

Untangling the Tangle-Web: Web Construction Behavior of the Comb-Footed Spider *Steatoda triangulosa* and Comments on Phylogenetic Implications (Araneae: Theridiidae)

Suresh P. Benjamin^{1,2,3} and Samuel Zschokke¹

Accepted August 9, 2002; revised September 20, 2002

*Theridiidae typically construct a three-dimensional web often described as “irregular.” The web consists of a supporting structure and lines under tension termed gumfooted lines. We used automated methods to observe web construction in the theridiid *Steatoda triangulosa* under laboratory conditions. Web construction lasted several nights. After orientation, spiders built a three-dimensional structure of several threads radiating sideways and downward from the retreat. To build gumfooted lines, they started from the retreat, moved along a structural thread, then dropped down to attach the thread to the lower substrate. On returning, they coated the lowest part of the thread with viscid silk before moving up along the same thread back to the structural thread. They then continued moving along the same structural thread to drop down again to build the next gumfooted line. This behavior was continued until the spiders had built a series of gumfooted lines (a bout). There were regular intervals between the construction of two bouts. Thus, a single web included many bouts built in different stages. We show that gumfooted lines are not homologues to sticky web elements of orb-weavers and present new synapomorphic characters that support the monophyly of Theridiidae + Nesticidae and the monophyly of araneoid sheet web weavers. Further, the time*

¹Department of Integrative Biology, Section of Conservation Biology, University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland.

²Department of Zoology, South Parks Road, Oxford OX1 3PS, England.

³To whom correspondence should be addressed. e-mail: Suresh.Benjamin@unibas.ch. Fax: +41612670832.

allocation pattern for different behavioral stages and the fine structure of a gumfooted line are presented.

KEY WORDS: web construction; behavioral patterns; capture thread; viscid silk; phylogeny; *Steatoda*; Theridiidae; theridioids.

INTRODUCTION

Comparative studies are an important tool in evolutionary biology. They reveal similarities and dissimilarities that require explanation and thus suggest new hypotheses (Harvey and Pagel, 1991). The spider's web is a record of its behavior (Vollrath, 1988) and, as such, is ideally suited for comparative studies of the evolution of behaviours. Comparative studies of web construction behavior and deducing relationships in spiders are popular (Eberhard, 1982; Coddington, 1986c, and references therein). However, most behavioral studies to date are on orb-webs. As noted by Eberhard (1990b), the ratio of papers on orb-webs to those on non-orb-webs is about 2:1, although the number of species is actually the reverse. When Hormiga *et al.* (1995), Scharff and Coddington (1997), and Griswold *et al.* (1988) inferred the phylogeny of Orbiculariae, they encountered severe limitations in deducing homologies of well-known orb-weaver motor patterns in non-orb-weaver orbicularians, because of the absence of data.

The neglect of non-orb-webs might be due to the bias of humans, who find symmetrical objects more attractive than nonsymmetrical ones, or perhaps due to the high variability of theridiid web construction behavior, which makes it tiresome to observe. The fact that these webs are often built during the night does not make things easier.

Comb-footed spiders, or Theridiidae, typically construct a three-dimensional web often described as "irregular." The web consists of a supporting structure (SSt: RT + RTt in Fig. 1) and lines under tension, termed gumfooted lines (GFs), which connect the SSt and the substrate (SB; GF in Fig. 1). Theridiid webs generally are suspended beneath a covering object or, as in *Steatoda*, extend from a retreat. Bases of GFs are the only part in the web that contain viscid silk. To date they have been considered as homologous to viscid elements found on webs of other orb-weavers (Griswold *et al.*, 1998).

Theridiid webs have been described before, however, these studies, except those by Szlep (1965) and Lamoral (1968), described only the spider's web, and not its construction behavior. Wiehle (1931) first described the web of *S. triangulosa* (*Teutana triangulosa*). Hopfmann (1935) described the web of *S. bipunctata*. Webs of *Latrodectus tredecimguttatus*, *L. pallidus*, *L. revivensis*, *L. variolus*, and *L. bishopi* were described by Szlep (1965,

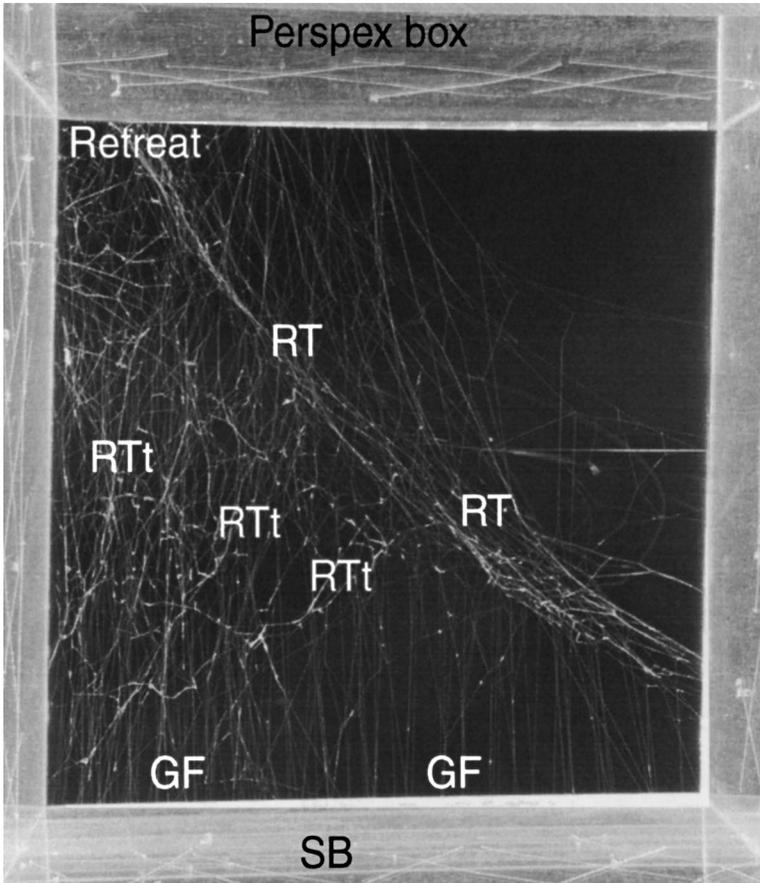


Fig. 1. The web of *Steatoda triangulosa*, lateral view, photographed in the laboratory; perspex box partly shown. GF, gumfooted lines; RT, radiating threads; RTt, peripheral web elements originating from RT; SB, substrate.

