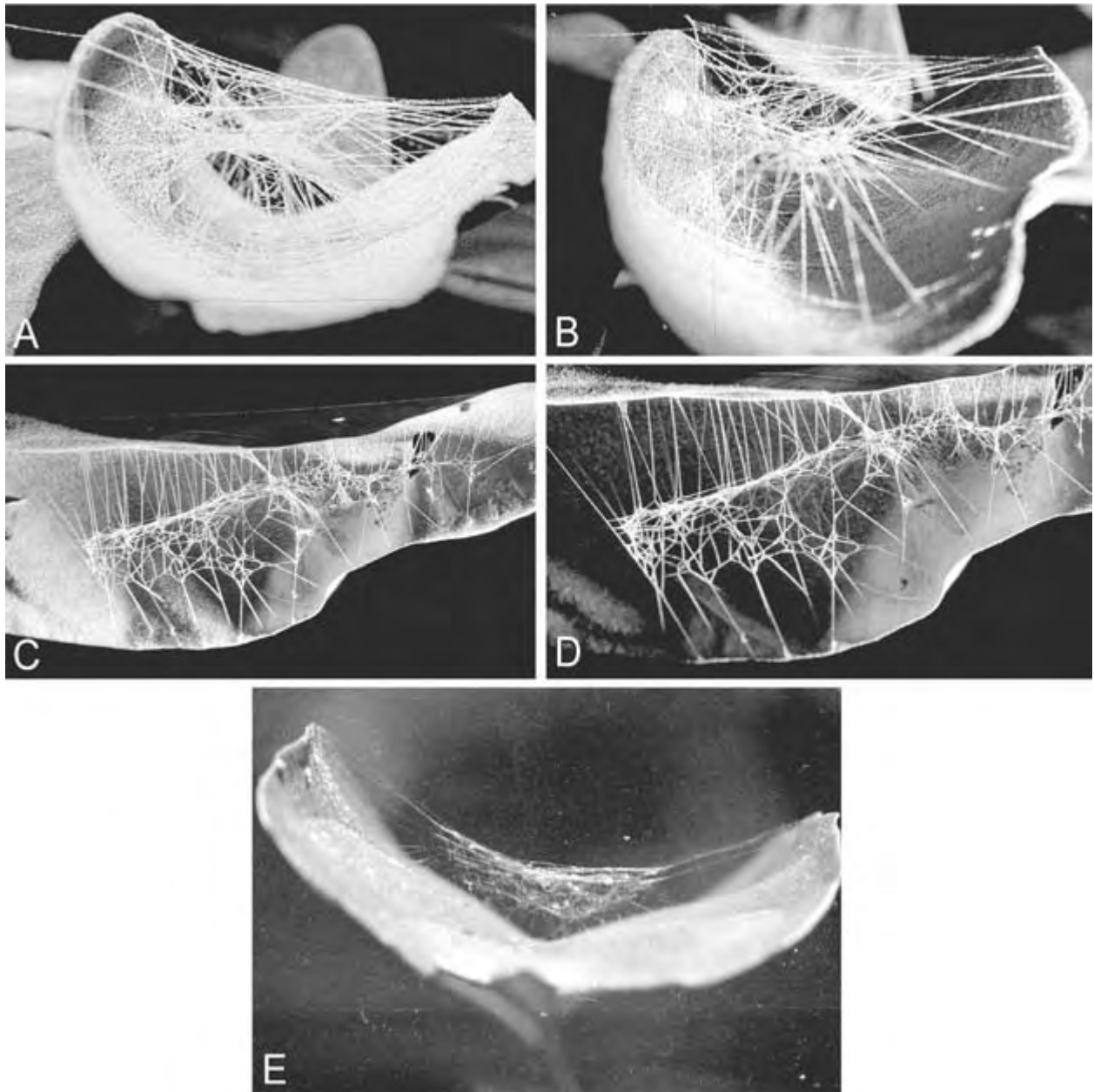


Figure 36 *Achaearanea*. A A. nr. *tepidarium* #3662. Lateral view; B Lateral view of same web; C A. nr. *tepidarium* #3713. Lateral view, showing central platform to which approximately vertical gumfoot lines are attached. This leaf was bent more than about 20 others in which similar webs were seen. The gumfoot lines were not sticky only at their tips, but along the bottom third to half of the line. The tangle was not sticky; D A. nr. *tepidarium* II #3713 Closer view of same web as C; E A. nr. *triguttata* #48 Lateral view of strong dorsal sheet, with spider resting on its underside. Approximate widths of photos (cm): A 5.1; B 5.4; C 14.5; D 11.4; E 4.2.

Theridiid web building hints at less stereotypy, though our present knowledge is very limited. The possible importance of focusing on behaviour rather than the resulting web is illustrated in *Latrodectus* and *Steatoda*, where knowledge of the intermediate stages of web construction can reveal underlying patterns that are difficult to perceive in the finished web (Fig. 45) (Lamoral, 1968). Nevertheless even within the genus *Achaearanea* there is a surprising diversity of building

behaviour. The sheet weaver *A. tessellata* performs a ‘drunken wandering’ behaviour, and also has a unique way of attaching its dragline to other lines while filling in its sheet (Jürger & Eberhard, 2006); neither behaviour pattern has apparent homologies with the behaviour used to build gumfoot webs in congeneric species (Benjamin & Zschokke, 2003). This hints that building behaviour per se may also be unusually diverse in theridiids, but much further work will be needed

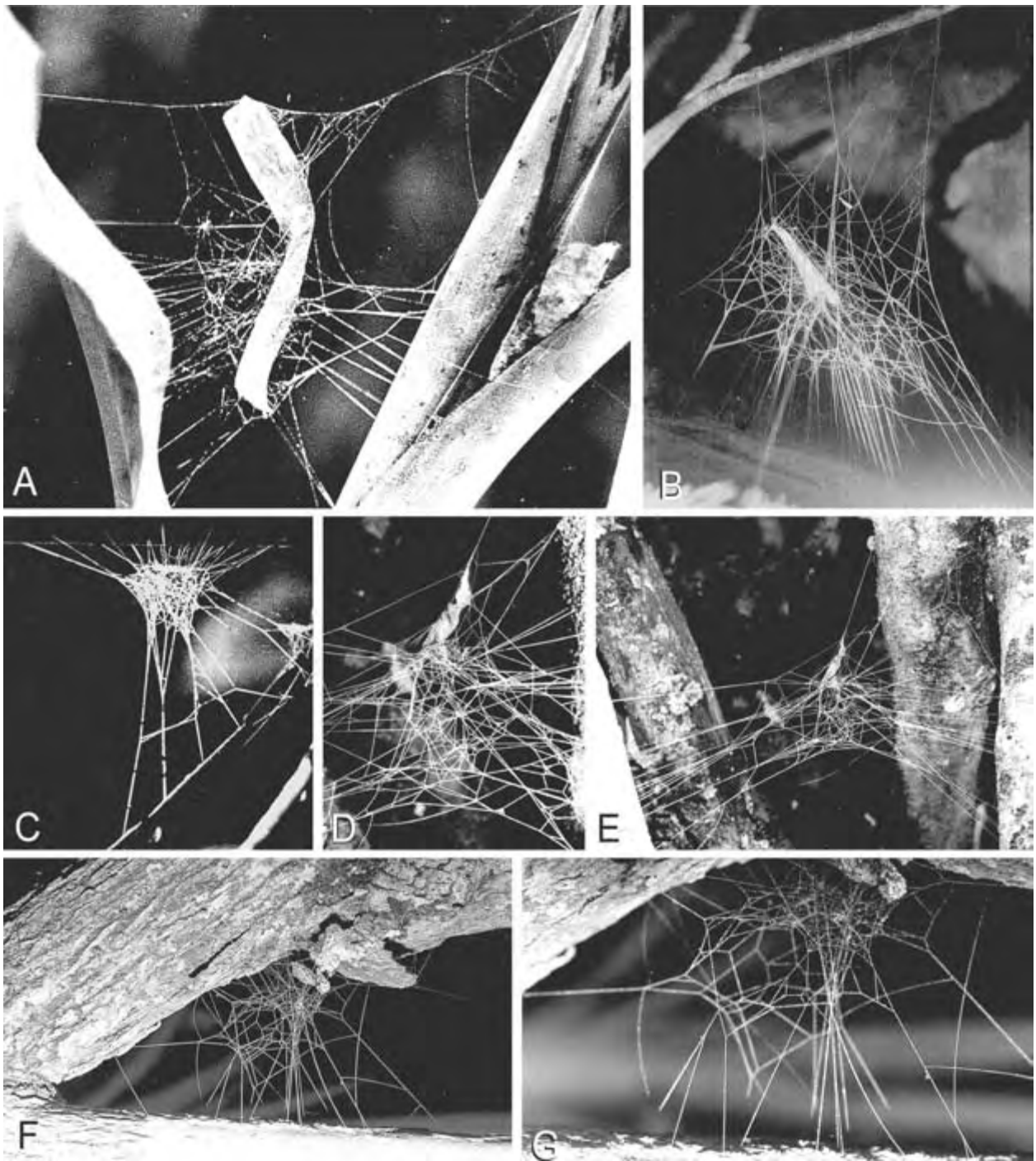


Figure 37 *Achaearanea*. A *A. florendita* #122. Lateral view. Only the tips of the gumfoot lines were sticky; B *A. florens* #2368. Lateral view, showing in some cases how several gumfoot lines were attached to a given tangle line that ran more or less parallel to the substrate (a rock). Only the distal approximately 3 mm of each gumfoot line was sticky; C *A. florendita* #205. Lateral view. Only the tips of about 10 of the short lines running more-or-less perpendicular to the surface above were sticky; D–E *A. florens* #FN21 103C. Dorso-lateral views. Three different sets of gumfoot lines were attached to three different trunks. Many of the lines at the mouth of the curled leaf retreat were clearly radially oriented; F–G *A. florendida* #FN21–103. Lateral views. Some of the shorter lines that are more or less perpendicular to the lower branch were sticky at their tips. Some of the lines in the small tangle where the spider rested were oriented more or less radially. Approximate widths of photos (cm): A 11.0; B 13.6; C 11.1; D 14.6; E 42.5; F 14.6; G 11.9.

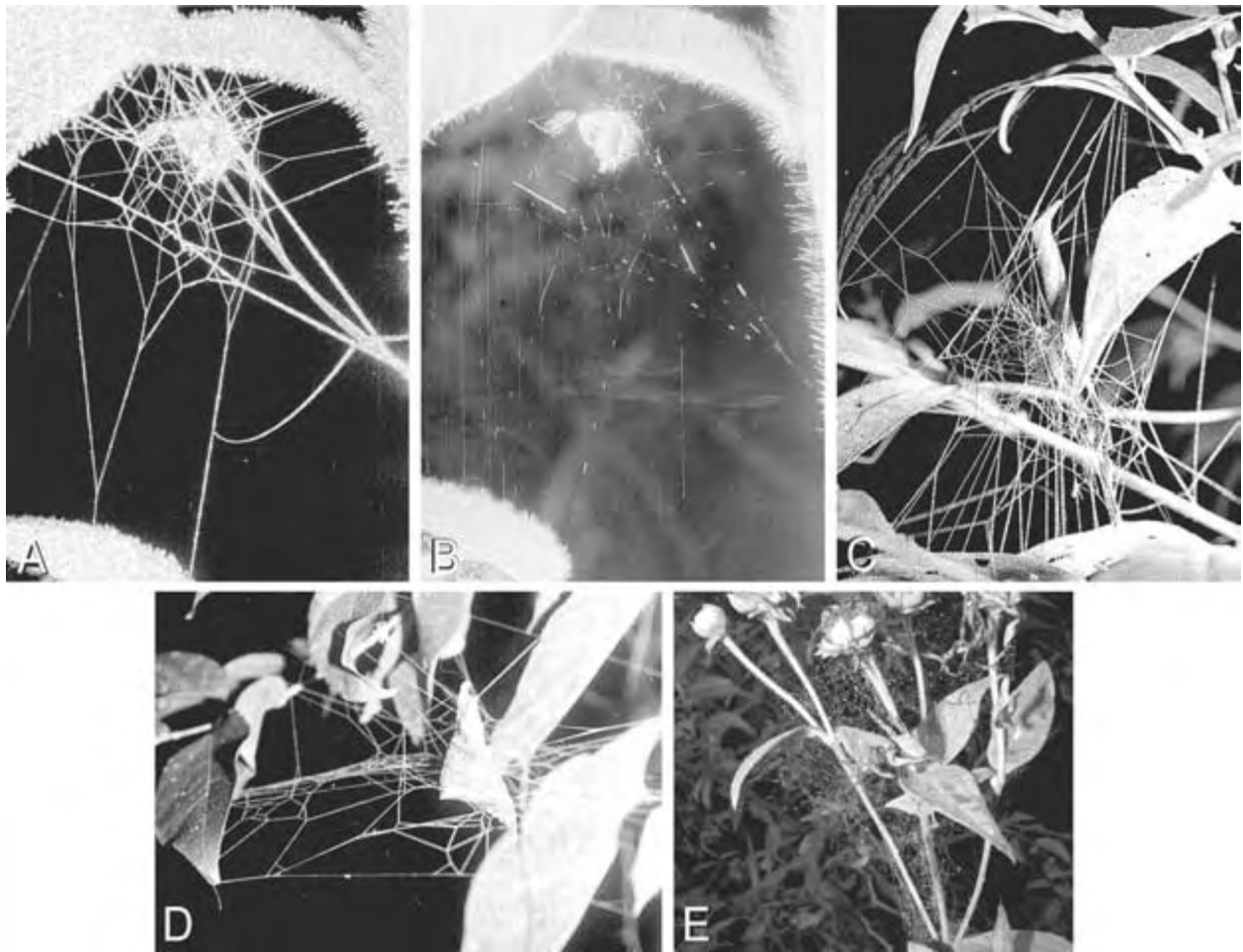


Figure 38 *Achaearanea*. A–B *A. nigrovittata* #1453a. A with powder; B without powder; C *A. triguttata* #3570. Lateral view; Long lines to leaf below with sticky tips; D, *A. nigrovittata* #2681. Lines had very sparse spots of sticky material; E, *A. picadoi* (Ecuador), a tangle in which most lines were sticky. Approximate widths of photos (cm): A 6.6; B 6.6; C 16.2; D 13.0; E 25.

to document this. Prey attack behaviour in Theridiidae also cannot yet be evaluated quantitatively, but seems to show a mix of very plastic traits (Japyassú & Gonçalves Jotta, 2005) and very conservative traits (Barrantes & Eberhard, 2007).

It should be noted that the behavioural characters in orb weavers may tend to show less homoplasy than other characters simply due to sparse observations limiting the discovery of polymorphism and other homoplasy. However, web characters suffer from exactly the same sampling limitation (typically only a single, or very few, webs observed per species) as the behaviour patterns, so we believe the trend in orb weavers toward lower homoplasy in behavioural units than in the end product of the behaviour (finished web design) is real. However, the second major theridiid pattern we have documented, widespread and repeated convergences in web traits, cannot be explained by our focus on the designs of webs rather than the behaviour patterns that are used to build them.

Why are theridiid webs so evolutionarily flexible?

Theridiid web characters exhibit more homoplasy than morphological characters of the same animals (Agnarsson, 2004), than web and behavioural characters in related, orb weaving spiders (Kuntner, 2005, 2006; Kuntner *et al.*, 2008), and than behavioural traits in other, more distantly related taxa (de Quieroz & Wimberger, 1993). Why might theridiid web construction be different? Eberhard (2000b) argued that a similar hyper-diversity of web types in the theridiosomatid genus *Wendilgarda* and even within a single species (e.g. Eberhard, 1990b) could be explained by how variant behaviours originate. The argument is that due to relaxation of selection for behavioural consistency due to changes in the basic *Wendilgarda* web form, the ‘random’ intraspecific and intra-individual variance in *Wendilgarda* behaviour has become much greater than is typical in other orb weavers. Subsequently, increased behavioural variance that resulted from this ‘imprecision’ facilitated the origin of substantially new web forms.

