Convergent evolution of eye ultrastructure and divergent evolution of vision-mediated predatory behaviour in jumping spiders

K. F. SU,* R. MEIER,* R. R. JACKSON,†‡ D. P. HARLAND†§ & D. LI*

*Department of Biological Sciences, National University of Singapore, Singapore
†School of Biological Sciences, University of Canterbury, Christchurch, New Zealand
‡International Centre of Insect Physiology and Ecology (ICIPE), Thomas Odhiambo Campus, Mbita Point, Kenya
§Structural Biology Group, Canesis Network Ltd, Lincoln, New Zealand

Abstract

All jumping spiders have unique, complex eyes with exceptional spatial acuity and some of the most elaborate vision-guided predatory strategies ever documented for any animal of their size. However, it is only recently that phylogenetic techniques have been used to reconstruct the relationships and key evolutionary events within the Salticidae. Here, we used data for 35 species and six genes (4.8 kb) for reconstructing the phylogenetic relationships between Spartaeinae, Lyssomaninae and Salticoida. We document a remarkable case of morphological convergence of eye ultrastructure in two clades with divergent predatory behaviour. We, furthermore, find evidence for a stepwise, gradual evolution of a complex predatory strategy. Divergent predatory behaviour ranges from cursorial hunting to building prey-catching webs and araneophagy with web invasion and aggressive mimicry. Web invasion and aggressive mimicry evolved once from an ancestral spartaeine that was already araneophagic and had no difficulty entering webs due to glue immunity. Web invasion and aggressive mimicry was lost once, in *Paracyrba*, which has replaced one highly specialized predation strategy with another (hunting mosquitoes). In contrast to the evolution of divergent behaviour, eyes with similarly high spatial acuity and ultrastructural design evolved convergently in the Salticoida and in *Portia*.

Introduction

Jumping spiders (Family: Salticidae) have high spatial acuity eyes that can support a very rich and complex repertoire of vision-mediated predatory behaviour. With 5035 described species in 553 genera, the Salticidae is the most speciose spider family (Platnick, 2006). Yet the position of Salticidae within the Araneae and the relationships within Salticidae have only recently been addressed using numerical cladistic techniques (e.g. Maddison & Hedin, 2003; Maddison & Needham, 2006). Of the major groups within the Salticidae (Maddison &

Hedin, 2003; Maddison & Needham, 2006), it is the Salticoida (higher salticids) that accounts for 90% of the species. Yet the relatively species-poor Lyssomaninae and Spartaeinae, which have both been variously described as 'primitive' or 'basal', are crucial for understanding the higher level systematics and early evolution of salticids. Whereas there is good evidence for the monophyly of the Salticoida, the monophyly of the Lyssomaninae and Spartaeinae and their position within the Salticidae remain controversial (Maddison & Hedin, 2003).

Salticid eye ultrastructure

Information on the retinal anatomy of salticids comes from TEM studies of 28 species, in 25 genera (Land, 1969; Eakin & Brandenburger, 1971; Wanless, 1980a, 1982; Williams & McIntyre, 1980; Blest & Price, 1984;

Correspondence: Daiqin Li, Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543.
Tel.: +65 65164372; fax: +65 67792486;
e-mail: dbslidq@nus.edu.sg

Blest & Sigmund, 1984, 1985; Blest, 1985; Blest *et al.*, 1988). It is the unique forward-facing anterior-median pair of eyes (principal eyes) that allow for high spatial acuity vision (Homann, 1928; Crane, 1949; Land, 1969) enabling some species to have a spatial resolution of ≈0.04°, whereas the highest spatial acuity known for insects of similar size is only ≈0.4° (Land & Nilsson, 2002; human eye: ≈0.007°).

In all salticids, the retina lies at the end of a long eye tube, and at the front end of the eye tube is a large corneal lens (Land, 1971, 1985). Immediately in front of the retina there is a second lens that turns the principal eye into a telescope (Williams & McIntyre, 1980). The retina is divided into four tiers and it is the rearmost layer (layer I) that takes primary responsibility for tasks requiring high spatial acuity (Land, 1969; Blest *et al.*, 1988, 1990). The receptors in the central region of layer I are especially slender in transverse section and packed close together, providing the sampling mosaic needed for exceptional spatial acuity (Land & Nilsson, 2002). What makes layer I of particular interest is that across the Salticidae, and especially within the Lyssomaninae and Spartaeinae, there are numerous differences in receptor structure that are linked to eye performance. Although all salticids have higher spatial acuity than that found in other spiders, we here restrict the term 'high acuity' to salticid species that have retinas organized with minimal optical pooling and a particularly tight, regular sampling mosaic that provides spatial acuity of ≈0.04°. High spatial acuity is found in the Salticoida and some spartaeines (*Portia*). The price for having a finer grain receptor mosaic is reduced sensitivity to light, resulting from a lower photon catch per receptor. In salticids with high spatial acuity, this potential loss in sensitivity is compensated for by increases in the length of the photoreceptors and receptor structure changes that allow receptors to act as light guides (Blest *et al.*, 1990).

However, in the absence of a phylogenetic tree, it remains unclear whether high spatial acuity was already a feature of the salticid stem species or evolved multiple times. Here, we address this question by tracing high spatial acuity on a phylogenetic tree.

Diverse predatory behaviours

It was suggested that acute vision might have been essential for the evolution of the complex predatory behaviours of Salticidae (Jackson, 1992; Jackson & Pollard, 1996). Most salticoid species that have been studied are cursorial hunters that see prey from a distance, stalk until close and then attack by leaping (Drees, 1952; Forster, 1977, 1982; Richman & Jackson, 1992). They prey primarily on insects and building webs is not normally part of the spiders' repertoire. However, every studied spartaeine departs from this repertoire. Spartaeines adopt different predatory strategies (Table 1). This includes various combinations of web building,

araneophagy, web invasion and aggressive mimicry (Jackson & Pollard, 1996).

Prey-catching webs

The term 'web' most appropriately refers to silk structures that are considerably larger than the web-building spider and are used in prey capture (Jackson, 1985a; Shear, 1994). Except for some spartaeines, lyssomanines and a few salticoids, web building is absent in salticids. The spinning of cocoon-like nests is common in the Salticoida, but these cocoons function as nests used for resting, moulting, mating and egg laying (Jackson, 1979). Few web-building salticids are known within salticoids, and they are *Plexippus paykulli* (Jackson & Macnab, 1989; also see Hallas & Jackson, 1986), *Pellenes arciger* (Lopez, 1986), *Euryattus* sp. (Jackson, 1985b) and *Simaetha* sp. (Jackson, 1985c). The only spartaeines known to build space webs are *Portia* and *Gelotia*, whereas other spartaeines, and lyssomanines only spin small silk sheets (Jackson, 1990e, 1992), or in the case of *Spartaeus* (Jackson & Pollard, 1990) sheets of moderate size. In some instances, these silk sheets may play a role in prey capture.

Araneophagy

Specialized predation on other spiders (araneophagy) is another unusual predatory strategy of spartaeines. Various salticid species occasionally feed on other spiders (Jackson, 1986; Edwards & Jackson, 1993), but araneophagic salticids have prey-specific capture behaviour and show a distinctive preference for spiders as prey (Jackson, 1992; Jackson & Pollard, 1996; Li *et al.*, 1997; Jackson *et al.*, 1998; Jackson & Li, 1998; Jackson, 2000; Li, 2000). Araneophagy is found in the spartaeine genera *Brettus, Cocalus, Cyrba, Gelotia, Holcolaetis, Mintonia, Neobrettus, Phaeacius* and *Portia* (see Table 2 and Jackson, 1990b; Li & Jackson, 1996a; Jackson *et al.*, 1998; D. Li, unpublished data). It ranges from hunting or ambushing of spiders outside the webs (e.g. on tree trunks and boulders: *Holcolaetis* and *Phaeacius*) (Jackson & Hallas, 1986b; Jackson, 1990d; R.R. Jackson, unpublished data) to the capturing of host spiders after invading their webs (Jackson, 1992; Jackson & Pollard, 1996). Web-invading araneophagic spartaeines enter alien webs to prey on the web-building spider, and have glue immunity; i.e. they have the remarkable ability to walk, without adhering, across cribellate and ecribellate sticky webs. This is a surprising feature because no salticid builds sticky webs (Jackson & Pollard, 1996).

