

Webs of theridiid spiders: construction, structure and evolution

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Understanding the web construction behaviour of theridiid (comb-footed) spiders is fundamental to formulating specific evolutionary hypotheses and predictions regarding the reduction of orb-webs. We describe for the first time in detail the web construction behaviour of *Achaearanea tepidariorum*, *Latrodectus geometricus*, *Theridion sisyphium* and *T. varians* as well as webs of a range of other theridiids. In our survey we distinguish four major web types. Among webs with gumfooted lines, we distinguish between webs with a central retreat (*Achaearanea*-type) and those with a peripheral retreat (*Latrodectus*-type). Among webs without gumfooted lines, we distinguish between those which contain viscid silk (*Theridion*-type) and those with a sheet-like structure, which do not (*Coleosoma*-type). Theridiid gumfoot-webs consist of frame lines that anchor them to surroundings and support threads which possess viscid silk. Building of gumfooted lines constitutes a unique stereotyped behaviour and is most probably homologous for Nesticidae and Theridiidae. Webs remained in place for extended periods and were expanded and repaired, but no regular pattern of replacement was observed. We suggest that the cost of producing and maintaining viscid silk might have led to web reduction, at least in theridiids. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, 78, 293–305.

ADDITIONAL KEYWORDS: behavioural patterns – character evolution – capture thread – resource allocation – viscid silk – web construction – web reduction.

INTRODUCTION

Behavioural patterns are subject to natural selection in the same way as morphological characteristics. Animals can be regarded as being designed by natural selection to make best use of the energy or resources they invest in behaviour (McFarland, 1978). Spiders build a diverse range of webs, each optimally adapted, on which they depend to survive and reproduce. The consequences of building a non-functional web would be drastic – hunger, inability to find a mate, less protection from predators, or the waste of valuable resources.

Numerous detailed hypotheses have been suggested to explain trends in web evolution (Griswold *et al.*,

1998 and references). Nevertheless, as mentioned in Griswold *et al.* (1998: 23): ‘The picture suggested by this study is much simpler: the orb-web is monophyletic, the araneoid sheet web is monophyletic and derived from an orb, and the “gum foot” web of theridiid-necticid lineage is monophyletic and derived from a sheet’. However, in the same study they mention the lack of information on the web construction behaviour of theridiids and constraints thus caused: ‘The diversity of theridioid web architecture is still very poorly known’, and ‘the lack of descriptions for other non-orb architectures frustrated detailed comparison’ (Griswold *et al.*, 1998: 43). Evidently, formulation of specific evolutionary hypotheses and predictions regarding the reduction of orb-webs to gumfoot and sheet-webs has been hampered by lack of information (see also Heimer & Nentwig, 1982; Eberhard, 1990; Hormiga, Eberhard & Coddington, 1995; Scharff & Coddington, 1997).

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The comb-footed spiders of the family Theridiidae constitute one of the largest groups of spiders, consisting of 2209 species in 73 genera (Platnick, 2002). Several authors have described theridiid webs. However, whereas most authors described the web in detail, the building behaviour was described anecdotally. The building process of theridiid webs may be more organized than suspected, as subsequent additions to the web may obscure the primary construction pattern. The aim of this study is to describe the web structure and building behaviour of *Achaearanea tepidariorum*, *Latrodectus geometricus*, *Theridion sisyphium*, *T. varians* and the web structure of a wide range of other theridiids. It also briefly addresses questions concerning the evolution of reduced webs, prey capture behaviour, foraging theory and plasticity in behaviour.

MATERIAL AND METHODS

STUDY SPECIES

Achaearanea tepidariorum (C. L. Koch, 1841) is a cosmopolitan spider common in northern and central Europe. It is mostly found in greenhouses and sometimes in houses. Adults attain a body length of 5–7 mm (females) or 3–4 mm (males) (Heimer & Nentwig, 1991; Roberts, 1995). *Latrodectus geometricus* C. L. Koch, 1841 is a cosmopolitan spider found around man-made habitats (Levy, 1998; Knoflach & van Harten, 2002). Adults attain a body length of 8–9 mm (females) or 3–4 mm (males). *Theridion sisyphium* (Clerck, 1757) and *T. varians* Hahn, 1833 are common Holarctic species of the genus. Adults attain a body length of 2.5–4 mm (females) or 2.5–3 mm (males) (Heimer & Nentwig, 1991; Roberts, 1995). All spiders except, *Latrodectus geometricus*, were collected as subadults or adults from Innsbruck, Austria and surroundings and maintained under laboratory conditions. The *L. geometricus* used in this study was laboratory reared at the Department of Zoology, University of Oxford.

Spiders were kept and observed in 8 × 8 × 16 cm and 20 × 20 × 20 cm perspex (PS) boxes. *A. tepidariorum*, *T. sisyphium* and *T. varians* were fed daily with two to three *Drosophila* sp., *L. geometricus* was fed with small crickets (*Gryllus campestris*). The controlled environmental conditions of the rearing cum observation room were 24.5 ± 2°C and a reverse L/D light cycle of 12/12. The introduction of the spider always took place at night (dark period).

OBSERVATIONAL PROCEDURE

Theridiids mostly build their web during the night and are easily disturbed by light, leading to an interruption in building. Conventional observation with

normal light was therefore impractical. Moreover, the initiation of web building was highly unpredictable, requiring observation throughout the night.

Our observational set up consisted of an infrared illuminated background in combination with an infrared-sensitive video camera. Captured live images were transferred from the camera to a computer where they were analysed in real time and the position of the spider recorded at a rate of 14 frames per second. Study methods are described in detail in Benjamin & Zschokke (2002). This approach was devised to record movement in two dimensions.

To record movement in three dimensions we used the set-up and methods described in Zschokke (1994) and Zschokke & Vollrath (1995); this involved the use of two synchronized observation units, each of which consisted of a video camera and an image scanner VP112 (HVS Image Ltd, Hampton, UK). The first camera was placed above the perspex box and the second in front of it. To obtain a 3-D movement pattern, recorded data of both units were combined using software described in Zschokke (1994); the patterns were viewed with Rotator (Kloeden, 1996).

