

## A phylogenetic classification of jumping spiders (Araneae: Salticidae)

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**Abstract.** The classification of jumping spiders (Salticidae) is revised to bring it into accord with recent phylogenetic work. Of the 610 recognized extant and fossil genera, 588 are placed at least to subfamily, most to tribe, based on both molecular and morphological information. The new subfamilies Onomastinae, Asemoneinae, and Eupoinae, and the new tribes Lapsiini, Tisanibini, Neonini, Mopsini, and Nannenini, are described. A new unranked clade, the Simonida, is recognized. Most other family-group taxa formerly ranked as subfamilies are given new status as tribes or subtribes. The large long-recognized clade recently called the Salticoida is ranked as a subfamily, the Salticinae, with the name Salticoida reassigned to its major subgroup (the sister group to the Amycoida). Heliophaninae Petrunkevitch and Pelleninae Petrunkevitch are considered junior synonyms of Chrysillini Simon and Harmochirina Simon respectively. Spartaeninae Wanless and Euophryini Simon are preserved despite older synonyms. The genus *Meata* Żabka is synonymized with *Gedea* Simon, and *Diagondas* Simon with *Carrhotus* Thorell. The proposed relationships indicate that a strongly ant-like body has evolved at least 12 times in salticids, and a strongly beetle-like body at least 8 times. Photographs of living specimens of all 7 subfamilies, 30 tribes, and 13 subtribes are presented.

**Keywords:** Phylogeny, taxonomy, systematics, biogeography

Jumping spiders, with more than 5800 species described (World Spider Catalog 2015), are familiar in all non-polar terrestrial ecosystems, and yet there has not been a new comprehensive classification of the family in more than a century. Eugène Simon's 1901–1903 landmark classification of salticids was remarkable for its breadth, covering the family's world-wide diversity. He separated the Salticidae by cheliceral dentition into three large sections (Pluridentati, Fissidentati, Unidentati), an arrangement that Simon suggested, correctly, to be somewhat artificial. His further division of the family into 69 groups is also rather artificial, because heavy reliance on basic body shape led him to group superficially similar species that we now recognize as unrelated. Petrunkevitch (1928) and Roewer (1954) substantially maintained Simon's arrangement. The next major advance was from Prószyński (1976), who used genitalic characteristics, radically reorienting salticid classification to be considerably more natural than Simon's. However, it included only a small fraction of the family's genera, and subsequent work (e.g., Maddison & Hedin 2003a; Bodner & Maddison 2012) has shown the basic form of male genitalia — the general shape of the tegulum and embolus — to be frequently convergent, holding insufficient information to resolve the family reliably. Wanless (1980c, 1981a, et seq.) brought cladistic reasoning to salticids, clarifying relationships among non-salticine salticids. Despite these advances, the relationships of most salticid genera remained unclear.

Five developments now enable a comprehensive new phylogenetic classification of the family. First, an increase in taxonomic effort during the last several decades by Prószyński, Wesolowska, Żabka, Logunov, Galiano, Wanless, Zhang, Maddison, Peng, Ruiz, Marusik, and others has made many species better known. Second, these authors, along with Edwards, Szűts, and others, have improved our phylogenetic interpretations of morphological variation. Third, the compilation of online libraries of illustrations (Prószyński 1995, 2015; Metzner 2015) has greatly facilitated inspection and comparison of morphological variation across the family, giving clues to the placement of many genera. Fourth, electronic catalogs

(Platnick 2014; World Spider Catalog 2015) have assisted many aspects of this work, providing a complete list of target genera to be placed. Molecular phylogenetic studies are the fifth major development. They have approached a sufficient breadth of coverage so as to represent most of the distinctive groups of genera (Hedin & Maddison 2001; Maddison & Hedin 2003a, b; Andriamalala 2007; Su et al. 2007; Maddison et al. 2008, 2014; Bodner & Maddison 2012; Zhang & Maddison 2013, 2014; Ruiz & Maddison in press). They also have enough support that we can be confident of the basic structure of the family (Bodner & Maddison 2012; Maddison et al. 2014).

In order to generate the classification, we would ideally perform a phylogenetic analysis for all genera of salticids based on scored character data, both molecular and morphological. Such formal data are not available for most of the genera, and waiting for them would leave us without a good classification for years. However, we have a strong scaffold from the molecular phylogeny, and we can identify where most salticid genera would attach to it, based on similarities in genitalic and somatic features, even if we lack clear synapomorphies. The classification proposed here (Tables 1 and 2) is therefore based on both molecular and morphological information. It is, of course, tentative, but by placing most salticid genera into groups, it increases the chances that each will be considered further, no doubt leading to revisions in the arrangement.

### METHODS

The list of genera to be placed in groups was compiled from Platnick's (2014) catalog version 15 by special modules in Mesquite 3.01 (Maddison & Maddison 2014), which allowed easy tabulation of species and geographic distribution. To this were added new genera and synonymies from some more recent papers (Wesolowska et al. 2014; Żabka 2014; Caleb et al. 2015; Dunlop et al. 2015; Patoleta & Żabka 2015; Richman 2015; Zhang & Maddison 2015; Edwards in press; Ruiz & Maddison in press). Although an attempt was made to include all described genera, a few species described after the date of Platnick (July 2014) are missing from the counts.

Counts of species currently in subtribes and tribes are given, but I did not attempt to decide for every species whether it belonged in the tribe or subtribe. Rather, the counts for a taxon are derived from the counts of species currently assigned to its contained genera. Given the state of salticid taxonomy, there are some genera that contain species properly belonging to different tribes, and so some will be misassigned in the counts given. These species counts should therefore not be relied upon for quantitative analyses; they are intended merely to convey a sense of diversity.

Authors of family-group taxon names are given in Table 1, and of generic names in Table 2, rather than listed in the text on first use. Synonymies under each taxon include any synonyms and changes of rank, as well as the names used by Simon (1901, 1903), Petrunkevitch (1928), Roewer (1954) and Prószyński (1976).

**Family-group taxa and ranking.**—My goal is not to question generic limits, but to place existing genera within suprageneric taxa (subfamilies, tribes and subtribes). A few family-group taxon names for salticids were proposed in the 19th century: Attidae by Sundevall (1833), Salticidae by Blackwall (1841), Lyssomanidae by Blackwall (1877), Dendryphantidae by Menge (1879), Athamii and Simonellii by Peckham et al. (1889), and Synemosinae, Ballinae, Marptusi and Phidippi by Banks (1892). F.O. Pickard-Cambridge's *Biologia Centrali Americana* (section containing salticid classification published 1900) added Synageleae, Amyceae, and Homalotteae. However, one major work provided most of the names needed for our current family-group taxa: Simon's second edition of *Histoire Naturelle des Araignées* (1901, 1903). Simon gave the first comprehensive and detailed classification of the family, adding dozens of names for taxa through his many "groups".

Salticid classification moved from Simon's groups toward a system of taxa ranked as subfamilies beginning with Petrunkevitch (1928), who dispensed with the rank of "group", instead consolidating Simon's 69 groups to form 23 subfamilies, a few of which were new. Roewer (1954) maintained Petrunkevitch's subfamilies, but layered them over top of Simon's groups and a few new groups of his own. Prószyński (1976) and most of the subsequent literature has focused on subfamily as the primary rank for suprageneric taxa within Salticidae. Since Prószyński (1976), one subfamily has been added by each of Wanless (1984a), Bodner & Maddison (2012), Edwards (in press), and Ruiz & Maddison (in press).

In recent years, unranked taxa such as the Amycoidea (Maddison & Hedin 2003a) have been established for salticid groups. This has been convenient, especially while our understanding of salticid relationships was changing rapidly. However, these unranked groups, along with the failure to place many genera into higher taxa, has left the classification in disarray, with subfamilies (such as Heliophaninae) existing alongside Simon's groups (such as Hasarieae) of unclear rank, and with many genera unplaced. Although ranks carry no biological meaning, a system of ranked taxa can be useful to provide a predefined low-resolution subset of highlighted clades for non-experts and alphabetizers. I therefore attempt to regularize salticid taxa into standard ranks.

There are two primary consequences of the review of ranking. First, most subfamilies are demoted to tribes, as per status changes indicated in Table 1. The traditional use of

"subfamily" in salticids is too fine-grained, with dozens of subfamilies and little chance for a formal higher order structure. Salticid systematists may have been inclined to use such small subfamilies because of the difficulty of finding broader relationships before molecular data were available. The new classification has 7 subfamilies and 30 tribes (Table 1).

Second, the name "Salticoidea", previously applied to the enormous clade of familiar salticids, will change its meaning to a stricter sense (to exclude the Amycoidea) so as to permit the larger clade to be renamed as a formal subfamily, the Salticinae. Several other unranked taxa that serve to group tribes together remain within the Salticinae, including the Amycoidea, Astioidea, Marpissoida and Saltafresia.

The use of tribes and subtribes leads to ambiguity in the meaning of the adjectival forms "salticine", "spartaeine", "dendryphantine", "plexippine", and "aelurilline". If not otherwise specified, by default I use "salticine" to refer to the subfamily, "spartaeine" to the tribe, and the last three to the respective subtribes. For the last three, this convention most closely maintains previous use of the terms.

**Phylogenetic decisions.**—The broader structure of this classification is based primarily on recent molecular phylogenetic results (Fig. 1; Hedin & Maddison 2001; Maddison & Hedin 2003a; Su et al. 2007; Maddison et al. 2008, 2014; Bodner & Maddison 2012; Zhang & Maddison 2013; Ruiz & Maddison in press), as well as a few unpublished molecular results. I would not have relied so much on the molecular results were they nonsensical to the morphological patterns, but they are not. The groups discovered by molecular data have coherence in general body form, in genitalia, and in geographical distribution. However, we lack precise morphological synapomorphies to corroborate many of our groups. While such synapomorphies no doubt exist, to date we have examined too few character systems in too little detail to have found them. I have given preference to molecular data primarily because we have hundreds of molecular characters, but only a few well gathered and consistently described morphological characters.

The molecular phylogeny is merely a skeleton, as molecular data have been gathered for only about half of the genera (Table 2 marks genera for which molecular data are available). Thus, I have added flesh to the bones by attaching other genera by morphological data, with varying degrees of certainty. In some cases, clear synapomorphies link a genus to a group well placed by molecules (e.g., *Kima* and others sharing the loss of retromarginal cheliceral teeth and ant-like body with the well-placed *Leptorchestes*). In other cases, there are no documented linking traits well demonstrated to be derived, but an overwhelming resemblance in many traits establishes a placement firmly (e.g., *Simaethula* as a simaethine). Under each tribe or subtribe, if there are no molecular data or previous literature justifying the inclusion of a genus, I give some indication as to why it is placed there. In making such choices, I am reassured by our experience in gathering molecular data: in many cases we have guessed by morphology that a genus would be in a particular group even though we lacked clear synapomorphies, and the molecular data have almost always corroborated our guess.

Molecular synapomorphies are indicated for some of the new tribes and subfamilies. Insofar as these are single nucleotide site changes, they do not supply strong evidence for monophyly,

but are given for the sake of the formal diagnosis of the new taxa. No attempt was made to list such molecular synapomorphies for other taxa.

In order to assess morphological similarities and synapomorphies, besides consulting the literature, I made heavy use of Prószyński's (2015) compilation of drawings, and to a lesser extent Metzner's (2015). Not only does Prószyński's compilation bring together in one place most of the illustrations in the literature, but it also includes many illustrations of Prószyński's that are not otherwise published, including of type specimens. This resource had an important influence at every stage of this project, for every tribe and subtribe, even where not directly cited below. Without it, the current classification would have taken far longer to achieve.

**Palps.**—Since Prószyński's (1976) work, the male palp has been an important focus of salticid systematics. It provides convincing or potential synapomorphies for many groups: Onomastinae, Lyssomaninae, Spartaetina, Holcolaetina, Marpissoida, Ballini, Dendryphantina, Neonini, Mopsini, Chrysillini, Euophryini, Aelurillina, and Plexippini. Several axes of variation are evident: whether the embolus is movable, whether the bulb is circular, and whether the functional tegulum appears divided by a cleft. A thorough review is beyond the scope of this paper, but some distinctions used in the discussion of taxa are explained here.

"Fixed embolus" is used to refer to an embolus that is more or less immovable relative to the tegulum, being fused thereto. "Freely movable embolus", in contrast, refers to an embolus (often spiral in form) that has substantial freedom of movement relative to the tegulum, with an extensive embolic hematodocha. There is not always a clear distinction between fixed and free, as some species have a small embolic hematodocha that permits a slight bend of the embolus away from the tegulum. Several clades have both fixed- and movable-embolus palps (e.g., Amycoidea, Astioida, Marpissoida, Euophryini, Aelurillini).

For fixed-embolus palps, there are two basic forms, a narrower oval form (e.g., *Hypaeus*, *Menemerus*, *Freya*, *Clynotis*, *Anarrhotus*, *Pellenes*, *Sitticus distinguendus* (Simon, 1868)) and a circular form (e.g., *Amycus*, *Afraflacilla*, *Chira*, *Myrmarachne*, *Epeus*, *Habronattus*, *Sitticus fasciger* (Simon, 1880)). The former typically have the embolus originating at about 9:00 to 10:00 (as on a clock face, left palp, ventral view), while the latter have the embolus arising at 8:00, or 5:00, or 2:00, or even further counterclockwise. These variants appear to be simply points along a continuum of rotation of the bulb, with the embolus getting longer and the bulb more circular as the origin of the embolus is rotated further counterclockwise. Many clades, well supported by molecular and other morphological data, separately show a diversity of rotations. Indeed, the exemplary genera noted above are respectively paired phylogenetically, with *Hypaeus* and *Amycus* both amycines, *Menemerus* and *Afraflacilla* both chrysillines, and so on. This strongly indicates considerable homoplasy in bulb rotation, and is the reason I mostly ignore the degree of rotation (embolus length), unlike Prószyński (2015), whose classification (unpublished by the rules of the ICZN 2012) appears to be heavily influenced by degree of rotation. Similar homoplasy is seen in the rotation of the spiral embolus in movable-embolus palps, where the embolus can vary from a simple curve to

more than 720 degrees of spiralling (repeated in the marpissoids and many euophryine subclades).

Those fixed-embolus palps with a short embolus (i.e., bulb narrow, oval, less rotated) often have a cleft cutting diagonally from the base of the embolus across the functional tegulum, as in freyines (Galiano 1982, fig. 2) and hasariines (Logunov 1999a, fig. 24). This cleft is also seen in palps that have a movable embolus, as in dendryphantines, where the cleft forms the "tegular ledge" of Maddison (1996, fig. 3). The two regions on either side of the cleft have been named variously by authors: the more basal region (toward the subtegulum) is called the "shoulder" of the tegulum by Maddison (1996), the tegulum proper by Logunov & Cutler (1999), and the basal division of the tegulum by Edwards (in press). The region distal to the cleft (toward the embolus) is called the radix by Logunov and Cutler (1999), and the distal division of the tegulum by Edwards (in press). In more circular, rotated bulbs, this cleft is less distinct and may be absent.

## CLASSIFICATION

A summary of the classification is given in Table 1, and is presented in relation to recent phylogenetic results in Fig. 1. The placement of salticid genera into subfamilies, tribes, subtribes, and unranked clades is given in Table 2, and repeated in machine-readable form in supplemental materials, online at <http://dx.doi.org/10.1636/R15-55.s1>. Photographs of living representatives of each of these groups are shown in Figs. 2–136.

There are four categories of genera that I leave as "*incertae sedis*". Among the extant species, some are poorly enough known that we cannot even decide whether they are salticines or not ("*Salticidae incertae sedis*", 9 genera). Others are well enough described that we know they belong to the Salticinae, but their placement is unclear, usually because we lack clear synapomorphies to place them ("*Salticinae incertae sedis*", 48 genera). The fossil genera (Dunlop et al. 2015) include some that are clearly non-salticines ("*Fossil Salticidae incertae sedis*, not in the Salticinae", 7 genera) and others poorly enough known that we cannot place them in, or exclude them from, any subfamily ("*Fossil Salticidae incertae sedis*", 6 genera). All remaining genera of salticids, 540 in total, have been placed to tribe, major clade, or subfamily.

### Family Salticidae Blackwall, 1841

Sundevall, 1833: Attidae  
 Blackwall, 1841: Salticidae  
 F.O. Pickard-Cambridge, 1900: Salticidae  
 Simon, 1901: Salticidae  
 Peckham & Peckham, 1909: Attidae  
 Petrunkevitch, 1928: Salticidae  
 Roewer, 1954: Salticidae

**Remarks.**—See Edwards (2011) regarding the synonymy of *Attus* with *Salticus*, and thus the preference for Salticidae over Attidae.

**Monophyly:** Jumping spiders are united by the large anterior median eyes in the form of a long cone (Scheuring 1914; Ramírez 2014) whose retinas are vertical strips (Land 1969a; Blest et al. 1990) and by the eye arrangement: medium-sized anterior lateral eyes (ALE) just beside or behind the anterior

Table 1.—Summary of classification.

- Family Salticidae** Blackwall, 1841  
**Subfamily Onomastinae** Maddison, *subfam. nov.*  
**Subfamily Asemoneinae** Maddison, *subfam. nov.*  
**Subfamily Lyssomaninae** Blackwall, 1877  
**Subfamily Spartaecinae** Wanless, 1984  
    **Tribe Spartaecini** Wanless, 1984, *stat. nov.*  
        **Subtribe Spartaecina** Wanless, 1984, *stat. nov.*  
        **Subtribe Holcolaetina** Simon, 1901, *stat. nov.*  
    **Tribe Cocalodini** Simon, 1901, *stat. nov.*  
    **Tribe Lapsiini** Maddison, *trib. nov.*  
**Subfamily Eupoinae** Maddison, *subfam. nov.*  
**Subfamily Hispaninae** Simon, 1901  
**Subfamily Salticinae** Blackwall, 1841  
    **Clade Amycoidea** Maddison & Hedin, 2003  
        **Tribe Gophonini** Simon, 1901, *stat. nov.*  
        **Tribe Sitticini** Simon, 1901, *stat. nov.*  
        **Tribe Bredini** Ruiz & Maddison, 2015, *stat. nov.*  
        **Tribe Scopocirini** Simon, 1901, *stat. nov.*  
        **Tribe Thiodinini** Simon, 1901, *stat. nov.*  
        **Tribe Sarindini** Simon, 1901, *stat. nov.*  
        **Tribe Simonellini** Peckham, Peckham & Wheeler, 1889, *stat. nov.*  
        **Tribe Huriini** Simon, 1901, *stat. nov.*  
        **Tribe Amycini** F.O. Pickard-Cambridge, 1900, *stat. nov.*  
    **Clade Salticoida** Maddison & Hedin, 2003, new delimitation  
        **Tribe Agoriini** Simon, 1901, *stat. nov.*  
        **Tribe Baviini** Simon, 1901, *stat. nov.*  
    **Clade Astioida** Maddison, Bodner & Needham, 2008  
        **Tribe Myrmarachnini** Simon, 1901, *stat. nov.*  
        **Tribe Neonini** Maddison, *trib. nov.*  
        **Tribe Astiini** Simon, 1901, *stat. nov.*  
        **Tribe Mopsini** Maddison, *trib. nov.*  
        **Tribe Viciriini** Simon, 1901, *stat. nov.*  
            **Subtribe Viciriina** Simon, 1901, *stat. nov.*  
            **Subtribe Simaethina** Simon, 1903, *stat. nov.*  
    **Clade Marpissoida** Maddison & Hedin, 2003  
        **Tribe Ballini** Banks, 1892, *stat. nov.*  
        **Tribe Tisanibini** Maddison, *trib. nov.*  
        **Tribe Dendryphantini** Menge, 1879, *stat. nov.*  
            **Subtribe Synagelina** F.O. Pickard-Cambridge, 1900, *stat. nov.*  
            **Subtribe Itatina** Simon, 1901, *stat. nov.*  
            **Subtribe Marpissina** Simon, 1901, *stat. nov.*  
            **Subtribe Dendryphantina** Menge, 1879, *stat. nov.*  
    **Clade Saltafresia** Bodner & Maddison, 2012  
        **Tribe Nannenini** Maddison, *trib. nov.*  
        **Tribe Hasariini** Simon, 1903, *stat. nov.*  
        **Tribe Chrysillini** Simon, 1901, *stat. nov.*  
    **Clade Simonida** Maddison, *nov.*  
        **Tribe Leptorchestini** Simon, 1901, *stat. nov.*  
        **Tribe Euophryini** Simon, 1901, *stat. nov.*  
        **Tribe Salticini** Blackwall, 1841, *stat. nov.*  
        **Tribe Aelurillini** Simon, 1901, *stat. nov.*  
            **Subtribe Aelurillina** Simon, 1901, *stat. nov.*  
            **Subtribe Freyina** Edwards, 2015, *stat. nov.*  
            **Subtribe Thiratoscirtina** Bodner & Maddison, 2012, *stat. nov.*  
        **Tribe Plexippini** Simon, 1901, *stat. nov.*  
            **Subtribe Plexippina** Simon, 1901, *stat. nov.*  
            **Subtribe Harmochirina** Simon, 1903, *stat. nov.*

median eyes (AME), behind which are the smallest eyes, behind which are the medium-sized posterior eyes. The smallest eyes, which are sometimes almost as large as the others, are here and traditionally referred to as the posterior medians (PME), although Homann (1971) argues that they are homologous to the posterior laterals of other spiders. This placement of the PMEs and posterior lateral eyes (PLE) results from a strong curvature of the posterior eye row, which can be considered another synapomorphy (Ramírez 2014). The jumping behaviour (Parry & Brown 1959; Hill 2010b), more precise than in other spiders, likely implies synapomorphies in cuticle, muscle or nervous systems, but they have not been described. Ramírez (2014) indicates several other possible synapomorphies for the family: loss of cylindrical gland spigots, gain of a median apophysis, and reversal to prograde leg orientation. Molecular data concur that the family is monophyletic (Maddison et al. 2014).

*Subdivision:* The basic division of the family established here, into 7 subfamilies, is based on both morphological (Wanless 1980c, 1985; Maddison 1988, 1996; Ramírez 2014) and molecular (Maddison et al. 2014) data. Table 1 presents the classification of salticids to the level of subtribe. Each of the 7 subfamilies, 30 tribes, and 13 subtribes will be considered in turn. The genera assigned to each are listed in Table 2.

With the recognition of the familiar and well-established clade as the subfamily Salticinae, the phylogeny (Fig. 1; Maddison et al. 2014) dictates that we recognize the Hispaninae and Spartaecinae as distinct subfamilies. The Eupoinae are distinctive and of unclear affiliation, and therefore provisionally separated. Most tentative is the separation of the former Lyssomaninae (Wanless 1980c) into three subfamilies, the Onomastinae, Asemoneinae, and Lyssomaninae. These three collectively have been treated as a separate family (Banks 1892; Roewer 1954) or subfamily (Galiano 1976b). They are superficially similar, sharing translucent green or yellow bodies, long legs, complex palps and the ALE placed behind and above the AME to form a second separate eye row. Their complex palps could represent a symplesiomorphy, and so do not provide evidence for their joint monophyly. Both the translucent greenish foliage-dwelling body form and displaced ALEs could be synapomorphies uniting the three groups, but alternatively they could be ancestral for the family or convergent, as other salticids show independent origins of both long-legged green body forms (e.g., *Epeus*, *Orthrus*, *Sidusa*) and displaced ALEs (e.g., *Athamas*, *Mantisatta* – see Wanless 1980c). Benjamin (2010) suggested that his morphological data support the monophyly of the former Lyssomaninae *sensu lato*, but this conclusion does not follow from his analysis, as only a single non-lyssomanine taxon was included. Wanless (1980c) suggested the Lyssomaninae *sensu lato* may be polyphletic, dividing it into three groups that correspond to the three subfamilies recognized here. Molecular analyses suggest that the Onomastinae, Asemoneinae, and Lyssomaninae may not form a clade (Maddison & Needham 2006; Su et al. 2007; Maddison et al. 2008; Bodner & Maddison 2012; Maddison et al. 2014). They are treated as separate subfamilies here, despite ambiguity in the molecular results. Even if they were to fall into a single monophyletic group, their molecular divergences are as deep as those separating other subfamilies (Maddison et al. 2014).

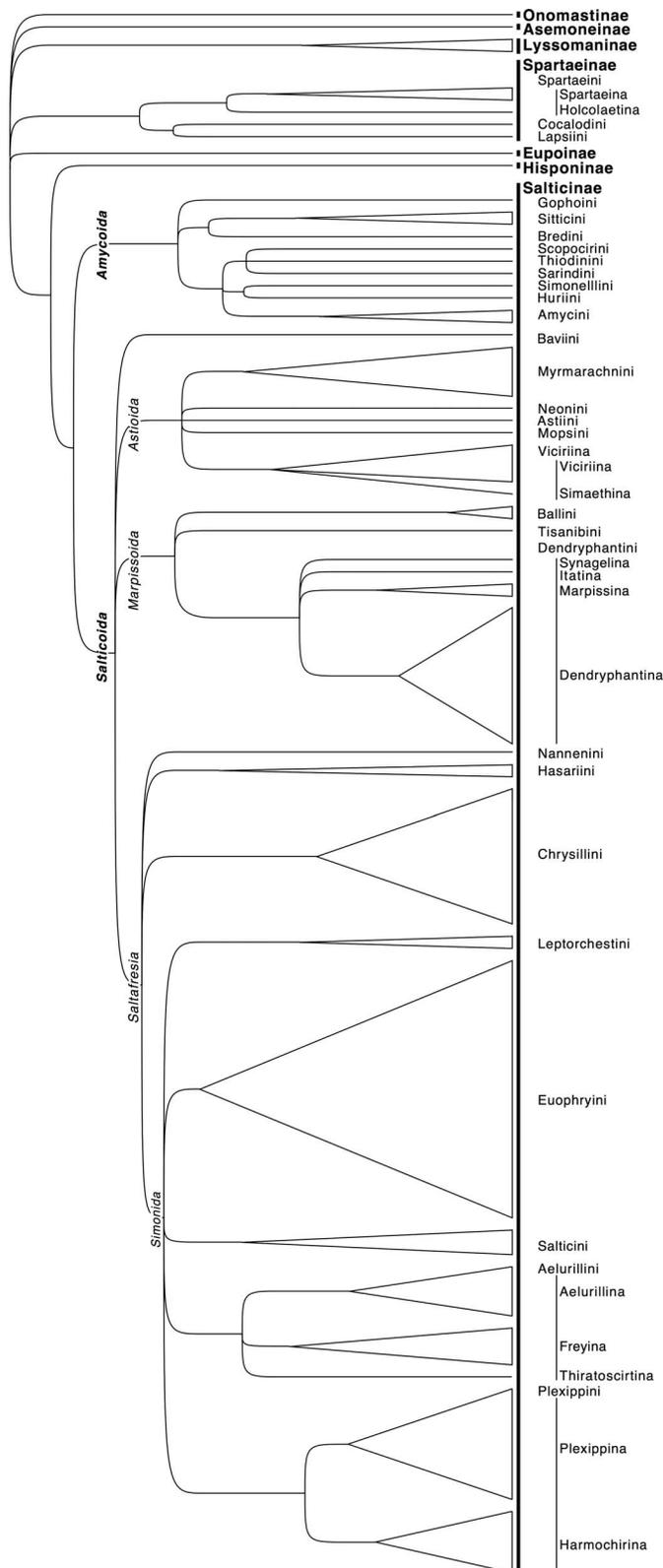


Figure 1.—Summary phylogeny of Salticidae showing higher taxa, based primarily on molecular results of Maddison et al. (2014) and others (see text). The Agorini, somewhere within the Salticoida, is not shown. The span of each terminal clade is drawn approximately proportional to its number of described species. Divergence depths are

Putative ancestral states for salticids in various characters can be inferred from the discussions of synapomorphies under particular clades. Three worth mentioning here are the presence of a median apophysis (Maddison 2009), the presence of large posterior median eyes (Wanless 1984a), and the presence of a claw on the female palp (Maddison 1996). Relatively few salticids show these features, and those that have any one of these are instantly marked as falling outside the Salticinae.