Two kinds of web invasion are used by spartaeines. In web invasion without aggressive mimicry (*Cocalus*), *Cocalus murinus* stalks very slowly across webs to prey on the resident spider (Jackson, 1990b). *Cocalus* generally do not venture far into the web and sometimes stay on the edge for hours (Jackson, 1990b). All the remaining web-invading spartaeines (*Brettus, Cyrba, Gelotia, Neobrettus*

Table 1 List of species, character scores and references.

Species	Web-building	Glue immunity	Araneophagy	References
Spartaeinae				
Cocalus murinus Simon	1	1	2	Jackson (2000), Cerveira *et al.* (2003), D. Li, unpublished data
Cyrba algerina (Lucas)	1	1	3	Jackson & Hallas (1986b), Jackson (1990a, 2000), Jackson & Li (1998)
Cyrba ocellata (Kroneberg)	1	1	3	Wanless (1984), D. Li, personal observation
Cyrba sp.	1	1	3	New species; D. Li, unpublished data
Gelotia springopalpis Wanless	1	1	3	Jackson (1990c), D. Li, unpublished data
Holcolaetis vellerea Simon	1	0	1	Wanless (1985), R. R. Jackson, unpublished data
Mintonia ramipalpis (Thorell)	1	0	1	Wanless (1984), D. S. H. Tay & D. Li, unpublished data
Neobrettus tibialis (Proszynski)	1	1	3	T. M. Wong & D. Li, unpublished data
Paracyrba wanlessi Zabka & Kovac	?	?	0	Zabka & Kovac (1996), J. R. W. Woon and D. Li, unpublished data
Phaeacius malayensis Wanless	1	0	1	Jackson (1990d), Li (2000)
Phaeacius yixin Zhang & Li	1	0	1	Zhang and Li (2005), D. Li, unpublished data
Portia africana (Simon)	1	1	3	Jackson & Hallas (1986a), Li *et al.* (1997)
Portia fimbriata (Doleschall)	1	1	3	Jackson & Blest (1982), Li & Jackson (1996b)
Portia heteroidea Xie & Yin	1	1	3	D. Li, unpublished data
Portia jianfengensis Song & Zhu	1	1	3	D. Li, unpublished data
Portia labiata (Thorell)	1	1	3	Jackson & Hallas (1986a), Li *et al.* (1997)
Portia sp.	1	1	3	D. Li, unpublished data
Portia quei Zebka	1	1	3	D. Li, personal observations
Spartaeus jianfengensis Song & Chai	1	0	0	D. Li, personal observations
Spartaeus platnicki Song, Chen & Gong	1	0	0	D. Li, personal observations
Spartaeus thailandicus Wanless	1	0	0	Wanless (1987), Jackson & Pollard (1990)
Spartaeus wildtrackii Wanless	1	0	0	Wanless (1987), D. Li, personal observation
Yaginumanis wanlessi Zhang & Li	?	?	?	Zhang and Li (2005)
Lyssomaninae				
Asemonea sichuanensis Song & Chai	1	0	0	Wanless (1980a), Jackson (1990e), D. Li, unpublished data
Lyssomanes viridis (Walckenaer)	1	0	0	Jackson, 1990e
Onomastus nigrimaculatus Zhang & Li	1	0	0	Zhang and Li (2005); D. Li, unpublished data

Web-building: 0 = absent, 1 = present. Glue immunity: 0 = absent, 1 = present. Araneophagy: 0 = absent, 1 = ambush predation, 2 = web invasion only, 3 = aggressive mimicry.

and *Portia*) deploy aggressive mimicry with *Portia*'s strategy being the most complex (see Table 1 and Wilcox *et al.*, 1996; Tarsitano & Jackson, 1997; Clark & Jackson, 2000; Jackson *et al.*, 2002; Jackson & Li, 2004). Here the web invader uses signalling (vibrations on the web) to control the behaviour of host spider.

The highly versatile and complex predatory strategies in the spartaeines have attracted considerable interest (Jackson & Blest, 1982). However, in the absence of a phylogenetic tree, all evolutionary inferences were highly speculative. A hypothesis concerning the joint evolution of high-acuity vision and intricate predatory strategies was outlined in the first detailed study of *Portia*'s predatory strategy (Jackson & Blest, 1982; Jackson, 1986). It was suggested that salticid ancestors, prior to the evolution of refined high-acuity eyes, were web-building spiders that lived in habitats where webs of various spider species were abundant and often contiguous. Another important part of the hypothesis (Jackson & Blest, 1982) was that ultrastructural modifications of salticid retinas

underlying high-acuity vision evolved in conjunction with a web-invading predator that was becoming a wide-spectrum aggressive mimic. This hypothesis can be rigorously tested using phylogenetic tools.

Materials and methods

Taxon sampling

Our data set comprised 35 species, including 22 species from 10 genera of the subfamily Spartaeinae, three species from the subfamily Lyssomaninae, one species from the *Cocalodes* group, five from Salticoida, and four outgroup species from four other families that are considered closely related to Salticidae, *Misumenops nepenthicola* (Thomisidae), *Cheiracanthium* sp. (Miturgidae) and *Oxyopes birmanicus* (Oxyopidae) and *Hibana* sp. (Anyphaenidae) (Simon, 1901; Petrunkevitch, 1933; Bristowe, 1938; Lehtinen, 1967, 1975; Ono, 1987; Coddington & Levi, 1991; Table 1).

Table 2 Taxonomic and locality information of the specimens included in the molecular analyses and GenBank accession numbers.

Species	Locality	28S1	28S2	18S	COI	H3	16S	ND1
Ingroup								
Asemonea sichuanensis	China: Sichuan	EF419017	EF419051	EF418986	EF419082	NA	NA	NA
Cocalus murinus	Singapore	EF419019	EF419053	EF418988	EF419084	EF419116	EF418959	EF419140
Cosmophasis umbratica	Singapore	EF419020	NA	NA	EF419085	EF419117	EF418960	EF419141
Cyrba algerina	Kenya	EF419021	EF419054	EF418989	EF419086	NA	EF418961	EF419142
Cyrba ocellata	China	EF419022	EF419055	EF418990	EF419087	NA	EF418962	EF419143
Cyrba sp.	Kenya	EF419023	EF419056	EF418991	EF419088	NA	NA	NA
Gelotia springpalpis	China: Hainan	EF419024	EF419057	NA	EF419089	EF419118	NA	NA
Holcolaetis vellerea	Kenya	EF419025	EF419058	EF418992	EF419090	EF419119	EF418963	EF419144
Ligurra latidens	Singapore	EF419026	EF419059	EF418993	EF419091	EF419120	EF418964	EF419145
Lyssomanes viridis	USA: Florida	EF419027	EF419060	EF418994	EF419092	EF419121	EF418965	EF419146
Mintonia ramipalpis	Singapore	EF419028	EF419061	EF418995	EF419093	EF419122	EF418966	EF419147
Neobrettus tibialis	Malaysia: Genting Highlands	EF419030	EF419063	NA	EF419095	EF419124	NA	NA
Onomastus nigrimaculatus	China: Yunnan	EF419031	EF419064	EF418997	EF419096	EF419125	EF418968	EF419149
Paracyrba wanlessi	Malaysia: Gombak	EF419033	EF419066	EF418999	EF419098	NA	NA	NA
Phaeacius malayensis	China: Yunnan	EF419034	EF419067	EF419000	EF419099	NA	EF418970	EF419151
Phaeacius yixin	China: Hainan	EF419035	EF419068	EF419001	NA	NA	EF418971	EF419152
Plexippus paykulli	Singapore	EF419036	NA	EF419002	EF419100	EF419127	EF418972	EF419153
Portia africana	Kenya	EF419037	EF419069	EF419003	EF419101	EF419128	NA	NA
Portia fimbriata	Singapore	EF419038	EF419070	EF419004	EF419102	EF419129	EF418973	EF419154
Portia heteroidea	China: Sichuan	EF419039	EF419071	EF419005	EF419103	EF419130	EF418974	EF419155
Portia jianfengensis	China: Haianan	EF419040	EF419072	EF419006	EF419104	NA	EF418975	EF419156
Portia labiata	Singapore	EF419041	EF419073	EF419007	EF419105	EF419131	EF418976	EF419157
Portia quei	China: Yunnan	EF419042	EF419074	EF419008	EF419106	EF419132	EF418977	EF419158
Portia sp.	China: Sichuan	EF419043	EF419075	EF419009	EF419107	EF419133	EF418978	EF419159
Rhene sp.	Malaysia: Cameron Highlands	EF419044	NA	EF419010	EF419108	EF419134	EF418979	EF419160
Spartaeus jianfengensis	China: Hainan	EF419045	EF419076	EF419011	EF419109	NA	EF418980	EF419161
Spartaeus platnicki	China: Hainan	EF419046	EF419077	EF419012	EF419110	EF419135	EF418981	EF419162
Spartaeus thailandicus	China: Yunnan	EF419047	EF419078	EF419013	EF419111	EF419136	EF418982	EF419163
Spartaeus wildtrackii	Malaysia	EF419048	EF419079	EF419014	EF419112	EF419137	EF418983	EF419164
Thiania bhamoensis	Singapore	EF419049	EF419080	EF419015	EF419113	EF419138	EF418984	EF419165
Yaginumanis wanlessi	China: Sichuan	EF419050	EF419081	EF419016	EF419114	EF419139	EF418985	EF419166
Outgroup								
Cheiracanthium sp.	Singapore	EF419018	EF419052	EF418987	EF419083	EF419115	NA	NA
Hibana sp.	GenBank	AY297295	NA	NA	AY297422	NA	AY296713	AY297358
Misumenops nepenthicola	Singapore	EF419029	EF419062	EF418996	EF419094	EF419123	EF418967	EF419148
Oxyopes birmanicus	Singapore	EF419032	EF419065	EF418998	EF419097	EF419126	EF418969	EF419150