Abbreviations used in the text and figures are given in Table 1. The number of observed behavioural sequences or bouts is given in Table 2. Although only a single *L. geometricus* was observed, the difficulty of obtaining them and the sparseness of our knowledge justifies reporting our observations. The spider's movement patterns during resting and gumfoot building were easily distinguishable in our recordings. In contrast, the movement patterns during the explorative stage, structure building and thread connections made during filling in of the web were almost indistinguishable from one another. For statistical analysis, we therefore did not differentiate between these three types of behaviour and defined the time spent on

Table 1. Abbreviations on figures and in text; after Coddington (1986)

A	Attach
Alt	Alternate leg movements, e.g. Alt L1
DL	Dragline
GF	Gumfooted lines, threads with viscid basal portions
L	Leg pairs 1–4 (numbered from front to rear)
KN	Knock-down trap, non-viscid
R	Retreat
RT	Radiating threads, SSt extending from a peripheral point to the substrate
SB	Substrate, bottom of perspex box
SH	Sheet, non-viscid
SSt	Supporting structure, a silken line
VSi	Viscid silk lines

Table 2. The number of webs and bouts observed

	Individuals/webs	Structure	Gumfooted lines or viscid elements
<i>A. tepidariorum</i>	5/7	36	45
<i>L. geometricus</i>	1/3	23	9
<i>T. sisyphium</i>	1/2	11	14
<i>T. varians</i>	1/2	14	7

Table 3. Webs studied with study region, type of web and source

Species	Origin	Type of web	Source
<i>Achaeearanea lunata</i>	Europe	<i>Achaeearanea</i> -type	Present study
<i>A. tepidariorum</i>	Europe	<i>Achaeearanea</i> -type	Present study
<i>A. tessellata</i>	Mexico	<i>Coleosoma</i> -type	Present study, Eberhard, 1972
<i>Anelosimus jucundus</i>	Mexico/Panama	Modified (see text)	Present study, Nentwig & Christenson, 1986
<i>Argyrodes attenuatus</i>	Colombia	Modified (see text)	Eberhard, 1979
<i>Chryso cambridgei</i>	Mexico	<i>Theridion</i> -type	Present study
<i>C. spiniventris</i>	Sri Lanka	<i>Achaeearanea</i> -type	Present study
<i>Coleosoma blandum</i>	Sri Lanka	<i>Coleosoma</i> -type	Present study
<i>Episinus angulatus</i>	Europe	Modified (see text)	Bristowe, 1958; Roberts, 1995
<i>Latrodectus geometricus</i>	Cosmopolitan	<i>Latrodectus</i> -type	Present study
<i>L. mactans</i>	South Africa	<i>Latrodectus</i> -type	Lamoral, 1968
<i>L. pallidus</i>	Israel	<i>Latrodectus</i> -type	Szlep, 1965
<i>L. purcelli</i>	South Africa	<i>Latrodectus</i> -type	Lamoral, 1968
<i>L. revivensis</i>	Israel	<i>Latrodectus</i> -type	Szlep, 1965
<i>L. variolus</i>	USA	<i>Latrodectus</i> -type	Szlep, 1966
<i>Pholcomma gibbum</i>	UK	<i>Achaeearanea</i> -type?	Holm, 1938; Jones, 1992
<i>Phoroncidia studo</i>	Colombia	Modified (see text)	Eberhard, 1981
<i>P. pukeiwa</i>	New Zealand	Modified (see text)	Marples, 1955
<i>Spintharus</i> sp.	?	Modified (see text)	Stowe, 1985
<i>Steatoda triangulosa</i>	Europe	<i>Latrodectus</i> -type	(Benjamin & Zschokke, unpub. data) Wiehle, 1937, 1949
<i>S. bipunctata</i>	Europe	<i>Latrodectus</i> -type	Hopfmann, 1935
<i>S. lepida</i>	South Africa	<i>Latrodectus</i> -type	Lamoral, 1968
<i>Theridion bergi</i>	Brazil	<i>Latrodectus</i> -type	Xavier <i>et al.</i> , 1995
<i>T. impressum</i>	Europe	<i>Theridion</i> -type	Wiehle, 1937, 1949
<i>T. sisyphium</i>	Europe	<i>Theridion</i> -type	Present study
<i>T. varians</i>	Europe	<i>Theridion</i> -type	Present study
<i>Tidarren haemorrhoidale</i>	Mexico	<i>Coleosoma</i> -type	Present study
<i>T. sisyphoides</i>	Mexico	<i>Coleosoma</i> -type	Present study
<i>Theridula</i> sp.	?	Modified (see text)	Stowe, 1985

structure construction as the time not spent on gum-foot building or resting.

In addition to our automated recordings, we observed single web constructions of *A. tepidariorum* directly, to describe leg movement patterns during thread manipulation. Additionally, the finished webs were photographed to compare them with the recorded movement pattern.

DATA ANALYSIS

Data were analysed using software and methods described in Benjamin & Zschokke (2002). For descriptive statistics we used StatView (SAS Institute, 1998). To compare time allocation and number of bouts built during successive days we used the Wilcoxon signed rank test.

RESULTS

CONSTRUCTION OF SUPPORTING STRUCTURE

Achaearanea tepidariorum

Achaearanea tepidariorum mostly started building during the night and began with an early or explorative stage, in which the spider in periodic bursts of activity moved around the space where the web was later built. It moved with alternate (Alt) L1 move-

