

Jumping spider phylogeny (Araneae: Salticidae)

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Abstract. A phylogenetic analysis of five sequenced genes (*28S*, *16S*, *EF1- α* , *COI*, *ND1*) from 81 genera of jumping spiders (Salticidae) and five outgroups supports the monophyly of the Dendryphantinae and Euophryinae and refines the concepts of the Plexippinae and Pelleninae. The clade that excludes lyssomanines and spartaeines and contains the bulk of salticid species is formally named as the Salticoida. The previously proposed clade delimited by an embolus articulated and separated from the tegulum by a developed distal hematodocha (as opposed to fused immovably to the tegulum) is rejected, suggesting the ‘free embolus’ evolved independently several times. Three major clades are discovered, the Marpissoida (including Dendryphantinae, Marpissinae and smaller groups such as synagelines), the Plexippoida (plexippines plus pellenines) and the Amycoida (including Amycinae, Sitticinae, Hyetusseae, Hurieae, Synemosyninae). The amycoids form a large neotropical radiation from which only a single known group (*Sitticus* and *Attulus*) has reached the Old World. The marpissoids also constitute a major New World group with relatively few species in the Old World. In contrast, the Plexippoida is predominantly an Old World group (except for the spectacular radiation of *Habronattus* in North America), as is the Heliophaninae. These results suggest that much of salticid diversification occurred after the separation of the continents of the Old World and New World.

Additional keywords: arachnids, continental biogeography, molecular systematics.

Introduction

The several thousand species of jumping spiders (family Salticidae) represent diverse body forms, behaviours and ecological relationships. An understanding of their phylogenetic relationships would not only allow us to form an adequate classification of genera and subfamilies, facilitating efforts to discover new species and distinguish among them, but would also open the group to phylogenetically-based studies of evolutionary processes. For instance, comparative studies of the evolution of salticid vision (e.g. Blest 1983, 1985; Blest *et al.* 1990), predatory behavior (Jackson and Pollard 1996) and chromosomes (e.g. Maddison 1982) all require a phylogenetic context for the interpretation of repeated evolutionary patterns.

Understanding phylogenetic relationships within this large clade has long been considered problematical. Eugène Simon, after discussing the difficulties of dividing salticids into genera, comments ‘The classification of genera is no less difficult; to give an idea of their interconnections, I place them in groups, which I refer to three sections, perhaps somewhat artificial, based on the armature of the lower margin of the

chelicerae...’ (1901: 387; our translation). His modesty about the classification’s artificiality is to some extent deserved, but the classification was nonetheless pathbreaking. Many of Simon’s groupings show remarkable insights into the family that we are only now rediscovering. F. O. Pickard-Cambridge (1901) and Petrunkevitch (1928) proposed alternatives to Simon’s classification, but neither was substantially closer to our present view. Prószyński’s (1976) partial classification represented another major advance, establishing the categorization of salticid male genitalia into major forms (for example, the ‘euophryine’ palp with a terminal, spiral embolus) and clarifying many placements. However, the general form of the palp is too simple to provide sufficient information for a detailed classification and has probably been subject to occasional homoplasy. Subsequent progress in delimiting major groups has been made by Wanless (1984), Rodrigo and Jackson (1992) and Maddison (1987, 1988, 1996), but much of the phylogenetic structure of this large family remains unresolved.

We here extend the work of Hedin and Maddison (2001a), who examined the utility of various genes in studying

phylogeny of the salticid subfamily Dendryphantinae, to consider the entire family. Our goals are to use molecular data to test some previously published hypotheses about salticid phylogeny, in order to arrive at an outline of the phylogenetic structure of the family. Although our sampling includes 81 salticid genera scattered broadly across the family, the sampling is biased toward New World taxa and much of the family's diversity (>500 genera described) is not included in this study. For this reason, our results are necessarily preliminary.

Authors of most genera and species discussed are presented in the Appendices.

Results from previous studies

There has been little consensus on what group of spiders is sister to the salticids. Suggested allies include the oxyopids (Simon 1901; Lehtinen 1975), thomisids (Simon 1901; Lehtinen 1967), clubionoids (Petrunkevitch 1933: 355; Bristowe 1938; Ono 1987), zodarioids (Lehtinen 1967) and web-building spiders (Blest and Carter 1987), but to date none of these suggestions has been backed by much evidence. Coddington and Levi (1991) tentatively place clubionids and anyphaenids as the nearest relatives of salticids. If there is any consolation to this confusion regarding the sister-group to the salticids, it is that we can with reasonable certainty demonstrate the monophyly of the family and some of the basal divisions within it, thus lessening the need to know the sister-group exactly for purposes of outgroup analysis within the family.

Salticid monophyly is supported by the peculiar eye structure yielding excellent vision and corresponding vision-based behavior. In particular, the anterior median eyes are enlarged and tube shaped, with the retina strip-shaped and tiered (Scheuring 1914; Land 1969; Blest and Sigmund 1984). Each of these features may be cited as a synapomorphy uniting the salticids. The fully developed system of eye muscles described by Scheuring (1914) appears unique to salticids, although eye muscles are inadequately studied among salticids and spiders as a whole. The complex branching of intestinal diverticula over the brain (Millot 1931) may also delimit the family, though there have not been studies of the diverticula of lyssomanines, whose narrower ocular area may not accommodate complex diverticula.

Previous work suggests that salticid phylogeny began with three major lineages (Wanless 1984; Maddison 1988, 1996): the lyssomanines (Wanless 1980), the spartaeines (Wanless 1984) and a large group consisting of the remaining salticids. The former two groups are sometimes considered the 'primitive' salticids, the last group the 'advanced' salticids. Such designations, however, typically reflect a focus biased to the familiar synapomorphies of speciose groups, rather than any evidence for a difference in total number of evolved apomorphies. Indeed, the spartaeines include many remarkable species (Jackson and

Blest 1982; Jackson and Hallas 1986; Jackson 1990) and there is reasonably good evidence for their monophyly (Wanless 1984; Rodrigo and Jackson 1992). Whether the lyssomanines are monophyletic is not clear (see Wanless 1980). The vast majority of salticid species fall into the third group, referred to as the Salticine Division by Maddison (1996). The Salticine Division is here recognised formally as the new taxon **Salticoida** (of unspecified rank). Morphological characters delimiting this clade will be considered in the Discussion.

More than 90% of described salticid species are members of the Salticoida. Previous work on relationships within the salticoids has resulted in contradictory proposals of subfamilies or subfamily-level groups (e.g. Simon 1901, 1903; Pickard-Cambridge 1901; Petrunkevitch 1928; Prószyński 1976; Maddison 1987, 1996), some of which are proposed with little supporting evidence. It is not our intention here to review comprehensively all published suggestions about salticoid phylogeny, but rather to concentrate on those most relevant to our data. Among the proposed groups whose monophyly will be examined here are the Marpissinae (Barnes 1958), Dendryphantinae (Maddison 1996), Heliophaninae (Prószyński 1976; Maddison 1987), Plexippinae (Maddison 1988, 1996), Euophryinae (Prószyński 1976), Pelleninae (Prószyński 1976) and the free-embolus group (Maddison 1988, 1996). We will also discuss the biogeographical implications of our results, in particular the divisions between the New and Old World faunas.

Materials and methods

Although the data formally analysed here are molecular, we will present informally some supporting morphological synapomorphies. Terms for morphological features in general follow those of Maddison (1996).

We name several new higher-level taxa (e.g. Salticoida, Amycoida). Except where specified otherwise, these are to be treated as without formal rank. We leave these taxa unranked to avoid provoking adjustments in the rank of many existing taxa (e.g. subfamilies to tribes) while salticid classification is still in a state of considerable flux.

Taxon sampling

We sampled 89 species for DNA sequencing (Appendix 1), including the five outgroups. The 84 salticid species represent 81 recognised salticid genera, of which about 60% are genera found primarily in the New World. These genera were selected to be broadly scattered throughout the salticids according to our previous notions of salticid phylogeny. New World diversity appears to be fairly well represented, but some major groups particularly in the Old World are absent or inadequately sampled. Notably absent from our sample are hispanines, which are well represented in Madagascar and the Baltic amber fauna (Wanless 1981; Prószyński and Zabka 1983), and the astiines of Australasia (Wanless 1988).

Three unidentified salticids from Ecuador, Costa Rica and the Philippines were included. That from Ecuador has a body form somewhat like *Tutelina* Simon, but males have long jaws somewhat reminiscent of *Myrmarachne* and a *Sitticus*-like palpus. That from Costa Rica resembles a *Platycryptus*, but is less hirsute. That from the Philippines is a female, elongate and yellow, resembling an *Epeus* in body form, but pluridentate.

Sequencing

Protocols used for specimen preservation, DNA extraction, amplification and sequencing of *28S*, *16S*, *ND1* (nicotinamide adenine dinucleotide dehydrogenase subunit 1) and *COI* (cytochrome oxidase 1) genes and entry of data to computer files are described by Hedin and Maddison (2001a). Protocols for the *EF1- α* (elongation factor 1- α) gene follow those of Hedin and Maddison (2001b).

Phylogenetic analysis

Sequences were aligned for phylogenetic analysis as described by Hedin and Maddison (2001a). Protein-coding data, containing no internal length variation, were aligned manually. *16S* and *28S* data were aligned using ClustalX (Thompson *et al.* 1997) to produce alternative alignments under different gap opening/gap extension costs. We then chose an alignment whose preliminary phylogenetic analysis best matched that produced by an elision matrix (Wheeler *et al.* 1995) of all the alignments (see Hedin and Maddison 2001a).

Both parsimony and maximum likelihood were used as criteria for reconstructing phylogenetic trees. Most parsimonious trees were sought using PAUP* versions 4.0b8 and 4.0b10 (Swofford 2001, 2002) on Macintosh G4 or Dell Windows Me computers and NONA 2.0 (Goloboff 1999) on a Dell Windows Me computer. Maximum likelihood trees were sought with PAUP*. Our descriptions of methods and estimated parameters will use terms and acronyms (e.g. MAXTREES, TBR, SPR, rmatrix) used in the command terminology of PAUP* (Swofford 2001), except where discussing NONA explicitly.

Data from different genes or gene regions (mitochondrial *16S*, *ND1*, *COI*; nuclear *28S*, *EF1- α*) were analysed separately. In addition, we performed parsimony analyses combining different gene regions as follows: All gene regions (89 taxa \times 3411 sites); all mitochondrial regions (*COI*, *ND1*, *16S*; 89 taxa \times 2085 sites); mitochondrial protein coding genes (*COI+ND1*, 89 taxa \times 1440 sites). The last combination, mitochondrial protein coding genes, was also analysed using likelihood.

