

Homology, behaviour and spider webs: web construction behaviour of *Linyphia hortensis* and *L. triangularis* (Araneae: Linyphiidae) and its evolutionary significance

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Abstract

Linyphiidae is the second largest family of spiders. Using *Linyphia hortensis* and *L. triangularis*, we describe linyphiid sheet-web construction behaviour. Orb-web construction behaviour is reviewed and compared with that of nonorb-weaving orbicularians. Phylogenetic comparisons and the biogenetic law are applied to deduce behavioural homology. *Linyphia* webs were constructed gradually and in segments over a period of many days and had a long lifespan. Two construction behaviours, supporting structure and sticky thread (ST) (within the sheet) were observed. ST construction behaviour in linyphiids is considered homologous to sticky spiral construction in orb-weavers. Overall web construction conformed to the pattern of alternate construction of sticky and nonsticky parts as observed in theridiids. Linyphiids had no problem in switching between structure construction and ST construction even during a single behavioural bout. Both web construction behaviours in linyphiids were nonstereotypic, which is unusual in orbicularians. This might be due to the loss of control mechanisms at genetic level, probably by macro mutation. Lack of stereotypic behaviour might have played a substantial role in the origin of the diverse web forms seen in nonorb-weaving orbicularians. This hypothesis is consistent with patterns observed in the orbicularian phylogeny.

Introduction

Our knowledge of evolutionary history is derived from phylogenies, reconstructed by sampling and grouping characters. Harvey & Pagel (1991) illustrated the richness of evolutionary questions that can be approached with phylogenies. The use of behavioural traits as characters in phylogenetic reconstruction is of recent appearance. Initial striving in this regard was confronted with scepticism. Critiques questioned the ability to accurately identify homology, as behavioural characters were thought to be highly variable (Atz, 1970; Brown, 1975; Greene, 1994; Proctor, 1996). de Quieroz & Wimberger (1993) and Paterson *et al.* (1995) compared levels of homoplasy between morphological and behavioural

characters and found no evidence that behavioural characters were more homoplasious than morphological characters. Wenzel (1992) demonstrated that homology statements for behavioural characters could be postulated in the same way as in morphological characters.

de Quieroz & Wimberger (1993) and Paterson *et al.* (1995) have emphasized the need for studies to incorporate behavioural characters to address problems of higher level phylogenetic reconstruction. However, few such studies exist. In a review of 882 published phylogenies, Sanderson *et al.* (1993) found that fewer than 4% of the studies relied on behaviour. Proctor (1996) reviewed 291 phylogenies to find out that only just 6% of them included behavioural characters. Most studies did not include behavioural characters because they were unavailable and too costly to determine (Wenzel, 1992; Greene, 1994; Proctor, 1996). The authors depended instead on optimizing behaviour onto an already existent tree to reveal its evolutionary history (Wenzel, 1992; Greene, 1994).

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Homology is still the basic concept of comparative biology (Wagner, 1989a,b), and the distinction between homology and analogy provides the foundation for systematic biology (de Pinna, 1991; Wenzel, 1992). However, the terms have been the source of disagreement for centuries. Phylogenetically defined, homologous traits are those that can be traced continuously to a common ancestor (Wenzel, 1992; Greene, 1994). Wenzel (1992) convincingly argued that Remane's (1952) criteria: position, special quality and connection by intermediates could be adopted to identify homologous behavioural character states (for definition of criteria see Wenzel, 1992). However, homologies cannot be distinguished from analogies in the absence of phylogenetic information (Wenzel, 1992, 1993). In operational terms, homologies are features that define monophyletic groups. If characters are allowed to weigh themselves, 'true' homologies (Synapomorphies) will be concordant and will support each other whereas analogies will not form a pattern (Patterson, 1982; de Pinna, 1991; Wenzel, 1992, 1993). Thus, homologies need to be confirmed by congruence with other characters (Patterson, 1982; de Pinna, 1991). Criteria of homology nevertheless are useful to recognize putative homologies, which are either corroborated or refuted by a cladogram that best fits all data (Nelson, 1994).

Web construction behaviour has several features that makes it a good model system for understanding the ability of deducing behavioural homology. It is largely innate, and can easily be analysed and compared (Eberhard, 1982; Coddington, 1986c). The end-product of the behaviour, the web, can also be analysed and compared. Furthermore, the fine structure of webs and spigot morphology of spinnerets used to produce corresponding fibres provides corroborative evidence of homology (Jackson, 1971; Coddington, 1989; Peters, 1990; Benjamin *et al.*, 2002).