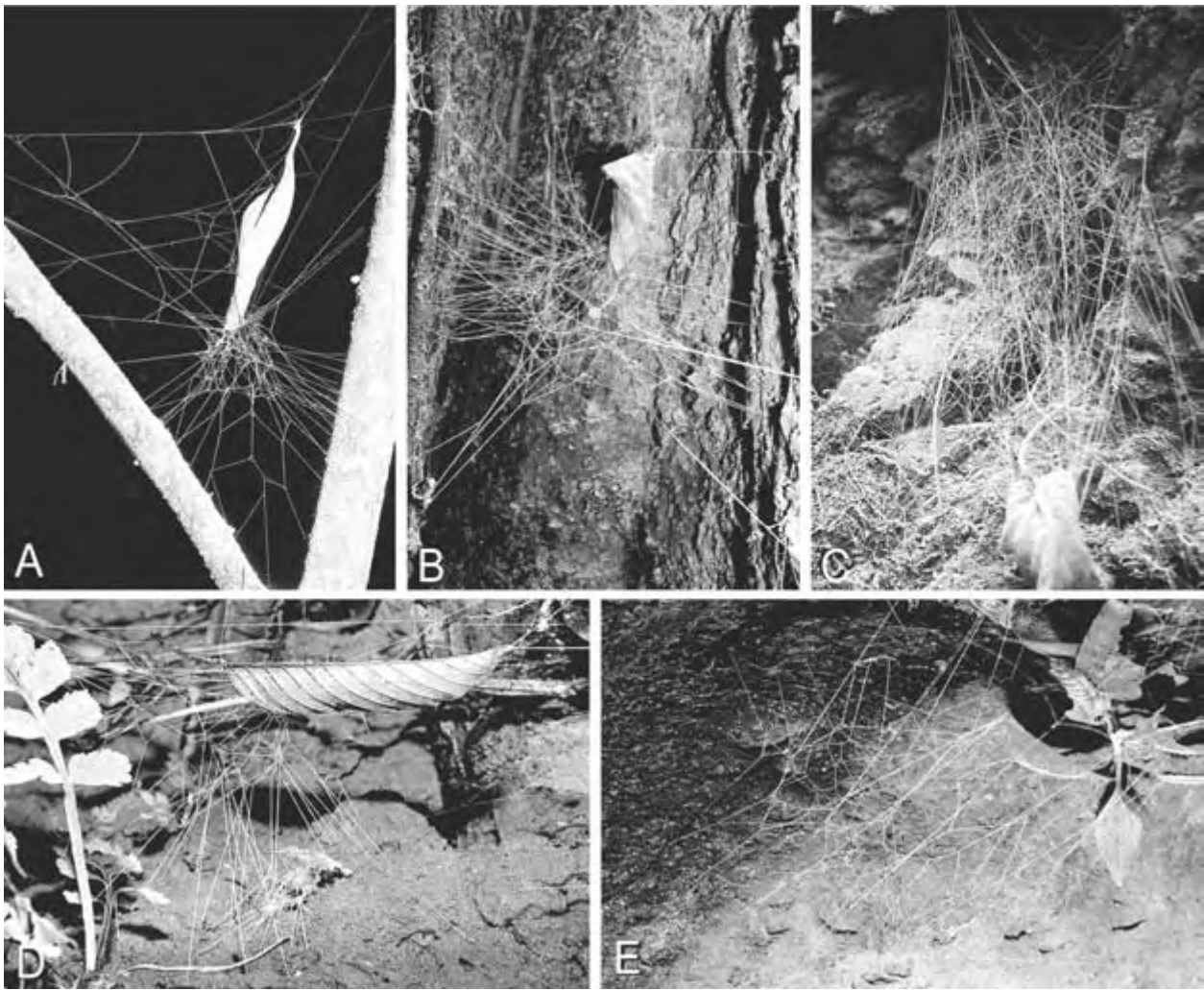


Figure 39 *Achaearanea taeniata*. A #1284. Lateral view. The multiple lines more or less perpendicular to the branches had sticky tips; B #1303. Lateral view. The lines more or less perpendicular to the substrate were sticky at their tips. Many spiderlings but no egg sacs were present in the curled leaf with the spider; C #424. Lateral view. The only sticky material was at the tips of multiple parallel lines running toward the rock near the retreat (upper right of web). The large tangle seemed not to have any function other than protection; D #3623. Lateral view with gumfoot lines to ground below; E. Lateral view of additional portion of web in D, with additional gumfoot lines. Approximate widths of photos (cm): A 11.9; B 15.6; C 21.6; D 15.5; E not known.

The situation in Theridiidae is at least partially compatible with this idea, in that intraspecific variation seems to often be substantial (e.g. Agnarsson, 2004; Table 2A). Perhaps the most spectacular illustration is in the allied family Synotaxidae, in which two different species of *Synotaxus* both show what appear to be profound intraspecific variation in the basic organisation of their webs. Some webs in each species (Figs 2D, 3C) have rectangular modules that are built one after the other (Eberhard, 1977); other webs of each species (Figs 2G, 3D, E) entirely lack these modules (see also Eberhard, 1995). Similarly, some long sticky lines in *Theridion hispidum* webs are connected at regular intervals with short, non-sticky lines, producing regular hexagonal patterns (Fig. 26A, B, G); but others entirely lack these connections (Fig. 26C). The intraspecific variation in the very

simple webs of *Phoroncidia pukeiwa* is also substantial, as expected (Marples, 1955). Not only the lines themselves, but also the behaviour used to lay them is variable in theridiids. A standard comment in accounts of web building by theridiids is that the sites of the lines and the order of their placement are variable (Szlep, 1965, 1966; Lamoral, 1968, Benjamin & Zschokke, 2002, 2003; Jürger & Eberhard, 2006). Thus variant behaviour patterns that could be candidates to give rise to new web forms may often appear in a species.

At a further taxonomic remove, the diversification of web forms in non-orbweaving orbicularians in general, in association with the loss of stereotypic building behaviour (at least in linyphiids – Benjamin *et al.*, 2002; Benjamin & Zschokke, 2004) is also in accord with the behavioural imprecision

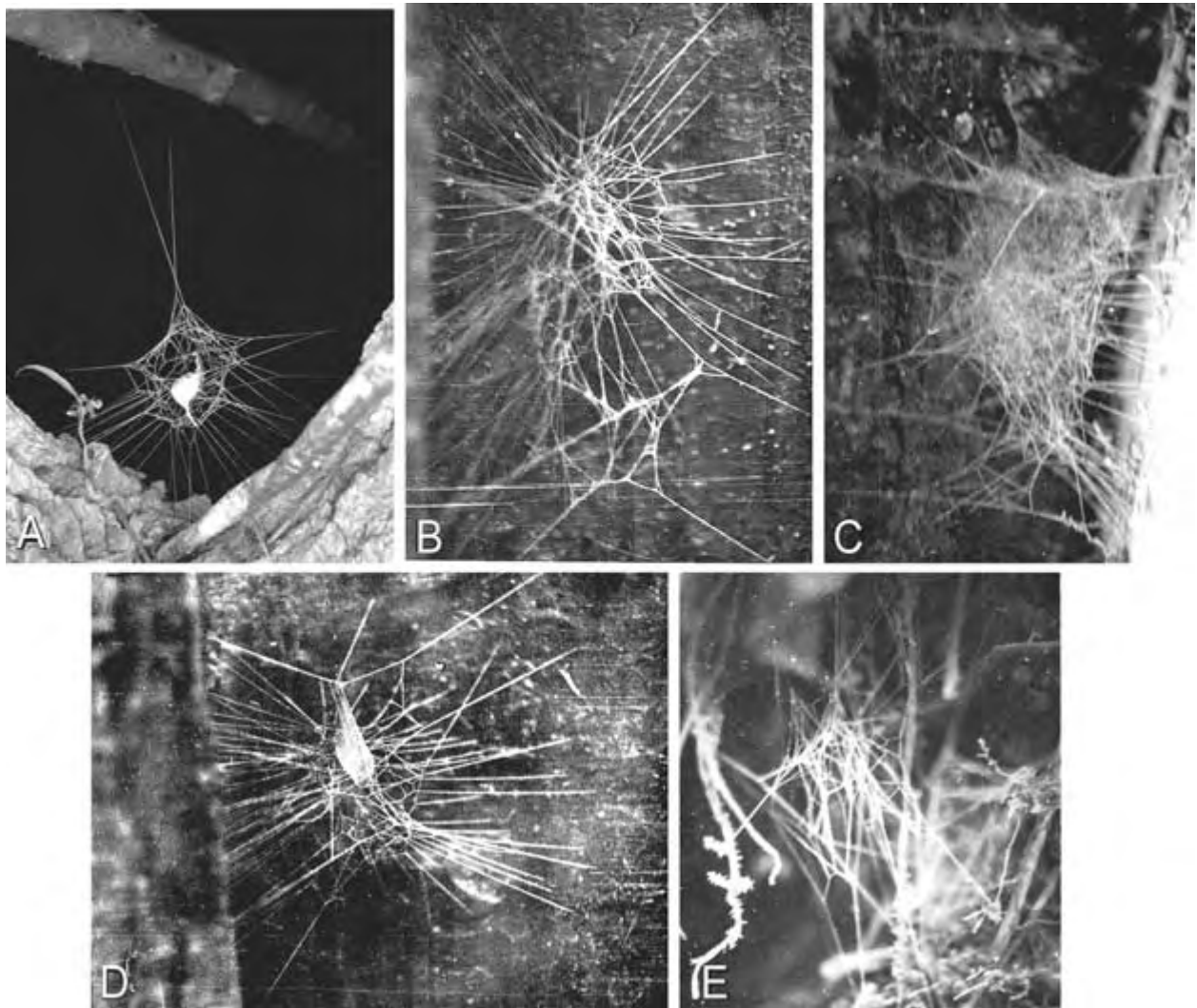


Figure 40 *Achaearanea*. A *A. sp. 6* (Fannies Island, S. Africa). The spider rested inside a folded leaf retreat suspended in the centre of the web. Most of the longer straight lines were gumfoot lines; B *A. maricaoensis* #479. Lateral view. There was a leaf suspended in the web, but the spider rested in a conical silk retreat; C *A. maricaoensis* #429. The spider was in a clear retreat; D *A. maricaoensis* #478; E *A. maricaoensis* #426. The only stickiness was at the tip of a single line down to the substrate. Approximate widths of photos (cm): A 7; B 12.3; C 9.5; D 15.0; E 9.0.

hypothesis (contrary to the conclusion of Benjamin & Zschokke, 2004). The relative uniformity of the webs within Linyphiidae, however, does not easily fit this hypothesis. The summary of linyphiid web forms (Benjamin & Zschokke, 2004), while admittedly only fragmentary, included only four designs among 12 species in 10 genera. Although only two species have been studied, and perhaps at only a superficial level, it appears that linyphiids have especially non-stereotyped construction behaviour (Benjamin & Zschokke, 2004). The implication is that within this very large family (>4200 species, Platnick 2006) with non-stereotyped construction there is very little web diversity. Fragmentary data suggest that similar web designs occur in the related families Cyatholipidae (Griswold, 2001) and Pimoidae (Hormiga, 1994). As we intimated in the Introduction, we suspect that the categories recognised

by Benjamin and Zschokke (2003) for theridiid web designs were overly simple; this may also be a problem with their characterisation of linyphiid webs. Perhaps it is too early to draw conclusions from data in Linyphiidae. We note, however, still another apparent contradiction of the behavioural imprecision hypothesis, in the only moderate diversity in the web forms of another group with highly reduced webs, the uloborid genus *Miagrammopes* and allied genera. Lubin 1986 (p. 157) notes that *Miagrammopes* webs 'vary in both number and arrangement of sticky lines'. It is possible that the predicted diversification did not occur because the derived web form is especially advantageous, and that selection has resulted in relative uniformity. The problem is that many factors undoubtedly come into play in the evolution of webs, and a hypothesis of this sort can only predict a trend, not the outcome of every

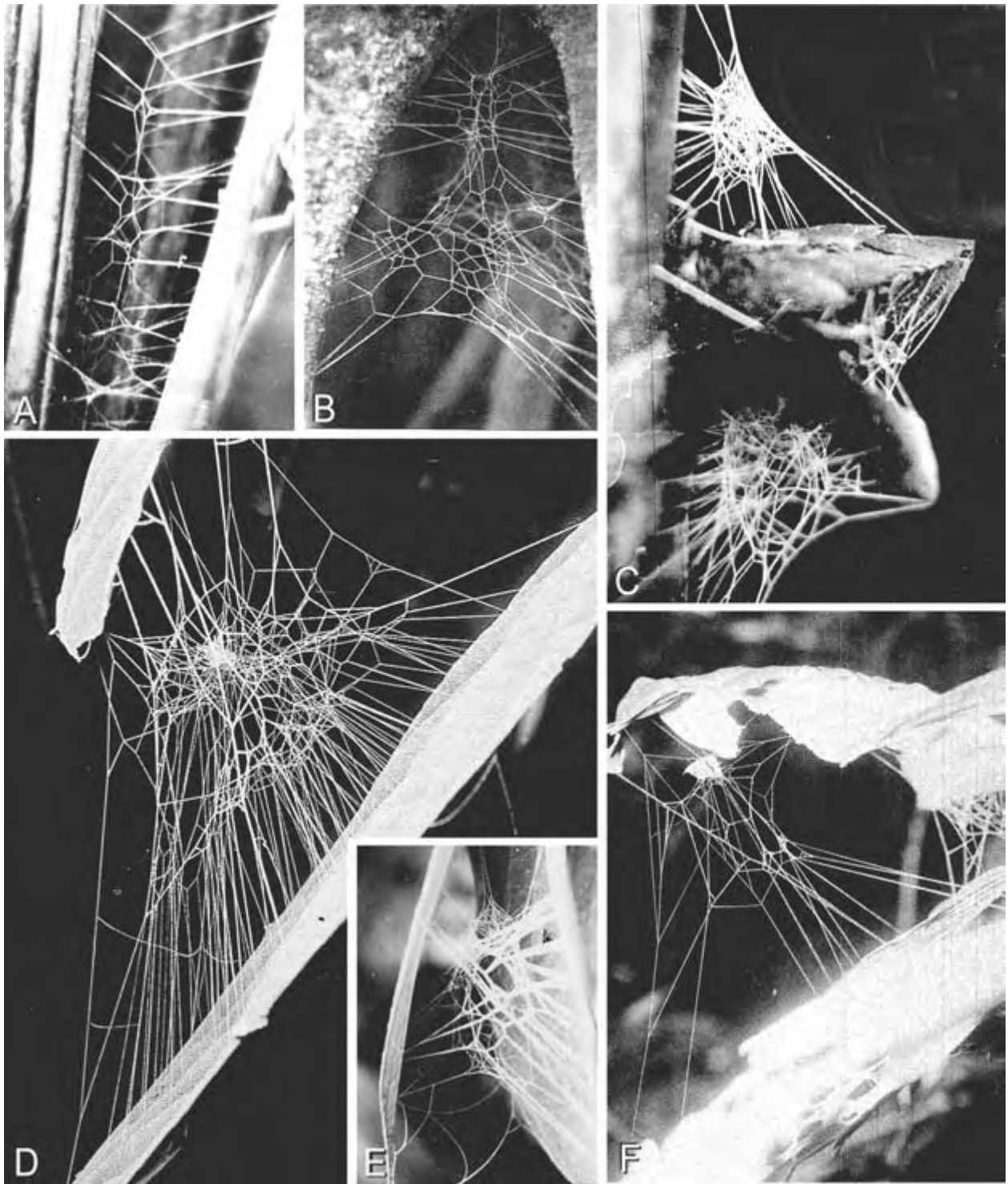


Figure 41 *Achaearanea*. A A. nr. *kaspi* #170. Lateral view. The lines more or less perpendicular to the substrate were sticky along nearly their entire length; a few lines connecting these lines were also sticky; B A. nr. *kaspi* #498. Lateral view of web between prop roots of tree. The spider rested at the top, against the tree. The only sticky material was at the tips of the lines more or less perpendicular to the substrate. About two-thirds of the web was farther back inside this cavity; C A. *hirta* #252. Lateral view of two webs on bamboo stem. The stickiness in both webs was confined to the tips of the lines that were more or less perpendicular to the substrate; D A. nr. *isana* #3247. The only glue was at the tips of the many long lines that ran to the substrate below. Most of these gumfoot lines were attached to lines more or less parallel to the substrate at the edge of the tangle; E A. nr. *isana* II #417. Lines to both leaves had stickiness on them, in some at the tip of the line but in others part way up. No stickiness was noted in the central sheet. The spider had two egg sacs in a cup-shaped silk retreat in the tangle that opened downward; F A. nr. *isana* II #3268 (very near #3247). All long lines to substrate and many (about half) of the lines in the tangle were sticky. Approximate widths of photos (cm): A 8.3; B 6.7; C 6.4; D 14; E 10.1; F 10.8.