With multiple gene regions and multiple analytical methods available, we faced the task of choosing how to use the data to achieve a single interpretation. A single analysis combining data from all genes has the advantage of being based on more data than any other single analysis and for this reason we performed the all-genes parsimony analysis. To perform a parallel analysis with likelihood is technically difficult at present, in part because of the computational burden of large likelihood analyses, in part because the programs available did not allow different gene regions to use different models of evolution, as needed for genes of such different functional and genomic categories (coding, non-coding; mitochondrial, nuclear). Thus, we performed separate likelihood analyses for the different gene regions. Performing separate analyses offers additional insights, for it allows us to determine how robust our conclusions are to variation in assumptions and the class of gene. Insofar as different genes are expected to have different evolutionary dynamics and to be more likely evolving independently than sites in the same gene, we consider independent support for a clade from different genes and analytical methods to add considerably to our confidence in the results. We distilled these various results into a single summary tree (see Fig. 6) subjectively, because quantitative consensus methods do not yet consider sufficient information about the provenance of each tree, such as whether they are deduced by separate analytical methods and independent gene regions.

Parsimony

The unordered states assumption (Fitch 1971) was used. Gaps were treated as missing data. Sites were weighted equally. For most PAUP* runs, the initial search consisted of 20 000 random addition sequence replicates, each saving at most five trees in order to narrow the search (D. Maddison 1991), using tree bisection reconnection (TBR) branch

swapping (Swofford 2001). Only most parsimonious trees were saved. These were used as input trees in a second round of TBR branch swapping, not constrained except by MAXTREES of 100 000. For the data set combining all genes, two additional parsimony searches were performed. First, a PAUP* heuristic search was performed as above, except that at most 500 trees were saved in each of 2000 random addition sequence replicates. Second, a NONA search was performed on the combined data by the command 'nix -10 50 20'. PAUP* branch and bound analysis was used for the *EF1- α* data. Replicability of clades was assessed by a PAUP* non-parametric bootstrap analysis (Felsenstein 1985) with 100 to 500 replicates. In each replicate, 20 random addition sequence replicates obtained starting trees for TBR branch swapping, holding no more than 1000 trees.

Likelihood

Likelihood analyses were performed for each of the individual gene regions and for the combined mitochondrial protein-coding genes (*COI* and *ND1*), which might be expected to behave according to similar models.

Because of the computational difficulty of simultaneously estimating parameters of the model of evolution and the tree, we used a successive-approximations approach as a heuristic approximation for a simultaneous estimation. First, a neighbour joining tree was obtained under the assumptions of HKY85 (Hasegawa *et al.* 1995) distances, empirical base frequencies and gamma-distributed rate variation. This tree was used to estimate the 6 parameters of a general time-reversible (GTR) model using likelihood and this model was used to obtain a second, refined neighbour joining tree using maximum likelihood (ML) distances. This tree was used to assess likelihood of various parameter combinations, from simpler to more complex rate matrix models and from simpler to more complex rate variation models. This was done to choose a model of evolution for use in the full likelihood tree search. Included among the rate matrix models examined was a five-parameter rate matrix model (rclass = (a b a c d e)), because preliminary analyses suggested that this model may fit nearly as well as the full six-parameter model for several data sets. The model chosen corresponded to the simplest model whose log likelihood was not significantly different than that of the most complex model (Goldman 1993; Sullivan and Swofford 1997). In practice, the decision was unequivocal: in all cases the chosen model was better than the next best by at least 14 ln likelihood units (e.g. $P = 0.05$ for χ^2 , 1 d.f. is at 3.84). In three of the analyses (*EF1- α* , *ND1*, *COI+ND1*), the ln likelihood of the five-parameter rate matrix model was within 0.04 to 1.3 units of the most complex model and was thus acceptable.

The model chosen was then used in a tree search. An initial tree was obtained by random addition sequence, then followed by subtree pruning regrafting (SPR) branch swapping, followed usually by TBR branch swapping. Because of their slow speed, the likelihood searches were usually not completed. To obtain the most from this imperfect situation, we used a flexible strategy involving different numbers of separate searches and rearrangements for the different datasets, with decisions based on whether a search appeared to be stagnating or improving likelihood quickly. Details for each search are given in results.

Bayesian analysis

For the *28S* gene, a Bayesian analysis was performed using MrBayes 2.01 (Huelsenbeck and Ronquist 2001). The same six-parameter GTR rate matrix and gamma shape parameter used in the *28S* likelihood analysis were employed for the MrBayes analysis. Three separate analyses were performed, each using the parameter command 'mcmc ngen = 100000 samplefreq = 100 nchains = 4'. For each, the posterior probabilities reached a plateau after about 15 000 generations and therefore trees sampled during the last 80 000 generations were examined. Using the 2403 trees examined (3 runs \times 801 sampled from

last 80000 generations), a majority rules consensus tree was made using PAUP* to count the frequency of appearance of various clades.

Results

Sequence data from four gene regions, totalling approximately 2.8 kb per taxon, were gathered for most of the 89 sample taxa (Appendix 1). *EF1- α* data were generated for 17 taxa. Some *ND1*, *COI*, *16S* and tRNA sequences are incomplete at either the 5' or 3' ends in a small number of taxa (Appendix 1); these regions were coded as having missing data for these taxa only. All sequences have been deposited in GenBank (see Appendix 1) and are available as NEXUS files at <http://salticidae.org/papers/MaddisonHedinSalticidae03/> (accessed 14 July 2003) and as Accessory Material on the journal's website.

28S

28S data were gathered for 85 taxa. The alignment chosen by the elision comparison method (Hedin and Maddison 2001a) had gap opening/extension costs of 24/6. The aligned matrix included 826 sites.

Figure 1 summarises results from phylogenetic analyses of 28S data. The parsimony tree search found 572 trees of 4330 steps; bootstrap percentages shown in Fig. 1). For likelihood, the six-parameter rate matrix with gamma rate variation and a proportion of invariant sites was chosen (rmatrix = (0.75424029 1.7835781 1.6703748 0.45466362 3.6527885) rates = gamma shape = 0.595039 pinvar = 0.139963; Table 1). The search began with 15 random addition sequence searches with SPR swapping and a rearrangement limit of 1000. The five replicates yielding highest likelihoods were selected for further swapping (SPR, REARRLIMIT = 10000), which failed to improve likelihoods. The three best replicates resulting were selected for further swapping (TBR, REARRLIMIT = 100000), which also failed to improve likelihoods. 500000 additional rearrangements on trees from the best replicate likewise failed to improve likelihood. The $-\ln$ likelihoods of the trees from the three replicates were 19130.259 (five trees), 19131.262 (two trees), 19132.105 (five trees). We examined both the consensus of the five best trees and of the 10 trees from the three best replicates. The Bayesian analysis and likelihood supported similar clades (see Fig. 1).

EF1- α

Data were gathered for 17 taxa. Fig. 2 shows the results of phylogenetic analyses. The branch and bound parsimony tree search found a single tree of 347 steps. For likelihood, the estimated model was a five-parameter rate matrix with codon position specific rates (rclass = (a b a c d e) rmatrix = (4.5996868 14.529896 4.5996868 2.5439187 17.950776) rates = 0.197222:pos1, 0.086039:pos2, 2.716739:pos3; Table 1). 100 random addition sequence likelihood searches

with SPR swapping were performed (without rearrangement limit). A single tree of $-\ln$ likelihood 2260.428 was found. The likelihood and parsimony trees differed in their placements of *Chalcotropis*, *Frigga* and *Amycus* (likelihood grouped these as a clade; whereas parsimony placed these as sisters to plexippoids, marpissoids and plexippoids + marpissoids combined respectively).

16S

Data for *16S* were gathered for 85 taxa. The alignment chosen via the elision comparison method (Hedin and Maddison 2001a) had gap opening/extension costs of 24/4. The aligned matrix included 645 sites.

Table 1. $-\ln$ likelihoods under various models of molecular evolution using initial candidate trees for each of the gene regions analysed by likelihood

Likelihood of model chosen for subsequent analyses shown in bold			
	Substitution model	Equal rates	Variable rates
			<i>Gamma</i>
28S	Jukes–Cantor	22495.82325	19775.35787
	F81	22646.98416	19907.11530
	HKY85	22205.45925	19374.86493
	a b a c d e		19238.63491
	GTR	22004.39982	19212.63622
			<i>Codon position</i>
EF1- α	Jukes–Cantor	2642.26013	2386.79003
	F81	2633.67072	2373.39570
	HKY85	2550.91959	2277.74666
	a b a c d e		2263.13324
	GTR	2527.48034	2263.09636
			<i>Gamma</i>
16S	Jukes–Cantor	23738.32208	20834.11748
	F81	22818.89384	19504.52468
	HKY85	22800.15478	19380.19793
	a b a c d e		18906.56698
	GTR	21936.17715	18850.88056
			<i>Codon position</i>
COI	Jukes–Cantor	33651.58096	29895.87313
	F81	33233.46274	29023.08211
	HKY85	32898.76392	28392.66792
	a b a c d e		27964.43485
	GTR	31479.51637	27689.13978
			<i>Gamma</i>
ND1	Jukes–Cantor	17909.92530	16835.74576
	F81	17697.30417	16458.55721
	HKY85	17409.98813	16023.00998
	a b a c d e		15617.85475
	GTR	16918.71647	15617.35422
			<i>Codon position</i>
COI+ND1	Jukes–Cantor	16321.74395	15379.52548
	F81	16128.99319	15036.58605
	HKY85	15869.32183	14645.56977
	a b a c d e		14269.37893
	GTR	15421.59715	14268.14248