Linyphiidae is the second largest family of spiders with 4214 described species in 559 genera (Platnick, 2003). It is

also the largest family of northern European spiders containing over 400 species (Roberts, 1995). Well over 650 species have been described for America north of Mexico (Hormiga, 2000). Peculiarly, linyphiid web construction behaviour has never been described, currently it is the only major araneoid family in which the web construction behaviour is largely unknown. When Scharff & Coddington (1997) and Griswold *et al.* (1998) inferred the phylogeny of Orbicularia, they encountered severe limitations in deducing homologies of well known orb-weaver motor patterns in nonorb-weaving orbicularians, because of the lack of data. Recent description of the web construction behaviour of derived orbicularians (Eberhard, 2001; Benjamin & Zschokke, 2002b, 2003) and the description of linyphiid web construction behaviour in this study, make comparison finally possible.

Most linyphiids construct sheet-webs with no retreat and move upside-down on the under side of the sheet. This sheet (primary sheet) is connected to the vegetation on all sides and consists of structural and sticky threads (ST) (Hopfmann, 1935; Wiehle, 1956; Kullmann, 1961, 1962; Scharff, 1990; Benjamin *et al.*, 2002). The diversity of linyphiid web architecture is barely known. Most webs appear to consist of a primary sheet (Kullmann, 1961, 1962; Scharff, 1990), some additionally have a knock-down trap extending above the sheet (Nielsen, 1932; Hopfmann, 1935; Wiehle, 1956; Kullmann, 1962; Benjamin *et al.*, 2002), or a second sheet (secondary sheet) below the primary sheet (Scharff, 1990; Benjamin *et al.*, 2002; Hormiga, 2002). Table 1 summarizes the scanty information available.

Some decades ago, an accepted opinion in arachnology was that orb-webs had evolved from 'primitive' gumfooted-webs or from sheet-webs as an adaptation for catching insects more efficiently (cf. discussions in Coddington, 1986b; Shear, 1986). However, recent cladistic analyses indicate that orb-webs are ancestral to gumfooted- and sheet-webs (Coddington, 1990; Griswold *et al.*, 1998), but see (Kullmann, 1972; Eberhard, 1982;

Table 1 Diversity of linyphiid webs.

Species	Primary sheet	Secondary sheet	Knock-down structure	Source
<i>Bathyphantes pallidus</i>	present	absent	absent	(Griswold <i>et al.</i> , 1998)
<i>Drapetisca socialis</i>	present	absent	absent	(Kullmann, 1961; Schütt, 1995)
<i>Frontinella communis</i>	present	present	present	(Pointing, 1965; Pointing, 1966)
<i>F. pyramitela</i>	present	present	present	(Griswold <i>et al.</i> , 1998)
<i>Linyphia hortensis</i>	present	absent	absent	present study
<i>L. triangularis</i>	present	present	present	(Hopfmann, 1935; Wiehle, 1956; Benjamin <i>et al.</i> , 2002); present study
<i>Obscuriphantes obscurus</i>	present	absent	present	(Kullmann, 1962)
<i>Orsonwelles</i> spp.	present	present	present	(Hormiga, 2002)
<i>Macrargus rufus</i>	present	absent	absent	(Buche, 1966)
<i>Mecynidis scutata</i>	present	present	present?	(Scharff, 1990)
<i>Neriene montana</i>	present	present	present	personal observation
<i>Microlinyphia pusilla</i>	present	present	present	(Benjamin <i>et al.</i> , 2002)

Shear, 1986, 1994; Wunderlich, 1994). The hypothetical web transition involved a shift in trapping function, from catching prey flying from above to catching prey walking, jumping or flying from below. This involved the transfer of ST from the radial supporting structure (SSt) of orb-webs to irregular sheets (as found in linyphiids) and a further transfer of ST from the sheet directly to the substrate below (as found in most theridiids). The loss of radial symmetry of orb-webs is considered to be an adaptation to be better able to fill available horizontal space (Griswold *et al.*, 1998) or a defensive adaptation (Blackledge *et al.*, 2003).

If the evolutionary relationships postulated by Griswold *et al.* (1998) hold, we can expect identical patterns in the behaviours of orb weavers and their derived sister linyphiids. Homologous web elements might be built using similar behaviours and using similar threads produced with identical silk glands. Corroborative evidence might be expected in the fine structure of comparable web elements. Additionally, the evolution of web types in orbicularians is subjected to test via the comparative method (Brooks & McLennan, 1991; Harvey & Pagel, 1991; Schuh, 2000) and biogenetic rule (Wenzel, 1993).

Methods

Description of web construction behaviour of *Linyphia*

Study species

Spiders were kept and observed in $8.5 \times 9.5 \times 14.5$ cm (*Linyphia hortensis* Sundevall, 1830), $16 \times 16 \times 16$ cm and $20 \times 20 \times 20$ cm [*L. triangularis* (Clerck, 1757)] perspex boxes. They were fed with two to three *Drosophila* sp. per day. 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. Spiders were always introduced during the dark period. Web construction of four *L. hortensis*¹ individuals, all juveniles (three females and one male) were analysed. They built a total of 14 webs. Additionally, web construction of two sub-adult *L. triangularis* females were analysed (four webs).