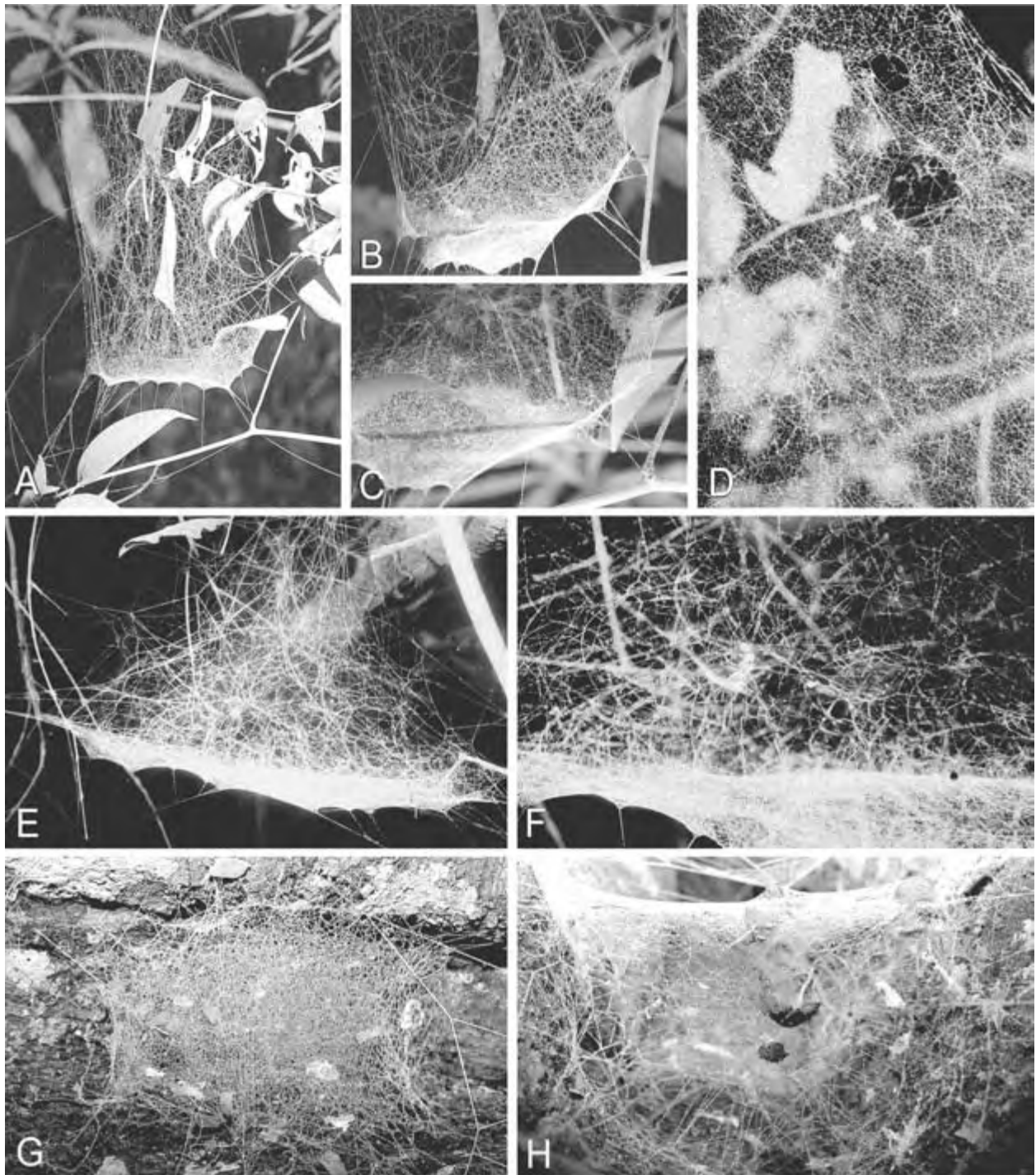


Figure 42 *Achaearanea*. A–C *A. sp. nr. porteri* #3680. There were multiple lines from the mouth of the retreat to the sheet (A). B and C, The mesh of the sheet was larger near the edge; D–F *A. tessellata* #1816 Dorsal view in D, showing holes presumably from damage or prey capture; lateral views in E and F. Many lines in the tangle above the sheet were slack, and some tended to converge on the retreat, which had small pieces of debris (F). No sticky silk was noted; G–H *A. nr. porteri* #3609. G, Dense non-sticky sheet covering web built in vertical groove in tree trunk (photo rotated 90°). This sheet extended all the way to the trunk (apparently not leaving room for prey to walk under), and was not connected with the gumfoot lines; H, End-on view along groove, showing more or less radial array of gumfoot lines centred on the soft-walled retreat. The retreat had small pieces of plant material incorporated in its walls that the spider pulled closed around itself when disturbed (a second empty soft-walled retreat was inside a curled leaf). Approximate widths of photos (cm): A 15.8; B 11.3; C not known; D not known; E 30.2; F not known; G 12; H 13.

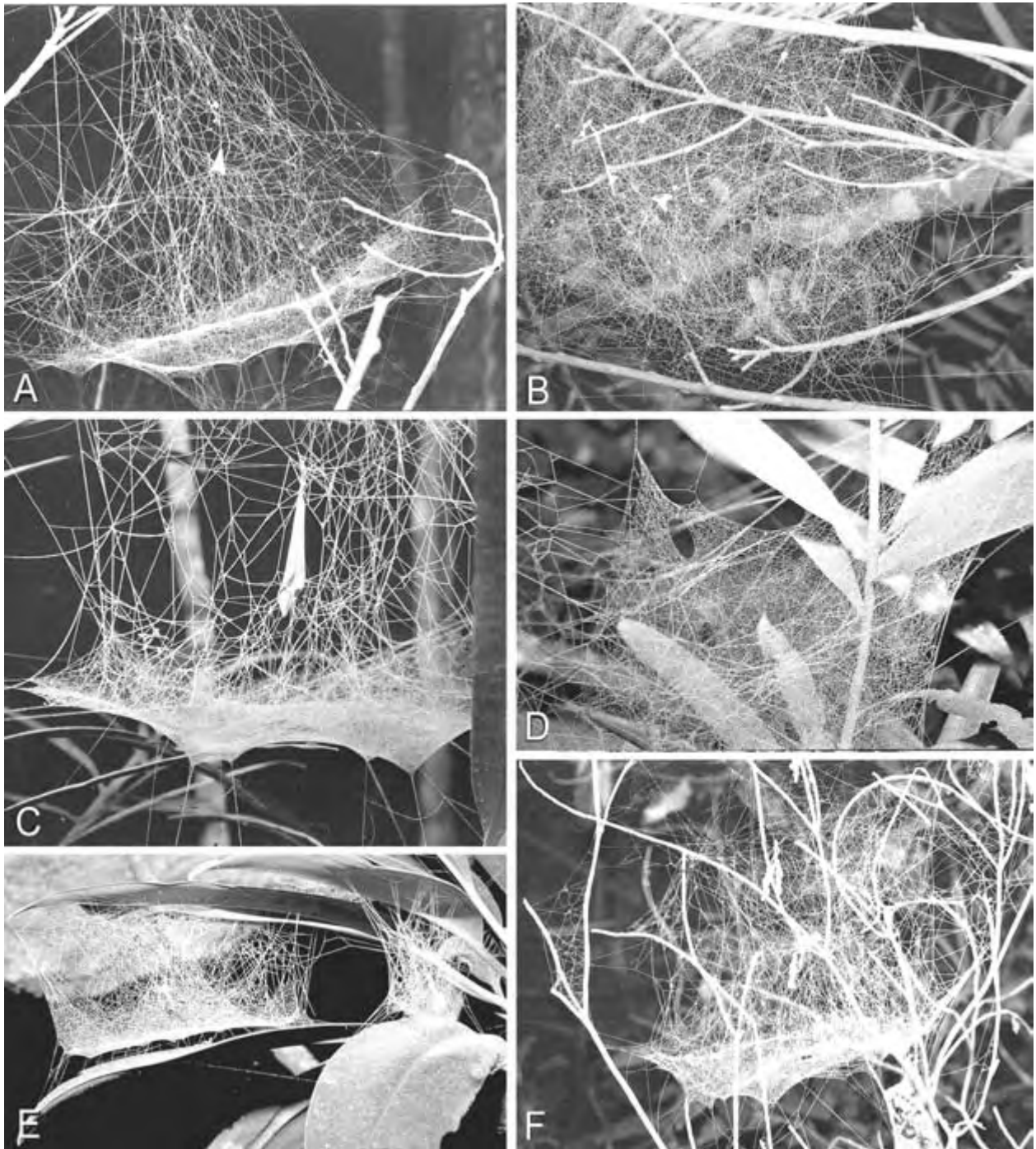


Figure 43 *Achaearanea* sp. nr. *porteri*. A #3693. Lateral view; B, Dorsal view of sheet of web in A; C #3694, Lateral view; D, Dorsal view of sheet in web in C. The mesh size in the sheet directly under the mouth of the retreat (not visible) was larger than nearby; E #3696; F #3704. The lines in the central portion of the tangle above the sheet tended to converge on the mouth of the retreat; there was a hole in the sheet immediately below the retreat. Approximate widths of photos (cm): A 27.2; B not known; C 14.7; D not known; E 21.4; F 41.7.

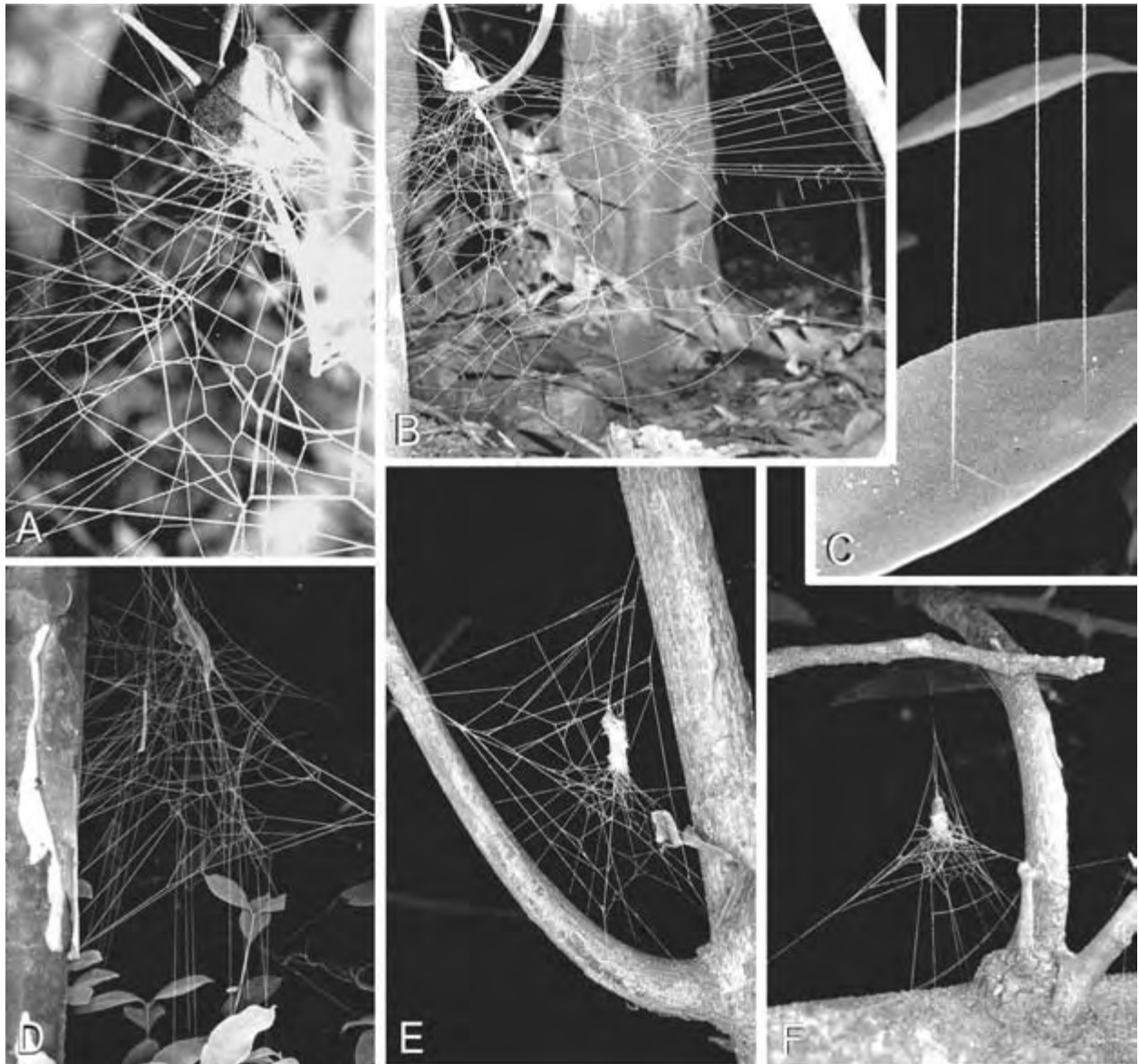


Figure 44 *Achaearanea*. A–B *A. sp. nr. tepidarium* II #3655. Lateral view. There were more or less horizontal gumfoot lines that were more or less perpendicular to substrates on both sides of the web. C–D *A. sp. 7* (Ranamofana, Madagascar). C, spider rested inside a rolled leaf retreat suspended in the uppermost section of the web, straight lines are gumfoot lines, both to the tree trunk and to leaves; E–F *A. sp. 4* (Fanies Island, S. Africa). Spider in a silk reinforced leaf retreat suspended in web, gumfoot lines leading to the substrate below the retreat. Approximate width of the photos (in cm): A, 7.2 B, 24.9; C, 4; D, 10; E, 7; F, 7.

single case. The sample is too small to test for possible trends. Our tentative overall impression is that the rapid divergence in theridiid webs may have a similar explanation to that for the diversity in *Wendilgarda* webs, but that the behavioural imprecision hypothesis clearly needs further testing.

The limitations and trends of this study

The reader should keep in mind several serious limitations of this study. There are a number of problems associated with the assumptions made in tracing the phylogeny of web

characters (see the methods section). In addition, we photographed only a single web for many species, and the webs of several theridiids show substantial intraspecific variability (Table 2). Theridiids probably often adjust the forms of their webs to the spaces they have available in which to build, and also add lines, including sticky lines, on subsequent nights (Lamoral, 1968; Xavier *et al.*, 1995; Benjamin & Zschokke, 2003; Jürger & Eberhard, 2006; Barrantes & Weng, 2007) (exceptional species that rebuild their webs daily, like most orb weavers, include *Phoroncidia* spp. and *Latrodectus indistinctus* in South Africa – Lamoral, 1968). We thus supposed, for instance, that the spider in the web of

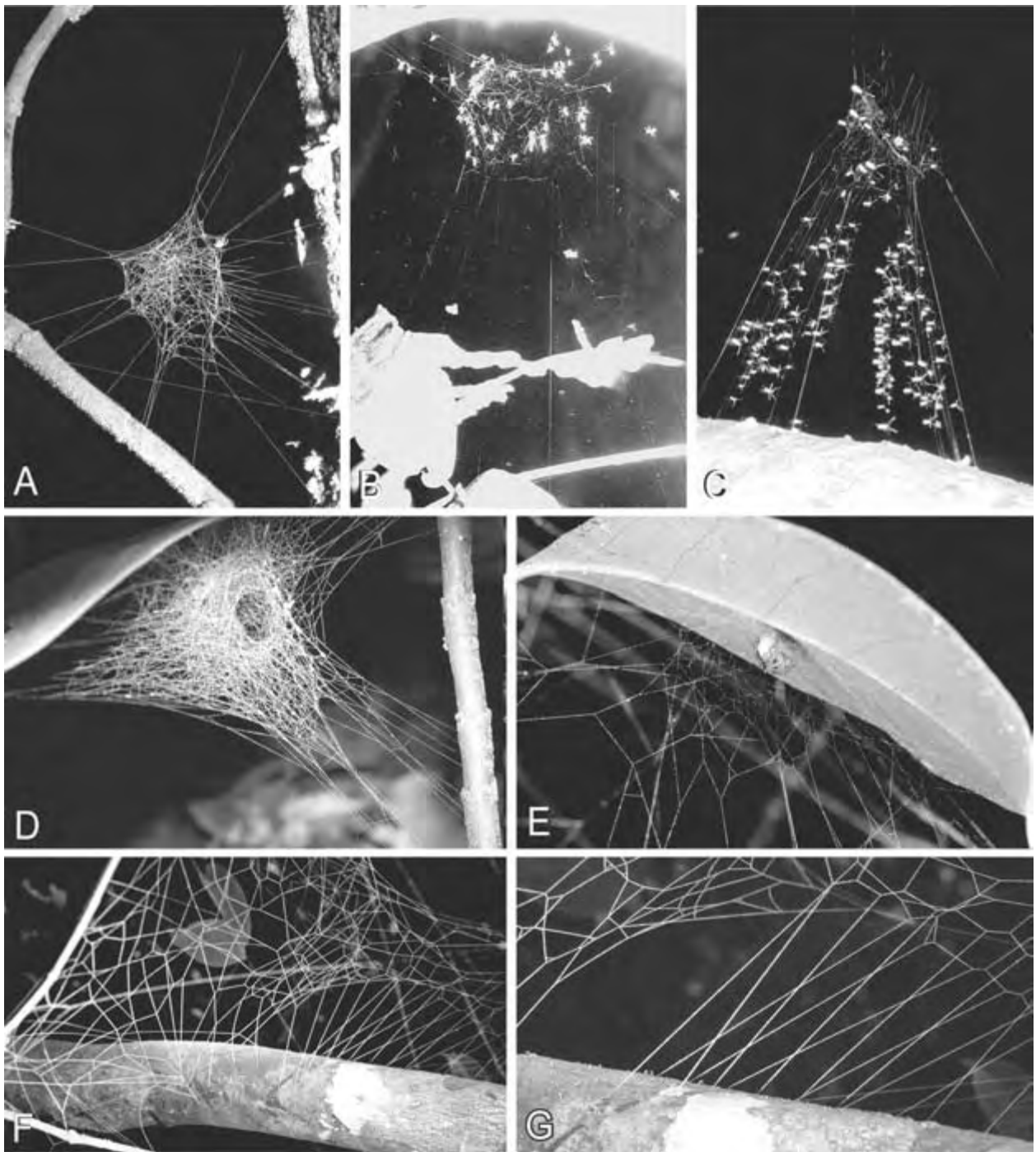


Figure 45 *Achaearanea*. A *A. sp. 9* (Ecuador). Spider resting inside central 'ball' of silk, most of the long lines are gumfoot lines; B *A. machaera* #1253. An aggregation of small flies rested on the web. C *A. sp.* (Guyana). An aggregation of *Nematoceros* flies on web; D *A. sp. 8* (Ecuador), spider rested inside the central tube, long lines to stem are gumfoot lines; E *A. sp. 3* (Ranamofana, Madagascar), spider rested on underside of live leaf; F–G *A. sp. 5* (Ranamofana, Madagascar), gumfoot lines attached to non-sticky tangle web. Approximate width of the photos (in cm): A, 6.2 B, 7.6; C, 5; D, 6; E, 8; F, 25; G, 10.