1966). Lamoral (1968) studied the webs of *S. lepida*, *L. mactans*, *L. geometricus*, and *L. purcelli*. Webs of the genus *Phoroncidia*, reduced to a single or a few lines of silk were described by Marples (1955) (*Ulesanis pukeiwa* Marples, 1955) and Eberhard (1981b). The web of *Achaearanea riparia* (*Theridium saxatile*) was described by Freisling (1961), the “sheet-web” of *Achaearanea tessellata* by Eberhard (1972), and the web of *Argyrodes attenuatus* by Eberhard (1979). Further notes on a range of theridiid webs are given by McCook (1889) and Nielsen (1932).

In the present contribution we describe the web construction behavior of *Steatoda triangulosa* and compare it with the known construction behavior

of Araneidae, Theridiosomatidae, Tetragnathidae, Linyphiidae, and Synotaxidae. We discuss the resulting implications for the evolution of web diversity in orbicularians, within a phylogenetic framework. We also present the time allocation pattern for different behavioral stages and the fine structure of a GF.

METHODS

Study Species

The spider family Theridiidae currently includes 2201 described species in 76 genera; 123 species are placed in *Steatoda* (Platnick, 2002). *Steatoda triangulosa* (Walckenaer, 1802) is a cosmopolitan spider common in central Europe. It is mostly found within or close to synanthropic habitats. Adults attain a body length of 4–5.2 mm (females) or 3.5–4 mm (males) (Roberts, 1995).

Handling of Spiders

Spiders used in this study were collected as subadults or adults from Basel, Switzerland, and surroundings and maintained under laboratory conditions. They were kept in 8 × 8 × 16-cm perspex (PS) boxes and fed daily with two or three *Drosophila* sp. and, occasionally, with ants. All spiders were observed in 8 × 8 × 16-, 10 × 10 × 14.5-, or 20 × 20 × 20-cm PS boxes. The controlled environmental conditions of the rearing and observation room were 24.5 ± 2°C and a reverse L/D light cycle of 12/12 h. The introduction of the spider into the box always took place at night (dark period).

Data Collection

Preliminary observations suggested that *S. triangulosa* builds its web during the night and that it is easily disturbed by light, typically leading to an interruption in construction. This made manual as well as conventional video observations with normal (white) light impractical. Moreover, the initiation of web construction was highly unpredictable, requiring observation throughout the night. Our observational setup 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 analyzed in real time. The position of the spider

was recorded at a rate of 14 frames per second. Study methods are described in detail by Benjamin and Zschokke (2002a, b). This approach permitted recording in two dimensions.

To record the spider's movements in three dimensions, we used the setup and methods described by Zschokke (1994) and Zschokke and Vollrath (1995b), but with infrared light rather than normal light. This setup differed from the first one by the use of two synchronized observation units. Each unit consisted of a videocamera and a VP112 image scanner (HVS Image Ltd., P.O. Box 100, Hampton TW12 2YD, UK). The first unit's camera was placed above the PS box, and the second unit's camera in front of it. To obtain a three-dimensional (3D) movement pattern, recorded data of the units were combined using software described by Zschokke (1994). The 3D movement patterns were viewed with Rotator (Kloeden, 1996).

We successfully recorded the construction of 25 webs built by eight subadult females. In these webs, we analyzed 130 GF construction bouts and 135 SSt construction bouts. The spider's movement patterns during resting and GF construction are easily recognizable in our recordings. In contrast, the movement patterns during the explorative stage, SSt construction, and thread connections made during filling-in were almost indistinguishable from one another. For statistical analysis we therefore did not differentiate these three types of behavior and define the time spent on SSt construction as the time not spent on GF construction or resting.

Additionally, the finished web was photographed to compare it with the movement pattern. To describe leg movement patterns during thread manipulation, parts of single web constructions were observed directly. The GFs were prepared for SEM (scanning electron microscope) study using procedures of Benjamin *et al.* (2002).

Data Analysis

Data were analyzed using software and methods described by Benjamin and Zschokke (2002a). For descriptive statistics we used the StatView program package (SAS Institute, 1998). To compare time allocation and number of bouts on successive days we used the Wilcoxon signed rank test.

Abbreviations and Terms

Abbreviations used in the figures and text are given in Table I and are mostly modified from Coddington (1986c) and Zschokke (1999). A "bout" is a series of similar behaviors (Coddington, 1986c); thus a single GF bout

Table I. Abbreviations Used in the Figures and Text^a

A	Attach
Alt	Alternate leg movements, e.g., Alt L1
DL	Dragline
GFs	Gumfooted lines; threads with viscid bases
L	Leg pairs 1–4 (numbered from front to rear)
PS	Perspex
RTs	Radiating threads
RTt	Peripheral web elements originating from RTs
SB	Substrate; bottom of perspex box
SSt	Supporting structure; RT + RTt

^aAfter Coddington (1986c) and Zschokke (1999).

incorporates the construction behavior of several GFs. By cut-and-reel behavior we mean moving by cutting and reeling the previously laid dragline (DL) while constructing a new thread. This behavior is performed by most araneids (Coddington, 1986c). New abbreviations are kept to a minimum. Unfortunately, the introduction of new abbreviations was unavoidable, as the use of some published abbreviations might have implied homology for nonhomologous behaviors. Thus we use radiating threads (RTs) instead of radii. We define a “thread” as a strand of two or more fibers produced simultaneously by two or more spinnerets (Zschokke, 2000). When we cite species names we first give the current nomenclature of Platnick (2002); the name used in the original published work is given parentheses.

RESULTS

General Description of Web Construction

Spiders always started construction during the night. During the day they rested with outstretched L1. When the spiders were introduced during the day, they always built few horizontal threads at the top of the box and rested at their meeting point until dark, prior to construction. Web construction began with an explorative stage, in which the spider, in periodic bursts, of activity, dropped down and walked around or moved in the space where the web was presumably planned. The spider moved about with Alt L1 movements and with a single L4 holding the dragline (DL). The spider let out silk while dropping but occasionally did not attach DL to the substrate (SB). In some cases the spider dropped down on the DL, stopped short of the SB, and then moved up on the DL. It was difficult to observe any stereotypic pattern during this stage. This stage lasted a relatively short time (3 to 15 min).

Structure

The structure consists of radiating threads (RTs) extending from a peripheral point to the SB. Although they were not arranged in geometrically regular arrays, most of them originated primarily from a single peripheral point (retreat in Fig. 6a). The RTs were held in tension by threads extending from them in all directions of the box (RTt in Figs. 1 and 6a). Structural elements never contained viscid silk. Almost all GFs were attached to RTs.

