

The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence

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ABSTRACT

A number of taxonomically diverse species of araneoid spiders adorn their orb-webs with conspicuous silk structures, called decorations or stabilimenta. The function of these decorations remains controversial and several explanations have been suggested. These include: (1) stabilising and strengthening the web; (2) hiding and concealing the spider from predators; (3) preventing web damage by larger animals, such as birds; (4) increasing foraging success; or (5) providing a sunshield. Additionally, they may have no specific function and are a consequence of stress or silk regulation. This review evaluates the strength of these explanations based on the evidence. The foraging function has received most supporting evidence, derived from both correlative field studies and experimental manipulations. This contrasts with the evidence provided for other functional explanations, which have not been tested as extensively. A phylogenetic analysis of the different decoration patterns suggests that the different types of decorations are as evolutionary labile as the decorations themselves: the analysis shows little homology and numerous convergences and independent gains. Therefore, it is possible that different types of decorations have different functions, and this can only be resolved by improved species phylogenies, and a combination of experimental and ultimately comparative analyses.

Keywords: Araneidae; Uloboridae; Tetragnathidae; Stabilimenta; Araneae; Behaviour; Phylogeny.

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I. INTRODUCTION

Orb-web spiders (Araneoidea, Deinopoidea) spin circular or ellipsoid webs consisting of a sticky spiral that overlays an array of non-adhesive radial threads. Frame threads, attached to the substratum, hold the radials and spiral in place. The mostly two-dimensional orb is orientated vertically (e.g. the garden spider *Araneus diadematus*), horizontally (many uloborids) or at an inclination (e.g. tetragnathids). Some orb-web spiders spin horizontal webs with extensive scaffolding structures (e.g. the tent spider *Cyrtophora citricola*), while others have lost the web-building habit altogether (e.g. the bolas spider *Dicrostichus furcatus*). Although orb-webs are inconspicuous, a number of taxonomically diverse species (Scharff & Coddington, 1997) spin conspicuous silk designs on the surface of the web. McCook (1889) called these silk structures 'decorations'; Simon (1895) subsequently introduced the term 'stabilimenta', and numerous other names including 'device', 'adornment' or 'structure' have been used over the decades (Nentwig & Heimer, 1987). The best known example of web decorations are those spun by spiders in the genus *Argiope* that consist either of white silk zig-zag bands attached to adjacent radii at the web hub, or a silk disc at the web centre (Fig. 1).

The function of these structures has been the subject of continued debate since their first description, and there has been little consensus. For example, they may act to camouflage the spider by obscuring its outline (Schoener & Spiller, 1992), prevent web damage by larger animals, such as birds (Eisner & Nowicki, 1983), provide a sunshield for the spider (Humphreys, 1992), stabilise and strengthen the web (Robinson & Robinson, 1970), or increase foraging success (Craig & Bernard, 1990). Alternatively, these decorations may result from regulating silk production (Peters, 1993) or reflect a stressful physiological state (Nentwig & Rogg, 1988). These explanations are not mutually exclusive (although this is often assumed); it is, in

fact, likely that web decorations serve different roles in different species, and even multiple functions for a single species.

Research into the function of web decorations has been taxonomically biased. Most studies have focused on the linear or cruciate web decorations constructed by *Argiope* spp. or *Uloborus* spp., and to a lesser extent the discoid, spiral, tuft or debris decorations spun by other species and/or juvenile spiders (see Table 1). Of a total of 43 publications that discuss a possible function for web decorations, 26 were specifically concerned with the web decorations constructed by *Argiope* spp. (Table 1) and only 21 published reports attempt to test one or more functional explanations. Furthermore, only three of the functional explanations have been tested directly by experimental manipulations; the remainder have been examined by either correlative studies or field observations. The goal of this review is to summarise the research that has investigated the function of web decorations and to provide a phylogeny of the various decoration patterns.

II. OCCURRENCE AND TYPES OF WEB DECORATIONS

We found reports of web decorations in 78 species from 22 genera of orb-web spiders (Table 2) whose webs are exposed during the day (Eberhard, 1990; Scharff & Coddington, 1997). There are no records of decorations in spiders whose webs are exposed only at night. Twenty species of spiders in the family Uloboridae, 52 species in the family Araneidae and six species in the family Tetragnathidae spin web decorations (Table 2). Within the well-known genus *Argiope*, 21 species were reported to decorate their webs (Table 2). Although web decorations are one of the most studied phenomena in spiders, the data in Table 2 undoubtedly suffer from at least three defects. Due to ontogenetic, individual and population-level variability (see below), the ethological occurrence and diversity of web decoration

in a particular species may be under-sampled; although capable of making a given decoration, it may not yet have been observed. Second, not all species in groups known to decorate their webs have been studied. Third, some of the observations listed in Table 2 are based on reports in old, relatively 'popular' literature that may not be accurate.

Silk decorations have been grouped according to their basic pattern (Table 3, Fig. 1). The juveniles of many species of *Argiope* spin silks into discs (e.g. Nentwig & Heimer, 1987) and spiders in the family Uloboridae often spin a decorative spiral at the web-centre (Nect, 1990). Adult *Argiope* spp. add zig-zag bands to the web, in either a linear pattern arranged vertically across the hub, or a cruciate pattern, where up to four zig-zag bands form a diagonal cross (Table 3, Fig. 1). *Argiope savignyi* sometimes spins a silk disc, sometimes a cruciate pattern and sometimes combines both types (Nentwig & Heimer, 1987). The common feature of these types of silk decoration is that they are located near the hub of the web, and may occasionally extend into the adjacent spiral region. By contrast, the silk tufts spun by *Gasteracantha* and *Witica* species (Table 3, Fig. 1) are placed on the frame threads while some species of *Micrathena* place them throughout the spiral region of the web (C. L. Craig, personal observations).

Some species incorporate organic material, such as bits of vegetation or the remains of captured prey near the centre of the web. These structures have also been described as web decorations. When *Cyclosa caroli* reaches reproductive maturity, it incorporates sequentially laid egg sacs into a string of pellets (Hingston, 1927; Craig, 1989). Similarly, prey remains in *Nephila*, *Cyrtophora* and *Nephilengys* are mostly attached to the barrier web surrounding the orb (Edmunds & Edmunds, 1986). *Cyrtophora* also attach numerous egg cocoons above the web (Elgar, Pope & Williamson, 1983; Edmunds & Edmunds, 1986), and *Cyrtophora citricola* incorporates debris in the silk retreat above the hub (Kullmann, 1958). *Phonognatha graeffei* attaches a leaf retreat to the web structure (Thirunavukarasu, Nicolson & Elgar, 1996).

III. SILK PRODUCTION

Orb-web spiders have up to six different types of silk-producing glands from which at least nine different types of proteins are produced (Kovoor, 1987). Specifically, araneoid spiders produce a minimum of eight different proteins that produce three types of silk fibroin and three types of protein glue (Craig,

1997). Their silks are used to produce the frame and sticky catching threads of the orb web, sperm webs and egg sacs (Foelix, 1992). The decorative silks spun by *Argiope bruennichi* and *A. lobata* are produced in the aciniform glands and are also used to wrap prey (Peters, 1993). Like all silks, decorative silks are secreted *via* tiny spigots. Hence, web decorations are actually composed of loosely arranged, individual fibres (Peters, 1993). Individual spigots are found in clusters, or spinning fields, on each of the spinnerets. Comparison of the anterior, posterior and median spinnerets reveals that *A. lobata* has almost twice as many aciniform spigots as *Araneus diadematus*, a non-decorating web spinner (Peters, 1993). By contrast, the web decorations of spiders in the Deinopoidea (e.g. *Uloborus walckenaerius* and *U. plumipes*), the sister taxon to Araneoidea, use silks produced in the aciniform gland as well as the piriform glands (Peters, 1993).

The reflective properties of web decorations also differ from other silks incorporated into the web. The decorations spun by *A. argentata*, *U. glomosus* (100% reflective at 370 nm varying to approximately 70% reflectance at 640 nm; Craig & Bernard, 1990) and *Octonoba sybotides* (Watanabe, 1999a), as well as their catching silks, are ultraviolet (UV) reflective (Craig, Bernard & Coddington, 1994), while the viscid silk spun by *A. argentata* exhibits low reflectivity in the UV (Craig & Bernard, 1990).

IV. VARIABILITY IN DECORATION PATTERNS

(1) Ontogenetic variation

Spiders display considerable within-species ontogenetic variation in decorating behaviour. The most commonly reported ontogenetic changes are those of juveniles that initially decorate their webs with discoid decorations, but spin linear or cruciate decorations during later stadia and when they are sexually mature. For example, juveniles of *A. savignyi* (Nentwig & Heimer, 1987), *A. flavipalpis* (Ewer, 1972; Edmunds, 1986), *A. aetherea* (Clyne, 1969) and *A. keyserlingi* (M. E. Herberstein, personal observations) usually construct discoid decorations but they construct cruciate decorations after they attain sexual maturity. Similarly, juvenile *A. aurantia* and *A. trifasciata* (Tolbert, 1975) spin discoid decorations but the adults spin linear decorations. *A. argentata*, however, spin both linear and discoid decorations as juveniles but adults spin only cruciate designs (C. L. Craig, personal observations).