Three species of lyssomanines (refer to Table 1) were included because Lyssomaninae has been proposed as the sistergroup of Spartaeinae (Wanless, 1980a, b, 1984; Blest & Carter, 1987; Maddison, 1988; Rodrigo & Jackson, 1992; Maddison & Hedin, 2003; Maddison & Needham, 2006). Five species of the Salticoida were chosen to represent the major groups recognized by Maddison & Hedin (2003): euophryines (*Thiania bhamoensis*), heliophanines (*Cosmophasis umbratica*), marpissoids (*Rhene sp.* indt.) and plexippoids (*P. paykulli*).

DNA extraction and sequencing

The DNA from whole spiders or spider legs was extracted using a modified CTAB extraction protocol (Shajahan, 1995). PCR was used to amplify DNA fragments from six genes (primers in Table 3). Cycling conditions for the primers started with an initial 95°C denaturation, followed by 30 cycles of 1 min at 95 °C, 1 min at 55 °C (28S), 50 °C (18S and H3), 46 °C (16S/ND1) or 48 °C (COI) and 1.5 min at 72 °C, and a final 2-min extension at 72 °C. PCR was carried out using the Hotstart Ex-*Taq* (Takara, Shiga, Japan). The amplified fragment was purified with the QIAquick PCR Purification kit (Qiagen, Valencia, USA). The purified PCR products were sequenced directly in both directions using an ABI 3100 (Applied Biosystems, Foster, California).

Phylogenetic analyses

Fragments were assembled into contigs in Sequencher (Gene Codes Corp., Ann Arbor, MI, USA). Multiple alignments were carried out in Clustal X (Higgins & Sharp, 1988) for 28S and 16S using the gap opening/gap extension ratios recommended by Maddison & Hedin (2003). Afterwards the alignments were manually adjusted in MacClade 4.06 OS X (Maddison & Maddison, 2003). 18S was first aligned in Clustal X (gap opening/gap

Table 3 List of primers

Gene	Primer
COI	C1-J-2309 (Masta, 2000)
	C1-N-2776 (Maddison & Hedin, 2003)
18S	18Sa2.0 (Giribet *et al.*, 1999)
	18S9R (Giribet *et al.*, 1999)
28S1	28S ÒOÓ (Maddison & Hedin, 2003)
	28S ÒCÓ (Maddison & Hedin, 2003)
28S2	28SRd4.5a (Whiting *et al.*, 1997)
	5Õ-GAC TTC CCT TAC CTA CAT-3Õ
	(Hausdorf, 1999)
Histone 3	H3aR (Colgan *et al.*, 1998)
	H3aF (Colgan *et al.*, 1998)
16S/ND1	N1-J-12261 (Maddison & Hedin, 2003)
	LR-N-12945 (Maddison & Hedin, 2003)

extension ratio: 15/6.66) (Higgins & Sharp, 1988) and manually adjusted in MacClade 4.06 OS X (Maddison & Maddison, 2003). The DNA sequences for protein-encoding genes were aligned based on amino acid sequences in DAMBE (Xia & Xie, 2001), using a gap opening/gap extension ratio of 10 : 0.1 and the protein weight matrix BLOSUM. The leading and trailing bases that had been discarded by DAMBE were re-inserted.

The data set was subjected to a parsimony analysis in TNT version 1.0 (Tree Analyses Using New Technology; Goloboff *et al.*, 2000). To explore if the indels in the alignments affects the resulting phylogenetic hypothesis, two separate analyses were carried out. The first with gaps treated as missing data and the second with gaps treated as fifth character state. A driven search was carried out at level 99 on TNT (with sectorial search), and the minimum length was found three times. Support for internal nodes was assessed using bootstrap and Bremer support. Bootstrap values were calculated in TNT (100 replicates) by using the 'New Tech' option utilizing the same search parameters as mentioned above. Bremer support values were computed in PAUP* version 4.0b10 (Swofford, 2002) using TreeRot (Sorenson, 1999; 100 random sequence-addition repetitions, TBR for each constrained search).

A Bayesian analysis was conducted in MrBayes 3.1 (Huelsenbeck & Ronquist, 2001). The GTR + I + G model was favoured by the Akaike information criterion and hierarchical likelihood ratio testing was implemented in MrModeltest version 2.2 (Nylander, 2004). The data set was analysed for 3 000 000 generations and a tree was sampled every 300 generations. Chain stationarity was achieved after 1 200 000 (burn-in) and 4000 trees were subsequently discarded. Three independently repeated analyses resulted in similar tree topologies, comparable clade probabilities and substitution model parameters, which suggested that reasonable estimates of the posterior probability (PP) distributions had been obtained.

Analyses of gene partitions

To assess whether mitochondrial or nuclear data provided greater amounts of support, partitioned Bremer supports (PBS) were determined for mitochondrial and nuclear genes with gaps coded as fifth character state. The amount of homoplasy and divergence in the nuclear and mitochondrial genes was assessed using the consistency index (CI), retention index (RI) and pairwise distances, as determined in PAUP* version 4.0b10 (Swofford, 2002).

Characters pertaining to predatory behaviour and eye ultrastructure

An extensive literature review on the predatory behaviours of Spartaeinae and eye ultrastructure of Salticidae was carried out and provided the following characters that were mapped onto the phylogenetic tree using MacClade 4.06 OS X (Maddison & Maddison, 2003) (Table 1). (1) Web building is defined as building of silk devices that are larger than the host spider and are used in prey capture: absent = 0; present = 1 (see Jackson, 1985a, 1992; Shear, 1994; Jackson & Pollard, 1996; Li & Jackson, 1996a; Jackson & Wilcox, 1998; Harland & Jackson, 2004). (2) Araneophagy is defined as targeting and preferring spiders as prey in standardized prey-choice experiments: absent = 0; ambushing = 1; web invasion = 2; aggressive mimicry = 3. The character was once mapped as additive (ordered) and once as nonadditive (unordered). (3) Glue immunity is the ability to enter and walk across sticky webs: absent = 0, present = 1. (4) With regard to high spatial acuity eyes, the literature data are comparatively incomplete, and it is here assumed that congeneric species share similar eye ultrastructure morphology. Given these uncertainties, only one unambiguous character was defined. High spatial acuity eyes with elongated and single rhabdomere receptors optimally placed throughout the layer I retina: absent = 0, present = 1 (Blest *et al.*, 1990). Such high spatial acuity has been confirmed for the following salticoid genera: *Amycus*, *Corythalia*, *Fluda*, *Holoplatys*, *Itata*, *Jollas*, *Helpis*, *Metaphidippus*, *Myrmarachne*, *Phiale*, *Plexippus*, *Scopocira*, *Synemosyna*, *Thiodina* and *Trite* and the spartaeine genus, *Portia* (Blest & Carter, 1987; Blest *et al.*, 1990). A lack of high spatial acuity eyes is known for: *Allococalodes*, *Asemonea*, *Brettus*, *Chinoscopus*, *Cyrba*, *Lyssomanes*, *Spartaeus* and *Yaginumanis* (see Blest & Carter, 1987; Blest *et al.*, 1990). Based on these data, we can here code the following genera as lacking high spatial acuity: *Asemonea*, *Cyrba*, *Lyssomanes*, *Spartaeus* and *Yaginumanis*, and the following as having high spatial acuity: *Plexippus* and *Portia*.