Observational procedure

Spiders mostly build their web during the night and are easily disturbed by light, leading to an interruption in building. Thus, manual and conventional video observation with normal light was impractical. Moreover, the initiation of web building is 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. The position of the spider was recorded at a rate of 14 frames per second. Study methods are described in detail in Benjamin & Zschokke (2002a). This approach permitted recording in two dimensions.

To record the spiders movements in three dimensions (3D), we used the setup and methods described in Zschokke (1994) and Zschokke & Vollrath (1995a), but with infrared light rather than visible light. This setup differed from the first one by the use of two synchronized observation units. Each unit 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 3D-movement pattern, recorded data of both units were combined using software described in Zschokke (1994). The 3D movement patterns were viewed with Rotator (Kloeden, 1996).

In addition, selected parts of web constructions were observed directly.

Behavioural ontogeny and evolution

We consider the complex web construction behaviours of orbicularians and regard the series of component behaviours as if they were developmental steps towards a large unit (behavioural ontogeny *sensu* Wenzel, 1993). The components are then compared across taxa according to their distinctive characteristics and position in the sequence (Eberhard, 1982; Coddington, 1986c, 1990; Wenzel, 1993). This information is then represented as a flow chart where the boxes represent major homologous phases or types of behaviour and arrows connect these to show major transitions (Wenzel, 1993). We used the character trace option of MacClade 4.0 (Maddison & Maddison, 2000) to phylogenetically map the behavioural characters. We use this method by which the characters are mapped onto the tree for a qualitative assessment of the homology hypothesis as described in Coddington (1988, 1994). The phylogenies used in this investigation are modified from Coddington (1986a) and Griswold *et al.* (1998).

Results

Web construction behaviour of *Linyphia*

Linyphia hortensis

Web construction of *L. hortensis*, which was analysed 14 times, occurred mostly during the night and began with a short exploratory stage with the spider moving in the space where the web was later built. The webs only consisted of a horizontal sheet of SSt and ST laid onto it (Fig. 1). Construction began as the spider

¹The juvenile specimens belong to the genus *Linyphia*; most probably they are *Linyphia hortensis*. The sister species *L. alpicola* van Helsdingen, 1969 occurs at much higher elevations (Konrad Thaler, personal communication); vouchers are deposited at the Natural History Museum, Basel.

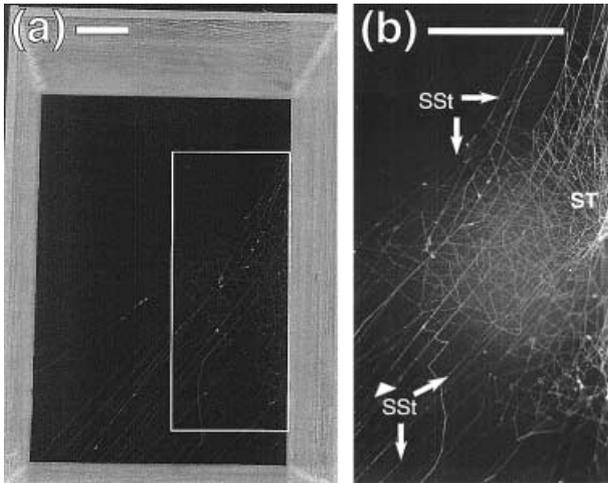


Fig. 1 (a) Typical web of *Linyphia hortensis*, viewed from above. (b) Close up (slightly different camera position). SSt, supporting structure; ST, sticky thread; scale bar, 2.0 cm.

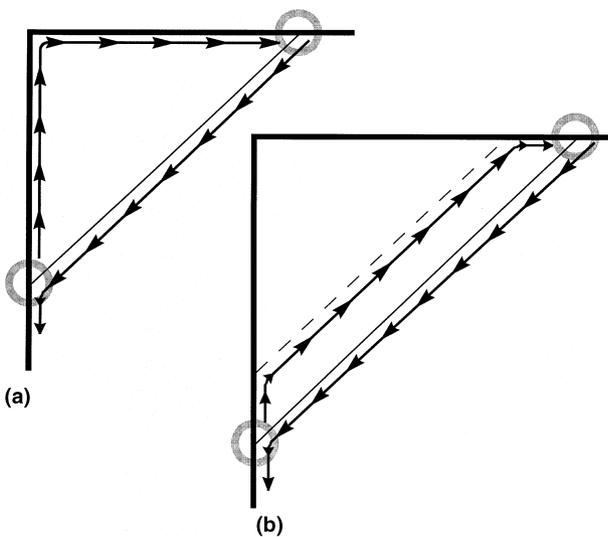


Fig. 2 Diagrammatic representation of the structure construction behaviour of *Linyphia hortensis* (schematic and not to scale, viewed from above). Thick lines represent substrate (sides of perspex box), dashed lines represent threads laid earlier in the sequence and circles denote attachment points.

moved about with a single leg of leg pair 4 (L4) holding the dragline (DL). Initially, the spider attached its DL to a side of the box and moved along the side of the box to attach DL. Then it walked back along the newly attached DL and reinforced it by doubling (Fig. 2a). No stereotyped movements with L1–L3 were observed.