Some Baltic Amber salticids have a characteristic constriction behind the PME, and hence are here considered to be hisponines. The remainder (e.g., *Eolinus*) are clearly non-salticines that cannot yet be placed to any subfamily. Although Wunderlich (2004) considered them “Cocalodinae”, his concept of the subfamily was paraphyletic, without synapomorphies. I therefore consider the non-hisponine Baltic salticids to be non-salticine Salticidae *incertae sedis*. While the Baltic Amber is striking for its lack of Salticinae, the younger Dominican Amber appears remarkably modern, including extant genera in such salticine groups as the euophryines and gophines (Wunderlich 1982; Wunderlich 1988; Wolff 1990; Penney 2008).

**Subfamily Onomastinae Maddison, subfam. nov.**

<http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:74993737-8A80-48B6-8660-6EF149DD7A6E>  
(1 genus; Fig. 2)

**Type genus.**—*Onomastus* Simon, 1900

**Remarks.**—Delicate, translucent and long-legged, with highly complex palps, from the Asian tropics. As in lyssomanines and asemoneines, the ALE are above the AME, forming two separate rows. Benjamin (2010) divides *Onomastus* into two groups, a Southeast Asia clade with a broad conductor and epigynal folds, and a South Asia clade with a medial branch on the median apophysis and a TA3 tegular apophysis.

**Monophyly and Diagnosis:** Wanless (1980b) proposes the distinctive tegular apophysis as a synapomorphy for onomastines (Wanless 1980b, fig. 3E). Benjamin (2010) indicates two additional synapomorphies for *Onomastus* species, the absence of the retrolateral tibial apophysis (Benjamin 2010, fig. 4A) and the dorsal origin of the embolus (Benjamin 2010, figs. 9A, 15A).

**Subfamily Asemoneinae Maddison, subfam. nov.**

<http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:018DD4F2-4695-4E50-A287-DD8ADFC151E2>  
(5 genera; Figs. 3, 4)

**Type genus.**—*Asemonea* O. Pickard-Cambridge, 1869

**Remarks.**—The African and Asian asemoneines are translucent and long-legged (Wanless 1980a, c), resembling onomastines and lyssomanines. They correspond to Wanless’s (1980c) “Group III” among the lyssomanines *sensu lato*. *Asemonea* is widely distributed in the African and Asian tropics. Most of the rest of the group’s diversity is in Africa, with four genera occurring in Madagascar.

← shown approximately proportional to their inferred ages from Bodner & Maddison (2012) and Zhang & Maddison (2013), with ages not included therein interpolated subjectively using branch lengths from Maddison et al. (2014).

*Monophyly and Diagnosis:* This group is distinguished by the unusually medial position of the PME, distinctly closer to the midline than is the inner edge of the ALE, an apparent synapomorphy (Wanless 1980c, figs. 2D, E, F). Molecular data (Maddison et al. 2014) unite the three sampled asemoneines, *Asemonea*, *Goleba* and *Pandisus*. Logunov (2004) suggests *Hindumanes* is near *Pandisus*, sharing their minute PLE.

**Subfamily Lyssomaninae** Blackwall, 1877  
(2 genera; Figs. 5–7)

Blackwall, 1877: Lyssomanidae  
Peckham & Peckham, 1886: Lyssomaneae  
Peckham, Peckham & Wheeler, 1889: Lyssomaneae,  
Lyssomanii  
Thorell, 1895: Lyssomaninae  
F.O. Pickard-Cambridge, 1900: Lyssomaneae  
Simon, 1901: Lyssomaneae  
Petrunkevitch, 1928: Lyssomaninae  
Roewer, 1954: Lyssomanidae  
Galiano, 1976b: Lyssomaninae

**Remarks.**—Lyssomanines are translucent and long-legged, usually green or yellow, from the American tropics (Galiano 1980, 1998; Logunov & Marusik 2003b; Logunov 2014). They dwell on foliage, especially large leaves. As in asemoneines and onomastines, the ALE are above the AME, forming a second separate row. Two genera are described, although Maddison et al.'s (2014) results suggest that *Lyssomanes* may be paraphyletic with respect to *Chinoscopus*.

*Monophyly:* Wanless (1980c) suggests the membranous secondary conductor as a possible synapomorphy of lyssomanines (Wanless 1980c, figs. 2G, H). Molecular data (Maddison et al. 2014) strongly support the monophyly of the group.

**Subfamily Spartaeinae** Wanless, 1984  
(29 genera; Figs. 8–20)

Simon, 1901: Boetheae, Cocaleae, Cocalodeae, Codeteae, Cyrbeae, Holcolaetiae, Lineae  
Petrunkevitch, 1928: Boethinae  
Roewer, 1954: Boethinae, Boetheae, Cocaleae, Cocalodeae, Codeteae, Holcolaetiae, Lineae  
Wanless, 1984a: Spartaeinae  
Wunderlich, 2004: Cocalodinae

**Remarks.**—Wanless's Spartaeinae and his "*Cocalodes* group", along with the lapsiines, are united here in the subfamily Spartaeinae. The names used for the subfamily and its contained groups are discussed below under "Problematic names".

*Monophyly:* Among non-salticid salticids, the Spartaeinae lack the distinctive green or yellow translucence of the lyssomanines, onomastines and asemoneines, lack the ocular constriction on the carapace of hisponines, and lack the small shiny bodies of eupoines. In this regard, the Spartaeinae appear generalized, united only by possibly ancestral character states. Together they have no known morphological synapomorphies. It was not necessarily expected therefore that they would be monophyletic. Rodrigo & Jackson (1992) concluded that their

morphological data supported the monophyly of the group (ignoring the lapsiines, of which they were unaware), but this conclusion does not follow from their analyses, because the latter included only a single taxon outside the group (*Asemonea*). Nonetheless, the molecular data (Maddison et al. 2014) clearly show that spartaeines, cocalodines and lapsiines form a clade. Similarly generalized salticids such as *Eolinus* and *Cenattus* are known from Paleogene Baltic amber, but there is no evidence to date that they are also part of this clade.

Appearing frequently in the Spartaeinae are PMEs notably larger than in the Salticinae. However, large PMEs are also seen in some asemoneines, and some Spartaeinae have small PMEs. While PME size is therefore problematical as evidence for monophyly, it can serve as an informal identification aid: all known living salticids with large PMEs that are not *Lyssomanes*-like (i.e., are not translucent and long-legged) belong to the Spartaeinae.

The subgroups of Spartaeinae are clearly defined by geographical range, if not by morphology. The Spartaeini has known synapomorphies, but the Cocalodini and Lapsiini are not distinguished by any documented morphological synapomorphies, appearing simply to be generalized salticids. In practice, they are best distinguished by molecular data or location (Lapsiini are American; Cocalodini are Australasian except for the distinctive *Depreissia*; Spartaeini are Afro-Eurasian, except for a few Australasian species).

**Tribe Spartaeini** Wanless, 1984

Synonymy given under subtribe Spartaeina

**Remarks.**—This group was first recognized by Wanless (1985) when he proposed that *Holcolaetis* and *Sonoita* — the present Holcolaetina — are closely related to what is here called the Spartaeina. Su et al. (2007)'s concept of Spartaeinae matches the tribe Spartaeini here.

Many of the Spartaeini are known to eat other spiders, to build webs, and to invade webs of other spiders (Su et al. 2007). The Spartaeini are primarily African and Asian, with a few representatives in Europe and Australasia.

*Monophyly:* Wanless (1985) proposes abdominal secretory organs as a synapomorphy uniting the members of this group (Wanless 1984b, figs. 16–21; Wanless 1985, fig. 12B). The molecular data (Maddison et al. 2014) strongly support their monophyly.

**Subtribe Spartaeina** Wanless, 1984  
(16 genera; Figs. 8–13)

Simon, 1901: Boetheae, Cocaleae, Codeteae, Cyrbeae, Lineae  
Petrunkevitch, 1928: Boethinae  
Roewer, 1954: Boetheae, Cocaleae, Codeteae, Lineae  
Wanless, 1984a: Spartaeinae

**Remarks.**—This is the Spartaeinae of Wanless (1984a), delimited by the presence of a tegular furrow. It is restricted to the tropics and subtropics of the Old World (Wanless 1978b, 1979, 1981b, c, 1984a, b, 1987). The best-known member is the araneophagous *Portia* (Jackson & Blest 1982; Jackson & Hallas 1986a, 1990; Jackson & Wilcox 1990, 1993;

Jackson 1992a, b, 1995; Clark & Jackson 2000; Jackson et al. 2001, 2008b; Jackson & Nelson 2011; Cross & Jackson 2014). The habitats of Spartaeina range from tree trunks (*Phaeacius*, *Mintonia*) to foliage (*Brettus*, some *Neobrettus*) and suspended litter near the ground (*Taraxella*).

**Monophyly:** A furrow in the tegulum just retrolateral from the base of the embolus, running parallel to the periphery of the tegulum, delimits this group (“tegular furrow”, Wanless 1984a, figs. 35A, C, E). It does not appear to be homologous with the tegular furrow of Ramírez (2014, fig. 157) or the cleft behind the tegular ledge of Maddison (1996). Loss of the median apophysis (Wanless 1984a) is a synapomorphy, but convergent with losses in salticines, hisponines and lyssomanines. In addition, the conductor is lost or extremely reduced in most, though not all (Wijesinghe 1992). The group is strongly supported by molecular data (Su et al. 2007; Maddison et al. 2014).

**Subtribe Holcolaetina** Simon, 1901  
(2 genera; Fig. 14)

Simon, 1901: Holcolaetiae  
Roewer, 1954: Holcolaetiae

**Remarks.**—A strictly African group notable for the prominent conductor on the palp (Wanless 1985). Unlike the Spartaeina, holcolaetines retain a distinct median apophysis. *Holcolaetis* is a large, flat bark dweller reminiscent of *Marpissa* or *Balmaceda*, but instantly recognizable as a non-salticine by its large PME.

**Monophyly:** Wanless (1985) suggests the two genera of holcolaetines share as synapomorphies “the characteristic form of the tegulum, median apophysis and distal haematodocha in males and epigynal flanges in females”. The first three of these have not been well explained as synapomorphies, but the epigynal flanges are distinctive (Wanless 1985, fig. 11J). Molecular data support their joint monophyly (Maddison et al. 2014).

**Tribe Cocalodini** Simon, 1901  
(6 genera; Figs. 18–20)

Simon, 1901: Cocalodeae  
Roewer, 1954: Cocalodeae  
Wunderlich, 2004: Cocalodini, Cocalodinae  
Maddison, 2009: Cocalodinae

**Remarks.**—Cocalodines are non-salticine salticids with large PMEs (except in *Cucudeta* and *Depreissia*), restricted (except for *Depreissia*) to Australasia east of Wallace’s Line (Wanless 1982; Maddison 2009). They are common components of the fauna of New Guinea, with varied body forms (Maddison 2009). Habitats vary, from foliage (*Cocalodes*, some *Tabuina*) to tree trunks (*Allococalodes*, *Yamangalea*, some *Tabuina*) and leaf litter (*Cucudeta*).

**Monophyly:** With the possible exception of the large size of the median apophysis (Maddison et al. in press), there are no known morphological synapomorphies of the group. However they are the only salticids east of Wallace’s Line with a median apophysis on the palp. The molecular data (Maddison et al. 2014) clearly place the five Australasian genera together. The

sixth genus, *Depreissia*, is placed only tentatively with the cocalodines. Known from central Africa and Borneo (Wesołowska 1997; Deeleman-Reinhold & Floren 2003; Szűts & Wesołowska 2003), *Depreissia* resembles an ant or wasp (Christa Deeleman-Reinhold, pers. comm.). Its placement outside the Salticinae is strongly supported by its median apophysis (Maddison et al. in press), absence of a cymbial apical groove cradling the embolus (Maddison et al. in press), and by molecular data (Maddison et al. in press). Molecular data suggest it is the sister group to the remaining cocalodines (Maddison et al. in press).

**Tribe Lapsiini** Maddison, trib. nov.

<http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:173197EF-71CA-4615-8786-4D33210B3BAC>  
(5 genera; Figs. 15–17)

**Type genus.**—*Lapsias* Simon, 1900

**Remarks.**—The Neotropical lapsiines are the only non-salticines other than lyssomanines in the New World. Following Simon’s early description of four *Lapsias* species from Venezuela, no other species were correctly added to this group for more than a century. Recently, several species and four new genera were added (Maddison 2006, 2012; Makhan 2007; Ruiz & Maddison 2012; Ruiz 2013a). Some live on leaf litter (*Soesiladeepakius*, some *Lapsias*), others on foliage (*Galianora sacha* Maddison, 2006), others on mossy tree trunks (*Thrandina*, *Galianora bryicola* Maddison, 2006, other *Lapsias*). The only lapsiine with substantially large PMEs is *Thrandina*.

**Monophyly and Diagnosis:** There is no known morphological synapomorphy for this group. The molecular data strongly support its monophyly, although the unusual *Thrandina* branches deep (Maddison et al. 2014). Diagnostic characters can be found in the molecular data: in the alignments submitted by Maddison et al. (2014) to the Dryad data repository (<http://dx.doi.org/10.5061/dryad.v53h1>), site 110 in CO1 has G in *Thrandina parocula* Maddison, 2006 and the two species of *Galianora* (the only three lapsiines sampled for that gene) versus C in all other salticids sampled. Similarly, in 18S rRNA, sites 522 (A vs. G) and 543 (T vs. C) supply apparent synapomorphies for lapsiines.

**Subfamily Eupoinae** Maddison, subfam. nov.

<http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:BE3B9C99-A02F-40C4-8FF4-A20117EE2771>  
(3 genera; Figs. 21, 22)

**Type genus.**—*Eupoa* Žabka, 1985

**Remarks.**—Known from subtropical Southeast Asia (southern China, Vietnam, Thailand), these are the only known minute litter-dwelling non-salticines, resembling *Neon* or *Neonella*. Other litter-dwelling non-salticines (e.g., *Cucudeta*, *Soesiladeepakius*, some *Lapsias*) are larger-bodied. There are three genera described (Žabka 1985; Zhou & Li 2013a, b; Logunov & Marusik 2014). Their phylogenetic placement is uncertain, but both the molecular data and morphological features indicate they are non-salticines (Maddison et al. 2007, 2014). Zhou & Li (2013a, figs. 90, 91) illustrate the insertion of the highly complex palps into the epigynum.

**Monophyly and Diagnosis:** Eupoines can be recognized by the complex palps (Žabka 1985; Zhou & Li 2013a; Logunov & Marusik 2014), small size, the dorsal abdominal scutum in

the male, anterior eye row wider than posterior (Logunov & Marusik 2014), and the paired pale spots on the abdomen. The last two features could be synapomorphies, though they are weak. The complex palps will likely supply some morphological synapomorphies, but none has been clearly articulated. Molecular data (Maddison et al. 2007, 2014) indicate that eupoinines are distinctive from all of the other subfamilies, but these data do not give evidence for the monophyly of the group, as they are available for only one species (*Eupoa nezha* Maddison & Zhang, 2007). Logunov & Marusik (2014) suggest that the three genera are so close that they might best be considered a single genus. On the other hand, the apparent diversity in palp form is great.

**Subfamily Hisponinae** Simon, 1901  
(9 genera; Figs. 23–27)

Simon, 1901: Hisponeae, Tomocyrbeae  
Petrunkevitch, 1942: Gorgopsininae  
Roewer, 1954: Hisponeae, Tomocyrbeae

**Remarks.**—The only extant subfamily of salticids recognizable in Baltic Amber, this group is diverse in Madagascar but nowhere else. Outside of Madagascar, the Seychelles and Africa, they are known from only a few specimens from Asia (Wanless 1981a; Maddison & Piascik 2014). The constriction behind the small eyes is distinctive. This group has received attention in recent years (Wanless 1981a; Prószyński & Żabka 1983; Wesołowska 1993; Wesołowska & Haddad 2009, 2013, 2014; Szűts & Scharff 2009; Maddison & Piascik 2014), but many species remain to be described.

**Monophyly:** The transverse furrow or constriction in the carapace just behind the small eyes (Fig. 23) can be considered a synapomorphy of hisponines, as can the dual copulatory ducts in females (Maddison & Piascik 2014, figs. 21–23). Molecular data support the monophyly of the group (Maddison et al. 2014).

**Relationships:** Molecular and morphological evidence places the Hisponinae as the sister group to the Salticinae (Bodner & Maddison 2012; Maddison et al. 2014; Ramírez 2014). Morphological synapomorphies potentially uniting the two subfamilies are:

- (1) Reduction of PMEs (Wanless 1984; homoplasious: also reduced in *Cyrba*, *Cucudeta*, *Lyssomanes*, *Onomastus*, *Pandisus*).
- (2) Medial displacement of gnathocoxal glands (see Maddison 1996). In hisponines, the medial displacement can be seen in images of *Hispo* sp. (Bemarah) (<http://www.morphbank.net/bisichen/?id=497568>) in the SpiderATOL collection in MorphBank (M. Ramírez, <http://www.morphbank.net/myCollection/?id=799626>).
- (3) Asymmetrical tarsal claws (Simon 1901: 385; Maddison 1996; Ramírez 2014).
- (4) Female palp tarsal claw reduced (Ramírez 2014). In hisponines it is reduced to a nubbin (Ramírez 2014), in salticines lost entirely.
- (5) Loss of conductor of palp (Ramírez 2014).

- (6) Presence of a cymbial apical groove that cradles the tip of the embolus (Maddison et al. in press).

The first three of these had been considered synapomorphies of salticines by Maddison (1988, 1996), but at the time hisponines were unstudied (and indeed, implicitly considered as salticines).

**Subfamily Salticinae** Blackwall, 1841

Blackwall, 1841: Salticidae  
Maddison, 1996: Salticine Division  
Maddison & Hedin, 2003a: Salticoida

**Remarks.**—This large clade, known in the past as the “advanced salticids” (e.g., Wanless 1984a), the “Salticine Division” (Maddison 1996), or the Salticoida (Maddison & Hedin 2003a), includes about 93% of the known species of salticids. Its former name Salticoida is reapplied in this classification to a narrower group excluding the Amycoidea, so as to permit this major long-recognized clade to receive the formal rank of subfamily. Thus, the Salticinae is divided into two major clades, the Amycoidea and the Salticoida. Salticines are known throughout the world, including temperate and arctic regions.

**Monophyly:** The monophyly of the Salticinae has been well demonstrated by both morphological (Maddison 1988, 1996; Ramírez 2014) and molecular data (Bodner & Maddison 2012; Maddison et al. 2014). The following can be considered synapomorphies for the Salticinae:

- (1) Tarsal claw absent on female palp (Maddison 1988, 1996; Ramírez 2014).
- (2) Median apophysis absent on male palp (see Maddison 2009). It is also absent in some spartaeines, hisponines and lyssomanines. Some authors have interpreted structures in salticines as median apophyses (Logunov & Hereward 2006; Szűts & Rollard 2007; Logunov & Azarkina 2008b), but none appears homologous to that of basal salticids. The median apophysis of basal salticids is distinctive: a sclerite arising from the ventral face of the tegulum, surrounded by the tegulum but separated from it by a membrane, and with a special relationship to the spermophore (usually, a loop of the narrowing spermophore approaches the median apophysis before bending back and entering the embolus).
- (3) Medial mound of slit sense organs on the chelicerae (Maddison 1988, 1996; Ramírez 2014).
- (4) Inter-cheliceral sclerite reduced (Maddison 1988, 1996; Ramírez 2014).
- (5) More complex tracheal system (Galiano 1976b; Wanless 1980c, 1981a; Ramírez 2014).
- (6) An abrupt gait. Salticine locomotion is different from that of all or most non-salticines, involving motions that seem more abrupt. This could relate to the difference in tracheation. The gait difference has not been well

characterized, and so any synapomorphy cannot be described clearly, but an experienced collector can quickly recognize most non-salticines by their soft-edged, almost serene motions. Such a gait has been noted for the Spartaeinae (Maddison 2006, 2009) and Hisponinae (<https://www.youtube.com/watch?v=HXDkUkLnK5g>).

- (7) Cymbium constricted at tibial joint, usually with distinct prolateral notch (Edwards in press).

The following may be synapomorphies of salticines, but have not been studied in enough members (e.g., in amycoids) to know where on the phylogeny they evolved:

- (8) Loss of tarsal scopula of tenant setae (Ramírez 2014, character 161).  
 (9) Loss of trichobothrial distal plate transverse ridge (Ramírez 2014, character 182).  
 (10) Reduction of male PMS minor ampulates to one (Ramírez 2014, character 274).  
 (11) Loss of cymbium dorsal chemosensory patch (Ramírez 2014, character 324).

The following are derived features present in Salticinae but absent in most or all non-salticines. They have not been examined in hisponines, and therefore could be synapomorphies either for Salticinae, or for the clade uniting Salticinae and Hisponinae.

- (12) Retinal strip of AME boomerang-shaped (as opposed to straight) (Blest et al. 1990).  
 (13) AME rhabdomeres rotated to eliminate suture lines (Blest et al. 1990).

A shorter and more anteriorly placed dorsal apodeme (fovea) of the carapace may also provide a synapomorphy (Wanless 1984). As well, salticines have, in general, greater heterogeneity of setae on legs than non-salticines. Salticine legs show a seemingly chaotic variety of setal lengths in addition to macrosetae, scales, and trichobothria. In contrast, the leg setae of many or all non-salticines appear as a uniform pelt. As with gait, differences in setae are not thoroughly studied.

**Clade Amycoida** Maddison & Hedin, 2003  
 (63 genera; Figs. 28–55)

Maddison & Hedin, 2003a: Amycoida

**Remarks.**—This diverse clade dominates the Amazon basin and stands as a major group in salticids — sister group to the enormous Salticoida — and yet is absent from the Old World except for *Sitticus*. Their body forms span the range of salticid diversity: long legged foliage-dwellers (the Amycini), ant-like forms (*Synemosyna*, *Sarinda*), beetle-like forms (*Cylistella*), flat bark dwellers (*Breda*), and unremarkable ground-dwellers (*Sitticus*). Most of what we know about the group is due to the efforts of Galiano (1957, 1958, 1963b, 1964a, b, c, 1965, 1966a, b, 1968b, 1971a, b, 1975, 1976a, 1977, 1985, 1987, 1988, 1989, 1991a, b), and more recently, Ruiz and colleagues (Ruiz & Brescovit 2005a, 2006a, b, 2013; Costa & Ruiz 2014; Patello & Ruiz 2014; Ruiz & Maddison in press). There are

about 430 described species, but this is almost certainly only a small fraction of the total extant. For instance, there are currently 11 species of *Amycus* recognized from all of the Neotropics, but in about two months of collecting within a 10 km radius at Cuyabeno, Ecuador, I found about 20 species.

In each of the 9 contained tribes except the Gophoini and the Bredini, the palpal bulb has a fixed embolus and is usually circular, though occasionally oval.

**Definition:** A formal definition was given by Ruiz & Maddison (in press): the Amycoida is the smallest clade containing *Cotinusa*, *Amycus*, *Sitticus*, *Breda*, *Sarinda* and *Synemosyna*.

Here I follow the classification of Ruiz & Maddison (in press), except for the re-ranking of their subfamilies as tribes. As they treat the amycoids fully, the account here is abbreviated. See Ruiz & Maddison (in press) for synapomorphies and molecular support for the individual tribes.

**Monophyly:** This group was first recognized on the basis of molecular data, which strongly support its monophyly (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014; Ruiz & Maddison in press). To date, there is no known morphological synapomorphy, though an unusual loop of the sperm reservoir of the palp is present near the subtegulum (Galiano 1968b, fig. 2; Prószyński 1980, fig. 5; Ruiz & Brescovit 2013, fig. 17 [left side]). It is rare to see such a loop in salticids with circular and fixed-embolus palps. Euophryines and others have a similar loop, but usually further from the subtegulum than in amycoids (Ruiz & Maddison in press).

Molecular data (Maddison, unpublished) show that *Asaracus*, once thought to be an amycoid (Ruiz & Brescovit 2008b), is a freyine near *Chira*. *Orvilleus* and *Toloella* are amycoids by their genitalia, but they are poorly studied and cannot yet be assigned to a tribe. *Albionella* and *Udalmella*, listed as Salticinae *incertae sedis*, could be amycoids.