Results

We obtained about 4.8 kb of sequences data for 35 species each (Table 2). Using equal weighting parsimony analysis of the gap = missing data set, we
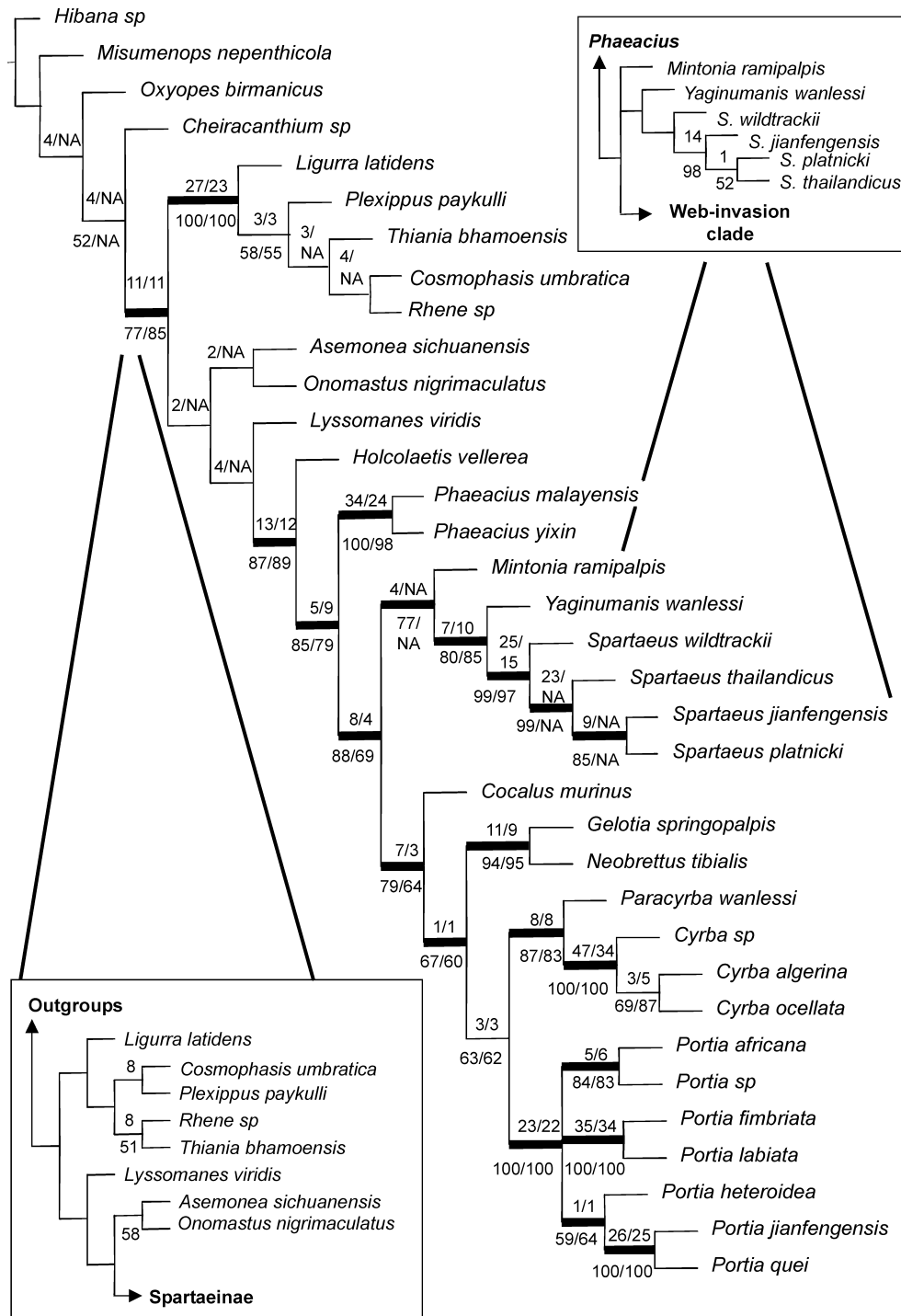
Fig. 1 Strict consensus tree of the MPTs (most parsimonious trees) from the analysis using gaps. (a) and (b) indicate areas that differ from the gaps = missing data tree. Bootstrap values are added below the nodes (bootstrap for gaps = fifth state/gaps = missing values). Numbers above each node refer to Bremer support values. Bold lines indicate nodes supported with 100 posterior probability in the Bayesian analysis.

found five parsimonious trees (length: 6166) whereas using the gap = fifth character state analysis yielded three parsimonious trees (length: 6907; Fig. 1). The trees had similar topologies, bootstrap support (BS) and Bremer supports (BrS) (see Fig. 1). The posterior probability tree from the Bayesian analysis yielded a nearly

Table 4 Partitioned Bremer support values for each gene partition (gaps = fifth character state).

Partitions	PBS
COI	63.8
16S	27
ND1	56.6
18S	34.9
28Sh	14.3
HIST	17.6
28S	147.9
All mitochondrial genes	147.3
All nuclear genes	214.7

identical tree. The only discrepancy is the lack of support in a few branches and conflict within the genus *Spartaeus* (Fig. 1). More than two-thirds of all the clades on the phylogram have 100% PP (see bold lines in Fig. 1).

The data support monophyly of Salticidae in all analyses, with a BS of 77, BrS of 11 and a PP of 100. The Spartaeinae is monophyletic (BS 85, BrS 5 and PP 100) (Fig. 1), with *Holcolaetis* being sistergroup to the remaining spartaeines (BS 87, BrS 13, PP 100) (Fig. 1). The Salticoida is monophyletic (BS 100, BrS 27, PP 100), whereas the Lyssomaninae are paraphyletic in the parsimony and Bayesian analyses. On the parsimony tree, *Lyssomanes* or *Asemonea + Onomastus* are sistergroup to the Spartaeinae and these two subfamilies are then sistergroup to the Salticoida (Fig. 1). On the Bayesian posterior probability tree, the higher level relationships within Salticidae remain unresolved.

Performance of gene partitions

Nuclear genes provided greater overall support than mitochondrial genes (Table 4). The overall highest support (*ca* 50%) comes from 28S1 (PBS = 147.9), which exceeds the support from all mitochondrial genes (PBS = 147.3) (Table 4). The second and third best performers were COI (PBS = 63.8) and ND1 (PBS = 56.6) respectively (Table 4). The poorest performer was 28S2 (PBS = 14.3). The mitochondrial gene COI had the lowest average CI (0.315) and RI (0.299) values of all the partitions, whereas the nuclear gene 18S had the highest average CI (0.638) and RI (0.650) values (Table 5). The 16S gene partition showed the greatest pairwise distance of all the partitions, whereas 28S2 partition showed the lowest pairwise distance (Table 6).

Evolution of behaviour and spatial acuity

Araneophagy evolved once at the base of Spartaeinae and was lost twice. Web invasion with aggressive mimicry evolved from simple web invasion. When araneophagy is coded as unordered, there is a second equally parsimonious optimization where simple web invasion is derived from web invasion with aggressive mimicry. Silk sheets

Table 5 CI and RI values for the seven gene partitions (gaps = fifth character state).