Table 1. Summary of studies that propose functions for the web decorations of various orb-web spiders

Function	Species	Test	Source
Anti-predator	<i>Argiope aurantia</i> , <i>Argiope trifasciata</i>	Indirect (laboratory experiment)	Blackledge (1998 <i>b</i>)
	Various <i>Argiope</i> spp.	None (review)	Blackledge (1998 <i>a</i>)
	Various	None (review)	Eberhard (1990)
	<i>Uloborus diversus</i>	None	Eberhard (1973)
	Various	None	Edmunds & Edmunds (1986)
	<i>Argiope flavipalpis</i>	None	Edmunds (1986)
	<i>A. flavipalpis</i>	None	Ewer (1972)
	Various	None (review)	Hingston (1927)
	<i>A. aurantia</i> , <i>A. trifasciata</i>	Direct (laboratory experiment)	Horton (1980)
	<i>Argiope argentata</i>	Indirect (field observation)	Lubin (1975)
	Various uloborids	None (review)	Lubin (1986)
	<i>Argiope pulchella</i>	Indirect (field observation)	Marson (1947 <i>a</i>)
	<i>Cyclosa insulana</i>	None	Marson (1947 <i>b</i>)
	<i>C. insulana</i>	Indirect (field observation)	Neet (1990)
	<i>A. argentata</i> , <i>Argiope aemula</i>	Indirect (field correlation)	Robinson & Robinson (1978)
	<i>A. argentata</i>	None	Schoener & Spiller (1992)
	Foraging	<i>A. aurantia</i> , <i>A. trifasciata</i>	Indirect (field correlation)
<i>A. argentata</i>		Direct (laboratory experiment)	Craig & Bernard (1990)
<i>A. argentata</i>		Indirect (field correlation)	Craig (1991)
<i>Argiope aetherea</i>		Indirect (field correlation)	Elgar <i>et al.</i> (1996)
<i>Argiope appensa</i>		Indirect (laboratory experiment)	Hauber (1998)
<i>A. keyserlingi</i>		Indirect (field correlation)	Herberstein <i>et al.</i> (2000)
<i>Argiope keyserlingi</i>		Indirect (laboratory experiment)	Herberstein (2000)
<i>A. trifasciata</i>		Indirect (field correlation)	Tso (1996)
<i>A. aurantia</i> , <i>A. trifasciata</i>		Direct (field experiment)	Tso (1998 <i>a</i>)
<i>Cyclosa conica</i>		Indirect (field correlation)	Tso (1998 <i>b</i>)
<i>Octonoba sybotides</i>		Direct (laboratory experiment)	Watanabe (1999 <i>a</i>)
		Indirect (field correlation)	

Mechanical	Various	None	Comstock (1912)
	Various	None	Comstock (1940)
	Various	None	McCook (1889)
	<i>A. argentata</i>	None	Robinson & Robinson (1970)
	<i>Nephila clavipes</i>	Indirect (field observation)	Robinson & Robinson (1973b)
	<i>Argiope picta</i> , <i>A. aemula</i> ,	None	Robinson & Robinson (1974)
	<i>A. reinwardti</i> , <i>A. argentata</i>		
	<i>A. argentata</i> , <i>A. aemula</i>		
	Various <i>Argiope</i> spp.		
	various		
Non-functional			
Reflex	<i>Argiope bruennichi</i>	None (review)	Robinson & Robinson (1978)
Several	Various	None	Simon (1895)
	Various	None (review)	Neutwig & Heimer (1987)
Silk regulation	<i>A. bruennichi</i> , <i>A. lobata</i> , <i>Uloborus</i>	None (review)	Rabaud (1932)
	<i>plumipes</i> , <i>U. walckenaerius</i>	None (review)	Cloudsley-Thompson (1995)
	<i>A. argentata</i>	None (review)	Scharff & Coddington (1997)
		None	Peters (1993)
Stress			Nentwig & Rogg (1988)
Thermoregulation	<i>Neogea</i> sp.	Indirect (field observation & laboratory experiment)	Humphreys (1992)
Web protection	Various <i>Argiope</i> spp.	Indirect (field observation)	Blackledge (1998a)
	<i>A. aurantia</i>	None (review)	Blackledge & Wenzel (1999)
	<i>Argiope florida</i> , <i>A. aurantia</i>	Direct (field experiment)	Eisner & Nowicki (1983)
	<i>A. appensa</i>	Direct (field experiment)	Kerr (1993)
		Indirect (field observation)	

Table 2. *Patterns of web decorations in orb-web spiders (Na = not available)*

Taxon	Decoration type	Habitat	Source
Uloboridae			
<i>Conifaber parvus</i>	Linear	Forest	Lubin <i>et al.</i> (1982)
<i>Lubinella morobensis</i>	Spiral, linear	Na	Lubin (1986)
<i>Octonoba octonarius</i>	Discoid, spiral, linear	Na	Peaslee & Peck (1983)
<i>O. sybotides</i>	Discoid, linear, spiral	Na	Watanabe (1999a)
<i>O. varians</i>	Spiral	Na	Yaginuma (1960)
<i>Philoponella herediae</i>	Discoid	Forest floor	Opell (1987)
<i>P. republicana</i>	Linear	Monsoon forest understory	Opell (1979)
<i>P. tingens</i>	Linear	Na	Opell (1979)
<i>P. undulata</i>	Linear	Tropical forest understory	Lubin (1986)
<i>Uloborus americanus</i>	Linear	Na	Comstock (1912)
<i>U. bispiralis</i>	Linear	Tropical understory	Lubin <i>et al.</i> (1982)
<i>U. centiculatus</i>	Linear	Cactus hedges	Hingston (1927)
<i>U. conus</i>	Linear	Tropical forest understory	Lubin <i>et al.</i> (1982)
<i>U. crucifasciens</i>	Cruciate	Against tree trunks	Hingston (1927)
<i>U. diversus</i>	Spiral, linear	Na	Eberhard (1973)
<i>U. filifasciens</i>	Linear, cruciate	Palm leaves	Hingston (1927)
<i>U. glomosus</i>	Discoid, linear	Urban (campus)	Cushing & Opell (1989)
<i>U. plumipes</i>	Spiral, linear	Na	Marples (1969); Peters (1993)
<i>U. scutifasciens</i>	Linear, irregular mat	Against tree trunks	Hingston (1927)
<i>Zosis geniculatus</i>	Discoid, linear	Na	Lubin (1986)
Araneidae			
<i>Arachnura</i> sp.	Debris	Na	N. Scharff (pers. comm.)
<i>Argiope aemula</i>	Cruciate	Na	Robinson & Robinson (1974)
<i>A. aetherea</i>	Cruciate	Urban (campus)	Elgar <i>et al.</i> (1996)
<i>A. appensa</i>	Cruciate	Edges, and forest gaps	Kerr (1993)
<i>A. argentata</i>	Cruciate	Grass clearing	Craig & Bernard (1990)
<i>A. aurantia</i>	Cruciate	Prairie	Tso (1998a)
<i>A. aurocincta</i>	Cruciate	Parkland	Robinson & Robinson (1980)
<i>A. bruennichi</i>	Linear	Grassland	Malt (1993)
<i>A. catenulata</i>	Tri-radiate	'Among trees'	Hingston (1927)
<i>A. clarki</i>	Linear	Between trunks of palms	Hingston (1927)
<i>A. doboensis</i>	Discoid, cruciate	Tree trunks	Robinson & Lubin (1979)
<i>A. flavipalpis</i>	Discoid, cruciate	Lower shrub	Edmunds (1986)
<i>A. florida</i>	Cruciate	Na	Eisner & Nowicki (1983)
<i>A. keyserlingi</i>	Discoid, cruciate	Shrub	Herberstein <i>et al.</i> (2000)
<i>A. lobata</i>	Linear	Na	Robinson & Robinson (1974)
<i>A. minuta</i>	Cruciate	Na	Yaginuma (1960)
<i>A. picta</i>	Cruciate	Na	Robinson & Robinson (1974)
<i>A. pulchella</i>	Cruciate	Mango trees	Marson (1947a)
<i>A. radon</i>	Linear	Over river	Levi (1983); Robinson & Robinson (1980)
<i>A. reinwardti</i>	Cruciate	Na	Robinson & Robinson (1974)
<i>A. savignyi</i>	Discoid, cruciate	Na	Nentwig & Heimer (1987)
<i>A. trifasciata</i>	Discoid, linear	Prairie	Tso (1998a)
<i>Caerostris</i> sp.	Linear	Na	J. A. Coddington (pers. obs.)
<i>Cyclosa bifida</i>	Debris	Na	Bristowe (1941)

Table 2. (cont.)

Taxon	Decoration type	Habitat	Source
<i>C. caroli</i>	Discoid, spiral, debris	Na	Levi (1977)
<i>C. conica</i>	Linear, debris	Shrubs	Bristowe (1941)
<i>C. centrifasciens</i>	Debris	On trees	Hingston (1927)
<i>C. cylindrifasciens</i>	Silk cylinder	Mangroves	Hingston (1927)
<i>C. insulana</i>	Discoid, spiral, debris	Rubber trees	Marson (1947b)
<i>C. micula</i>	Spiral	Na	Bristowe (1941)
<i>C. turbinata</i>	Linear, debris	Na	Rovner (1976)
<i>Cyrtophora bifurcata</i>	Debris	Na	Levi (1977)
<i>C. citricola</i>	Debris	Na	Kullmann (1958)
<i>C. hirta</i>	Debris	Na	M. A. Elgar (pers. obs.)
<i>C. moluccensis</i>	Debris	Na	M. A. Elgar (pers. obs.)
<i>Gasteracantha brevispina</i>	Debris	Na	Hingston (1927)
<i>G. cancriformis</i>	Linear, tufts	Na	Marples (1969)
<i>G. curvispina</i>	Tufts	Under bushes	Edmunds & Edmunds (1986)
<i>G. germinata</i>	Tufts	Na	Simon (1895)
<i>G. minax</i>	Linear, tufts	Shrub	Mascord (1970)
<i>Gea eff</i>	Cruciate	Tall grass	Levi (1983)
<i>Isoxya cicatricosa</i>	Linear	Grass	Edmunds & Edmunds (1986)
<i>Micrathena sexspinosa</i>	Linear	Na	Nentwig & Heimer (1987)
<i>Neoscona domiciliorum</i>	Linear	Na	McCook (1889)
<i>N. arabesca</i>	Linear	Na	McCook (1889)
<i>Neogea egregia</i>	Linear	Na	Levi (1983)
<i>Parawixia tuberculata</i>	Debris	Na	Yaginuma (1960)
<i>Singa</i> sp.	Na	Na	Wiehle (1929)
<i>Wilica crassicauda</i>	Linear	Na	Levi (1986)
<i>W. crassispina</i>	Linear, tufts	Na	Nentwig & Heimer (1987)
<i>Zilla</i> sp. 1	Linear	Bushes, forest edge	Robinson & Robinson (1980)
<i>Zilla</i> sp. 2	Linear	Na	Robinson & Robinson (1980)
Tetragnathidae			
<i>Nephila clavipes</i>	Linear	Forest edges	Robinson & Robinson (1973b)
<i>N. edulis</i>	Linear, debris	Forest	M. A. Elgar (pers. obs.)
<i>N. maculata</i>	Linear (juveniles)	Various	Robinson & Robinson (1973a)
<i>N. plumipes</i>	Linear, debris	Mangroves	M. A. Elgar (pers. obs.)
<i>N. tetragnathoides</i>	Linear, debris	Coconut plantations	M. A. Elgar (pers. obs.)
<i>Nephilengys cruentata</i>	Debris	Urban	Edmunds & Edmunds (1986)

Uloborids also show ontogenetic change in web-building behaviour. Immature *Uloborus conus* built linear decorations, while adults rarely built any (Lubin *et al.*, 1982). *Zosis geniculatus* adults constructed disks more than linear decorations, while in juveniles linear decorations were more frequent (Lubin, 1986).

