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Salticid spider phylogeny revisited, with the discovery of a large Australasian clade (Araneae: Salticidae)

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Abstract

DNA sequence data from four gene regions (28S, 18S, 16S-ND1, and CO1) were gathered from 65 jumping spider (salticid) taxa to supplement previously gathered molecular data for the family's phylogeny. The additional taxa are mostly from Australasia and other regions of the Old World. Bayesian and parsimony analyses support a clade, here called the Astioida, representing a large proportion of the Australasian fauna. Included in the Astioida are, for example, the robust-bodied *Simaetha* and *Mopsus*, the flattened bark-dweller *Holoplatys*, the delicate foliage-dweller *Tauala*, the antlike *Myrmarachne* and the litter-dwelling *Neon*. One astioid, *Rhondes neocaledonicus*, is returned to that genus from its placement in *Hasarius*. Another newly supported clade, the Aelurilloida, includes the aelurillines, the freyines, and the *Bacelarella* group of genera. Other newly delimited clades are the *Philaeus* group (*Philaeus*, *Mogrus*, *Carrhotus* and others), the Leptorchesteae (*Leporchestes*, *Yllenus* and *Paramarpissa*) and the Hasarieae (*Hasarius*, *Habrocestum* and *Chinattus*). These results concur with previous discoveries (e.g., Amycoida, Marpissoida) in suggesting that salticid clades are largely restricted to continental regions.

Key words: Araneae, Salticidae, Salticoida, Astioida, Aelurilloida, jumping spider, arthropod phylogeny

Introduction

Jumping spiders (Salticidae) form a clade of about 5000 described species (Platnick 2008), characterized by a unique high-resolution visual apparatus (Land 1969; Eakin & Brandenburger 1971). These species are distributed on all continents except Antarctica, and show a great diversity of behaviours (Jackson & Pollard 1996) and body forms (Simon 1901, 1903). Early work on their systematics and phylogenetic relationships put much emphasis on the general form of the body, using it to delimit large groups (Simon 1901, 1903) as well as to assign North American species into European genera such as *Icius* Simon, *Pseudicius* Simon and *Habrocestum* Simon (e.g., Peckham & Peckham 1909). However, as more attention was paid to genitalic characters later in the 20th century (e.g., Prószyński 1976), it became clear that the New World species were misplaced in these Old World genera. Indeed, recent molecular phylogenetic studies (Maddison & Hedin 2003; Maddison & Needham 2006; Maddison *et al.* 2007) have revealed both convergence of body forms and a deep biogeographical divide between the Old World and New World. This was emphasized by the discovery of the clade Amycoida (Maddison & Hedin 2003), which is perhaps the dominant Neotropical group (in terms of numbers of species and phenotypic diversity) but which has only one relatively small and uniform lineage (*Sitticus* Simon) in the Old World. Conversely, the Heliophaninae and Plexippinae are both major Old World

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groups with only a few New World species (Maddison & Hedin 2003).

However, our understanding of worldwide salticid phylogeny and these biogeographical patterns is hampered both by the paucity of species from the Old World tropics included in molecular analyses to date (Maddison & Hedin 2003) and by the lack of comprehensive morphological phylogenetic studies. Here we begin to rectify the former by expanding our molecular data to include many more species from the Old World, with an emphasis on Australasian taxa.

We have chosen to focus on the Australasian fauna because few suggestions have been made for the phylogenetic placement of many of its genera. Some common genera would appear by morphology to fall easily within known groups: *Maratus* Karsch, *Cytaea* Keyserling, *Servaea* Simon and *Zenodorus* Peckham & Peckham all appear to be members of the Euophryinae according to genitalia, for example. Others appear plausibly close to groups outside of the region. *Simaetha* Thorell and *Opisthoncus* L. Koch by body form and genitalia are similar to genera within the Plexippoida or Marpissoida. *Mopsus* Karsch and *Sandalodes* Keyserling appear to have a movable embolus and in this respect resemble dendryphantines, euophryines and ballines. *Clynotis* Simon and related species are quite similar to the New World marpissines, to the extent that one species is currently placed within an otherwise Neotropical genus ("*Breda*" *jovialis* L. Koch). However, there is one fairly large group recognized as perhaps endemic to the region: the Astieae, in which Wanless (1988) includes 6 primarily Australian genera with no clear affinities to other salticids.

Material and methods

Taxon sampling. Previous work has provided sequences for several genes for 107 taxa (89 from Maddison & Hedin 2003; 17 additional from Maddison & Needham 2006; 1 additional from Maddison *et al.* 2007). In our analyses here we use those sequences and add sequences from 65 additional taxa. Among the sequences used from these previous papers are those from the outgroups, namely *Xysticus* sp., *Hibana* sp., *Cesonia* sp., and *Cheiracanthium* sp., representing the families Thomisidae, Anyphaenidae, Gnaphosidae, and Miturgidae respectively (for more details on these specimens see Maddison & Hedin, 2003). Because the sister group of the Salticidae is not well resolved, these outgroups were chosen to represent a diversity of families of Dionycha, wherein lie the Salticidae.

In addition to a large sample of genera from Australia and New Caledonia, the taxa newly sequenced include well-known Eurasian genera whose phylogenetic placement is poorly understood, such as *Philaeus* Thorell, *Carrhotus* Thorell, *Mogrus* Simon, *Yllenus* Simon, and *Leptorchestes* Thorell. A sample of species from Ghana is also included. A full list of the species newly sequenced is given in Appendix 1.

We composed our data matrices by adding the new sequences to those of Maddison and Hedin (2003), Maddison and Needham (2006) and Maddison *et al.* (2007), with one exception. We have identified Maddison and Hedin's "cf. *Neaetha*" as *Pellenes bulawayoensis* Wesolowska, and because of concerns with the quality of the original sequences, we have replaced this taxon's sequences with newly obtained ones (Appendix 1). Also, we have identified Maddison and Hedin's "unident. (Phil.)" as a *Stagetilus* sp., and their "unident. (Ec.)" as *Rishaschia* sp. We refer to their "unident. (C.R.)" as "Costa Rica indet.".

Because some of the species are unidentified and from regions whose salticid faunas are poorly known, we offer illustrations of some specimens from New Caledonia and Ghana (Figs. 1–7), so that they may be more easily identified at a later date. The specimen identified as "cf. *Mopsus*" from New Caledonia (d202) has a palp that resembles that of *Mopsus mormon*, but the body is coloured with varied shades of brown.

Sequencing. Four gene regions were amplified by PCR and sequenced: the nuclear 28S and 18S, and the mitochondrial 16S–ND1 and CO1. Primers used are those of Maddison and Needham (2006) except that for many specimens we used primer ZX1 from Mallatt and Sullivan (1998) for 28S instead of primer 28SO. PCR and sequencing were done as by Maddison and Needham (2006). Sequences were obtained from the chromatogram files using Phred (Ewing & Green 1998; Ewing *et al.* 1998; Green & Ewing 2002) and Phrap (Green 1999) as operated via the chromaseq package (D. Maddison & W. Maddison in prep.) for Mesquite (Maddison & Maddison 2006), following the procedures used by Maddison and Needham (2006).