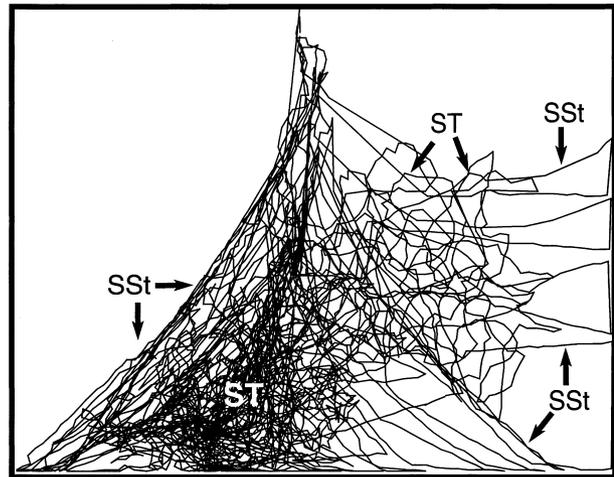


Fig. 3 Track of the movements during SSt and ST construction of *Linyphia hortensis*, viewed from above. SSt, supporting structure; ST, sticky thread.

To construct the next thread, the spider moved away, on the same plane, from the original attachment point and attached DL. The spider then moved along the previously laid thread to its other end, moved away from its attachment point and attached DL. Then it moved back along the newly attached DL and reinforced it by doubling (Figs 2b and 3). Alternatively, the spider attached DL to existing threads instead of the sides of the box. During SSt construction, the spider held DL with a single L4 all the time and released new DL behind it. Breaking and replacing pre-existing threads, i.e. cut-and-reel behaviour *sensu* Coddington (1986c) was never observed. How the spider assessed the spacing between two threads could not be determined.

Construction of ST was by hanging onto the structural threads and moving in semicircles (Figs 3 and 4). The spider stopped at regular intervals to attach the thread with the spinnerets by moving its abdomen upward towards the structure. The ST was never held with any of its legs. The spider was never seen to turn back following an attachment and move back along the newly laid thread. No cut-and-reel behaviour was observed. The spider did not make any obvious tapping movements between attachments, as orb-weavers do. The spider did not appear to differentiate between SSt and previously laid ST during attachments.

There was no clear pattern during ST construction, however the movements appeared to be around a 'central point' (Figs 3 and 4). The 'central points' differed between bouts. There were no clear transition points between SSt and ST construction. Moreover, the spider appeared to have no problem in switching between SSt and ST construction even during a single behavioural bout.

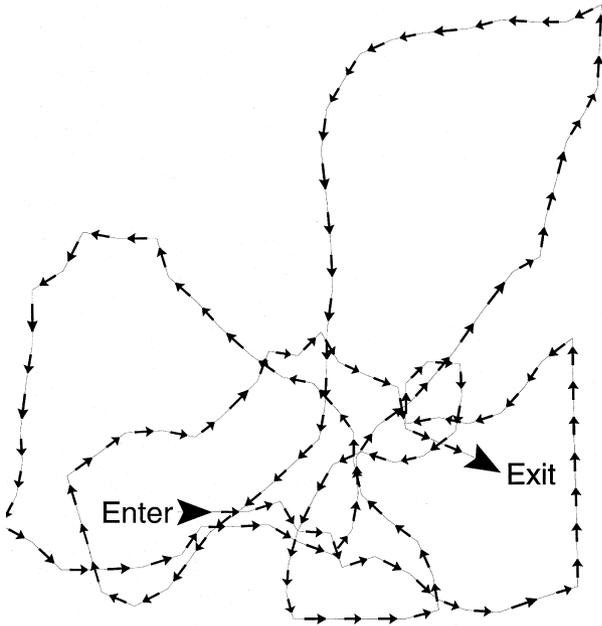


Fig. 4 Diagrammatic representation of movement pattern during sticky thread construction of *Linyphia hortensis* (viewed from above).

Linyphia triangularis

Recordings of *L. triangularis* suggest that they use similar behaviours to construct the sheet. SSt construction was similar to that of *L. hortensis*. The same can be said for ST construction behaviour (Fig. 5). Spiders stopped at regular intervals to attach ST with the spinnerets by moving its abdomen upward towards the structure. The ST was never held with any of its legs.

Again, as in *L. hortensis*, there appeared to be no clear transition points between SSt and ST construction and the spider appeared to have no problem in switching

between SSt and ST construction even during a single behavioural bout (Fig. 5).

Web construction behaviour in orb-weavers, a review

In the following, we present a summary of the web construction of araneid orb-weavers to facilitate comparison with that of nonorb-weaving orbicularians.