**Tribe Gophoini** Simon, 1901  
 (8 genera; Figs. 28–30)

Simon, 1901: Thiodineae [based on a misinterpretation of *Thiodina*], Gophoeae  
 Petrunkevitch, 1928: Thiodininae  
 Roewer, 1954: Thiodininae, Thiodineae  
 Ruiz & Maddison, 2015: Gophoinae

**Remarks.**—This group, long known as the thiodinines, cannot retain that name with the discovery that the name *Thiodina* had long been misapplied (Bustamante et al. 2015; Ruiz & Maddison in press). Thus, Thiodineae and Thiodininae are not synonyms of Gophoini, but are listed in the synonymy above because the literature's past concept of Thiodininae refers to this clade. The type genus is *Gophoa* Simon, 1901, currently considered a junior synonym of *Cotinusa* Simon, 1900 (see Ruiz & Maddison in press). The best-known genus is *Colonus* (formerly known as *Thiodina*). Gophoinae are elongate, often with a carapace-leg stridulatory apparatus (Maddison 1987) and paired bulbous setae on the first legs (Hill 2012). While their motions are often deliberate and slow, they are excellent jumpers, seeming to tense strongly before popping in long jumps.

**Tribe Sitticini** Simon, 1901  
 (10 genera; Figs. 32–34)

Simon, 1901: Sitticeae

Petrunkévitch, 1928: Sitticinae  
 Roewer, 1954: Sitticinae, Sitticeae  
 Prószyński, 1976: Sitticinae  
 Ruiz & Maddison, 2015: Sitticinae

**Remarks.**—This is the only amycoid group to have reached the Old World. The bulk of its described species are in Eurasia, studied extensively by Prószyński (1968, 1971b, 1973, 1980). However, the deeper diversity of the group is South American (Galiano 1987, 1989, 1991a, b; Ruiz & Brescovit 2005a, 2006a, b). Sitticines are distinctive in having lost the retromarginal cheliceral tooth (as in leptorchestines and some euophryines and aelurillines) and in having third legs much shorter than the fourth. They are ground dwellers, with few exceptions (e.g., *Sitticus palustris* (Peckham & Peckham, 1883) lives on marsh vegetation).

**Tribe Bredini** Ruiz & Maddison, 2015  
 (2 genera; Fig. 31)

Ruiz & Maddison, 2015: Bredinae

**Remarks.**—These flat salticids dwell in suspended litter and on tree trunks. Two genera are described (Ruiz & Brescovit 2013). They were once thought to be marpissines (e.g., Edwards 2006) but molecular data have shown them to be amycoids. In retrospect, the sperm duct loop in the tegulum is typical for amycoids (Ruiz & Brescovit 2013, fig. 15).

**Tribe Scopocirini** Simon, 1901  
 (2 genera; Figs. 39, 40)

Simon, 1901: Scopocireae  
 Roewer, 1954: Scopocireae  
 Ruiz & Maddison, 2015: Scopocirinae

**Remarks.**—The chelicerae and palps of males are unusual in *Scopocira* (Costa & Ruiz 2014). *Gypogyna* is only tentatively placed with *Scopocira* (Ruiz & Maddison in press).

**Tribe Thiodinini** Simon, 1901  
 (9 genera; Figs. 36–38)

Simon, 1901: Thiodineae  
 Simon, 1903: Hyetusseae  
 Mello-Leitão, 1917: Arachnomureae  
 Roewer, 1954: Hyetusseae  
 Ruiz & Maddison, 2015: Thiodininae

**Remarks.**—The name “Thiodinini” now applies to what would have formerly been called the Hyetusseae (Ruiz & Maddison in press), because of the reinterpretation of *Thiodina* (Bustamante et al. 2015). The thiodinines include both elongate (e.g., *Cyllodania*, *Arachnomura*) and high-bodied (e.g., *Titanatus*) forms (Ruiz & Maddison in press).

**Tribe Sarindini** Simon, 1901  
 (7 genera; Figs. 47, 48)

Simon, 1901: Sarindeae, Zuningae [sic]  
 Roewer, 1954: Sarindeae, Zunigae  
 Ruiz & Maddison, 2015: Sarindinae

**Remarks.**—Of the two major groups of ant-like amycoids, the sarindines are the more robust, appearing more like *Formica* or *Camponotus* ants than does *Synemosyna*.

**Tribe Simonellini** Peckham, Peckham & Wheeler, 1889  
 (4 genera; Figs. 41–46)

Peckham, Peckham & Wheeler, 1889: Simonellii  
 Banks, 1892: Synemosinae  
 F.O. Pickard-Cambridge, 1900: Synemosyneae  
 Simon, 1901: Synemosyneae  
 Roewer, 1954: Synemosyneae  
 Prószyński, 1976: Synemosyninae  
 Ruiz & Maddison, 2015: Simonellinae

**Remarks.**—This group is a strange mix of small beetle-like salticids (*Cylistella*, Figs. 44, 45) and ant-like salticids (Figs. 41–43, 46), including *Synemosyna*, often an excellent mimic of the elongate ant *Pseudomyrmex*. See Ruiz & Maddison (in press) for the use of the name “Simonellini”. The type genus is *Simonella* Peckham & Peckham, 1885, a junior synonym of *Synemosyna* Hentz, 1846.

**Tribe Huriini** Simon, 1901  
 (6 genera; Fig. 35)

Simon, 1901: Hurieae  
 Ruiz & Maddison, 2015: Huriinae

**Remarks.**—Most huriines have a typical, unremarkable salticid body form (Fig. 35). Huriines have been studied by Galiano (1985, 1988).

**Tribe Amycini** F.O. Pickard-Cambridge, 1900  
 (13 genera; Figs. 49–55)

F.O. Pickard-Cambridge, 1900: Amyceae  
 Simon, 1901: Amycieae  
 Petrunkévitch, 1928: Magoninae  
 Roewer, 1954: Magoninae, Amycieae  
 Maddison & Hedin, 2003a: Amycinae  
 Ruiz & Maddison, 2015: Amycinae

**Remarks.**—This large and speciose group of mostly foliage-dwellers includes many with translucent legs, and males with a high clypeus. Many are excellent jumpers: I measured a 5.2 mm juvenile *Hypaeus* aff. *porcatus* (Taczanowski, 1871) from Yasuní, Ecuador jump 25 cm on a horizontal surface (more than 45 times its body length). The third leg is longer than the fourth (Ruiz & Maddison in press), as in many Simonida.

**Clade Salticoida** Maddison & Hedin, 2003, **new delimitation**  
 (427 genera; Figs. 56–136)

**Remarks.**—This clade, sister group to the primarily-Neotropical Amycoida, includes the vast bulk of described species in the Salticinae, although our counts are likely skewed against the Amycoida by the relatively little attention paid to the South American fauna. The relationships among the subgroups of Salticoida are ambiguous, but some analyses (Bodner & Maddison 2012) suggest that baviines, marpissoids

and astioids may form a clade, which would then be sister to the Saltafresia.

**Definition:** This clade has been recognized (e.g., node 3, Maddison et al. 2014), but not previously given a name. The name “Salticoida” is used for it here, reassigning the name from its former meaning (the current Salticinae), as explained under Salticinae. The Salticoida is now defined formally as the smallest clade containing baviines, marpissoids, astioids and the Saltafresia.

**Monophyly:** There are no known morphological synapomorphies of this group, and yet it is reconstructed with confidence by combined molecular datasets as well as by individual genes (28S rRNA, 18S rRNA, *wingless*, myosin HC; Maddison et al. 2014).

**Tribe Agoriini** Simon, 1901  
(2 genera; Figs. 56, 57)

Simon, 1901: Agorieae  
Petrunkevitch, 1928: Agoriinae  
Roewer, 1954: Agoriinae

**Remarks.**—This group includes only *Agorius* and *Synagelides*, unusual ant-like salticids from Asia and Australasia (Szűts 2003a; Logunov & Hereward 2006; Prószyński 2009a). *Agorius* holds the first legs curled and raised in life, like antennae (Fig. 56). The relationships of the group are unclear by both morphological and molecular data, but evidence suggests they are within the sister group to amycoids, i.e., within the Salticoida (Maddison et al. 2014). Their current placement outside of the major clades Saltafresia, Marpissoida and Astioida reflects ignorance and not evidence for exclusion. We simply do not know their relationships, and they may fall within one of those groups. The multiple-genes salticine analysis of Maddison et al. (2014: fig. 18) places them as sister to the chrysilines, but not firmly so, as the group is placed elsewhere by other analyses and individual genes. The palps of some species are unusual, but the simpler ones (Prószyński 2009a, figs. 27, 28) resemble those of chrysilines or hasariines.

**Monophyly:** *Synagelides* and *Agorius* have a male palp with unusually-proportioned segments, the femur being smaller than the robust patella (e.g., Logunov & Hereward 2006, fig. 4). In addition, the first leg has a tibia that is usually bent dorsally and with macrosetae closely packed in the distal half (Prószyński 2009a, figs. 16–22). In addition to these apparent synapomorphies, molecular data place *Synagelides* and *Agorius* together (Maddison et al. 2014).

**Tribe Baviini** Simon, 1901  
(3 genera; Figs. 58, 59)

Simon, 1901: Bavieae  
Roewer, 1954: Bavieae

**Remarks.**—The baviines, elongate and resembling marpissines, are common on large-leaved plants and suspended litter in Southeast Asian forests. They are speciose, despite the paucity of species currently described. The palp is of typical oval form with a fixed embolus and tegular ledge (i.e., with a cleft running retrolaterally across the bulb from the base of embolus).

**Monophyly:** Although the elongate and flattened body form (Figs. 58, 59) is consistent, it may not provide a synapomorphy for the group, as the same body form may be plesiomorphic in the possibly related marpissoids. The palps are fairly consistent, with a fixed embolus (e.g., Żabka 1988, figs. 29, 37, 52), generally like viciriines or marpissines, but without any known distinctive features. Molecular data, however, show that *Stagetilus* and *Bavia* fall together (Maddison et al. 2014). *Piranthus* is placed tentatively here on the basis of the close similarity in body form and markings with many *Bavia*.

**Clade Astioida** Maddison, Bodner & Needham, 2008  
(55 genera; Figs. 78–89)

Maddison, Bodner & Needham, 2008: Astioida

**Remarks.**—The astioids form one of the two major radiations of Australasia (the other, euophryines). The group is almost restricted to Australasia, the Pacific Islands, and Southeast Asia, with only *Neon* and *Myrmarachne* having extended beyond to Europe, Africa and the Americas. Alongside the Marpissoida and Saltafresia, this is one of the three major subgroups of the Salticoida. The form of the body is varied, including the ant-like *Myrmarachne*, the robust beetle-like simaethines, the delicate astiines, and the majestic mopsines. This group has become known especially through the efforts of Żabka and colleagues (Żabka 1987a, 1990a, 1991a, b, 1992a, b, 1994, 1995, 2000, 2001, 2002, 2003, 2004, 2009, 2014; Żabka & Gray 2002, 2004; Gardzińska & Żabka 2010; Żabka & Patoleta 2014; Patoleta & Żabka 2015).

The division of the group into five tribes is based on the combined results of Maddison et al. (2008, 2014) and Bodner & Maddison (2012), which show a major subclade (here called the Viciriini) and four smaller clades outside that.

**Definition:** The group was proposed by Maddison et al. (2008). It is here defined formally as the smallest clade including *Neon*, *Myrmarachne*, *Mopsus*, *Astia*, *Viciria*, *Trite* and *Simaetha*.

**Monophyly:** There are no known morphological synapomorphies, but the Astioida is well supported by molecular data (Maddison et al. 2008, 2014; Bodner & Maddison 2012). The embolus is generally fixed to the tegulum, but in some there appears to be a movable embolus (*Neon*, *Mopsus*), which however is not spiralled in the same manner as euophryines or marpissoids.

Because of the diversity of genitalia in this group, it is difficult to assess which unsequenced salticid genera are in fact astioids. However, the biogeographical pattern is strong, and we can guess that any salticid with a fixed embolus occurring in Australasia that is not obviously a member of another group (e.g., not a plexippine or chrysiline) is likely to be an astioid. Thus, among the genera listed as Salticinae *incertae sedis*, I suspect that *Aruana*, *Grayenulla*, *Hinewaia*, *Maddisonia*, *Proszynellus*, *Pseudomaevia*, and *Pseudosynagelides* are all astioids. *Muziris* could also be an astioid.

**Tribe Myrmarachnini** Simon, 1901  
(7 genera; Figs. 78, 79)

F.O. Pickard-Cambridge, 1900: Toxeae, Toxeinae  
Simon, 1901: Myrmarachneae, Ligonipedeae  
Petrunkevitch, 1928: Myrmarachninae  
Roewer, 1954: Myrmarachninae, Myrmarachneae, Ligonipeae

**Remarks.**—The mymarachnines form the most speciose clade of ant-like jumping spiders, most species of which are in the enormous genus *Myrmarachne* (Galiano 1969; Wanless 1978a; Edwards & Benjamin 2009; Edwards 2013; Benjamin 2015). There is great variability in appearance: depending on the colour, and the width and contours of the body, different species resemble different groups of ants. *Myrmarachne* has been the focus of studies of mimicry (Nelson et al. 2005; Edmunds 2006; Ceccarelli & Crozier 2007; Ceccarelli 2008; Nelson & Jackson 2009b; Huang et al. 2011), social behavior (Jackson et al. 2008a; Nelson & Jackson 2008), predatory behavior (Jackson 1986c; Jackson & Willey 1994), and sexual selection (Pollard 1994). Apart from a few Neotropical species of *Myrmarachne*, the group is entirely Old World. Edwards & Benjamin (2009) present a review of the group with a morphological phylogeny.

The name Toxeinae is not used as it was replaced, before 1961, by Myrmarachneae/Myrmarachninae because of synonymy of the type genus (ICZN 1999, article 40.2).

**Monophyly:** The morphological features that confer their striking resemblance to ants — e.g., narrow body with constrictions in the thorax — are synapomorphies, although they have evolved elsewhere in the family several times. Most distinctive, then, are the genitalia. The bulb is round, with the fixed embolus looping one or more times around it. Instead of faithfully following the periphery of the bulb, some loops of the embolus typically fall beneath and across the tegulum (e.g., Edwards & Benjamin 2009, figs. 4A, C, 7). The epigynum has a stereotyped arrangement, with the loops of the copulatory ducts eventually reaching the midline near the posterior margin then proceeding together side by side to the anteriorly-placed fertilization ducts (Prószyński 1992b, figs. 87, 92; Edwards & Benjamin 2009, fig. 7).

**Tribe Neonini** Maddison, **trib. nov.**

<http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:69DB2118-1C16-41E3-B914-150E0B96435A>

(1 genus; Fig. 80)

**Type genus.**—*Neon* Simon, 1876

**Remarks.**—Although initially familiar from the Holarctic region, *Neon* is now recognized as extending to Southeast Asia (Logunov 1998) and as having “radiated widely” in Australia (Richardson et al. 2006; Richardson 2013). It is not surprising, therefore, that molecular data have placed it in the primarily Australasian Astioida (Maddison et al. 2008).

**Monophyly and Diagnosis:** Small salticids with a relatively cubic carapace, a freely movable embolus (Logunov 1998, fig. 21) that is often spiraled (e.g., Gertsch & Ivie 1955, figs. 19, 24; Prószyński 1976, fig. 438), and long macrosetae under the first leg’s tibia. One possible synapomorphy is the shift of the embolus to arise on the prolateral side of the bulb. Although this shift is often seen in species with a fixed embolus, it is less common among species with a freely movable embolus.

An undescribed second lineage of neonines, larger-bodied, has been found in New Guinea (Maddison, unpublished data). The genus *Ananeon* (Richardson 2013) may be a neonine.

**Tribe Astiini** Simon, 1901

(11 genera; Figs. 82, 83)

Simon, 1901: Astieae  
Roewer, 1954: Astieae

**Remarks.**—This tribe more or less matches Wanless’s Astieae (1988), as supplemented by Žabka (1995, 2009) and Prószyński & Deeleman-Reinhold (2010). Typically long-legged and somewhat delicate-bodied, these spiders are Australasian and Southeast Asian. The astiine *Orthrus* was formerly placed with lyssomanines (Simon 1901), based on its eye placement and delicate translucent green body (Fig. 82).

**Monophyly:** The palp has a simple bulb, with embolus and tegulum fused and typically without elaboration. Wanless (1988) gives as two of their characteristics that they are pluri-dentate, and that they have the posterior lateral eyes “separated from lateral margins of the carapace by a distinct space when viewed from above” (e.g., Wanless 1988, fig. 9A). Although these characteristics in themselves might give little confidence in monophyly, molecular data support the group (Maddison et al. 2008).

Žabka (2009) suggests *Astilodes* may belong in the Astieae. Žabka (1995) places *Megaloastia* within the Astieae. *Parahelpis* is closely similar to *Helpis* (Gardzińska & Žabka 2010). Prószyński & Deeleman-Reinhold (2010) suggest *Katya* may belong to the Astieae, and indeed it has close similarities in its body and genitalia with *Orthrus*, particularly the overhanging lip of the epigynum and spermathecal configuration.

**Tribe Mopsini** Maddison, **trib. nov.**

<http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:99FA80D3-FF59-4C84-A1C7-347D280D0077>

(3 genera; Fig. 81)

**Type genus.**—*Mopsus* Karsch, 1878

**Remarks.**—This group of Australasian salticids includes just a handful of species in three genera, and yet is familiar through the often-photographed *Mopsus*.

**Monophyly and Diagnosis:** Large and robust Australasian salticids, with the embolus arising hidden behind the distal end of the tegulum and directed obliquely retrolateral (Žabka 2000, fig. 2). Žabka (2000) recognized the relationship of *Mopsus*, *Sandalodes*, and *Mopsolodes*, noting the similarities in male palps. The embolus appears movable, with a distinct embolic hematodocha (Maddison, unpublished data). Molecular data confirm the relationship of *Mopsus* and *Sandalodes* (Maddison et al. 2008). Those molecular data had suggested *Clynotis* was also closely related, which would be puzzling as *Clynotis* has a rather different embolus, possibly immovable. However, reexamination has shown that the 28S rRNA sequence used for *Clynotis severus* (L. Koch, 1879) by Maddison et al. (2008) is almost certainly a contaminant, as it is identical to that of the specimen of *Sandalodes scopifer* (Karsch, 1878). When reanalyzed with this sequence excluded, *Clynotis* groups more reasonably with the vicirini *Ocrisiona jovialis* (L. Koch, 1879) and *Holoplatys*.

**Tribe Vicirini** Simon, 1901

(33 genera; Figs. 84–89)

Simon, 1901: Viciriae, Rogmocrypteae  
Simon, 1903: Tritae, Simaetheae  
Roewer, 1954: Tritae, Rogmocrypteae, Simaetheae, Viciriae

**Remarks.**—Members of this tribe show many body forms, including the elongate *Viciria*, the wide-bodied *Simaetha*, the flat *Holoplatys*, and the more mundane *Trite* and *Opisthonus*.

One distinctive group, the simaethines, is separated as a subtribe. The remaining viciriines are diverse enough to deserve subdivision, but their phylogenetic relationships are too poorly known to assign them to subtribes even tentatively. The consequence of this is that *Viciria* is (necessarily) within the subtribe Viciriina, but all other non-simaethine viciriines remain as Viciriini *incertae sedis*. Of the four Simon group names that could apply to this tribe, Viciriini is chosen as it has priority over Triteae and Simaetheae (appearing in 1901 with diagnostic characters in the key of p. 517) and *Viciria* is better known than *Rogmocrypta*.

**Monophyly:** There are no known morphological synapomorphies of this group. The most comprehensive molecular data (Maddison et al. 2014) put *Trite*, *Nungia* and the simaethines together, while other studies (Maddison et al. 2008; Bodner & Maddison 2012) add to these *Viciria*, *Corambis*, *Holoplatys*, *Opisthonus*, *Penionomus*, *Rhondes*, and some of their relatives. See note under Mopsini regarding molecular support for *Clynotis* being a viciriine.

*Paraplatoidea*, *Zebraplatys*, *Holoplatys* and *Ocrisiona* are considered by Żabka (1992a) to form a monophyletic group. Żabka and Gray (2004) suggest *Huntiglennia* is related to *Zebraplatys*. Prószyński (2015) suggests that *Avarua* may be *Trite*, and indeed it resembles the viciriine *Corambis*. Żabka (1987a) concludes that *Tara* is closely related to *Clynotis*. By both body and genitalia, *Clynotis albobarbatus* L. Koch, 1879 and *Diplocanthopoda hatamensis* (Thorell, 1881) appear to be close to, or belong within, *Nungia*, of which there are several undescribed species in New Guinea (Maddison, unpublished data). The molecular data from cf. *Lystrocteisa* and cf. *Rogmocrypta* (Maddison et al. 2008) suggest that *Lystrocteisa* and *Rogmocrypta* are viciriines, at least if similarities of the sequenced specimens to those genera represent relationship. Two additional genera are included tentatively within the Viciriini, *Abracadabrella* and *Paraphilaeus*. Their placement is based on the fact that they resemble viciriines like *Opisthonus* in having paired abdominal markings resembling those of dendryphantines, along with palps generally resembling some viciriines. It is likely the case that several other Australasian genera like *Grayenulla* (Żabka 1992b) and *Hinewaia* (Żabka & Pollard 2002a) are also viciriines, but the data are unclear, and they are left as Salticinae *incertae sedis*.

**Subtribe Simaethina** Simon, 1903  
(13 genera; Figs. 87, 88)

Simon, 1903: Simaetheae  
Roewer, 1954: Simaetheae

**Remarks.**—These wide-bodied, often beetle-like salticids are distinctive components of Southeast Asian and Australasian faunas. They form a subgroup of the Viciriini.

**Monophyly:** The palp's bulb is round to oval, with a short embolus (e.g., Prószyński 1984a, p. 77, 1987, p. 107; Żabka 1994, fig. 1B). Among salticids with a fixed embolus, only the simaethines have such wide bodies with robust carapaces, with the exception of the tiny *Cylistella* in the amycoids. There

are other salticids with such a wide body (e.g., *Beata*, *Coccorchestes*, *Omoedus*, *Pachyballus*, *Rhene*, *Rhetenor*), but these are marpissoids or euophryines, with a freely movable embolus. The molecular data confirm that the wide-bodied astioids form a clade (Bodner & Maddison 2012; Maddison et al. 2014, unpublished data).

*Urogelides* is included as it appears close to *Uroballus*, sharing elongate spinnerets (Żabka 2009). *Iona* is placed by Prószyński (2015) with the simaethines. *Simaethula* is considered by Żabka (1994) to be a relative of *Simaetha*. The type species of *Stertinius* is not well known, but other species placed in the genus (Prószyński & Deeleman-Reinhold 2013) share the unusual cymbial extension of some *Irura* species (Peng et al. 1993). Having robust bodies and genitalia typical of simaethines are *Mantius* (Workman & Workman 1894; Prószyński 1984a), *Phyaces* (Wanless 1986), *Porius* (Prószyński 1984a), and *Poecilorchestes* (Prószyński 1971a). *Flacillula*, *Microhasarius*, *Pilia*, *Simaethulina*, and *Stergusa*, listed as Salticinae *incertae sedis*, could also be simaethines. *Stergusa*, at least for the species described by Prószyński & Deeleman-Reinhold (2010), has the palp typical of a simaethine, but at the same time these are very similar in body and palp to the euophryine *Sobasina*. The placements of *Microhasarius* and *Pilia* are especially important to resolve, as an available family-group name (Simon 1903) is based on each.

**Clade Marpissoida** Maddison & Hedin, 2003  
(90 genera; Figs. 60–77)

Maddison & Hedin, 2003a: Marpissoida

**Remarks.**—Although the largest tribe of marpissoids (Dendryphantini) is primarily a New World group, the other two tribes are restricted to the Old World (ballines and tisanibines).

**Definition:** After its original conception, Marpissoida was expanded to include the ballines (Bodner & Maddison 2012) and then the tisanibines (Zhang & Maddison 2014). However, given that the placement of tisanibines with the marpissoids is not made with full confidence (Zhang & Maddison 2014), the definition of the Marpissoida will be conditional: The Marpissoida is the smallest clade containing the Dendryphantina, Marpissina, Ballini and the Tisanibini, except if *Tisaniba* is not a close relative of the other three, in which case the Marpissoida would be the smallest clade containing the Dendryphantina, Marpissina, and Ballini.

**Monophyly:** The embolus is ancestrally spiral and movable, with a well-developed embolic hematodocha. The spiral typically appears edge-on in ventral view (Maddison 1996, fig. 64c; Edwards 1999, fig. 14), as its axis is parallel to the axis of the palp, unlike that of euophryines whose axis is usually perpendicular to that of the palp (Zhang & Maddison 2015). A simple open spiral is seen in ballines, tisanibines, synagelines and itatines, while a compacted spiral is seen in dendryphantines (Maddison 1996). Within the Marpissina, however, the embolus has become secondarily fixed. While the spiral embolus and the full development of the embolic hematodocha could be synapomorphies of the Marpissoida, they are also present in hisponines (Szűts & Scharff 2009) and euophryines (Zhang & Maddison 2015). The marpissoids are well supported by

molecular data (Bodner & Maddison 2012; Maddison et al. 2014) with some ambiguity about the inclusion of tisanibines (Zhang & Maddison 2014; Maddison et al. 2014).

**Tribe Ballini** Banks, 1892  
(15 genera; Figs. 60–63)

Banks, 1892: Ballinae  
Simon, 1901: Balleae, Copocrosseae  
Roewer, 1954: Balleae, Copocrosseae  
Benjamin, 2004: Ballinae

**Remarks.**—Members of this Old World group have unusual and varied body forms, with some resembling beetles (*Ballus*, *Pachyballus*), others ants (*Afromarengo*, *Leikung*, *Marengo*). Two contrasting extremes are the wide-bodied *Pachyballus* and the narrow and tailed *Mantisatta* (Cutler & Wanless 1973). Benjamin (2004) reviews the group and its phylogeny. Andriamalala (2007) found that convergent evolution of remarkable cheliceral horns in *Padilla* was uncorrelated with environment, suggesting the action of sexual selection.