Genes	CI/RI values for most parsimonious trees			
	1	2	3	Average
COI				
CI	0.315	0.315	0.316	0.315
RI	0.299	0.298	0.301	0.299
16S				
CI	0.431	0.432	0.432	0.432
RI	0.418	0.421	0.419	0.419
ND1				
CI	0.348	0.347	0.348	0.348
RI	0.353	0.351	0.353	0.352
18S				
CI	0.638	0.638	0.638	0.638
RI	0.65	0.65	0.65	0.65
28Sh				
CI	0.525	0.525	0.524	0.525
RI	0.527	0.527	0.526	0.527
Hist3				
CI	0.385	0.387	0.385	0.386
RI	0.468	0.471	0.468	0.469
28S				
CI	0.457	0.456	0.456	0.456
RI	0.491	0.49	0.49	0.49

CI and RI values are averages. CI, consistency index; RI, retention index.

Table 6 Uncorrected pairwise distances (in percentage).

Genes	Within Spartaeinae	Across all species
COI	0.8–18.0	0.8–23.2
16S	0–30.3	0–37.3
ND1	0.3–26.2	0.3–30.8
18S	0–7.5	0–10.5
28Sh	0–5.3	0–7.4
H3	0–16.1	0–20.6
28S	0.3–28.4	0.3–31.5

were at the base of the Spartaeinae and Lyssomaninae, and large space webs have evolved twice. Eyes with high spatial acuity have evolved twice in Salticidae.

Discussion

Salticid evolution

Resolving the relationships within the speciose Salticidae is one of the main priorities in reconstructing the tree-of-life for spiders, and much progress has been made in recent years (Maddison & Hedin, 2003; Maddison & Needham, 2006). In Maddison & Hedin (2003), the focus was on the relationships within the most speciose salticid clade, Salticoida. Our study is complementary in addressing the higher level relationships between Salticoida, Spartaeinae and Lyssomaninae. Maddison & Hedin

(2003) discussed morphological evidence for the monophyly of Salticidae, which was also supported in their analyses based on molecular data. Here, we again find support for the monophyly of Salticidae (BS 77, BrS 11 and PP 100). The same applies to the Salticoida (BS 100, BrS 27 and PP 100) that were already strongly supported in previous studies (Maddison, 1996; Maddison & Hedin, 2003; Maddison & Needham, 2006). But in our study, we also present strong molecular evidence for the monophyly of Spartaeinae based on a comparatively large taxon sample (BS 85, BrS 5 and PP 100; Fig. 1). We find that similar to Maddison & Needham (2006), *Holcolaetis*, a member of the *Cocalodes* group (*Allococalodes, Cocalodes, Holcolaetis* and *Sonoita)* is sistergroup to the Spartaeinae *sensu stricto*, and should thus be included in the Spartaeinae.

However, one important issue in salticid systematics remains unsatisfactorily resolved. Ever since Blackwall (1877) first proposed a separate family for the lyssomanines, there has been uncertainty regarding its monophyly. Maddison & Needham (2006) suggested splitting the lyssomanines into two groups. Our tree similarly suggests that the Lyssomaninae is paraphyletic and forms a grade in the same clade that also includes the Spartaeinae. However, the support for this conclusion in the parsimony analyses is weak and lacking on the Bayesian tree. Overall, our tree is quite different from some previous hypotheses that considered both the Lyssomaninae and Spartaeinae to be basal grades within the Salticidae (Wanless, 1984; Maddison, 1988, 1996; Rodrigo & Jackson, 1992). In our analyses, the nuclear genes out-performed the mitochondrial genes in providing overall support (PBS). However, this is mostly due to 28S1, which provide more support than all the mitochondrial genes combined. Hence, the results show that different sections of the same gene (28S) can provide vastly different amounts of support.

Divergent evolution of predatory behaviour in Salticidae

Our study documents strongly divergent evolution of predatory behaviour in the Salticidae, where the behaviours range from cursorial hunting and building prey-catching webs to araneophagy involving web invasion and aggressive mimicry. When the multistate character 'araneophagy' is coded as ordered, araneophagy evolved once at the base of the Spartaeinae and was lost twice (in *Spartaeus* and *Paracyrba*; Fig. 2). This suggests that the ancestral spartaeine was araneophagic, but with araneophagy being expressed as hunting or ambushing spiders on tree trunks and boulders as seen in the spartaeines *Holcolaetis* and *Phaeacius* (Jackson, 1990d; Li, 2000; R. R. Jackson, unpublished data). Web invasion and aggressive mimicry evolved later within the Spartaeinae. This scenario requires that different modes of araneophagy be homologized across salticids. For exam-

ple, araneophagy by ambushing is homologized with araneophagy by invading webs and one could argue against our treatment of the character and regard 'araneophagy' alone as insufficient evidence for homology. However, we submit that even though the behaviours for prey catching are very different, the search image and preference for spiders could be the homologous trait. Alternatively, one could regard ambush predation and web invasion as discrete characters, and then araneophagy would have evolved twice in Spartaeinae, once as ambush predation and once as web invasion in the web-invasion clade (see below).

Web invasion, glue immunity and aggressive mimicry

Web invasion when mapped onto the salticid tree has evolved once in what we will refer to as the web-invasion clade (*Portia + Cyrba + Gelotia + Cocalus + Neobrettus + Paracyrba*; Fig. 2). There are two modes of web invasion, one without (*Cocalus*) and one with aggressive mimicry (*Portia, Cyrba, Gelotia* and *Neobrettus*), where the web invader uses signalling routines for controlling the behaviour of the resident spider. We find that web
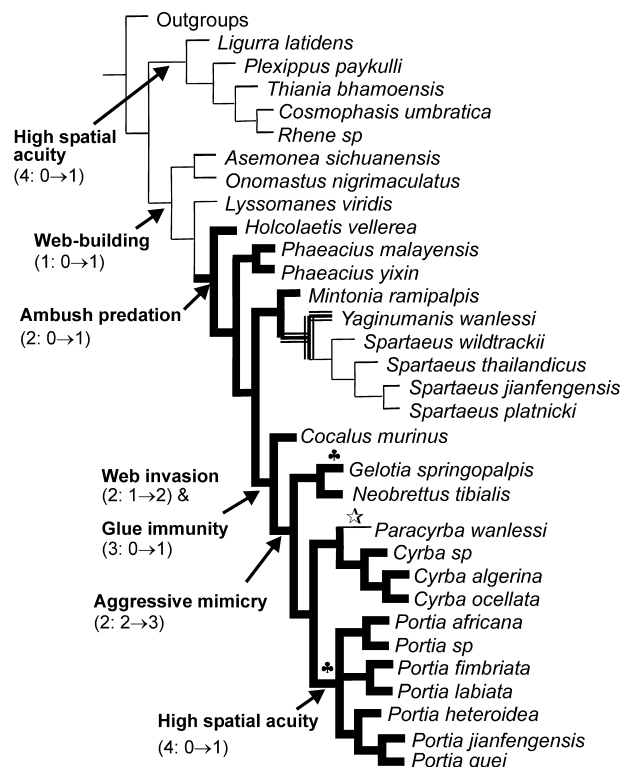

Fig. 2 Evolution of predatory behaviours in Salticidae (bold black lines = araneophagy present, thin lines = araneophagy absent, shaded lines = feeding behaviour unknown). ☆ indicates Loss of web invasion, aggressive mimicry, and araneophagy. ♣ indicates building of large space webs. Numbers in brackets refer to character and states. Character 2 is mapped additively.

invasion has been lost once in *Paracyrba* (Fig. 2), which lives in the hollow interior of decaying bamboo internodes where it preys on aquatic insects, especially mosquito larvae (Zabka & Kovac, 1996). It also has a distinctive preference for mosquitoes over other insects; i.e. it has replaced one highly specialized predation strategy with another (J. R. W. Woon and D. Li, unpublished data).