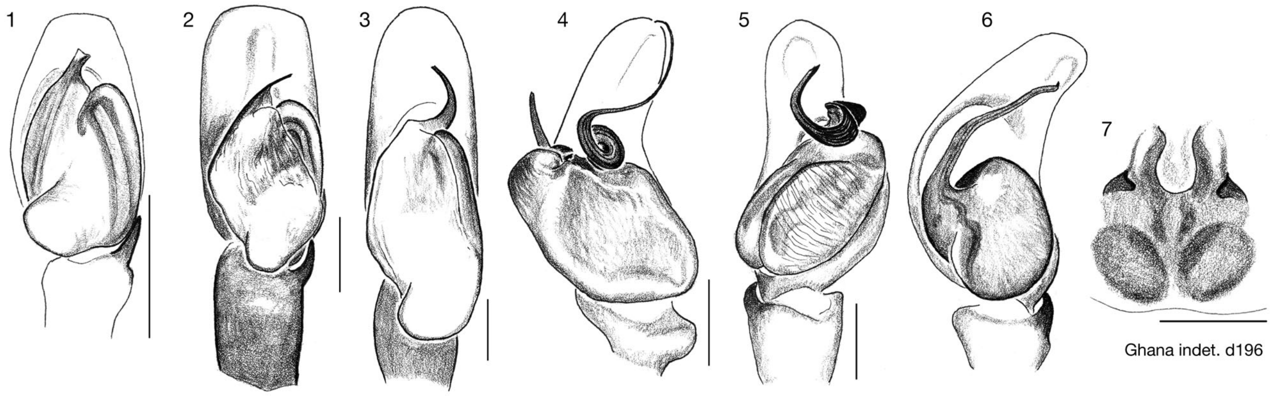
Sequence alignment. Multiple sequence alignments were carried out using ClustalX (Thompson *et al.* 1997) with gap opening and gap extension costs set either to 24 and 6 respectively ("24–6") following Maddison and Hedin (2003) or 8 and 4 ("8–4") to provide an alternative alignment. The protein coding sequences of ND1 and CO1 and the conservative 18S in general seemed to have aligned easily with few indels except in regions of 18S. For these regions, only the 24-6 alignments were used. For the non-coding regions of 16S-ND1 and for 28S, both 24–6 and 8–4 alignments were analyzed. Also, minor editing of the alignments for the ribosomal sequences was done manually using Mesquite (Maddison & Maddison 2006) to correct obvious misalignments of short blocks (5–10 bases) near the ends of sequences. One additional complication arose at the start of ND1: the automatic alignment inserted many indels at the start of ND1 so as to obscure its boundary with the poorly-aligned adjacent non-coding region. We used the amino acid translation to recognize what bases actually belonged to ND1, generating a clear boundary for ND1. Once this boundary was found, the non-coding region in front of it, including 16S and a tRNA, was realigned on its own either with 24–6 or 8–4 parameters. Alignments have been deposited in TreeBASE (treebase.org, accession number: S2168).

Phylogenetic analysis. Phylogenetic analyses were performed using parsimony and Bayesian methods. Bayesian analyses were done using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). MrModeltest (Nylander 2004) was used in combination with PAUP* (Swofford 2002) to choose the appropriate model, which for all matrices was the GTR invariant-gamma model (nst=6 rates=invgamma). Model parameters were permitted to differ among data partitions, with the partitions defined as follows: 28S; 18S; 16S; ND1 first, second, and third codon positions; CO1 first, second, and third codon positions. When ND1 and CO1 were included together in an analysis, they were united to yield 3 partitions (ND1+CO1 first, second, and third codon positions) instead of 6. Each analysis was run via a command of the form "mcmcp ngen= 50000000 printfreq=1000 samplefreq=1000 nchains=4 savebrlens=yes;". The All-Genes 24-6 matrix was analyzed most thoroughly, with a Bayesian analysis run for 150 million generations. The All-Genes matrix with 8-4 alignment was run for 50 million generations, individual gene regions for 10 million generations. After completion, Tracer (Rambaut & Drummond 2005) was used to determine when the posterior probabilities had stabilized. Both runs output by MrBayes during a single analysis were used if they stabilized to approximately the same posterior probabilities. Stabilization was judged by eye in the Tracer plot, and trees from the point of stabilization to the end of the analysis were collected into a single tree file, which was then imported into PAUP* (Swofford 2002) for generation of a majority rules consensus tree of sampled trees.

Parsimony analyses were done using PAUP* (Swofford 2002), treating character states as unordered (one step for any state change). Gaps were treated as missing data. Analyses followed the methods of Maddison and Needham (2006), using 20000 constrained random addition sequence replicates, whose trees were then used as starting points for an unconstrained search.

Analyses were performed on the gene regions separately and combined. We present the results of 8 analyses, four on the matrix combining all genes (28S, 18S, 16S–ND1, CO1), two on the 28S sequences alone, and two on the 16S-ND1 sequences alone. On the All-Genes data, a Bayesian analysis was performed on both the 24-6 and 8-4 alignments, and similarly a parsimony analysis was performed on both alignments. On the 28S sequences, a Bayesian analysis was performed on both the 24–6 and 8–4 alignments, and similarly for the 16S–ND1 sequences. In addition to these 8 analyses, we explored other analyses (e.g., CO1 alone, all mitochondrial alone, 18S alone), but these either agreed substantially with what we present, or they gave little resolution.

With this study we add to our understanding of salticid phylogeny, but we continue to work actively to sample many other unstudied taxa. Salticid classification is currently in disorder: it is a mix of formally ranked subfamilies (e.g., Euophryinae, Dendryphantinae), ambiguously ranked groups of Simon (1901, 1903) (e.g., Astiae, Hasariae), unranked but formally named taxa (e.g., Salticoida, Amycoida), and informal groups discussed in the literature but not formally named as taxa (e.g., lapsiines, freyines). However, we will not here undertake a comprehensive reform of the formal ranked classification of salticid subfamilies, because it is premature to do so: we anticipate many new phylogenetic results in the near future. Nonetheless, we need names to discuss clades. For this reason, we here give names to two large clades — the Astioida and Aelurilloida. Each encompasses several subfamilies, and is unranked. Formal definitions of these new names await further study. In addition, two smaller clades are even more informally named: "the *Philaeus* group" and "the *Bacelarella* group". Both would be approximately of subfamilial rank according to the rankings currently used in the family.



cf. *Lystrocteissa* *Penionomus* cf. *Rogmocrypta* cf. *Nimbarus* *Pochyta* cf. *pannosa* Ghana indet. d193 Ghana indet. d196

FIGURES 1–7. Genitalia of some of the more poorly identified taxa sequenced. 1 Left palp of cf. *Lystrocteissa* sp. (voucher d054), which is small and narrow-bodied. 2 Left palp of *Penionomus* sp. (d122), medium sized, fairly robust, and bronze. 3 Left palp of cf. *Rogmocrypta* sp. (d205), small, with body form reminiscent of *Sitticus*. 4 Left palp of cf. *Nimbarus* sp. (d218), whose long tibial apophysis extends dorsally over the cymbium. 5 Left palp of *Pochyta* cf. *pannosa* Simon (d217), whose tegulum appears to be twisted so as to expose the basal hematadocha. 6 Left palp of Ghana indet. d193. 7 Epigynum of Ghana indet. d196, with two anteriolateral epigynal pockets.

Results and discussion

DNA sequences obtained are listed in Appendix 1, and results of phylogenetic analyses are summarized in Figures 8–11. Figure 8 shows full details of taxa included. Figures 9–11 are compressed (already established clades such as the Amycoida, Marpissoida and others are shown without internal resolution) and somewhat trimmed (a second species of *Massagris* Simon and *Phintella* Strand are not shown). This is done to permit enlarging the typeface for legibility of taxon names.

In the Bayesian analysis of the All-Genes matrix with the 24–6 alignment, trees sampled from the last 140 million generations of both of the two runs were combined to yield a majority rules consensus to estimate posterior probabilities for clades (280000 trees sampled, Fig. 8). For the 8–4 alignment, the majority rules consensus tree was taken from the last 40 million generations from both runs (80000 trees sampled). With the 28S analysis, the last 9 million generations of both runs were used (18000 trees sampled). With the 16S–ND1 analysis, one 24–6 run stabilized to lower likelihood than the other, and thus we used the other run after its stabilization (last 6.8 million generations; 6800 trees sampled).

Support for the clades we discuss below was in general strong, with posterior probabilities estimated at nearly 100% for many of the nodes in the All-Genes analysis (Figs. 8, 9). The 24–6 and 8–4 alignments yielded similar results throughout (Fig. 9), although they disagreed about some clades in a few analyses, or yielded slightly different posterior probabilities.