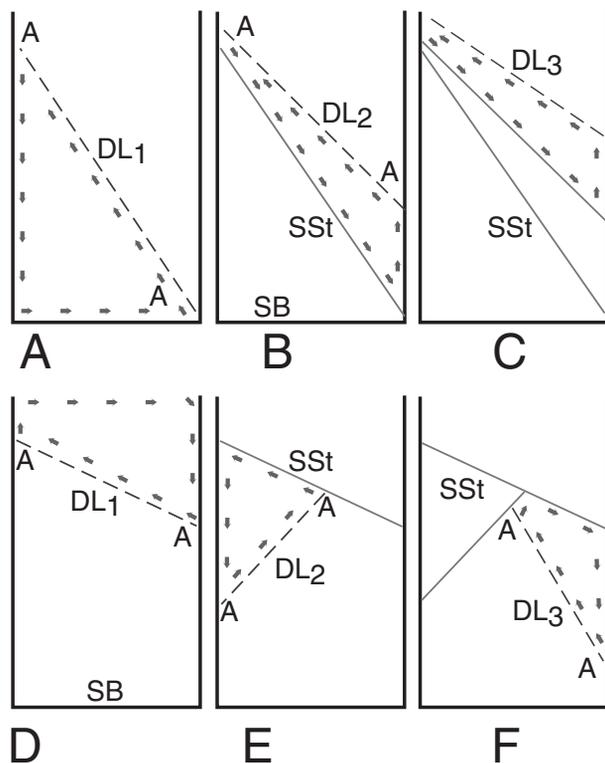


Figure 1. Movements of *Achaearanea tepidariorum* (A–C), *Theridion sisyphium* and *T. varians* (D–F), during construction of SSt, frontal view (schematic and not to scale). A, early stages: the spider initially made an attachment at the upper periphery of the box, dropped down, then moved away from the periphery on SB, stopped, attached and then doubled DL. B & C, later stages: the spider initially moved away from the upper periphery of the box and along an existing thread, stopped, attached and then doubled DL. D, early stages: the spider initially made an attachment at the upper periphery of the box, then moved away along the peripheral borders, stopped, attached and then doubled DL. E & F, later stages: the spider initially moved away from the upper periphery of the box and along an existing thread, then moved away from the thread along the peripheral borders of the box, stopped, attached and then doubled DL.

ments and with a single L4 holding the dragline (DL). Structural thread construction behaviour was highly variable. Basically, the spider attached its DL to an upper peripheral point of the box, dropped down or moved away to the central part of the box on substrate (SB) and attached DL to SB. Then DL was reinforced by doubling (Fig. 1A). The spider's behaviour was highly variable; no fixed patterns were detected.

During later phases the spider used existing supporting structure (SSt) as scaffolding to expand the web. Its movements were variable but still followed the same behaviour. After making an attachment to the upper periphery of the box, the spider moved along an existing line to the opposite side and attached DL.

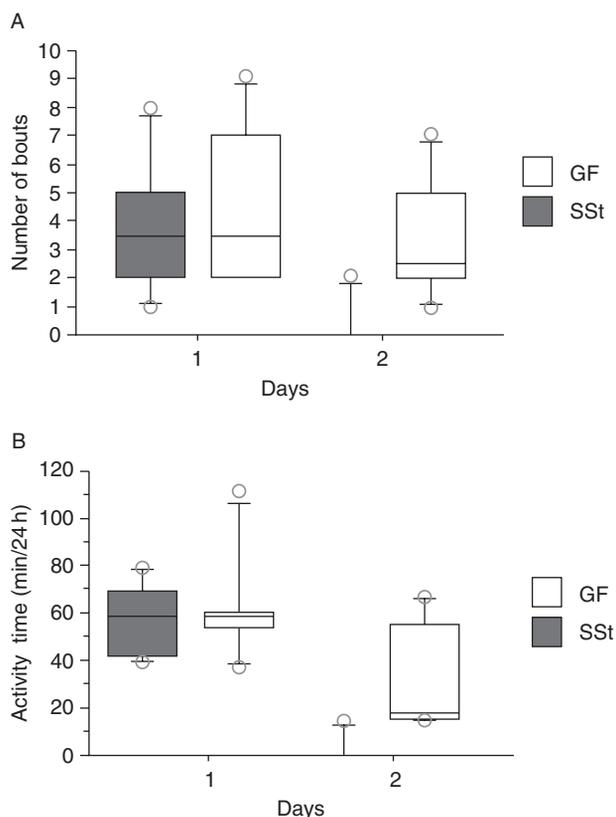


Figure 2. Activity of *Achaearanea tepidariorum* during construction of GF and SSt. A, the number of GF and SSt bouts performed. The number of the latter during the first night was significantly higher than during the second ($Z = -2.201$; $P = 0.027$). B, activity time of *A. tepidariorum*. During the first day, the spider allocated more time to build SSt than during the second ($Z = -2.201$; $P = 0.027$). We calculated activity time as the number of min/24 h for the first 48 h; 10th, 25th, median, 75th and 90th percentiles are plotted. Values above the 90th and below the 10th percentiles are plotted.

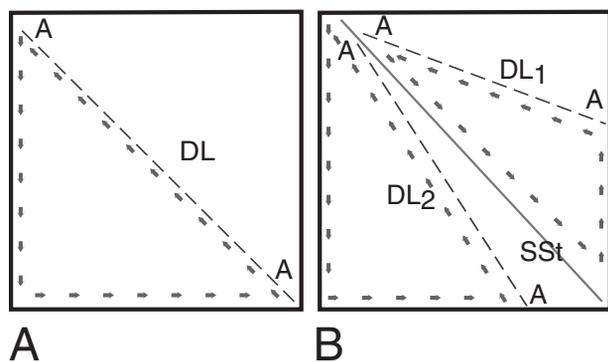


Figure 3. Movements of *Theridion sisypium* and *T. varians* during SSt construction, seen from above (schematic and not to scale). (A) Early and (B) later stages of construction. Description as in Fig. 1.

Finally, DL was reinforced by doubling (Figs 1A–C, 5A). We never observed cut-and-reel behaviour. The structure consisted of threads extending from a central point of the box to surroundings. Structural elements never contained viscid silk. All GFs were attached at one end to structural threads. During the first night (first 24 h) more SSt were built (Fig. 2A,B) than during the second night ($Z = -2.201$; $P = 0.027$), and more time was allocated to build them ($Z = -2.201$; $P = 0.027$).

Latrodectus geometricus

The structure consisted of radiating threads (RT) extending from a peripheral point to the substrate. Radiating thread construction behaviour was highly variable. Basically the spider first attached its DL to an upper peripheral point of the box, moved away to the central section, on SB and attached DL to SB. Then DL was reinforced by doubling. During later phases of web construction the spider used existing SSt as scaffolding in the processes of expanding the web. Its movements were variable but still followed the same basic pattern.

Theridion sisypium and *T. varians*

The spider first attached its DL to an upper peripheral point of the box, moved downwards along the peripheral walls of the box and attached DL. Then DL was reinforced by doubling (Figs 1D–F, 3A,B, 5B). During later phases of web building the spider used existing SSt to expand the web. The spider rarely dropped down. In addition to bouts of SSt and viscid silk lines *T. sisypium* and *T. varians* built a silk lined retreat (R in Fig. 5B). The building behaviour was highly variable and appeared not to be stereotyped.