During the first steps of orb-web construction, the spider explores the area and establishes the so-called proto-hub, a structure where several threads (the proto-radii) attached to the substrate come together in a single point. The establishment of the proto-hub is a lengthy and highly variable process with continuous laying of new threads and moving or removing some of the previously laid ones. During this stage, the spider may rest at any time, be it for a few minutes or for several hours. So far, this stage has been described in detail for a few exemplary species only (Eberhard, 1972, 1990a; Zschokke, 1996). After the proto-hub has been established, the spider usually no longer reaches the substrate and exclusively walks on its own, previously laid threads. The spider is thus no longer exposed to the unpredictability of the substrate and can therefore build the following stages using more stereotyped behavioural patterns. In the next stage, the spider constructs the frame and the radii. Frame threads are built using the same basic pattern by all species except *Nephila* spp. (Zschokke & Vollrath, 1995b). The spider walks out along an existing 'exit' radius to attach a thread. It then walks back on the newly laid thread towards the hub. During this walk-back, it briefly stops and attaches DL to the newly laid thread. After reaching the hub, it walks outwards along the next lower radius where it attaches DL to form the frame. It then continues along this frame thread towards the upper radius and then back to the hub. To build a secondary radius (i.e. a radius constructed without simultaneous construction of a frame

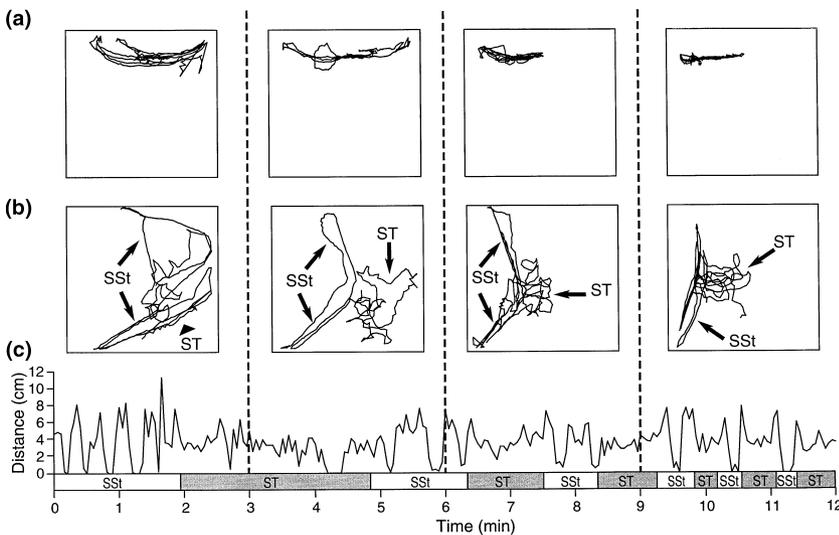


Fig. 5 Exemplary path and activity pattern of one *Linyphia triangularis* during 4 × 3 min of web construction. (a) Frontal views of the path. (b) Path as seen from above. Size of box = 20 × 20 × 20 cm. (c) Corresponding activity pattern at a resolution of 3 s. The spider moved a total distance of 852 cm. SSt, supporting structure; ST, sticky thread.

thread; Zschokke, 1999), the spider walks out along an existing radius to the frame, then down a few steps along the frame where it attaches DL (the 'provisional radius') and then clambers back to the hub along the provisional radius. Most araneid and tetragnathid species completely reel up (cut-and-reel behaviour; Peters, 1937) the provisional radius when producing the definitive one, whereas a few species leave the outer half of the provisional radius in place, thus producing a definitive one which is partially doubled (Eberhard, 1981; Zschokke, 2000). Uloborids do not use cut-and-reel behaviour during radius construction and thus build radii, which are doubled all the way. The order of the radius construction follows the same patterns in all species: the spider always places the new radius below an existing one and – except *Nephila* spp. – never with a large gap where it will later add another radius (Peters, 1937; Reed, 1969). It also tends to build the radii above the hub before those below it (Vollrath *et al.*, 2002) and it seems to add the radii in an order to balance the forces at the hub (Wirth & Barth, 1992).

When the spider builds the radii, it continuously circles the hub to find a gap to place the next radius (Zschokke, 1995). During this circling it continuously attaches DL to the radii, thus forming the hub structure. After the insertion of the last radius, this circling continues in most species before it changes suddenly, without interruption, into the construction of the coarsely meshed, nonsticky auxiliary spiral, built from the centre to the periphery of the web (Zschokke & Vollrath, 1995b). After completion of the auxiliary spiral, the spider makes its only rest after the establishment of the proto-hub, presumably to switch the production of silk, before building the finely meshed sticky spiral from the periphery towards the centre. During sticky spiral construction, the spider uses the auxiliary spiral to stabilize the web, as a bridge to cross from one radius to the next and – at least in some araneid species – as a guide for the placement of the sticky spiral (Zschokke, 1993). During construction of the sticky spiral, the auxiliary spiral is taken down part by part (Wiehle, 1927). Sticky spiral construction is never interrupted to construct SSt (Eberhard, 2000), except in *Nephila* spp., which has been observed on several occasions (four of 25 web constructions observed in the laboratory) to add SSt during construction of the sticky spiral (unpublished observations) and in *Araneus arihastulus*, which builds the auxiliary spiral in the lowest part of the web after it has built the sticky spiral in the uppermost part (Forster & Forster, 1985). Araneid, tetragnathid and theridiosomatid spiders finally complete the web by modifying the hub.