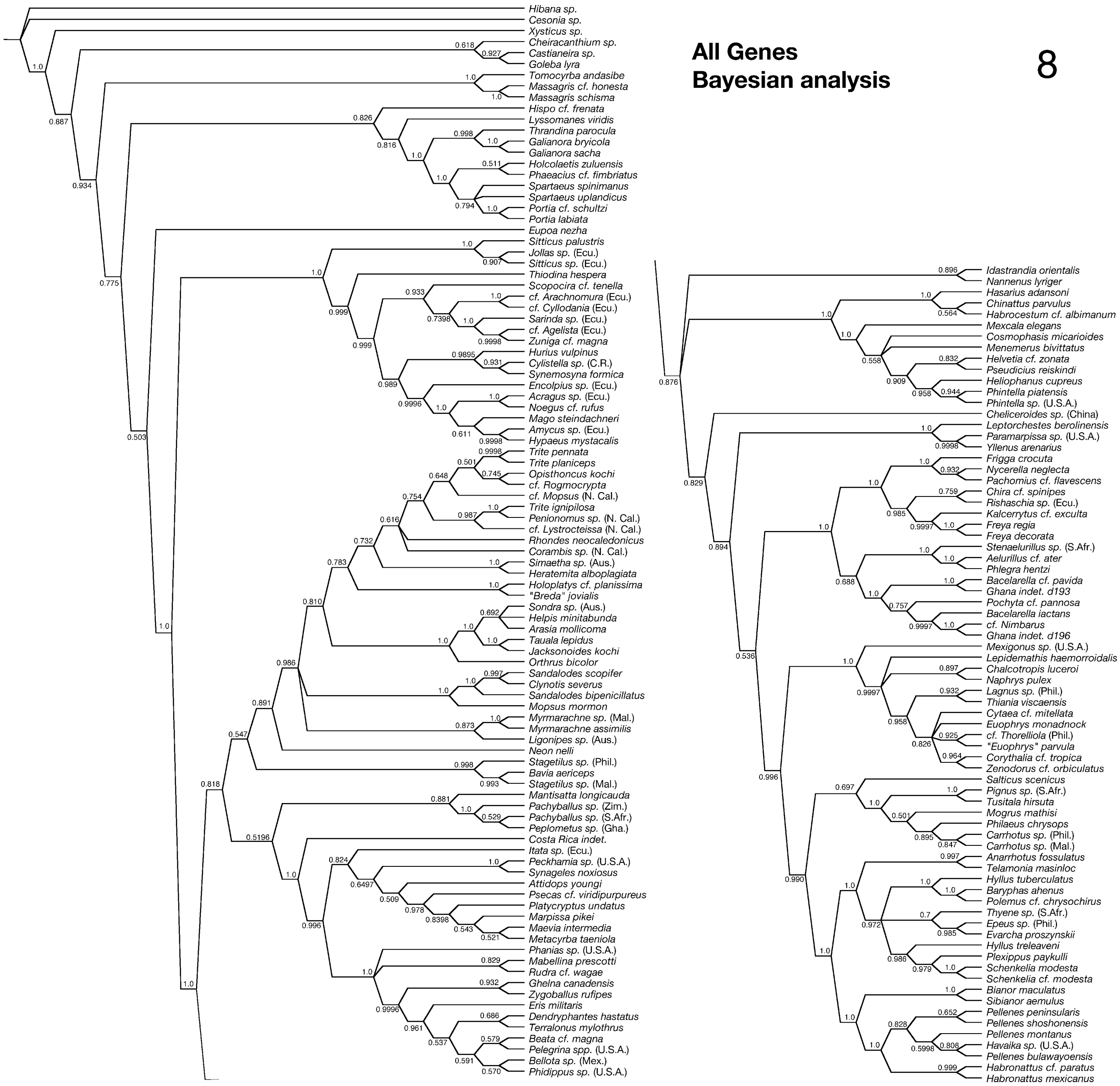
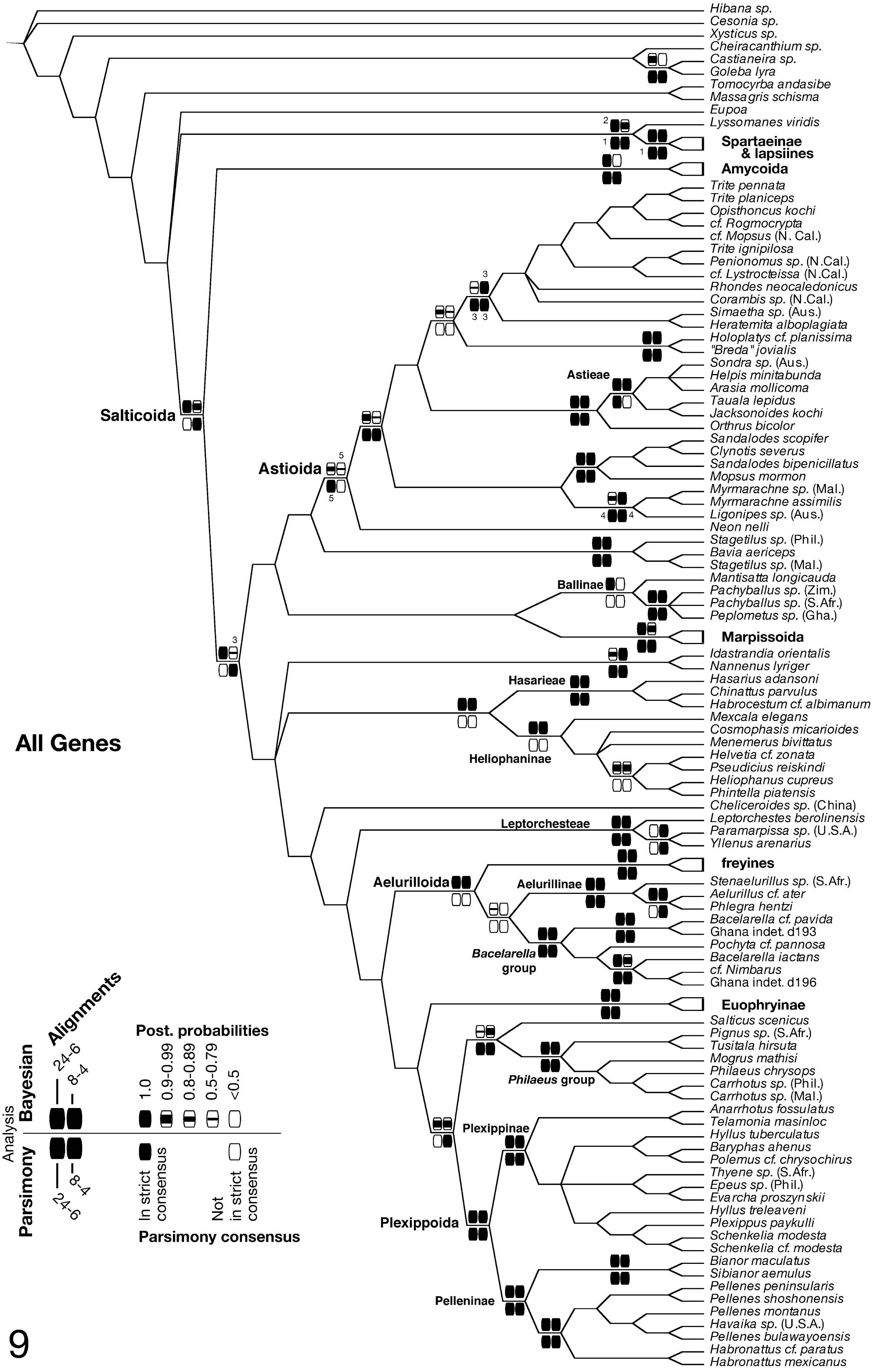


FIGURE 8. Tree from Bayesian analyses of combined matrix of all gene regions (28S, 18S, 16S–ND1, CO1) using 24-6 alignment. Tree shown is majority rules consensus of 280,000 trees sampled from generations 10 million through 150 million from each of two MrBayes runs. Beside branches are estimated posterior probabilities of clades.

The analysis with All-Genes shows patterns similar to those seen in previous studies: a reasonably well-supported Salticoida, poor resolution of the basal divergences of the Salticoida, but with good resolution of smaller groups within the Salticoida (Figs 8, 9). We judge two results of the 24–6 All-Genes analysis to be erroneous: the grouping of *Goleba* Wanless among the outgroups, and the placement of *Hispo* Simon apart from the other hisponines (*Tomocyrba* and *Massagris*). *Goleba*'s placement may have arisen from sparse taxon sampling and long branches in the basal part of the tree. As for *Hispo*, the furrow between the posterior median and posterior lateral eyes is good morphological evidence that it belongs with *Tomocyrba* and *Massagris*. Its apparent misplacement is not surprising because we lack 28S sequence for *Hispo*, and thus its placement is primarily dependent on the fast evolving mitochondrial genes. Other analyses on particular subsets of gene regions were attempted but they had little resolution (18S, CO1), and thus these regions have contributed to the analysis only through the All-Genes analysis.