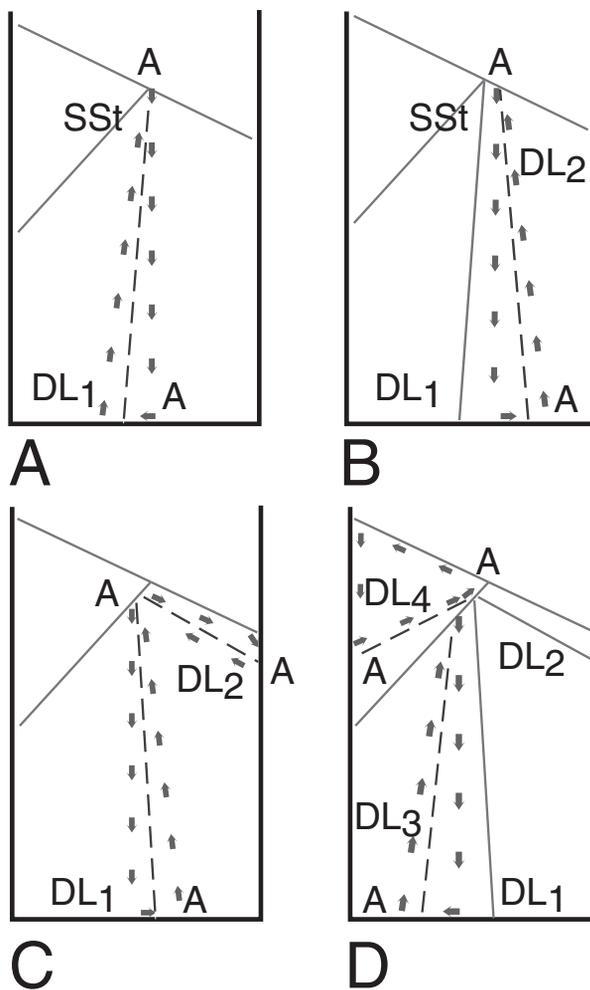


Figure 4. Movements of *Achaearanea tepidariorum* during GF construction, frontal view (schematic and not to scale). A & B, the spider attached DL to the supporting thread, then dropped down to SB, moved one body length along SB, attached DL to SB, and then turned around and moved up doubling DL. C & D, during a second type of GF building behaviour the spider dropped down to SB to build a single GF, then moved to a peripheral side of the box along an existing SSt to build a GF attached to the side of the box.

CONSTRUCTION OF GUMFOOTED LINES

Achaearanea tepidariorum

To build gumfooted lines (GF), the spider moved away from the central section of the web along an existing SSt, and then started groping with one L1 holding DL with the other; Alt plucking movements were not observed. When the starting point was determined, it attached DL to the supporting thread. The spider then dropped down paying out DL with a L1 forward tap of

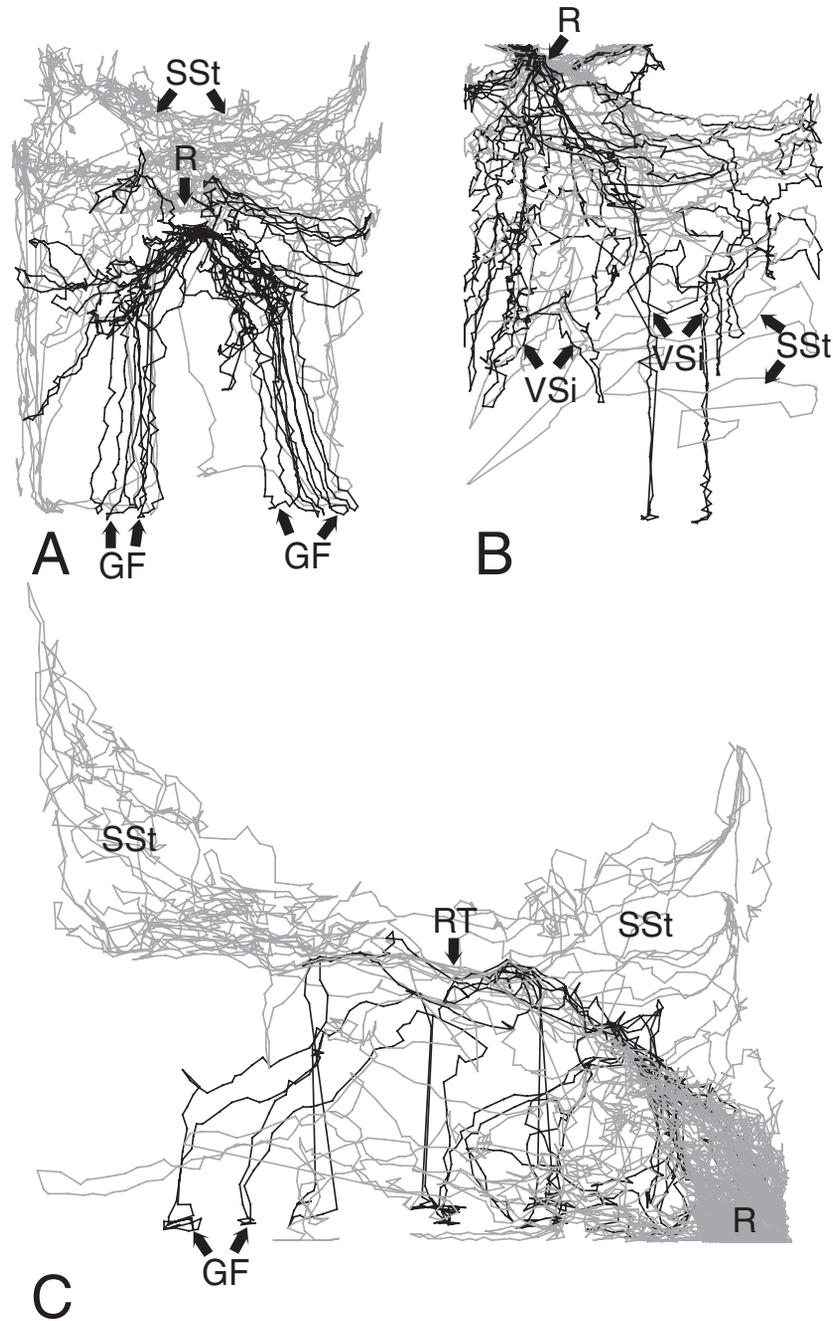


Figure 5. Tracks of the movements during SSt (grey lines) and GF construction (black lines). A, *Achaearanea tepidariorum*, lateral view. B, *Theridion sisyphium*, lateral view. C, *Latrodectus geometricus*, lateral view. Size of box: $8 \times 8 \times 16$ cm (A & B); $20 \times 20 \times 20$ cm (C).

substrate (SB). It turned around and moved approximately its body length along SB, attached DL to SB by dipping the posterior part of the abdomen (Fig. 4A); during the attachment process DL was held with one outstretched L1. The spider then turned around towards DL and went up with L1 holding the existing

silk line and with L4 holding the new thread; Alt L4 pulling movements were not visible. During its upward journey, it coated the gumfoot at the basal part with viscid silk, probably directly with the spinnerets (Figs 4A,B, 5A). Building the basal part and its attachment to SB is the slowest during gumfoot

building (mean = 1.28 mm/s; min. = 0.71 mm/s; max. = 2.48 mm/s; $N(\text{GF}) = 10$). The spider never moved back and forth along DL or applied viscid silk with leg movements. We never observed cut-and-reel behaviour during GF construction.