Species	Character #	Character states and references
A. Differences within species		
Theridiidae <i>Achaearanea florendita</i>	6	clear 'star' web (Fig. 37C); tangle is clearly not spherical and contains large curled leaf (Fig. 37A)
Theridiidae <i>Achaearanea</i> sp. nr. <i>isana</i> II	4	some gumfoot lines sticky only at tip Fig 41D); others also sticky part way up line (Fig. 41E) tangle not sticky (Fig. 41D); about half of the tangle lines sticky (Fig. 41F)
Theridiidae <i>Achaearanea</i> sp. nr. <i>kaspi</i>	2, 4	nearly entire 'gumfoot' line sticky (not just at tip) and also a few tangle lines sticky (Fig. 41A); only tips of gumfoot lines sticky (Fig. 41B)
Theridiidae <i>Achaearanea maricaoensis</i>	19	tent retreat in tangle (Fig. 40B); dead leaf retreat in tangle (Fig. 40D)
Theridiidae <i>Achaearanea maricaoensis</i> , nr. <i>porteri</i>	19	retreat single curled leaf; tent (which in <i>A. nr. porteri</i> includes bits of debris)
Theridiidae <i>Achaearanea taeniata</i>	–	very large tangle above gumfoot lines (protection? knockdown?) (Fig. 39C); small tangle above gumfoot lines (Fig. 39A)
Theridiidae <i>Achaearanea tessellata</i>		retreat single curled leaf; retreat small pieces debris (Fig. 42F)
Theridiidae <i>Anelosimus pacificus</i>	19	retreat not modified (Fig. 16A); retreat formed by connecting living leaves with silk (notes)
Theridiidae <i>Argyrodes antipodiana</i>	1, 10, 16	sticky tangle (Whitehouse, 1986); only dry lines to steal prey from other spiders or kill them (Whitehouse, 1986)
Theridiidae <i>Chryso sulcata</i>	–	long sticky lines between leaves (Fig. 19D); same across fold in single large leaf (notes)
Theridiidae <i>Enoplognatha ovata</i>	10, 16	web of own (Nielson, 1931; Bristowe, 1958); steal prey and kill other, linyphiid and theridiid spiders (Bristowe, 1958).
Theridiidae <i>Keijia tinctoria</i>	10	no web of own, prey on other spiders (Jones 1983); dense tangle with sheet below (Fig. 23D)
Theridiidae <i>Latrodectus geometricus</i>	1	gumfoot lines (usual); gumfoot lines missing when web is high off the ground (Lamoral, 1968)
Theridiidae <i>Latrodectus hesperus</i>	4	gumfoot lines; sticky glue extends up line up to 3 cm, and occasionally present in middle layer (Kaston, 1970)
Theridiidae <i>Latrodectus mactans</i>	1, 4	gumfoot lines; no gumfoot lines (usually). No sticky lines in middle layer; sticky lines in middle layer (Kaston, 1970)
Theridiidae <i>Neottiura</i> sp.	5	long lines more or less radial and sticky all along and a few branch (Fig. 31); long lines with only distal 1/3 sticky, most or all branch near tip notes
Theridiidae <i>Theridion hispidum</i>	19	spider under living leaf or twig; curl living leaf
	7	web planar (Fig. 25A, D, E); not planar (Fig. 26C, D)
Theridiidae <i>Theridion nigroannulatum</i>	19	retreat under leaf (Fig. 29H); retreat in curled leaf (Fig. 29B)
Theridiidae <i>Theridion</i> nr. <i>melanosticum</i>	7	web planar; web not planar (Fig. 26E notes)
Theridiidae <i>Theridion purcelli</i>	3	gumfoot/no gumfoot lines (Lamoral, 1968)
Synotaxidae <i>Synotaxus turbinatus</i>	–	regular array of sticky lines in rectangular modules (Fig. 2D); without modules (Fig. 2G)
Synotaxidae <i>Synotaxus ecuadorensis</i>	–	regular array of sticky lines in rectangular modules (Fig. 3C); without modules (Fig. 3D, E)
B. Differences within genera		
<i>Achaearanea</i> sp. 3	18	retreat under living leaf (Fig. 45E)
<i>Achaearanea</i> (several)		retreat single curled leaf (e.g. Fig. 39A, 44D)
<i>Achaearanea tessellata</i> , sp.4		small pieces of plant debris (some) (Fig. 44E, F)
<i>Achaearanea</i> (several)	6	typical gumfoot (e.g. Fig. 41D)
<i>Achaearanea</i> sp. 1, 2, 6, 9, <i>florendita</i> , <i>hirta</i>		star web (e.g. Figs. 37C, 45A, B)
<i>Achaearanea taeniata</i>	–	gumfoot lines attached directly to tangle near mouth of retreat (Fig. 39D)
<i>Achaearanea florens</i> , nr. <i>islana</i>		gumfoot lines attached to lines more or less parallel to substrate in tangle below mouth of retreat (Fig. 37B, 41D)
<i>Achaearanea</i> nr. <i>tepidariorum</i>		gumfoot attached on both sides of central sheet (Fig. 36D)
<i>Achaearanea tessellata</i> , nr. <i>porteri</i>	11	dense horizontal sheet at or near lower edge of dense tangle (Fig. 43A, E)

Table 2 The flexibility of web design within different taxonomic categories of theridiids (data for species not followed by references are from this paper; "–" refers to characters that were not included in our analysis for lack of sufficient data).

Species	Character #	Character states and references
<i>Achaearanea</i> (several)		no sheet
<i>Achaearanea</i> nr. <i>porteri</i> (#3609)	20	dense vertical sheet covers web in groove of tree trunk
<i>Achaearanea</i> nr <i>porteri</i> (#3696), others		no vertical sheet at edge of web
<i>Achaearanea</i> (several)	22	no sheet
<i>Achaearanea triguttata</i> , nr. <i>porteri</i>		dense sheet at edge that 'protects' web (Fig. 35D, 36D, 42G,H)
<i>Achaearanea apex</i>		
<i>Ameridium</i> sp. 1 (#157), <i>lathropi</i>	1	typical gumfoot (Fig. 24A, notes)
<i>Ameridium paidiscum</i>		no sticky lines seen (Fig. 24C)
<i>Anelosimus</i> (several)	12	cup-shaped sheet under dense tangle (solitary and group living species) (e.g. Fig. 15B, F, G)
<i>Anelosimus eximius</i>		horizontal sheet under dense tangle (large colonies) (Fig. 14E)
<i>Anelosimus vittatus</i> (= <i>T. vittatum</i>), <i>pacificus</i>		no sheet, delicate web abundantly provided with small balls of glue (Fig. 16, Nielsen, 1931)
<i>Chrosiothes tonala</i>	10, 18	very few dry lines, used only as sites from which to drop onto termite columns, no retreat (Eberhard, 1991)
<i>Chrosiothes</i> nr. <i>portalensis</i>		dense, very regular horizontal sheet under thick tangle, single curled leaf retreat (Fig. 8, 9)
<i>Argyrodes antipodiana</i>	1, 10	sticky tangle (Whitehouse, 1986)
<i>Argyrodes argyrodes</i> , <i>elevatus</i>		dry lines only in order to gain access to webs of other spiders to steal prey (Kullmann, 1959a; Vollrath, 1979)
<i>Keijijia</i> sp. (#1192)	1	no sticky lines, at least in outer 2/3 of a dense tangle (Fig. 23C)
<i>Keijijia</i> sp. n (#2331)		lines edge more sparse tangle almost all covered with glue (Fig. 23E), possibly egg sac web
<i>Keijijia</i> nr. <i>tincta</i>		small sheet in lower part of dense tangle between leaves (Fig. 23D)
<i>Latrodectus bishopi</i>	19	roll leaf into cone (Szlep, 1966)
<i>Latrodectus</i> (several)		retreat in shelter at or beyond edge (Szlep, 1965; Lamoral, 1968; Kaston, 1970; Benjamin and Zschokke, 2003)
<i>Latrodectus variolus</i> , <i>bishopi</i> , <i>mactans</i>	3, 4	sticky lines in tangle, usually no gumfoot lines (Szlep, 1966; Kaston, 1970)
<i>Latrodectus geometricus</i> , <i>hesperus</i> , <i>indistinctus</i>	3	sticky balls on gumfoot lines, usually not in tangle (Lamoral, 1968; Benjamin & Zschokke, 2003; Kaston, 1970)
<i>Latrodectus pallidus</i> , <i>revivensis</i>	13	small sheet ('platform') in tangle with radial organisation (Szlep, 1965)
<i>Latrodectus tridecimguttatus</i> , <i>variolus</i>		sheet in tangle without radial organisation (Szlep, 1965)
<i>Steatoda moesta</i>	1, 3	2 horizontal sheets, no sticky lines (Fig. 7, notes)
<i>Steatoda lepida</i> , <i>bipuncta</i>		gumfoot under approx sheet (Lamoral, 1968) (Nielsen, 1931 says sheet also has sticky lines)
<i>Theridion impressum</i>	8	'random' sticky lines in dry tangle (Benjamin and Zschokke, 2003)
<i>Theridion pictum</i> , <i>hispidum</i>		central trellis-work (Bristowe, 1958, Fig. 26B, F))
<i>Theridion evexum</i> , <i>adjacens</i>	18, 19	curl living leaf to form retreat (Fig. 20B, 28D)
<i>Theridion nigroannulatum</i>		under unmodified leaf (some) (Fig. 29D, H, 30E)
<i>Theridion</i> sp. 2		under leaves connected with silk (Fig. 28F)
<i>Theridion hispidum</i> , <i>melanosticum</i>	9	isolated or small groups of balls of glue (Figs. 25D, 26F)
<i>Theridion orlando</i> , <i>schlingeri</i> , <i>adjacens</i>		contiguous stretches covered with balls (Fig. 27B, D, 28D)
<i>Theridion hispidum</i> , sp. 2	11	planar, non-horizontal sheet (Figs. 25A, 28E)
<i>Theridion adjacens</i>		3-dimensional (Fig. 28D)
<i>Tidarren haemorrhoidale</i> , <i>Tidarren sisypoides</i>	11	dense non-sticky tangle with domed sheet in its midst (Fig. 32D)
<i>Tidarren</i> sp. SAE 10–9A ¹		moderate tangle with detritus retreat, dense cup-shaped sheet at bottom

Table 2 Continued

Characters	Taxa
1(1) no sticky silk	some <i>Steatoda</i> ; some <i>Latrodectus</i> ; some <i>Chrosiothes</i> ; <i>Thwaitesia</i> ; <i>Selkirkiella</i> ; <i>Argyrodes</i> and related genera; <i>Cephalobares</i> ; <i>Meotipa</i> ; some <i>Ameridion</i> ; some <i>Achaearanea</i>
2(1) no sticky line to substrate	Synotaxidae; <i>Theridon</i> spp.; <i>Achaearanea</i> spp.
3(1) no gumfoot	some <i>Latrodectus</i> ; <i>Phoroncidia</i> ; <i>Chryso</i> spp.; <i>Rugathodes</i> ; some <i>Theridion</i> ; some <i>Achaearanea</i>
4(1) sticky to substrate not sticky at tip	some Nesticidae;
5(1) distal ends gumfoot split	<i>Neottiura</i> sp.; <i>Nesticus</i> sp. and <i>Eidmanella pallida</i> (Coddington, 1986; Griswold et al., 1998)
6(1) star gumfoot webs	<i>Chryso spiniventris</i> (Benjamin & Zschokke, 2003); <i>Achaearanea</i> spp.; <i>Theridion</i> sp. (Agnarsson, 2004)
7(0) sticky lines in tangle	<i>Argyrodes antipodiana</i> (Whitehouse, 1986); <i>Theridion</i> spp.; <i>Achaearanea</i> spp.; <i>Chryso</i> spp.; <i>Theridula</i> .sp. n
7(1) sticky lines sheet, or more or less planar array	<i>Synotaxus</i> spp.; some <i>Chryso</i> ; some <i>Latrodectus</i> ; some <i>Theridion</i>
9(1) isolated balls sticky material	<i>Synotaxus</i> spp. (Eberhard, 1977, 1995); <i>Theridion hispidum</i> and <i>T. nr. melanosticum</i>
11(1) tightly meshed horiz. Sheet in extensive tangle	<i>Achaearanea tessellata</i> and <i>A. nr. porteri</i> ; <i>Chrosiothes portalensis</i>
12(2) cupped sheet at bottom of tangle	<i>Anelosimus</i> spp. (some social); <i>Tidarren</i> sp. (SAE10–9A); <i>Achaearanea wau</i> (social) (Lubin, 1982)
12(3) planar, open-meshed sheet to which vertical adhesive lines are attached	<i>Latrodectus</i> spp.; <i>Achaearanea nr. tepidariorum</i>
14(3) few, long, nonsticky lines	<i>Ariamnes attenuatus</i> (Eberhard, 1979); <i>Thwaitesia</i> sp. (Agnarsson, 2004); <i>Chrosiothes tonala</i> (Eberhard, 1991)
17(0) retreat at edge or beyond edge	<i>Theridium sisyphium</i> (Nielsen, 1931; Bristowe, 1958); <i>Latrodectus</i> spp. (Szlep, 1965)
19(4) curl living leaf	<i>Chryso</i> spp.; <i>Enoplognatha</i> spp. (Nielsen, 1931; Bristowe, 1958; Shinkai & Takano, 1987); <i>Latrodectus bishopi</i> (Szlep 1966); <i>Theridion</i> spp. (Comstock, 1967; Shinkai & Takano, 1984)
21(2) rest against leaf	<i>Synotaxus</i> spp.; <i>Chryso</i> spp.; <i>Theridion</i> spp.
22(1) dense sheet at edge of web (probably protective)	<i>Theridion melanurum</i> (Nielsen, 1931); <i>Achaearanea rostrata</i>
Other traits	
Prey on other spiders	<i>Enoplognatha ovata</i> (Bristowe, 1958); <i>Neospintharus</i> spp. (e.g. Whitehouse et al., 2002); <i>Theridion tinctum</i> (Jones, 1983); <i>Rhomphaea</i> spp. (Whitehouse, 1987; W. Eberhard unpub.), <i>Thwaitesia</i> spp. (Agnarsson, 2004), and <i>Faiditus</i> spp. (W. Eberhard unpub)
Mouth of retreat is continuous with lower surface sheet	<i>Tidarren</i> spp.; <i>Chrosiothes nr. portalensis</i>
Long sticky vertical lines, and a small dry tangle above	<i>Chryso ecuadorensis</i> ; <i>Gaucelmus calidus</i> (Nesticidae)
Sticky lines across depression in leaf	<i>Chryso vallensis</i> ; <i>Neottiura</i> sp. (some webs in each species)
Steal prey of other	<i>Enoplognatha ovatum</i> (Bristowe, 1958); <i>Argyrodes</i> spp, <i>Neospintharus</i> , <i>Faiditus</i> spp. Agnarsson, 2004), <i>Achaearanea tepidariorum</i> (Kullmann, 1959b)
Approximately radial lines converge at retreat ²	<i>Achaearanea tessellata</i> (Jürger and Eberhard, in press); <i>A. apex</i> (Fig. 35G); <i>Latrodectus pallidus</i> (Szlep, 1965); <i>Neottiura</i> sp. (Fig. 31C)

Table 3 Especially striking convergences in web traits in different groups of Theridiidae and closely related families documented in Figs 49–59; independent derivations separated by ‘;’ (data are from webs in photographs in this study unless otherwise specified).