All Genes
Hibana sp.
Cesonia sp.
Xysticus sp.
Cheiracanthium sp.
Castianeira sp.
Goleba lyra
Tomocyrba andasibe
Massagris schisma
Eupoa
Lyssomanes viridis
Spartaeinae & lapsiines
Amycoida
Salticoida
Trite pennata
Trite planiceps
Opisthoncus kochi
cf. Rogmocrypta
cf. Mopsus (N. Cal.)
Trite ignipilosa
Penionomus sp. (N.Cal.)
cf. Lystrocteissa (N.Cal.)
Rhondes neocaledonicus
Corambis sp. (N.Cal.)
Simaetha sp. (Aus.)
Heratemita alboplagiata
Holoplatys cf. planissima
"Breda" jovialis
Astieae
Sondra sp. (Aus.)
Helpis minitabunda
Arasia mollicoma
Tauala lepidus
Jacksonoides kochi
Orthrus bicolor
Astioida
Sandalodes scopifer
Clynotis severus
Sandalodes bipenicillatus
Mopsus mormon
Myrmarachne sp. (Mal.)
Myrmarachne assimilis
Ligonipes sp. (Aus.)
Neon nelli
Stagetilus sp. (Phil.)
Bavia aericeps
Stagetilus sp. (Mal.)
Ballinae
Mantisatta longicauda
Pachyballus sp. (Zim.)
Pachyballus sp. (S.Afr.)
Peplometus sp. (Gha.)
Marpissoida
Idastrandia orientalis
Nannenus lyriger
Hasarieae
Hasarius adansoni
Chinattus parvulus
Habrocestum cf. albimanum
Mexcala elegans
Cosmophasis micarioides
Menemerus bivittatus
Heliophaninae
Helvetia cf. zonata
Pseudicius reiskindi
Heliophanus cupreus
Phintella piatensis
Cheliceroides sp. (China)
Leptorchesteae
Leptorchestes berolinensis
Paramarpissa sp. (U.S.A.)
Yllenus arenarius
freyines
Aelurilloida
Aelurillinae
Stenaelurillus sp. (S.Afr.)
Aelurillus cf. ater
Phlegra hentzi
Bacelarella cf. pavida
Ghana indet. d193
Bacelarella group
Pochyta cf. pannosa
Bacelarella iactans
cf. Nimbarus
Ghana indet. d196
Euophryinae
Salticus scenicus
Pignus sp. (S.Afr.)
Tusitala hirsuta
Mogrus mathisi
Philaeus group
Philaeus chrysops
Carrhotus sp. (Phil.)
Carrhotus sp. (Mal.)
Plexippinae
Anarrhotus fossulatus
Telamonia masinloc
Hyllus tuberculatus
Baryphas ahenus
Polemus cf. chrysochirus
Thyene sp. (S.Afr.)
Epeus sp. (Phil.)
Evarcha proszynskii
Hyllus treleaveni
Plexippus paykulli
Schenkelia modesta
Schenkelia cf. modesta
Plexippoida
Bianor maculatus
Sibianor aemulus
Pellenes peninsularis
Pellenes shoshonensis
Pellenes montanus
Havaika sp. (U.S.A.)
Pellenes bulawayoensis
Habronattus cf. paratus
Habronattus mexicanus
Pelleninae
Analysis
Bayesian
Parsimony
Alignments
24-6
8-4
Post. probabilities
1.0
0.9-0.99
0.8-0.89
0.5-0.79
<0.5
In strict consensus
Not in strict consensus
Parsimony consensus

9

Our results corroborate previously recognized groups such as the Marpissoida and Amycoida, and reveal several new clades, including a large radiation of Australasian salticids. We will discuss the results group by group.

Astioida *(new)*. A large portion of the sampled species from Australia and New Caledonia fall within a single clade (Figs. 8, 9) that we will name the Astioida, after the contained Astieae (Simon 1901; Wanless 1988). This clade is supported exactly or with some modification by all analyses with the All-Genes matrix. It is supported by the Bayesian analysis on the 24–6 alignment (estimated posterior probability 0.891; excluding *Neon* Simon 0.986), by the Bayesian analysis on the 8–4 alignment (but with *Mantisatta* Warburton included, posterior probability 0.73), and by parsimony with both alignments (but with *Neon* excluded or *Mantisatta* included). It is also supported in the analysis of 28S (Fig. 10).

Because the support for the proposed Astioida is reasonable, we will provisionally accept it as a single clade. However, it is not without doubt, and in particular some subgroups may belong elsewhere. The Astioida can be divided into five major subgroups, each of which appears consistently in various analyses: (1) the Astiae proper (possibly including *Orthrus* Simon), (2) the antlike genera *Myrmarachne* MacLeay and *Ligonipes* Karsch, (3) a clade with *Mopsus* and *Sandalodes* (see Zabka 2000), (4) a large clade of diverse body forms including *Opisthoncus*, *Trite* Simon, *Holoplatys*, and *Simaetha*, and (5) *Neon*. While the inclusion of *Neon* and *Myrmarachne* among the Astioida may be in most doubt (e.g., Fig. 11), these may (as suggested by the All-Genes analysis) be basal astioids, and thus their failure to group with the others by mitochondrial genes may be due to those genes' high rate of evolution. *Neon* and *Myrmarachne* are unusual among the Astioida also for being broadly distributed outside Australasia. Also, *Mantisatta*, placed with the Ballinae in the All-Genes analysis (and with which it shares similar genitalia), in some analyses is grouped as sister to *Neon*, and may belong in the Astioida.

The Astioida includes species of diverse body forms: robust and broad beetle-like species (*Heratemita* Strand, *Simaetha*), narrow bodied elongate forms (*Corambis* Simon, *Holoplatys*), antlike species (*Myrmarachne*), and unremarkable species resembling dendryphantines or plexippines (*Opisthoncus*). Diversity in the Astioida and their convergences with other groups can be seen by examining Simon's (1901–1903) classification, which scatters the astioids among many groups based largely on general body form: he placed *Arasia* Simon and *Helpis* Simon in the Astieae with what we now recognize as lapsiines and some members of the Amycoida; *Orthrus* in the Lyssomaneae; *Holoplatys* and *Corambis* in the Marpissae; *Sandalodes* in the Hylleae, *Philaeus* and others; *Mopsus* in the Thyeneae. The Astioida thus include pluridents, unidents and fissidents (Simon 1901, 1903). Because of our results here, we support Patoleta's proposal (unpublished PhD thesis, cited by Prószyński in his 2002 online Catalogue of Salticidae) to undo Zabka's (1988) combination *Hasarius neocaledonicus* to return the species to *Rhondes*.

Morphological synapomorphies for the Astioida are not yet known; its members are relatively little studied. Astioida genitalia in general are simple, with the embolus fixed to the tegulum. However, some species (*Mopsus*, *Sandalodes*, *Neon*) appear to have a movable embolus. The member of the Astioida about which

FIGURE 9. Summary of phylogenetic analyses on combined matrix of all gene regions (28S, 18S, 16S–ND1, CO1). Tree shown is majority rules consensus of trees sampled from the Bayesian analysis of the 24–6 aligned data. Spots show strength of support from this and other analyses. Top row refers to Bayesian analyses (24–6 and 8–4 alignments). Darkness of spot shows estimated posterior probability of clade as explained at left. Bottom row refers to presence of clade in strict consensus of all most parsimonious trees (black, present; white, absent). Lack of support spots on a branch does not necessarily indicate the branch was poorly supported; for instance, support is not shown on branches within the Plexippoida and other groups because their internal relationships are not our focus of study. With the 24–6 alignment, 1170 most parsimonious trees were found of length 31378; with the 8–4 alignment, 72 trees were found of length 30377. Footnotes: [1] *Eupoa* included in clade. [2] *Hispo* included in clade. [3] *Corambis* excluded from clade. [4] *Corambis* included in clade. [5] *Mantisatta* included in clade.

most phylogenetic commentary has been made is *Neon*, which as we note above is only tentatively included within the group. Logunov (1998) supports a relationship of *Neon* with *Neonella* Gertsch and *Sitticus*. However, the traits Logunov cites as shared with *Neonella* (two teeth on cheliceral promargin, one on retromargin; fourth leg longest; few but strong macrosetae; embolus with spicules; primary and secondary receptacles present) do not appear to be synapomorphies of the two or even of a small clade (Logunov does not claim they are), and at least some of these occur in many other salticids. There is little special that *Neon* and *Neonella* are known to have in common apart from small size. The relationship with *Sitticus* is supported by the presence of well-marked primary and secondary receptacles (Logunov 1998), but the distribution of this condition across the Salticidae has not been described. Thus, there are no known morphological synapomorphies uniting specifically *Sitticus*, *Neonella* and *Neon* alone or in a small clade. Our data strongly support a placement of *Sitticus* elsewhere, in the Amycoida (see below).