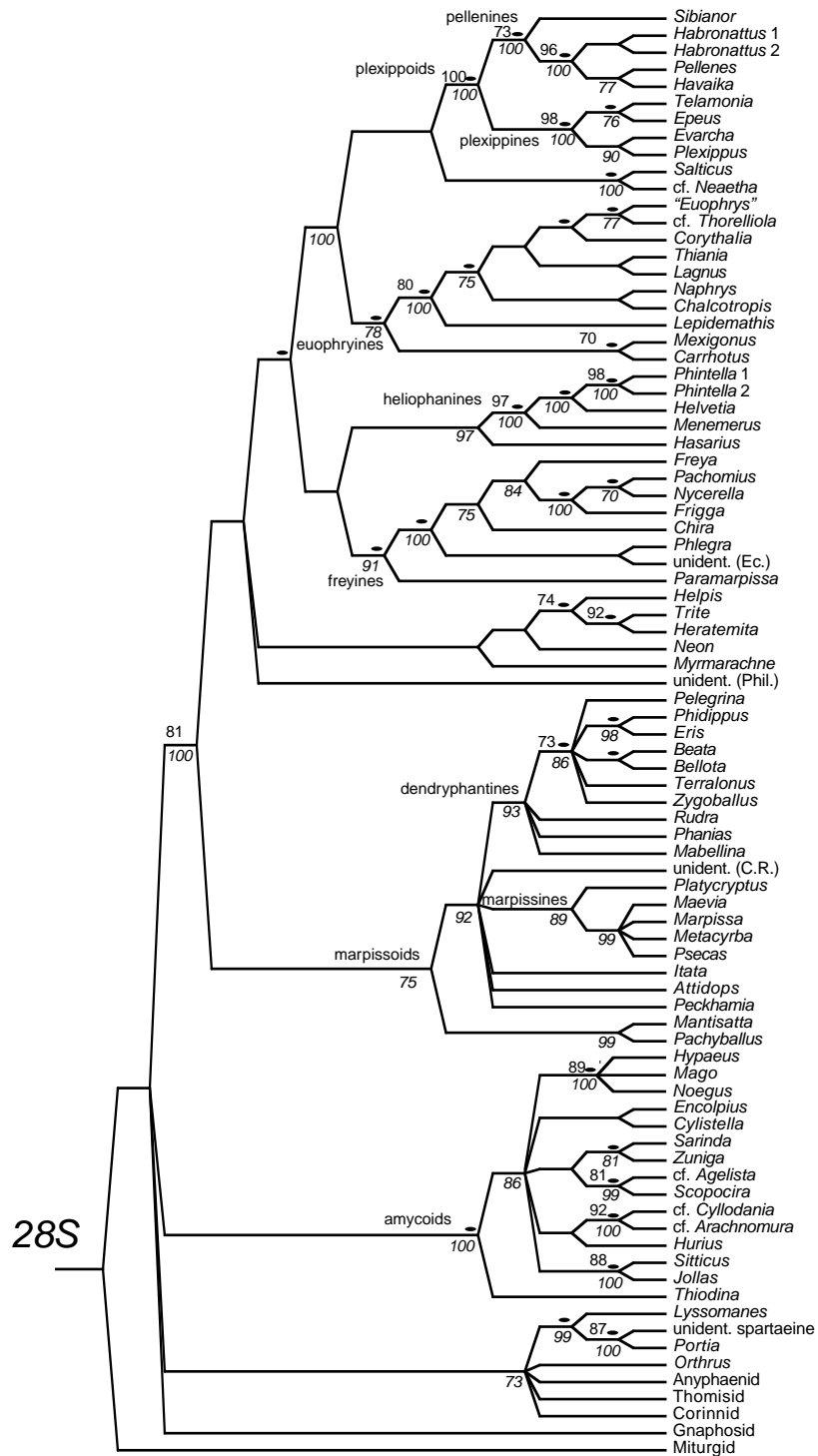


Fig. 1. Phylogeny from 28S: Consensus tree of 10 trees from three best MLE replicates after 4 rounds of swapping. All resolved clades also appear in consensus of five trees from best MLE replicate after five rounds of swapping. Spots show clades in strict consensus of parsimony analysis (572 trees of 4330 steps). Numbers above lines show % of 100 parsimony bootstrap replicates with clade if $\geq 70\%$. Italicised numbers below lines show % trees with clade from Bayesian MCMC search.

Figure 3 shows the results of phylogenetic analyses for *I6S*. The parsimony search found 12 trees of 4750 steps. The six-parameter rate matrix with gamma rate variation and a proportion of invariant sites were chosen for likelihood (rmatrix = (7.6107667 10.726309 17.833743 0.32636122 37.242308) rates = 0.689798:pos1, 0.192537:pos2, 2.117665:pos3; Table 1). The search began with eight random addition sequence searches (SPR, REARRLIMIT = 2000), from which the three best replicates ($-\ln$ likelihoods of 18712.620, 18716.257, 18716.766) were chosen for further swapping. An additional 100000 TBR rearrangements improved the $-\ln$ likelihoods of the three replicates to 18690.557, 18691.267 and 18676.371 respectively. The best replicate ($-\ln L = 18676.371$) with three equally likely trees was used to represent likelihood results.

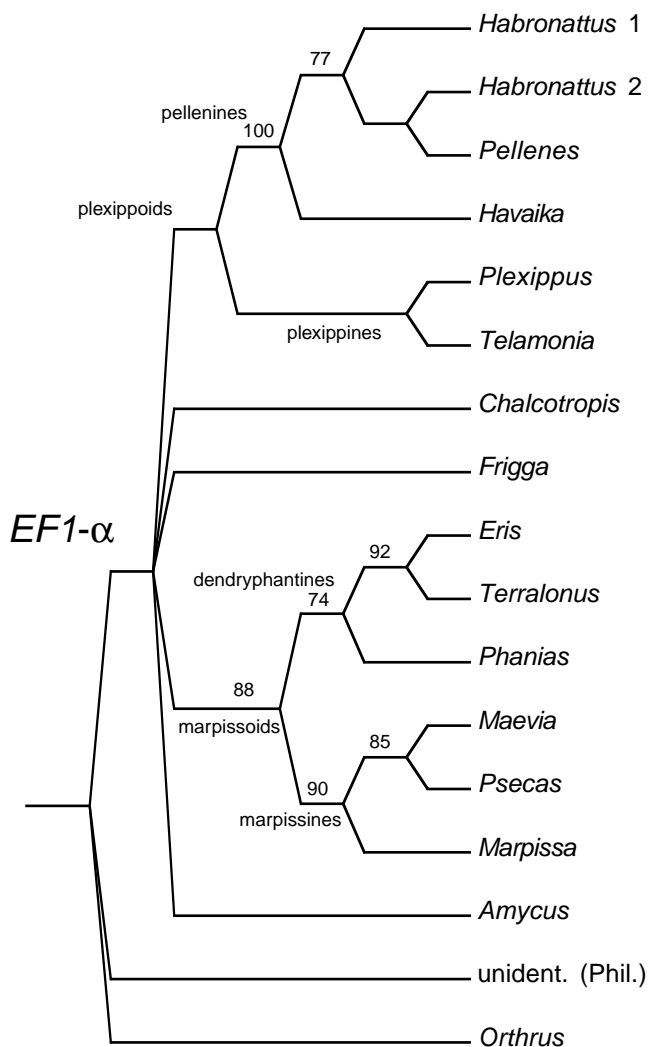


Fig. 2. Phylogeny from *EF1- α* : Strict consensus of results from branch and bound parsimony and best tree from likelihood searches. Percentage of 100 bootstrap replicates showing clade with parsimony analysis indicated if $\geq 70\%$. Tree rooted at *Orthrus* based on results of other analyses.

COI

Data were gathered for 82 taxa, yielding a matrix with 1047 sites. Results of phylogenetic analyses are indicated in Figs 4 and 6. Parsimony searches were not performed using *COI* data only. The six-parameter rate matrix with codon position specific rates was chosen for likelihood (rmatrix = (0.19211957 9.7879133 3.5426362 1.589561 3.2996761) rates = 0.317739:pos1, 0.117411:pos2, 2.564850:pos3; Table 1). The search began with 50 random addition sequence searches (SPR, REARRLIMIT = 1000), from which the five best replicates were chosen for further swapping (TBR, REARRLIMIT = 500000). The second round, in which each replicate completed swapping within the rearrangement limit, resulted in $-\ln$ likelihoods of 27337.360, 27325.858, 27321.239, 27359.645 and 27343.543 for the five replicates. The single tree from the replicate of highest likelihood was used for the data summaries shown in Figs 4, 6.

ND1

Data were gathered for 85 taxa, yielding a matrix with 393 sites. Parsimony searches were not performed using *ND1* separately. The five-parameter rate matrix with codon position specific rates was chosen for likelihood (Table 1).

The search began with 30 random addition sequence searches (SPR, REARRLIMIT = 5000), from which the five best replicates ($-\ln$ likelihoods of 15419.196, 15422.860, 15424.852, 15433.761, 15433.916) were chosen for further swapping. A second round of swapping (SPR, REARRLIMIT = 10000) resulted in improvement of likelihood scores (respectively, $-\ln L$ of 15400.935, 15409.262, 15421.640, 15426.196, 15428.959), as did a third round (SPR, REARRLIMIT = 50000; $-\ln L$ of 15379.493, 15363.364, 15386.207, 15393.852, 15399.925). SPR swapping was carried to completion on the best replicate but resulted in no improvement of likelihood (15363.364); 1 tree resulted and was used to represent the likelihood results.

Combined COI and ND1 analyses

These protein coding regions of the mitochondria were combined in several parsimony and likelihood analyses (Fig. 4). The parsimony analysis on the nucleotide data resulted in a single tree of 10393 steps. The concatenated *COI+ND1* matrices were translated to amino acid sequence using the *Drosophila* mtDNA translation code in MacClade 4 (Maddison and Maddison 2000). Parsimony analysis of the amino acid data resulted in 6720 trees of 1966 steps. For likelihood, the model of evolution was estimated on that subset of the taxa for which sequences of both genes was available; however, searches were conducted using the full set of taxa represented by either *COI* or *ND1* sequences. The inferred model was the five-parameter rate matrix with

codon position specific site variation (rmatrix = (4.003657 3.6774476 4.003657 2.2962842 18.57292) rates = 0.689798:pos1, 0.192537:pos2, 2.117665:pos3; Table 1). The search began with 30 random addition sequence

searches (SPR, REARRLIMIT = 5000), followed by continued swapping on the four best replicates (-ln likelihoods of 46920.525, 46923.979, 46928.171, 46933.004). Four additional rounds of swapping (SPR,