(2) Population variation

The proportions of individuals that decorate their

webs can vary greatly between different populations. For instance, *A. flavipalpis* in West Africa (Edmunds, 1986) and *U. diversus* in Arizona, USA (Eberhard, 1973) almost always spun web decorations. By contrast, only 25% of individuals of *A. appensa* observed on Guam constructed web decorations (Hauber, 1998), while on neighbouring Pacific islands the frequency of web decorations in *A. appensa* varied between 3.6% and 76% (Kerr, 1993). Similarly, the proportion of *A. argentata* that never

Table 3. Summary of the types of web decorations and their possible location on the web (see Fig. 1 for schematic representations)

Type	Location on web	Example	Source
Silk			
Discoid	Hub	Juvenile <i>Argiope argentata</i>	Nentwig & Heimer (1987)
Spiral	Hub	<i>Lubinella morobensis</i>	Lubin (1986)
Linear	Hub	<i>Argiope trifasciata</i>	Horton (1980)
Cruciate	Hub	<i>A. argentata</i>	Craig & Bernard (1990)
Tufts	Orb, frame	Various <i>Gasteracantha</i> spp.	Edmunds (1986)
Debris			
Prey remains	Orb, barrier web	<i>Nephila plumipes</i>	Austin & Anderson (1978)
Egg sacks	Orb, frame, barrier web	<i>Cyrtophora citricola</i>	Edmunds & Edmunds (1986)

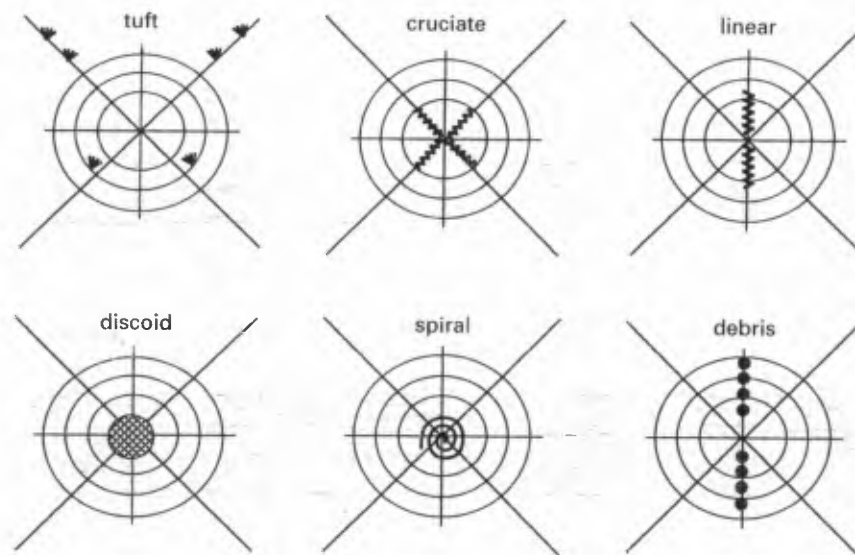


Fig. 1. Schematic representation of various web decoration types in orb-web spiders.

decorated their webs ranged from 65% in Panama (Robinson & Robinson, 1970) to between 58% and 78% on Santa Cruz Island, Galapagos (Lubin, 1975). These data may either reflect facultative changes in the decorating behaviour according to local environmental conditions, or indicate a genetic basis for web-decorating behaviour (Edmunds, 1986).

(3) Individual variation

Individuals of the same species display different decorating behaviours that may be influenced by changes in local physical factors. For example, *A. aetherea* spun more web decorations in dim light than in bright light (Elgar, Allan & Evans, 1996). By

contrast, *U. diversus* constructed more circular and linear decorations following nights of bright illumination compared with nights of low light level (Eberhard, 1973). Food availability also affected decorating behaviour. For example, *A. aurantia*, *A. trifasciata* (Blackledge, 1998b) and *A. keyserlingi* (Herberstein, Craig & Elgar, 2000) construct more and larger web decorations when they are maintained on a high-energy diet than when maintained on a low-energy diet. *Octonoba sybotides* was more likely to construct spiral decorations when food deprived while food-satiated individuals tended to form linear decorations (Watanabe, 1999b). Furthermore, when *A. keyserlingi* was fed the same amount of prey, the number and size of decorations was greater when prey encounter rates were low

predictable than when they were constant (Herberstein et al., 2000). The effects of feeding regimes were less pronounced for *A. trifasciata* foraging in the field, which suggests that other environmental factors, in addition to nutrition, influence the decorating behaviour (Tso, 1999).

Finally, experimental data suggest that selection may favour unpredictable decorating behaviour. For example, the stingless bee, *Trigona fluviventris*, learned to avoid the webs of *A. argentata* that were decorated identically over successive days. When the orientation of decorations was varied, however, *T. fluviventris* were more likely to be intercepted and hence captured in the web (Craig, 1994a, b). Correlative field studies further demonstrated that when a population of webs spun by *A. argentata* were decorated identically over three successive days, they intercepted fewer prey on days 2 and 3 compared with day 1. However, when webs in a second population were decorated randomly, they intercepted the same number of insects on each of the three days of the experiment (Craig, 1994a, b). By contrast some *A. flavipalpis* spun the same pattern more often than expected, while other individuals frequently changed the decoration pattern on a daily basis (Edmunds, 1986).

V. PHYLOGENETIC ANALYSIS OF DECORATION PATTERNS

We analysed the different patterns of decorations (as defined by Fig. 1) on a composite phylogeny (Fig. 2) of orb-web spiders produced by melding the latest relevant phylogenies from the literature. The phylogeny of Uloboridae is taken from Coddington (1990), of Araneidae from Scharff & Coddington (1997), of Tetragnathidae from Hormiga, Eberhard & Coddington (1995), of Orbiculariae from Griswold *et al.* (1998), and of Entelegynae from Griswold *et al.* (1999). Two characters, presence or absence of decorations (Fig. 2) and type of decoration patterns (see Table 2), were then traced at the generic level using MacClade 3.0 (Maddison & Maddison, 1992).

The first character is binary, and the second was treated as unordered. We made no *a priori* assumptions about any phylogenetic transformation series linking different types of decorations. A number of genera in Table 2 exhibit more than one type of decoration, thus making those terminals in Fig. 2 'polymorphic'. We checked MacClade's interpretation of polymorphic taxa by adding as

many dummy terminals as necessary within each genus to represent the various decoration types monomorphically. The lack of species-level cladograms for genera exhibiting diverse patterns is unfortunate. For example, if *Nephila tetragnathoides* were basal to the remaining *Nephila* in Table 2, the presence of a debris decoration in *Nephilengys* would make the debris pattern primitive for *Nephila*. Contrariwise, if *N. clavipes* and *N. maculata* were basal, the linear pattern would be inferred as primitive. Similar effects are possible in *Argiope*, *Uloborus*, *Cyclosa*, and *Gasteracantha*.

For the Uloborids (Fig. 3A) these data imply that linear or discoid decorations are primitive because only these two patterns are present in each of the four web-decorating genera in the cladogram. Spiral or cruciate patterns, such as in *U. crucifasciens* or *U. diversus* (Table 2) evolved *de novo*. The debris pattern is reconstructed to be primitive for *Nephila* (Fig. 3B) by outgroup comparison to *Nephilengys*. In *Witica* (Fig. 4A), tufts, debris, or both may be primitive, but the debris pattern is *de novo* to *Cyrtophora*. In *Neogea* and *Gea*, the patterns are monomorphic, and thus either the linear or cruciate pattern is plesiomorphic for *Argiope*; discoid and 'tri-radiate' (Table 2) are reconstructed as *de novo* in *Argiope*. However, the polymorphic *Argiope* species tend also to be the better known ones. Further observations may reveal that currently monomorphic genera such as *Gea* may also be polymorphic. Linear decorating patterns are *de novo* in *Micrathena* and *Caerostris*, but could be homologous and plesiomorphic for *Gasteracantha*, by outgroup comparison to *Isoxya* (Fig. 4A). Finally, all decorating patterns are *de novo* in *Cyclosa* (Fig. 4B).

Considering just the presence or absence of web decoration at the generic level (Fig. 2), these data require at least nine gains and one loss to explain the distribution of web decorations within Orbiculariae (Scharff and Coddington, 1997). Compared to other comparative data on orbicularians the fit of 'web decorations' to the cladogram is worse than any other character used by Scharff and Coddington (1997). In other words, there seem to be frequent evolutionary changes in web decorations. This pattern more or less repeats at the level of decoration patterns – states are far more likely to be convergent between genera than homologous. Although without phylogenies it is impossible to be precise, the diversity of patterns within genera will also require many hypotheses of convergence to be explained. This high degree of lability in the evolution of web decorations certainly supports the possibility that different types of web decorations have different