We suspect that the Astioida will include many other Australasian genera not sampled here such as *Ocrisiona* Simon (Zabka 1990), *Ligurra* Simon and others (Zabka 1994), *Sobasina* Simon, and possibly *Diolenius* Thorell. Few genera that we include among the Astioida are known from outside of Australia, New Zealand and nearby islands. *Holoplatys* and *Orthrus* are known from mainland Asia, as are *Simaetha*-like genera (e.g., *Ligurra*). However, only two groups currently recognized as within the Astioida are distributed broadly beyond Australasia and southeast Asia: the genera *Neon* and *Myrmarachne*. Both are widespread in the Old World and have a few species in the New World.

Leptorchesteae. An unexpected result was the strong support for a relationship among *Yllenus* Simon, *Paramarpissa* F.O. Pickard-Cambridge and *Leptorchestes* Thorell. The first is an Old World ground-dwelling genus resembling *Habronattus* F.O. Pickard-Cambridge, the second is a small tree-bark dwelling group from the American deserts, and the third is an Old World ant mimic. Their relationship is strongly supported in the All-Genes analysis, the 28S analysis, and partially supported (*Leptorchestes* and *Yllenus*) in the 16S–ND1 analysis. Simon (1901) placed *Yllenus* with *Sitticus*; Prószyński (1976) placed it in the Aelurillinae. Logunov (1998) suggested *Yllenus* is most probably near *Menemerus* and *Plexippus*, although no data were cited. *Menemerus* is strongly supported as belonging with the Heliophaninae by molecular data (here and Maddison & Hedin 2003); *Plexippus* belongs with *Evarcha*, *Hyllus* and others according to genitalic and somatic characters (Maddison 1996a) and DNA data (Maddison & Hedin 2003). Logunov and Cutler (1999) provisionally placed *Paramarpissa* with *Icius* and *Pseudicius* based on similar spermathecal structure. However, they do not indicate whether this similarity is a synapomorphy (restricted and derived). This association appears unlikely, as *Pseudicius* is strongly supported as a member of the Heliophaninae by our DNA data and previous somatic and genitalic data (Maddison 1987). However, more recent comments by Logunov and Marusik (2003) propose a relationship between *Yllenus* and *Paramarpissa* based on similar palpi. The relationship with the ant-like *Leptorchestes* was unexpected, but we know of nothing in genitalia or other features that would preclude it. We will use Simon's (1901) name for this group, although it is unclear whether other genera currently included with *Leptorchestes* (*Kima* Peckham & Peckham, *Enoplomischus* Giltay; see Wesolowksa & Szeremeta 2001) should remain. This group known from a few disparate genera may be small, for we know of no other genera unsampled for molecular phylogeny that are obvious candidates for membership in this group.

The *Philaeus* group. A broadly-supported group consists of 5 genera from Eurasia and Africa: *Philaeus* Thorell, *Carrhotus* Thorell, *Mogrus* Simon, *Tusitala* Peckham and Peckham and *Pignus* Wesolowska. The support from the All-Genes and 28S analyses is uncomplicated; the 16S–ND1 analysis supports the group but with *Tomocyrba* Simon included (erroneously, as it is a distantly related basal salticid, a member of the Hisponinae — see Maddison & Needham 2006). Although not obvious in *Carrhotus*, these genera share a prominent lobe on the palp bulb just counterclockwise from the base of the embolus (left palp, ventral view). These genera were scattered by Simon (1901, 1903) among the Hylleae, Aelurilleae and Hasarieae; by Prószyński (1976) among the Heliophaninae, Hyllinae, and Plexippinae. Logunov (1995) proposed a relationship among

Mogrus, *Plexippoides* Prószyński, *Epeus* Peckham and Peckham, *Afraflacilla* Berland and Millot, and *Pseudicius*, based on several genitalic characters. None of these characters appears to be a synapomorphy of the group: the lobe-like terminal apophysis is present more broadly in plexippines (Maddison 1996a) and heliophanines (Maddison 1987), while many other salticids share the other features (curved cymbium, conspicuous distal haematodocha, simple sperm duct, lack of epigynal pocket, simple copulatory openings, prominent accessory glands, distinct spermathecae). Other morphological and DNA data separate these genera (placing *Afraflacilla* and *Pseudicius* in the Heliophaninae, and *Epeus* in the Plexippinae). Because the morphological data available do not contradict our proposed group, we will accept it based on DNA data. As there is no available name for this group, we will use the informal name "*Philaeus* group" for it. The All–Genes analysis gives good support of a relationship of the *Philaeus* group with *Salticus* Latreille and the Plexippoida (Figs. 8, 9).

Hasarieae. A very strongly supported group includes three sampled genera: *Hasarius* Simon, *Habrocestum* Simon, and *Chinattus* Logunov. These share a compact body, similar markings and a small pocket hidden on the dorsal surface of the back edge of the epigynum (Logunov 1999, figs. 17 and 45). The relationship between *Chinattus* and *Habrocestum* has been suggested already (Logunov 1999; Edwards 2002), but the link to *Hasarius* is new. Although Simon (1903) included many genera in the Hasarieae (including many now considered euophryines), we redefine the group to include the three genera sampled here. Based on similar morphology, we tentatively place *Habrocestoides* Prószyński, *Hasarina* Schenkel, and *Mikrus* Wesolowska also within the Hasarieae.

***Bacelarella* group.** Several species from Ghana with diverse genitalia all fell, to our surprise, as a single clade. Because we have as yet little information as to what described genera might belong here, we will not erect a formal name for this group, but refer to them as the *Bacelarella* group. Jocqué and Szûts (2001) describe a radiation of *Bacelarella* Berland and Millot in west African forests; our results suggest that this may be part of a larger radiation that has generated genitalic forms more diverse than found in most recognized subfamilies — cf. *Nimbarus* (Fig. 4) has a long dorsal tibial apophysis, *Pochyta* cf. *pannosa* (Fig. 5) appears to have the tegulum folded back so as to expose the basal hematodocha, and Ghana indet. d193 (Fig. 6) has the embolus fixed to the tegulum. The separation of *Bacelarella iactans* and *B. cf. pavida* (Fig. 8) suggests that *Bacelarella* as conceived by Szûts and Jocqué (2001) is polyphyletic, assuming that our sampled Ghanan species do not all belong in one genus.

Aelurilloida *(new)*. The All-Genes Bayesian analyses and one of the 28S analyses indicate a relationship among the aelurillines, freyines, and the *Bacelarella* group (Figures 8, 10). The 16S–ND1 analysis puts the freyines and *Bacelarella* group together (with a few other genera). Because of the strong support from the All-Genes Bayesian analyses, we will give this provisional clade a name, the Aelurilloida.

Heliophaninae. *Pseudicius* Simon, *Cosmophasis* Simon and *Mexcala* Peckham and Peckham, as expected based on morphology, were placed within the Heliophaninae.

Euophryinae. *Cytaea* Keyserling, as expected from its genitalia, fell clearly within the Euophryinae.

Plexippoida. Maddison and Hedin (2003) showed that the Pelleninae and Plexippinae are sister groups, together comprising the Plexippoida. With our new sequences we have confirmed, as expected (Maddison 1996a), that *Hyllus* C.L. Koch and *Thyene* Simon are plexippines. In addition, the African *Polemus* Simon, *Baryphas* Simon, and *Schenkelia* Lessert are plexippines, as is the Asian *Anarrhotus* Simon. In the pellenines, *Bianor* Peckham & Peckham and *Sibianor* Logunov are related. *Pellenes montanus* and therefore also its close relative (or senior synonym) *P. lapponicus* Sundevall are confirmed to be pellenines (Logonuv & Marusik 2000), and not members of the plexippine *Evarcha* Simon as proposed by Logunov *et al.* (1999). *Cheliceroides* Zabka, which resembles (at least superficially) *Evarcha*, groups with the Plexippoida by 16S–ND1 (Fig. 11), but the more complete matrix excludes it from the Plexippoida and shows it branching deep within the Salticoida (Figs. 8, 9). Perhaps further sampling from southeast Asia will find close relatives of *Cheliceroides*.