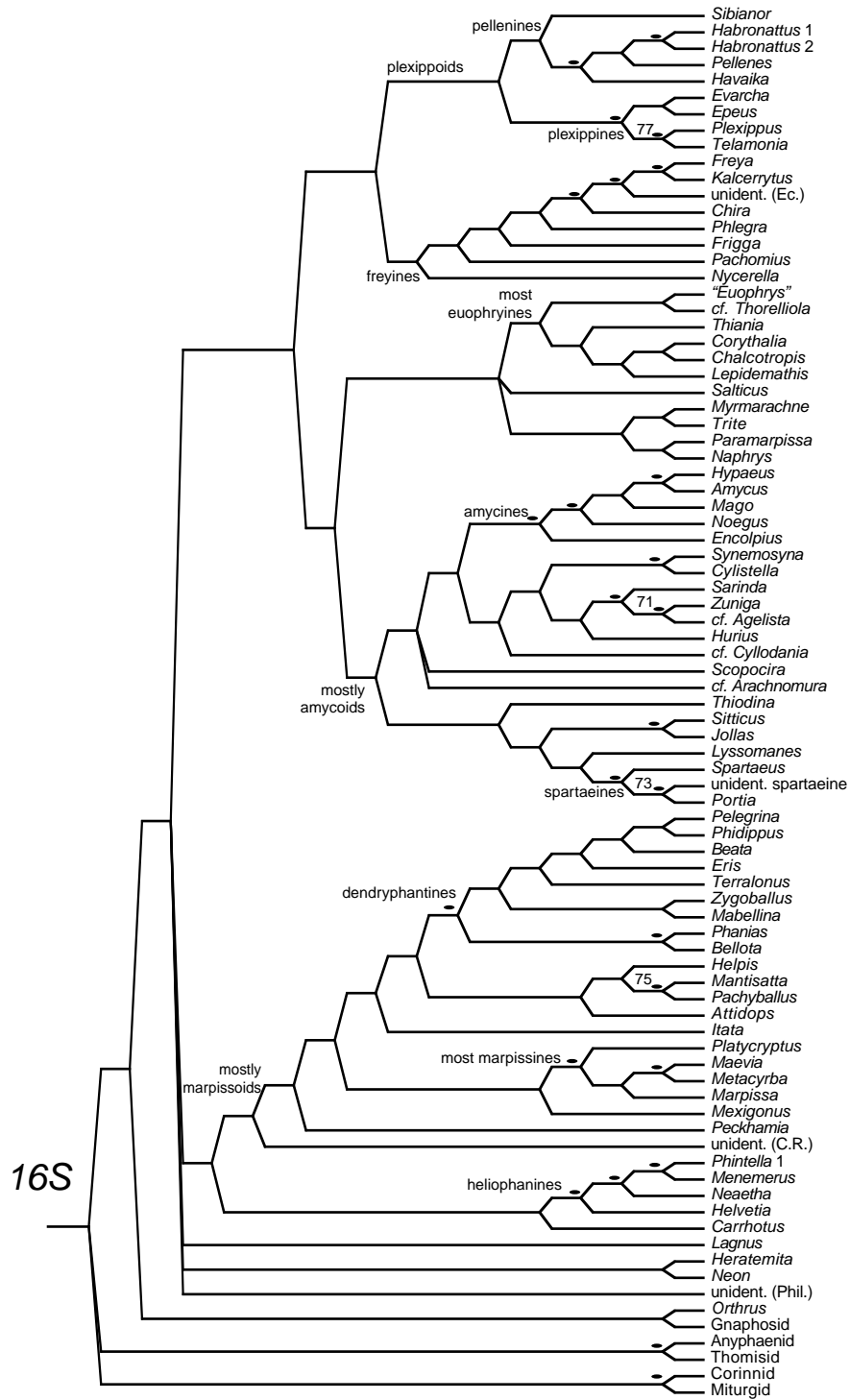


Fig. 3. Phylogeny from 16S: Strict consensus of 3 best trees from likelihood analysis. Spots show clades appearing in parsimony analysis. Numbers show % of 100 parsimony bootstrap replicates showing clades if $\geq 70\%$.

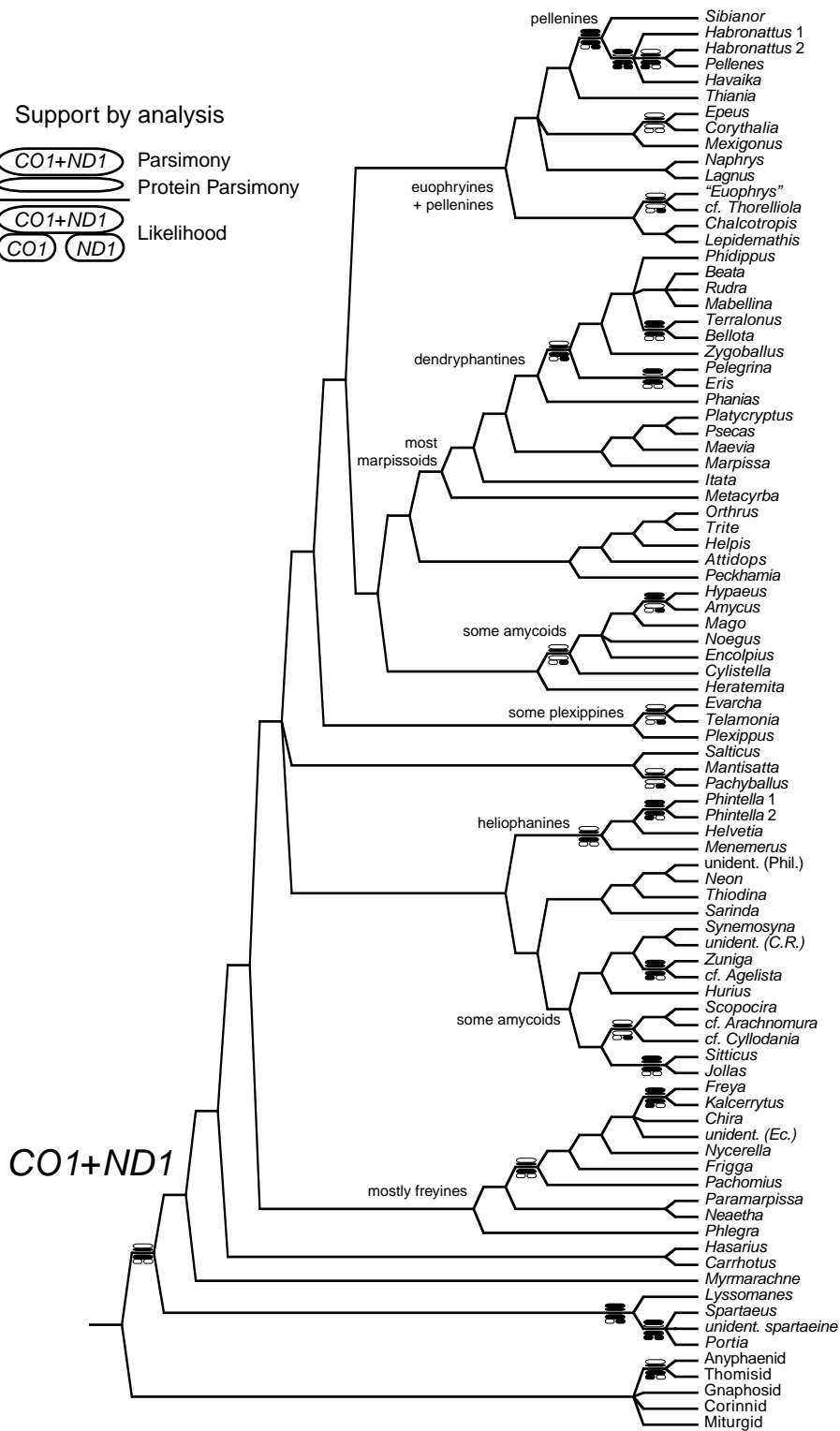


Fig. 4. Phylogeny from mitochondrial protein coding genes (*CO1* and *ND1*): Strict consensus of 6720 trees from parsimony analysis of sequence data translated to amino acids, with some resolution added from other analyses. Symbols show support by parsimony on the nucleotide and protein sequences (above branch) and by likelihood on the combined and separate *CO1* and *ND1* genes (below branch), as explained in legend. Black indicates support for clade as shown and white indicates no clear support for clade. No symbol is shown on those branches supported only on the tree shown, i.e. the parsimony analysis of protein sequence.

REARRLIMIT = 10000; SPR, 20000; SPR, 20000; TBR, 100000) brought the $-\ln$ likelihoods to 46862.773, 46861.031, 46882.839, 46907.208 respectively. The best two replicates were subjected to further TBR swapping until completion, resulting in final $-\ln$ likelihoods of 46815.972 and 46862.773. The best replicate with a single tree ($-\ln L = 46815.972$) was used to represent the likelihood results.

Combined mitochondrial gene analysis

The mitochondrial gene regions (*16S*, *COI* and *ND1*; NCHAR of aligned matrix = 2910) were combined in a parsimony analysis that found 2 trees of 15385 steps. Resulting clades are indicated by symbols in Fig. 5.

All genes analysis

All five gene regions were combined (NCHAR of aligned matrix = 3411) for parsimony analysis. The three separate tree searches (PAUP*: 20000 random addition sequences with NCHUCK = 5, CHUCKSCORE = 1 followed by open TBR swapping; PAUP*: 2000 random addition sequences with NCHUCK = 500, CHUCKSCORE = 1 followed by open TBR swapping; NONA: ratchet by command 'nix -10 50 20') all found the same two trees with 20267 steps. The strict consensus of these two trees is shown in Fig. 5.

Discussion

We present a summary phylogeny (Fig. 6) to synthesise the results of our various analyses. The diagram is marked to indicate support by various gene regions and analytical methods. We will discuss some notable clades and then consider the implications of the phylogeny. A partial classification of salticids summarising placement of some of the genera discussed below is presented in Appendix 2.

Basal divisions of Salticidae

Only four non-salticoid salticids were included in the analysis, one lyssomanine and three spartaeines (*Portia*, *Spartaeus*, 'unident. spartaeine'). In several analyses these were placed near the outgroups as expected (Fig. 5). The spartaeines and (spartaeines + *Lyssomanes*) are both supported as monophyletic by both parsimony and likelihood analyses of *28S*, *16S* and *COI+ND1* data independently. The phylogenetic distances involved may be sufficiently long to make such conclusions unreliable using these genes; however, we tentatively accept the relationship of lyssomanines and spartaeines.

With the exception of the placement of *Orthrus*, clear support for the monophyly of the remaining salticids, the Salticoida, is given in the all-genes parsimony analysis, the *28S* parsimony and likelihood analyses and the protein-translated *COI+ND1* parsimony analysis. The *16S* analyses provide some support for salticoid monophyly. In exception there were conflicting placements of *Lyssomanes* and the

gnaphosid. The placement of *Orthrus*, an Australasian plurident, was unstable. A few analyses (all genes, *28S*) suggest it belongs outside the Salticoida. *Orthrus* is little studied and it is not known which if any of the described salticoid morphological synapomorphies it possesses.