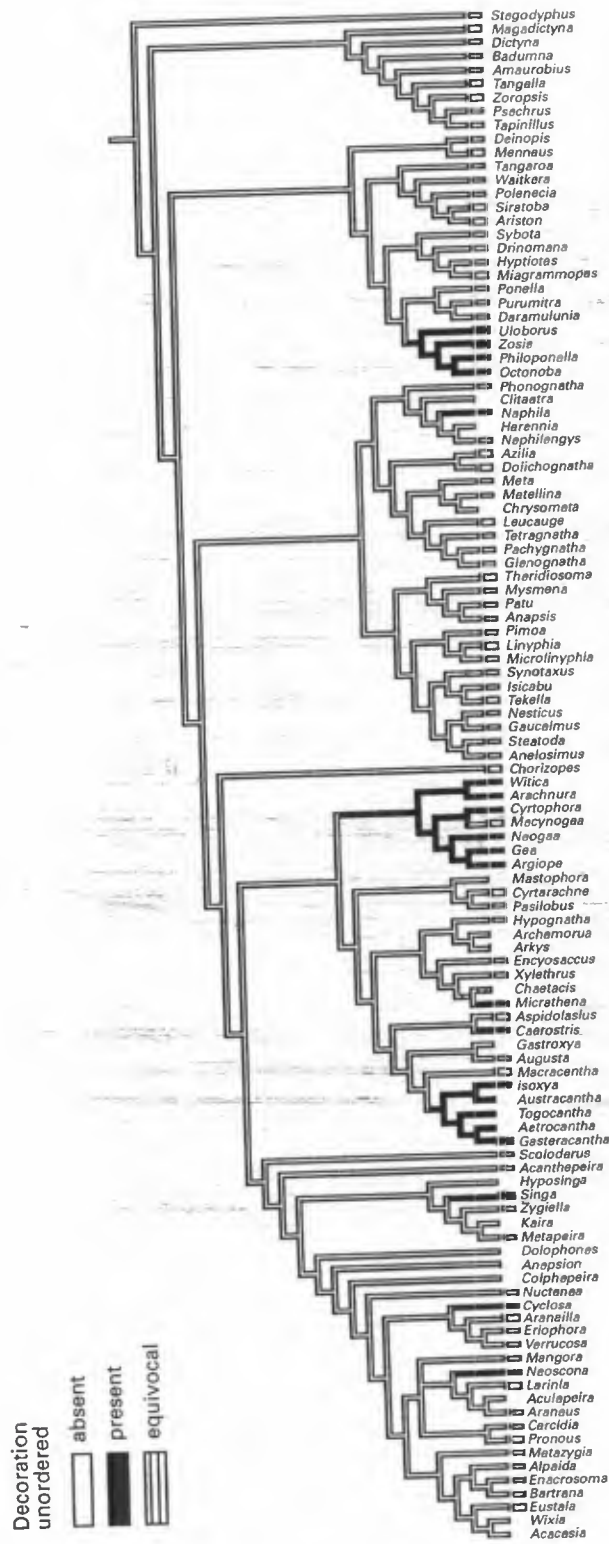


Fig. 2. Cladogram adapted from Scharff & Coddington (1997) tracing decorations on an equally weighted tree. See text for further details.

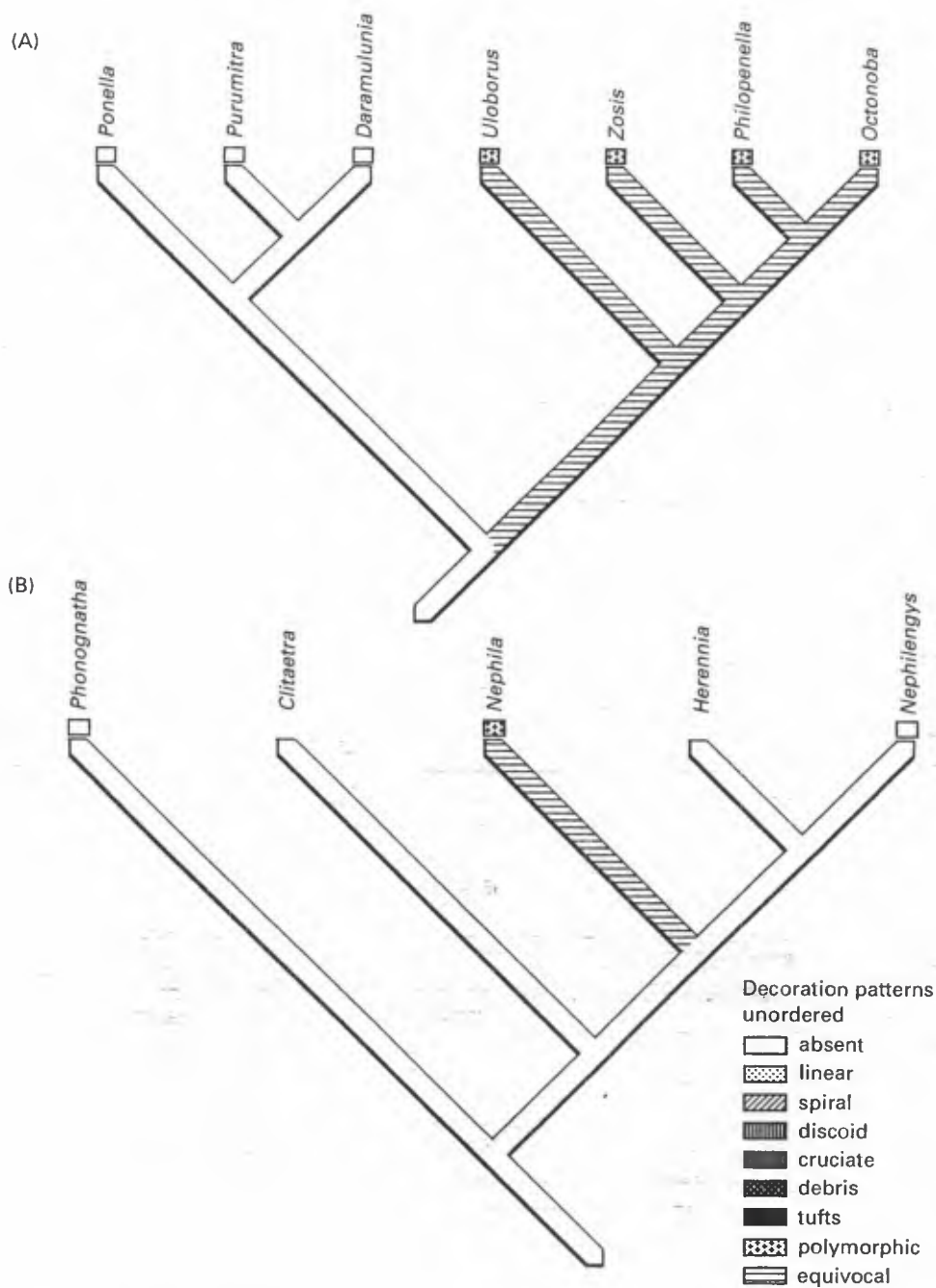


Fig. 3. Cladogram tracing decoration patterns on equally weighted tree for Uloboridae (A) and Tetragnathidae (B). See text for further details.

functions. Moreover, it is likely that the same type of decoration differs in function between species.

behaviour. We discuss each in turn, together with a critical analysis of the available evidence.

VI. FUNCTIONAL EXPLANATIONS

The evolutionary significance of decorating behaviour has attracted considerable debate, and there are several general explanations for the function of this

(1) Mechanical function

Simon (1895) was the first to ascribe a mechanical function to the cruciate decorations constructed by *A. argentata*, suggesting that the silk ribbon 'strengthens the position occupied by the spider'.

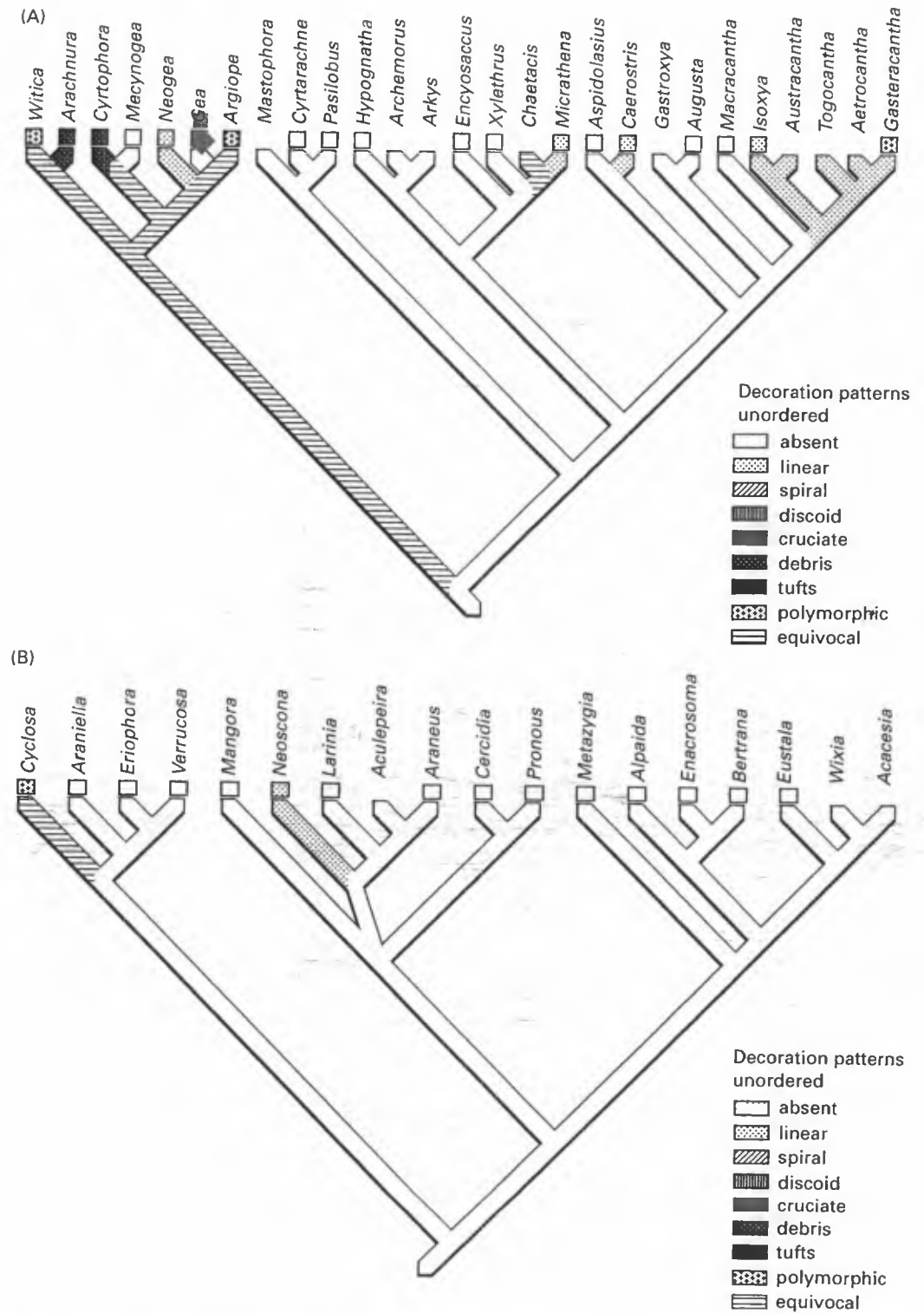


Fig. 4. Cladogram tracing decoration patterns on an equally weighted tree for Araneidae. The tree is split into parts (A, B) for clarity. See text for further details.