After attaching GF to the structural thread, the spider continued moving along SSt to build the next GF (Figs 4B, 5A). This behaviour continued until it had completed a bout of GF construction (a bout included 1–27 GFs; $N = 31$; mean 8). During a second type of GF building behaviour the spider dropped down to SB, and moved back up, building a single GF as described above, then moved to a peripheral side of the box along an existing SSt, to build the next GF attached to the side of the box (Figs 4C,D, 5A).

Latrodectus geometricus

The spider moved outwards along a radiating thread (RT in Fig. 5C) from the peripheral retreat to the substrate, to the central section, then turned 90°, moved a bit and attached DL to the supporting thread. It then dropped down paying out DL, settled on the substrate, turned around and attached DL to SB by dipping the posterior part of the abdomen. The spider then turned around and went up to attach GF to SSt. After attaching, it continued moving along the same or another structural thread to drop down again to build the next GF (Fig. 5C). This behaviour continued until the spider had built a bout of GF. In addition to bouts of SSt and GF, *L. geometricus* built a silk-lined retreat (R in Fig. 5C).

Theridion sisypium and *T. varians*

No gumfooted lines were built. The spider moved along a SSt in a random pattern laying viscid silk lines (at least we were unable to observe any constant pattern or stereotyped behaviour), which gave the finished web a net-like appearance (Fig. 5B) (see Wiehle, 1937: fig. 3, 1949: fig. 30). Observations of web samples with a compound microscope showed the entire length to be of viscid silk.

DESCRIPTION OF ADDITIONAL THERIDIID WEBS

Achaearanea tessellata

Achaearanea tessellata (Keyserling, 1884) constructs a 'sheet-web' identical to the 'sheet-web' of *C. blandum* (Fig. 6C).

Chryso cambridgei

Chryso cambridgei (Petrunkevitch, 1911) builds a web without gumfooted lines, consisting of a two dimensional structure interconnected with viscid lines (Fig. 7A,B).

Chryso spiniventris

The web of *Chryso spiniventris* (O. P.-Cambridge, 1869) from Sri Lanka is very similar to that of *A. tepidariorum* and *A. lunata* (Fig. 6B). It consists of an irregular, three-dimensional retreat connected to the surroundings with strong anchor lines and with gumfooted lines extending from the retreat to the substrate. The retreat is also the retreat of the spider, but unlike *Achaearanea* no vegetation fragments are collected (Fig. 6B).

Coleosoma blandum

Coleosoma blandum O. P.-Cambridge, 1882 from Sri Lanka builds a 'sheet-web' without gumfooted lines or any other viscid elements (Fig. 6D). It is outwardly similar to a linyphiid sheet-web and consists of a dense sheet connected with anchor threads to the vegetation (SH in Fig. 6D). Threads that function as a knockdown trap (KN) extend above the sheet (KN in Fig. 6D). The spider rests within a retreat made of detritus or a leaf suspended in the centre of the knockdown trap, above the sheet (R in Fig. 6E). The building behaviour of *C. blandum* is different from that of any theridiid observed by us (Benjamin, unpublished observations).

DISCUSSION

COMPARING WEBS AND BEHAVIOURAL HOMOLOGIES

The most interesting observation in our study is that the building process of theridiid webs is more organized than previously thought, particularly during the building of gumfooted lines. The interpretation of theridiid webs as 'highly irregular' or 'tangle' webs (Hopfmann, 1935; Comstock, 1940; Levi & Levi, 1962; Szlep, 1965, 1966; Shear, 1986, 1994) might be due to authors describing the end product and not the behaviour.

Theridiid webs observed remained in place for extended periods, were expanded and repaired, but the spiders appeared to exhibit no regular pattern of web replacement. In contrast to most orb-webs, theridiid webs are constructed gradually and in segments over a period of many days and have a longer life span (Carico, 1986; Eberhard, 1987; Opell, 1999).

Structure construction behaviour in theridiids is highly variable. Even the same spider employed variable behaviours to build successive webs. Such behavioural flexibility during later construction stages is unknown in orb-web builders except for some theridiosomatids (Eberhard, 2001). Araneid orb-weavers like *Araneus diadematus* only perform highly variable behaviours during the first construction stage, leading to the proto-hub. Thereafter its behaviour becomes stereotyped and highly predictable (Zschokke, 1996). After SSt construction, except for *A. tessellata*,