Lack of unanimous support for the monophyly of the Salticoida is not troubling because these genes are less than ideal for resolving phylogenetic questions of this depth. Monophyly of the Salticoida is well supported by numerous apparent morphological synapomorphies, presented by Maddison (1988) and summarised briefly by Maddison (1996). These include:

- (i) Short, anteriorly placed fovea on carapace (Wanless 1984).
- (ii) Eyes between anterior eye row and posterior eyes strongly reduced in size (Wanless 1984).
- (iii) Cell bodies of anterior lateral eye photoreceptors displaced to side (Homann 1971; Blest 1983).
- (iv) Retinal strip of anterior median eyes sharply curved (Blest and Sigmund 1984).
- (v) Six arms of pigmented glia surround secondary eye photoreceptors, as opposed to four or fewer in *Lyssomanes* and the spartaeines (Eakin and Brandenburger 1971; Blest and Sigmund 1984).
- (vi) Absence (or perhaps great reduction) of a tarsal claw on the female palpus. The tarsal claw is present in lyssomanines and spartaeines (Wanless 1980, 1982, 1984), as in other spiders, but lacking in the Salticoida (Maddison 1988).
- (vii) Gland openings on upper surface of endite (gnathocoxal glands, Legendre 1953) displaced medially (Maddison 1996: figs 14, 15) and dividing a patch of setae away from the medial scopula. Non-salticoids and non-salticoids generally have the distal placement, except for a gnaphosid and araneoids (Maddison 1988).
- (viii) Asymmetrical tarsal claws (Simon 1901: 385; Harm 1973; Hill 1977). In the Salticoida, the posterior tarsal claw has one-third as many teeth or fewer (0–5 teeth) than the anterior claw (7–24 teeth), whereas most non-salticoids have about as many teeth on both claws (exceptions: *Philodromus* Walckenaer and *Cyrba* Simon; Maddison 1988).
- (ix) Cluster of slit sense organs on the medial edge of the basal segment of the chelicerae, associated with a seta and appearing as an unpigmented mound in posterior view (Maddison 1996: fig. 13), absent in the lyssomanines, spartaeines and other families studied by Maddison (1988).
- (x) Sclerite between the posterior medial bases of the chelicerae very small, at most 1/4 as long as the anterior-posterior thickness of the chelicera (Maddison 1996: fig. 13). In non-salticoid salticids and most non-salticoids the sclerite is at least 1/3 as long as

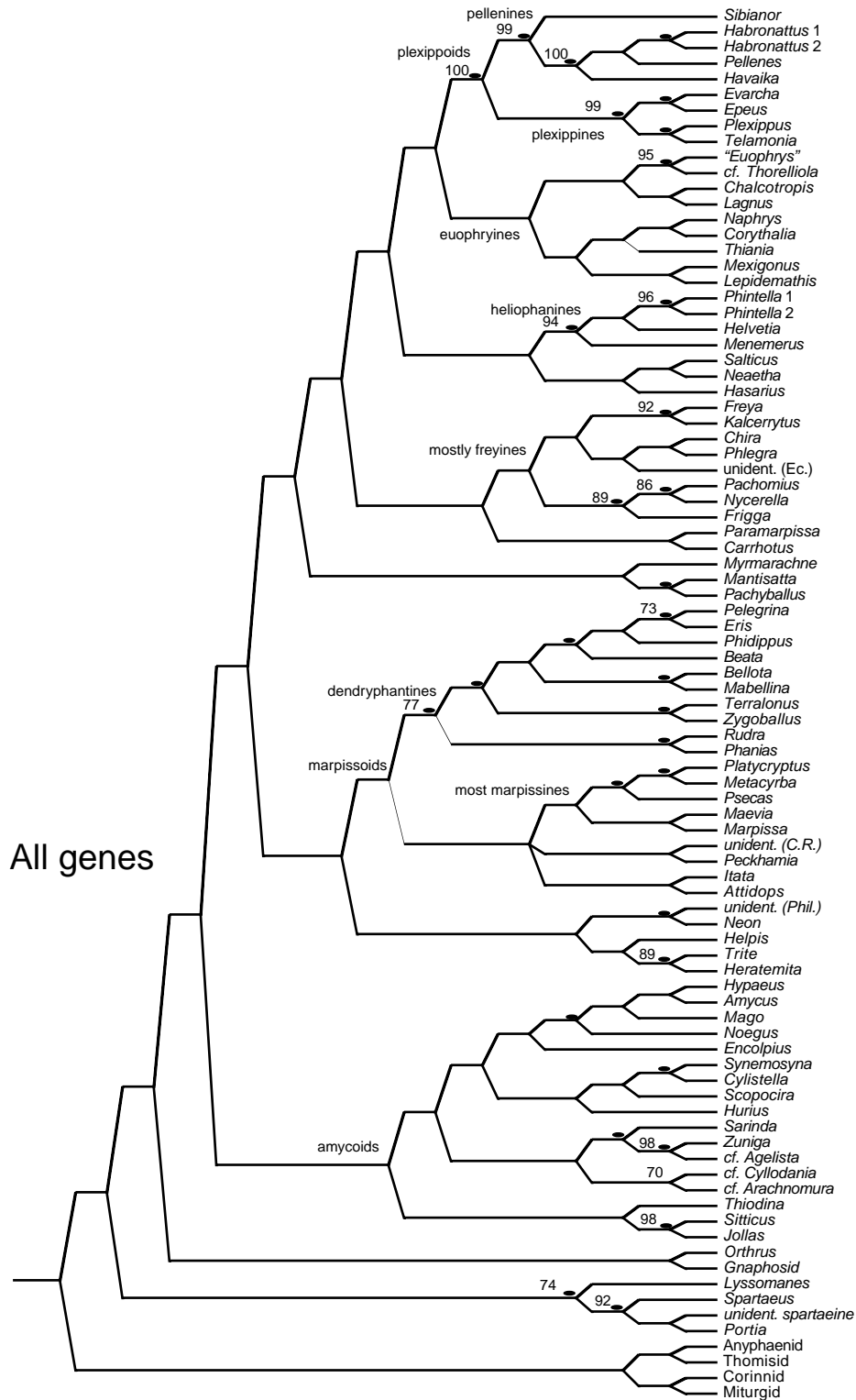


Fig. 5. Phylogeny from parsimony analysis with all genes combined; strict consensus of two trees of 20267 steps. Numbers show % of 500 parsimony bootstrap replicates showing clade if $\geq 70\%$. Spots show clades also appearing in combined parsimony analysis of mitochondrial sequence alone.

the thickness of the chelicera (Maddison 1988, 1996: fig. 13).

Dendryphantinae (sampled genera included: Beata, Bellota, Eris, Mabellina, Pelegrina, Phantias, Phidippus, Rudra, Terralonus, Zygoballus)

In our analyses, the dendryphantines as delimited by Maddison (1996) are monophyletic, as previously confirmed by Hedin and Maddison (2001a). Thus, it appears that the phenotypic synapomorphies proposed by Maddison (1996) are valid. These are:

(i) Carina on ventrolateral edge of the male chelicerae (Maddison 1996: fig. 10).

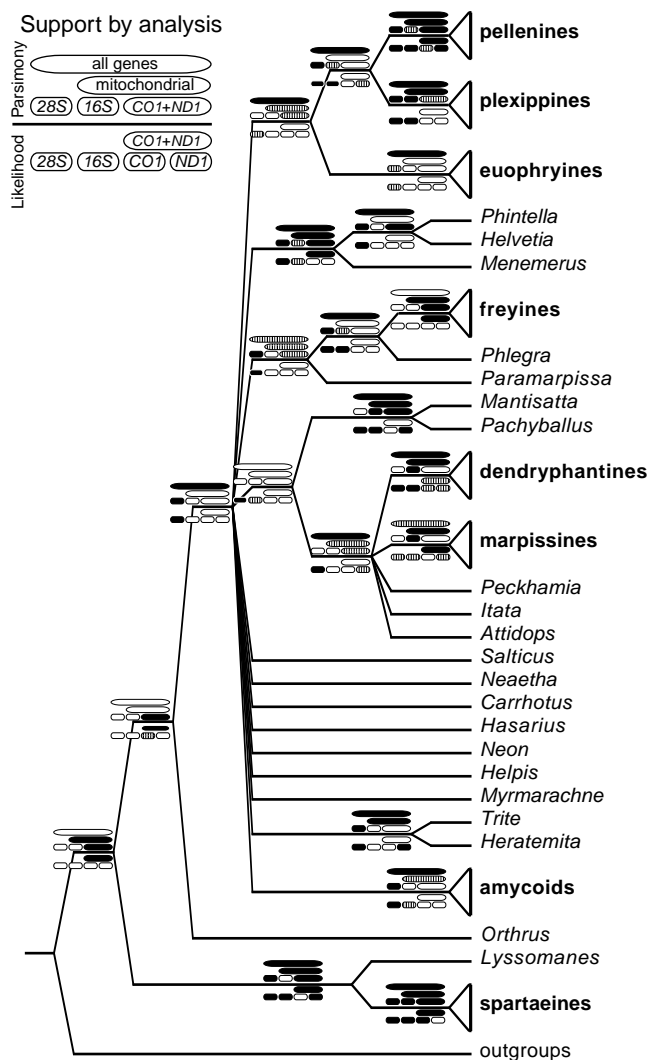


Fig. 6. Summary of phylogenetic analyses. Symbols show support by parsimony (above branch) and by likelihood (below branch) for various genes or combinations of genes (left to right), as explained in legend. Black indicates support for clade as shown, hatched indicates support for clade plus or minus one or two terminal taxa and white indicates no clear support for clade. See Discussion for list of what sampled taxa fall in the clades shown as triangles.

(ii) Coil of embolus folded back so as to be hidden behind the basal part of the embolus (Maddison 1996: fig. 9).

(iii) Epigynal openings S-shaped, with entry toward the lateral in the anterior half and toward the medial in the posterior half (Maddison 1996). Genera include *Dendryphantes*, *Macaroeris* and *Rhene* in the Old World and many in the New World (Maddison 1996). Phylogenetic relationships within the dendryphantines were studied by Maddison (1996) and Hedin and Maddison (2001a).

Marpissinae (sampled genera included: Maevia, Marpissa, Metacyrba, Platycryptus, Psecas)

Barnes (1958) included among the marpissines the genera *Marpissa*, *Maevia*, *Metacyrba* (the current *Metacyrba* plus *Platycryptus*), *Menemerus* and *Paramaevia*. With the exception of *Menemerus* (which falls within the heliophanines), Barnes's proposed group is monophyletic among the North American species. Included in our sample is an unidentified Costa Rican specimen ('new genus' of G. S. Bodner and G. B. Edwards, unpublished data) that is ambiguously a marpissine, falling outside the group in several analyses. Similar genera unsampled for molecular data but presumed to be marpissines are *Balmaceda*, *Breda*, *Fuentes*, *Mendoza*, *Paramaevia* and *Parkella*.

Marpissoida

A strongly supported result of our analyses is the close relationship between the marpissines and dendryphantines. In retrospect, this is not surprising, as the groups share similarity of typical body form—carapace boxy, with a flat top (contrasting, for instance, with the eye tubercles and rounded form of a euophryine carapace) and first legs robust. Morphometric studies to articulate precisely such differences would be valuable. The palpus in both groups is typically narrow and shoe-shaped, although the embolus is more freely articulated in the dendryphantines.

We here propose a new taxon, **Marpissoida** (of unspecified rank), to include the marpissines and dendryphantines. Also included are a series of other groups with a spiral, moveable embolus. These are the antlike *Peckhamia* (and presumably, the similar *Synageles*, *Descanso* and *Cheliferooides*), the beetle-like *Attidops* (and presumably, the similar *Admestina*) and the elongate *Itata*. One major group with a freely articulated spiral embolus, the euophryines, is not included with the marpissoids. The issue of embolus evolution is discussed later.