Accordingly, the silk bands may enable the spider to adjust the mechanical state of the completed web (Robinson & Robinson, 1970). Therefore, the variability in web decorations may reflect differences

in the amount of mechanical adjustment required to strengthen the web (Robinson & Robinson, 1970). For example, Robinson & Robinson (1970) attributed a mechanical strengthening function

the zigzag bands on the moulting platforms of *Nephila clavipes*.

This idea has been tested indirectly by comparing the frequency with which decorations are added to webs at sites characterised by different wind conditions. The proposed role of decorations is to stabilise webs in windy sites, where they are likely to require 'mechanical support'. Hence, more decorations should be added to webs in windy sites than to webs spun under calmer conditions. These observations provide little supporting evidence; there was no difference in the frequency of decorations spun by *A. argentata* in habitats exposed to strong winds and those in sheltered habitats (Lubin, 1975; Nentwig & Rogg, 1988). Nevertheless, Nect (1990) reports an increase in the frequency of circular decorations in *Cyclosa insulana* on windy days. However, these observations were conducted on three separate days, two of which were classified as 'calm' and data on wind speed (or any other environmental variables including rate of prey capture) are not provided (Nect, 1990). Wind speed manipulated in the laboratory had no effect on the decorating behaviour of *A. argentata* (Nentwig & Rogg, 1988).

A mechanical function of web decorations seems unlikely, although the idea has not been tested extensively. For example, it is not known whether decorated webs are more stable than undecorated webs, nor is it clear how web decorations could stabilise or strengthen the web. Indeed, other types of web decorations, particularly debris or tuft decorations (Fig. 1), seem an unlikely strengthening tool because the decorating silk is generally laid as an unstressed mass and often only attached to a single thread (Eberhard, 1973, 1990). Perhaps the strongest supporting evidence will come from comparative studies that compare the mechanical stability of webs constructed by decorating and non-decorating species.

(2) Anti-predator function

Web decorations may protect spiders from predatory attacks. There are thought to be several different protective mechanisms that depend, in part, on the various types of decorations. Pellets of prey remains or egg sacks may act as a decoy, confusing the predator who attacks the pellet rather than the spider (Hingston, 1927). Spiral or discoid decorations may conceal and hide the spider from predators (Eberhard, 1973; Ewer, 1972) and cruciate or linear bands may change the apparent shape

of the spider, making it less obvious to predators (Edmunds, 1986). Cruciate decorations may also increase the apparent size of the spider by appearing as extensions of pairs of legs, and thus protect it from gape-limited predators (Schoener & Spiller, 1992). Web decorations, including the silk tufts used by *Gasteracantha* spp., may protect spiders indirectly by advertising the presence of the web, which may be a negative stimulus to some avian predators (Horton, 1980).

The anti-predator function for web decorations has been examined in a number of ways. First, variation in web decorations has been interpreted to reflect the relative abundance of predators. For example, the frequency of decorating *A. argentata* on different islands in the Galapagos is associated with the number of potential predators (Lubin, 1975). Spiders on Daphne Island, which lacks potential spider predators, only rarely spin web decorations, whereas spiders spun decorated webs more frequently on Santa Cruz Island, which maintains a higher diversity of predators such as birds and lizards. However, there are no reports of direct predatory attacks by any of the suggested predators (Lubin, 1975). It is also possible that there may be other differences between the two islands that affect decorating behaviour.

A survey of *A. argentata* in the Bahamas showed that cruciate decorations were mostly spun by medium-sized spiders but not by small or large spiders (Schoener & Spiller, 1992). *A. argentata* may use cruciate decorations to increase their apparent size to predatory lizards (*Anolis* spp.), whose gape size places an upper limit on the size of their prey. Consequently, medium-sized spiders benefit most from spinning decorations but small spiders could not increase their apparent size beyond the gape size of the lizard and large spiders are already large enough (Schoener & Spiller, 1992). While this explanation is certainly possible, the mortality rate due to predatory attack of differently sized *A. argentata* was not measured nor was the response of lizards towards decoration size tested experimentally (Schoener & Spiller, 1992).

Finally, the variation in web decorating may reflect a trade-off between foraging efficiency and predator avoidance (Blackledge, 1998*b*). Thus, well-fed spiders might invest more energy into predator avoidance by spinning more decorations compared with food-deprived animals. Laboratory experiments revealed that food-deprived *A. trifasciata* constructed fewer web decorations than well-fed spiders (Blackledge, 1998*b*).

A more direct approach attempts to demonstrate experimentally that the risk of predation is reduced by decorations. Captive blue jays (*Cyanocitta cristata*) were allowed to choose individuals of *A. argentata* and *A. trifasciata* without a web, spiders in undecorated webs and spiders in decorated webs. The birds attacked spiders without a web most frequently, and spiders in undecorated webs more frequently than those in decorated webs (Horton, 1980). These data are consistent with the anti-predator function, but the decorations may not have acted to camouflage or conceal the spider, but rather the birds may have learned to associate web decorations with a negative stimulus – a sticky web (Horton, 1980).

The anti-predatory function of decorations is widely cited (Table 1) despite the paucity of experimental evidence. The absence of decorating behaviour in nocturnal species is consistent with the anti-predator explanation because few visual predators are likely to be active at night. However, records of the prey of diurnal sphecid predators reveal no consistent patterns. For example, the predominant genera captured by *Sceliphron laetum* in Madang, PNG were *Argiope*, *Gasteracantha* and *Neoscona* (Elgar & Jebb, 1999); only the latter is not known to decorate webs. By contrast, *S. madraspatanum conspicillatum* rarely captured *Argiope* spp., but preyed more frequently on species of *Araneus* and *Neoscona* (Adato-Barrion & Barrion, 1981). Of course, it is difficult to interpret these data without knowledge of the abundance and accessibility of the different genera.

However, the possibility that predators may also learn to associate web decorations with prey location is a strong argument against an anti-predator function (Robinson & Robinson, 1970). In a field experiment, crickets attached to screens were offered as prey to wild birds in the field. The crickets were placed in the centre of a 'model stabilimentum' consisting of a white zig-zag stitching arranged in a cruciate pattern. Eventually, the birds showed a preference for crickets with models over crickets without models (Robinson & Robinson, 1970).

(3) Improving foraging success

There are essentially two mechanisms by which web decorations may increase the foraging success of web-building spiders. First, they may attract pollinating insects by reflecting UV light in patterns similar to UV markers on flowers. Second, UV patches created by web decorations may indicate gaps in vegetation, which elicits flight behaviour in

many insects (Craig & Bernard, 1990). A foraging function has been tested extensively using spider that construct cruciate, linear and discoid decorations (eg. Craig, 1991; Craig & Bernard 1990; Hauber, 1998; Tso, 1996, 1998a, b; Watanabe, 1999a; see Table 1), and there are two lines of supporting evidence. First, the presence and the number and size of decorative bands were related to the presence of prey and to prey interception rates of the web. Second, more direct studies using choice experiments and field experiments showed that insects approach UV-reflecting web decorations more frequently than webs without UV-reflecting decorations.

The orientation and presence of decorative silk on webs spun by naturally foraging *A. argentata* were manipulated, and the prey-capture rates were estimated by recording the web-damage pattern caused by prey interceptions (Craig & Bernard 1990). Decorated webs intercepted significantly more insects than undecorated webs and the presence of the spider itself, which is characterised by reflecting abdomen, further enhanced prey-capture rates. Moreover, a within-web comparison showed that the vertical web half containing the decorative band also intercepted more prey than the undecorated web half (Craig & Bernard, 1990).

A further field study measured the prey-interception rates at *A. argentata* webs under three conditions: interception rates of solitary spider web interception rates of webs within 3 m of at least one other web, and interception rates of webs with both the spider and the decorations removed (Craig 1991). Webs of *A. argentata* foraging within 3 m of each other intercepted more insects than solitary foraging individuals. Furthermore, within the clusters, decorated webs captured more prey than undecorated webs (Craig, 1991). However, when the spiders and the decorations were removed solitary webs intercepted insects at similar rates to webs in a cluster (Craig, 1991).

The presence of web decorations was also related to prey interception in *A. trifasciata* (Tso, 1996). Decorated and undecorated webs did not differ in size, but decorated webs intercepted more flying insects than undecorated webs. However, the web half containing a decorative band did not capture more flying insects than the web half without decorative band (Tso, 1996). Similarly, *A. keyserlii* captured more prey on webs with decoration band than on undecorated webs (Herberstein, 2000). Observations of *A. appensa* on Guam revealed differences in the prey-interception rates

decorated and undecorated webs, and no increase in prey interception in the decorated quadrants of the same webs (Hauber, 1998). This result was confounded by differences in web size: decorated webs were significantly smaller than undecorated webs. After controlling for this size difference, decorated webs intercepted more prey per unit web area than undecorated webs (Hauber, 1998).

The relationship between web decorations and prey capture has been examined in field studies of *Cyclosa conica*, which constructs linear decorations in its horizontal web (Tso, 1998b) and *Octonoba sybotides*, which utilises linear and spiral decorations (Watanabe, 1999a). Decorated webs of *C. conica* intercepted 150% more insects than undecorated webs, even though they were 19% smaller than undecorated webs (Tso, 1998b). Similarly, when the webs of *O. sybotides* were adorned with either spiral or linear decorations, they intercepted more insects compared with undecorated webs. The size of decorated and undecorated webs did not differ (Watanabe, 1999a), although the mesh height of webs decorated with spirals was smaller than that of undecorated webs. However, this may not affect the conclusions because webs with a smaller mesh must also be more visible to insect prey than webs with a larger mesh (Craig, 1986; Watanabe, 1999a).

Three manipulative experiments provide more conclusive evidence in support of a foraging function. In choice experiments, *Drosophila* spp. flies were confronted with identical webs spun by *Uthoborus glomosus* (Craig & Bernard, 1990) and *O. sybotides* (Watanabe, 1999a). The web in one arm of a Y-maze was illuminated with white light containing a UV component, while the web in the other arm was illuminated with white light without a UV component. Flies approached and were captured in webs containing UV-reflecting decorations more frequently than in webs that did not reflect UV.

Furthermore, isolated bands of decorations built by *A. aurantia* were transferred onto an artificial web consisting of a synthetic adhesive mesh and exposed in the field (Tso, 1998a). In a control group, a similar-sized area of non-decorative silk was introduced into identical artificial webs. The artificial webs were then installed adjacent to already existing *A. aurantia* web sites. Artificial webs containing decoration bands captured significantly more flying insects than those in the control group, while web site or date had no effect on prey capture (Tso, 1998a).