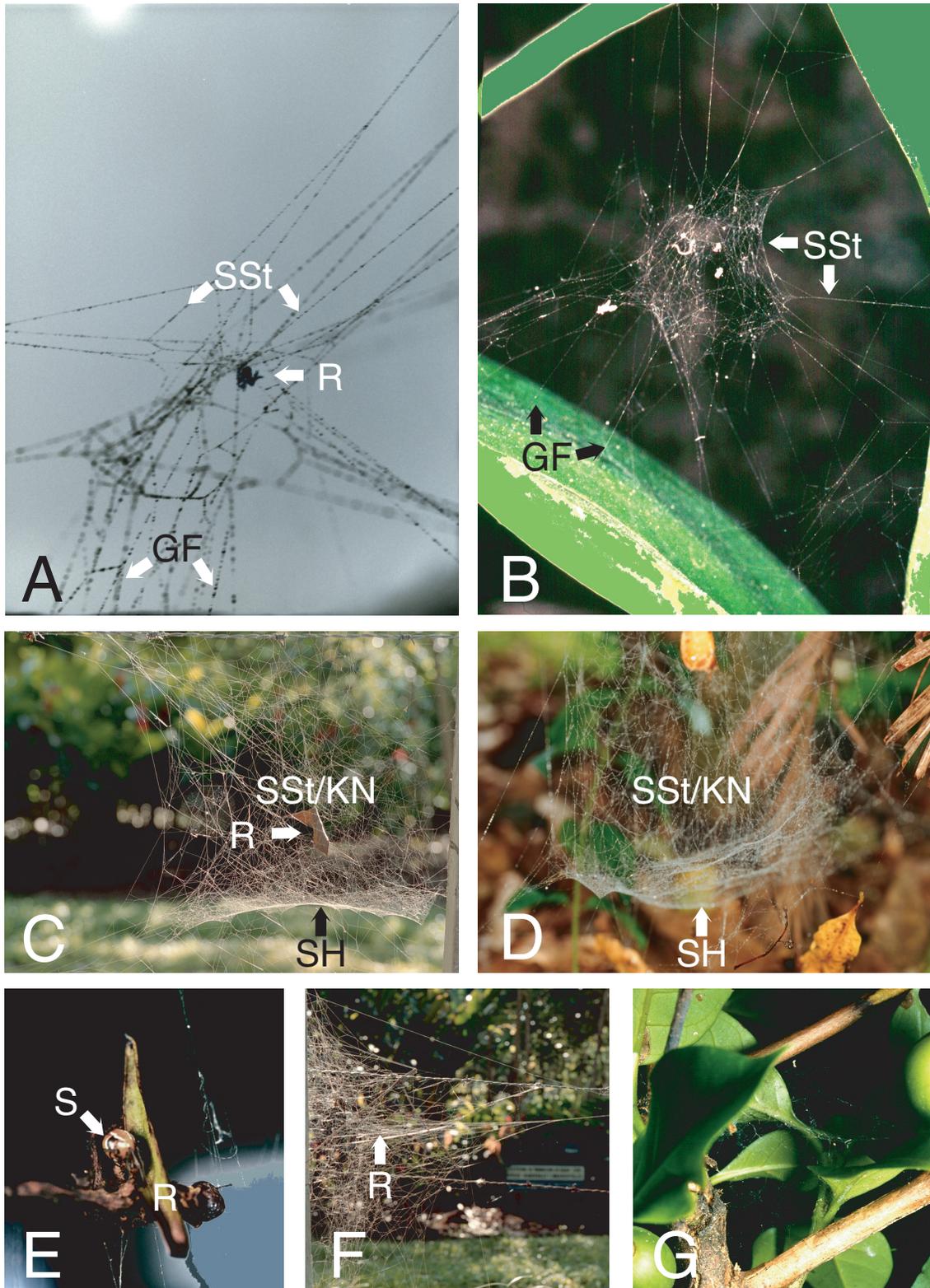


Figure 6. Webs of Theridiidae. A, *Achaearanea*-type web of *Achaearanea tepidariorum*. B, *Achaearanea*-type web of *Chrysso spiniventris*. C, 'sheet-web' of *Achaearanea tessellata*. D, 'sheet-web' of *Coleosoma blandum*. E, retreat above the sheet of the 'sheet-web' of *C. blandum*. F, the tangle web of *Tidarren sisypoides*. G, the tangle web of *Anelosimus jucundus*. Webs A, B and D were coated with water to make them more visible for photography.

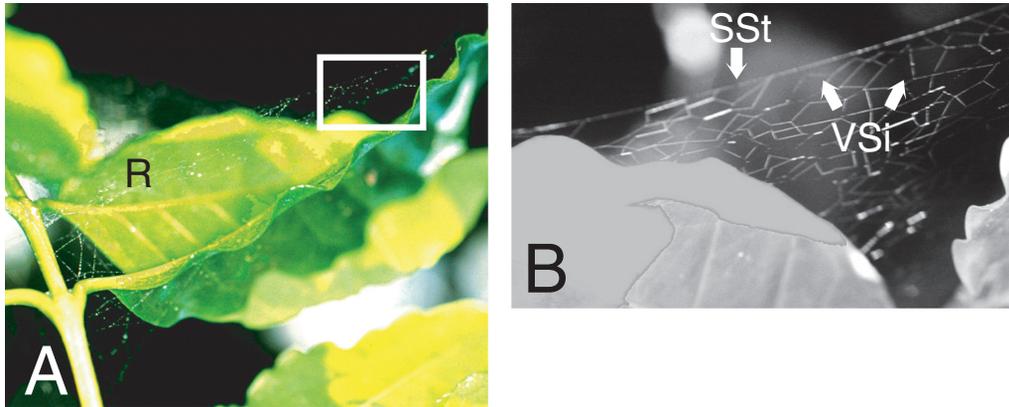


Figure 7. Web of *Chrysso cambridgei*. A, 2-D web with viscid silk lines. B, close-up.

C. blandum and *Tidarren* spp., all theridiids observed by us added viscid elements to the structure. The building of gumfooted lines in *Achaearanea* and *Latrodectus* (Lamoral, 1968) constitutes a unique stereotyped behaviour or a unique motor pattern and is most probably homologous for Theridioids (Theridiidae + Nesticidae, clade 9, *sensu* Griswold *et al.*, 1998).

The structure constructed by *A. tepidariorum* consisted of an irregular, three-dimensional retreat connected to the surroundings with strong anchor lines. In comparison, *S. triangulosa* starts with an initial structure of radiating threads (RT) extending from a peripheral point to the substrate (Benjamin & Zschokke, unpublished data). Similarly, *Latrodectus* initially lays several RT, extending out of its retreat towards surrounding objects (Szlep, 1965; Lamoral, 1968). Although they are not arranged in geometrically regular arrays, almost all of them primarily originate from a single peripheral point.

Achaearanea tepidariorum and *A. lunata* (Benjamin & Zschokke, unpublished data) started to build GF from more or less the central section of the web. During construction, the spider moved from the retreat to the periphery. The GF construction behaviour of *Latrodectus* and *Steatoda* (Benjamin & Zschokke, unpublished data) is different. They start from the peripheral retreat, move along a structural thread, then drop down at regular intervals to attach the thread to the lower substrate, coating the lowest part of the thread with viscid silk on returning.