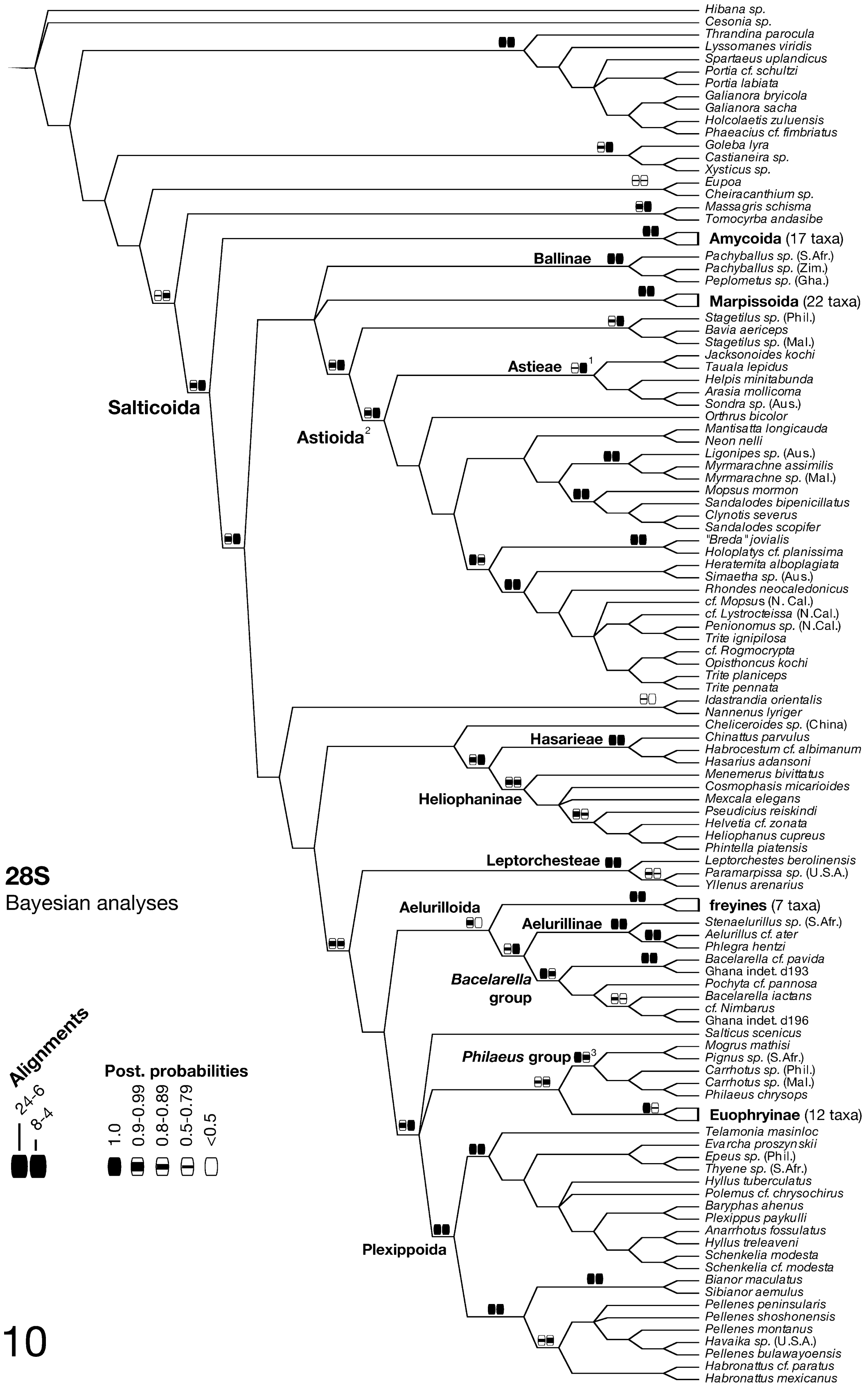


FIGURE 10. Phylogenetic analyses of 28S sequences. Tree shown is majority rules consensus of trees sampled from the Bayesian analysis of 24–6 aligned data. Spots show strength of support with 24–6 and 8–4 alignments. Darkness of spot shows estimated posterior probability of clade. Footnotes: [1] *Orthrus* included in clade. [2] *Mantisatta* included in clade. [3] *Carrhotus* sp. (Phil.) excluded from clade.

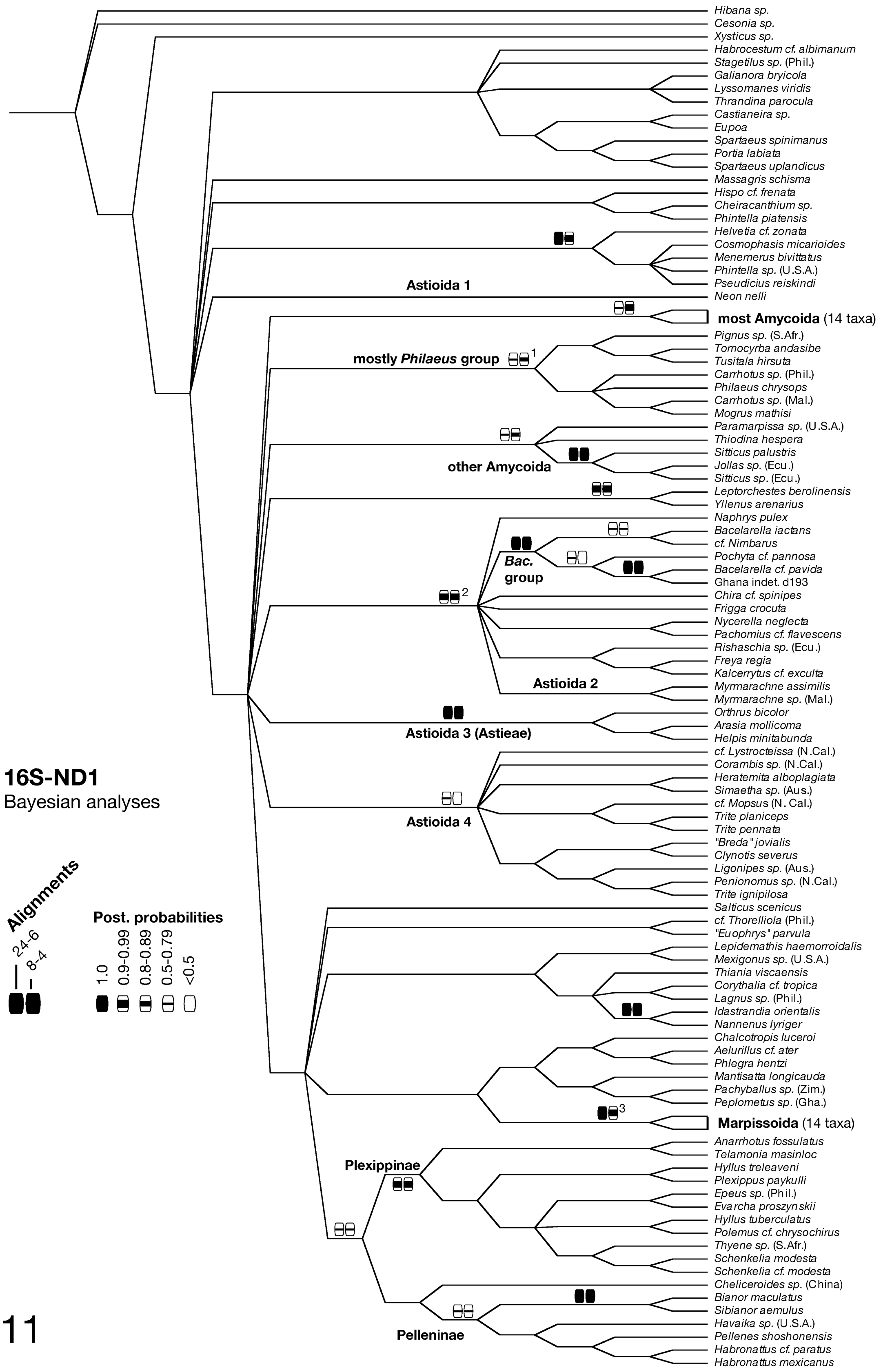


FIGURE 11. Phylogenetic analyses of 16S–ND1sequences. Tree shown is majority rules consensus of trees sampled from the Bayesian analysis of 24–6 aligned data. Spots show strength of support with 24–6 and 8–4 alignments. Darkness of spot shows estimated posterior probability of clade. Footnotes: [1] *Tomocyrba* excluded from clade. [2] *Naphrys* and *Myrmarachne* excluded from clade. [3] *Hispo* included in clade.