Blackledge and Wenzel (2000) recently published the results of an experimental study that tested the

response of honeybees to silks spun by ancestral (*Pterinochilus* sp.) and derived spiders (*A. aurantia*) against a grass background. On the basis of their experiments they argue that they were unable to train bees to associate an award with UV-reflecting silk concluding that decorations spun by orb-spinning spiders are cryptic to bees which would not be able to discriminate UV-reflecting silk from background vegetation.

Blackledge and Wenzel (2000) hypothesise that the reflectance spectra of the decorative silks are flat but, regrettably, do not provide data to test this assertion. This is important because the only spectral data available show a 30% variation in the reflectance spectrum of decoration silks spun by *A. argentata* (100% reflective at 370 nm varying to approximately 70% reflectance at 640 nm; Craig & Bernard, 1990). It is unknown whether there were any differences in the spectral properties of the ancestral and derived silks or the silks and their background. Further, most vegetation [with the exception of densely hairy or glaucous leaves and foliage (Frolich, 1976)] absorbs light in the UV to blue (330–420 nm) region of the spectrum and reflects light in the green region of the spectrum and above (> 550 nm). As a result, the contrast between the web decoration and a green background is high (see Figs 2a and b in Craig & Bernard, 1990). Blackledge & Wenzel (2000) have shown that honeybees had difficulty associating the decorative silks with the sugar reward, but learning is a different behaviour from perception. In fact, honeybees have more difficulty learning to associate a sugar water reward with UV-reflecting objects than objects that reflect any other wavelength (Menzel & Erber, 1978). Finally, the achromatic reflectance (brightness) of the silks and the background was not measured. Thus, we cannot determine if the observed choices were made in response to brightness or colour of the silks and their background. The experiments cited above show that understanding insect responses to colour, pattern and brightness is extremely complex and will require tightly controlled experiments that address one variable at a time.

In a field experiment (Blackledge & Wenzel, 1999), *A. aurantia* in decorated webs captured fewer prey than spiders in webs that had the decorations removed, suggesting that web decorations do not function to increase foraging success, but actually reduce it. This study is puzzling, since Tso (1998b) used the same species (see above) and reported the opposite effect: artificial traps containing decorations intercepted more prey than control traps

containing non-decorative silk. There are several possible explanations. Blackledge & Wenzel (1999) did not control for web size in their study, but Tso (1998b) used identical traps in both treatments. Thus, random differences in web size between the control and experimental groups may have biased the results reported by Blackledge & Wenzel (1999). Further, the effect of decorated and undecorated webs was estimated using the foraging success of the spiders rather than the interception rates of the webs alone (see Tso, 1998b). Variation in the attack behaviour of the resident spider may further result in contradictory outcomes. Alternatively, it is possible that web decorations serve different functions in different populations of the same species. The decorations built by *A. aurantia* in Ohio, USA (Blackledge & Wenzel, 1999) may have different effects on the prey population compared with *A. aurantia* in Michigan, USA (Tso, 1998b) and therefore serve a different function.

Several other studies that investigate the source of variation in decorating behaviour have also provided data that are consistent with a foraging function. For example, individual *A. aetherea* adjusted their decorating behaviour according to light conditions. In dim light they adorned their webs with more and larger cruciate decorations than in bright light, presumably increasing the amount of UV-light reflected (Elgar et al., 1996). These patterns are consistent with a foraging function resulting from UV-reflection: if decorations increase prey interception spiders should increase the number and size of web decorations in dim light in order to increase the amount of reflected UV-light. Similarly, if web decorations are part of a foraging strategy, spiders should vary the decorating behaviour in response to variation in the rate of prey encounter (Herberstein et al., 2000). *A. keyserlingi* were maintained on the same quantity of prey but at different prey encounter rates. When prey arrival was constant, spiders spun fewer web decorations compared with variable prey-capture rates (Herberstein et al., 2000). It is important to note that a mechanical or anti-predator function does not predict these changes in decorating behaviour according to ambient light condition or prey encounter rates.

Nevertheless, the response of spiders to variation in satiation level does not appear to be consistent with a prey-attraction function: food-deprived spiders reduced the number and size of web decorations, while food-satiated spiders spun more decorations (Blackledge, 1998b). In *A. keyserlingi* (Herberstein et al., 2000) and *A. trifasciata* (Tso,

1999), food-deprived spiders also increased the size of their webs. These patterns may reflect a trade-off between the costs and benefits of decorating behaviour. In the field, decorated webs suffer from greater web damage due to prey interception (Hauber, 1998). Consequently, hungry spiders may reduce web damage of their larger webs by spinning fewer decorations (Herberstein et al., 2000). It may also be that web decorations target specific types of prey. In this case, starving spiders could be predicted to spin large, undecorated webs that intercept prey non-specifically while well-fed spiders build smaller, decorated webs capturing only those insects that provide a specific resource.

Finally, the general absence of decorating behaviour among nocturnal spiders, is also consistent with a foraging function. Comparative analyses between the prey-selected by decorating and non-decorating species may provide further insights into a foraging function.

(4) Decreasing web damage

The web decorations constructed by *Argiope* species or the silk tufts spun by *Gasteracantha* species are conspicuous structures, and may advertise the presence of webs to birds or other larger animals that may otherwise encounter and destroy the web (Eisner & Nowicki, 1983). This idea was tested experimentally by placing paper replicates of cruciate decorations made by *A. florida* on the vacant orb webs of various species of nocturnal web-building spiders. During the day, webs with a paper strip suffered a lower degree of destruction than unadorned webs (Eisner & Nowicki, 1983). It is difficult to assess these data because the source of web destruction is not identified and there are a number of potentially biasing effects (see also Craig & Bernard, 1990). For example, there was no control for differences in the ability of webs to absorb insect kinetic energy, the primary factor causing web breakdown and which varies greatly between the webs of different species (Craig, 1987). Hence, some webs are destroyed when they intercept large or fast-flying insects, while others are unaffected. It is unlikely that the kinetic properties of the webs spun by six different araneid species are identical, and therefore the differences in damage may be caused by varying rates of insect interception. Similarly, the reflective properties of the pieces of paper used in their study were not measured and it is likely that they differed from those of silk decorations, which

may have very different effects on insect prey or even birds.

However, a recent field experiment using the webs and decorations of *A. aurantia* showed that webs with decorations suffered less damage than webs that had all decorations removed (Blackledge & Wenzel, 1999), while the presence of the spider in the web did not affect the rate of web damage. Empty frames were initially set up in a triangular arrangement on a mown lawn and birds were lured to the middle of the arena with a dish of bird seed. After a period of acclimatisation, two of the three empty frames were replaced by a web containing decorations and a web where all decorations had been removed. While Blackledge & Wenzel (1999) did not provide information on the source of web destruction, they observed several birds actively avoid webs that contained decorations.

In a different approach, Kerr (1993) related the frequency of web-decorating behaviour with the presence of birds on different Pacific islands. Only 16.4% of *A. appensa* spun decorated webs on Guam, where the introduction of the brown tree snake (*Boiga irregularis*) has eliminated all of the native birds over the past 30 years (but see Hauber, 1998). By contrast, between 41.9% and 56.9% of *A. appensa* on the neighbouring islands of Rota, Tinian and Saipan, where the bird fauna remains intact, decorated their webs (Kerr, 1993). Perhaps the extinction of birds on these islands reduced or eliminated selection for web-decorating behaviour. This evolutionary scenario suggests that the cost of decorating is very high if this behaviour is to be lost in such a short time interval.

The main argument against an advertisement function is that many spiders that build decorations locate their webs in sheltered positions (see Table 2; Eberhard, 1990) such as tree buttresses (e.g. *Lubinella* spp.), tall grass (e.g. *Argiope* spp.) shrubs and understory (e.g. *Gasteracantha* spp.) where birds are unlikely to fly through and damage the web (Eberhard, 1990). Experimental designs that expose these webs outside their natural shelter (e.g. on a mown lawn in Blackledge & Wenzel, 1999) may not provide biologically relevant information.

(5) Thermoregulation

A few studies suggest a thermoregulatory function for disc-shaped decorations. Humphreys (1992) found that the discs constructed by juvenile *Neogea* spp. provided shade to spiders foraging in sites characterised by high temperatures. When tempera-

tures exceeded 40 °C, the spider moved under the disc where it was protected. The disc cut the transmission of light by 60%, reducing the body temperature of the spider by 1.8 °C (Humphreys, 1992). It is likely that this shuttling behaviour evolved secondarily, with the animal taking advantage of an existing structure. However, web decorations are found in a variety of different light conditions, and more frequently under dim light (Elgar *et al.*, 1996). Furthermore, linear or cruciate decorations do not shade the spiders' body and are thus of limited thermoregulatory benefit.

VII. NON-FUNCTIONAL EXPLANATIONS

Nentwig & Heimer (1987) argue that the high degree of unexplained variation in decorating behaviour, together with a body of contradictory evidence, indicates that web decorations are unlikely to have an evolutionary function. Instead, web-decorating behaviour may simply arise as a consequence of non-specific stress reactions (Nentwig & Rogg, 1988) or silk regulation (Peters, 1993).

Under laboratory conditions, *A. argentata* varied their decorating behaviour in response to extreme temperatures, the presence of males, moulting and age, factors that were thought to raise levels of stress (Nentwig & Rogg, 1988). However, these patterns were not replicated under field conditions, where variation in temperature, humidity, illumination and wind velocity failed to explain differences in web-decorating behaviour (Nentwig & Rogg, 1988). Peters (1993) suggests that web decorations are a by-product of silk regulation. Not all of the silk from the aciniform (Araneidae) and piriform (Uloboridae) glands is used in wrapping prey, and thus the superfluous silk is transferred into the decorations (Peters, 1993). This idea has not been tested empirically.

There are several objections to the non-functional explanation of silk decorations. First, the energetic cost of silk production is high (Peakall & Witt, 1976; Opcll, 1998). Therefore, it is unlikely that natural selection will maintain web-decorating behaviour unless it provides some benefit. Furthermore, it would be surprising if a non-functional trait evolved independently several times, as appears to be the case.