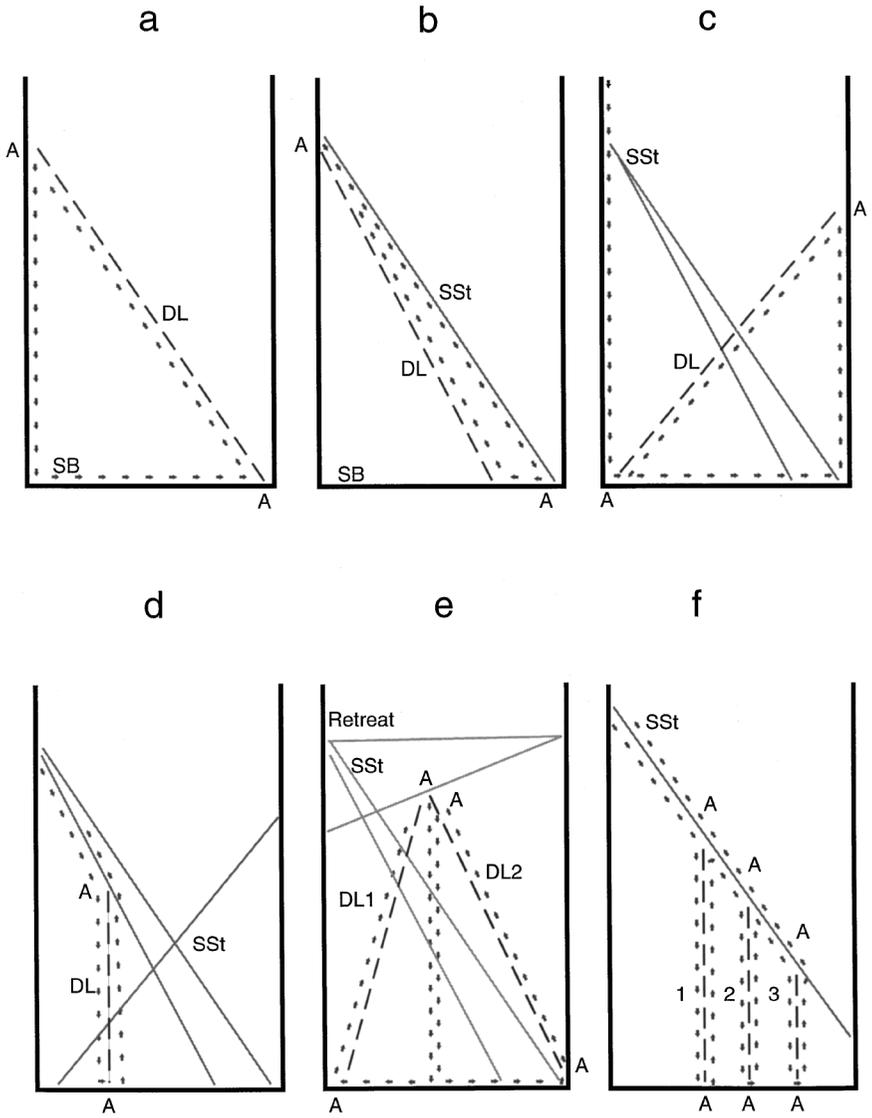
RT construction behavior was highly variable. Basically the spider would first attach its DL to an upper peripheral point of the box, then move away to the central part of the SB and attach its DL. Then the DL was reinforced by doubling. We observed two behavioral patterns that were performed often (Figs. 2a and b). During a third type of RT construction behavior the spider dropped down to the SB, attached its DL to the SB, moved to the opposite side, moved up the peripheral side of the box, attached the DL, and doubled it (Fig. 2c).

During later phases of web construction the spider used existing SSt as scaffolding in the processes of expanding the web. The spider's movements were variable but still followed the same basic pattern. After making an attachment to the upper periphery of the box, the spider moved along an existing line to the SB, moved away on the SB, and attached its DL. Finally, the DL was reinforced by doubling (Figs. 1d and e). We never observed cut-and-reel behavior. In a gradual process, *S. triangulosa* expanded the web by adding SSt and GFs to the existing web.

Gumfooted Lines

The construction behavior of GFs is the most stereotyped of all theridiid construction patterns (Figs. 1f and 6b). RTs, which serve as a suspension structure, were always in place before the spider began constructing GFs.

To build a GF the spider moved away from the periphery along an existing radiating thread to more or less the central part of the web. It then started groping (waving actively) with L1 to determine the position of existing GFs. When the starting point was determined, it attached its DL to the supporting thread. The spider then dropped down, paying out DL. At the same time it groped with Alt L1 and L2 for surrounding GFs. We once observed the spider holding an existing GF with one leg and groping with the other. It then dropped down to the SB with an L1 forward tap, turned around, and attached DL to the SB by dipping the posterior part of the abdomen. The



spider then turned around and went up, with L1 holding the existing silk line and with L4 holding the new thread. During its upward journey, it coated the GF at the most basal part with viscid silk by applying viscid silk directly with the spinnerets (Figs. 2f and 6b). The spider never moved back and forth along the DL or applied viscid silk with leg movements. Construction of the basal part and its attachment to the SB are the slowest during GF construction (0.06 to 0.37 mm/s).

After attaching the GF to the structural thread, the spider then continued moving along the same or another structural thread to drop down again to build the next GF (Fig. 2f). This behavior was continued until the spider had completed a bout of GF construction (a GF bout included 1 to 17 GFs; $n = 20$; median = 6.5). There were regular intervals between two GF construction bouts. Hence a single web included many GF bouts. We never observed cut-and-reel behavior during GF construction. A GF consisted of two pairs of thread; the thin pair probably of minor ampullate gland thread and the thick pair of major ampullate gland thread (Fig. 3).