Marpissoida. Maddison and Hedin (2003) delimited the Marpissoida to include the Dendryphantinae, Marpissinae and a few other genera. Our new sequences for *Synageles noxiosa* show that it is, unsurprisingly, sister to *Peckhamia* Simon (Fig. 8).

Amycoida. The Amycoida (Maddison & Hedin 2003) remains a well supported clade. We have added to the analysis *Sitticus palustris* Peckham and Peckham. It goes with the *Sitticus* sp. from Ecuador and the *Jollas* sp. (Fig. 8), confirming that the Holarctic *Sitticus* do indeed belong with the Neotropical *Sitticus,* within the Amycoida. Logunov (1998) had suggested *Jollas* is less closely related to *Sitticus* than is *Neon* based on genitalic peculiarities of *Jollas*, but such autapomorphies would not rule out a close relationship of *Jollas* and *Sitticus*. Apart from the male's coppery sheen, *Jollas* in many respects (genitalia, body form, leg proportions, and so on) resembles closely many small species of *Sitticus*. The DNA data support a *Jollas*-*Sitticus* relationship to the exclusion of *Neon* (which is not a member of the Amycoida by any molecular analysis).

Basal salticids. The Salticoida are monophyletic according to Bayesian and one of the parsimony analyses on all genes (Fig. 9). Outside this are the so-called "basal salticids", including the lyssomanines, spartaeines, lapsiines, hisponines, and *Eupoa* Zabka. These results match those previously reported by Maddison & Needham (2006) and Maddison *et al.* (2007) based on a smaller sample of species.

As yet poorly sampled among our taxa are southeast Asian and rainforest African salticids. The southeast Asian ground-dwelling *Nannenus* Simon and *Idastrandia* Strand group together strongly, but are consistently isolated from the other major groups. *Bavia* Simon and *Stagetilus* Simon, foliage or suspended litter dwellers which superficially resemble *Marpissa* C.L. Koch or *Metacyrba* F. O. Pickard-Cambridge, are shown in Figures 8 and 9 as sister to the Astioida, but in other analyses they fall as sister to the Marpissoida.

These phylogenetic results continue to strengthen the pattern (Maddison & Hedin 2003) of large clades being mostly confined to a continental region, and continental regions being dominated by a few clades: the Marpissoida, Amycoida, Euophryinae and the freyines in the Americas; the Heliophaninae, Plexippoida, Aelurillinae in Eurasia and much of Africa; and the Astioida and Euophryinae in Australasia. However, the picture is still incomplete. With better phylogenetic sampling, especially from rainforest Africa and other regions of Asia and Australasia, we will be in a position to understand more fully the biogeography of salticid diversification.

Our choice to use DNA data was based in part on the speed by which it may be gathered. We would have preferred a joint molecular-morphological analysis, but sadly the morphological data are not yet available in a form that can be analyzed. Morphology has informed the current study, but indirectly — our sampling of taxa and interpretation of results would have been severely hampered had the senior author not had decades of experience with salticid morphology. Direct and thorough morphological studies will be important for a complete understanding of the phylogeny of the Salticidae. We are starting to understand their morphology, for instance through recent studies of genitalia (Logunov 1998; Logunov & Cutler 1999; Maddison 1996a; Prószyński 1976). In particular, the discovery that the "tegulum" of some salticids may be a composite of two sclerites (Logunov & Cutler 1999; Logunov 1999) could provide the basis for understanding many new characters in palpi. However, these studies have involved only a few characters and been completed in too few genera. Single characters described in a handful of taxa do not permit analysis. At the moment, therefore, we do not have the morphological data to analyze. In addition, to understand data as phylogenetic evidence, we need analyze them using logical (synapomorphy) or quantitative (e.g., parsimony) phylogenetic methods, which have rarely been used in systematic studies within the Salticidae. At the very least, a character when used as phylogenetic evidence should be described as an explicit claim of a synapomorphy with a clearly stated distribution. Few papers have attempted to make precise claims of morphological synapomorphies across the breadth of the Salticidae (e.g. Wanless 1984; Maddison 1987, 1996a). Even better would be a formal matrix of many characters scored in many genera. Quantitative analysis of a morphological matrix has been undertaken very rarely in the Salticidae (e.g., Rodrigo & Jackson 1992). Morphological data are vital not only for a more comprehensive phylogeny but also for a deeper understanding of the spiders' evolution (Maddison 1996b). It is our hope that the DNA data will stimulate comprehensive studies to score and analyze well-defined morphological characters formally across a broad range of genera.

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APPENDIX 1. Specimens newly sequenced for molecular phylogenetic analysis. All specimens deposited in Spencer Entomological Museum (UBC-SEM). Voucher codes are included with specimens on small labels of form "WPM Voucher DNA d046"". Columns marked 28S, 18S, 16S-ND1, and CO1 show sequence length in parentheses (as used in analyses) and GenBank accession numbers. * identified by M. Zabka

Species	Voucher	Locality	28S	18S	16SND1	CO1
Astioida						
Arasia mollicoma (L. Koch)*	d046	AUSTRALIA: New South Wales: Munmorah Area	(659) EU815483	(1660) EU815532	(597) EU815550	(976) EU815598
"Breda" jovialis (L. Koch)	d021	AUSTRALIA: SOUTH AUSTRALIA: Adelaide (S 34.9 E 138.6)	(669) EU815472		(913) EU815543	(971) EU815588
Clynotis severus (L. Koch) *	d023	AUSTRALIA: New South Wales: Jarvis Bay	(749) EU815473		(901) EU815544	
Corambis sp. (N. Cal.)	d203	NEW CALEDONIA: Pouembout (S 21.12 E 164.95)			(907) EU815575	
Holoplatys cf. *planissima* (L. Koch)*	d045	AUSTRALIA: New South Wales: Munmorah Area	(734) EU815482			(967) EU815597
Jacksonoides kochi (Simon)	d011	AUSTRALIA: Queensland: Cow Bay (S 16.2 E 145.4)	(765) EU815466	(1313) EU815526		(974) EU815582
Ligonipes sp. (Aus.)*	d048	AUSTRALIA: Ku-ring-gai Chase National Park	(533) EU815484		(921) EU815551	(965) EU815599
cf. *Lystrocteissa* sp. (N. Cal.)	d054	NEW CALEDONIA: Col d'Amieu (S 21.55 E 165.85)	(632) EU815485		(603) EU815552	
Mopsus mormon Karsch	d018	AUSTRALIA: Queensland: Cow Bay (S 16.226 E 145.437)	(745) EU815470	(1355) EU815529		(979) EU815586
cf. *Mopsus* (N. Cal.)	d202	NEW CALEDONIA: Prony (S 22.32 E 166.82)	(746) EU815518		(905) EU815574	(970) EU815623
Myrmarachne sp. (Mal.)	d162	MALAYSIA: PAHANG: Tanah Rata (N 4.46 E 101.40)	(749) EU815507		(814) EU815565	(972) EU815616
Ophisthoncus kochi Zabka	d015	AUSTRALIA: SOUTH AUSTRALIA: Adelaide (S 34.9 E 138.6)	(748) EU815468	(1571) EU815528		(968) EU815584
Penionomus sp. (N. Cal.)	d122	NEW CALEDONIA: Mt. Do summit (S 21.75 E 166.00)	(759) EU815498		(838) EU815561	(978) EU815610
Rhondes neocaledonicus (Simon)	d201	NEW CALEDONIA: Prony (S 22.32 E166.82)	(759) EU815517			
cf. *Rogmocrypta* sp.	d205	NEW CALEDONIA: Col d'Amieu (S 21.55 E 165.85)	(742) EU815519			
Sandalodes bipenicillatus (Keyserling)	d019	AUSTRALIA: Queensland: Stratbroke Island	(752) EU815471			(958) EU815587
Sandalodes scopifer (Karsch)	d026	AUSTRALIA: Queensland (S 24.82 E 149.75)	(750) EU815476			(969) EU815591
Simaetha sp. (Aus.)	d027	AUSTRALIA: Queensland: Cow Bay (S 16.2 E 145.4)	(683) EU815477		(899) EU815546	(981) EU815592
Sondra sp. (Aus.)	d078	AUSTRALIA: New South Wales: Gerringong (S 34.736 E 150.791)	(753) EU815489			(955) EU815602
Tauala lepidus Wanless	d024	AUSTRALIA: Queensland: Cow Bay (S 16.2 E 145.4)	(700) EU815474			(971) EU815589
Trite ignipilosa Berland	d206	NEW CALEDONIA: Aoupinie (S 21.17 E 165.32)	(719) EU815520		(906) EU815576	(930) EU815624
Trite pennata Simon	d035	NEW CALEDONIA: Mt. Koghis (S 22.18 E 166.02)	(708) EU815478		(899) EU815547	(902) EU815593
Plexippoida						
Anarrhotus fossulatus Simon	d103	MALAYSIA: Pahang: Taman Negara	(749) EU815492		(916) EU815557	(949) EU815605
Baryphas ahenus Simon	d134	SOUTH AFRICA: Kwazulu-Natal Province: Tembe Elephant Park (S 26.979 E 32.400)	(587) EU815501			(971) EU815612
Bianor maculatus (Keyserling)	d017	AUSTRALIA: SOUTH AUSTRALIA: Glenelg (S 34.973 138.511)	(691) EU815469		(893) EU815542	(971) EU815585
Hyllus treleaveni Peckham & Peckham	d040	SOUTH AFRICA: Kwazulu-Natal Province: Phinda (S 26.866 E 32.274)	(755) EU815480	(1624) EU815531	(907) EU815548	(980) EU815595
Hyllus tuberculatus Wanless & Clark	d200	GHANA: Kakum Forest (N 05.349 W 01.383)	(756) EU815516		(875) EU815573	(970) EU815622
Pellenes bulawayoensis Wesolowska	d075	SOUTH AFRICA: Kwazulu-Natal Province: Sodwana Bay (S 27.54 E 32.66)	(755) EU815488			
Pellenes montanus (Emerton)	d154	USA: Wyoming: Freemont Lake Rd. (N 42.003 W 109.752)	(736) EU815506			
Polemus cf. *chrysochirus* Simon	d197	GHANA: Kakum Forest (N 05.349 W 01.383)	(755) EU815513		(905) EU815570	(977) EU815619
Schenkelia cf. *modesta* Lessert	d198	GHANA: Kakum Forest (N 05.349 W 01.383)	(755) EU815514		(897) EU815571	(997) EU815620
Schenkelia modesta Lessert	d074	SOUTH AFRICA: Kwazulu-Natal Province: Phinda (S 26.866 E 32.274)	(755) EU815487		(908) EU815554	(972) EU815601