Theridion sisyphium and *T. varians* built a structure extending sideways from a peripheral retreat; all attachments were made to the sides of the box and not to SB. During the construction of viscid silk lines, the spider attached them to SSt at both ends, instead of one end each to SSt and SB as in *A. tepidariorum* and *L. geometricus*. This behaviour might be unique for *Theridion* and related genera. *Achaearanea*, *Latrodectus*

and *Steatoda* never attached GFs to existing SSt at both ends. However, *Theridion* viscid silk lines are built in bouts, as are GFs in other Theridiidae. The SSt building behaviour of *T. sisyphium* and *T. varians* differed from that of *A. tepidariorum*. *Theridion* rarely dropped down to SB during later stages, instead it attached the threads to the peripheral sides of the box or to existing SSt. Judging from the completed webs, *C. cambridgei* might have constructed viscid elements in the same manner.

In the absence of a phylogeny, the interpretation of the evolution of the diverse range of webs and their corresponding behaviours is somewhat arbitrary. Additionally, most genera might not be monophyletic (Forster *et al.*, 1990). Nevertheless, it is appropriate to discuss implications of the described behavioural characters on the theridiid interrelationship hypotheses proposed by Levi & Levi (1962) and Forster *et al.* (1990).

The webs and construction behaviours of *Latrodectus* and *Steatoda* indicate a close relationship. Forster *et al.* (1990) considered *Latrodectus*, together with *Anelosimus*, *Enoplognatha*, and *Steatoda*, to be basal theridiids because of the presence of a colulus. Thus, we might consider the behaviour of *Latrodectus* and *Steatoda* to be the primitive condition in theridiids.

Theridula has a web with long viscid lines that help capture flying prey (Stowe, 1985). *Anelosimus* constructs a three-dimensional web without viscid elements; a structure (SSSt) wrapped around branches (Eberhard pers. comm.; Foelix, 1996: fig. 209; Levi, 1967; Tietjen, 1986: fig. 2). *Anelosimus jucundus* (O. P.-Cambridge, 1896) does not build gumfooted lines or a sheet similar to that of *Coleosoma* or *A. tessellata* (Fig. 6G; Nentwig & Christenson, 1986: fig. 2).

Coleosoma was placed close to *Theridion* because of the absence of a colulus (Levi & Levi, 1962). Based on the presence of a hoodlike paracymbium, *Anelosimus*,

Chrosiothes, *Chryso*, *Coleosoma*, *Helvibis*, *Nesticodes*, *Rugathodes*, *Spintharus*, *Tekellina*, *Theridula*, *Thwaitesia* and *Thymoites* are considered to form a monophyletic group (Forster *et al.*, 1990). The genera *Anelosimus*, *Chryso*, *Coleosoma* and *Theridion* do not build gumfooted lines. *Achaearanea tessellata* (Keyserling, 1884) constructs a 'sheet-web' identical to that of *C. blandum* (Fig. 6C; Eberhard, 1972). However, the relationships of *A. tessellata* to *Coleosoma* are unclear. Most probably *A. tessellata* is misplaced in *Achaearanea* (*Achaearanea* might be polyphyletic; Forster *et al.*, 1990).

The placement of *Tidarren* has been enigmatic to date (Knoflach & van Harten, 2000). The webs of *Tidarren sisypoides* (Walckenaer, 1842) and *Tidarren haemorrhoidale* (Bertkau, 1880) contain no gumfooted lines or viscid elements (Fig. 6F; Benjamin, unpublished data). We suggest that *Tidarren* might be related to *A. tessellata* and *Coleosoma*.

Chryso was originally defined for an assemblage of American species (Levi, 1955, 1962). The subsequent inclusion of Asian species might have rendered the genus polyphyletic. Our study of webs of *Chryso* (American species) and *Theridion* suggest that Levi (1955, 1962) might have been correct in postulating that they are related.

Chrosiothes, *Episinus* and *Spintharus* have unique web architecture (Bristowe, 1958; Stowe, 1985; Forster *et al.*, 1990; Roberts, 1995). The web of *Episinus angulatus* (Blackwall, 1836) consists of two gumfooted lines held by L1 and L2. The spider hangs upside down on a few SSSt threads, facing the substrate (Holm, 1938; Roberts, 1995: 261). However, it is not clear whether this derived web architecture defines a monophyletic group (Forster *et al.*, 1990).

Derived webs are also known from *Argyrodes*, *Pholcomma* and *Phoroncidia*. *Argyrodes* species make webs consisting of a few non-viscid lines strung across vegetation, intended for other spiders wandering inadvertently onto the web (Eberhard, 1979; Stowe, 1985). Some do not construct webs at all, and are kleptoparasitic. *Pholcomma* appears to construct a unique derived web described in detail by Holm (1938) and Jones (1992). *Phoroncidia* constructs webs with 1–3 GF; the spider sits on a twig with L1 holding a SSSt thread (Marples, 1955; Eberhard, 1981).

In summary, as a result of our survey of theridiid webs (Theridiidae excluding Hadrotarsinae, which are not known to build webs), we recognize four major web types, with corresponding behaviours: Types 1 and 2 which have gumfooted lines and Types 3 and 4 which do not, but which have (Type 3) or do not have (Type 4) viscid elements in their webs. Type 1 is an *Achaearanea*-type web with a central retreat (Fig. 8A; Stowe, 1985: fig. 3; Griswold *et al.*, 1998: fig. 2a, b). Type 2 is a *Latrodectus*-type web with a peripheral retreat

(Fig. 8B; Wiehle, 1937: fig. 2). Type 3 is a *Theridion*-type web with viscid elements (Fig. 8C; Wiehle, 1937: fig. 3) and Type 4 a *Coleosoma*-type web without viscid elements but with a sheet and KN structure (Fig. 8D). However, a phylogenetic analysis that takes into account all the available data is required to establish whether these behavioural types generally define natural groups.

EVOLUTION OF REDUCED WEBS IN THERIDIIDS

In theridiids, webs may often have been reduced or modified. The obvious direction of evolution seems to be from a *Steatoda* or *Latrodectus*-type gumfoot-web to a *Coleosoma*-type web without gumfooted lines or any viscid elements. The web of *A. tepidarium* may constitute an intermediate form. The reduction of webs to a few gumfooted lines in *Phoroncidia*, the derived webs of *Spintharus* and *Episinus* and the absence of a web construction behaviour in *Argyrodes* all suggest that modification of web construction behaviour may have occurred many times independently. The evolutionary trend seems to be from extensive to reduced amounts of viscid silk in webs, and finally to total absence.