¹Sketchy verbal descriptions suggest possibly similar webs for other synotaxid genera such as *Meringa*, *Mangua*, *Runga*, and *Chileotaxus* (Griswold et al., 1998).

²or at resting site.

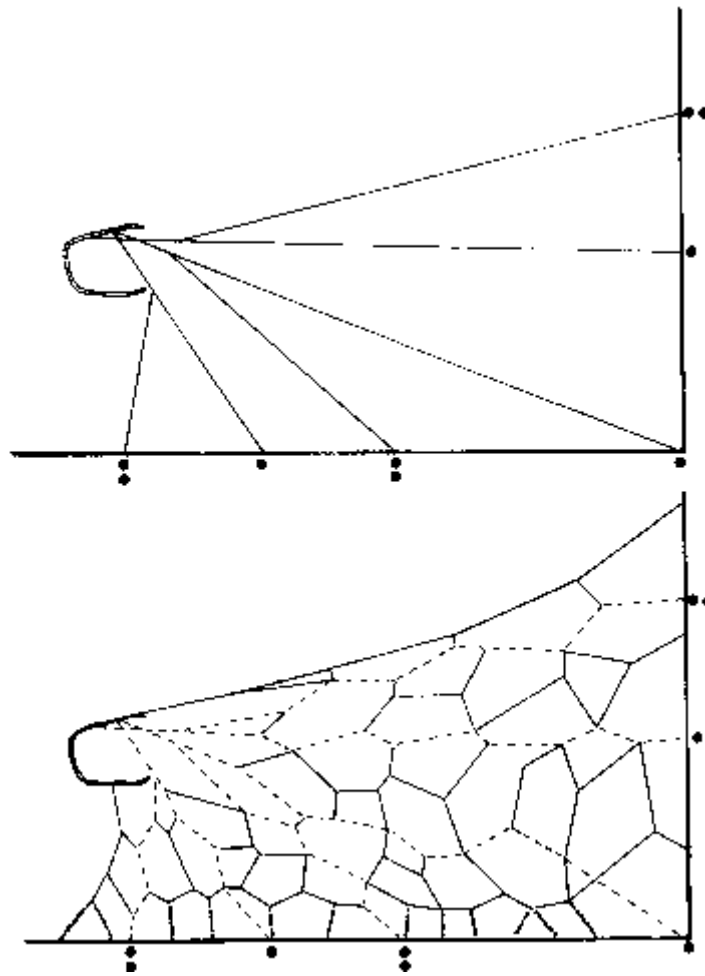


Figure 46 Schematic representation of the construction process in *Steatoda lepida*, showing how an orderly placement of lines can be obscured by subsequent lines (after Lamoral, 1968).

A. maricaoensis with only a single gumfoot line (Fig. 40E) would have subsequently built other gumfoot lines as in the webs of other individuals of this species (Fig. 40B-D), but cannot be sure. We have probably seriously underestimated the variation in some species. In general we have no data on possible ontogenetic changes in the species we studied, nor data on possible interpopulation variation (as occurs e.g. in *Anelosimus eximius* – J. Purchell, pers. comm.). In essence, we know that certain traits occur, but generally do not know the ranges of traits that occur. An underestimate of this sort will bias us to underestimate homoplasy (in cases in which we have failed to see the homoplasious variants), but not to overestimate it. Similarly, we have data on relatively few species in each genus; calculations based very conservatively on the 2300 known species of theridiids (thus ignoring the substantial numbers of undescribed species) and the 166 species in this study suggest a coverage on the order of only 7%. Again, the expected effect of this ignorance will be to underestimate the amount of homoplasy. In general, the limitations

of this study have probably caused us to underestimate rather than overestimate the amount of support for one of our two major conclusions, that convergence is especially widespread in theridiid webs.

Another problem is the unsettled nature of the taxonomy of several theridiid genera. Recent taxonomic work on *Anelosimus*, for example, has redistributed ‘*Anelosimus*’ species into nine different theridiid genera (Agnarsson, 2004, 2005, Agnarsson & Kuntner, 2005, Agnarsson *et al.*, 2007). Some other genera such as *Theridion*, *Achaeearanea* and *Chrysso* also appear to be polyphyletic. One is led to question whether the combination of striking within-taxon diversity and between taxon convergence may be due to taxonomic error. This explanation is particularly appealing, for instance, in the genus *Chrosiothes*. However, even if groups like *Chrosiothes* turn out not to be monophyletic, it seems certain that their current members are all related (e.g. they are all spintharines, in the case of *Chrosiothes*); hence the within-taxon diversity would not disappear, but would simply

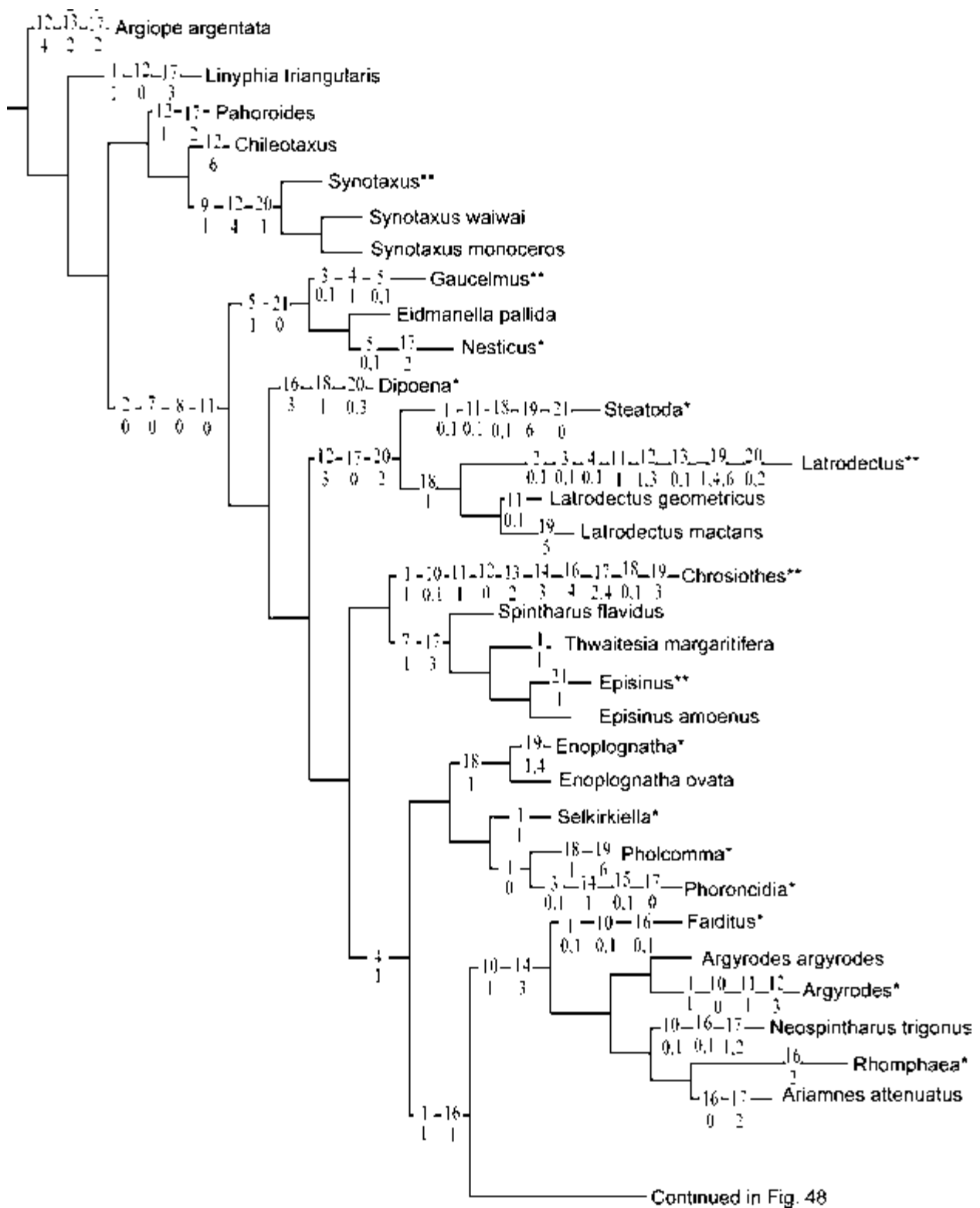


Figure 47 All characters are mapped on the consensus phylogeny, part 1. Numbers inside circles are character numbers, numbers below refer to character states, more than one state are given when polymorphism is present

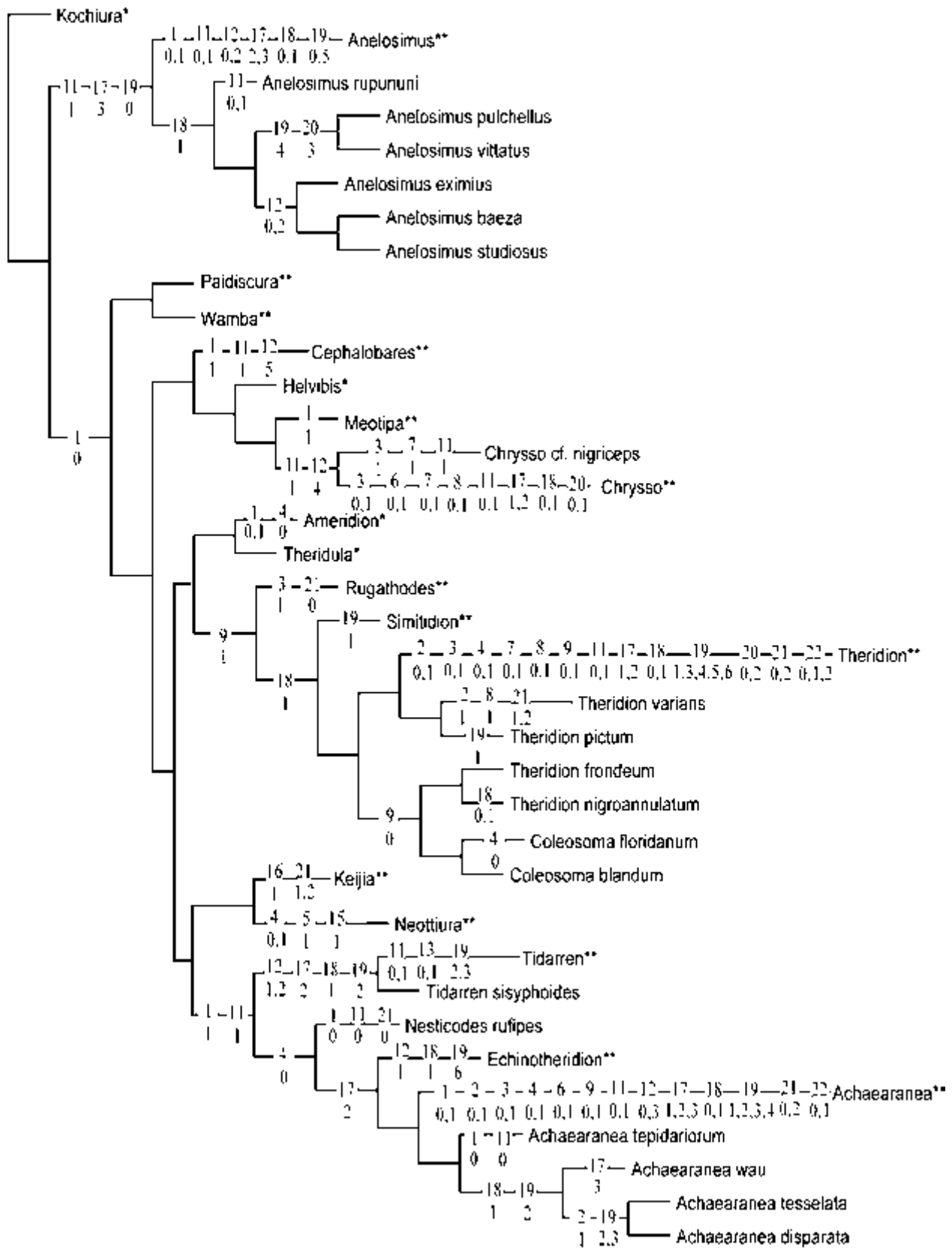
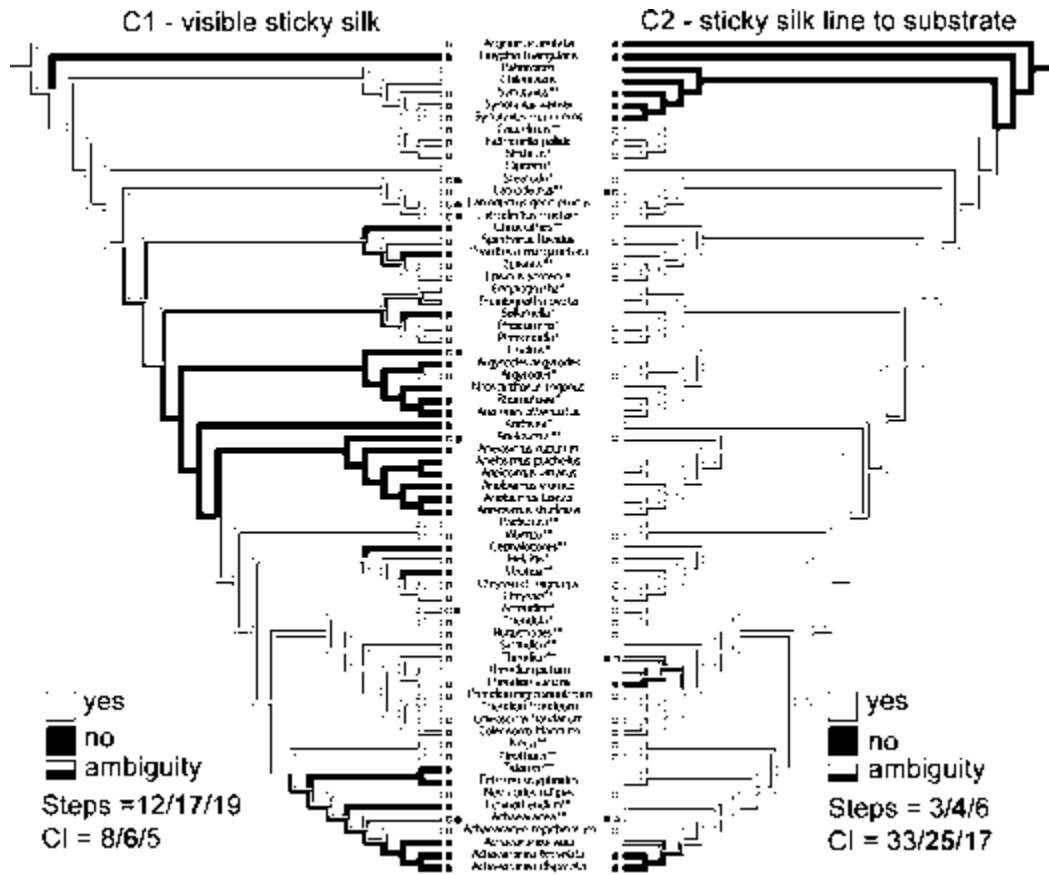


Figure 48 All characters are mapped on the consensus phylogeny, part 2. Numbers inside circles are character numbers, numbers below refer to character states, more than one state is given when polymorphism is present



Figures 49–59 Mapping of individual characters. States are indicated with boxes as shown in legend, and matching colour in branches, polymorphism is shown by more than one box associated with a taxon, ambiguity by bi-coloured branches. Steps are counted as minimum ignoring polymorphism/minimum counting polymorphism (but ignoring states in composite taxa if not unique, i.e. if present in some congeners)/maximum counting polymorphism. CIs are calculated accordingly for each step counting scheme. Bold numbers are the preferred. Asterisk identify dummy taxa, double asterisk novel branches (see Methods for detail). **Figure 49** Mapping of characters 1–2.

be transferred to a more inclusive (subfamily) taxon. Also, the general overall agreement between the morphological and molecular phylogenies of theridiids (Agnarsson, 2004; Arnedo *et al.*, 2004) indicates that evolutionary flexibility, not mistaken phylogenetic groupings, explains the majority of the observed homoplasies. As is clear from Figs 47–48, only major rearrangements of the phylogenetic tree would dramatically reduce web character homoplasy, and would thus strongly contradict both morphological and molecular characters.