The stress-response interpretation is counter-intuitive; spiders that experience stress should not deplete their nutritional resources further by producing more costly silk. In fact, spiders spin

decorations under extremely benign laboratory conditions that minimise or eliminate 'stress' (e.g. Herberstein et al., 2000). The inter-specific variation in web-decorating behaviour provides little support for either the stress-response or silk-regulation explanations. For example, such explanations should apply equally to spiders that build webs during the day or night, but web decorating is not found in nocturnal species. Additionally, it is not clear why spiders belonging to the genus *Argiope* suffer higher stress levels or need to regulate silk more than spiders of, say, the genus *Araneus* that do not decorate their webs (Table 1). Finally, web decorations are typically constructed immediately after the orb web is completed. Even if the spiders have produced superfluous silk, it seems unlikely that they would discard it at the beginning of a foraging bout when an unknown quantity of silk is needed to wrap prey.

While an excess of silk probably does not induce decorating behaviour, it is likely that the availability of silk in the glands will affect the frequency and size of web decorations. The amount of wrapping silk expended by *A. aetherea* has been manipulated experimentally by offering some spiders more prey, which was consequently wrapped but not ingested (I. M. Tso, unpublished data). These spiders spun fewer or smaller decorations in subsequent webs than spiders whose silk reserves were not depleted. At the end of the foraging period, the spider's reserve of aciniform silk was never completely exhausted, and spiders were always able to release more silk to wrap-prey (I. M. Tso, unpublished data).

VIII. CONCLUSION

The function of web decorations remains an unresolved issue. At least seven different functional explanations have been proposed, but only a few functions have been tested directly. The foraging function has been tested most extensively on linear, cruciate and circular decorations and is supported by several experiments and correlative field studies (e.g. Craig & Bernard, 1990; Craig, 1991; Hauber, 1998; Tso, 1996, 1998a, b; Watanabe, 1999a). The anti-predatory function (Horton, 1980) and the web advertisement function (Blackledge & Wenzel, 1999) have been investigated for linear, cruciate and circular decorations built by *Argiope* spp. By contrast, the other functions and other types of decorations have not been tested as extensively.

Assigning a specific function to web decorations is made difficult for a number of reasons. First, the

selective pressures responsible for the evolution of web decorations may differ from those identified by contemporary studies as maintaining the behaviour. Second, the convergent nature of decorations and their patterns implies that different types of decorations serve different functions in different species. For example, the relationship between prey capture and web decorations is confirmed for the linear and cruciate types, particularly in *Argiope* spp. and may also apply to disc-shaped decorations spun by some Uloboridae (Craig & Bernard, 1990; Watanabe, 1999a). However, it is not clear whether debris types have similar functions. In fact, it is not clear whether the eggsacs placed in the web of *Cyclosa*, *Arachnura* and *Cyrtophora* species should be considered as decorations equivalent to the linear, circular or cruciate patterns. Keeping eggsacs in the web may allow the spider to protect the eggs from predators, parasites and parasitoids (see Elgar et al., 1983). While these egg sacs may provide additional concealment, the selective 'route' is fundamentally different to those species that use aciniform silk bands. Similarly, the prey items placed in bands in the webs of *Nephila* species may function primarily as food storage, with concealment being a selectively neutral consequence.

Finally, the different types of decorations constructed by juvenile and adult spiders also impede an attempt to assign particular functions. While ontogenetic changes suggest distinct mechanisms or perhaps different functions for the different decorations types, these are still poorly understood. The vast majority of studies have been concerned with adult rather than juvenile spiders.

Several steps may help to resolve the ongoing controversy regarding the function of web decorations. First, it may be helpful to identify four phylogenetic clusters of web decorations: 'uloborine' uloborids, 'argiopine' and 'gasteracanthine' araneids and 'nephiline' tetragnathids. Within these clusters, similar web decorations may have similar functions as a result of common ancestry. Extrapolations from one phylogenetic locus to another are unlikely to be relevant in resolving this debate. Second, the different decorating patterns may describe different phenomena that have undergone different selective routes. Therefore, the functions of the various types of decorations may or may not be convergent. For example, debris structures should not be termed 'decorations' or 'stabilimenta', but should be treated as separate behavioural phenomena. Two main clusters remain within the 'true' silk types of decorations. The 'bright white' silk bands

spun frequently by species in the 'argiopine' and 'uloborine' cluster, which may be convergent in form and function, (although evidence is not very strong at this stage), and the more dull decorations that are spun less frequently by species in the 'gasteracanthine' and 'nepheline' clusters.

Finally, inter-specific comparative studies that combine field observations, experimental studies and the life histories of decorating and non-decorating spiders should give the clearest insight into the selective factors that have influenced the evolution of decorating behaviour among spiders.

IX. ACKNOWLEDGMENTS

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X. REFERENCES

- ADATO-BARRION, A. M. & BARRION, A. T. (1981). Spider prey of *Sceliphron madraspatanum conspicillatus* (Hymenoptera: Sphecidae). *Kalikasan* **10**, 122-125.
- AUSTIN, A. D. & ANDERSON, D. T. (1978). Reproduction and development of the spider *Nephila edulis* (Koch) (Araneidae: Araneae). *Aust. J. Zool.* **26**, 501-518.
- BLACKLEDGE, T. A. (1998a). Signal conflict in spider webs driven by predators and prey. *Proc. R. Soc. Lond. B.* **265**, 1991-1995.
- BLACKLEDGE, T. A. (1998b). Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). *J. Zool. Lond.* **246**, 21-27.
- BLACKLEDGE, T. A. & WENZEL, J. W. (1999). Do stabilimenta in orb webs attract prey or defend spiders? *Behav. Ecol.* **10**, 372-376.
- BLACKLEDGE, T. A. & WENZEL, J. W. (2000). The evolution of cryptic spider silk: a behavioral test. *Behav. Ecol.* **11**, 142-145.
- BRISTOWE, W. S. (1941). *A comity of spiders*. The Ray Society, London.
- CLOUDSLEY-THOMPSON, J. L. (1995). A review of the anti-predator devices of spiders. *Bull. Br. Arachnol. Soc.* **10**, 81-96.
- CLYNE, D. (1969). *A guide to Australian spiders*. Thomas Nelson, Ltd. Australia.
- CODDINGTON, J. A. (1990). Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneocladia: Araneoidea, Deinoidea). *Smithsonian Contrib. Zool.* **496**, 1-52.
- COMSTOCK, J. H. (1912). *The spider book*. Doubleday, Page & Company, New York.
- COMSTOCK, J. H. (1940). *The spider book*. Doubleday, Doran & Company, Inc., New York.
- CRAIG, C. L. (1986). Orb visibility: the influence of insect flight behaviour and visual physiology on the evolution of web designs within the Araneoidea. *Anim. Behav.* **34**, 54-68.
- CRAIG, C. L. (1987). The significance of spider size to the diversification of spider-web architectures and spider reproductive modes. *Am. Nat.* **129**, 47-68.
- CRAIG, C. L. (1989). Alternative foraging modes of orb web weaving spiders. *Biotropica* **21**, 257-264.
- CRAIG, C. L. (1991). Physical constraints on group foraging and social evolution: observations on web-spinning spiders. *Funct. Ecol.* **5**, 649-654.
- CRAIG, C. L. (1994a). Limits to learning: effects of predator pattern and colour on perception and avoidance-learning by prey. *Anim. Behav.* **47**, 1087-1099.
- CRAIG, C. L. (1994b). Predator foraging behavior in response to perception and learning by its prey: interactions between orb-spinning spiders and stingless bees. *Behav. Ecol. Sociobiol.* **35**, 45-52.
- CRAIG, C. L. (1997). Evolution of arthropod silks. *Annu. Rev. Entomol.* **42**, 231-267.
- CRAIG, C. L. & BERNARD, G. D. (1990). Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* **71**, 616-623.
- CRAIG, C. L., BERNARD, G. D. & CODDINGTON, J. A. (1994). Evolutionary shifts in the spectral properties of spider silks. *Evolution* **48**, 287-296.
- CUSHING, P. E. & OPELL, B. D. (1989). Disturbance behaviours in the spider *Uloborus glomosus* (Araneae, Uloboridae). *Can. J. Zool.* **68**, 1090-1097.
- EBERHARD, W. G. (1973). Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. *J. Zool. Lond.* **171**, 367-384.
- EBERHARD, W. G. (1990). Function and phylogeny of spider webs. *Annu. Rev. Ecol. Syst.* **21**, 341-372.
- EDMUNDS, J. (1986). The stabilimenta of *Argiope flavipalpis* and *Argiope trifasciata* in West Africa, with a discussion of the function of stabilimenta. In *Proceedings of the 9th International Congress of Arachnology, Panama 1983* (eds W. G. Eberhard, Y. D. Lubin and B. C. Robinson.), pp. 61-72. Smithsonian Institution Press, Washington.
- EDMUNDS, J. & EDMUNDS, M. (1986). The defensive mechanisms of orb weavers (Araneae: Araneidae) in Ghana, West Africa. In *Proceedings of the 9th International Congress of Arachnology, Panama 1983* (eds W. G. Eberhard, Y. D. Lubin and B. C. Robinson.), pp. 73-89. Smithsonian Institution Press, Washington.
- EISNER, T. & NOWICKI, S. (1983). Spider web protection through visual advertisement: role of the stabilimentum. *Science* **219**, 185-187.
- ELGAR, M. A., ALLAN, R. A. & EVANS, T. A. (1996). Foraging strategies in orb-spinning spiders: ambient light and silk decorations in *Argiope aetherea* Walckenaer (Araneae: Araneoidea). *Aust. J. Ecol.* **21**, 464-467.
- ELGAR, M. A. & JEBB, M. (1999). Nest provisioning in the mud-dauber wasp *Sceliphron laetum* (F. Smith): body mass and taxa specific prey selection. *Behaviour* **136**, 147-159.
- ELGAR, M. A., POPE, B. & WILLIAMSON, I. (1983). Observations on the spatial distribution and natural history of *Cyrtophora*