APPENDIX 1 (continued)

Species	**Voucher**	**Locality**	28S	18S	16SND1	CO1
Thyene sp. (S. Afr.)	d073	SOUTH AFRICA: Kwazulu-Natal Province: Phinda (S 26.866 E 32.274)	(755) EU815486		(855) EU815553	(960) EU815600
***Philaeus* group**						
Carrhotus sp. (Mal.)	d106	MALAYSIA: Sabah: Mt. Kinabalu (N 06.008 E 116.543)	(516) EU815494		(874) EU815559	(968) EU815606
Mogrus mathisi (Berland & Millot)	d192	SOUTH AFRICA: Northern Province: Pietersberg (S 23.894 E 29.499)	(673) EU815508		(908) EU815566	
Philaeus chrysops (Poda)	d025	ITALY: Calabria: Gozza (N 38.413 E 16.335)	(720) EU815475	(1449) EU815530	(925) EU815545	(958) EU815590
Pignus sp.	d041	SOUTH AFRICA: Kwazulu-Natal Province: Tembe Elephant Park (S 26.979 E 32.400)	(641) EU815481		(911) EU815549	(970) EU815596
Tusitala hirsuta Peckham & Peckham	d080	SOUTH AFRICA: Mpumalanga Province: Badplaas Resort, Embuleni Nature Resort		(1660) EU815533	(906) EU815555	
***Bacelarella* group**						
Bacelarella cf. *pavida* Szuts & Jocqué	d195	GHANA: Kakum Forest (N 05.349 W 01.383)	(755) EU815511	(1608) EU815538	(899) EU815569	(876) EU815618
Bacelarella iactans Szuts & Jocqué	d194	GHANA: Kakum Forest (N 05.349 W 01.383)	(756) EU815510		(906) EU815568	
cf. *Nimbarus* sp.	d218	GHANA: Kakum Forest (N 05.349 W 01.383)	(762) EU815523		(844) EU815578	
Pochyta cf. *pannosa* Simon	d217	GHANA: Kakum Forest (N 05.349 W 01.383)	(756) EU815522		(890) EU815577	
Ghana indet. d193	d193	GHANA: Kakum Forest (N 05.349 W 01.383)	(758) EU815509		(722) EU815567	(955) EU815617
Ghana indet. d196	d196	GHANA: Kakum Forest (N 05.349 W 01.383)	(761) EU815512			
Other groups						
Acragus sp. (Ecu.)	d130	ECUADOR: NAPO: Estación Biológica Jatun Sacha (S 1.067 W 77.617)	(754) EU815499			
Aelurillus cf. *ater* (Kroneberg)	d140	KAZAKHSTAN: Almaty Region (N 43.643 E 75.805)	(753) EU815504	(843) EU815536	(757) EU815564	(968) EU815615
Bavia cf. *aericeps* Simon	d079	MALAYSIA: Sabah: Poring Hot Springs	(746) EU815490			(972) EU815603
Cheliceroides sp. (China)	d222	CHINA: Guangxi: Tianlin County, Langping Village	(638) EU815524		(782) EU815579	
Chinattus parvulus (Banks)	d009	USA: North Carolina (N 35.341 W 83.878)	(755) EU815464	(1596) EU815525		(965) EU815581
Cosmophasis micarioides (L. Koch)	d006	AUSTRALIA: Queensland: Cow Bay (S 16.2 E 145.4)	(705) EU815463		(907) EU815540	(974) EU815580
Cytaea cf. *mitellata* (Thorell)	d010	AUSTRALIA: Queensland: Cow Bay (S 16.2 E 145.4)	(761) EU815465			
Freya decorata (C.L. Koch)	d211	ECUADOR: NAPO: Estación Biológica Jatun Sacha (S 1.067 W 77.617)	(757) EU815521	(1656) EU815539		
Habrocestum cf. *albimanum* Simon	d132	SOUTH AFRICA: Western Cape Prov. (S 32.603 E 19.040)	(755) EU815500		(829) EU815562	(972) EU815611
Idastrandia orientalis (Szombathy)	d108	MALAYSIA: Sabah: Mt. Kinabalu (N 06.008 E 116.543)	(766) EU815496	(953) EU815535	(838) EU815560	(975) EU815608
Leptorchestes berolinensis (C.L. Koch)	d086	POLAND: Lublin	(692) EU815491	(1658) EU815534	(913) EU815556	(877) EU815604
Mexcala elegans Peckham & Peckham	d037	SOUTH AFRICA: Kwazulu-Natal Province: Sodwana Bay (S 27.543 E 32.664)	(675) EU815479			(959) EU815594
Nannenus lyriger Simon	d105	MALAYSIA: Pahang: Taman Negara (N 04.381 E 102.399)	(777) EU815493		(898) EU815558	
Pachyballus sp. (S.Afr.)	d141	SOUTH AFRICA: Kwazulu-Natal Province: Lake St. Lucia. Makakatana (S 28.237 E 32.410)	(752) EU815505	(1657) EU815537		
Peplometus sp. (Gha.)	d199	GHANA: Kakum Forest (N 05.349 W 01.383)	(758) EU815515		(745) EU815572	(942) EU815621
Pseudicius reiskindi Proszynski	d137	INDONESIA: E. Kalimantan, Mahakam River, Kota Bangun	(565) EU815502		(832) EU815563	(956) EU815613
Stagetilus sp. (Mal.)	d107	MALAYSIA: Sabah: Kiabau (N 05.832 E 117.225)	(763) EU815495			(952) EU815607
Stenaelurillus sp. (S. Afr.)	d139	SOUTH AFRICA: Limpopo, Soutpansberg (S 23.034 E 30.013)	(752) EU815503			(965) EU815614
Synageles noxiosus (Hentz)	d113	USA: Mississippi: Marshall County (N 34.832 W 89.471)	(550) EU815497			(975) EU815609
Yllenus arenarius Menge	d013	POLAND: Kozki (N 52.361 E 22.870)	(750) EU815467	(1329) EU815527	(903) EU815541	(739) EU815583