Web invasion with and without aggressive mimicry only evolved in Spartaeinae. Based on the complexity of the behaviour, one may surmise that the simple web-invasion technique used by *Cocalus* may be intermediate between araneophagy through ambushing and araneophagy using web invasion and aggressive mimicry. We indeed find this hypothesis compatible with our phylogenetic tree, and it is unambiguously supported when araneophagy is coded as an ordered character. The Spartaeinae thus constitute a good case for the stepwise, gradual evolution of a complex behaviour. Aggressive mimicry evolved via, ambush araneophagy, simple web invasion before arriving at araneophagy via web invasion with aggressive mimicry. However, when the various modes of araneophagy are coded as unordered, the simultaneous origin of web invasion and aggressive mimicry in the web-invasion clade with a subsequent loss of aggressive mimicry in *Cocalus* is equally parsimonious.

One adaptation that is needed for web invasion and that is seen in all spartaeine web invaders is glue immunity. Experiments have revealed that the majority of salticids have difficulty walking across sticky webs, but some spartaeines have evolved glue immunity (Jackson, 1992; Jackson & Pollard, 1996). For example, ambush predators like *Phaeacius* never enter webs voluntarily and get stuck when experimentally placed onto sticky webs, whereas all web-invading spartaeines never adhere to sticky or nonsticky webs (Jackson, 1990d, 1992). Hence, glue immunity to sticky webs is an autapomorphy supporting the web-invasion clade, whereas the ability to enter nonsticky webs evolved earlier in spartaeines incapable of web invasion. All previous hypotheses had suggested that the spartaeine ancestor was likely to be a wide-spectrum aggressive mimic resembling extant *Portia* (Jackson & Blest, 1982). One important implication of our results is that web invasion and aggressive mimicry are not an ancestral trait of Salticidae, and instead evolved within the Spartaeinae.

Web building

We will here only consider as webs silk devices that are considerably larger than the resident spider and are used in prey capture (Jackson, 1985a; Shear, 1994). Most salticids do not build webs (Jackson, 1979). Within Spartaeinae, large space webs have evolved twice independently in *Portia* and *Gelotia*. The rest of the lyssomanines and spartaeines, build small silk sheets (Jackson,

1990e, 1992), or in the case of *Spartaeus* (Jackson & Pollard, 1990), sheets of moderate size, which often have a role in prey capture. Our tree suggests that the ancestor of lyssomanines and spartaeines built such silk sheets (Fig. 2). However, the ancestral character state for Salticidae remains uncertain. Several of the potential sistergroups of Salticidae (e.g. Thomisidae and Oxyopidae) are polymorphic with regard to building prey-catching webs. Resolving the ancestral state for Salticidae will thus not only require identifying the sistergroup of Salticidae, but is also dependent on having additional information on the distribution of prey-catching webs within the closely related families.

Convergent evolution of eye ultrastructure

We observe a remarkable case of convergent evolution of eye ultrastructure in the Salticoida and the spartaeine, *Portia*, which have evolved divergent predatory strategies (cursorial hunting vs. aggressive mimicry). Both have independently evolved a similar layer I eye ultrastructure that provides high spatial acuity (Fig. 2). The layer I fovea of *Portia* and the Salticoida are entirely made up of regularly packed light-guiding rhabdomeres, with receptors containing only a single rhabdomere that is positioned maximally distant from the rhabdomeres of adjacent receptors (Williams & McIntyre, 1980; Blest *et al.*, 1990). This reduces ambiguity as it lowers the chance that light guided down one rhabdomere in a receptor cell gets passed into a rhabdomere in a neighbouring cell. Both Salticoida and *Portia* also have narrow receptors with small transverse profile and correspondingly less photopigment, making them less sensitive per unit length. This potential loss in sensitivity is at least partly abrogated in the salticoids and *Portia* by an increased receptor length and a reduction of the optical density of the cytoplasm surrounding the rhabdomere so that on entering the light is trapped within the rhabdomere by total internal reflection, i.e. they act as light guides. In salticoids, the cytoplasm surrounding the rhabdomeres contains no organelles other than microtubules, whereas in *Portia* even the microtubules are completely lost (Blest & Price, 1984).

Within the Salticidae, the loss of organelles and/or microtubules in the cytoplasm is unique to *Portia* and Salticoida as is the simultaneous occurrence of narrow and long receptors in a layer I fovea that entirely consists of single-rhabdomere receptors. Other spartaeines may have only one or the other feature, such as somewhat lengthened rhabdomeres (e.g. *Cyrba*) or a mixture of single and double rhabdomere receptors in the layer I fovea (e.g. *Spartaeus*). Reconstructing the precise pathway that led to high spatial acuity vision within the Spartaeinae would be very rewarding. However, it will require the systematic study of additional species and more standardized morphological descriptions.

Evolution of behaviour and eye ultrastructure

We can use our tree to test previous hypotheses with regard to the evolution of prey catching behaviour and the origin of high spatial acuity. Previously, it has been hypothesized that high spatial acuity evolved in conjunction with web invasion and aggressive mimicry, as invading spiders with the ability to exploit a sensory system independent of web dynamics would gain an adaptive advantage over the host (Jackson & Blest, 1982). However, based on our phylogenetic tree, the 'lyssomanines' are more closely related to the spartaeines than to the Salticoida, and therefore, araneophagy is derived within this clade, and not the Salticidae. Furthermore, web invasion and aggressive mimicry are derived within the Spartaeinae. Hence, araneophagy and web invasion are not ancestral salticid traits. Furthermore, the exceptionally high spatial acuity seen in *Portia* has evolved within the web-invasion clade, probably from eyes of intermediate spatial acuities like those that are observed in *Spartaeus*. It is important to remember that even salticids that do not practice aggressive mimicry may be among the most vision-dependent spiders and generally have better spatial acuity than most web-building spiders.

Conclusions

Our study was able to resolve many outstanding issues in salticid evolution. We were able to establish the monophyly of Spartaeinae including *Holcolaetis*. However, more work including a larger taxon sample will be needed to resolve 'lyssomanine' relationships. We demonstrate that similar eye ultrastructure that is capable of supporting high spatial acuity has evolved at least twice in the jumping spiders, once in the Salticoida and once within the aggressive mimicry clade in the Spartaeinae; i.e. predatory behaviour specialized for web invasion preceded the origin of sophisticated eyes and even eyes with lower spatial acuity can support such behaviour. We were also able to demonstrate that this case of convergence involves spiders with vastly divergent predatory behaviours.

Acknowledgments

References

Blackwall, J. 1877. A list of spiders captured in the Seychelle Islands by Professor E. Perceval Wright, M. D., F. L. S.; with descriptions of species supposed to be new to arachnologists. *Proc. R.I.A.* **3**: 1–22.

Blest, A.D. 1985. The retinal mosaics of the principal eyes of some neotropical jumping spiders: optical trade-offs between sizes and habitat illuminances. *J. Comp. Physiol. A* **157**: 391–404.

Blest, A.D. & Carter, M. 1987. Morphogenesis of a tiered principal retina and the evolution of jumping spiders. *Nature* **328**: 152–155.

Blest, A.D. & Price, G.D. 1984. Retinal mosaics of the principal eyes of some jumping spiders (Salticidae: Araneae): adaptations for high visual acuity. *Protoplasma* **120**: 172–184.

Blest, A.D. & Sigmund, C. 1984. Retinal mosaics of the principal eyes of two primitive jumping spiders, *Yaginumanis* and *Lyssomanes*: clues to the evolution of salticid vision. *Proc. R. Soc. Lond. B* **221**: 111–125.

Blest, A.D. & Sigmund, C. 1985. Retinal mosaics of a primitive jumping spider, *Spartaeus* (Araneae: Salticidae: Spartaeinae): a phylogenetic transition between low and high visual acuities. *Protoplasma* **125**: 129–139.

Blest, A.D., McIntyre, P. & Carter, M. 1988. A re-examination of the principal retinae of *Phidippus johnsoni* and *Plexippus validus* (Araneae: Salticidae): implications for optical modelling. *J. Comp. Physiol. A* **162**: 47–56.

Blest, A.D., O'Carroll, D.C. & Carter, M. 1990. Comparative ultrastructure of Layer I receptor mosaics in principal eyes of jumping spiders: the evolution of regular arrays of light guides. *Cell Tissue Res.* **262**: 445–460.