Two genera of remarkably dissimilar body form (*Pachyballus*, a round flat beetle-like spider, and *Mantisatta*, an extremely thin transparent grass-like spider) are strongly supported as sister-groups. Both have a terminally coiled embolus and, in that regard, resemble some of the marpissoids (e.g. *Attidops* and *Itata*), with whom our data suggest a possible relationship (Fig. 6). If *Mantisatta* and

Pachyballus are sister to the marpissoids, they would probably be joined by other Old World genera such as *Ballus* C. L. Koch and *Marengo* Peckham & Peckham.

A feature that may unite the marpissoids with a few other groups such as *Habrocestum* Simon (and the similar *Habrocestoides* Prószyński and *Chinattus* Logunov) and the freyines is the presence of a distinct tegular ledge (fig. 3 of Maddison 1996), a cuticular flap and furrow cutting across the surface of the tegulum from the base of the embolus to the retrolateral margin. Logunov (1999) used different terms, considering the tegular ledge in *Habrocestoides* to mark the division between two sclerites, the radix and the tegulum. Our data do not indicate a relationship between the freyines and the marpissoids, but neither do they rule it out.

Euophryinae (sampled genera included: *Chalcotropis*, *Corythalia*, 'Euophrys', *Lagnus*, *Lepidemathis*, *Mexigonus*, *Naphrys*, *Thiania* and cf. *Thorelliola*)

Prószyński (1976) proposed a delimitation of the Euophryinae based heavily on genitalic similarity. The genera he included have an embolus that is a coiled spiral at the distal end of the tegulum. Although other salticids have a terminal spiral embolus (Maddison 1996), the genera placed by Prószyński in Euophryinae (Prószyński 1976: plates 11–24) have the embolus and tegulum with a particular form: (1) the plane of the spiral of the embolus is more or less parallel to the longitudinal axis of the palpus; and (2) a loop in the sperm duct projects toward the centre of the tegulum. As well, euophryine epigyna commonly show two spiral grooves (related to the openings) that frame two circular areas of relatively transparent, flat integument.

Our molecular data provide some support for the monophyly of this group, primarily via the all genes analysis (Fig. 5). *28S* puts the group nearly monophyletic, *COI+ND1* has it paraphyletic with respect to some plexippoids and *16S* puts most but not all euophryines together. Although not fully convincing, this alleviates some of Maddison's (1996) concern that the Euophryinae may be a paraphyletic group from which many other groups arose. It should be noted, however, that we sampled only a small proportion of euophryine genera. As many as 75 genera could be considered euophryines on the basis of genitalic characters, including those sampled, and *Anasaitis*, *Ascylltus*, *Athamas*, *Bathippus*, *Canama*, *Chalcoscirtus*, *Chapoda*, *Cobanus*, *Cytaea*, *Euophrys*, *Euryattus*, *Hypoblemum*, *Jotus*, *Lagnus*, *Maeota*, *Maratus*, *Omoedus*, *Pensacola*, *Pseudeuophrys*, *Pystira*, *Saitis*, *Servaea*, *Sidusa*, *Siloca*, *Spilargis*, *Talavera* and *Zenodorus*.

Plexippinae (sampled genera included: *Plexippus*, *Evarcha*, *Telamonia* and *Epeus*)

Maddison (1988, 1996) proposed that a modified serrula on the male endite and a bump on the tegulum delimit the plexippines, including *Plexippus*, *Hyllus*, *Evarcha*, *Thyene*,

Telamonia, *Harmochirus* and part of *Bianor*. The lateral-most teeth on the serrula are elongate and curved, unique as far as we know among the salticids (Fig. 7). The bump on the tegulum mentioned by Maddison is just counterclockwise of the base of the embolus on the left palp viewed from below, unlike the bump of heliophanines, which is just clockwise. Some, although not all, plexippines have distinct tufts of hairs in the region of the small eyes (e.g. *Thyene* and *Hyllus*). Maddison's suggestion that only some *Bianor* species are plexippine is based on the observation that *Sibianor aemulus* (formerly in *Bianor*) shows the two proposed plexippine synapomorphies, whereas the type species, *Bianor maculatus*, does not (see Maddison 1988).

Our molecular data strongly indicate that the sampled plexippines (including *Epeus*) are indeed monophyletic but that they do not include *Sibianor aemulus*, which is more closely related to *Pellenes* and *Habronattus*. This would suggest that Maddison's proposed plexippine synapomorphies on the serrula and tegulum do not delimit the plexippines per se, but rather the larger group of plexippines plus pellenines. If so, we lack morphological synapomorphies for the plexippines.

Our data do not speak clearly to relationships within the plexippines as relationships among the four included taxa varied according to the different genes analysed.

Pelleninae (sampled genera included: *Pellenes*, *Habronattus*, *Havaika*, *Sibianor*)

Prószyński's (1976) Pelleninae included *Pellenes*, *Habronattus*, *Evarcha*, *Neaetha*, *Bianor* (now divided into *Bianor* and *Sibianor*; Logunov 2000), *Maevia*, *Hasarius* and *Yaginumella*. Our molecular results support a close relationship of *Pellenes*, *Habronattus*, *Sibianor* and the Hawaiian *Havaika*. These, along with *Bianor*, *Harmochirus*, *Microbianor* and *Modunda*, we will consider to be the pellenines. These share an epigynum with the guide for the tibial apophysis moved forward from the epigastric furrow (e.g. Griswold 1987; Logunov 2000). Except in *Habronattus paratus* and some species of *Pellenes*, the lateral edge of the



Fig. 7. Lateral terminus of serrula of male endite characteristic of plexippines (species shown, *Evarcha hoyi*). Note that terminal edge (at left) is long and sinuate.

epigynal opening is long, sclerotised and semicircular. Also sharing the distinctive pellenine genitalic features, and bearing a strong resemblance and body form to the other pellenines, is *Neaetha*. It was a surprise to us, therefore, that the specimen we tentatively identify as a species of *Neaetha* Simon ('cf. *Neaetha*' in the tables and figures) showed no clear affinities to the pellenines. At present the placement of *Neaetha* must be considered uncertain. The remaining groups must be removed from the Pelleninae. Our analyses and those of Maddison (1988) suggest that *Evarcha* and *Yaginumella* are plexippines, that *Maevia* is a marpissine (as it had been to Barnes 1958) and that *Hasarius* is not a pellenine and of unclear affinity.

Most of our analyses support the close relationship of *Pellenes*, *Habronattus* and *Havaika*, with *Sibianor* being more distant.

Plexippoida

Our data strongly support a close relationship between the plexippines and pellenines; we therefore propose the new taxon **Plexippoida** (of unspecified rank) to contain both groups. That these are related is not surprising: there has been taxonomic confusion between them. *Sibianor* (as *Bianor*) was considered a pellenine, Maddison (1996) considered it a plexippine and now it returns to the pellenines. *Evarcha* was formerly considered a synonym of *Pellenes* and is now considered a plexippine (Maddison 1996). The tegular bump and serrular modification mentioned above in regards to plexippines appear to be synapomorphies of the plexippoids as a whole, being shared by both the plexippines and a basal pellenine (*Sibianor*) and therefore subsequently lost in the line leading to *Pellenes*, *Habronattus* and *Havaika*.

Several of our analyses suggest that the closest relative of the plexippoids may be the euophryines. The all-genes parsimony analysis supports this most clearly. Support from the mitochondrial parsimony analyses and the 28S likelihood analysis was ambiguous. One feature uniting many (but not all) plexippoids and euophryines is the relatively long third leg. Whether this could reflect a unique adjustment to the jumping mechanism is not known.

Aelurillines and freyines

Of all the aelurillines (including *Aelurillus*, *Langona* and others), we only sampled one genus (*Phlegra*). Thus, although we cannot speak to the monophyly of the group, we can discuss possible close relatives. Among the neotropical salticids are a number of genera that resemble plexippoids in general body form and markings, including *Phiale* and *Freya*, which have been informally known as 'freyines'. Freyine genera sampled here are *Chira*, *Freya*, *Frigga*, *Kalcerrytus*, *Nycerella* and *Pachomius*. The unidentified specimen from Ecuador groups with the freyines. Freyines lack the morphological synapomorphies of the plexippoids

and pellenines. Our data confirm that they are not closely related to the plexippoids. Their monophyly is supported by the mitochondrial protein coding genes. A close relationship of the freyines with *Phlegra* is supported by three gene regions: 28S, 16S and the mitochondrial protein coding genes. 28S and 16S genes suggest that *Phlegra* (and presumably the aelurillines along with it) arose from within the freyines. There is weaker support for a relationship of *Paramarpissa* with the aelurillines and freyines.

We are not proposing a formal group for the freyines, nor that the freyines be included within the aelurillines, merely that these are probably close relatives.

Heliophaninae (sampled genera included: *Phintella*, *Helvetia*, *Menemerus*)

Maddison (1987) proposed a leg-carapace stridulatory mechanism as a synapomorphy of a group of genera including *Phintella*, *Heliophanus*, *Icius*, *Pseudicius* and *Marchena*. This clade, a subgroup of the Heliophaninae, is speciose in the Old World but includes only a few species in New World genera (*Helvetia*, *Marchena*, *Theriella* and *Yepoella*). A broader group, approximately matching Prószyński's (1976) concept of the Heliophaninae, is delimited by a bump on the tegulum about 90° clockwise from the base of the embolus in the left palpus viewed from below (Maddison 1987).

Our sample included *Phintella* and *Helvetia* (with the leg-carapace stridulatory mechanism) and *Carrhotus* (in Prószyński's concept of Heliophaninae but without the stridulatory mechanism). *Phintella* and *Helvetia* are strongly supported as relatives. *Carrhotus* is of ambiguous placement; there is no support for it being a heliophanine. There was consistent strong support for a relationship of *Phintella* and *Helvetia* with *Menemerus*. Thus *Menemerus* can rightly be considered a heliophanine.

Our data showed hints of relationships between the heliophanines and *Salticus*, *Hasarius* and *Neaetha* (all genes analysis, *COI-ND1* parsimony, 28S likelihood (*Hasarius* only)). Until more Old World genera are sampled, the molecular data will probably remain unclear about the true relatives of the heliophanines.

Amcyoida (sampled genera included: cf. *Agelista*, *Amcyus*, cf. *Arachnomura*, *Cylistella*, cf. *Cyllodania*, *Encolpius*, *Hurius*, *Hypaeus*, *Jollas*, *Mago*, *Noegus*, *Sarinda*, *Scopocira*, *Sitticus*, *Thiodina*, *Zuniga*)

Our data suggest that a large proportion of the neotropical salticid fauna form a single radiation, only one group of which has reached the Old World (*Sitticus/Attulus*). This clade includes diverse body forms, from the long-legged amycines to the antlike *Synemosyna* and other genera. We propose a new taxon, **Amcyoida** (of unspecified rank), for this group.