Still another potential problem is that we optimised characters in the phylogenies using parsimony. Parsimony favours homology hypotheses over convergence hypotheses; but one of

the major findings of this study is that convergence is rampant in theridiid webs. Convergence may be even more common than we have conservatively estimated using parsimony reconstruction. We may well be mistaken, for instance, in supposing that the gumfoot design is plesiomorphic for theridiids. The overall effect of using parsimony, however, will necessarily be to underestimate rather than overestimate the total numbers of convergences.

In sum, several of the limitations of this study reinforce rather than weaken our two major general conclusions. They seem likely to have caused us to underestimate rather than overestimate both the frequency of homoplasy, and that of intrageneric divergence.

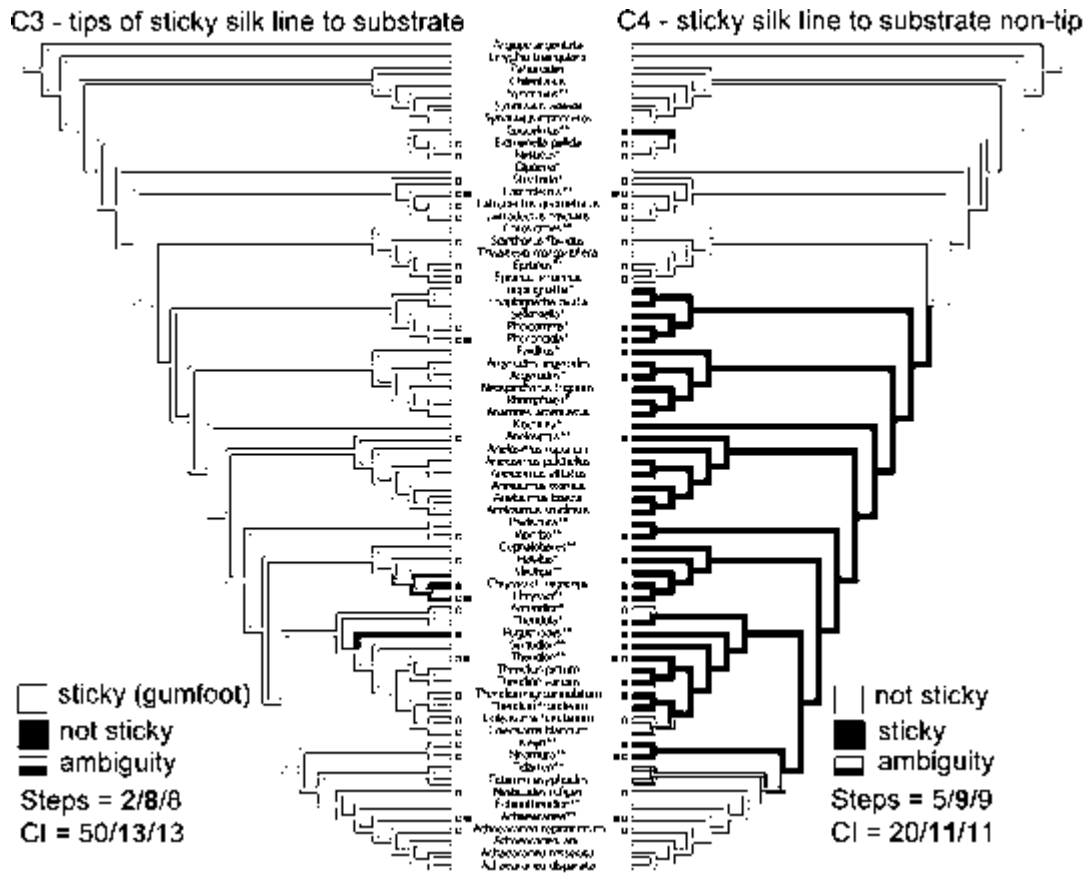


Figure 50 Mapping of characters 3–4.

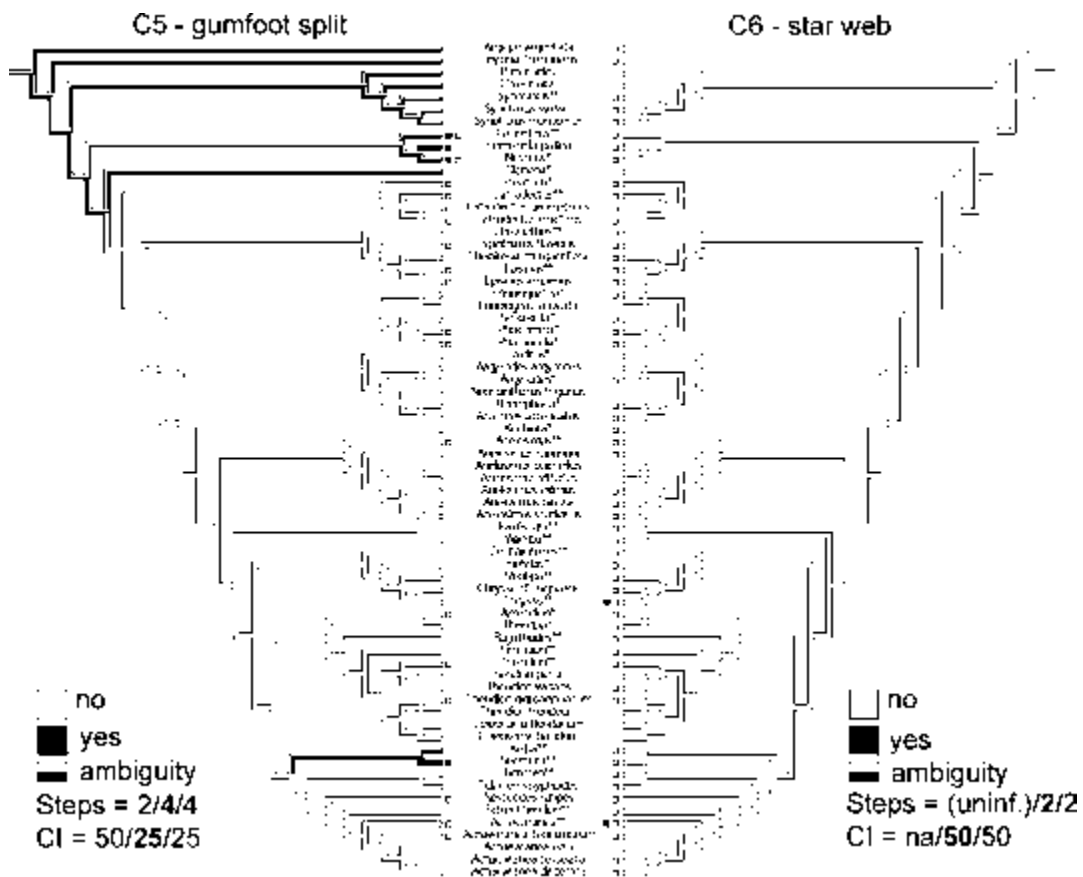


Figure 51 Mapping of characters 5–6.

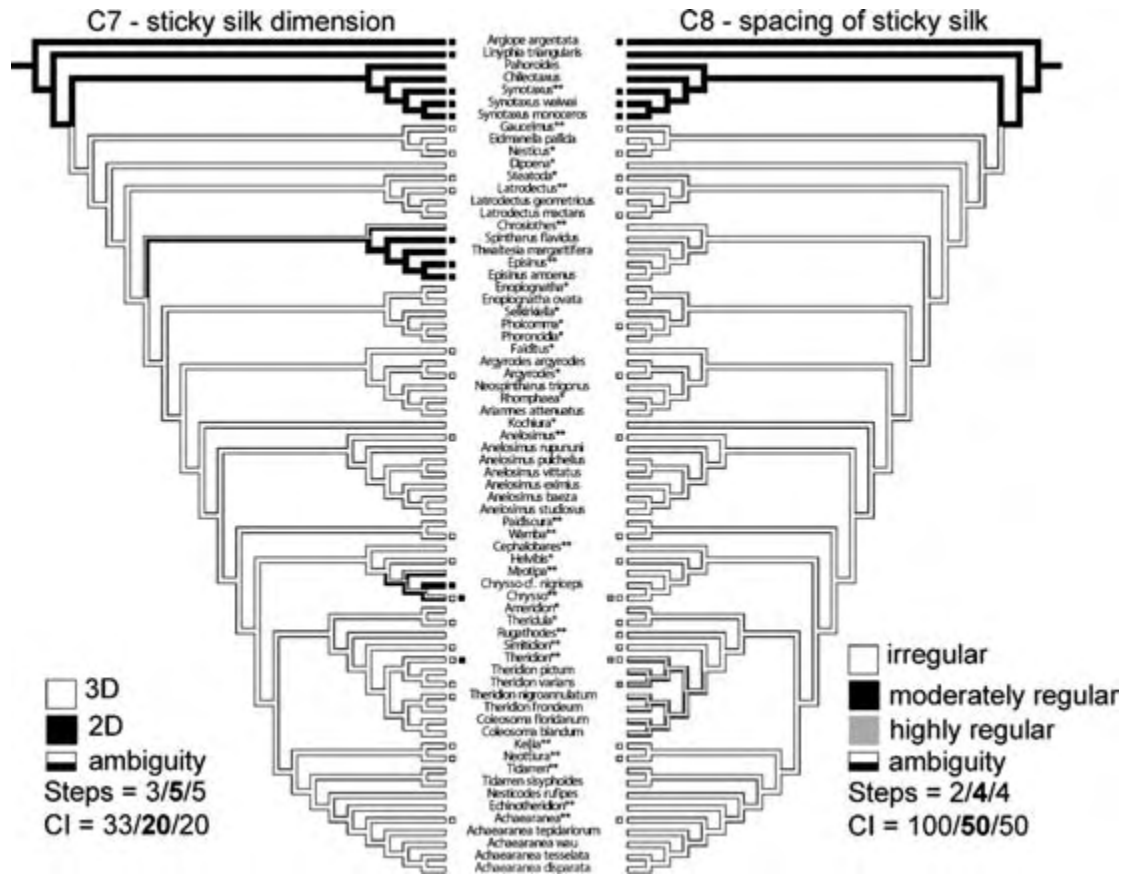


Figure 52 Mapping of characters 7–8.

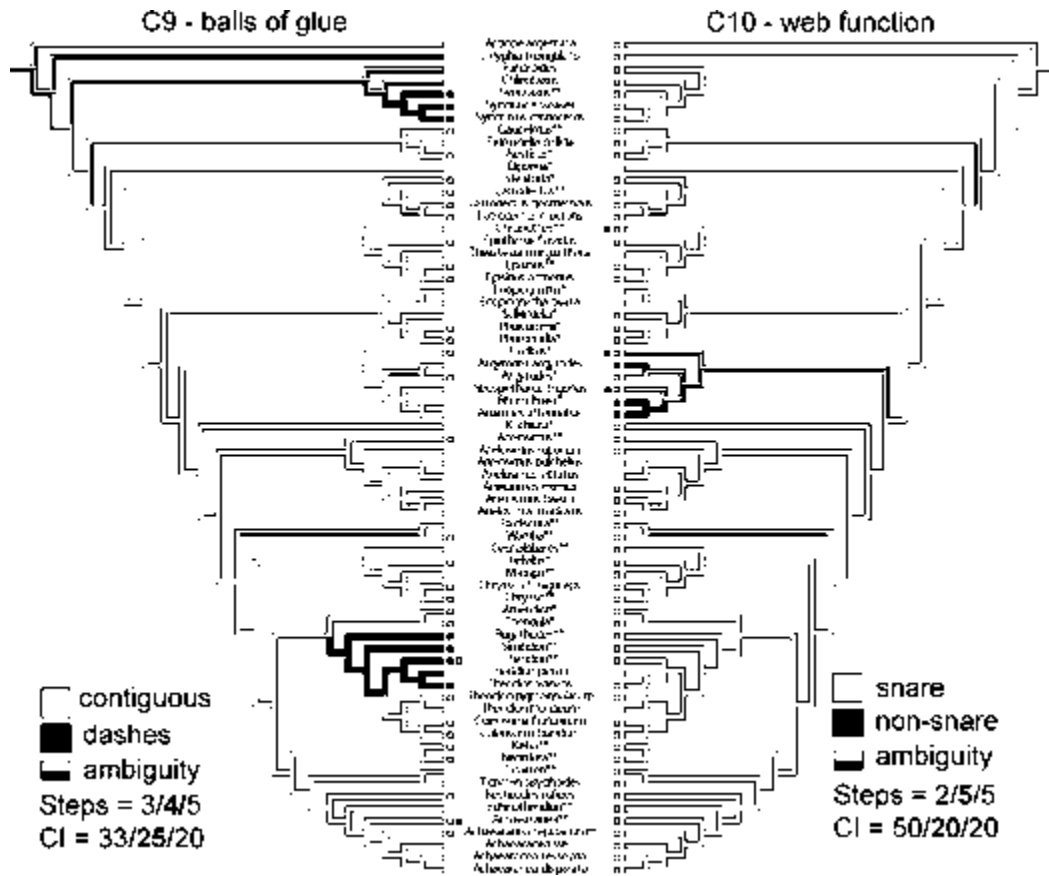


Figure 53 Mapping of characters 9–10.

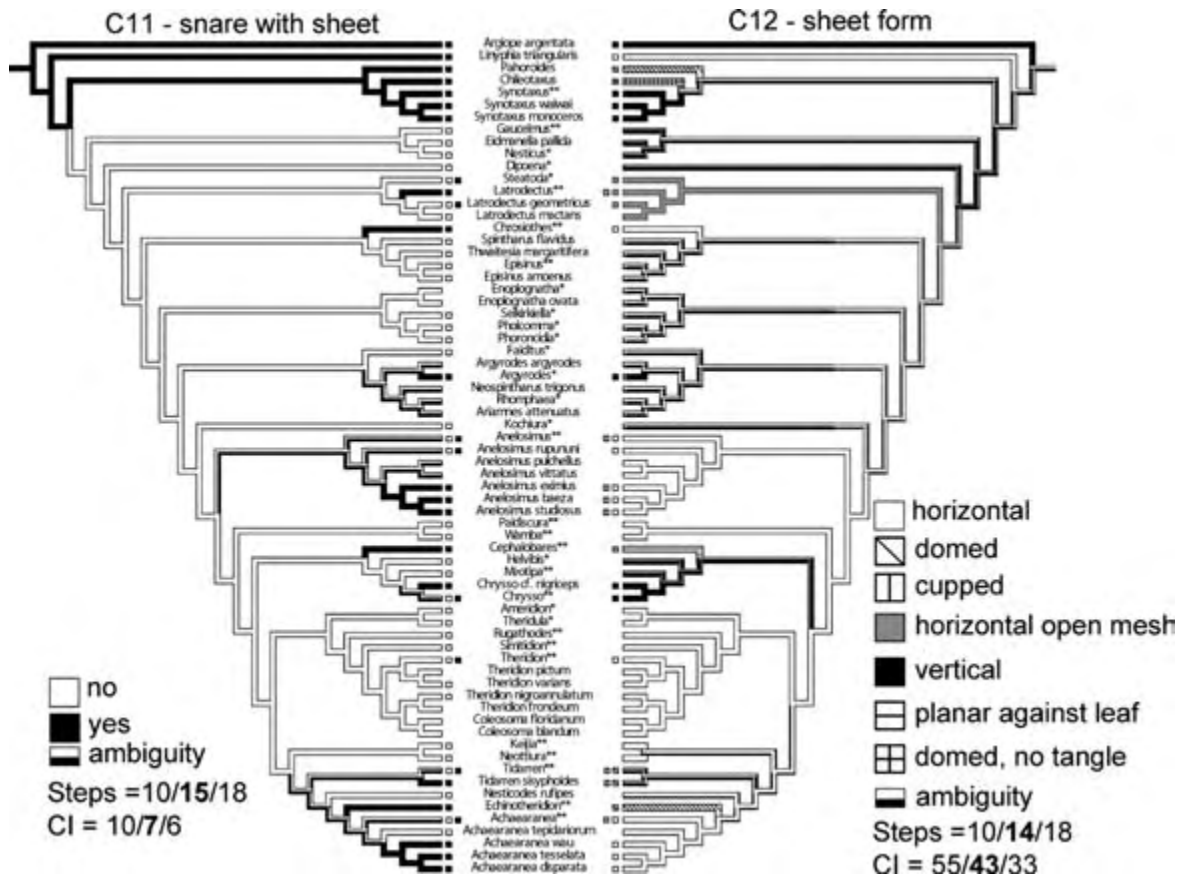


Figure 54 Mapping of characters 11–12.