Discussion

Web construction behaviour of *Linyphia*

The spiders performed two types of behaviours, one to construct the more or less parallel SSt and a second to

construct the ST. *Linyphia hortensis* webs were expanded, but the spiders appeared to exhibit no regular pattern of web replacement. Webs were constructed gradually and in segments over a period of many days and had a longer lifespan than most orb-webs. In our laboratory observations, where spiders were fed regularly and amply, and had no possibility to relocate their webs, we did not observe spiders to stop building or to remove parts of their web during up to 7 days. Similar web construction patterns were observed in theridiids (Benjamin & Zschokke, 2002b, 2003). In contrast, most orb-webs are built in a single run, removed every night and replaced (Wiehle, 1927). When orb-weavers stay at the same place, they re-use large parts of the anchor and frame threads, but rebuild all radii and the spirals (Carico, 1986; Zschokke & Vollrath, 2000). Orb-weavers ingest silk as they take down their webs and recycle this silk in subsequent webs (Breed *et al.*, 1964; Peakall, 1971; Opell, 1998, 1999).

We observed no regular pattern in SSt construction behaviour in *L. hortensis*, apart from the construction behaviour described. Even the same spider employed variable movements to build successive webs. ST construction behaviour was surprisingly simple. *Linyphia hortensis* was able to alternatively construct SSt and ST. As described recently, theridiids rest or move to the retreat before the onset of a new gumfooted line (GF) bout (Benjamin & Zschokke, 2002b, 2003).

Phylogenetic implications

We never observed linyphiids to cut-and-reel during either SSt or ST construction. Whereas, we are certain that it did not occur during ST construction, we were merely unable to observe it during SSt construction. However, the observation that structural threads contain doubled strands (four fibres of two different thickness; Peters & Kovoor, 1991; Benjamin *et al.*, 2002) may support the notion that linyphiids do not cut-and-reel during SSt construction. *Steatoda triangulosa*, *Achaearanea tepidariorum* and most probably other theridiids do not cut-and-reel (Benjamin & Zschokke, 2002b, 2003). The same also applies to *Synotaxus* (Eberhard, 1982). Except for *Nephila*, all other orb-weavers cut-and-reel (uloborids cut-and-reel frames but not radii, other orb weavers cut-and-reel frames and radii; Eberhard, 1982; Coddington, 1986c). This might turn out to be a character synapomorphic for nephilines and 'araneoid sheet web weavers'.

Sticky thread construction behaviour in linyphiids can be considered homologous to the orb-weaver sticky spiral, as the threads originate from the same glands (Peters & Kovoor, 1991; Benjamin *et al.*, 2002) and the spider moves in circles (Fig. 4), albeit in a nonstereotypic manner. In contrast, theridiid GF are possibly not homologous to the orb-weaver sticky spiral (nonhomologous states in two independent transformation series;

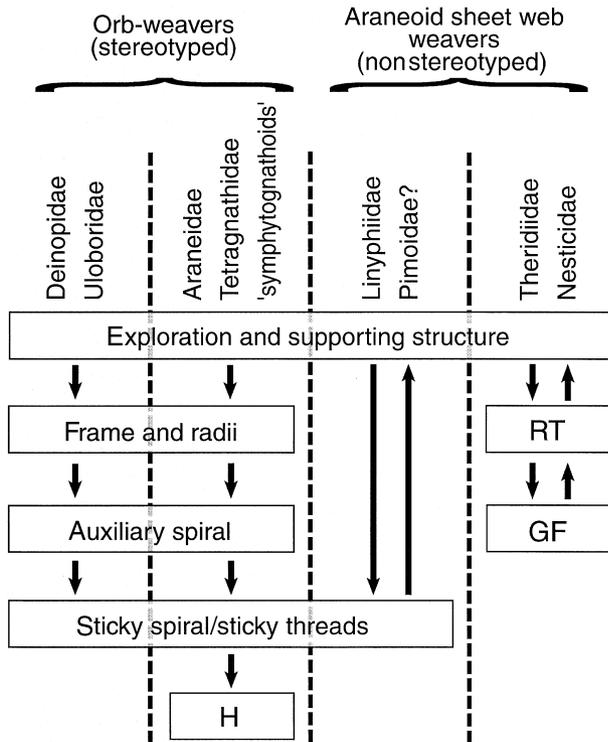


Fig. 6 General sequence of bouts during web construction in Orbiculariae. The bouts (series of similar behaviours) are ordered top to bottom as they arise during web construction, boxes represent homologous behaviours. The web building behaviour of Synotaxidae and Cyatholipidae are hardly known, making placement difficult. Some bouts in Nephilinae might be reversible and hub modification is absent. 'symphytognathoids', *sensu* Griswold *et al.* (1998) include the families Anapidae, Mysmenidae, Symphytognathidae and Theridiosomatidae. Species of the theridiosomatid genus *Wendilgarda* build a range of nonorb-webs (Eberhard, 2000). Note the irreversibility of the sequence in the orb-weaving families. GF, gumfooted lines; H, hub modification; RT, radiating threads (non-sticky threads extending to the substrate).