Included in the Amycoidea are the amycines (Galiano 1968), ant-like genera such as *Synemosyna* and *Sarinda* (e.g. Galiano 1964a–1964c 1965, 1966), the Hyetusseae (including *Agelista*, *Arachnomura*, *Cyllodania* and *Hyetussa* Simon), the sitticines (including *Sitticus*, *Jollas*, *Attulus*, *Ailluticus*), the Hurieae (Galiano 1987) and the thiodinines (including *Banksetosa*, *Cotinusa*, *Nilacantha* and *Thiodina*). In addition to the genera already mentioned, probable members include *Admesturius*, *Atelurius*, *Atomosphyrus*, *Cyllodania*, *Erica*, *Fluda*, *Gypogyna*, *Hyetussa*, *Maenola*, *Martella*, *Parafluda*, *Scoturius*, *Simonurius*, *Simprulla*, *Synemosyna*, *Tanybelus*, *Titanattus*, *Toloella* and *Vinnius*. All (except perhaps the thiodinines) have an embolus fixed to the tegulum. One feature shared by species in many of these genera is the looping of the embolus over the dorsal surface of the cymbium. This trait is by no means universal and occurs only in species with a particularly long embolus. Our placement of *Sitticus* within the amycoids is novel. It differs from Petrunkevitch's (1928) suggestion of a relationship with *Neon* and Logunov's (2000) suggestion of a relationship with *Bianor* and relatives. Our placement suggests that had *Sitticus* not lost its retromarginal cheliceral teeth, it could very well be plurident, as are many of the amycoids.

Within the Amycoidea, most relationships are uncertain; however, there are a few consistent results in our analyses. The amycines proper (*Amycus*, *Noegus*, *Hypaeus*, *Mago* and *Encolpius*) appear to form a monophyletic group. *Sitticus* and *Jollas*, as expected, are close relatives. However, there is no clear molecular evidence that the antlike amycoids (*Sarinda*, *Synemosyna* and *Zuniga* in our sample) form a monophyletic group. This is perhaps not surprising: amycoid ant mimics take various body forms and could very well be derived independently several times from groups like the Hyetusseae, which themselves show some antlike traits (e.g. black-tipped first legs that are waved like antennae). Ant mimicry has evolved independently elsewhere in the salticids (among our sampled taxa, for example, in the dendryphantines (*Bellota*), other marpissoids (*Peckhamia*) and the myrmarachnines (*Myrmarachne*)).

Polyphyly of the free-embolus group

Maddison (1988, 1996) proposed that salticids with a 'free embolus', i.e. a fully expandable distal hematodocha and a movable embolus-tegulum articulation, form a monophyletic group. This group would include dendryphantines, euophryines, *Ballus*, *Synageles*, *Mopsus* Karsch and others. We find no support for this proposal in our molecular data. In contrast, the Euophryinae is a distinct, monophyletic group that may be more closely related to the plexippoids.

This suggests that the free, spiral embolus is either independently derived more than once, or such a free embolus has been lost repeatedly by fusion to the tegulum. The placement of *Itata*, *Attidops* and the synagelines (*Peckhamia*) and possibly others (*Pachyballus*, *Mantisatta*)

with the dendryphantines suggests that at least their articulated, spiral embolus is homologous with that of the dendryphantines. Relationships within the Marpissoida are not well enough resolved to determine whether the marpissine palp, with a fixed embolus, represents a secondary fusion of a free embolus.

The independent derivation of a free, spiral embolus may be supported by the fact that it differs in details. The spiral in dendryphantines and *Attidops*, for example, appears (primitively) to be oriented perpendicular to the longitudinal axis of the palpus. The plane of the spiral of the embolus in euophryines, in contrast, lies parallel to the axis of the palpus (Prószyński 1976: figs 93–232).

Two other groups placed by Maddison (1988) in the free-embolus group are the aelurillines (e.g. *Phlegra*) and the thiodinines. The *Phlegra* embolus is spiral and appears to have a distinct hematodocha (fig. 18 of Maddison 1996), but it is hidden behind the tegulum. Our results suggest that *Phlegra* may be a freyine. Thiodinines may have an articulated embolus, but the embolus is not spiral. This group appears to belong with the amycoids. Both of these placements suggest that taxa with a freely articulated embolus may be scattered throughout the phylogeny of salticids.

Old World v. New World

The reconstructed phylogeny suggests a deep biogeographical division between the Old World and New World. With the exception of the euophryines, major speciose groups are either restricted, or nearly restricted, to one hemisphere or the other. Although this pattern may be overturned with more Old World sampling, at present it is strong.

For instance, almost all neotropical salticid species appear to belong to four groups: amycoids, marpissoids, freyines and euophryines. Euophryines are found abundantly in the Old World, but the other three groups are apparently poorly represented (unless, of course, many unsampled Old World taxa belong within these groups). Amycooids, which are so diverse in body forms and numerous in genera and species in the neotropics, are represented in the Old World, as far as known, by a single group (*Sitticus* and *Attulus*). One of the two major groups of marpissoids, the marpissines, is represented in the Old World by *Marpissa* and *Mendoza* only. The other major marpissoid group, the dendryphantines, is perhaps the most speciose group of salticids in North and Central America and yet is represented in the Old World by a few small clades. If *Ballus*, *Marengo* and similar salticids are marpissoids, then they may represent the largest marpissoid radiation in the Old World. Freyines are absent in the Old World, unless the aelurillines (including *Phlegra*) are derived within the freyines.

Conversely, two groups that are diverse in the Old World, the heliophanines and the plexippines, have few species in the New World. There is one Nearctic heliophanine species

(*Marchena minuta*) and several neotropical species (in *Helvetia*, *Yepoella* and *Theriella*). Whether these represent a single clade is not known. New World plexippines are likely to have been introduced recently—*Evarcha* as boreal migrants, *Plexippus* as a cosmopolitan salticid ambassador.

These are not the only large clades far more diverse in one hemisphere than the other. Aelurillines, with many Old World species, have only a single known New World species. The spartaeines, by published reports, are restricted to the Old World, although the neotropical *Lapsias* may belong with them (having a tarsal claw on the female palp and at least some species with large small eyes).

Difference in species number cannot be used on its own to interpret biogeographical history. The phylogenetic placement of the species matters also. Although we know little about the relationships within each of these clades, it seems likely that the amycoids and marpissoids in the Old World, and the plexippines and heliophanines in the New World, represent a few migration events from groups diversifying in the other hemisphere. This is perhaps clearest for the plexippines as each of the few New World species has many close relatives in the Old World.

If indeed each major group diversified primarily in one hemisphere, it would suggest that much of the diversification of salticoids has occurred since continental drift limited communication between the Old World from the New World by the late Mesozoic (Wing and Sues 1992). The factors that explain the occurrence of high diversity on the euophryines within both hemispheres are unclear.

Our view of the deep biogeography of salticids will become clarified as additional taxa are sampled. In particular, our sample of Old World taxa is weak. The reader will notice that many of the unassociated genera near the base of the summary tree (*Salticus* through *Myrmarachne*) are Old World genera. Placements of these genera were strongly inconsistent from one analysis to the next. By adding Old World species, we would start to find close relatives of these genera, breaking up long phylogenetic branches, which can promote better resolution of other interrelationships (Hillis 1998).

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Appendix 1. Specimens sequenced for molecular phylogenetic analysis

Columns labelled *ND1*, *16S*, *COI*, *28S* and *EF1- α* indicate sequence length obtained in parentheses followed by GenBank accession numbers. *Habronattus* #1 in the figures is *H. cf. paratus*; #2 is *H. mexicanus*. *Phintella* #1 is *P. pitatisensis*; #2 is *P. sp.*