**Monophyly:** Benjamin (2004) lists 6 putative morphological synapomorphies for the ballines: (1) an embolic coil of more than 360°, lying flat on the tegulum; (2) a subtegulum that extends over the tibia; (3) a narrow septum on the epigynum, (4) long copulatory ducts and spermatheca with internal spicules; (5) an enlarged femur 1 with dark lateral bands; and (6) small to medium body size with enlarged tibia 1. However, the primary argument for these comes from an analysis that included just one outgroup taxon, and therefore cannot speak to the monophyly of the group. Trait (1) is seen in synagelines and tisanibines, while (3), (4), (5) and (6) are seen in other salticids. Nonetheless, among Old World salticids, ballines are recognizable for the embolus, the pale longitudinal trough on the tegulum (Benjamin 2004, fig. 20A), robust first legs, and resemblance to beetles, pseudoscorpions, or ants. The molecular data suggest they are indeed monophyletic (Bodner & Maddison 2012), although these studies do not include the atypical *Cynapes*.

Among the genera listed as Salticinae *incertae sedis*, *Ligdus* could be a balline, and *Homalattus* could be either a balline (*Pachyballus*), or a dendryphantine (*Rhene*).

**Tribe Tisanibini** Maddison, *trib. nov.*

<http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:9A96C04C-E0B5-42CB-8D8E-5F7AFAC79133>  
(2 genera; Figs. 64, 65)

**Type genus.**—*Tisaniba* Zhang & Maddison, 2014

**Remarks.**—Tisanibines are small leaf-litter dwellers in tropical forests of Southeast Asia. Although common in some areas (Zhang & Maddison 2014), they were entirely undescribed until recently (Logunov & Azarkina 2008b; Zhang & Maddison 2014).

**Monophyly and Diagnosis:** As in other marpissoids such as ballines and synagelines, the embolus is a spiral with axis parallel to that of the palp (Zhang & Maddison 2014). The body form is unusual among marpissoids, however, as the males are small, black, shiny, and with a dorsal abdominal scutum (Fig. 65). Molecular data (Zhang & Maddison 2014) show

that *Tisaniba* is outside the Ballini and the Dendryphantini. A molecular synapomorphy of tisanibines is suggested by the broad sample alignments submitted by Zhang & Maddison (2014) to the Dryad data repository (<http://dx.doi.org/10.5061/dryad.984fn>), wherein site 138 of the 28S rRNA alignment has A in all four tisanibines sampled and different bases in other salticids.

Of the two genera placed here, *Tisaniba* and *Saaristattus*, the former is chosen as the type genus, rather than the older name *Saaristattus*, because the molecular data justifying the group's placement come from the type species of *Tisaniba*, and *Saaristattus* is only tentatively associated with *Tisaniba*.

**Tribe Dendryphantini** Menge, 1879  
(73 genera; Figs. 67–77)

Menge, 1879: Dendryphantidae  
See also listings under subtribes

**Remarks.**—The Dendryphantini, including the synagelines, itatines, marpissines and dendryphantines proper, matches the original content of the Marpissoida (Maddison & Hedin 2003a), before ballines and tisanibines were added to the latter by Bodner & Maddison (2012) and Zhang & Maddison (2014). The Dendryphantini are primarily in the New World.

**Monophyly:** There are no known morphological synapomorphies. The monophyly of the group is well supported by molecular data (Hedin & Maddison 2001; Maddison & Hedin 2003a; Maddison et al. 2014).

*Semorina* by genitalia appears to be in the Dendryphantini (Gustavo Ruiz, pers. comm.), but within which subtribe is unclear.

**Subtribe Synagelina** F.O. Pickard-Cambridge, 1900  
(6 genera; Figs. 67–70)

F.O. Pickard-Cambridge, 1900: Synageleae  
Simon, 1901: Synageleae, Peckhamieae  
Petrunkevitch, 1928: Synagelinae, Peckhamiinae  
Roewer, 1954: Synagelinae, Synageleae, Peckhamiinae

**Remarks.**—In parallel to the ballines, this group's morphological spectrum extends from forms resembling ants (*Synageles*, *Peckhamia*) to beetles (*Attidops*) and pseudoscorpions (*Admestina*, *Cheliferoidea*). The ant-like species are unusual in waving the second pair of legs like antennae (Fig. 68), rather than the first, which is typical for other ant-like salticids. Except for some species of *Synageles*, synagelines are entirely New World (Platnick 1984; Cutler 1988; Piel 1992; Edwards 1999).

**Monophyly:** There are no clear morphological synapomorphies of the group as a whole. The embolus typically is distinctly spiralled, in some cases winding several times, resembling many ballines (Edwards 1999). Molecular data support the group (Bodner & Maddison 2012; Maddison, unpublished data).

The second leg of *Descanso* has a darkened tip and is held aloft while walking (Gustavo Ruiz, unpublished data), which, combined with the body form and the spiral embolus (Galiano 1963a, 1986), confirm its placement in the Synagelina.

**Subtribe Itatina** Simon, 1901  
(1 genus; Fig. 66)

Simon, 1901: Itateae  
Petrunkevitch, 1928: Itatinae  
Roewer, 1954: Itatinae, Itateae

**Remarks.**—A single Neotropical genus of elongate spiders, green or yellowish, resembling baviines. It is here considered a distinct tribe as it falls outside the other major groups (Maddison & Hedin 2003a; Maddison et al. 2008; Zhang & Maddison 2014), without a clear sister group relation to any of them.

*Monophyly:* Although there are no described morphological synapomorphies for *Itata*, its species are recognizable by their elongate shape and yellow-green colour (Fig. 66) among New World salticids. The embolus has a distinct spiral.

**Subtribe Marpissina** Simon, 1901  
(9 genera; Figs. 71, 72)

Banks, 1892: Marptusi  
F.O. Pickard-Cambridge, 1900: Marptuseae  
Simon, 1901: Marpisseae  
Simon, 1903: Maeviaeae  
Petrunkevitch, 1928: Marpissinae, Maeviinae  
Roewer, 1954: Marpissinae, Marpisseae, Maeviinae, Maeviaeae  
Prószyński, 1976: Marpissinae

**Remarks.**—This mostly New World group includes many tree trunk or suspended litter dwellers, in contrast to the primarily foliage-dwelling dendryphantines. The North American *Maevia inclemens* (Walckenaer, 1837) is notable for having strikingly dimorphic males (Peckham & Peckham 1889; Painter 1913; Clark & Uetz 1992, 1993; Clark 1994; Clark & Morjan 2001; Clark & Biesiadecki 2002).

The old name Marptusi Banks was based on *Marptusa* Thorell, 1877, an unjustified replacement for *Marpissa* C.L. Koch, 1846 (Simon 1903), and thus a junior objective synonym thereof. On this basis, Simon (1901) rejected Marptusi and preferred Marpisseae. The preference for Marpisseae is therefore to be maintained (ICZN 1999, article 40.2).

*Monophyly:* The palp is narrow and in general resembles that of dendryphantines, but in many marpissines (e.g., *Fuentes* and *Balmaceda*, Edwards 2006), the embolic hematodocha is reduced and the embolus fixed to the tegulum and not spiral, presumably representing a secondary loss of the movable spiral embolus. However, this does not provide a synapomorphy for the group as a whole. Among New World salticids the group can be partially recognized by the general form of the palp and the slightly flattened or elongate body (Figs. 71, 72), but this simple characterization led us astray with *Breda*, assumed to be a marpissine by its resemblance to genera such as *Fuentes*, but in fact an amycoid (Ruiz & Maddison in press). Molecular data support the Marpissina (Maddison & Hedin 2003a).

The group was recognized approximately by Barnes (1958), but he included *Menemerus*, since shown to be a chrysiline (Maddison & Hedin 2003a). The concept of the group here is almost precisely that of Edwards (2006), with the exception that he included *Breda*. *Mendoza* is closely related to *Marpissa*

(Logunov 1999b). Gustavo Ruiz (pers. comm.) indicates that *Empanda* is a marpissine.

**Subtribe Dendryphantina** Menge, 1879  
(56 genera; Figs. 73–77)

Menge, 1879: Dendryphantidae  
Banks, 1892: Phidippi  
F.O. Pickard-Cambridge, 1900: Phidippeae  
Simon, 1901: Dendryphanteae, Rheneae  
Simon, 1903: Rudreae, Zygoballeae  
Petrunkevitch, 1928: Dendryphantinae, Zygoballinae  
Roewer, 1954: Dendryphantinae, Dendryphanteae, Donalidaeae, Rheneae, Rudreae, Zygoballinae, Zygoballeae  
Prószyński, 1976: Dendryphantinae

**Remarks.**—Although well known in Eurasia for *Dendryphantes*, *Rhene*, and *Macaroeris*, this group is primarily from the Americas (Maddison 1996). Dendryphantines dominate the species diversity of salticids in many areas of North America. The largest subclade consists of high-bodied and reasonably robust spiders such as *Phidippus* and *Dendryphantes*; outside of that is a series of less speciose lineages that include more elongate or flattened spiders such as *Hentzia* and *Phanias* (Hedin & Maddison 2001). *Phidippus* (Edwards 2004) includes some of the largest salticids in the world, sometimes exceeding 20 mm in length while also being broad and high-bodied. *Phidippus* has been the subject of many studies, of movement and foraging (Givens 1978; Hill 1979, 2010a, b; Freed 1984; Edwards & Jackson 1993; Hoefler & Jakob 2006; Baker 2007; Stankowich 2009), vision and neurophysiology (Land 1969a, b; Hill 1975; Sivertson 1985; Jackson 1986a; Blest et al. 1988; Hoefler et al. 2002; Baker et al. 2009; Bednarski et al. 2012; Spano et al. 2012; Menda et al. 2014), learning and experience (Edwards & Jackson 1994; Skow & Jakob 2006; Jakob et al. 2007; Kasumovic et al. 2009), and mating behavior (Jackson 1977a, b, c, 1978, 1980a, b, c, d, e, 1981a, b, 1982; Edwards 1982; Robertson & Stephens 2002; Hoefler 2007, 2008; Elias et al. 2008, 2010; Sivalingham et al. 2010). At least three separate lineages are in the Old World, represented by *Rhene*, *Macaroeris*, and *Dendryphantes*.

*Monophyly:* Maddison's (1996) composition of the Dendryphantinae, confirmed for many genera by molecular data (Hedin & Maddison 2001; Maddison & Hedin 2003a), was supported by several proposed synapomorphies: a carina on the underside of the male chelicera (Maddison 1996, fig. 10), the coil of the spiral embolus folded back so as to be hidden behind the base of embolus (Maddison 1996, fig. 64), and S-shaped epigynal openings (Maddison 1996, fig. 4). Males of many species have dark bodies with longitudinal white bands on either side of the thorax and continuing onto the abdomen (Fig. 77). Sexual dimorphism often involves enlarged chelicerae and first legs in males.

The genera listed here under Dendryphantina follow Maddison (1996), with some genera added, including *Pseudofluda* and *Naubolus* (Edwards et al. 2005). Gustavo Ruiz (pers. comm.) indicates that the poorly studied *Anokopsis*, *Alcmena*, *Pseudopartona* and *Monaga* are all dendryphantines. *Mirandia*, by Badcock's (1932) illustration, appears to be a dendryphantine. Based on the body form, shape of the palp and the sperm

duct loop, both *Planiemen* (Wesołowska & Harten 1994) and *Xuriella* (Wesołowska & Russell-Smith 2000) are provisionally considered to be close to *Rhene*, although if so the embolus would be modified from the typical form. The palps of the two known male specimens of *Tuvaphantes* are highly unusual, without a recognizable spermophore or embolus (Logunov 1993). I suspect they are teratologies, as they closely resemble deformed palps in other otherwise-identifiable salticids I have seen (Maddison, unpublished data). For example, Levi's illustration of the palp of *Phidippus opifex* (McCook, 1883) (= *P. octopunctatus* (Peckham & Peckham, 1883)) in Gardner (1965, fig. 1) shows a similar, presumably deformed palp (compare to Edwards' 2004 fig. 11 of the same species). *Homalattus*, listed as Salticinae *incertae sedis*, could be either a dendryphantine (*Rhene*) or a balline (*Pachyballus*).

**Clade Saltafresia** Bodner & Maddison, 2012  
(277 genera; Figs. 90–136)

Bodner & Maddison, 2012: Saltafresia

**Remarks.**—The Saltafresia is the third and largest of the three major clades of the Salticoida *sensu stricto*. Despite the size of the group (more than 3000 species), it is rather conservative in body form, having relatively few species of ant-like, beetle-like, highly elongate or other unusual body forms. Saltafresians are largely Afro-Eurasian, with the exception of many euophryines and the freyines.

Although the molecular data are to some extent ambiguous, there is evidence for a subclade consisting of the Plexippini, Aelurillini, Leptorchestini, Salticini and the Euophryini (Bodner & Maddison 2012; Maddison et al. 2014, node 4). I name it here as the **Simonida**, in honour of Eugène Simon. It is formally defined as the smallest clade including the type genera of those 5 groups. Frequently seen among the Simonida are relatively robust legs — e.g., *Cytaea*, *Aelurillus*, *Freya*, *Pellenes*, *Evarcha*, *Hyllus*, *Plexippus* and *Yllenus*. Insofar as they might remind us of humans, these spiders appear as strong-legged athletes. Longer third legs, possibly accompanied by a shift in jumping mechanics, evolved several times in this subclade (e.g., Figs. 112, 117, 123, 125, 136; Otto & Hill 2012b).

**Definition:** The Saltafresia was defined by Bodner & Maddison (2012) as the smallest clade containing the Plexippini, the Aelurillini, Euophryini, Chrysillini, Leptorchestini, Hasariini, Salticini and *Nannenus*.

**Monophyly:** There is no known morphological synapomorphy of the Saltafresia, but the group is reasonably well supported by molecular data (Bodner & Maddison 2012; Maddison et al. 2014).

**Tribe Nanneni** Maddison, **trib. nov.**

<http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:235D0370-6EBD-4A5B-B190-31914A98C1BD>  
(3 genera; Figs. 97–99)

**Type genus.**—*Nannenus* Simon, 1902

**Remarks.**—This small Southeast Asian group makes up a poorly known but common component of Southeast Asian faunas, especially on leaf litter (Prószyński & Deeleman-Reinhold 2012; Maddison & Piascik, unpublished data). Only two

generic names can be unequivocally assigned to the group (*Nannenus* and *Idastrandia*), but the number of genera is likely to grow as the many undescribed species become known.

**Monophyly and Diagnosis:** The macrosetae under the first tibia tend to be long (Szombathy 1915, fig. 5d; Prószyński 1987, p. 69), as in some thiratoscirtines and *Neon*, but this may be merely an adaptation to litter-dwelling. The embolus is fixed to the tegulum (Prószyński 1983b, fig. 7; Prószyński & Deeleman-Reinhold 2012, figs. 98, 100), with the possible exception of "*Bathippus*" *pahang* Zhang, Song & Li, 2003. Neither the macrosetae nor fixed embolus provides a clear synapomorphy for the group. Nonetheless, molecular data unite them (Zhang & Maddison 2013; Maddison et al. 2014, unpublished data), and they are relatively easy to recognize by being small to medium-sized compact-bodied salticids, relatively setose, Southeast Asian, and with an embolus that is generally more delicate than that of the hasariines. In the concatenated alignment submitted by Bodner & Maddison (2012) to TreeBASE (<http://purl.org/phylo/treebase/phylo/study/TB2:S13034>) are two synapomorphies for nanneniines, with site 737 (within 28S rRNA) showing T in nanneniines *versus* C in others, and site 2171 (within ND1) showing C *vs.* T.

*Langerra* is placed here only tentatively because its type species has not been studied recently. Although the species of *Langerra* studied for molecular phylogeny by Maddison et al. (2014) is clearly close to *Langerra longicymbium* Song & Chai, 1991, sharing its distinctive cymbial projection (Song & Chai 1991, fig. 7E), the question remains whether *L. longicymbium* belongs with the type species *L. oculina* Żabka, 1985. Females of the species studied by Maddison et al. (2014) have an epigynum (Maddison, unpublished data) that resembles that of *L. oculina* in having openings placed laterally beneath a transverse fold, with ducts proceeding anteriorly (Żabka 1985). Thus, the studied species' molecular placement with nanneniines can be provisionally considered to apply to *Langerra*. "*Bathippus*" *pahang* does not belong to the euophryine genus *Bathippus*; it is a nanneniine (Zhang & Maddison 2013). Among the genera listed as Salticinae *incertae sedis*, *Epidelaxia*, *Lechia* and *Leuserattus* could be nanneniines.

**Tribe Hasariini** Simon, 1903  
(15 genera; Figs. 100–102)

Simon, 1903: Hasarieae

Petrunkévitch, 1928: Hasariinae

Roewer, 1954: Hasariinae, Hasarieae, Diplocanthopodeae

**Remarks.**—The cosmopolitan *Hasarius adansonii* (Audouin, 1826) is the only widely known hasariine. In general they are ground dwellers, except for the trunk- or rock-dwelling *Gedea*. *Diplocanthopoda marina* Abraham, 1925 lives in the intertidal zone (Abraham 1925; Maddison, unpublished data). *Habrocestum* is reasonably speciose in Africa (Wesołowska & van Harten 1994, 2002, 2007; Wesołowska 2000, 2006b; Wesołowska & Russell-Smith 2000, 2011; Wesołowska & Haddad 2009; Haddad & Wesołowska 2013). Recent molecular work has assigned some small Southeast Asian genera to the group (Maddison et al. 2014). The single native New World species is the eastern North American *Chinattus parvulus* (Banks, 1895) (Edwards 2003a).

*Monophyly*: Hasariines are compact-bodied, often with distinctly white-edged palps that are held across the face. The palp's bulb is generally oval, with a reasonably robust embolus and a cleft across the face of the functional tegulum. A probable synapomorphy for the group is a small circular structure hidden in an overhanging lip at the back of the epigynum (see Logunov 1999a, figs. 17, 45), although a similar structure is seen in freyines (Edwards in press). Logunov (1999a) correctly surmises that *Chinattus* is related to *Habrocestum*. Although Logunov suggests that *Habrocestoides* is not near *Habrocestum* or *Chinattus*, the similarities to *Chinattus* in body form and genitalia, including the peculiar epigynal lip, suggest that *Habrocestoides* (for which molecular data are lacking) is a hasariine. The molecular data strongly link *Hasarius*, *Habrocestum*, *Chinattus*, and several other genera (Maddison et al. 2014).

*Meata* Żabka, 1985, known only from the female, is here synonymized with *Gedea* Simon, 1902 (**NEW SYNONYMY**), based on co-collecting and molecular data matching it with male *Gedea* (Maddison, unpublished data). *Curubis* is likely close to, or a synonym of, *Echeclus* (Maddison et al. 2014). *Hasarina*, *Imperceptus*, and *Madhyattus* are placed here based on the epigynum's overhanging lip with a circular notch; *Hasarina* in addition has a typical hasariine palp. *Mikrus* and *Uxuma* are included because of the resemblance of the palp to hasariines, and *Mikrus* in addition has a body and markings that strongly resemble *Chinattus*. Among the genera listed as Salticinae *incertae sedis*, *Ghumattus*, *Heliophanoides*, and *Jajpurattus*, *Pachypoessa*, and *Phausina* could be hasariines. Tentative molecular results (Maddison et al. 2014) suggest that *Bristowia* and *Cheliceroides* may be the sister group to the other hasariines. They are therefore included here provisionally.

#### Tribe Chrysillini Simon, 1901

(31 genera; Figs. 90–96)

Simon, 1901: Chrysilleae, Flacilleae

Simon, 1903: Silereae

Petrunkévitch, 1928: Heliophaninae

Roewer, 1954: Augusteae, Chrysilleae, Heliophaninae, Silereae

Prószyński, 1976: Heliophaninae

**Remarks.**—Formerly known as heliophanines (see Problematic Names, below), the chrysillines are ubiquitous throughout the Old World. They are generally small to medium sized foliage-dwellers with delicate legs, often brightly coloured, including the large genera *Heliophanus* (Wesołowska 1986; Rakov & Logunov 1997) and *Cosmophasis* (Żabka & Waldock 2012). Exceptions to the delicate body form include *Menemerus* and *Pseudicius*, typically bark or rock dwellers, and the relatively large-bodied *Epocilla*. The group has many species with interesting features: some fluoresce (Lim et al. 2007), some reflect and respond to UV light (Lim & Li 2006a, b, 2007; Land et al. 2007; Lim et al. 2008; Li et al. 2008), some are myrmecophages (Pekár & Haddad 2011), *Orsima* resembles a bug or wasp in reverse (Reiskind 1976), some live in nest aggregations (Jackson 1986b; Maddison 1987), and many have a stridulatory apparatus in both males and females (Maddison 1987). The embolus is fixed to the tegulum.

*Monophyly*: Many, though not all, chrysillines have a bump on the tegulum about 90° clockwise from the base of the

embolus (left palp ventral view; Maddison 1987; Maddison & Hedin 2003a). A smaller subset has distinctively swollen setal bases on the first femur and a rugose carapace side, suggested to be a stridulatory apparatus (Maddison 1987). Each of these could be a synapomorphy for a subclade of chrysillines, or for the group as a whole with subsequent losses. The Chrysillini is supported as monophyletic by molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014).

Most of the genera included without molecular data can be easily placed here by the classic form of the palp with the tegular bump. The genera *Afraflacilla*, *Heliophanillus*, and *Wesołowskana* all have the chrysilline palp as well as the leg-carapace stridulatory apparatus. Based on the palp and stridulatory apparatus, Ruiz et al. (2007) and Ruiz (2010) place the genera *Kupiuka*, *Matagaia*, *Plesiopiuka*, and *Theriella* into the chrysillines, which along with *Helvetia*, *Marchena*, and *Yepoella* are the only New World representatives. Prószyński (2015) suggests that *Tasa* and *Paraheliophanus* are heliophanines and that *Echinussa*, *Hakka* and *Helicius* are chrysillines, placements that are supported by their palps. *Chrysilla* and *Natta* have the classic chrysilline palp, as well as body forms like those of *Siler*, *Mexcala* and *Orsima*. *Augustea* is included because it appears to be a synonym of *Orsima* or *Chrysilla*. Based on my examination of the type specimen of *Rooseveltiella mutilla* Peckham & Peckham, 1907 in the Museum of Comparative Zoology, the body and markings of *Ogdenia* very closely resemble those of *Siler cupreus* Simon, 1889, though the epigynum has the openings oriented differently (Prószyński 1984b). Prószyński (2015) lists *Jaluticola hesslei* Roewer, 1944 as a synonym of *Menemerus bivittatus* (Dufour, 1831). The genus *Toticoryx*, listed as Salticinae *incertae sedis*, could be a chrysilline.

#### Tribe Leptorchestini Simon, 1901

(7 genera; Figs. 103–105)

Simon, 1901: Leptorchestae

Roewer, 1954: Leptorchestae

**Remarks.**—This small but heterogeneous group, unexpected before molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014), includes the pellenine-like *Yllenus* and the ant-like *Leptorchestes*. The only New World lineage is the elongate desert-dwelling *Paramarpissa*. The behavioural ecology of *Yllenus*, by far the largest leptorchestine genus (Logunov & Marusik 2003a) has been studied by Bartos (2002a, b, 2004, 2005, 2007, 2008; Bartos & Szczepko 2012; Bartos et al. 2013).

*Monophyly*: The only known morphological synapomorphy of this tribe is the loss of retromarginal cheliceral teeth (*Leptorchestes*: Wesołowska & Szeremeta 2001; *Paramarpissa*: Logunov & Cutler 1999; *Yllenus*: Logunov & Marusik 2003a), convergently lost in the Sitticini and some euophryines and aelurillines. Logunov & Marusik (2003a) suggested, without knowledge of the molecular results, that *Paramarpissa* and *Yllenus* may be related, based on the discreteness of a sclerite between the tegulum and the embolus, which they called the radix (Logunov & Cutler 1999, figs. 9–12; Logunov & Marusik 2003a, figs. 58–61). Although this sclerite may be common in salticids (hasariines, Logunov 1999a; freyines, Edwards in

press; euophryines, Zhang & Maddison 2015; see also comments on palps under Methods), its distinctness in *Paramarpissa* and *Yllenus* is unusual, and thus provides a synapomorphy for these two genera. *Leptorchestes* and related ant-like leptorchestines do not appear to have such a distinct “radix” (Wesołowska & Szeremeta 2001). The group as a whole is well supported by molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014).

*Kima* has palps very much like *Leptorchestes* (Wesołowska & Szeremeta 2001, figs. 12, 61). Photographs of the type specimen of *Araegeus mimicus* Simon, 1901 taken by Tamás Szűts show a spider whose body and epigynum closely resembles those of *Kima atra* Wesołowska & Russell-Smith, 2000. Wesołowska (2006a) places *Ugandinella* with *Leptorchestes* because of the ant-like form and the absence of a retromarginal cheliceral tooth.

**Tribe Euophryini** Simon, 1901  
(116 genera; Figs. 106–112)

Peckham, Peckham & Wheeler, 1889: Athamii  
Simon, 1901: Bythocroteae, Chalcoscirteae, Coccorchesteeae, Diolenieae, Evophrydeae, Saitideae, Sobasineae, Thianieae, Zenodoreae  
Simon, 1903: Athameae, Bellieneae, Cytaeae, Emathideae, Laufeieae, Servaeae, Spilargeae  
Petrunkevitch, 1928: Coccorchestinae, Cytaeinae, Spilarginae  
Roewer, 1954: Coccorchestinae, Cytaeinae, Spilarginae; Athameae, Bellieneae, Bythocroteae, Chalcoscirteae, Cytaeae, Diolenieae, Ematheae, Euophryeae, Laufeieae, Pensacoleae, Saiteae, Serveae, Sobasineae, Spilargeae, Thianieae, Zenodoreae.  
Prószyński, 1976: Euophryidinae  
Wanless, 1988: Euophryinae

**Remarks.**—Although speciose, euophryines are remarkably uniform in genitalia and body form except in tropical Australasia, where atypical forms such as *Diolenius*, *Sobasina*, *Paraharmochirus*, *Athamas* and *Coccorchestes* exist (Zhang & Maddison 2012b, 2015). Otherwise, the palp typically has a simple spiral embolus (Prószyński 1976; Zhang & Maddison 2015) and the epigynum has windows framed by circular folds that presumably guide the embolus. Elongate or ant-like body forms are rare. The Euophryini is the most cosmopolitan of all taxa ranked as tribes (Zhang & Maddison 2015) with high diversity in all tropics except African, and yet it also has a prominent role in the faunas of colder altitudes and latitudes. The group has recently been studied extensively by Zhang (Zhang & Maddison 2012a, b, c, d, 2013, 2015).