- hirta* (L. Koch) (Araneae: Araneidae) in Queensland, Australia. *Bull. Br. Arachnol. Soc.* **6**, 83–87.
- EWER, R. F. (1972). The devices in the web of the African spider *Argiope flavipalpis*. *J. Nat. Hist.* **6**, 159–167.
- FOELIX, R. F. (1992). *Biologie der Spinnen*. Georg Thieme Verlag, Stuttgart.
- FROLICH, M. W. (1976). Appearance of vegetation in ultraviolet light: absorbing flowers, reflecting backgrounds. *Science* **194**, 839–841.
- GRISWOLD, C. E., CODDINGTON, J. A., HORMIGA, G., & SCHARFF, N. (1998). Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zool. J. Linn. Soc.* **123**, 1–99.
- GRISWOLD, C. E., CODDINGTON, J. A., PLATNICK, N. I., & FORSTER, R. R. (1999). Towards a phylogeny of entelegyne spiders (Araneae, Entelegynae). *J. Arachnol.* **27**, 53–63.
- HAUBER, M. E. (1998). Web decorations and alternative foraging tactics of the spider *Argiope appensa*. *Ethol. Ecol. Evol.* **10**, 47–54.
- HERBERSTEIN, M. E. (2000). Foraging behaviour in orb-web spiders (Araneidae): do web decorations increase prey capture success in *Argiope keyserlingi* Karsch 1978? *Aust. J. Zool.* **48**, 217–223.
- HERBERSTEIN, M. E., CRAIG, C. L. & ELGAR, M. E. (2000). Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evol.-Ecol. Res.* **2**, 69–80.
- HINGSTON, R. W. G. (1927). Protective devices in spider's snares, with a description of seven new species of orb-weaving spiders. *Proc. Zool. Soc. Lond.* **28**, 259–293.
- HORMIGA, G., EBERHARD, W. G. & CODDINGTON, J. A. (1995). Web construction behavior in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae, Tetragnathidae). *Aust. J. Zool.* **43**, 313–343.
- HORTON, C. C. (1980). A defensive function for the stabilimenta of two orb weaving spiders (Araneae: Araneidae). *Psyche* **87**, 13–20.
- HUMPHREYS, W. F. (1992). Stabilimenta as parasols: shade construction by *Neogea* sp. (Araneae: Araneidae, Argiopinae) and its thermal behaviour. *Bull. Br. Arachnol. Soc.* **9**, 47–52.
- KERR, A. M. (1993). Low frequency of stabilimenta in orb webs of *Argiope appensa* (Araneae: Araneidae) from Guam: an indirect effect of an introduced avian predator. *Pacific Science* **47**, 328–337.
- KOVOOR, J. (1987). Comparative structure and histochemistry of silk-producing organs in arachnids. In *Ecophysiology of spiders* (ed. W. Nentwig), pp. 160–186. Springer Verlag, Berlin.
- KULLMANN, E. (1958). Beobachtung des Nützbaues und Beiträge zur Biologie von *Cyrtophora citricola* Forskal (Araneae, Araneidae). *Zool. Jb. Syst.* **86**, 181–216.
- LEVI, H. W. (1977). The orb-weaver genera *Cyclosa*, *Metazygia* and *Eustala* north of Mexico (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* **148**, 61–127.
- LEVI, H. W. (1983). The orb-weaver genera *Argiope*, *Gea*, and *Neogea* from the western Pacific region (Araneae: Araneidae, Argiopinae). *Bull. Mus. Comp. Zool.* **150**, 247–338.
- LEVI, H. W. (1986). The orb-weaver genus *Witica* (Araneae: Araneidae). *Psyche* **93**, 35–46.
- LUBIN, Y. D. (1975). Stabilimenta and barrier webs in the orb webs of *Argiope argentata* (Araneae, Araneidae) on Daphne and Santa Cruz Islands, Galapagos. *J. Arachnol.* **2**, 119–126.
- LUBIN, Y. D. (1986). Web building and prey capture in the Uloboridae. In *Spiders – Webs, behavior, and evolution* (ed. W. A. Shear), pp. 132–171. Stanford University Press, Stanford, CA.
- LUBIN, Y. D., OPELL, B. D., EBERHARD, W. G. & LEVI, H. W. (1982). Orb plus cone-webs in Uloboridae (Araneae), with a description of a new genus and four new species. *Psyche* **89**, 29–64.
- MADDISON, W. P. & MADDISON, D. R. (1992). MacClade: Interactive analysis of phylogeny and character evolution. Version 3.0. Sunderland, Massachusetts: Sinauer Associates.
- MALT, S. (1993). Trophical relations of selected web-building spiders (Araneae) in xerophil grasslands. *Boll. Acc. Gioenia Sci. Nat.* **26**, 253–261.
- MARPLES, B. J. (1969). Observations on decorated webs. *Bull. Br. Arachnol. Soc.* **1**, 13–18.
- MARSON, J. E. (1947a). Some observations on the ecological variation and development of the cruciate zigzag camouflage-device of *Argiope pulchella* (Thor.). *Proc. Zool. Soc. Lond.* **117**, 219–227.
- MARSON, J. E. (1947b). Some observations on the variations in the camouflage devices used by *Cyclosa insulana* (Costa), an Asiatic spider, in its web. *Proc. Zool. Soc. Lond.* **117**, 598–605.
- MASCORD, R. (1970). Australian spiders in colour. Charles E. Tuttle Co., Vermont.
- MCCOOK, H. C. (1889). *American spiders and their spinningwork*, I. Academy of Natural Sciences of Philadelphia, Philadelphia.
- MENZEL, R. & ERBER, J. (1978). Learning and memory in bees. *Scient. Am.* **239**, 102–109.
- NEET, C. R. (1990). Function and structural variability of the stabilimenta of *Cyclosa insulana* (Costa) (Araneae, Araneidae). *Bull. Br. Arachnol. Soc.* **8**, 161–164.
- NENTWIG, W. & HEIMER, S. (1987). Ecological aspects of spider webs. In *Ecophysiology of spiders* (ed. W. Nentwig), pp. 211–225. Springer Verlag, Berlin.
- NENTWIG, W. & ROGG, H. (1988). The cross stabilimentum of *Argiope argentata* (Araneae: Araneidae) – nonfunctional or a nonspecific stress reaction? *Zool. Anz.* **221**, 246–266.
- OPELL, B. D. (1979). Revision of the genera and tropical American species in the spider family Uloboridae. *Bull. Mus. Comp. Zool.* **148**, 445–549.
- OPELL, B. D. (1987). The new species *Philoponella herediae* and its modified orb-web (Araneae, Uloboridae). *J. Arachnol.* **15**, 59–63.
- OPELL, B. D. (1998). The material cost and stickiness of capture threads and the evolution of orb-weaving spiders. *Biol. J. Linn. Soc.* **62**, 443–458.
- PEAKALL, D. B. & WITT, P. N. (1976). The energy budget of an orb web-building spider. *Comp. Biochem. Physiol.* **54A**, 187–190.
- PEASLEE, J. E. & PECK, W. B. (1983). The biology of *Octonoba octonarius* (Muma) (Araneae, Uloboridae). *J. Arachnol.* **11**, 51–67.
- PETERS, H. M. (1993). Über das Problem der Stabilimente in Spinnennetzen. *Zool. Jb. Physiol.* **97**, 245–264.
- RABAUD, E. (1932). Le rôle du stabilimentum des toiles d'*Argiope fasciata*. *C. R. Acad. Sci.* **194**, 655–657.
- ROBINSON, B. C. & ROBINSON, M. H. (1974). The biology of some *Argiope* species from New Guinea: predatory behaviour and stabilimentum construction (Araneae: Araneidae). *Zool. J. Linn. Soc. Lond.* **54**, 145–159.
- ROBINSON, B. & ROBINSON, M. H. (1978). Developmental studies of *Argiope argentata* (Fabricius) and *Argiope aemula* (Walckenaer). *Symp. Zool. Soc. Lond.* **42**, 31–40.

- ROBINSON, M. H. & LUBIN, Y. (1979). Specialists and generalists: the ecology and behavior of some web-building spiders from Papua New Guinea. I. *Herennia ornatissima*, *Argiope ocyaloides* and *Arachnura melanura* (Araneae: Araneidae). *Pac. Ins.* **21**, 97-132.
- ROBINSON, M. H. & ROBINSON, B. (1970). The stabilimentum of the orb web spider, *Argiope argentata*: an improbable defence against predators. *Can. Ent.* **102**, 641-655.
- ROBINSON, M. H. & ROBINSON, B. (1973a). Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smith. Contr. Zool.* **149**, 1-76.
- ROBINSON, M. H. & ROBINSON, B. (1973b). The stabilimenta of *Nephila clavipes* and the origins of stabilimentum-building in araneids. *Psyche* **80**, 277-288.
- ROBINSON, M. H. & ROBINSON, B. (1980). Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pac. Ins. Mono.* **36**, 1-218.
- ROVNER, J. S. (1976). Detritus stabilimenta on the webs of *Cyclosa turbinata* (Araneae, Araneidae). *J. Arachnol.* **4**, 215-216.
- SCHARFF, N. & CODDINGTON, J. A. (1997). A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zool. J. Linn. Soc.* **120**, 355-424.
- SCHOENER, T. W. & SPILLER, D. A. (1992). Stabilimenta characteristics of the spider *Argiope argentata* on small islands: support of the predator-defense hypothesis. *Behav. Ecol. Sociobiol.* **31**, 309-318.
- SIMON, E. (1895). *Historie naturelle des Araignees*. Roset, Paris.
- THIRUNAVUKARASU, P., NICOLSON, M. & ELGAR, M. A. (1996). Leaf selection by the leaf-curling spider *Phonognatha graeffei* (Keyserling) (Araneoidae: Araneae). *Bull. Br. Arachnol. Soc.* **10**, 187-189.
- TOLBERT, W. W. (1975). Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae). *Psyche* **92**, 29-52.
- TSO, I. M. (1996). Stabilimentum of the garden spider *Argiope trifasciata*: a possible prey attractant. *Anim. Behav.* **52**, 183-191.
- TSO, I. M. (1998a). Isolated spider web stabilimentum attracts insects. *Behaviour* **135**, 311-319.
- TSO, I. M. (1998b). Stabilimentum-decorated webs spun by *Cyclosa conica* (Araneae, Araneidae) trapped more insects than undecorated webs. *J. Arachnol.* **26**, 101-105.
- TSO, I. M. (1999). Behavioral response of *Argiope trifasciata* to recent foraging gain: a manipulative study. *Am. Midl. Nat.* **141**, 238-246.
- WATANABE, T. (1999a). Prey-attraction as a possible function of the silk decoration of the uloborid spider *Octonoba sybotides*. *Behav. Ecol.* **5**, 607-611.
- WATANABE, T. (1999b). The influence of energetic state on the form of stabilimentum built by *Octonoba sybotides* (Araneae: Uloboridae). *Ethology* **105**, 719-725.
- WIEHLE, H. (1929). Weitere Beiträge zur Biologie der Araneen, insbesondere zur Kenntnis des Radnetzbaues. *Z. Morph. Ökol. Tiere* **15**, 262-306.
- YAGINUMA, T. (1960). Spiders of Japan in colour. Hoikusae, Osaka.