Species	Locality	<i>ND1</i>	<i>16S</i>	<i>COI</i>	<i>28S</i>	<i>EF1-α</i>	Specimen #
Lyssomanines & Spartaeines							
<i>Lyssomanes viridis</i> (Walckenaer)	USA: Florida	(390) AY297297	(577) AY296652	(891) AY297360	(754) AY297231	NA	160/161
<i>Portia labiata</i> (Thorell)	Philippines: Luzon	(387) AY297298	(594) AY296653	(960) AY297361	(752) AY297232	NA	206
<i>Spartaeus spinimanus</i> (Thorell)	Australia: Queensland	(390) AY297299	(585) AY296654	(1032) AY297362	NA	NA	199
unident. spartaeine	Philippines: Luzon	NA	(591) AY296655	(969) AY297363	(722) AY297233	NA	185/186
Ameyoids							
<i>cf. Agelista</i>	Ecuador: Manabi	(393) AY297300	(580) AY296656	(900) AY297364	(745) AY297234	NA	169
<i>Ameyus</i> sp.	Ecuador: Sucumbios	(393) AY297301	(576) AY296657	(969) AY297365	NA	(492) AY297218	171
<i>cf. Arachnomura</i>	Ecuador: Sucumbios	(393) AY297302	(577) AY296658	(1047) AY297366	(744) AY297235	NA	175
<i>Cyrtistella</i> sp.	Costa Rica	(393) AY297303	(578) AY296659	NA	(743) AY297236	NA	326
<i>cf. Cylodania</i>	Ecuador: Manabi	(393) AY297304	(574) AY296660	NA	(751) AY297237	NA	223/172
<i>Encolpius</i> sp.	Ecuador: Sucumbios	(393) AY297305	(578) AY296661	(1047) AY297367	(748) AY297238	NA	168
<i>Hurius vulpinus</i> Simon	Ecuador: Pichincha	(393) AY297306	(578) AY296662	(1047) AY297368	(743) AY297239	NA	213
<i>Hypaeus mystacalis</i> (Taczanowski)	Ecuador: Manabi	(393) AY297307	(562) AY296663	(1047) AY297369	(745) AY297240	NA	217
<i>Jollus</i> sp.	Ecuador: Sucumbios	(393) AY297308	(580) AY296664	(1047) AY297370	(734) AY297241	NA	162
<i>Mago steindachneri</i> (Taczanowski)	Ecuador: Sucumbios	(393) AY297309	(576) AY296665	(966) AY297371	(747) AY297242	NA	247
<i>Noegus cf. rufus</i> Simon	Ecuador: Sucumbios	(393) AY297310	(572) AY296666	(984) AY297372	(752) AY297243	NA	255/277
<i>Sarinda</i> sp.	Ecuador: Sucumbios	(393) AY297311	(578) AY296667	(1047) AY297373	(750) AY297244	NA	176
<i>Scopocetra cf. tenella</i> Simon	Ecuador: Sucumbios	(393) AY297312	(582) AY296668	(1047) AY297374	(742) AY297245	NA	165
<i>Sitticus</i> sp.	Ecuador: Manabi	(393) AY297313	(577) AY296669	(954) AY297375	(755) AY297246	NA	220
<i>Synemosyna formica</i> Hentz	USA: Massachusetts	(393) AY297314	(576) AY296670	(954) AY297376	NA	NA	122
<i>Thiodina</i> sp.	USA: Arizona	(390) AF328017	(581) AF327958	(1032) AF327987	(745) AF327930	NA	184/159
<i>Zuniga cf. magna</i> Peckham & Peckham	Ecuador: Manabi	NA	(476) AY296671	(1047) AY297377	(748) AY297247	NA	177
Plexippoids							
<i>Epets</i> sp.	Philippines: Luzon	(393) AY297315	(585) AY296672	(969) AY297378	(750) AY297248	NA	191
<i>Evarcha hoyi</i> (Peckham & Peckham)	USA: New Mexico	(393) AY297316	(581) AY296673	(963) AY297379	(750) AY297249	NA	232
<i>Habronattus cf. paratus</i> (Peckham & Peckham)	Ecuador: Manabi	(393) AF477276	(581) AF477276	(1047) AY297380	(753) AY297250	(478) AF477207	HA88A
<i>Habronattus mexicanus</i> (Peckham & Peckham)	USA: Texas	(393) AF477353	(581) AF477353	(909) AY297381	(749) AY297251	(478) AF359098	HA496A
<i>Hawaika</i> sp.	USA: Hawaii	NA	(581) AF477249	(1047) AY297382	(748) AY297252	(478) AF359058	127
<i>Pellenes shoshonensis</i> Gertsch	USA: California	(393) AF477252	(582) AF477252	(969) AY297383	(744) AY297253	(478) AF359060	HA430
<i>Plexippus paykulli</i> (Audouin)	USA: Florida	(390) AY297317	(584) AY296674	(957) AY297384	(748) AY297254	(319) AY297219	73
<i>Sibianor aemulus</i> (Gertsch)	Canada: Ontario	(393) AY297318	(577) AY296675	NA	(750) AY297255	NA	238
<i>Telamonia masinloc</i> Barrion & Litsinger	Philippines: Luzon	(285) AY297319	(584) AY296676	(960) AY297385	(750) AY297256	(501) AY297220	269
Euophryines							
<i>Chalcotropis luceroi</i> Barrion & Litsinger	Philippines: Luzon	(393) AY297320	(594) AY296677	(963) AY297386	(755) AY297257	(489) AY297221	153
<i>Corythalia cf. tropica</i> (Mello-Leitao)	Ecuador: Manabi	(390) AY297321	(582) AY296678	(969) AY297387	(760) AY297258	NA	222
' <i>Euophrys</i> ' <i>parvula</i> Bryant	New Zealand	(393) AY297322	(575) AY296679	(1047) AY297388	(754) AY297259	NA	190
<i>Lepidemathis haemorroidalis</i> (Simon)	Philippines: Luzon	(393) AY297323	(580) AY296680	(1041) AY297389	(693) AY297260	NA	262
<i>Mexigonus</i> sp.	USA: Arizona	(393) AY297324	(579) AY296681	(912) AY297390	(750) AY297261	NA	118
<i>Naphrys pulex</i> (Hentz)	USA: Massachusetts	(393) AY297325	(577) AY296682	(1047) AY297391	(755) AY297262	NA	119/120
<i>Thiania viscaensis</i> Barrion & Litsinger	Philippines: Luzon	(393) AY297326	(580) AY296683	(954) AY297392	(758) AY297263	NA	157
<i>cf. Thorelliola</i>	Philippines: Luzon	(393) AY297327	(577) AY296684	(1047) AY297393	(753) AY297264	NA	147

Appendix 1. (continued)

Species	Locality	NDI	I6S	COI	28S	EFL- α	Specimen #
<i>Paramarpissa</i> sp.	USA: Arizona	(390) AY297350	(591) AY296705	(831) AY297414	(748) AY297287	NA	313
<i>Phlegra fasciata</i> (Hahn)	USA: Missouri	(393) AY297351	(578) AY296706	(960) AY297415	(747) AY297288	NA	251
<i>Saliticus scenicus</i> (Clerek)	USA: Washington, Missouri	(393) AY297352	(579) AY296707	(972) AY297416	(748) AY297289	NA	107/115
<i>Trite planiceps</i> Simon	New Zealand	(393) AY297353	(581) AY296708	(960) AY297417	(750) AY297290	NA	197
unident. (Phil.)	Philippines: Luzon	(393) AY297354	(586) AY296709	(969) AY297418	(638) AY297291	(501) AY297230	202
Outgroups							
Corinnidae: <i>Castaneira</i> sp.	México: Sonora	(393) AY297355	(596) AY296710	(1047) AY297419	(739) AY297292	NA	320
Gnaphosidae: <i>Cesonia</i> sp.	México: Sonora	(387) AY297356	(600) AY296711	(1047) AY297420	(745) AY297293	NA	319
Miturgidae: <i>Cheiracanthium</i> sp.	México: Sonora	(375) AY297357	(611) AY296712	(1047) AY297421	(753) AY297294	NA	321
Anyphaenidae: <i>Hibana</i> sp.	México: Sonora	(393) AY297358	(585) AY296713	(1047) AY297422	(743) AY297295	NA	318
Thomisidae: <i>Xysticus</i> sp.	USA: Colorado	(387) AY297359	(582) AY296714	(1047) AY297423	(744) AY297296	NA	316

Appendix 2. Classification of salticid genera discussed in text

This is not intended to be an exhaustive classification of salticids; for some clades only examples are given

Lyssomaninae (See Wanless 1980)

Lyssomanes Hentz

Spartaeinae (See Wanless 1984)

Portia Karsch, *Spartaeus* Thorell, ?*Lapsias* Simon

Salticoida

Marpissoida

Marpissinae

Balmaceda Peckham & Peckham, *Breda* Peckham & Peckham, *Fuentes* Peckham & Peckham, *Maevia* C. L. Koch, *Marpissa* C. L. Koch, *Mendoza* Peckham & Peckham, *Metacyrba* F. P.-Cambridge, *Paramaevia* Barnes, *Parkella* Chickering, *Platycryptus* Hill, *Psecas* C. L. Koch

Dendryphaninae (See Maddison 1996)

Beata Peckham & Peckham, *Bellota* Peckham & Peckham, *Dendryphantes* C. L. Koch, *Eris* C. L. Koch, *Mabellina* Chickering, *Macarokeris* Wunderlich, *Pelegrina* Franganillo, *Phanias* F. Pickard-Cambridge, *Phidippus* C. L. Koch, *Rhene* Thorell, *Rudra* Peckham & Peckham, *Terralonus* Maddison, *Zygoballus* Peckham & Peckham

Other marpissoids

Admestina Peckham & Peckham, *Attidops* Banks, *Cheliferoidea* F. Pickard-Cambridge, *Descanso* Peckham & Peckham, *Itata* Peckham & Peckham, *Peckhamia* Simon, *Synageles* Simon

Euophryinae

Anasaitis Bryant, *Ascyltus* Karsch, *Athamas* O. Pickard-Cambridge, *Bathippus* Thorell, *Canama* Simon, *Chalcoscirtus* Bertkau, *Chalcotropis* Simon, *Chapoda* Peckham & Peckham, *Cobanus* F. Pickard-Cambridge, *Corythalia* C. L. Koch, *Cytaea* Keyserling, *Euophrys* C. L. Koch, *Euryattus* Thorell, *Hypoblemum* Peckham & Peckham, *Jotus* L. Koch, *Lagnus* L. Koch, *Lepidemathis* Simon, *Maeota* Simon, *Maratus* Karsch, *Mexigonus* Edwards, *Naphrys* Edwards, *Omoedus* Thorell, *Pensacola* Peckham & Peckham, *Pseudeuophrys* Dahl, *Pystira* Simon, *Saitis* Simon, *Servaea* Simon, *Sidusa* Peckham & Peckham, *Siloca* Simon, *Spilargis* Simon, *Talavera* Peckham & Peckham, *Thiania* C. L. Koch, *Thorelliola* Strand, *Zenodorus* Peckham & Peckham

Plexippoida

Plexippinae

Epeus Peckham & Peckham, *Evarcha* Simon, *Hyllus* C. L. Koch, *Plexippus* C. L. Koch, *Telamonia* Thorell, *Thyene* Simon, *Yaginumella* Prószyński

Pelleninae

Bianor Peckham & Peckham, *Habronattus* F. Pickard-Cambridge, *Harmochirus* Simon, *Havaika* Prószyński, *Microbianor* Logunov, *Modunda* Simon, *Pellenes* Simon, *Sibianor* Logunov

Aelurillinae + freyines

Aelurillus Simon, *Langona* Simon, *Phlegra* Simon, *Chira* Peckham & Peckham, *Freya* C. L. Koch, *Frigga* C. L. Koch, *Kalcerrytus* Galiano, *Nycerella* Galiano, *Pachomius* Peckham & Peckham, *Phiale* C. L. Koch

Heliophaninae

Heliophanus C. L. Koch, *Helvetia* Peckham & Peckham, *Icius* Simon, *Marchena* Peckham & Peckham, *Menemerus* Simon, *Phintella* Strand, *Pseudicius* Simon, *Theriella* Braul & Lise, *Yepoella* Galiano

Amycoidea

Admesturius Galiano, *Agelista* Simon, *Ailluticus* Galiano, *Amycus* C. L. Koch, *Arachnomura* Mello-Leitao, *Atelurius* Simon, *Atomosphyrus* Simon, *Attulus* Simon, *Banksetosa* Chickering, *Cotinusa* Simon, *Cylistella* Simon, *Cylloclania* Simon, *Encolpius* Simon, *Erica* Peckham & Peckham, *Fluda* Peckham & Peckham, *Gypogyna* Simon, *Hurius* Simon, *Hyetussa* Simon, *Hypaeus* Simon, *Jollas* Simon, *Maenola* Simon, *Mago* O. Pickard-Cambridge, *Martella* Peckham & Peckham, *Nilacantha* Peckham & Peckham, *Noegus* Simon, *Parafluda* Chickering, *Sarinda* Peckham & Peckham, *Scopocira* Simon, *Scoturius* Simon, *Simonurius* Galiano, *Simprulla* Simon, *Sitticus* Simon, *Synemosyna* Hentz, *Tanybelus* Simon, *Thiodina* Simon, *Titanattus* Peckham & Peckham, *Toloella* Chickering, *Vinnius* Simon, *Zumiga* Peckham & Peckham