After constructing a series of GFs the spider moved along SSt with L1 plucking behavior, which was followed by filling in the web. Filling-in is achieved in two ways: by interconnecting existing structural threads and by constructing new structural threads connecting the structure with upper parts of the box. Thread lines that become loose or thread lines of old



Fig. 2. Movements of *Steatoda triangulosa* during web construction (schematic and not to scale). (a) Early stages of SSt construction, to construct RTs. The spider initially made an attachment at the upper periphery of the box and dropped down, then moved away from the periphery on the SB, stopped, and attached, the DL. Finally, it doubled the DL. (b) Same as a; stages of SSt construction, to construct RTs. The spider initially moved away from the upper periphery of the box and along an existing RT, then moved away from the RT on the SB, stopped, and attached the DL. Finally, it doubled the DL. (c) Movements during a third type of RT construction behavior. The spider dropped down to the SB, attached the DL to the SB, moved to the opposite side, moved up the peripheral side of the box, attached the DL, and doubled it. (d) During later phases of web construction the spider used existing SSt as scaffolding in the process of expanding the web. After attaching the DL to the upper periphery of the box, it moved along an existing RT to the SB, dropped down, reeling out DL with Alt L4 movements, and attached the DL to the SB. Finally, the DL was reinforced by doubling. The spider probably did not cut-and-reel. (e) Probable sequence of behavior during later stages of SSt construction. These threads tense SSt by connecting to the SB in opposite directions. The spider's moments were the same as in d at the beginning, but after dropping down reeling out DL with Alt L4 movements, it moved away on the SB and attached the DL to the SB. Finally, the DL was reinforced by doubling. The spider then continued, without rest, to perform the same behavior in the opposite direction. (f) Same as e, during construction of three GFs. The spider started from the retreat, moving along an existing thread; it then dropped down at regular intervals to attach the thread to the SB, moving along the same structural thread to drop down again to build the next GF. Probably, on returning, it coated the lowest part of the thread with viscid silk. A, attach; Alt, alternate leg movements; DL, dragline; GF, gumfooted lines; RT, radiating threads; SB, substrate; SSt, supporting structure.

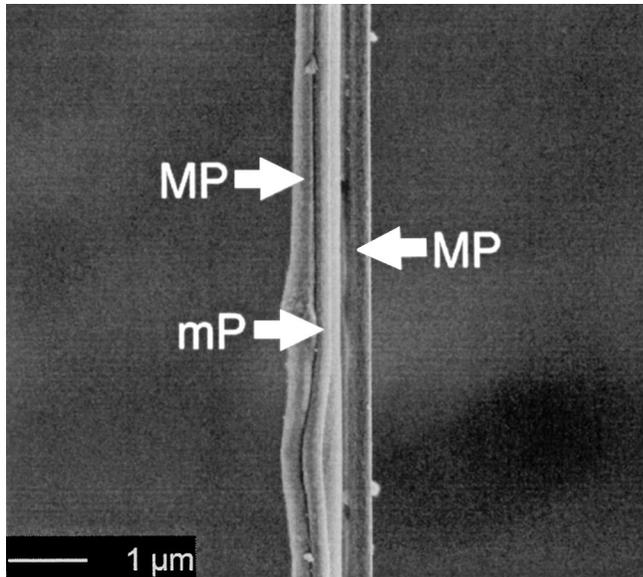


Fig. 3. Scanning electron micrograph of a GF above viscid elements; it consists of two fibers of minor and two fibers of major ampullate silk. mP, minor ampullate gland thread; MP, major ampullate gland thread.

webs are cut and bundled up by the spider. We never observed silk being eaten.

Web Construction Sequence and Time Allocation

The construction sequence consisted of alternating behavioral bouts of GF and SSt construction (Fig. 5). During the first day (first 24 h) more SSt were built (Fig. 4a) than during the second day ($Z = -3.06$, $P = 0.002$), and more time was allocated to build them during the first day than during the second day (Fig. 4b; $Z = -3.11$, $P = 0.002$). During the third day there were fewer SSt bouts (Fig. 4b) and they were significantly shorter than during the first day ($Z = -3.180$; $P = 0.0015$).

The spider normally performed a single GF bout during the first day, then more on the second and third days (Fig. 4a). After finishing a GF bout the spider most often interconnected structural threads. It also rested between successive bouts (Fig. 5). During the fourth day the spider allocated almost the same amount of time to the two types of bouts ($Z = -1.362$, $P = 0.173$).

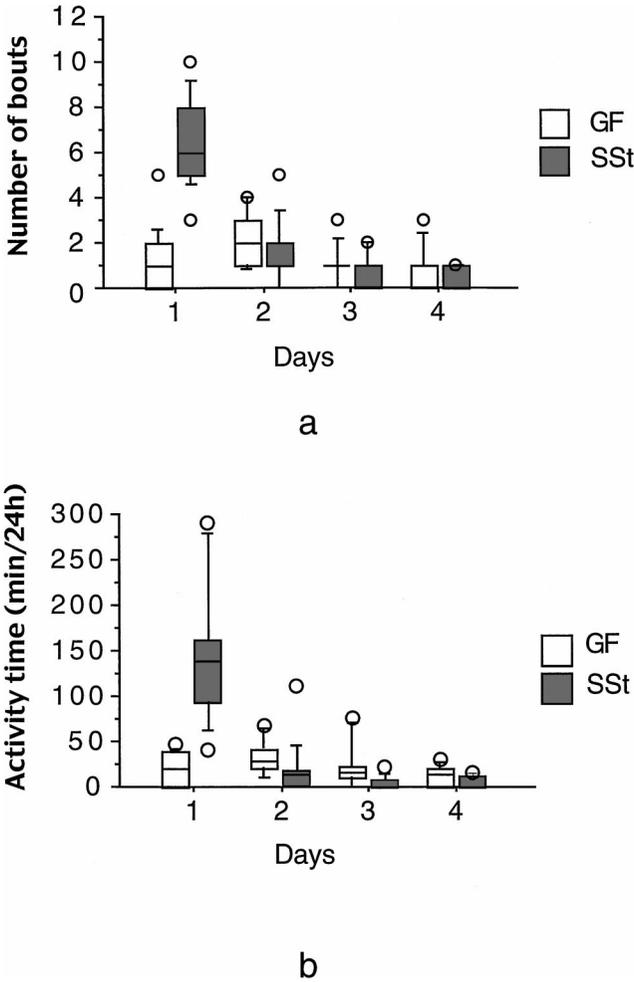


Fig. 4. The number of bouts performed and activity time of *Steatoda triangulosa* during web construction. (a) The number of GF and SSt bouts performed. The number of bouts during the first day was significantly higher than during the second day ($Z = -3.06, P = 0.002$). The number of GF and SSt bouts performed during the fourth day did not differ ($Z = -1.183, P = 0.237$). (b) The activity time during construction of GF and SSt. The spider allocates more time to building the structure during the first day than during the second day ($Z = -3.06, P = 0.002$). During the fourth day the time allocated to different bouts differs least ($Z = -1.36, P = 0.173$). We calculated the activity time as the number of minutes per 24 h. Data given are for the first 96 h of 25 webs constructed by eight individuals. The 10th, 25th, median, 75th, and 90th percentiles are plotted. Values above the 90th and below the 10th percentile are plotted as points.