Euophryines are little studied ecologically, though there are many reports of ant feeding (Edwards et al. 1974; Cutler 1980; Jackson & van Olphen 1991, Li et al. 1996, Jackson et al. 1998; Clark et al. 2000; Jackson and Li 2001). Crane (1948) examined the life history and courtship of *Corythalia* in exquisite detail. Perhaps the most widely known euophryines are the peacock spiders (*Maratus*, Fig. 112), whose males have remarkably diverse, complex and colourful ornaments (Žabka 1987b; Otto & Hill 2011a, 2012a, b, 2013a, b, 2014a, b, c; Waldock 2013, 2014) and courtship behaviours (Hill 2009; Otto & Hill 2010, 2011a, b; Girard et al. 2011).

Regarding the decision to use the name “Euophryini” for this group, see the discussion below under “Problematic Names”.

Prószyński & Deeleman-Reinhold (2013) explain the shift in spelling from “Euophryidinae”.

**Monophyly:** While other groups of salticids have a spiral embolus, its form in most euophryines is distinct from that in most other salticids in being an open spiral facing ventrally, with the axis of the spiral perpendicular to the axis of the palp (Maddison & Hedin 2003a). The loop of the sperm duct inside the tegulum (e.g., Zhang & Maddison 2015, fig. 8) is also partially distinctive, though also seen elsewhere (e.g., some dendryphantines such as *Phanias* and *Rhene*, Maddison 1996, figs. 20, 52). Most species with a long embolus also show distinctive “windows” in the epigynum (Maddison & Hedin 2003a; Zhang & Maddison 2015, fig. 39). Molecular data confirm the group is monophyletic, including the type genera of the Athamii and all of Simon’s euophryine groups (Zhang & Maddison 2013; Maddison et al. 2014).

The list of genera here included follows that of Zhang & Maddison (2015) with the following additions. *Baviola*, *Gorgasella*, and *Lauharulla* have been added as per the suggestion of Zhang & Maddison (2015), but not *Lechia* and *Panyisinus*, as their placement is too doubtful. *Platypsecas* is included following the tentative suggestion of Ruiz & Brescovit (2005b). *Pensacolops* and *Pseudocorythalia* are added based on figures in their original descriptions, showing euophryine genitalia. The new genera of Richardson (2013) are included except *Ananeon*, which is considered here Salticinae *incertae sedis*, possibly a neonine. *Rarahu* is included as it appears to be close to, or synonymous with, *Sobasina*, based on illustrations by Prószyński in Prószyński (2015). *Yacuitella* is included tentatively, as a possible close relative of *Amphidraus*, based on the form of the embolus, cheliceral teeth, and body. The Dominican amber fossil *Pensacolatus* seems clearly euophryine by its palp (Wunderlich 2004). *Udalmella* is not included, though it could be a derived *Tylogonus*, near *T. chiriqui* Galiano, 1994. *Stergusa* might be near *Sobasina*, or it could be a simaethine, and so is listed as Salticinae *incertae sedis*. *Tatari* and *Gambaquezonina*, possibly related, have a spiral embolus, but lack the sperm duct loop typical for euophryines (Berland 1938; Edwards 2009), and so are listed as Salticinae *incertae sedis*. Possible other euophryines among the genera listed as Salticinae *incertae sedis* are *Lechia*, *Leuserattus*, and *Muziris*.

**Tribe Salticini** Blackwall, 1841  
(7 genera; Figs. 113–115)

Blackwall, 1841: Salticidae  
Prószyński, 1976: Salticinae

**Remarks.**—It is remarkable that previous literature has made so little mention of the Salticini or Salticinae, taxa that must exist and contain *Salticus* by traditional nomenclatural rules. While this may be due in part to the past difficulty of finding the close relatives of *Salticus*, it is also due to our failure to correct Simon’s placement of *Salticus* in the Marpisseae, until Prószyński (1976) revived the required nominate subfamily. Recent molecular work (Maddison et al. 2014) consistently places *Salticus* as sister group to Maddison et al.’s (2008) “*Philaeus* group”. For this reason Maddison et al. (2014) placed the *Philaeus* group within the taxon that is here re-ranked as the Salticini.

The seven genera known to belong to the Salticini occur in Africa, with some extending into Europe and Asia. *Salticus* is the only genus that reaches the New World, with a handful of native species.

**Monophyly:** There are no known morphological synapomorphies of the tribe. The embolus is fixed, and in all but *Salticus* there is a prominent lobe on the tegulum (Peckham & Peckham 1903, plate XXII fig. 4A [*Pignus*]; Andreeva et al. 1981, figs. 1, 6 [*Mogrus*]; Prószyński 1984a, p. 149 [*Tusitala*], 1992b, fig. 7 [*Carrhotus*], 2003, figs. 403 [*Mogrus*], 503 [*Philaeus*]). Prószyński (2003) suggested that *Mogrus* and *Philaeus* are related.

The claimed type locality for *Diagondas viridiaureus* Simon, 1902, Brazil, is almost certainly a result of mislabelling (as for *Thiratoscirtus patagonicus* Simon, 1886: Tamás Szűts, pers. comm; Wesołowska & Russell-Smith 2011). No other specimens of *Diagondas* have been reported from South America. *D. viridiaureus* is very close to, or a senior synonym of, *Carrhotus malayanus* Prószyński, 1992, from southeast Asia (compare Prószyński 1992b: figs. 1–4 to Galiano 1963a: plate XV figs. 11–13; also, a male specimen recently collected by me in Borneo is a nearly perfect match to Galiano's drawings). *Diagondas* Simon, 1902 is therefore considered a junior synonym of *Carrhotus* Thorell, 1891, **NEW SYNONYMY**).

**Tribe Aelurillini** Simon, 1901  
(51 genera; Figs. 116–124)

Simon, 1901: Aelurilleae

Maddison, Bodner & Needham, 2008: Aelurilloida

**Remarks.**—This group of more than 500 species, called the Aelurilloida by Maddison et al. (2008), contains the distinctive aelurillines along with the Neotropical freyines and Afrotropical thiratoscirtines.

**Monophyly:** Although freyines and thiratoscirtines resemble each other in body form and markings, there are no known morphological synapomorphies to link them to each other or the somewhat more distinctive Aelurillina. The group is well supported by molecular data (Maddison et al. 2014).

**Subtribe Aelurillina** Simon, 1901  
(11 genera; Figs. 116–118)

Simon, 1901: Aelurilleae

Roewer, 1954: Aelurilleae

Prószyński, 1976: Aelurillinae

**Remarks.**—Although speciose, this ground-dwelling group is rather uniform in appearance, with a slightly narrowed carapace and stout legs. *Langelurillus* and *Phanuelus* are exceptions (Fig. 116; Caleb et al. 2015, figs. 26–37), being smaller and more compact, resembling small *Habrocestum*, *Naphrys* or *Ail-lutticus*. Among the best-known genera are *Aelurillus* and *Phlegra* (Azarkina 2002, 2003, 2004, 2006). Only a single species of this Afro-Eurasian group has reached the New World, *Phlegra hentzi* (Marx, 1890). Several aelurilline species are reported to live with or eat termites (Wesołowska & Cumming 2002; Wesołowska 2007; Wesołowska & Haddad 2009). Some *Langelurillus* and *Phanuelus* lack a tooth on the cheliceral retromargin (Wesołowska & Russell-Smith 2000; Caleb et al. 2015).

**Monophyly:** The palp has a distinctive appearance, with the tegulum oval, distally extended as a shield hiding the embolus, and proximally pointed (e.g., Logunov 1996a, fig. 32; Maddison 1996, fig. 18; Azarkina 2002, fig. 2). Logunov (1996a) proposes a pocket on the cymbium as a synapomorphy of the group (Logunov 1996a, figs. 2–4, 32). The embolus is spiral in many species, and separated from the tegulum by a hematodocha (e.g., Logunov, 1996b, figs. 1–5; Maddison 1996, fig. 18; Azarkina 2002, figs. 5, 6). The thorax is often marked by longitudinal bands of white or pale scales at or just medial to the PLE (Fig. 118).

**Subtribe Freyina** Edwards, 2015  
(26 genera; Figs. 119–121)

Edwards, 2015: Freyinae

**Remarks.**—A Neotropical group of medium- to large-bodied salticids typically having simple palps with a fixed embolus, resembling plexippines to some extent. It is the smallest and most morphologically uniform of the four major groups of Neotropical salticines (the other three being the Amycoidea, Marpissoida and Euophryini). The group was a focus of study by Galiano (1961, 1968a, 1970, 1978, 1979a, b, c, 1981a, b, c, 1982, 1983, 1984, 1994, 1995, 2000, 2001). Edwards (in press) reviews the group comprehensively and describes several new genera.

**Monophyly:** Edwards (in press) notes there are no known strongly diagnostic synapomorphies for the group, but suggests two traits that could be synapomorphies, though not universally present: (1) subdistal and subproximal prolateral leg tibial macrosetae, and (2) a very thick basal division of the tegulum with a groove in its distal side. Edwards (in press) describes freyines as often having a conductor that accompanies the embolus, an anterior eye row about 5% wider than the posterior, and conspicuous setal tufts on the basal leg segments. The male palp has a strong and distinct cleft cutting diagonally across the front face of the bulb, and often bears a proximal tegular lobe as in euophryines (Galiano 1979b, figs. 36–43, 1979c, figs. 5, 6, 1994, figs. 7–10, 2001, figs. 14, 17). The thorax is often marked by one medial and two lateral longitudinal bands of white or pale scales below the PLE (Figs. 119, 120), more or less the negative of the aelurilline pattern. However, these features are not perfectly diagnostic. Even still, in the context of the Neotropics, freyines are usually easy to recognize, lacking the unusual body forms of amycoids, the angular carapaces and freely movable embolus of the Marpissoida, and the spiral embolus of euophryines. If not for geographical distribution, they would be difficult to distinguish from thiratoscirtines. Nonetheless, when such Neotropical species are accumulated, they are found to hold together by molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012).

Among the genera listed as Salticinae *incertae sedis*, *Hisukatius* could be a freyine.

**Subtribe Thiratoscirtina** Bodner & Maddison, 2012  
(14 genera; Figs. 122–124)

Bodner & Maddison, 2012: Thiratoscirtinae

**Remarks.**—A group endemic to Africa, concentrated in the wetter tropics of Central and West Africa. In Gabon at least,

they are the most speciose and common group of salticids within the forests, while other groups such as plexippines and chrysilines dominate outside the forests (Bodner & Maddison 2012). Thiratoscirtines are remarkable for the large number of species that can be found on leaf litter sympatrically (Jocqué & Szűts 2001; Bodner & Maddison 2012). Most recent work on the group has been due to Szűts, Wesołowska and colleagues (Szűts & Jocqué 2001; Rollard & Wesołowska 2002; Szűts & Scharff 2005; Szűts & Rollard 2007; Wesołowska & Russell-Smith 2011; Wesołowska & Edwards 2012; Wesołowska & Haddad 2013).

**Monophyly:** Bodner & Maddison (2008) diagnosed the thiratoscirtines with molecular data, demonstrating their monophyly with data from five genes. The epigynum of thiratoscirtines often has an abrupt, deep and broad central depression, and often has a posterior tongue-like extension (Szűts & Jocqué 2001, fig. 4; Szűts & Rollard 2007, fig. 1C, Wesołowska & Russell-Smith 2011, figs. 171, 191, 199). The palps are almost always unusual, but seemingly in different ways. What might unite their atypicality has not been articulated. The embolus is usually fixed, but sometimes apparently not (e.g., Maddison et al. 2008, figs. 4, 5). When fixed, the embolus often appears to wander away from the tegulum in strange directions — e.g., *Pochyta fastibilis* Simon, 1903, *Thiratoscirtus capito* Simon, 1903. Indeed, this dissociation of the embolus from a typical path is what leads to the placement here of *Ajaraneola*, *Cembalea*, *Nimbarus*, and *Ureta*. This is tentative, however, as some Salticini (e.g., *Pignus*, Peckham & Peckham 1903, plate XXII fig. 4A) also have a loosely directed embolus. In some thiratoscirtine species, it appears that the subtegulum and hematodocha are unusually exposed (e.g., *Pochyta pannosa* Simon, 1903, Maddison et al. 2008, fig. 5). It may be that some functional shift in the bulb has released the thiratoscirtine palp to evolve in patterns not normally seen in salticids. Despite this lack of morphological clarity, when the non-plexippine salticines with generally freyine-like bodies in central African forests are studied, the molecular data clearly put them together as a group (Bodner & Maddison 2012).

*Gramenca* is placed here by its epigynum with posterior tongue; *Lamotella* by its palp closely resembling *Pochyta pulchra* (Thorell, 1899). Possible thiratoscirtines among the genera listed as Salticinae *incertae sedis* are *Hasarinella* and *Maltecora*.

**Tribe Plexippini** Simon, 1901  
(47 genera; Figs. 125–136)

Simon, 1901: Plexippeae  
Maddison & Hedin, 2003a: Plexippoida  
See further synonyms under subgroups.

**Remarks.**—This large group (nearly 800 species), first recognized by Maddison & Hedin (2003a) as the Plexippoida, is second among tribes only to the Euophryini in number of species, though that may reflect considerable attention by arachnologists, as they are often large, commonly collected by beating, and diverse in long-studied Eurasia. Compared to such groups as astioids or amycoids, they tend to be rather conservative in body form, with the elongate (e.g., *Telamonia*), beetle-like

(*Hermotimus*), or ant-like (*Eburneana*) body forms being only weakly so. However, it should be remembered that they are merely a subgroup of the Saltafresia, and likely considerably younger than the astioids or amycoids (Fig. 1). The Plexippini includes two subgroups, the Plexippina and the Harmochirina.

The embolus is fixed to the tegulum, which is usually circular or slightly oval in shape.

**Monophyly:** Two synapomorphies, a modified serrula on the male endite (Maddison & Hedin 2003a, fig. 7) and a lobe on the tegulum just clockwise (left palp, ventral view) from the base of the embolus (Prószyński 1987, p. 80; Marusik & Logunov 1998, figs. 1, 4; Wesołowska & van Harten 1994, fig. 151), were originally thought by Maddison (1988, 1996) to delimit what is here called the subtribe Plexippina, but insofar as they apply also to *Harmochirus* and close relatives, they are better considered synapomorphies of the Plexippini (see Maddison & Hedin 2003a), secondarily lost in the pellenine harmochirines. The Plexippini is strongly supported by molecular data (Maddison & Hedin 2003a; Bodner & Maddison 2012; Maddison et al. 2014).

*Vatovia*, assigned to Salticinae *incertae sedis*, could be in the Plexippini judging by figures in Caporiacco's (1940) original description.

**Subtribe Plexippina** Simon, 1901  
(32 genera; Figs. 125–130)

Simon, 1901: Plexippeae, Hylleae, Thyeneae  
Simon, 1903: Hermotimeae  
Petrunkevitch, 1928: Plexippinae, Hyllinae, Thyeninae  
Roewer, 1954: Plexippinae, Plexippeae, Barypheae, Hyllinae,  
Hylleae, Thyeninae, Thyeneae  
Prószyński, 1976: Plexippinae, Hyllinae  
Maddison, 1996: Plexippinae

**Remarks.**—This Old World group has only two native species in the New World, both *Evarcha*. It is approximately equivalent to Maddison's (1988, 1996) concept of the Plexippinae. Most are relatively large salticids with robust legs, including the familiar cosmopolitan *Plexippus paykulli* (Audouin, 1826). Their conservatism in body and genitalia makes generic limits problematical, with genera such as *Evarcha*, *Pancorius* and *Hyllus* difficult to distinguish except perhaps by size.

**Monophyly:** Although there are no known synapomorphies of this group, they are generally easy to recognize by the large size, usually round palp bulb, simple fixed embolus, and robust legs. Many species have tufts of setae beneath the PME that project laterally and forward (Žabka 1985, fig. 217; Wesołowska & van Harten 1994, figs. 150, 152). The molecular data for monophyly are strong (Bodner & Maddison 2012). The guide of the epigynum is often shifted anteriorly from the margin, as in the related harmochirines, but often split into two lateral pockets (e.g., *Evarcha*, *Hyllus*, *Pancorius*, *Yaginumella*).

Given their simple palps and generalized (though usually robust) body form, the limits of this group have been unsettled. Prószyński (1984b) was the first to recognize that species formerly placed in *Viciria* pertain to two very different groups, some belonging with the plexippine *Telamonia*, others remaining in *Viciria*, which is now placed in the Astioida.

*Pseudamycus* and *Artabrus* are included on the basis of an epigynum with a divided guide pocket. In *Pseudamycus*, it is divided into two separate lateral pockets as in *Evarcha* and *Pancorius*. *Taivala invisitata* Peckham & Peckham, 1907 (types in Museum of Comparative Zoology, examined) is close to, or a synonym of, *Pancorius dentichelis* Simon, 1899. As noted by Prószyński & Deeleman-Reinhold (2013), *Vailimia* is a plexippine (type specimen of *Vailimia masinei* Peckham & Peckham, 1907 in Museum of Comparative Zoology, examined). It is close to, and possibly a synonym of, *Pancorius*. Tamás Szűts (pers. comm.) was kind enough to supply photographs of the type specimen of *Pachynomastus kittenbergeri* Capporiaco, 1947, by which it appears to be very similar to *Thyene semiar-gentea* (Simon, 1884). *Afrobeatia* is placed here tentatively on the basis of the lateral pockets of the epigynum (Prószyński 1987), and the eye tufts reminiscent of *Hyllus* and *Thyene* (photograph of type supplied by Tamás Szűts, pers. comm.). *Dasycyptus* has an *Evarcha*-like palp (Prószyński 1987), but is poorly studied. Szűts & Scharff (2005) indicates that *Encymachus* “is most similar to the African *Hyllus*”. Prószyński (2015) indicates that *Pseudoplexippus unicus* Caporiaco, 1947 is a synonym of *Plexippus petersi* (Karsch, 1878). *Paraplexippus* is likely a synonym of *Plexippus*, based on Franganillo’s (1930) figures and comments. The robust body and eye tufts suggest that *Parajotus* belongs here, but this must be considered highly tentative. *Pharacocerus* resembles *Pancorius* in palp, robust body, and eye tubercles, but it may belong elsewhere. Possible plexippines among the genera listed as Salticinae incertae sedis are *Bokokius*, *Maltecora*, *Tamigalesus*, and *Yogotor*.

**Subtribe Harmochirina** Simon, 1903  
(15 genera; Figs. 131–136)

Simon, 1903: Harmochireae  
Petrunkevitch, 1928: Pelleninae  
Roewer, 1954: Harmochireae, Pelleninae  
Prószyński, 1976: Pelleninae

**Remarks.**—This subtribe includes two primary subgroups, the harmochirines *sensu stricto* (e.g., *Bianor*, *Harmochirus*, *Sibianor*) and the pellenines (e.g., *Pellenes*, *Habronattus*, *Havaika*, *Neaetha*). The pellenines are well known for the Holarctic *Pellenes* and the primarily-Nearctic *Habronattus* (Griswold 1987; Maddison & Hedin 2003b), the latter remarkable for its complex and colourful courtship traits (Peckham & Peckham 1889, 1890; Maddison & Stratton 1988; Richman & Cutler 1998; Maddison & McMahon 2000; Elias et al. 2003, 2005, 2006a, b, 2012; Hebets & Maddison 2005; Taylor & McGraw 2013; Taylor et al. 2014a), visual system (Zurek et al. 2015) and chromosomes (Maddison 1982; Maddison & Leduc-Robert 2013). The pellenines are athletic salticids, typically dwelling on open sunny ground like aelurillines and sitticines. In contrast, the harmochirines *sensu stricto* are usually compact, often beetle-like, with more delicate walking legs.

For explanation of the decision to use “Harmochirina” rather than “Pellenina”, see “Problematic Names”, below.

**Monophyly:** The epigynal notch receiving the male’s tibial apophysis has moved forward on the epigynum, yielding a more or less conical pocket flanked by two crescent shaped openings (e.g., Griswold 1987, figs. 108–149; Prószyński

2008, figs. 69–84; Logunov 2009, figs. 13, 31, 40). Although this has been obscured secondarily in some *Pellenes* and in *Habronattus paratus* (Peckham & Peckham, 1896), it is a synapomorphy of the group. Two of the three subgroups, the harmochirines *sensu stricto* and the pellenines, are strongly united by molecular data (Bodner & Maddison 2012; Maddison et al. 2014). The third subgroup, the ant-like *Eburneana*, is ambiguously linked to the first two by molecular data (Maddison et al. 2014), but can be placed in the group by the epigynal pocket.

*Iranattus* (Prószyński 1992a) and *Monomotapa* (Wesołowska 2000) share with *Pellolessertia* (Szűts & Scharff 2005) a robust carapace with PLE on tubercles, and with *Pellolessertia* and *Neaetha* extremely long third legs. (Prószyński 1992a says the long legs of *Iranattus* are the fourth pair, but his figures 35 and 36 appear to show they are the third pair.) Their palps are consistent with those of pellenines, and have an unusual cymbial extension like that seen in some *Pellenes* (e.g., *Pellenes bonus* Logunov, Marusik & Rakov, 1999), although similar extensions are seen elsewhere (e.g., the simaethine *Irura*). These features indicate a placement of *Iranattus* and *Monomotapa* with the pellenines, as *Pellolessertia* and *Neaetha* have typical harmochirine genitalia in both males and females. Denis’s (1947) figure of the epigynum of *Paranaetha* suggests it has the guide and atria typical of harmochirines. Thus, the pellenines provisionally include *Pellenes*, *Habronattus*, *Havaika*, *Neaetha*, *Iranattus*, *Monomotapa*, *Pellolessertia*, and *Paranaetha*; the harmochirines *sensu stricto* include *Harmochirus*, *Bianor*, *Sibianor*, *Napoca*, and *Microbianor*; the eburneanines include only *Eburneana*. Whether *Modunda* is a harmochirine *sensu stricto* or a pellenine is unclear.

**PROBLEMATIC NAMES**

With this review of salticid classification, several available suprageneric names have been found to be older than commonly used names. These are:

- Harmochireae Simon, 1903 is older than Pelleninae Petrunkevitch, 1928
- Chrysilleae Simon, 1901 is older than Heliophaninae Petrunkevitch, 1928
- Athamii Peckham, Peckham & Wheeler, 1889 is older than Euophrydeae Simon, 1901
- Cocalodeae, Cyrbeae, and Cocaleae Simon, 1901 are older than Spartaeinae Wanless, 1984.

In each case, the younger name has been used as a subfamily, while the older name was described as a taxon called simply a “group”, with unclear rank in the modern scheme. Through much of the 20th century, there was a tradition of describing new subfamilies without regard to older “group” names (e.g., Petrunkevitch 1928; Wanless 1984) as if the latter were not coordinate with subfamily names for priority. For example, Simon (1901) placed the nominate genus *Salticus* in the group Marpissae, and Roewer (1954) did likewise for several subfamilies (e.g., *Heliophanus* in the group Chrysilleae within the subfamily Heliophaninae). Bonnet (1955–1959), normally an activist in correcting errors, lists without comment synonymies showing older group names as synonyms beneath younger subfamily names. This treatment suggests that early 20th century

authors viewed “group” names as following rather different rules than subfamilies, as if they were informal and acceptably ignored. However, more recently, arachnologists have treated these group names as within the ranks of the family group, available as subfamilies or at other ranks. This shift in interpretation challenges us to consider older names that were long disregarded. The taxonomic rank of these “groups” could be considered ambiguous, but they have been considered below the rank of subfamily (e.g., Roewer 1954), as if equivalent to tribes.

While article 35.5 of the current code (ICZN 1999) might have permitted us to retain the younger higher-ranked subfamily names, this article would no longer apply once their rank is reduced to tribe, which I do for all but Spartaetinae.

The simplest case is perhaps Harmochireae/Pelleninae. Insofar as both have continued to be used (e.g., Logunov 2009), but not commonly in the literature, it is best to give way to priority, with subtribe Harmochirina taking precedence over the alternative choice Pellenina. However, the pellenines are still recognized, informally, as a subgenus of the Harmochirina.

In the other three cases, a strict application of the Code would likewise support older and more-or-less forgotten names to displace names currently in common use. Of these, the displacement of “Heliophaninae” is the least disruptive, as its uses in the literature are not extensive. While the group’s genera are among the most conspicuous salticids throughout the Old World, their collective labelling as heliophanines is not so conspicuous in the literature. Therefore, I use Chrysillini for the group, treating Heliophaninae as a junior synonym.

However, “Euophryinae” cannot be so painlessly set aside. Because of strong prevailing use in salticid systematics, I use Euophryini in preference to the older Athamii. Among the groups heretofore recognized as subfamilies, the Euophryinae is the largest and most widespread, with over 1000 species and 100 genera on all continents except Antarctica, from the tropics to cold temperate habitats (Zhang & Maddison 2015). Our current concept of this group dates to Prószyński’s (1976) landmark paper. While it is easy to recognize a salticid as belonging to the group, it has been difficult to distinguish genera (Zhang & Maddison 2015). Thus, for the last 40 years we have often spoken of “euophryines” and identified specimens as “euophryine”, without referring to the genus, both in the literature and in our informal parlance. The names “Euophryinae” and “euophryine” have come to be key parts of the vocabulary of salticid systematics (e.g., Prószyński 1976, 1983a, 2003, 2009b; Prószyński & Żabka 1980; Żabka 1980b, 2012; Griswold 1987; Logunov 1992, 1998; Maddison 1996; Wesolowska & Russell-Smith 2000; Wesolowska 2001, 2012; Żabka & Pollard 2002b, c; Edwards 2003a, b, 2004, 2009; Logunov & Kronstedt 2003; Maddison & Hedin 2003a; Benjamin 2004; Edwards et al. 2005; Ruiz & Brescovit 2005b, 2008a, b; Arnedo & Gillespie 2006; Andriamalala 2007; Ruiz et al. 2007; Su et al. 2007; Logunov & Azarkina 2008b; Azarkina 2009; Hill 2009, 2012; Otto & Hill 2011a, 2012a, b, 2013a, b, 2014a, b, c; Prószyński & Deeleman-Rheinhold 2012, 2013; Zhang & Maddison 2012a, b, c, d, 2013, 2015; Azarkina & Foord 2013; Edwards & Ruiz 2013; Richardson 2013; Ruiz 2011, 2013b; Waldock 2013, 2014; Wesolowska & Haddad 2013, 2014; Wesolowska et al. 2014). In contrast, the

older name Athamii (or Athameae) has been used rarely (Simon 1903; Roewer 1954; Galiano 1976b; Szűts 2003b), though enough to prevent its being considered a *nomen oblitum*. The use of Athamii/Athameae has been restricted to the rarely collected and little studied nominate genus *Athamas* of Australasia and Pacific Islands (Jendrzejewska 1995). Prószyński & Deeleman-Rheinhold (2013) recognized that *Athamas* is a euophryine, but did not address the priority of names, possibly because the Athamii/Athameae has been misattributed to Simon (e.g., Jendrzejewska 1995, Szűts 2003b). Because of the importance of the name “Euophryinae” to salticid systematics, I will use Euophryini as the name of the tribe.