Bristowe, E.S. 1938. The classification of spiders. *Proc. Zool. Soc. Lond.* **108**: 285–322.

Cerveira, A.M., Jackson, R.R. & Guseinov, E.F. 2003. Stalking decisions of web-invading araneophagic jumping spiders from Australia, Azerbaijan, Israel, Kenya, Portugal, and Sri Lanka: the opportunistic smokescreen tactics of *Brettus, Cocalus, Cyrba*, and *Portia*. *N. Z. J. Zool.* **30**: 21–30.

Clark, R.J. & Jackson, R.R. 2000. Speculative hunting by an araneophagic salticid spider. *Behaviour* **137**: 1601–1612.

Coddington, J.A. & Levi, H.W. 1991. Systematics and evolution of spiders (Araneae). *Annu. Rev. Ecol. Syst.* **22**: 565–592.

Colgan, D.J., Wilson, G.D.F., Livingston, S.P., Edgecombe, G.D., Macaranas, J., Cassis, G. & Gray, M.R. 1998. Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. *Aust. J. Zool.* **46**: 419–437.

Crane, J. 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. *Zoologica* **34**: 159–215.

Drees, O. 1952. Untersuchungen über die angeborenen verhaltensweisen bei Springspinnen (Salticidae). *Z. Tierpsychol.* **9**: 169–207.

Eakin, R.M. & Brandenburger, J. 1971. Fine structure of the eyes of jumping spiders. *J. Ultrastruct. Res.* **195**: 277–297.

Edwards, G.B. & Jackson, R.R. 1993. Use of prey-specific predatory behaviour by North American jumping spiders (Araneae: Salticidae) of the genus *Phidippus*. *J. Zool. Lond.* **229**: 709–716.

Forster, L.M. 1977. A quantitative analysis of hunting behaviour in jumping spiders (Araneae: Salticidae). *N. Z. J. Zool.* **4**: 51–62.

Forster, L.M. 1982. Vision and prey-catching strategies in jumping spiders. *Am. Sci.* **70**: 165–175.

Giribet, G., Carranza, S., Riutort, M., Baguna, J. & Ribera, C. 1999. Internal phylogeny of Chilopoda (Myriapoda, Arthropoda) using complete 18S rDNA and partial 28S rDNA sequences. *Philos. Trans. R. Soc. Lond. B* **354**: 215–222.

Goloboff, P., Farris, S. & Nixon, K. 2000. *T.N.T. Tree Analysis Using New Technology (BETA)*. ver. 1.0. Published by the authors, Tucumán, Argentina.

Hallas, S.E.A. & Jackson, R.R. 1986. Prey-holding abilities of the nests and webs of jumping spiders (Araneae, Salticidae). *J. Nat. Hist.* **20**: 881–894.

Harland, D.P. & Jackson, R.R. 2004. *Portia* perceptions: the *Umwelt* of an araneophagic jumping spider. In: *Complex Worlds from Simpler Nervous Systems* (F. R. Prete, ed.). pp. 5–40. MIT Press, Cambridge, MA.

Hausdorf, B. 1999. Molecular phylogeny of araneomorph spiders. *J. Evol. Biol.* **12**: 980–985.

Higgins, D.G. & Sharp, P.M. 1988. Clustal: a package for performing multiple sequences alignment on a microcomputer. *Gene* **73**: 237–244.

Homann, H. 1928. Beträge zur Physiologie der Spinnenaugen. I. Untersuchungsmethoden, II. Das Sehvermöen der Salticiden. *Z. vergl. Physiol.* **7**: 201–268.

Huelsenbeck, J.P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.

Jackson, R.R. 1979. Nests of *Phidippus johnsoni* (Araneae, Salticidae): characteristics, pattern of occupation, and function. *J. Arachnol.* **7**: 47–58.

Jackson, R.R. 1985a. Web-building jumping spiders. *Sci. Am.* **253**: 102–115.

Jackson, R.R. 1985b. The biology of *Euryattus* sp. indet., a web-building jumping spider (Araneae, Salticidae) from Queensland: utilization of silk, predatory behaviour, and intraspecific interactions. *J. Zool. Lond.* **1**: 145–173.

Jackson, R.R. 1985c. The biology of *Simaetha*, web-building jumping spiders (Araneae, Salticidae) from Queensland: cohabitation with social spiders, utilization of webs, predatory behaviour and intraspecific interactions. *J. Zool. Lond.* **1**: 175–210.

Jackson, R.R. 1986. Web building, predatory versatility, and the evolution of the Salticidae. In: *Spiders: Webs, Behavior, and Evolution*. (W. A. Shear, ed.), pp. 232–268. Stanford University Press, Stanford, CA.

Jackson, R.R. 1990a. Predtor–prey interactions between jumping spiders (Araneae, Salticidae) and *Pholcus phalangioides* (Araneae Pholcidae). *J. Zool. Lond.* **220**: 553–559.

Jackson, R.R. 1990b. Predatory versatility and intraspecific interactions of *Cyrba algerina* and *C. ocellata*, web-invading spartaeine jumping spiders (Araneae, Salticidae). *N. Z. J. Zool.* **17**: 157–168.

Jackson, R.R. 1990c. Predatory and nesting behaviour of *Cocalus gibbosus*, a spartaeine jumping spider (Araneae: Salticidae) from Queensland. *N. Z. J. Zool.* **17**: 483–490.

Jackson, R.R. 1990d. Predatory and silk utilisation behaviour of *Gelotia* sp. indet. (Araneae: Salticidae: Spartaeinae), a web-invading aggressive mimic from Sri Lanka. *N. Z. J. Zool.* **17**: 475–482.

Jackson, R.R. 1990e. Ambush predatory behaviour of *Phaeacius malayensis* and *Phaeacius* sp. indet., spartaeine jumping spiders (Araneae: Salticidae) from tropical Asia. *N. Z. J. Zool.* **17**: 491–498.

Jackson, R.R. 1990f. Comparative study of lyssomanines jumping spiders (Araneae: Salticidae): silk use and predatory behaviour of *Asemonea*, *Goleba*, *Lyssomanes*, and *Onomastus*. *N. Z. J. Zool.* **17**: 1–6.

Jackson, R.R. 1992. Eight-legged tricksters. *BioScience* **42**: 590–598.

Jackson, R.R. 2000. Prey preferences and visual discrimination ability of *Brettus*, *Cocalus* and *Cyrba*, araneophagic jumping spiders (Araneae: Salticidae) from Australia, Kenya and Sri Lanka. *N. Z. J. Zool.* **27**: 29–39.

Jackson, R.R. & Blest, A.D. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: utilization of webs and predatory versatility. *J. Zool. Lond.* **196**: 255–293.

Jackson, R.R. & Hallas, S.E.A. 1986a. Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. schultzi*, araneophagic web-building jumping spiders (Araneae: Salticidae): utilisation of silk, predatory versatility, and intraspecific interactions. *N. Z. J. Zool.* **13**: 423–489.

Jackson, R.R. & Hallas, S.E.A. 1986b. Predatory versatility and intraspecific interactions of spartaeine jumping spiders (Araneae: Salticidae): *Brettus adonis*, *B. cingulatus*, *Cyrba algerina* and *Phaeacius* sp. indet. *N. Z. J. Zool.* **13**: 491–520.

Jackson, R.R. & Li, D. 1998. Prey preferences and visual discrimination ability of *Cyrba algerina*, an araneophagic jumping spider (Araneae: Salticidae) with primitive retinae. *Isr. J. Zool.* **44**: 227–242.

Jackson, R.R. & Li, D. 2004. One-encounter search-image formation by araneophagic spiders. *Anim. Cogn.* **7**: 247–254.

Jackson, R.R. & Macnab, A.M. 1989. Display, mating and predatory behaviour of the jumping spider *Plexippus paykulli*, (Araneae, Salticidae). *N. Z. J. Zool.* **16**: 151–168.

Jackson, R.R. & Pollard, S.D. 1990. Web-building and predatory behaviour of *Spartaeus spinimanus* and *Spartaeus thailandicus*, primitive jumping spiders (Araneae, Salticidae) from Southeast Asia. *J. Zool. Lond.* **220**: 561–567.