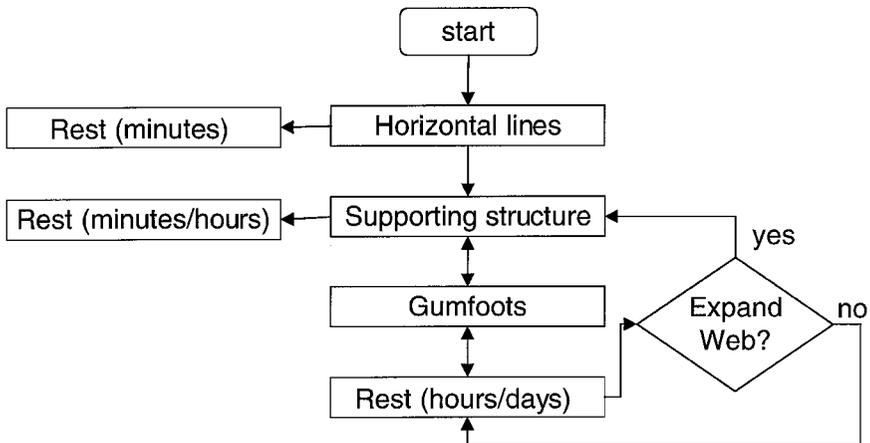


Fig. 5. General sequence of web construction of *Steatoda*. The web construction sequences consists of two main behavioral bouts, SSt and GF construction. The spider is able to expand the web by adding new SSt to existing ones and constructing new GFs. Note the spider's ability to rest between different stages. GF, gumfooted lines; SSt, supporting structure.

DISCUSSION

General Discussion

Theridiid webs have often been described as “highly irregular” or “tangle” webs (Hopfmann, 1935; Comstock, 1940; Levi and Levi, 1962; Szlep, 1965, 1966; Shear, 1986). However, the construction behavior of *Steatoda* is more stereotyped than initially expected. In most previous studies, authors described the end product of successive sequences of a highly organized and stereotyped behavior, and not the behavior per se. This is not peculiar to theridiids; Eberhard (1992) showed that the supposed “highly irregular” or “tangle” web of the pholcid *Modisimus guatuso* Huber 1998 (*Modisimus* sp.) was the end product of stereotyped and organized behavior. The irregular appearance of theridiid webs might be due to the absence of cut-and-reel behavior.

The explorative stage in *Steatoda* is very similar to that of other theridiids (Szlep, 1965, 1966; Lamoral, 1968) and orb-weavers (Eberhard, 1975, 1990a; Zschokke, 1996). The descents probably inform the spider of the presence of objects in the space where the web is to be built (Eberhard, 1975). The relatively short duration of this stage might be an artifact and may be due to the lack of structure in the observation area. In nature this could be the longest of all stages. In some orb-weavers this stage is relatively longer, for example, see Eberhard (1990a) and Zschokke (1996).

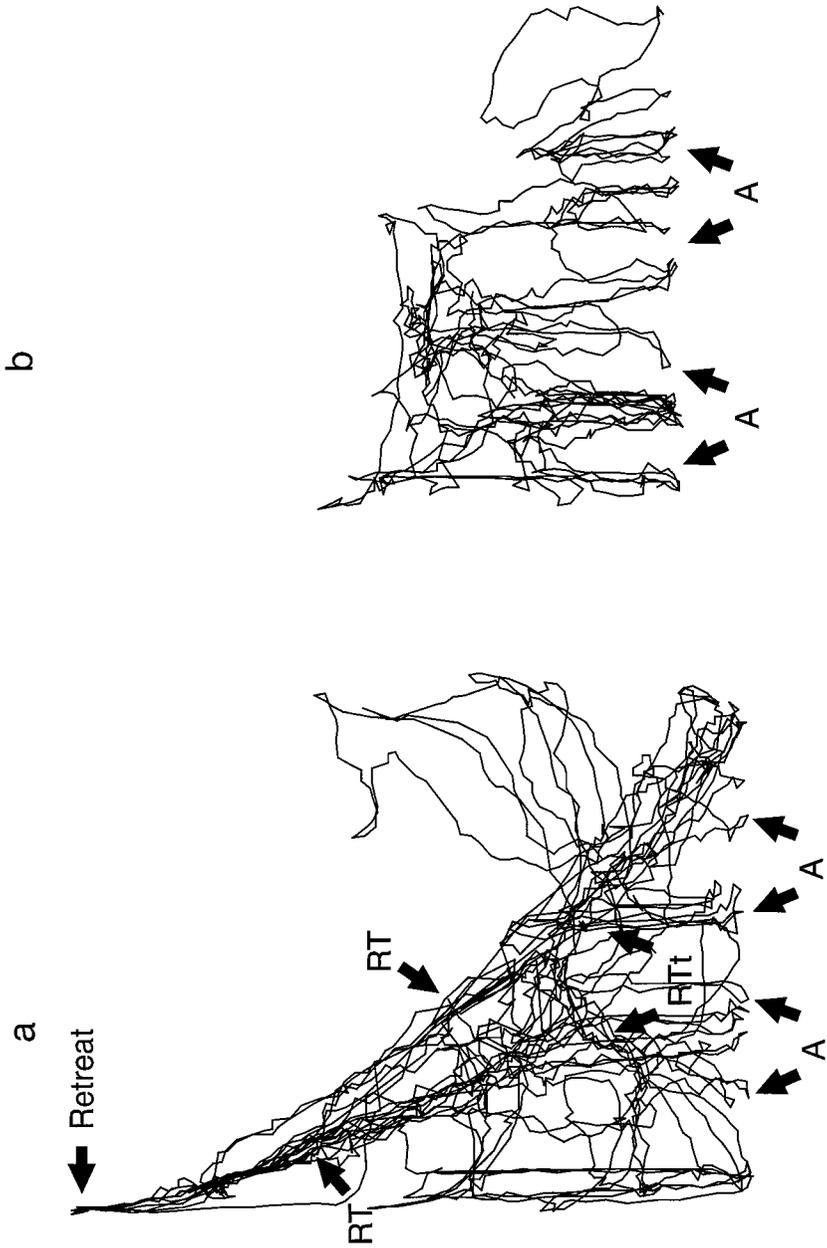


Fig. 6. Tracks of the movements of *Steatoda triangulosa*, lateral view. (a) During supporting structure construction. (b) During GF construction. A, attach; RT, radiating threads; RTt, peripheral web elements originating from RT. Size of box, 20 × 20 × 20 cm.