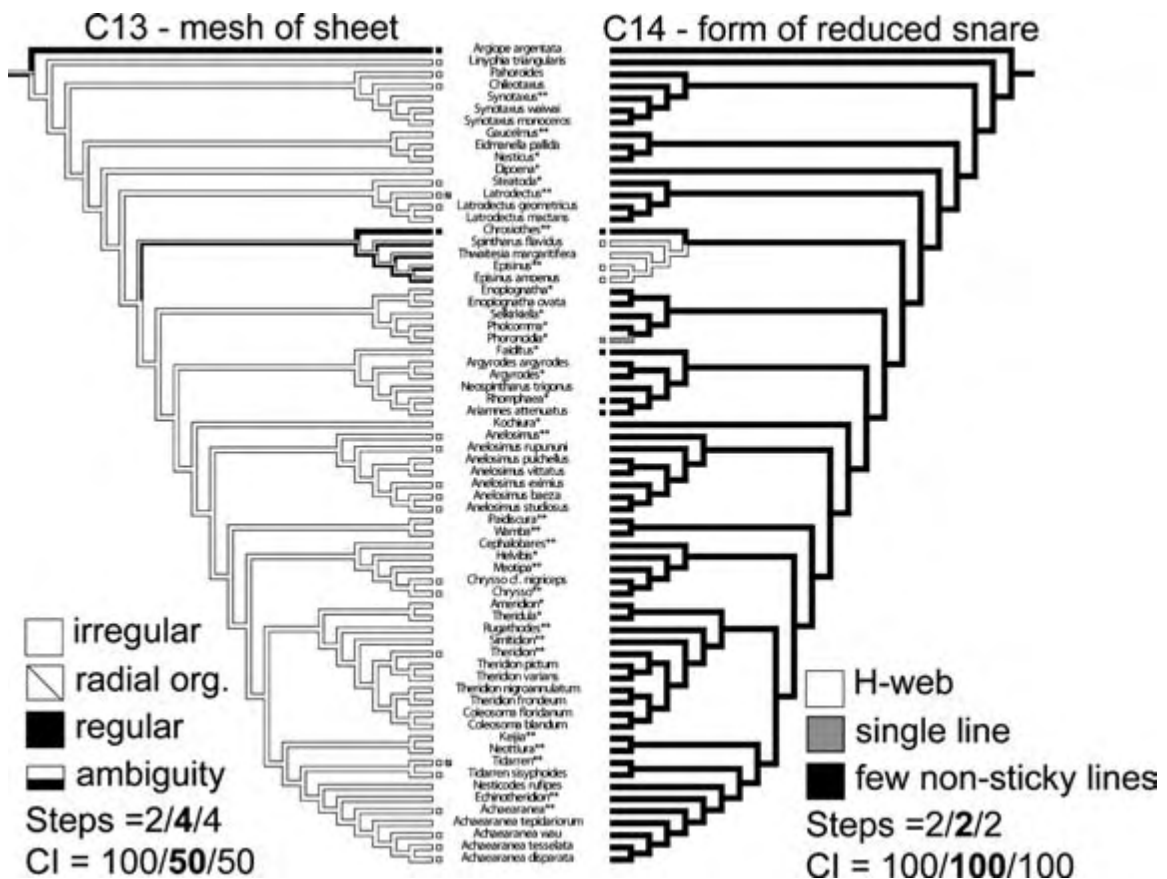


Figure 55 Mapping of characters 13–14.

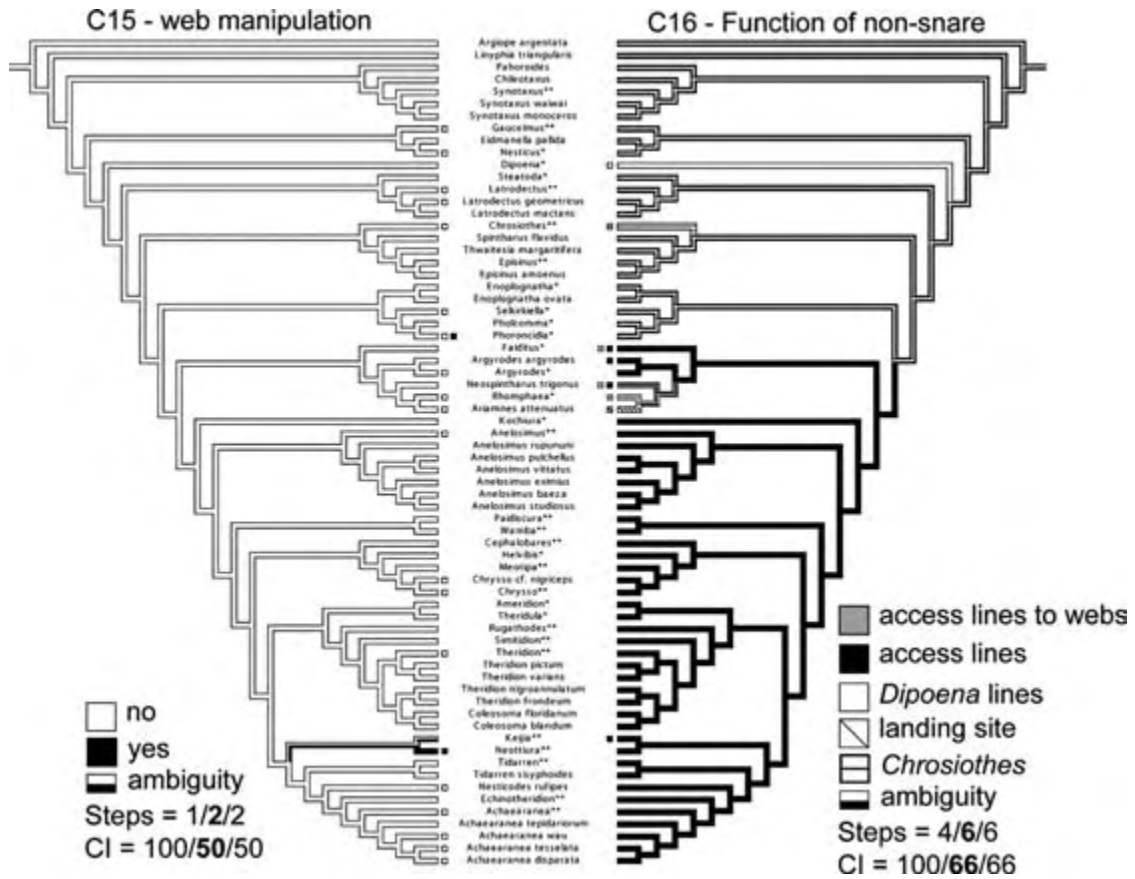


Figure 56 Mapping of characters 15–16.

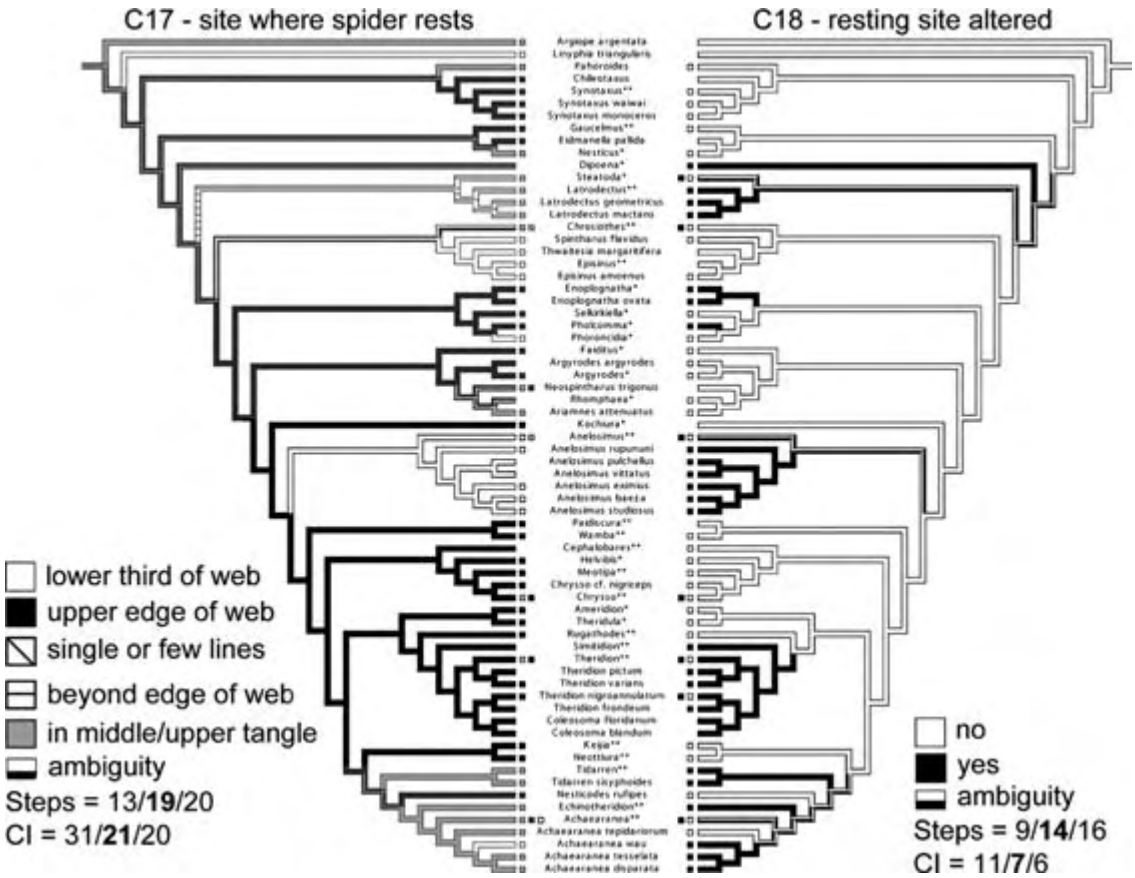


Figure 57 Mapping of characters 17–18.

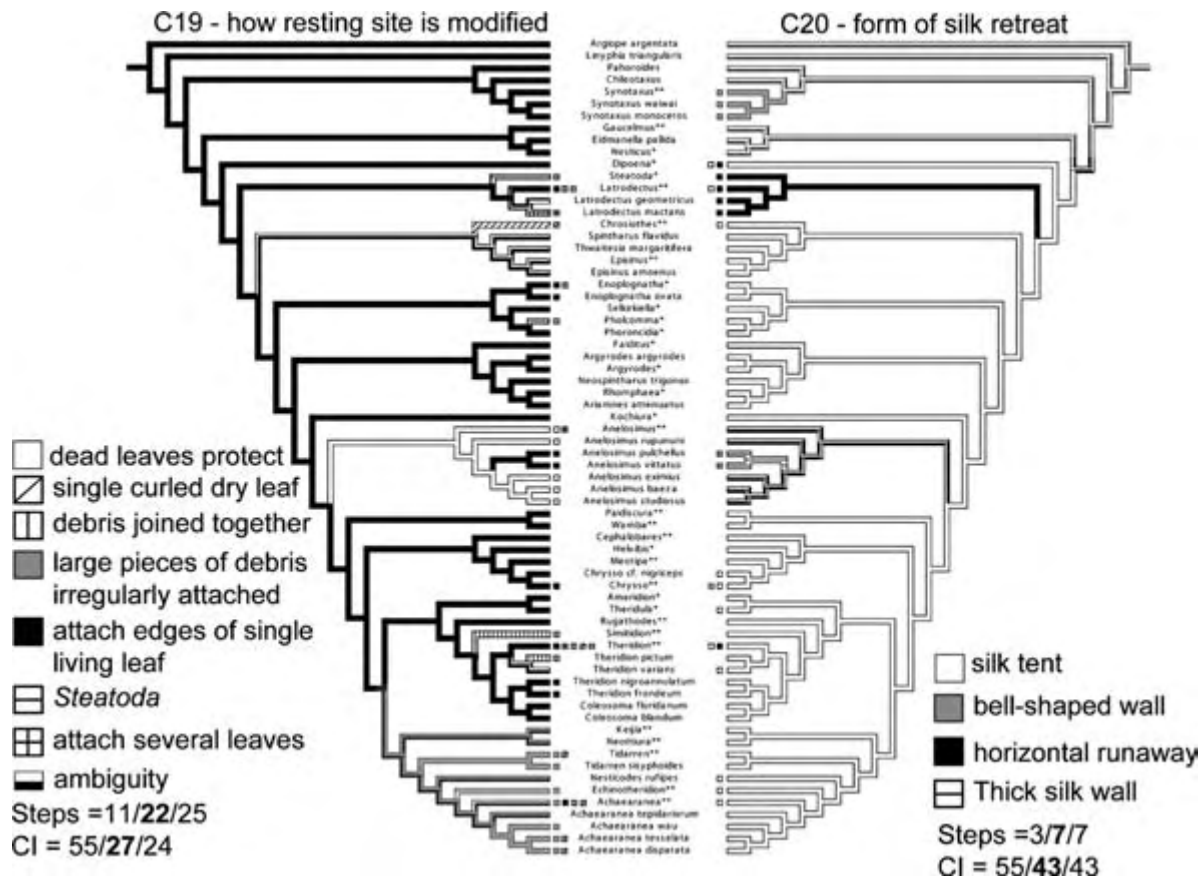


Figure 58 Mapping of characters 19–20.

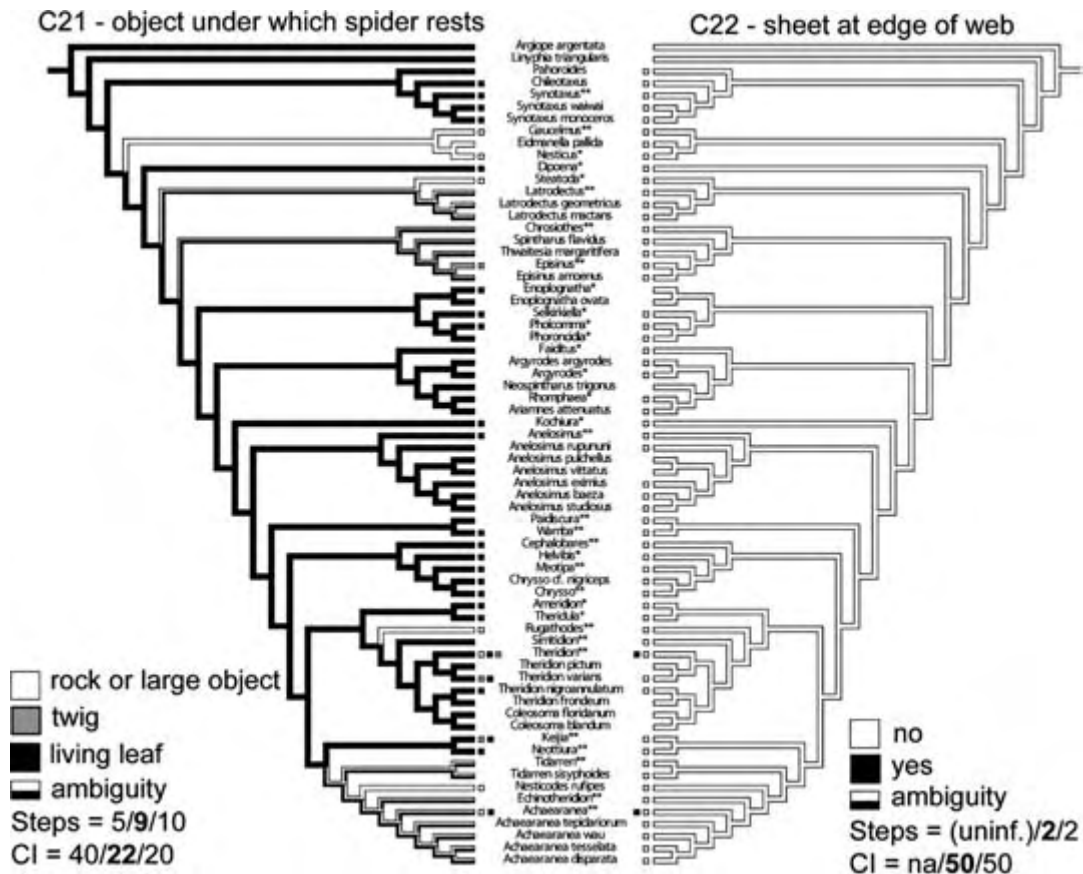


Figure 59 Mapping of characters 21–22.