Jackson, R.R. & Pollard, S.D. 1996. Predatory behaviour of jumping spiders. *Annu. Rev. Entomol.* **41**: 287–308.

Jackson, R.R. & Wilcox, R.S. 1998. Spider-eating spiders. *Am. Sci.* **86**: 350–357.

Jackson, R.R., Li, D., Barrion, A.T. & Edwards, G.B. 1998. Prey-capture techniques and prey preferences of nine species of ant-eating jumping spiders (Araneae: Salticidae) from the Philippines. *N. Z. J. Zool.* **25**: 249–272.

Jackson, R.R., Pollard, S.D. & Cerveira, A.M. 2002. Opportunistic use of cognitive smokescreens by araneophagic jumping spiders. *Anim. Cogn.* **5**: 147–157.

Land, M.F. 1969. Structure of retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *J. Exp. Biol.* **51**: 443–470.

Land, M.F. 1971. Orientation by jumping spiders in the absence of visual feedback. *J. Exp. Biol.* **54**: 119–139.

Land, M.F. 1985. Fields of view of the eyes of primitive jumping spiders. *J. Exp. Biol.* **119**: 381–384.

Land, M.F. & Nilsson, D.E. 2002. *Animal Eyes*. Oxford University Press, Oxford.

Lehtinen, P.T. 1967. Classification of the Cribellate spiders and some allied families, with notes on the evolution of suborder Araneomorpha. *Ann. Zool. Fenn.* **4**: 199–468.

Lehtinen, P.T. 1975. Notes on the phylogenetic classification of Araneae. In: Proceedings of the 6th International Arachnological Congress, Amsterdam 1974, pp. 27–34. Nederlandse Entomologische, Vereniging.

Li, D. 2000. Prey preference of *Phaeacius malayensis*, a spartaeine jumping spider (Araneae: Salticidae) from Singapore. *Can. J. Zool.* **78**: 2218–2226.

Li, D. & Jackson, R.R. 1996a. Prey-specific capture behaviour and prey preferences of myrmicophagic and araneophagic jumping spiders (Araneae: Salticidae). *Rev. Suisse Zool. hors serie* 423–436.

Li, D. & Jackson, R.R. 1996b. Prey preferences of *Portia fimbriata*, an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland. *J. Insect Behav.* **9**: 613–642.

Li, D., Jackson, R.R. & Barrion, A. 1997. Prey preferences of *Portia africana*, *P. labiata* and *P. schultzi*, araneophagic web-building jumping spiders (Araneae: Salticidae) from Kenya, the Philippines, and Sri Lanka. *N. Z. J. Zool.* **24**: 333–349.

Lopez, A. 1986. Construction de toiles en 'oile de bateau par une araignee salticid languedocine. *Bull. Soc. Arch. Beziers (ser. 6)* **2**: 65–68.

Maddison, W.P. 1988. *A revision of jumping spider species groups formerly placed in the genus Metaphidippus, with a discussion of salticid phylogeny (Araneae)*. Unpublished PhD thesis. Harvard University.

Maddison, W.P. 1996. *Pelegrina* Franganillo and other jumping spiders formerly placed in genus *Metaphidippus* (Araneae: Salticidae). *Bul. Mus. Comp. Zool.* **154**: 215–368.

Maddison, W.P. & Hedin, M.C. 2003. Jumping spider phylogeny (Araneae: Salticidae). *Invert Sys.* **17**: 529–549.

Maddison, D.R. & Maddison, W.P. 2003. *MacClade 4*, version 4.06. Sinauer, Sunderland, MA.

Maddison, W.P. & Needham, K.M. 2006. Lapsiines and hisponines as phylogenetically basal salticid spiders (Araneae: Salticidae). *Zootaxa* **1255**: 37–55.

Masta, S.E. 2000. Mitochondrial sequence evolution in spiders: intraspecific variation in tRNAs lacking the T psi C arm. *Mol. Biol. Evol.* **17**: 1091–1100.

Nylander, J.A.A. 2004. *MrModeltest v2*. Program Distributed by the Author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.

Ono, H. 1987. A new Japanese castianeirine genus (Araneae, Clubionidae) with presumptive prototype of salticoid eyes. *Bull. Nat. Sci. Mum. A (Zool.)* **13**: 13–19.

Petrunkevitch, A. 1933. An inquiry into the natural classification of spiders, based on a study of their internal anatomy. *Trans. Connect. Acad. Arts Sci.* **31**: 303–389.

Platnick, N.I. 2006. *The World Spider Catalogue*, version 6.5 [www document]. URL http://research.amnh.org/entomology/spiders/catalog/index.html.

Richman, D.B. & Jackson, R.R. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). *Bull. Br. Arachnol. Soc.* **9**: 33–37.

Rodrigo, A.G. & Jackson, R.R. 1992. Four jumping spider genera of the Cocalodes-group are monophyletic with genera of the Spartaeinae (Araneae: Salticidae). *N. Z. Nat. Sci.* **19**: 61–67.

Shajahan, R.M. 1995. Lower incubation temperature increases yield of insect genomic DNA. *BioTechniques* **19**: 332–334.

Shear, W.A. 1994. Untangling the evolution of the web. *Am. Sci.* **82**: 256–266.

Simon, E. 1901. *Hisoire Naturelle des Araignées*. Deuxième edition. Tome 2, fasc 3. Encyclopédie Roret, Paris. pp. 381–668.

Sorenson, M.D. 1999. *TreeRot*. Boston University, Boston, MA.

Swofford, D.L. 2002. *PAUP* Phylogenetic Analysis Using Parsimony (*and Other Methods)* Version 4.0b10. Sinauer Associates, Sunderland, MA.

Tarsitano, M.S. & Jackson, R.R. 1997. Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey. *Anim. Behav.* **53**: 257–266.

Wanless, F.R. 1980a. A revision of the spider genera *Asemonea* and *Pandisus* (Araneae: Salticidae). *Bull. Br. Nat. Hist. (Zool.)* **39**: 213–257.

Wanless, F.R. 1980b. A revision of the spider genus *Onomastus* (Araneae, Salticidae). *Bull. Br. Nat. Hist. (Zool.)* **39**: 179–188.

Wanless, F.R. 1982. A revision of the spider genus *Cocalodes* with a description of a new related genus (Araneae: Salticidae). *Bull. Br. Mus. Nat. Hist. (Zool.)* **42**: 263–298.

Wanless, F.R. 1984. A review of the spider subfamily Spartaeinae nom. N. (Araneae: Salticidae) with descriptions of six new genera. *Bull. Br. Nat. Hist. (Zool.)* **46**: 135–205.

Wanless, F.R. 1985. A revision of the spider genus *Holcolaetis* and *Sonoita* (Araneae: Salticidae). *Bull. Br. Nat. Hist. (Zool.)* **48**: 249–278.

Wanless, F.R. 1987. Notes on spiders of the family Salticidae. 1. The genera *Spartaeus*, *Mintonia* and *Taraxella*. *Bull. Br. Nat. Hist. (Zool.)* **52**: 107–137.

Whiting, M.F., Carpenter, J.C., Wheeler, Q.D. & Wheeler, W.C. 1997. The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. *Syst. Biol.* **46**: 1–68.

Wilcox, R.S., Jackson, R.R. & Gentile, K. 1996. Spider web smokescreens: spider trickster uses background noise to mask stalking movements. *Anim. Behav.* **51**: 313–326.

Williams, D.S. & McIntyre, P. 1980. The principal eyes of a jumping spider have a telephoto component. *Nature* **288**: 578–580.

Xia, X. & Xie, Z. 2001. DAMBE: software package for data analysis in molecular biology and evolution. *Heredity* **92**: 371–373.

Zabka, M. & Kovac, D. 1996. *Paracyrba wanlessi*: a new genus and species of Spartaeinae from Peninsular Malaysia, with notes on its biology (Arachnida: Araneae: Salticidae). *Senck. Biol.* **76**: 153–161.

Zhang, J.X. & Li, D. 2005. Four new and one newly recorded species of the jumping spiders (Araneae: Salticidae: Lyssomaninae & Spartaeinae) from (sub)tropical China. *Raffles Bull. Zool.* **53**: 221–229.