Steatoda starts with an initial structure of RTs extending from a peripheral point to the SB (Fig. 5). In a similar behavioral sequence, *Latrodectus* initially lays several threads extending out of its retreat toward surrounding objects (Szlep, 1965; Lamoral, 1968). Although they are not arranged in geometrically regular arrays, almost all of them originate primarily from a single peripheral point. The peripheral point in our recordings corresponds to the retreat in nature. It is possible that in nature spiders first select a site with an appropriate retreat and then start web construction. *S. triangulosa*, in contrast to *Latrodectus*, never lines the retreat with silk. *A. riparia* builds a retreat lined with silk and detritus (Freisling, 1961). *Latrodectus* lays a DL while moving back and forth along a RT (Szlep, 1965). In *S. triangulosa* we would predict similar behavior, as RTs become more visible with time. We were unable to observe cut-and-reel behavior during structure construction; we are certain that it did not occur during GF construction, nevertheless, we cannot exclude its occurrence. Due to the difficult light conditions and the small size of the spider, we might have overlooked it. However, cut-and-reel behavior has never been reported in theridiids (Freisling, 1961; Szlep, 1965; Lamoral, 1968; Eberhard, 1979, 1981b).

During the second phase, GFs are built (Fig. 5). The movements during GF construction were the most unique and stereotyped of the whole web construction. During GF construction, the spider dropped down on a minor ampullate thread and doubled it with a major ampullate thread (Fig. 3). Capture threads of orb-weavers consist of two axial fibers of flagelliform silk; if GFs are made of flagelliform silk, they should be of equal thickness instead of two different thicknesses as in Fig. 3. During construction of threads with doubling as seen in GF construction, the first line remains loose, but the second line becomes tense (Peters, 1990). In GFs the thick fibers are tense and the thin fibers are loose, forming loops. The DL (used as bridging lines during movement) of Araneoidea is of minor ampullate thread and is doubled with major ampullate thread (Peters, 1990). *Latrodectus* seems to perform similar GF construction behavior (Szlep, 1965; Lamoral, 1968). We are not sure how GFs are connected to the SB or how they are coated with viscid silk. The GF-to-SB connection is a weak connection, which breaks at the slightest contact with prey (Wiehle, 1931; Kullmann, 1960; Szlep, 1965). An attachment disk would not break in this manner. To us, it appears that GF-to-SB connections are made of viscid silk.

The filling-in of the web after the termination of construction, by interconnecting existing structural threads and by constructing new structural threads connecting the structure with upper parts of the box, appears to be unique to theridioids. Similar behavior has been observed in *A. riparia* (Freisling, 1961). It was not clear if the spider was manipulating the tension of RTs and thereby, indirectly, of GFs or simply filling in the

web. Orb-weavers adjust tension during web construction (Eberhard, 1981a, 1990a).

Computerized observation, as in this study, requires a high contrast between the object and the background (Zschokke and Vollrath, 1995a; Benjamin and Zschokke, 2002a). Unfortunately this prevented us from offering the spider a more natural habitat, which may have modified its behavior. However, as *S. triangulosa* is found mostly within or close to synantropic habitats, the effect of the artificial conditions is probably minimal.

Phylogenetic Implications

Theridioids (Theridiidae + Nesticidae, Clade 9 [*sensu* Griswold *et al.*, 1998]) are probably some of the most derived spiders among araneoids (Coddington, 1986b). Theridiidae and Nesticidae are similar in their finished webs and, to a large extent, in their genital morphology (Griswold *et al.*, 1998). The spinneret morphology is well known and is similar in both families (Coddington, 1989; Forster *et al.*, 1990). Thus the identification of behavioral patterns unique to one family requires the understanding of the behavior of both. Nesticidae web construction behavior has never been described. However, we have studied webs of *Nesticus cellulanus* (Clerck, 1757) in detail. They do contain GFs. (Benjamin and Zschokke, unpublished data). In the absence of more detailed evidence suggesting otherwise, we may assume that both possess similar construction behavior.

GFs are characteristic of theridioids. Nothing similar has been described in other Araneoidea. *Wendilgarda* sp. (Theridiosomatidae) possesses an outwardly similar structure (Coddington and Valerio, 1980; Coddington, 1986a; Eberhard, 1989, 2001; Shinkai and Shinkai, 1997). However, the construction behavior of viscid parts in *Wendilgarda* sp. is more similar to that of orb-weavers (Eberhard, 2001). They add viscid lines with droplets to the existing nonviscid vertical line instead of coating a vertical line with viscid silk during DL doubling as in *Steatoda*. Sticky vertical lines in *Wendilgarda* might thus be homologous to the orb-weaver sticky spiral (cf. discussion by Eberhard, 2001).

Araneoid capture threads originate from six silk glands, two flagelliform glands and four aggregate glands. The core fiber is from the flagelliform gland and the aggregate glands produce aqueous glucoroproteins, which form the viscid material. The spigots are arranged in a characteristic form termed a triad or triplet (Sekiguchi, 1952; Peters, 1955; Kovoov and Lopez, 1982; Griswold *et al.*, 1998). However, GFs are only partly produced by the triads. The GF core fiber is of minor ampullate gland and major ampullate gland threads, and not flagelliform thread. Thus, only the viscid material in GFs

and araneoid capture threads are homologous (produced by corresponding structures). Contrary to Szlep (1965), because of the presence of viscid material and the unique construction behavior, we do not consider GF to be homologous to radii. GF construction behavior is unique for theridioids.

During GF construction *Steatoda* performs Alt L4 pull behavior and, during GF attachment to the SB, forward taps with L1. However, as Coddington (1986b) pointed out for L1 tapping behavior, the spider has few other options when hanging down on a vertical line. The theridiid *Achaearanea tepidariorum* attaches the GF to SSt with L3 and one L4 holding SSt and the other L4 holding the GF (Eberhard, 1982). *Steatoda* and probably other theridiids (Marples, 1955; Eberhard, 1979, 1981b, 1982), *Synotaxus* (Eberhard, 1982), and linyphiids (Benjamin and Zschokke; preliminary data on *Linyphia triangularis* and *Microlinyphia pusilla*) do not cut-and-reel. Except for *Nephila*, all other orb-weavers cut-and-reel (uloborids cut-and-reel frames but not radii, other orb-weavers cut-and-reel when constructing radii [Eberhard, 1982; Coddington, 1986c]). Nephilines also use an infrequent outward L1 tap and a frequent outward L4 downward slide (Coddington, 1986b). We once observed an individual *S. triangularis* drop down on a DL to build a GF with L2 in contact with an existing GF.