The case of Spartaetinae is more complex, but I use that familiar name instead of the alternatives because of its widespread use in literature on salticid behaviour and systematics, cited below. When Wanless (1984a) named the subfamily Spartaetinae because of homonymy of the former Boethinae’s type genus, he ignored the availability of Simon’s older group names Cocalodeae, Cyrbeae, and Cocaleae, possibly because he did not consider them as coordinate with family-group names. Noticing Wanless’s error, Wunderlich (2004) proposed Cocalodinae instead. At first glance, it would appear that the Code rules out Wunderlich’s change, with article 35.5 preventing Spartaetinae’s replacement by a lower ranked name (Cocalodeae). However, that article specifies that the older name be in use (despite this requirement seeming against the intent of the article), and Cocalodeae arguably was not in use. Thus, a direct reading of the Code leads us to the subfamily name as the Cocalodinae.

What would be the name of the tribe excluding *Codalodes* but including *Cyrba*, *Cocalus*, and *Spartaeus* (Table 2)? Besides Spartaetini, there are two competing names for this tribe, based on Cyrbeae or Cocaleae, of which I would choose Cyrbeae because the type genus is considerably more widespread. Here again, article 35.5 cannot protect the Spartaetini, for any of three reasons: (1) Spartaetini as a tribe does not outrank Simon’s group, if we treat groups as of tribal rank; (2) “Cyrbeae” has not been in use; (3) Cyrbeae does not represent a distinct taxon from the Spartaetini even at the lowest level, as *Cyrba* and *Spartaeus* have long been placed together even at the finest level (here, the same subtribe). This last requirement, for distinctness at the lowest level, I interpret as the spirit of the Code, implied by the example given in the Code for article 35.5. Even if 35.5 would protect the subfamily name Spartaetinae, the lower levels of tribe and subtribe would not be so protected, leading to the inconsistency that *Spartaeus* and *Cyrba* would find themselves together within the subtribe Cyrbina, tribe Cyrbini, subfamily Spartaetinae.

According to the cited articles of the Code and the principle of priority, therefore, the appropriate names for groups containing *Cyrba* and *Spartaeus* would be Cocalodinae: Cyrbini: Cyrbina, accepting Wunderlich (2004) as first revisor. However, there is a compelling argument to maintain current usage for stability. There is much work anchored to the name Spartaetinae in the literature of salticid behaviour (Blest 1984, 1987; Jackson & Hallas 1986b; Blest et al. 1990; Jackson 1990a, b, c, d, 2000, 2002; Jackson & Pollard 1990, 1996; Jackson & Li 1998; Harland et al. 1999; Bartos 2002b; Li 2000; Cerveira et al. 2003; Guseinov et al. 2004; Nelson & Jackson 2009a; Cerveira & Jackson 2011; Hu et al. 2012; Nelson et al. 2012; Cross & Jackson 2015) and systematics (Wanless 1984a,

b, 1985, 1987; Bohdanowicz & Prószyński 1987; Griswold 1987; Davies & Žabka 1989; Rodrigo & Jackson 1992; Wijesinghe 1992, 1994; Maddison 1996, 2006, 2009; Žabka & Kovac 1996; Galiano 1998, 2000; Logunov 1998; Žabka 1999; Szűts & Azarkina 2002; Deeleman-Reinhold & Floren 2003; Maddison & Hedin 2003a; Prószyński 2003; Edwards 2004; Zhang & Li 2005; Maddison & Needham 2006; Maddison et al. 2007, 2008, 2014; Su et al. 2007; Logunov & Azarkina 2008a; Wesołowska & Haddad 2009, 2013; Azarkina & Logunov 2010; Benjamin 2010; Hill 2012; Prószyński & Deeleman-Reinhold 2012; Ruiz & Maddison 2012; Ruiz 2013a; Zhang & Maddison 2013; Zhou & Li 2013a; Logunov & Marusik 2014; Ramírez 2014; Patoleta & Žabka 2015). To avoid disconnecting that literature from the classification, I use Spartaeinae: Spartaeini: Spartaeina.

### EVOLUTION AND BIOGEOGRAPHY

While the arrangement is presented here as a classification, it also represents the first time that explicitly phylogenetic relationships have been proposed for all (or most) genera of salticids. Such a classification has two roles. First, by placing together related genera, it promotes species discovery and taxonomic work, by assembling together those genera that might hold species relevant for a study, facilitating the search for already-described species. Second, it promotes exploration of evolutionary patterns in salticids.

**The age and biogeography of salticid radiations.**—Major clades of salticids are mostly restricted to a single continental area (Maddison & Hedin 2003a; Bodner & Maddison 2012). In the speciose Salticinae, the Amycoidea are primarily Neotropical, the Astioida primarily Australasian, the Marpissoida primarily in the Americas (especially Central and North America), and the Saltafresia (with the exception of the euophryines and freyines) primarily Afro-Eurasian. The Spartaeinae is similarly divided, with the Americas, Afro-Eurasia and Australasia occupied by the lapsiines, spartaeines, and cocalodines respectively. This pattern suggests that each major group diversified mostly in isolation from the others, after the continents were fully isolated about 35 million years ago (Maddison & Hedin 2003a; Bodner & Maddison 2012). This timing of salticid radiations is supported by dating of divergence times using molecular data and fossils (Bodner & Maddison 2012; Zhang & Maddison 2013). Even before molecular data clarified relationships, Žabka (1990b, 2000) and Žabka et al. (2002) pointed out the lack of any trace of a Gondwanan salticid fauna.

At present, each continental area has its own distinct fauna consisting primarily of a few groups — e.g., Amycoidea, Dendryphantini, Freyina, and Euophryini in the Neotropics, contrasted against Euophryini, Plexippina, Chrysillini, Spartaeina, and Astioida in the Asian tropics — but the faunas may have been even more distinct in the past. One is tempted to imagine a time in the mid-Cenozoic during which South America, North America, Afro-Eurasia and Australia each had its own major isolated radiation (the amycooids, marpissoids, saltafresians and astioids respectively).

It should be realized, however, that the relationships presented here are not entirely independent evidence for isolated radiations. The strength of this geographical pattern has likely influenced my assessments of the relationships of some poorly

studied genera, such that I may have been more likely to predict that an Australian salticine species with fixed embolus is an astioid rather than a marpissine, for example.

**Salticid eyes and vision.**—Many studies have explored various aspects of salticid vision: anatomy (Scheuring 1914; Land 1969a, 1985; Eakin & Brandenburger 1971; Homann 1971; Hill 1975; Oberdorfer 1977; Blest & Maples 1979; Williams & McIntyre 1980; Blest 1983, 1984, 1985, 1987; Blest & Price 1984; Blest & Sigmund 1984, 1985; Blest & Carter 1987; Blest et al. 1988; Blest et al. 1990; Hu et al. 2012; Zurek et al. 2015), neurophysiology and cognition (Land 1969b; Hill 1975; Duelli 1978; Hardie & Duelli 1978; Sivertson 1985; Baker et al. 2009; Spano et al. 2012; Zurek & Nelson 2012a, b; Nagata et al. 2012; Menda et al. 2014), opsins and colour sensitivity (Devoe 1975; Yamashita and Tateda 1976; Blest et al. 1981; Peaslee & Wilson 1989; Nakamura & Yamashita 2000; Lim & Li 2006a; VanderSal & Hebets 2007; Koyanagi et al. 2008; Nagata et al. 2010; Terakita & Nagata 2014; Taylor et al. 2014b), and behavioural responses (Drees 1952; Land 1972; Giulo 1979; Zurek et al. 2010; Bednarski et al. 2012; Dolev & Nelson 2014). Their visual systems have even inspired robotic camera systems (Tonet et al. 2008).

With this phylogenetic arrangement of salticids, we are now in a position to interpret evolutionary patterns in visual system diversity. Diversity is expected, given that the family is comparable, in species diversity and age, to groups such as the eutherian Mammalia or the passerine birds. Indeed, the Salticinae (and possibly the hisponines) differ distinctly from the other salticids in having the AME retina boomerang-shaped and the AME rhabdomeres rotated to eliminate suture lines (Blest et al. 1990). However, we are hampered in exploring evolutionary patterns by a lack of data from diverse taxa. For instance, the ultrastructure of the AME has been studied in the Lyssomaninae, Asemoneinae, Spartaeinae (Spartaeina, Cocalodini); Amycoidea (Gophoini, Sitticini, Scopocirini, Simonellini, Amycini); Astioida (Myrmarachnini, Astiini, Viciriini); Marpissoida (Dendryphantina, Itatina), and Saltafresia (Euophryini, Freyina), as compiled by Blest et al. (1990). The Plexippina is not included in this list, as the reported *Plexippus validus* Urquhart, 1893 is the euophryine *Servaea incana* (Karsch, 1878). Thus, there is scant coverage of the most diverse of the major clades, the Saltafresia. Nonetheless, we can conclude that there is convergence: the amycooids, astioids, and saltafresians each contain species with different conditions in whether the AME Layer 1 receptive segments are continuous or well separated (see Blest et al. 1990). Obtaining more data on anatomy and physiology of diverse salticids will be vital to understand how and why their remarkable eyesight has evolved.

**Salticids that look like ants, beetles, and other things.**—Ant-like body forms and behaviour in salticids are well known (Peckham & Peckham 1892; Cushing 1997; Ceccarelli 2008; Huang et al. 2011; Nelson 2011; Uma et al. 2013; Pekár 2014), and many of the spiders bearing them have special behaviours that enhance their resemblance to ants (Reiskind, 1972). The degree of resemblance, to human eyes, varies from mild (e.g., *Tutelina, Mexcala*) to highly convincing, with strangely constricted body parts and well-placed markings (e.g., *Synemosyna, Myrmarachne*).

A long-standing question is how many independent origins there are of ant-like bodies and behaviour in salticids

(Jackowska & Prószyński 1975). Pekár (2014) concludes that strongly ant-like bodies evolved in six salticid lineages. The more complete picture of salticid relationships presented here indicates that strong ant (or wasp) mimicry has evolved at least 12 or 13 times in salticids. The following list shows the scattered distribution of ant-like bodies:

Cocalodini: *Depreissia* (Wesołowska 1997; Deeleman-Reinhold & Floren 2003)

#### Amycoidea

Thiodinini: *Atomosphyrus* (see Ruiz & Maddison in press)

Sarindini: *Sarinda*, *Zuniga*, etc. (Figs. 47, 48)

Simonellini: *Synemosyna*, *Fluda*, *Erica* (Figs. 41–43, 46)

#### Salticoida

Agoriini: *Agorius*, *Synagelides* (Figs. 56, 57)

Astioidea: *Myrmarachne*, etc. (Figs. 78, 79)

#### Marpissoida

Ballini: *Marengo*, *Leikung*, etc. (Fig. 61)

#### Dendryphantini

Synagelina: *Synageles*, *Peckhamia*, etc. (Figs. 68, 69)

Dendryphantina: *Bellota*, etc. (Fig. 74)

#### Saltafresia

Chrysillini: *Yepoella* (Fig. 95)

Leptorchestini: *Leptorchestes*, *Kima*, etc. (Fig. 105)

Euophryini: *Sobasina*, *Paraharmochirus* (Zhang & Maddison 2015, figs. 836–841)

Plexippini: *Eburneana* (Fig. 133)

In this list are at least 12 independent evolutionary origins, because, in each case, the ant-like species are embedded within clades of non-ant-like species, or have close relatives that are not ant-like. The agoriines are probably a 13th independent origin. However, given the uncertainty in their phylogenetic placement, we cannot yet rule out their sharing an origin of ant-like bodies with some other salticoids. Another caveat is that the selective force for these body forms may not have always been ant mimicry. For example, Christa Deeleman-Reinhold (pers. comm.) suggests that the ant-like *Depreissia* may have been selected for resemblance to polistine wasps. Nonetheless, the phylogenetic distribution of ant-like bodies suggests an answer to the question posed by Jackowska & Prószyński (1975): a strongly ant-like form has neither evolved once, forming a single clade of ant-like salticids, nor in every species independently. Rather, it has evolved a handful of times, with some origins leading to a large diversification of many ant-like species (myrmarachnines, simonellines), and others only a few.

Other salticids are round, dark and shiny, strongly resembling beetles. A striking beetle-like appearance has evolved at least eight times in salticids: in the Amycoidea (*Cylistella*, Figs. 44, 45), the Astioidea (*Simaetha* and others, Fig. 88), the Ballini (*Pachyballus*, Fig. 60), the Dendryphantini (*Sassacus*, *Rhene*, *Rhetenor*, Fig. 76), and the Euophryini (*Coccorchestes*, Fig. 109).

A surprising pattern is that in at least four of these beetle-like lineages, close relatives of the beetle-like forms are ant-like (*Cylistella/Synemosyna*, *Pachyballus/Marengo*, *Sassacus/Bellota* and *Coccorchestes/Sobasina*). A somewhat less-striking beetle-like form (*Attidops*) has the ant-like *Synageles* and *Peckhamia* as close relatives.

*Orsima* (Chrysillini) has been reported as resembling a backwards insect, with the spinnerets like the insect's mouthparts (Fig. 90; Reiskind 1976). This is indeed convincing, and is replicated in some *Asemonea* (Asemoneinae; Fig. 4), and in different form in *Abracadabrella* (Astioidea?).

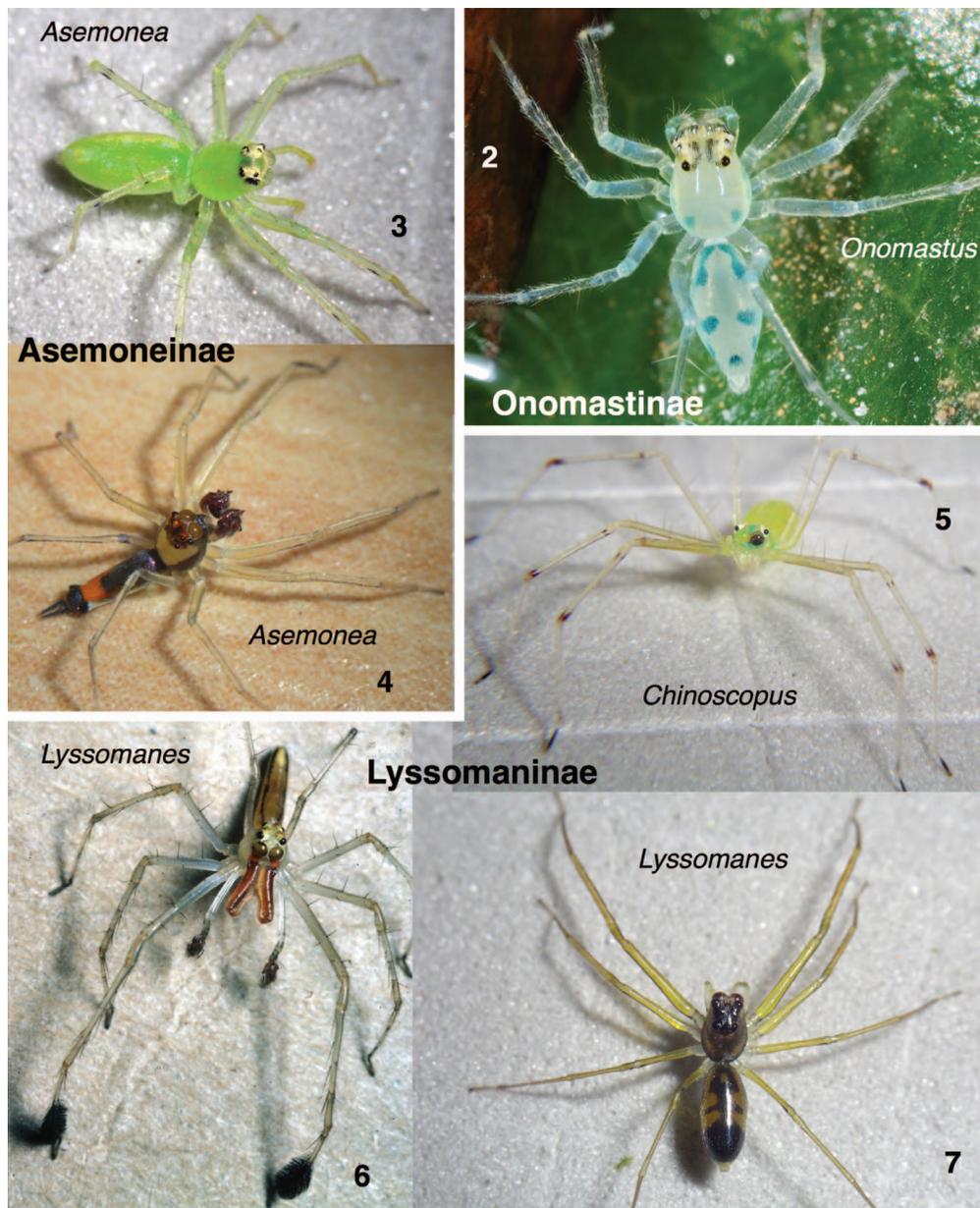
### PRIORITIES FOR FUTURE STUDY

Acquiring molecular data from many genes is the priority for resolving salticid relationships with greater clarity. However, for many salticid genera, finding more certain placement will require a better understanding of structures of the body and genitalia. While standard illustrations of palps and epigyna (both external and internal) are sufficient for species identification, they have not yet yielded many clear synapomorphies for groups. For that, we need to observe structures at much higher resolution than is usually done; a sketch at 80X magnification is not likely enough for phylogenetic work. We also need to go beyond genitalia to fine structures of the whole body. It is also critical that the morphological data be analyzed cladistically, seeking and explaining synapomorphies clearly and explicitly.

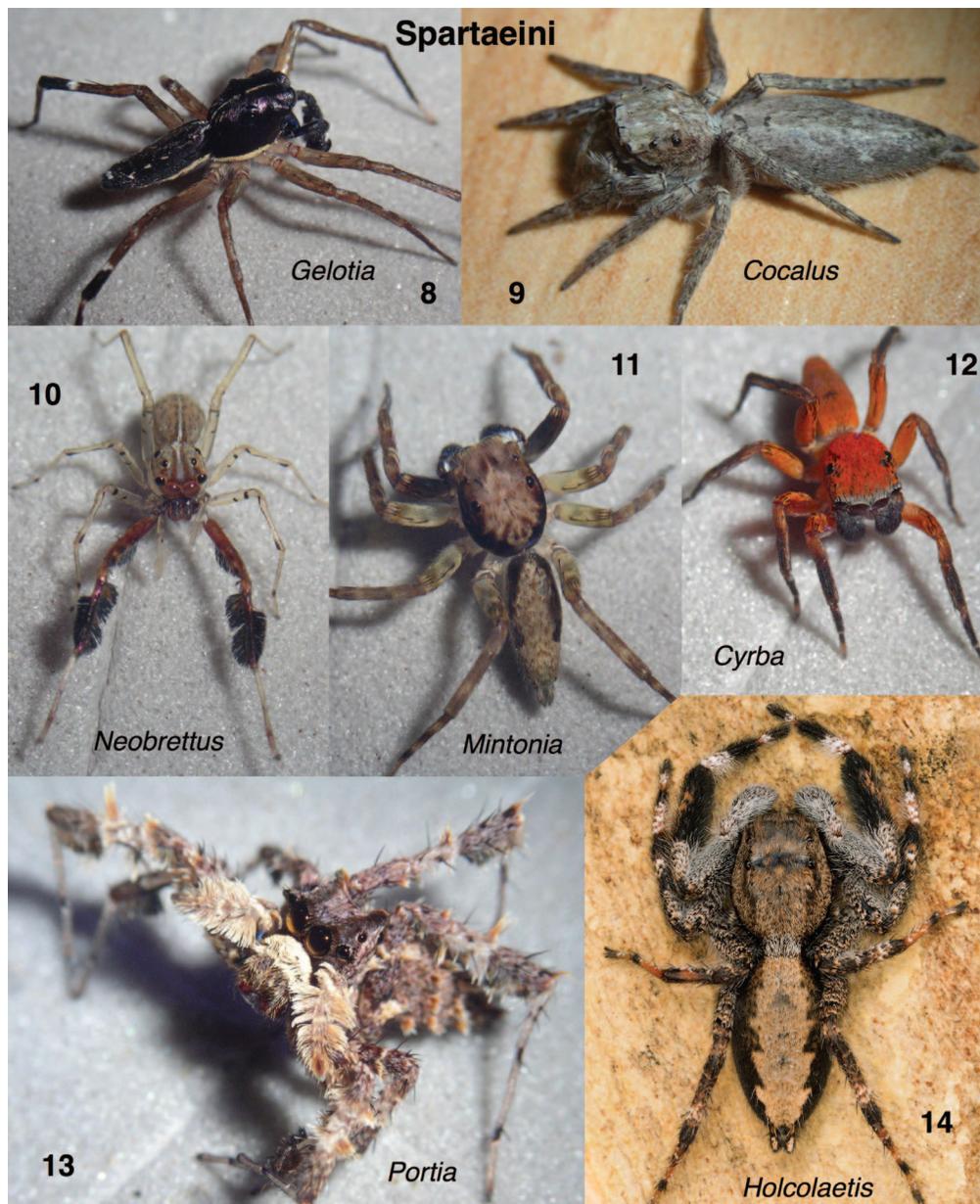
However, our greatest challenge is the size of the group compared to the number of active workers. The great bulk of work this century has been led by just a few people in each major continental area: Prószyński, Logunov, Marusik, Peng, and Azarkina for Eurasia; Wesołowska, Russell-Smith, Haddad, and van Harten for Africa and adjacent areas; Žabka for Australasia; Ruiz for the Americas; Maddison and Zhang for multiple areas. While each of the above has participated in describing at least 50 new species, the pace is far too slow given the family's size and the continuing loss of habitat. The need to recruit more workers is especially acute in the Neotropics, South Asia, Southeast Asia, and Australasia. Perhaps, as the family becomes better described and organized, young arachnologists will find it a less daunting vocation.

### ACKNOWLEDGMENTS

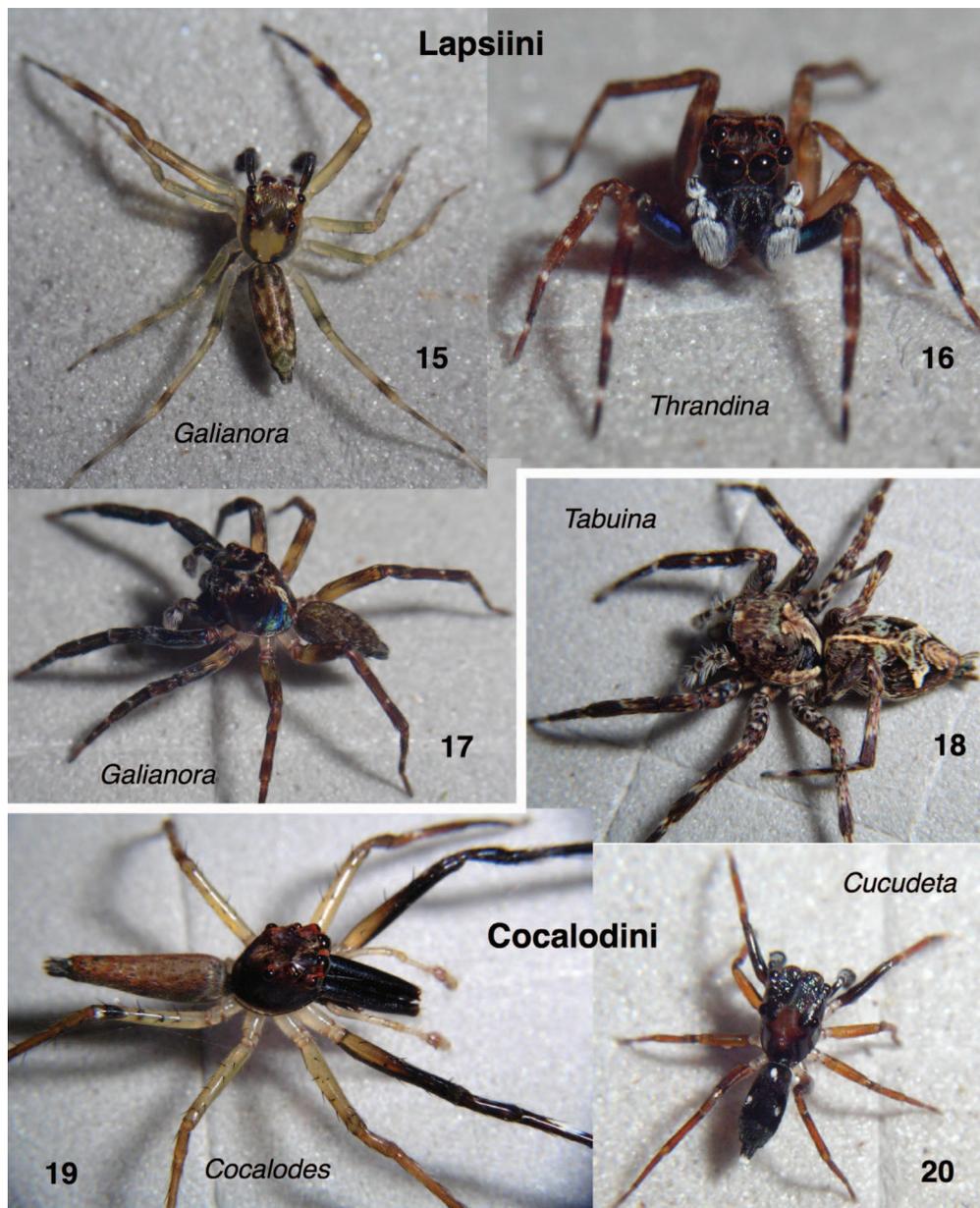
I thank David Maddison for sharing his wisdom, always, on systematics. I am grateful to G.B. Edwards for extensive discussion over the years about salticid relationships, and for hastening his publication on freyines on which this paper relied. I thank Gustavo Ruiz for his collaborations on salticid relationships, and for his hard work on various projects that served as prerequisites for this paper. He was generous and helpful with his advice, not only correcting errors but also permitting me to use his unpublished results on the placement of several Neotropical genera. I am grateful to Tamás Szűts for sharing his unpublished photographs of type specimens. Special thanks are due to Suresh Benjamin, Charles Haddad, Shuqiang Li, Jürgen Otto, Michael Schäfer, and Vida Van der Walt for permitting me to use their photographs of living spiders. Gustavo Ruiz, Martín Ramírez, Mark Harvey, G.B. Edwards, Michael Rix, and an anonymous reviewer gave helpful comments on the manuscript. I am thankful to Robert Suter, Rick Vetter, and Michael Rix for their extraordinary efforts in guiding this paper to publication. This paper was supported by an NSERC Discovery grant.