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Appendix 1

Character descriptions and comments

Webs

1. Visible glue: (0) present; (1) absent. Small balls of liquid close together on a line make the line brighter and more visible. In some groups the balls were large enough that the individual balls could be distinguished with the naked eye (Figs 11A, 25D, 26C, F), while in others their presence was judged by brighter spots or stretches on particular lines (Figs 29A, E). The balls of liquid decrease substantially in diameter in dry conditions in some species (*Theridion evexum*. – G. Barrantes pers. comm., *Gaucelmus calidus* W. Eberhard, unpub.) and can become nearly imperceptible. Our observations were all under field conditions. In addition to these ‘macroscopic’ balls

- of liquid, the webs of some *Anelosimus* species and of *Achaearanea tessellata* (G. Barrantes, in prep.) have very small balls of liquid that are only visible under a compound microscope. The webs of *Anelosimus pacificus* had small balls that were barely perceptible (without magnification) when they had accumulated dust. We usually did not assay for such small balls, which could provide additional characters, and all references below to sticky lines concern lines on which glue was visible to the naked eye under natural conditions. The only exception was *A. pacificus*, in which the balls were small, and their distribution was so uniform on nearly all the lines that their suspected presence had to be confirmed under the low power of a dissecting microscope.
2. Sticky silk on lines attached directly to substrate: (0) yes (Fig. 19C); (1) no (Figs 26C, D). This character applies only to species whose webs include sticky lines. Usually when webs have multiple sticky lines to the substrate, they are approximately parallel to each other, and are approximately perpendicular to the substrate (Figs 41A–D), but this was not always the case (Figs 16, 27D).
 3. Tips of sticky lines that are attached to the substrate: (0) sticky; (1) not sticky. State ‘0’ refers to the classic gumfoot lines of theridiids that have only a short stretch of glue (often only about 1 cm or less) at the very tip of the gumfoot line. Gumfoot lines are undoubtedly designed to capture walking prey (though the tangle portion of some gumfoot webs may allow the spider to capture flying prey, knocking them to the ground with an aerial tangle and then capturing them as they walk on the substrate – Lamoral, 1968). In species such as *Achaearanea tepidariorum* they are said to be laid under tension, and to have especially weak attachments to the substrate, thus easily breaking free and lifting a pedestrian prey from the substrate (Bristowe, 1958) (we know of no careful demonstration of such weak attachments, and we made no attempt to assay these traits; when such traits occur in this conjunction, gumfoot lines will constitute complex characters, worthy of greater weight). In some webs the portion of the line with glue at the tip was relatively short, and thus not easy to see (it was sometimes necessary to get one’s eyes very close to the substrate). We made this effort because we were interested in this particular trait, and thus believe that our evaluations are accurate. It is possible, however, that some literature evaluations underestimated the presence of glue near the substrate. Sticky lines attached to the substrate that had glue near the tip and also farther along toward the rest of the web were counted as ‘0’.
 4. Glue on sticky lines that were attached to the substrate occurred away from the tip of line: (0) no; (1) yes. On gumfoot lines, the glue is limited to just the distal tip of the line near the substrate, thus indicating that they function only to capture walking prey. Lines that have glue farther from the tip presumably function to capture flying or jumping prey, but not walking prey. With characters 1–4, a ‘classic’ gumfoot web, such as that of *A. tepidariorum*, codes as 1–0, 2–0, 3–0 and 4–0. If some but not all the lines to the substrate were sticky along most or all of their length, the web was scored as 1–0, 2–0, 3–0 and 4–1.
 5. Distal ends of gumfoot lines: (0) undivided (Figs 6C, D, 35E, 41D); (1) forked one or a few times (Figs 31C, D, *Eidmanella* Coddington 1986). Construction of fork-tipped gumfoot lines probably requires substantial modification of the sticky line construction behaviour that is described by Benjamin and Zschokke (2002), and may thus merit more weight.
 6. Form of outer boundary of tangle in gumfoot webs: (0) diffuse, tangle often extending to the substrate (Figs 44B, D); (1) clear boundary, usually somewhat removed from the substrate (‘star’ webs of Agnarsson, 2004) (Figs. 37C, 41C, 45A, B). The boundary of the tangle in star webs was sharply delimited by a loosely meshed wall of lines, and was attached to the substrate at a few points by relatively long anchor lines. Usually there was no object in star webs against which the spider rested, suggesting that this design provides protection for the spider.
 7. Dimensions in which sticky lines occurred in non-gumfoot webs: (0) 3 (Fig. 16); (1) 2 (Figs 2, 25A). Webs in which the sheet containing sticky lines was curved (e.g. Fig. 22A) were counted as being two-dimensional, despite the curve of the sheet. In one species (*Theridion nr. melanostictum*, Fig. 26E) the web photographed was built along a more or less straight twig whose branches lay in a single plane, and was highly planar, but other nearby webs of apparently the same species that were built on less planar supports were clearly three-dimensional; the web of this species was classified as three-dimensional. By choosing web supports that are planar over other possible building sites, the spider may determine that its web will be planar, so an environmental effect of this sort does not rule out an active role for the spider in making its web planar.
 8. Spacing between sticky lines: (0) not regular (Figs 16, 17D, 20A); (1) moderately regular (Figs 22B–F, 25A, C–E, 26F); (2) highly regular (Figs. 2A–G). We did not attempt to quantify the regularity of spacing; this would be extremely difficult if not impossible in many webs, especially those with sticky lines in three dimensions. Rather we counted as ‘regular’ cases in which the array of sticky lines suggested that the spider must somehow have performed some sort of measurement. We may have overestimated regularity, as it is possible that physical constraints on construction behaviour sometimes result incidentally in regular arrays of lines. Thus, for instance, the multiple lines in the sheet of *A. tessellata* that are attached to a given anchor line that runs to a supporting object are somewhat parallel and converge on each other, and give early stages of the sheet the appearance of regular spacing (Jürger and Eberhard in press). We did not attempt to evaluate the possible regularity of spacing between gumfoot lines where they attached to the substrate (this would be technically difficult); regularity of this sort is possible, and may occur in some webs with abundant gumfoot lines (e.g. Figs 36C, 41D). We judged the mesh in the portion of the web in which it was most uniform. In the early stages of

construction some webs may have more uniform mesh sizes, which are later obscured by the addition of further lines (Fig. 46).

9. Distribution of balls of glue: (0) contiguous stretches of numerous (probably always ≥ 10) balls (Fig. 11A); (1) single isolated balls (Figs 25D, 26C, F) or short 'dashes' of several balls (Figs. 2F, 38B); in both cases they were separated by stretches of at least 1 mm of line that lacked balls. When an author did not mention the distribution of balls of glue on sticky lines, we presumed that the balls were numerous and contiguous, because this made the stickiness more obvious and is typical for theridiids (and thus presumably expected by authors).
10. Apparent web function: (0) snare; (1) not a snare. In nearly all cases our classification was based on the web design, rather than on direct observations of spiders capturing prey. We assumed that webs with sticky lines not in the immediate vicinity of an egg sac function to snare prey. This assumption seems reasonable, although care is needed because sticky egg sac webs occur in *Steatoda* (Nielsen, 1931) and some *Latrodectus* (G. Barrantes, pers. comm.). Previous studies of at least one species have shown that nearly all of the web designs that we presumed do not function to snare prey have other functions (*Ariamnes* (= *Argyrodes*) *attenuatus* – Eberhard, 1979; *Faitidus* – Vollrath 1979; *Rhomphaea* – Whitehouse, 1987; *Chrosiothes tonala* – Eberhard, 1991). The classification of *Dipoena banksi* is uncertain, as the description of the web and prey capture behaviour (Gastreich, 1999) is too sketchy to allow confident conclusions. It is possible, for instance, that the web contains gumfoot lines, as suggested by the finding that other *Dipoena* species feed on ants and have apparently reduced webs (*D. castrata*, *mustelina*, *punctisparsa* in Shinkai and Takano, 1984, 'most species' in Jones, 1983).
11. Snare webs with clear sheet: (0) no (Figs 12A, 17A); (1) yes (Figs 15B, G, 43A–F). A 'sheet' was taken to be a planar or nearly planar array where lines were relatively dense compared with other portions of the web.
12. Form of sheet: (0) horizontal and more or less planar at bottom of tangle (Figs 9A, 43A–F); (1) domed sheet in midst of tangle (Figs 32D, 33C, D); (2) cupped sheet at bottom of tangle (Figs 14A, E, 15B, G); (3) more or less horizontal open-meshed plane to which gumfoot lines are attached (Figs 36C, D); (4) vertical sheet (Fig. 22A); (5) planar sheet against leaf (Fig. 18A–B). The distinction between planar horizontal sheets (state 1) and cupped sheets (state 2) was not always easy. Planar horizontal sheets were usually neither perfectly planar nor perfectly horizontal, and sometimes curled upward at the edge (e.g. Figs 43C, E); and in some species of *Anelosimus* (e.g. Fig. 15B) the cup was relatively flat. Nevertheless we feel that the difference is real. This character is meant to refer to the spider's ability to make planar arrays of lines, whether they are dry (e.g. *A. tessellata*) or sticky (e.g. *Chryso cambridgei*).
13. Regularity of orientations of lines in dense, non-sticky sheet: (0) irregular (Figs 43B, D); (1) irregular but with radial organisation perceptible (Fig. 33D); (2) highly regular (Figs 8A, B, E).
14. Web line number (tangle vs. line webs): (0) H web (Figs 10A, B); (1) single sticky line (Figs 11A, B); (2) tangle, numerous lines (most theridiids); (3) few long non-sticky lines (*Chrosiothes tonala* Eberhard, 1991, *Ariamnes attenuatus* Eberhard, 1979, *Dipoena banksi*). An additional state might be multiple sticky lines in three dimensions, but none are known in theridiids, but known in others such as the theridiosomatid *Wendilgarda galapagensis* Eberhard, 1990b). In *P. studo* the reduction in the web is associated with an apparent ability to attract prey to the web (Eberhard, 1981), presumably with a chemical attractant, so at least in this genus this is probably a complex character that deserves more weight. H-webs may also be associated with active web manipulation behaviour by the spiders (Holm, 1939); if so, they may also be complex and merit further weight.
15. Spider actively manipulates its web: (0) no; (1) yes. 'Yes' was scored if the spider altered tensions on the lines, either by tensing them (as in *Neottiura* sp.) or by relaxing and then tensing them (as in *Phoroncidia* spp.). Shaking the web following prey impact, as occurs in *Achaearanea tessellata* (G. Barrantes and J.-L. Weng, in prep.) (and probably many others) to locate prey was not counted as manipulation. Tensing and relaxing behaviour of this sort has evolved repeatedly in orb-weaving spiders (e.g. the uloborids *Hyptiotes* and *Miagrammopes*, and several theridiosomatids). Few theridiids have been observed capturing prey, so 'yes' may be under-represented.
16. Function of reduced non-sticky, non-snare webs: (0) landing site or bridge for prey to walk along, allowing spider to ambush them (*Ariamnes attenuatus* Eberhard, 1979); (1) a few resting lines connected with web of another spider, allowing access to this web from which prey can be removed (kleptoparasites), as in *Faitidus*, and *Argyrodes*; (2) same as (1) except access functions to facilitate attacks on the other spider; (3) lines from resting site to petiole of leaf where prey (*Pheidole* ants) walk (*Dipoena banksi* Gastreich, 1999); (4) a few widely spaced more-or-less horizontal lines along which spider travels and single line to the ground below, giving spider access to columns of foraging termites below and from which captured termites are suspended to allow further attacks (*Chrosiothes tonala*, Eberhard, 1991).

Protection

17. Site of retreat: (0) just at lateral edge or beyond the edge of the web (Fig. 6A); (1) at upper edge of web (Figs 2G, 15A, 23A, 45E); (2) in middle to upper part of the tangle (Figs 37D, 42F); (3) lower third of web (Fig. 14E); (4) single or few lines (Figs. 11A, B). Some species that rest against non-modified substrates such as leaves and rocks at the top of the web adopt apparent defensive postures such as a crouch (Fig. 45E), or pressing the body to the substrate and probably make it more difficult to see (the synotaxid *Synotaxus monoceros* in Agnarsson, 2004, the nesticid *Gaucelmus calidus*), though this is not true in others

- (Fig. 45E). We do not have enough data, however, to include this trait. In some species without retreats (e.g. *Argyrodes* spp.), the spider rests in the web with its legs tightly appressed in a way that, along with its body outlines serves to camouflage its spider-like outline (e.g. Whitehouse, 1986; Fig. 13D). Species resting in cramped shelters typically crouch with all their legs pressed against the body (e.g. many *Achaearanea*), and it seems that the spider itself experiences this position as stressful: *A. tessellata*, when it first begins to spin in the evening after crouching in its retreat all day, pauses and stretches its legs just like a dog or a person (W. Eberhard, unpub.) (thus emphasising that there is probably a reason, presumably adaptive, for assuming these positions). We have not coded defensive postures because there are very few descriptions available (and photos of 'resting' spiders in the literature may have been taken after the photographer caused the spider to extend its legs and become more visible); resting posture may be an informative character.
18. Resting site altered by spider to increase protection: (0) no; (1) yes. In all cases the modification by the spider decreases its own visibility (at least to humans), and possibly also reduces its physical exposure to attacks from outside the web while resting at its normal resting site. While state 1 is derived on the basis of comparison with outgroups such as linyphiids, synotaxids and nesticids, in many species state 0 is associated with resting in very sheltered sites (e.g. *Steatoda*, *Rugathodes bellicosus*, nesticids) where modifications to hide the spider may lack adaptive value, and is thus probably secondarily derived.
 19. Modifications of the resting site using objects: (0) spider rests under leaves or other detritus which is not apparently reoriented after it has fallen into the web (Fig. 16); (1) many small pieces of debris (including small pellets of soil or tiny leaves) joined tightly together so that the resulting object has a more or less inverted conical shape (Fig. 34B); (2) larger pieces of debris, which generally are not especially tightly connected together, and do not form consistent shapes (Fig. 15B); (3) single curled dry leaf, usually suspended so that it is oriented vertically, with the spider resting at lower end (Figs. 38D, 42A); (4) edges of a single living leaf are attached together so that the leaf becomes curled (Figs. 20B, 29B); (5) attach several leaves together, generally forming a roof under which the spider rests (Fig. 28G); (6) tightly meshed silk structure. Modifying the resting site with objects (character #19) instead of just modifying it with silk (character #20) was counted when any objects were included in the silk walls of the retreat. In some of these cases (see Nielsen, 1931), there was also silk in most of the walls of the retreat. Presumably state 3 is derived from resting under unmodified living leaves (e.g. Fig. 20C). Because the objects used by spiders as refuge probably often arrive in the form of detritus falling on the web, our data are very likely to seriously under-represent the amount of intra-specific variation. For example, in one species we have observed in detail (*A. tessellata*), spiders sometimes use a single curled leaf suspended so the tunnel is vertical, sometimes (when no curled leaf is present in the web) use multiple pieces of detritus, and sometimes (when there is no detritus in the web) make a small, inverted silken cup under which they rest. In all cases except *Achaearanea apex* (Fig. 35) the spider rested against or under objects suspended in their webs. In *A. apex* the multiple small objects were in the sheet at the top of the web, and the spider, which rested in the tangle just under this sheet, was not close to with any particular object (and was quite difficult to distinguish).
 20. Form of silk retreat structure: (0) silk tent consisting of increased density of the mesh of the tangle, also generally forming an inverted cone or cup; (1) a bell-shaped wall attached to lower surface of substrate where spider rests (Figs 4C, 45E); (2) runway that narrows to form a horizontal tube beyond the edge of the web (Fig. 6A); (3) silk wall behind which spider rests (*Dipoena castrata* – Shinkai and Takamoto, 1984). It was not easy to distinguish a bell-shaped wall from a small decrease in mesh size in the tangle where the spider rested; for instance, *Helvibis* sp. nov. nr. *thorelli* (Fig. 23A) was counted as lacking a bell-shaped wall, while *Theridion* nr. *melanostictum* (Fig. 26E) and *Theridion* nr. *orlando* II (Fig. 27D) were counted as having a bell-shaped wall. Presumably silk tents and bell-shaped walls were derived from a lack of modification (as in *Achaearanea tepidariorum*). It is also possible that spiders gradually add lines over the space of several days to the area where they rest, making distinctions even more difficult. In *A. tepidariorum* webs, for instance, there is sometimes a slightly domed sheet where the spider rests (Comstock, 1967), and sometimes this sheet is lacking (Bristowe, 1958). Detritus was incorporated in some tubular runways in *Latrodectus* (Szlep, 1965).
 21. Object (unmodified) against which spider rests: (0) rock or other large object (*Theridion bergi* – Xavier *et al.*, 1995); (1) twig (Figs. 27D, G); (2) living leaf (Figs. 16, 23A) or fruit or flower.
 22. Dense sheet of silk at edge of web: (0) no; (1) yes (Figs. 42G, H). These sheets are relatively strong. In *T. melanorum*, spiders begin to include these sheets only after they have produced an egg sac, suggesting that the sheets function as protection (Nielsen, 1931). These sheets are so obvious that when a verbal description did not mention a sheet, we assumed that it did not exist.