Two striking similarities between theridiids and synotaxids are the alternate construction of viscid and nonviscid parts and the unit-like construction of the web. The construction behavior in synotaxids is so characteristic that they were termed “unit webs” by Eberhard (1977, 1995). Preliminary observations suggest that the linyphiids have the same web construction behavior, i.e., alternate construction of viscid and nonviscid parts and unit-like construction (Benjamin and Zschokke; unpublished data on *L. triangularis* and *M. pusilla*). Judging by the finished webs of two other “araneoid sheet web weavers,” Pimoidae and Cyatholipidae might have similar behavior (Hormiga, 1994; Griswold, 1997). In contrast, orb-weavers build their webs in a single behavioral bout or unit and construct viscid parts only after the completion of the construction of nonviscid parts (Wiehle, 1927; Eberhard, 1987, 1990a; Zschokke and Vollrath, 1995a, b). Coddington (1989) considered this to be distinctive for orbicularians. Hence, although more taxa need to be examined, this implies that the two characters (alternate construction of viscid and nonviscid parts and unit-like construction; character states: present absent) might be synapomorphies for araneoid sheet web weavers.

Understanding the web construction behavior of theridiid 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 behavior of a theridiid. This study shows that theridiid webs are not so disorganized when viewed as behavior rather than web architecture. Furthermore, we were able to show that theridiid web

construction behavior should not generally be considered homologous to that of orb-weavers. However, a complete understanding of the construction behavior of highly diverse theridiids definitely requires the study of more taxa. The *Steatoda* web represents only one of many vastly diverse theridiid web architectures (Benjamin and Zschokke, 2000b).

ACKNOWLEDGMENTS

This research was supported by Swiss National Science Foundation Grant 31-55617.98 to S.Z. Part of this study was done during the first author's stay at the Department of Zoology, University of Oxford. He would like to thank Fritz Vollrath for inviting him to visit his laboratory and Fritz Vollrath, David Knight, Shao Zhengzhong, David and Caroline Steel, and Shobana Dissanayeke for their assistance, hospitality, and discussion; their generosity made his stay in Oxford a great pleasure. This study was presented at the Zoologia and Botanica 2001, Neuchâtel, Switzerland (attendance supported by the Swiss Zoological society), and the 15th International Congress of Arachnology, Badplaas, South Africa (attendance supported by the Swiss National Science Foundation). We also thank William Eberhard, Gustavo Hormiga, Yael Lubin, and two anonymous reviewers for their comments and suggestions on the manuscript. Their suggestions helped immensely to improve the quality of the manuscript. Brigitte Braschler is thanked for statistical advice and for sacrificing her favorite ants as food for our spiders. Marcel Düggelein and Richard Guggenheim of the SEM laboratory, University of Basel, helped with SEM work.

REFERENCES

- Benjamin, S. P., and Zschokke, S. (2002a). A computerised method to observe spider web construction behaviour in a semi-natural light environment. In Toft, S., and Scharff, N. (eds.), *European Arachnology 2000*, Aarhus University Press, Aarhus, pp. 117–122.
- Benjamin, S. P., and Zschokke, S. (2002b). Webs of theridiid spiders—Construction, structure and evolution. *Biol. J. Linn. Soc.* (in press).
- Benjamin, S. P., Düggelein, M., and Zschokke, S. (2002). Fine structure of sheet-webs of *Linyphia triangularis* (Clerck) and *Microlinyphia pusilla* (Sundevall), with remarks on the presence of viscid silk. *Acta Zool.* **83**: 49–59.
- Coddington, J. A. (1986a). The genera of the spider family Theridiosomatidae. *Smithson. Contrib. Zool.* **496**: 1–96.
- Coddington, J. A. (1986b). The monophyletic origin of the orb web. In Shear, W. A. (ed.), *Spiders—Webs, Behavior, and Evolution*, Stanford University Press, Stanford, CA, pp. 319–363.
- Coddington, J. A. (1986c). Orb webs in non orb weaving ogre-faced spiders (Araneae: Dinopidae): A question of genealogy. *Cladistics* **2**: 53–67.
- Coddington, J. A. (1989). Spinneret silk morphology: Evidence for the monophyly of orb-weaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. *J. Arachnol.* **17**: 71–95.

- Coddington, J. A., and Valerio, C. E. (1980). Observations on the web and behavior of *Wendilgarda* spiders (Araneae: Theridiosomatidae). *Psyche* **87**: 93–105.
- Comstock, J. H. (1940). *The Spider Book*, Comstock, Ithaca, NY.
- Eberhard, W. G. (1972). Observations on the biology of *Achaearanea tessellata* (Araneae: Theridiidae). *Psyche* **78**: 209–212.
- Eberhard, W. G. (1975). The 'inverted ladder' orb web of *Scoloderus* sp. and the intermediate orb of *Eustala* (?) sp. (Araneae, Araneidae). *J. Nat. Hist.* **9**: 93–106.
- Eberhard, W. G. (1977). 'Rectangular orb' webs of *Synotaxus* (Araneae: Theridiidae). *J. Nat. Hist.* **11**: 501–507.
- Eberhard, W. G. (1979). *Argyrodes attenuatus* (Theridiidae): A web that is not a snare. *Psyche* **86**: 407–413.
- Eberhard, W. G. (1981a). Construction behaviour and the distribution of tensions in orb webs. *Bull. Br. Arachnol. Soc.* **5**: 189–204.
- Eberhard, W. G. (1981b). The single line web of *Phorocidia studo* Levi (Araneae: Theridiidae): A prey attractant? *J. Arachnol.* **9**: 229–232.
- Eberhard, W. G. (1982). Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* **36**: 1067–1095.
- Eberhard, W. G. (1987). Web-construction behavior of anapid, symphytognathid and mys-menid spiders (Araneae). *J. Arachnol.* **14**: 339–356.
- Eberhard, W. G. (1989). Niche expansion in the spider *Wendilgarda galapagoensis* (Araneae, Theridiosomatidae) on Cocos Island. *Rev. Biol. Trop.* **37**: 163–168.
- Eberhard, W. G. (1990a). Early stages of orb construction by *Philoponella vicina*, *Leucauge mariana*, and *Nephila clavipes* (Araneae, Uloboridae and Tetragnathidae), and their phylogenetic implications. *J. Arachnol.* **18**: 205–234.
- Eberhard, W. G. (1990b). Function and phylogeny of spider webs. *Annu. Rev. Ecol. Syst.* **21**: 341–372.
- Eberhard, W. G. (1992). Web construction by *Modisimus* sp. (Araneae, Pholcidae). *J. Arachnol.* **20**: 25–34.
- Eberhard, W. G. (1995). The web and construction behavior of *Synotaxus ecuadoriensis* (Araneae, Synotaxidae). *J. Arachnol.* **23**: 25–30.
- Eberhard, W. G. (2001). Trolling for water striders: Active searching for prey and the evolution of reduced webs in the spider *Wendilgarda* sp. (Araneae, Theridiosomatidae). *J. Nat. Hist.* **35**: 229–251.
- Forster, R. R., Platnick, N. I., and Coddington, J. A. (1990). A proposal and review of the spider family synotaxidae (Araneae, Araneoidea), with notes on theridiid interrelationships. *Bull. Am. Mus. Nat. Hist.* **193**: 1–193.
- Freisling, J. (1961). Netz und Netzbauinstinkte bei *Theridium saxatile* Koch. *Z. Wiss. Zool.* **165**: 396–421.
- Griswold, C. (1997). *Scharffia*, a remarkable new genus of spiders from East Africa (Araneae, Cyatholipidae). *J. Arachnol.* **25**: 269–287.
- Griswold, C. E., Coddington, J. A., Hormiga, G. and Scharff, N. (1998). Phylogeny of the orb-web construction spiders (Araneae, Orbicularia: Deinopoidae, Araneoidea). *Zool. J. Linn. Soc.* **123**: 1–99.
- Harvey, P. H., and Pagel, M. D. (1991). *The Comparative Method in Evolutionary Biology*, Oxford University Press, Oxford.
- Hopfmann, W. (1935). Bau und Leistung des Spinnapparates einiger Netzspinnen. *Jena. Z. Naturw.* **70**: 65–112.
- Hormiga, G. (1994). A revision and cladistic analysis of the spider family Pimoidae (Araneoidea, Araneae). *Smithson. Contrib. Zool.* **549**: 1–104.
- Hormiga, G., Eberhard, W. G., and Coddington, J. A. (1995). Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae: Tetragnathidae). *Aust. J. Zool.* **43**: 313–364.
- Kloeden, C. (1996). *Rotater 3.5 for Macintosh*, University of Adelaide, Adelaide.