Fig. 6); as only the viscid substance of GF, but not the core thread, originates from corresponding glands as in orb-weavers and linyphiids (Benjamin & Zschokke, 2002b). Thus, we consider linyphiids to be more closely related to the orb weaver taxa (less 'derived') than theridiids.

Whereas most orb-weavers never interrupt sticky spiral construction to construct SSt (Wiehle, 1927; Eberhard, 1987b, 1990b, 2000; Zschokke & Vollrath, 1995a, b; but see above), the observed linyphiids had no problem in switching between SSt and ST construction even during a single behavioural bout (Figs 3 and 5). Alternate construction of SSt and ST was also observed for theridiids (Szlep, 1965; Lamoral, 1968; Benjamin & Zschokke, 2002b, 2003), for *Synotaxus* (Eberhard, 1977, 1995) and *Wendilgarda* (Coddington & Valerio, 1980; Eberhard, 1989, 2001; Shinkai & Shinkai, 1997). The

nonorbicularians *Psechrus* sp. (Eberhard, 1987a), *Fecenia singaporiensis* (Zschokke & Vollrath, 1995b) and *Titanoeca albomaculata* (Szlep, 1966) construct ST and SSt alternatively. Orb-weavers never walk across a ST that is already in place as observed by linyphiids in this study. However, the taxonomic importance of these characters is unclear as they occur in a broad range of taxa.

Another character that is constant in all orb-weavers is the centripetal tendency (construction beginning near the outer edge of the web and continuing towards the hub) in the spinning of ST (Coddington, 1986b, 1989; Eberhard, 1987a). A centripetal tendency in the spinning of ST also occurs in the nonorb-weaving *Fecenia singaporiensis* (Zschokke & Vollrath, 1995b). ST construction of *L. hortensis* and *L. triangularis* showed no such tendency. Its absence has been described for a range theridiids (Szlep, 1965; Lamoral, 1968; Benjamin & Zschokke, 2002b, 2003), *Wendilgarda* sp. (Coddington & Valerio, 1980; Eberhard, 1989, 2001; Shinkai & Shinkai, 1997), *Synotaxus* (Eberhard, 1977, 1995) and the nonorbicularian pholcid *Modisimus guatuso* (Eberhard, 1992).

The lack of stereotypy in web construction is unusual. Whereas most theridiids have a nonstereotypic SSt and a stereotypic GF construction behaviour, we found all construction stages in linyphiids to be nonstereotypic. Such behavioural flexibility during later construction stages is unknown in orb-web builders. Most orb-weavers perform highly variable behaviours only during the first construction stage leading to the proto-hub. Thereafter their behaviour, especially during the construction of the spirals, is very repetitive, stereotyped and highly predictable (Zschokke, 1996). Even the transition from SSt to ST construction, which is a clear and irreversible step in most orb-weavers (Eberhard, 1987a; Coddington, 1989), is reversible in the observed linyphiids and theridiids (Benjamin & Zschokke, 2002b, 2003).

In summary, we observed no regular patterns in *L. hortensis* and *L. triangularis* web construction behaviour. Webs were constructed gradually and in segments over a period of many days and had a long lifespan. Two construction behaviours, SSt and ST were observed and found to be nonstereotypic. ST construction behaviour is considered to be homologous to orb-weaver sticky spiral construction. Centripetal tendency during ST construction is absent in *Linyphia* spp. Apart from the behaviours of alternate construction of sticky and nonsticky elements and the unit like web construction behaviour, we observed no characters shared by *Linyphia* and theridiids.

This study shows that the use of Remane's (1952) criteria: position, special quality and connection by intermediates can be successfully adopted to identify behavioural homologous character states as performed in morphological studies. The application of phylogenetic comparison (Harvey & Pagel, 1991) and the biogenetic law (Wenzel, 1993) further facilitates the deduction of behavioural homology. We have made considerable progress towards the understanding of linyphiid web

construction. However, more taxa need to be examined if we are to gain a better understanding of the behaviour of this large and diverse family.