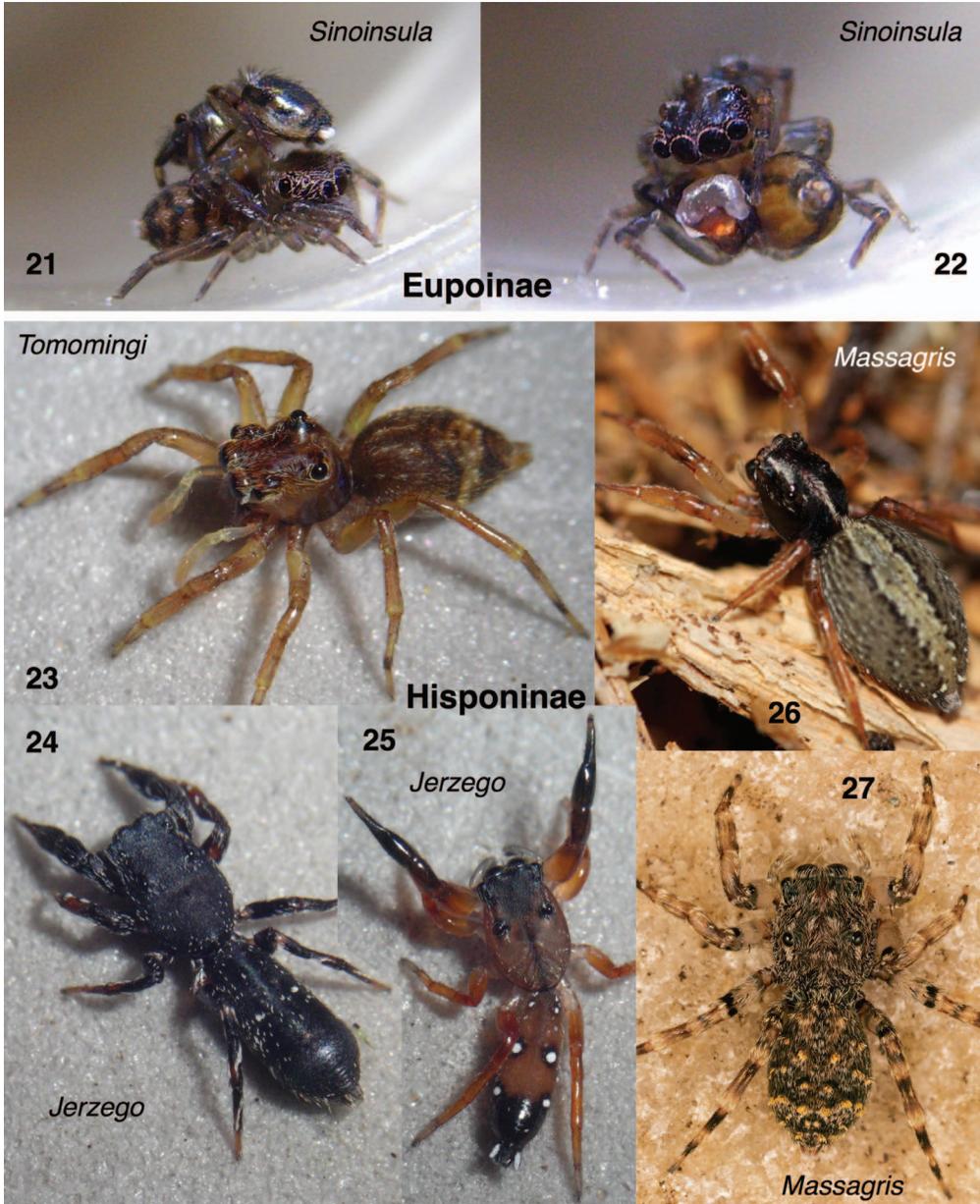
Figures 2–7.—**Onomastinae**: 2, *Onomastus pethiyagodai* Benjamin, 2010, female, Sri Lanka (photo from Benjamin 2010, fig. 18D). **Asemoneinae**: 3 *Asemonea* sp., female, Gabon: Lambaréné; 4, *Asemonea tenuipes* (O. Pickard-Cambridge, 1869), male, Singapore. **Lyssomaninae**: 5, *Chinoscopus* cf. *flavus* (Peckham, Peckham & Wheeler, 1889), female, Panama; 6, *Lyssomanes jemineus* Peckham, Peckham & Wheeler, 1889, male, México: Campeche; 7, *Lyssomanes tenuis* Peckham, Peckham & Wheeler, 1889, female, Ecuador: Yasuní. Figure 2 is © 2010 The Linnean Society of London, with permission. Figures 3–7 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



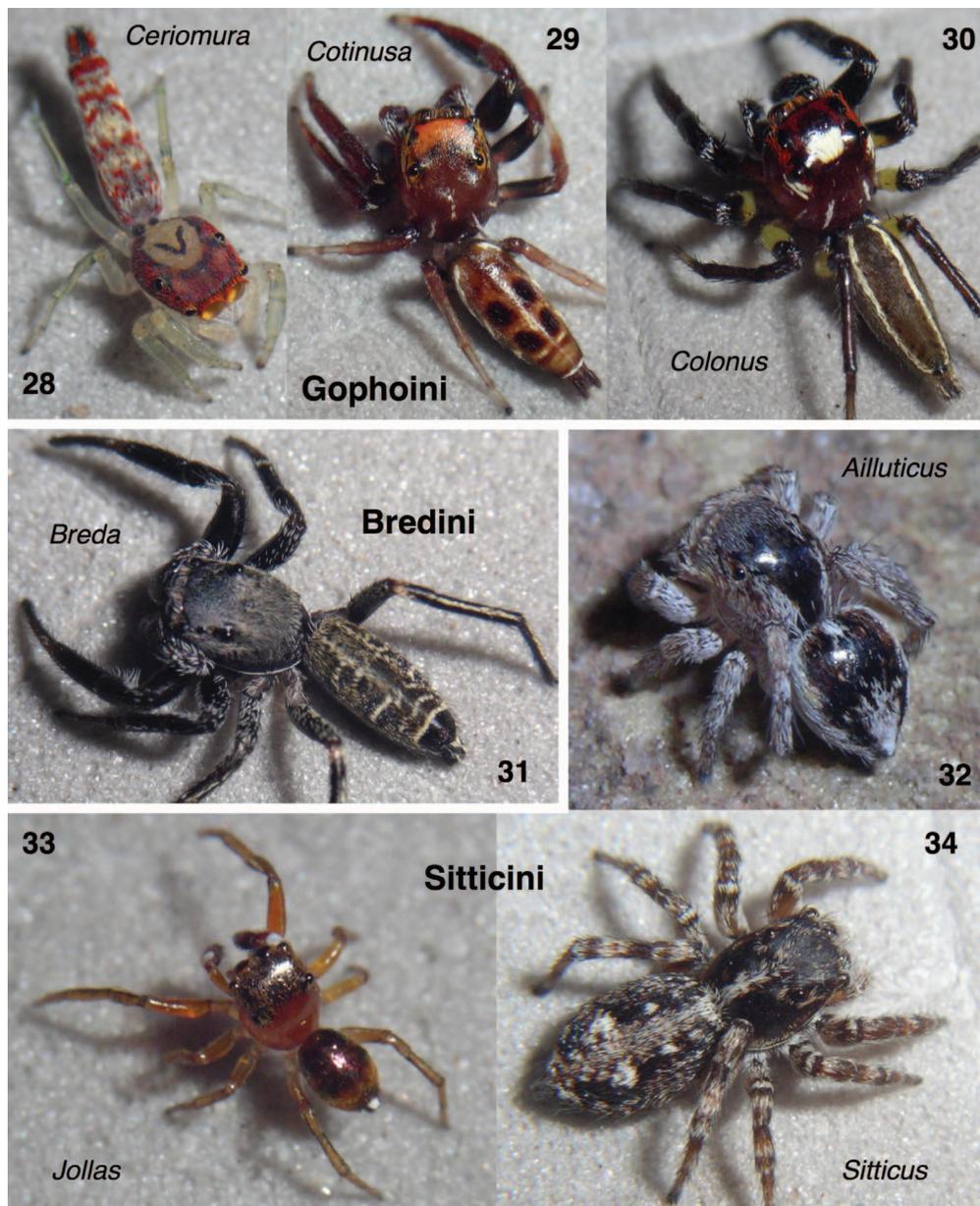
Figures 8–14.—Spartheinae. **Spartheini**: 8, *Gelotia bimaculata* Thorell, 1890, male, Malaysia: Sarawak: Kubah Nat. Pk.; 9, *Cocalus murinus* Simon, 1899, female, Singapore; 10, *Neobrettus* sp., female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 11, *Mintonia silvicola* Wanless, 1987, male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 12, *Cyrba* sp., male, Gabon: Estuaire, Cap Esterias; 13, *Portia* sp., female, Gabon: Ngounié: Waka Nat. Pk.; 14, *Holcolaetis vellerea* (Simon, 1910), male, South Africa: Pretoria: Kameeldrift, Pretoria (photo by Vida Van der Walt). Figures 8–13 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 14 is © 2014 Vida Van der Walt, used with permission.



Figures 15–20.—Spartaeinae. **Lapsiini**: 15, *Galianora sacha* Maddison, 2006, male, Ecuador: Orellana: Río Bigal Reserve; 16, *Thrandina parocula* Maddison, 2006, male, Ecuador: Napo: Río Guamani; 17, *Galianora bryicola* Maddison, 2006, male, Ecuador: Orellana: Río Bigal Reserve. **Cocalodini**: 18, *Tabuina varirata* Maddison, 2009, female, Papua New Guinea: Varirata National Park; 19, *Cocalodes longicornis* Wanless, 1982, male, Papua New Guinea: Varirata National Park; 20, *Cucudeta zalkai* Maddison, 2009 — Papua New Guinea: Southern Highlands Province, Wanakipa. Figures 15, 17–20 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 16 is © 2012 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



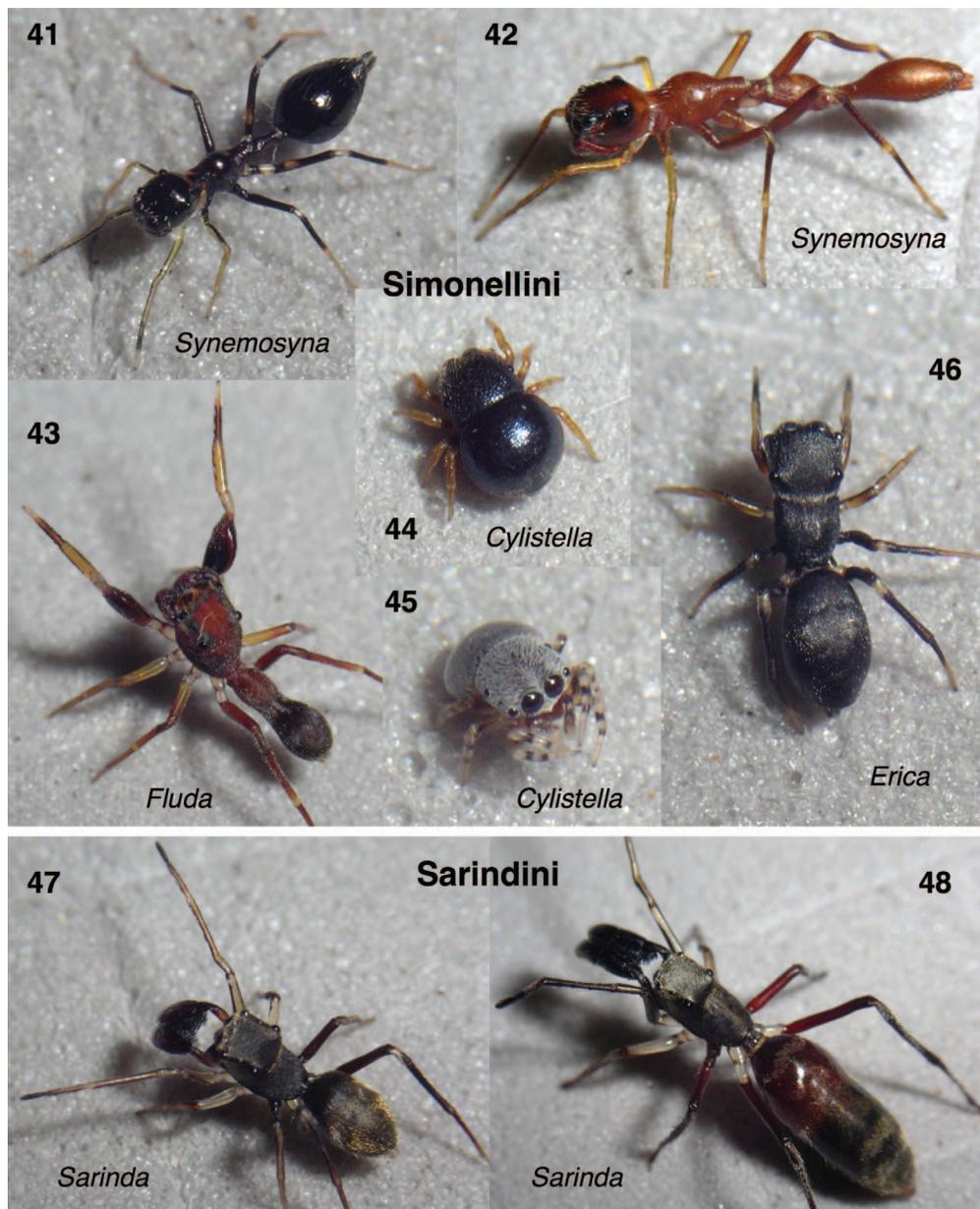
Figures 21–27.—**Eupoinae**: 21, 22, *Sinoinsula curva* (Zhou & Li, 2013), male and female in copula, China: Hainan: Mt. Limushan (photos by Yuanye Zhou). **Hisponinae**: 23, *Tomomingi* sp., female, Gabon: Monts de Cristal, Tchimbélé; 24, *Jerzego corticicola* Maddison, 2014, female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 25, *Jerzego* cf. *alboguttatus* (Simon, 1903), juvenile, Malaysia: Sarawak: Lambir Hills Nat.; 26, *Massagris honesta* Wesolowska, 1993, female, South Africa: Eastern Cape, Hogsback (photo by Charles Haddad); 27, *Massagris natalensis* Wesolowska & Haddad, 2009, female, South Africa: Kwazulu Natal, Ndumo (photo by Vida Van der Walt). Figure 21 is from Zhou & Li (2013a: fig. 118) and is © 2013 Magnolia Press, with permission. Figure 22 is © 2013 Yuanye Zhou & Shuqiang Li, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figures 23–25 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 26 is © 2010, Charles Haddad, used with permission. Figure 27 is © 2015 Vida Van der Walt, used with permission.



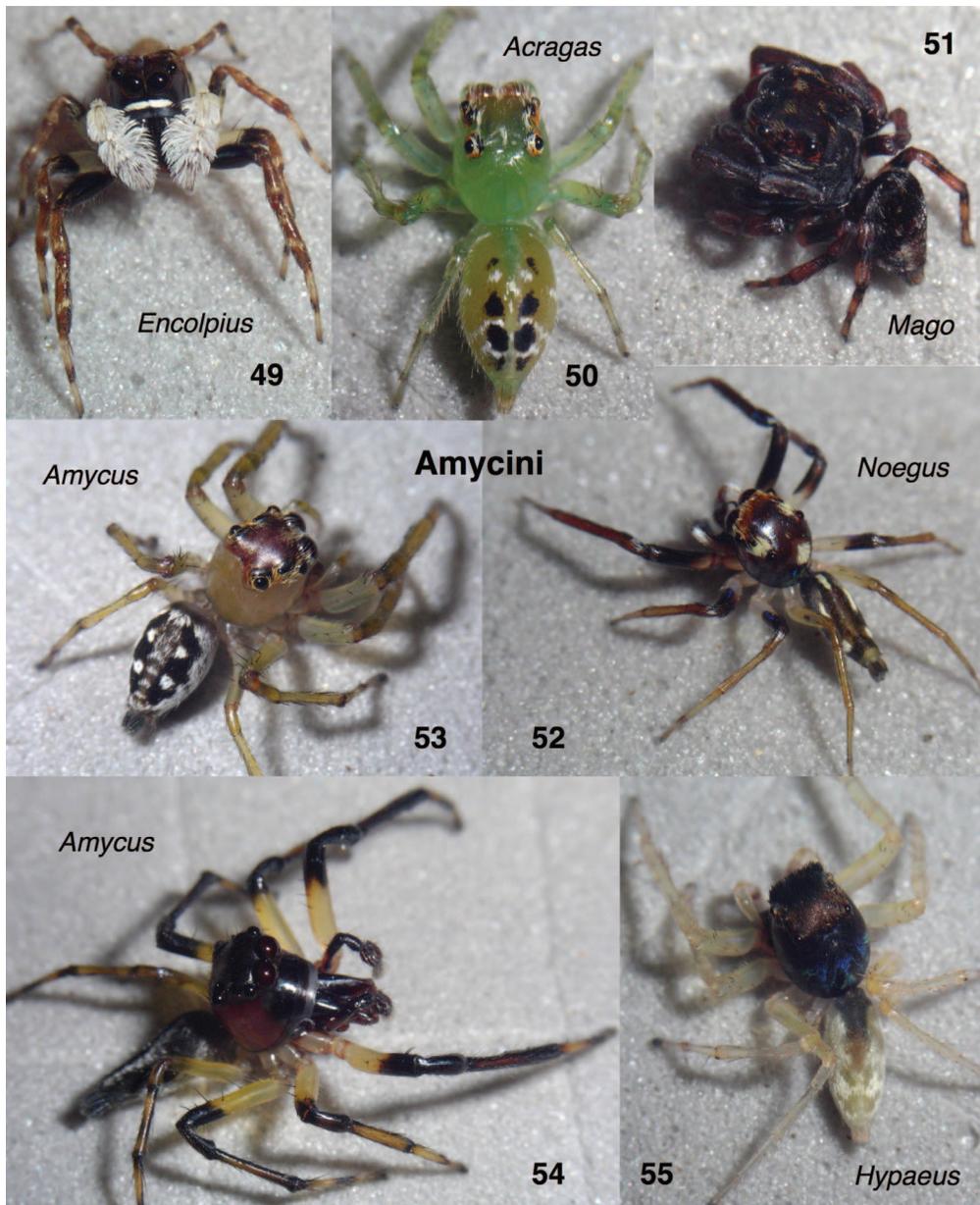
Figures 28–34.—Salticinae: Amycoida. **Gophoini:** 28, *Ceriomura* sp., female, Ecuador: Yasuní; 29, *Cotinusa* cf. *distincta* (Peckham & Peckham, 1888), male, México: Jalisco; 30, *Colonus* sp., México: Jalisco. **Bredini:** 31, *Breda akypueruna* Ruiz & Brescovit, 2013, male, Ecuador: Yasuní. **Sitticini:** 32, *Ailluticus nitens* Galiano, 1987, male, Uruguay: Canelones: Barra de Carrasco; 33, *Jollas* sp., male, Ecuador: Yasuní; 34, *Sitticus pubescens* (Fabricius 1775), female, Poland: near Neple. Figures 28–34 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 35–40.—Salticinae: Amycoidea. **Huriini**: 35, *Hurius* sp. male, Ecuador, Pichincha: near Paso de la Virgen. **Thiodinini**: 36, *Cyllodania* sp., female, Ecuador: Esmeraldas: Reserva Canandé; 37, cf. *Arachnomura* sp., male, Ecuador: Yasuní; 38, *Titanattus* sp., male, Ecuador: Pichincha: Bellavista Cloud Forest Reserve. **Scopocirini**: 39, *Gypogyna* sp., male, México: Jalisco; 40, *Scopocira* cf. *cepa* Costa & Ruiz, 2014, male, Ecuador: Yasuní. Figures 35–39 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 40 is © 2014 W. Maddison, released under a Creative Commons Attribution 4.0 International license.



Figures 41–48.—Salticinae: Amycoida. **Simonellini:** 41, *Synemosyna* sp., female, Ecuador: Esmeraldas: Reserva Canandé; 42, *Synemosyna* sp. female, Ecuador: Yasuní; 43, *Fluda* sp., male, Ecuador: Orellana: Río Bigal Reserve; 44, *Cylistella* sp., female, México: Jalisco, Chamela; 45, *Cylistella* sp., female, Ecuador: Yasuní; 46, *Erica* sp., female, Ecuador: Yasuní. **Sarindini:** 47, *Sarinda* sp., female, Ecuador: Yasuní; 48, *Sarinda* cf. *nigra* Peckham & Peckham, 1892, female, Ecuador: Yasuní. Figures 41–48 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



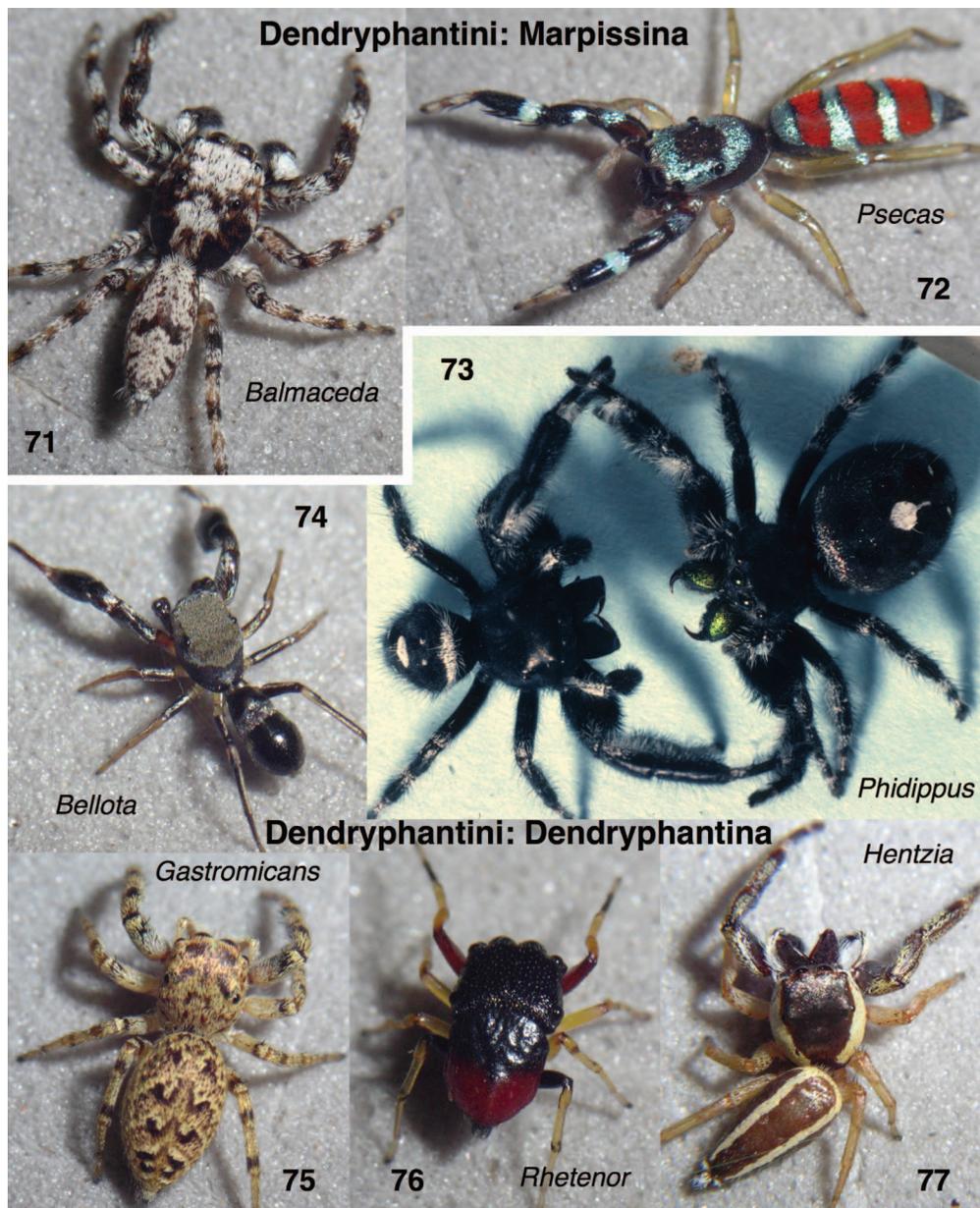
Figures 49–55.—Salticinae: Amycoidea. **Amycini**: 49, *Encolpius* sp., male, Ecuador: Napo: Río Guamani; 50, *Acragas longimanus* Simon, 1900, female, Ecuador: Yasuní; 51, *Mago* sp., male, Ecuador: Esmeraldas: Reserva Canandé; 52, *Noegus* cf. *actinosus* Simon, 1900, male, Ecuador: Yasuní; 53, *Amycus* sp., female, Ecuador: Yasuní; 54, *Amycus* sp., male, Ecuador: Yasuní; 55, *Hypaeus* aff. *porcatus* (Taczanowski, 1871), male, Ecuador: Yasuní. Figures 49–55 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 56–63.—Salticinae: Salticoida. **Agoriini**: 56, *Agorius* sp., male, Malaysia: Sarawak: Kubah Nat. Pk.; 57, *Agorius* sp., male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; **Baviini**: 58, unidentified baviine, male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 59, *Bavia* sp., female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; **Marpissoida**: **Ballini**: 60, *Pachyballus* sp., female, Gabon: Monts de Cristal, Tchimbélé; 61, *Leikung porosa* (Wanless, 1978), male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 62, *Mantisatta longicauda* Cutler & Wanless, 1973, female, Philippines: Laguna Province: Los Baños; 63, *Ballus chalybeius* (Walckenaer, 1802), female, Poland: Janów Podiaski. Figures 56–63 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 64–70.—Salticinae: Salticoida: Marpissoida. **Tisanibini:** 64, *Tisaniba mulu* Zhang & Maddison, 2014, female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 65, *Tisaniba mulu* Zhang & Maddison, 2014, male, Malaysia: Sarawak: Gunung Mulu Nat. Pk. **Dendryphantini: Itatina:** 66, *Itata* sp., male, Ecuador: Yasuní. **Dendryphantini: Synagelina:** 67, *Attidops youngii* (Peckham & Peckham, 1888), male, Canada: Ontario: Port Cunnington; 68, *Peckhamia* sp., female, México: Jalisco; 69, *Synageles* sp., female, U.S.A.: Arizona: Santa Rita Mountains; 70, *Admestina* sp., female, U.S.A.: Florida: Gainesville. Figures 64–70 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 71–77.—Salticinae: Salticoida: Marpissoida: Dendryphantini. **Marpissina:** 71, *Balmaceda* sp., male, Ecuador: Yasuní; 72, *Psecas* sp., female, Ecuador: Yasuní. **Dendryphantina:** 73, *Phidippus audax* (Hentz, 1845), male and female, Canada: Ontario: Burlington; 74, *Bellota* sp., male, Ecuador: Esmeraldas: Reserva Canandé; 75, *Gastromicans* sp., female, Ecuador: Yasuní; 76, *Rhetenor* sp., female, Ecuador: Yasuní; 77, *Hentzia* sp., male, Dominican Republic: Barahona: Parque Nacional Sierra Martín García. Figures 71–77 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