Web reduction is not an unusual phenomenon and has occurred repeatedly in Orbiculariae (Eberhard, 1990; Griswold *et al.*, 1998). Many adaptive advantages for reduced webs have been postulated (Kaston, 1964; Foelix, 1996). Most arguments are generally associated with increased functional efficiency of the web (Kaston, 1964; Stowe, 1978; Eberhard, 1982; Eberhard, 1990; Eberhard, 2001). Surprisingly, the costs of producing and maintaining viscid web elements for prey capture have been overlooked.

Viscid silk requires a humid or even aqueous environment in order to maintain its proper conformation and function as glue (for references see Benjamin, Duggelin & Zschokke, 2002; Higgins & Rankin, 1999). In addition, the strength and elasticity of viscid web elements depend on the appropriate degree of hydration (Higgins & Rankin, 1999; Higgins *et al.*, 2001). The mixture of hydrophilic and hygroscopic low molecular weight compounds in droplets may therefore attract and hold atmospheric water and prevent drying, improving the ability of the web to capture insects (Tillinghast & Townley, 1987; Townley *et al.*, 1991). Choline, a component of viscid silk, may function as an osmoprotectant (Higgins & Rankin, 1999; Higgins *et al.*, 2001). However, for spiders producing viscid silk, even on normal diets, choline might be sufficiently limiting as to require trade-offs in allocation (Higgins & Rankin, 1999).

Unlike in theridiids, daily removal and replacement of large parts of the orb-web by orb-weavers resolves

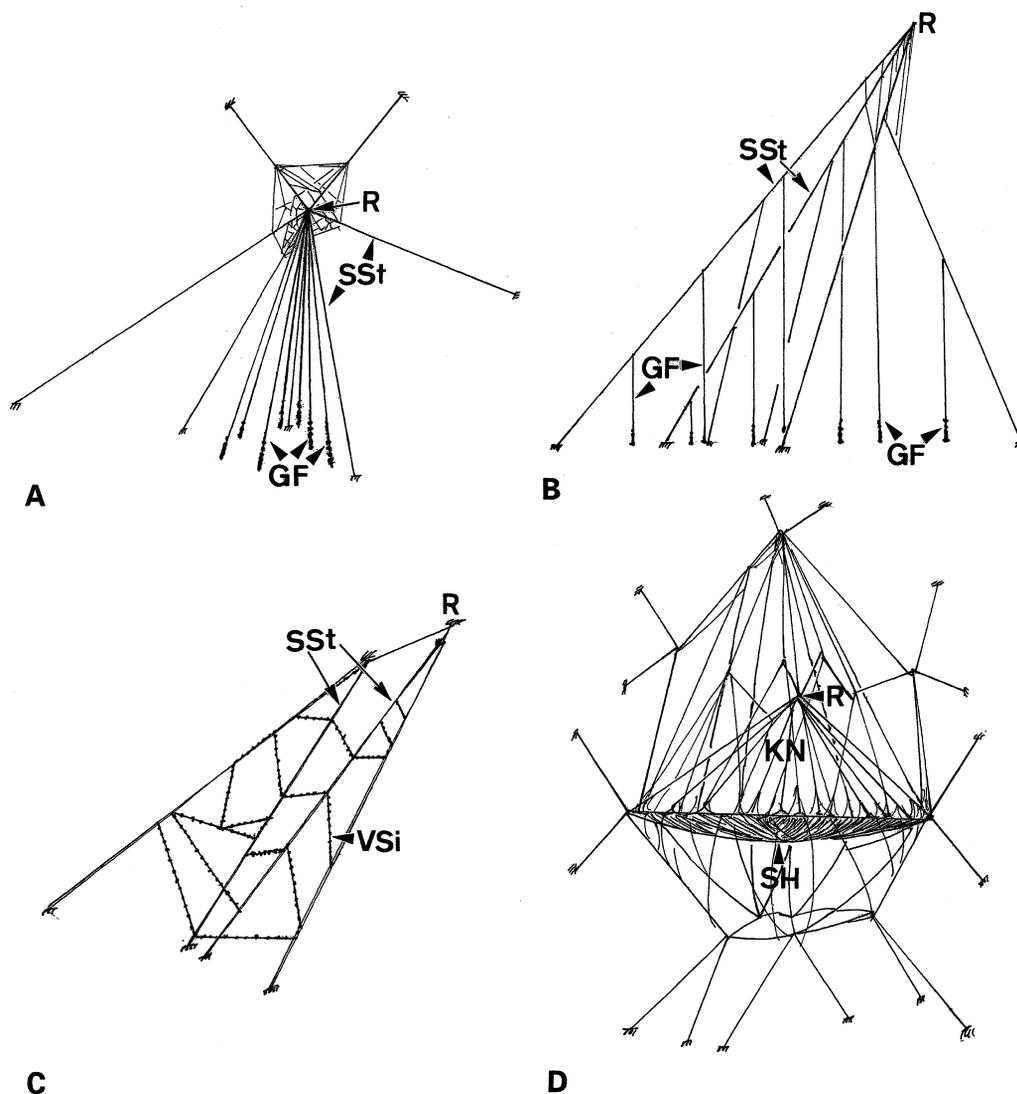


Figure 8. Schematic representation of theridiid webs (not to scale): A, *Achaearanea*-type web with a central retreat. B, *Latrodectus*-web with a peripheral retreat. C, *Theridion*-type web with viscid elements. D, *Coleosoma*-type without viscid elements but with a sheet and KN structure.

this problem. Orb-weavers ingest silk as they take down their webs and recycle it in subsequent webs to significantly improve the economy of web construction (Breed *et al.*, 1964; Peakall, 1971; Opell, 1998, 1999). The horizontal orb-weaving Cyrtophorinae neither produce viscid silk, nor do they perform web removal and replacement (Kovoor & Lopez, 1988; Levi, 1997). The sheet-web building Linyphiidae (at least Linyphiinae) produce viscid silk that dries up after a short time and the web is not replaced daily (Benjamin *et al.*, 2002). The striking fact is the convergent loss of viscid silk production in several orbicularian lineages. The cost of producing and maintaining viscid silk might be a long overlooked

driving force that leads to web reduction, at least in theridiids. Such an adaptation might have, by relieving the spider of the necessity to produce viscid silk, reduced its dependence on choline, thereby increasing its fitness.

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