Web evolution in Orbiculariae

Evolutionary factors leading to the divergence of web forms built by orbicularian spiders has attracted considerable interest. Different Orbicularians were present in the Early Cretaceous (Selden, 1989; Penney & Selden, 2002; Zschokke, 2003), so it is very likely that the divergence of this clade occurred before then. Orb-web construction behaviour is highly stereotyped and in several respects invariable (Eberhard, 2000). Different types of threads are laid in a specific order (Fig. 6), leg movements used to lay threads are highly constant. Details of orb-web construction behaviour are so conservative and consistent that they provide some of the best characters for defining araneoid taxa (Eberhard, 1982; Coddington, 1986c; Griswold *et al.*, 1998). These behaviours are innate, and major deviations would have a negative effect on the functional efficiency of the web and be disastrous for the spider (this could explain the evolutionary origin and maintenance of stereotypic construction behaviour). Thus, for the origin and divergence of nonorb-web construction behaviour, initially the ancestors of the two clades might have had to break away from the constraint of stereotypic construction behaviour, giving natural selection the raw material necessary to select from, leading to the extraordinary diversity of orbicularian nonorb-webs observed today.

It was only recently that Eberhard (1990c, 1995, 2000) proposed a plausible hypothesis to explain the evolutionary origin of the diverse and complex behaviours needed to construct orbicularian nonorb-webs. According to his hypothesis, novel behavioural patterns originate as variations resulting from imprecision in the production of behaviour rather than by mutations. New behaviours originate because of selective filtering of 'good' behavioural variations. When such behaviours are selectively neutral in respect to each other, the expressed number of behaviours increases.

Within the Orbiculariae, novel construction behaviours appeared, independently of each other, with the origin of the clade 'araneoid sheet web weavers' and in the theridiosomatid genus *Wendilgarda* (Fig. 7). The diversity of web forms is remarkable for 'araneoid sheet web weavers'. Web construction behaviour in the clades 'araneoid sheet web weavers' and *Wendilgarda* is not stereotyped and their web designs have diverged rapidly and independently (Eberhard, 2000; Benjamin & Zschokke, 2002b, 2003; Blackledge *et al.*, 2003). In contrast, construction behaviour in all other orbicularian clades appears to be fairly constant and highly stereotyped. These observations are inconsistent with Eberhard's hypothesis. As his hypothesis would predict that novel web designs should occur randomly in all

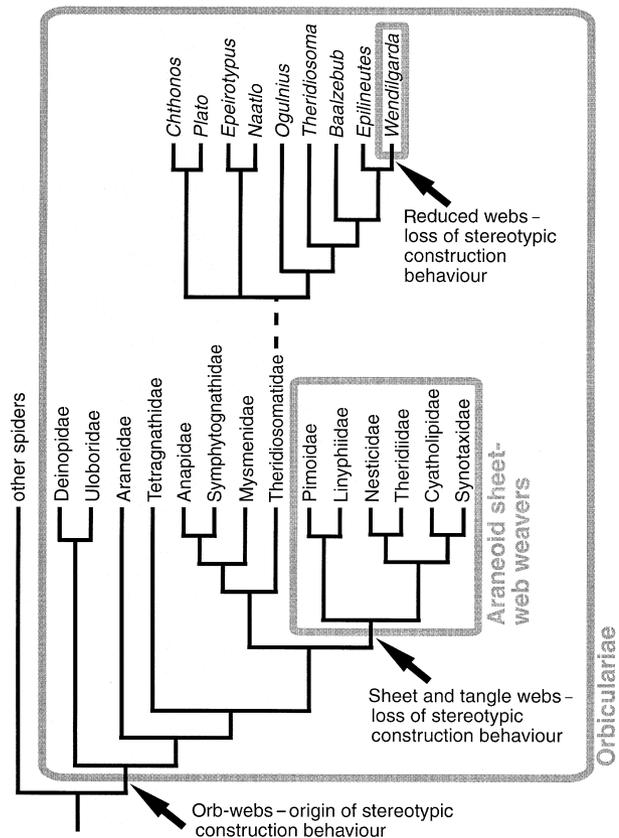


Fig. 7 The origin and loss of stereotypic behaviour of orb-web building traced onto the phylogeny of Orbiculariae based on morphological characters (modified from Coddington, 1986a; Griswold *et al.*, 1998). Novel construction behaviours appear with the origin of the clade 'araneoid sheet web weavers' and in the theridiosomatid genus *Wendilgarda*. In these two clades, the diversity of web forms is remarkable and web construction behaviour is not stereotyped. Webs of *Ogulnius*, which construct a radiating network of nonsticky threads on which the sticky silk spiral is placed in a more or less regular trajectory (Coddington, 1986a), can be considered as highly modified orb-webs.

orbicularian lineages, changes being gradual throughout evolutionary time. Thus, we suggest that the loss of control mechanisms, probably by macro mutation, that regulate stereotypic behaviour might have led to the origin of variation, which in turn produced a diverse range of behaviours. They were subject to natural selection, giving rise to diverse web forms seen in 'araneoid sheet web weavers' and in *Wendilgarda*. This hypothesis is consistent with patterns observed in the orbicularian phylogeny (Fig. 7).

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