- Kovoor, J., and Lopez, A. (1982). Anatomie et histologie des glandes séricigènes des *Cyrtophora* (Araneae, Araneidae): Affinités et corrélations avec la structure et la composition de la toile. *Rev. Arachnol.* **4**: 1–21.
- Kullmann, E. (1960). Beobachtungen an *Theridium tepidariorum* C. L. Koch als Mitbewohner von Cyrtophora-Netzen. *Deuts. Ent. Z.* **7**: 146–163.
- Lamoral, B. H. (1968). On the nest and web structure of *Latrodectus* in South Africa, and some observations on body colouration of *Latrodectus geometricus* (Araneae, Theridiidae). *Ann. Natal. Mus.* **20**: 1–14.
- Levi, H. W., and Levi, L. R. (1962). The genera of the spider family Theridiidae. *Bull. Mus. Comp. Zool.* **127**: 1–71.
- Marples, B. J. (1955). A new type of web spun by spiders of the genus *Ulesanis*, with the description of two new species. *Proc. Zool. Soc. Lond.* **125**: 751–760.
- McCook, H. C. (1889). *American Spiders and their Spinningwork I*, Academy of Natural Sciences of Philadelphia, Philadelphia. Nielsen, E. (1932). *The Biology of Spiders*, Levin and Munksgaard, Copenhagen.
- Peters, H. M. (1955). Über den Spinnapparat von *Nephila madagascariensis* (Radnetzspinnen; Fam. Argiopidae). *Z. Naturforsch. (C)* **106**: 395–464.
- Peters, H. M. (1990). On the structure and glandular origin of bridging lines used by spider for moving to distant places. *Acta. Zool. Fenn.* **190**: 309–314.
- Platnick, N. (2002). *The World Spiders Catalog*, Version 3.0 [online catalog], Merrett P., and Cameron H. D. (eds.), American Museum of Natural History, New York (<http://research.amnh.org/entomology/>).
- Roberts, M. J. (1995). *Spiders of Britain and Northern Europe*, Collins Field Guide, London.
- SAS Institute (1998). *Statview*, SAS Institute, Cary, NC. Scharff, N., and Coddington, J. A. (1997). A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zool. J. Linn. Soc.* **120**: 355–434.
- Sekiguchi, K. (1952). On a new spinning gland found in geometric spiders and its function. *Annot. Zool. Jpn.* **25**: 394–399.
- Shear, W. A. (1986). The evolution of web-construction behavior in spiders: A third generation of hypotheses. In Shear, W. A. (ed.), *Spiders—Webs, Behavior, and Evolution*, Stanford University Press, Stanford, CA, M pp. 364–400.
- Shinkai, A., and Shinkai, E. (1997). The web structure and the predatory behavior of *Wendilgarda* sp. (Araneae: Theridiosomatidae). *Acta arachnol.* **46**: 53–60.
- Szlep, R. (1965). The web-spinning process and web-structure of *Latrodectus tredecimguttatus*, *L. pallidus* and *L. revivensis*. *Proc. Zool. Soc. Lond.* **145**: 75–89.
- Szlep, R. (1966). The web structure of *Latrodectus variolus* Walckener and *L. bishopi* Kaston. *Israel J. Zool.* **15**: 89–94.
- Vollrath, F. (1988). Untangling the spider's web. *Trends Ecol. Evol.* **3**: 331–335.
- Wiehle, H. (1927). Beiträge zur Kenntnis des Radentzbaues der Epeiriden, Tetragnathiden und Uloboriden. *Z. Morph. Ökol. Tiere* **8**: 468–537.
- Wiehle, H. (1931). Neue Beiträge zur Kenntnis des Fanggewebes der Spinnen aus den Familien Argiopidae, Uloboridae und Theridiidae. *Z. Morph. Ökol. Tiere* **22**: 349–400.
- Zschokke, S. (1994). *Web Construction Behaviour of the Orb Weaving Spider Araneus diadematus* Cl., Ph.D. thesis, Universität Basel, Basel (<http://www.unibas.ch/dib/nlu/staff/sz/pub>).
- Zschokke, S. (1996). Early stages of orb web construction in *Araneus diadematus* Clerck. *Rev. Suisse Zool. H.S.* **2**: 709–720.
- Zschokke, S. (1999). Nomenclature of the orb-web. *J. Arachnol.* **27**: 542–546.
- Zschokke, S. (2000). Radius construction and structure in the orb-web of *Zilla diodia* (Araneidae). *J. Comp. Physiol. A* **186**: 999–1005.
- Zschokke, S., and Vollrath, F. (1995a). Unfreezing the behaviour of two orb spiders. *Physiol. Behav.* **58**: 1167–1173.
- Zschokke, S., and Vollrath, F. (1995b). Web construction patterns in a range of orb-weaving spiders (Araneae). *Eur. J. Entomol.* **92**: 523–541.