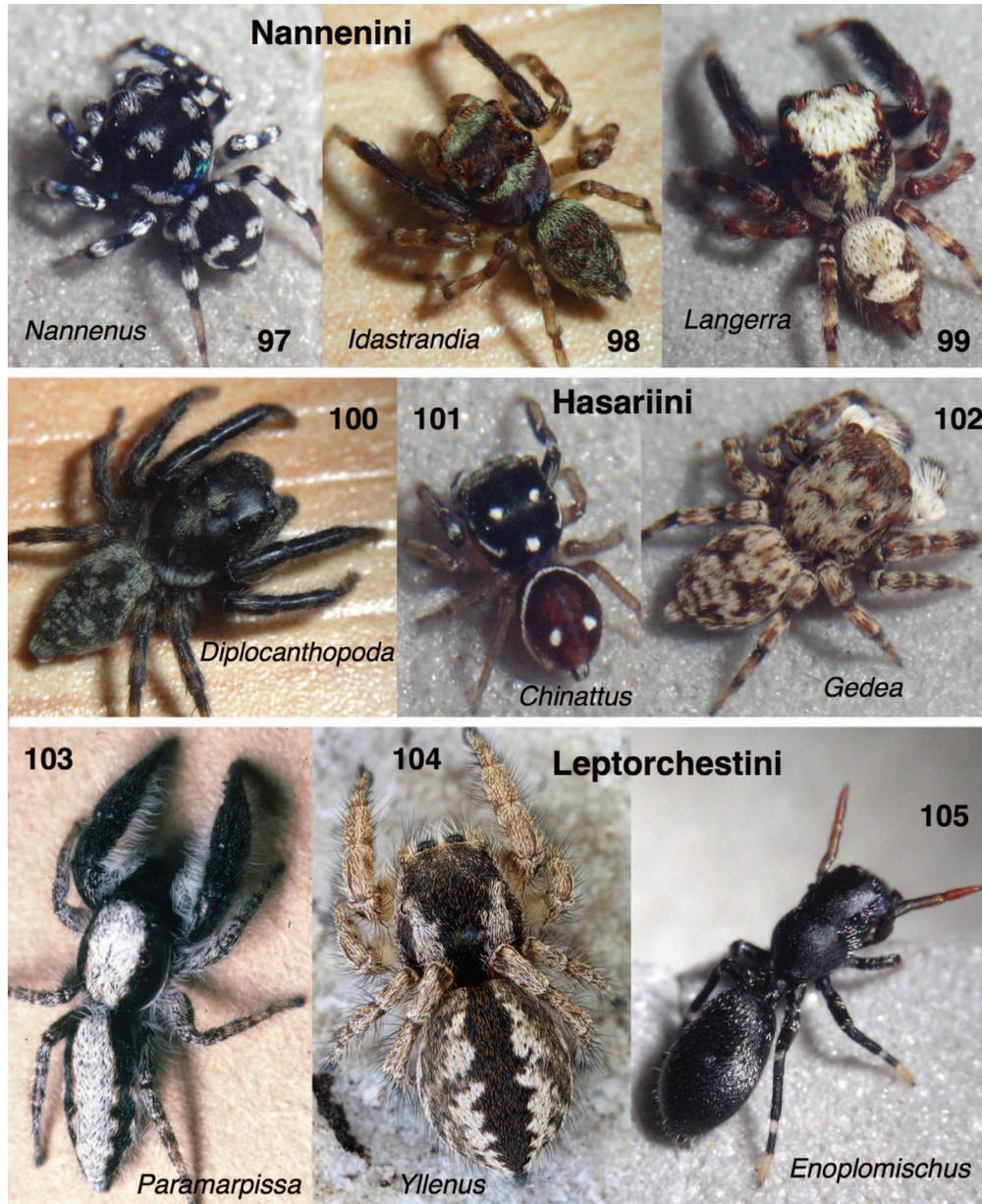
Figures 78–83.—Salticinae: Salticoida: Astioida. **Myrmarachnini:** 78, *Myrmarachne* sp., female, Gabon: Ngounié: Waka Nat. Park; 79, *Myrmarachne alticephalon* Yamasaki & Ahmad, 2013, male, Malaysia: Sarawak: Gunung Mulu Nat. Pk. **Neonini:** 80, *Neon* sp., female, U.S.A.: California: Monterey County. **Mopsini:** 81, *Mopsus mormon* Karsch, 1878, male, Australia: Queensland: Townsville (photo by Jürgen Otto). **Astiini:** 82, *Orthrus* cf. *muluensis* Wanless, 1980, male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 83, *Helpis minitabunda* (L. Koch, 1880), male, Papua New Guinea: Enga Province: Porgera. Figure 81 is © 2004 Jürgen Otto, used with permission. Figures 78–80, 82, 83 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



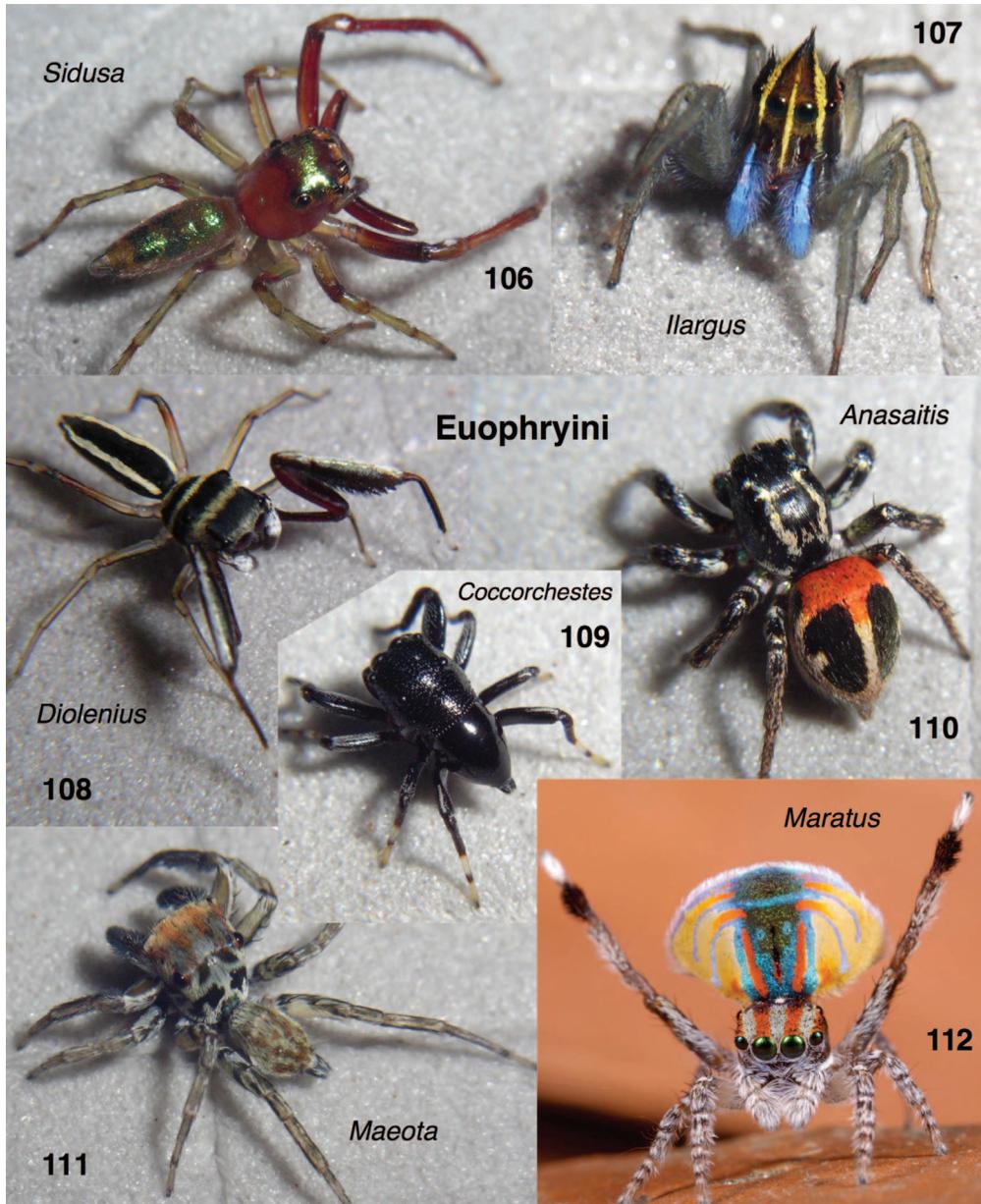
Figures 84–89.—Salticinae: Salticoida: Astioida. **Viciriini**: 84, *Nungia* sp., male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 85, *Holoplatys* sp., male, Papua New Guinea: Southern Highlands Province: Wanakipa; 86, *Viciria praemandibularis* (Hasselt, 1893), male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 87, *Uroballus* sp., male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 88, *Simaetha* sp., female, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 89, *Opisthonus* sp., female, Papua New Guinea: Enga Province: Kai-ingri. Figures 84–89 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 90–96.—Salticinae: Salticoida: Saltafresia. **Chrysillini**: 90, *Orsima ichneumon* (Simon, 1901), male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 91, *Menemerus bivittatus* (Dufour, 1831), female, Ecuador: Yasuní; 92, *Phintella* sp., male, Malaysia: Sarawak: Kubah Nat. Pk.; 93, *Heliophanus* sp., female, Poland: near Sary Babel; 94, *Epocilla* sp., female, Malaysia: Sarawak: Bako Nat. Pk.; 95, *Yepoella* sp., male, Ecuador: Sucumbios: Reserva Faunística Cuyabeno; 96, *Cosmophasis* sp., male, Papua New Guinea: Southern Highlands Province: Wanakipa. Figures 90–96 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 97–105.—Salticinae: Salticoida: Salfafresia. **Nanneniini**: 97, *Nannenus syrphus* Simon, 1902, male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 98, *Idastrandia* cf. *orientalis* (Szombathy, 1915), male, Singapore; 99, *Langerra* aff. *longicymbium* Song & Chai, 1991, male, Malaysia: Sarawak: Lambir Hills Nat. Pk. **Hasariini**: 100, *Diplocanthopoda marina* Abraham, 1925, male, Singapore; 101, *Chinattus* sp., male, Malaysia: Sarawak: Lambir Hills Nat. Pk.; 102, *Gedeia* sp., male, Malaysia: Sarawak: Gunung Mulu Nat. Pk. **Leptorchestini**: 103, *Paramarpissa* sp., male, U.S.A.: California: San Luis Obispo County; 104, *Yllenus vittatus* Thorell, 1875, female, Austria (photo by Michael Schäfer, from [http://www.kleinesganzgross.de/gallery\\_art.php?ID=85](http://www.kleinesganzgross.de/gallery_art.php?ID=85)); 105, *Enoplomisclus* sp. juvenile, Gabon: Ngounié: Waka Nat. Park. Figures 97–103, 105 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 104 is © 2014 Michael Schäfer, used with permission.



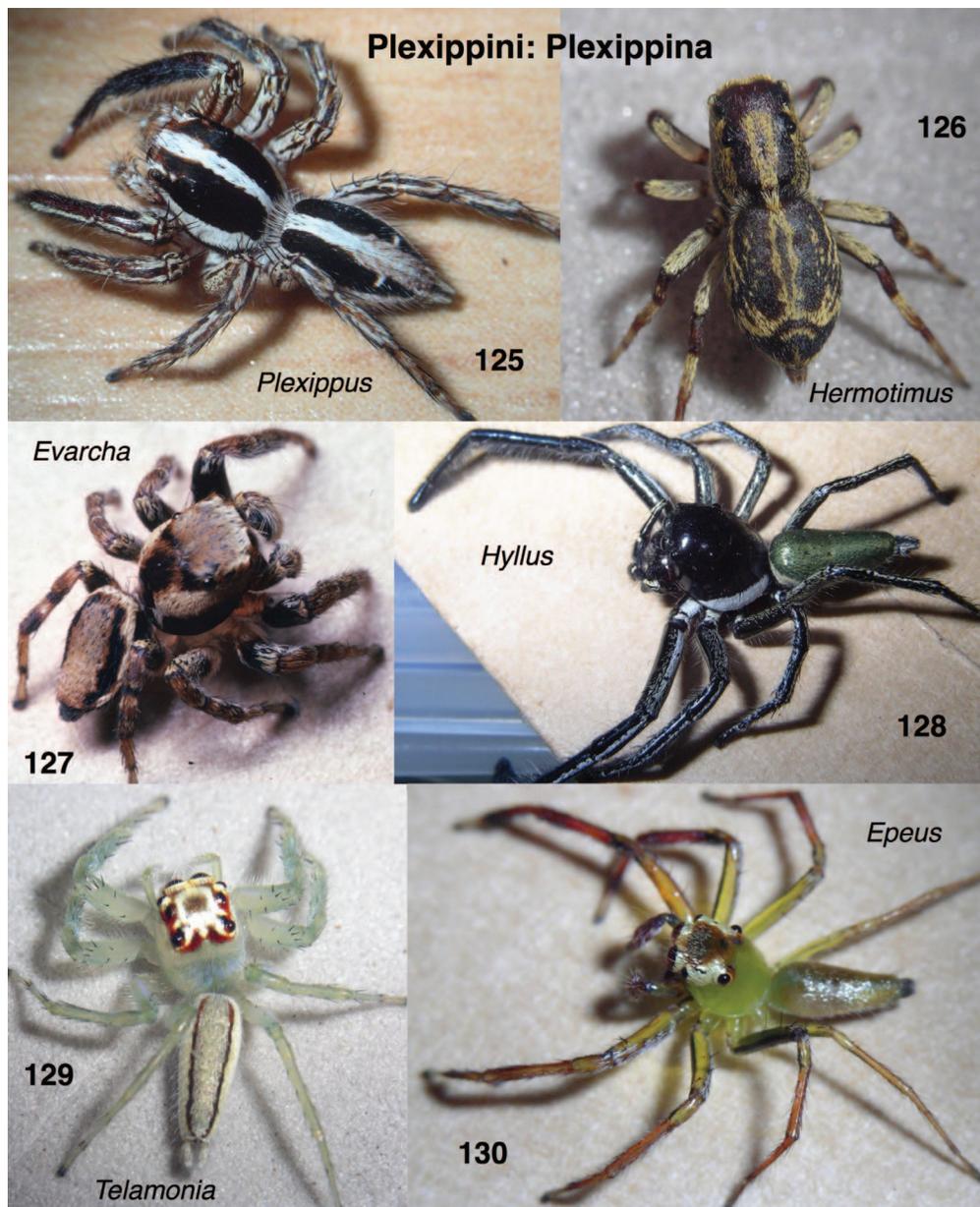
Figures 106–112.—Salticinae: Salticoida: Saltafresia. **Euophryini**: 106, *Sidusa* sp., male, Ecuador: Esmeraldas: Puerto Nuevo; 107, *Ilargus* sp., male, Ecuador: Pichincha: near Nono; 108, *Diolenius* sp., male, Papua New Guinea: Central Province: Varirata National Park; 109, *Coccochestes* sp., male, Papua New Guinea: Southern Highlands Province: Wanakipa; 110, *Anasaitis elegantissima* (Simon, 1888), female, Dominican Republic: La Altagracia: Punta Cana; 111, *Maeota* sp., male, Ecuador: Tena; 112, *Maratus volans* (O. Pickard-Cambridge, 1874), male (photo by Jürgen Otto). Figures 106–110 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 111 is © 2015 W. P. Maddison & J. Zhang, released under a Creative Commons Attribution (CC-BY) 3.0 license. Figure 112 is © 2010 Jürgen Otto, used with permission.



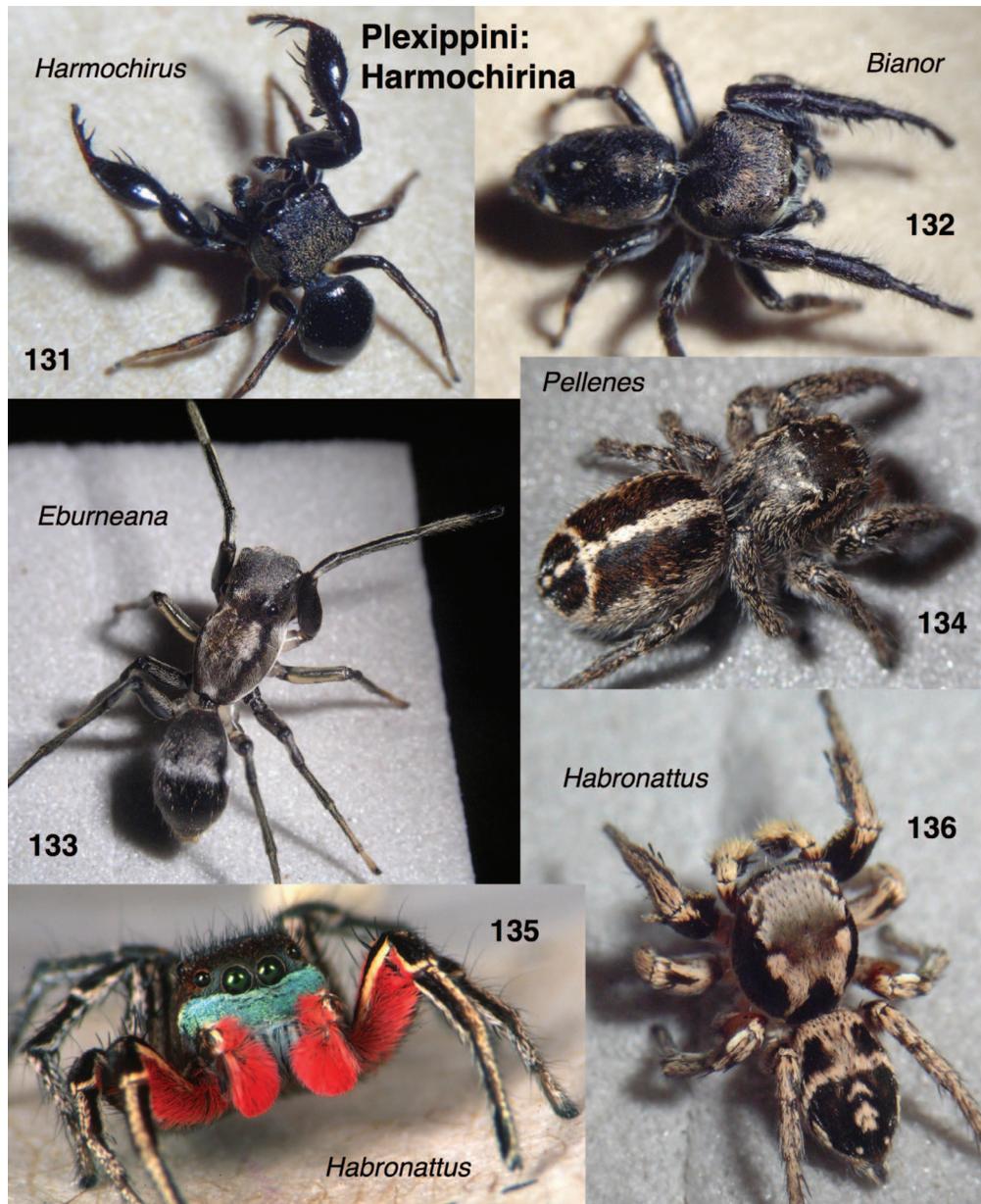
Figures 113–118.—Salticinae: Salticoida: Saltafresia. **Salticini:** 113, *Tusitala* sp., male, Gabon: Moyen-Ogououé: Lambaréné; 114, *Carrhotus sannio* (Thorell, 1877), male, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 115, *Salticus* sp., female, U.S.A.: Arizona: near Santa Rita Mountains. **Aelurillini: Aelurillina:** 116, *Langelurillus* sp., female, Gabon: Monts de Cristal, Tchimbélé; 117, *Stenaelurillus* sp., male, Gabon: Estuaire: Cap Esterias; 118, *Phlegra* sp., female, Germany: Saxony: Authausen. Figures 113–118 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 119–124.—Salticinae: Salticoida: Saltafresia: Aelurillini. **Freyina**: 119, *Freya decorata* (C.L. Koch, 1846), male, Ecuador: Yasuní; 120, *Asaracus* sp., male, Ecuador: Yasuní; 121, *Akela* sp., male, Ecuador: Napo: Río Salado at highway 45. **Thiratoscirtina**: 122, *Longarenius* sp., female, Gabon: Monts de Cristal, Tchimbélé; 123, *Thiratoscirtus* sp., male, Gabon: Monts de Cristal, Tchimbélé; 124, *Malloneta guineensis* Simon, 1902, male, Gabon: Ngounié: Waka Nat. Park. Figures 119–124 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 125–130.—Salticinae: Salticoida: Saltafresia: Plexippini. **Plexippina:** 125, *Plexippus paykulli* (Audouin, 1826), male, Singapore; 126, *Hermotimus* sp., female, Gabon: Ngounié: Waka Nat. Park; 127, *Evarcha falcata* (Clerck, 1757), male, Spain: Barcelona: Bagà; 128, *Hyllus* cf. *keratodes* (Hasselt, 1882), male, Malaysia: Selangor: near Ulu Gombak; 129, *Telamonia dimidiata* (Simon, 1899), female, Malaysia: Sarawak: Gunung Mulu Nat. Pk.; 130, *Epeus* sp., male, Malaysia: Pahang: Cameron Highlands. Figures 125–130 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.



Figures 131–136.—Salticinae: Salticoida: Saltafresia: Plexippini. **Harmochirina:** 131, *Harmochirus* sp., male, Malaysia: Selangor: Ulu Gombak Field Station; 132, *Bianor* sp., male, Malaysia: Pahang: Cameron Highlands; 133, *Eburneana* sp., male, Gabon: Monts de Cristal, Tchimbélé; 134, *Pellenes tripunctatus* (Walckenaer, 1802), female, Germany: Saxony: Authausen; 135, *Habronattus americanus* (Keyserling, 1885), male, U.S.A.: Idaho; 136, *Habronattus mexicanus* (Peckham & Peckham, 1896), male, México: Jalisco. Figures 131–136 are © 2015 W. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

Table 2.— Classification of genera of Salticidae. ? = placement especially tentative; \* = placement in part by molecular data (Hedin & Maddison 2001; Maddison & Hedin 2003a, b; Su et al. 2007; Andriamalala 2007, Maddison et al. 2008, 2014; Bodner & Maddison 2012; Zhang & Maddison 2013, 2014; Ruiz & Maddison 2015; Maddison, unpublished data). Available in machine-readable form online at <http://dx.doi.org/10.1636/R15-55.s1>, <http://doi.org/10.5886/gg3ud66w>, and <http://salticidae.org/classification/>. This table is © 2015 W. Maddison, released under a Creative Commons Attribution (CC - BY) 3.0 license.

### Subfamily Onomastinae

(12 species in 1 genus)

*Onomastus* Simon, 1900\*

### Subfamily Asemoneinae

(38 species in 5 genera)

*Asemonea* O. P.-Cambridge, 1869\*  
*Goleba* Wanless, 1980\*

*Hindumanes* Logunov, 2004  
*Macopaeus* Simon, 1900

*Pandisus* Simon, 1900\*

### Subfamily Lyssomaninae

(92 species in 2 genera)

*Chinoscopus* Simon, 1900\*

*Lyssomanes* Hentz, 1845\*

### Subfamily Spartaeinae

(165 species in 29 genera)

#### Tribe Spartaeini: Subtribe Spartaeina (111 species in 16 genera)

*Brettus* Thorell, 1895\*  
*Cocalus* C. L. Koch, 1846\*  
*Cyrba* Simon, 1876\*  
*Gelotia* Thorell, 1890\*  
*Meleon* Wanless, 1984\*  
*Mintonia* Wanless, 1984\*

*Neobrettus* Wanless, 1984\*  
*Paracyrba* Žabka & Kovac, 1996\*  
*Phaeacius* Simon, 1900\*  
*Portia* Karsch, 1878\*  
*Sparbambus* Zhang, Woon & Li, 2006\*  
*Spartaeus* Thorell, 1891\*

*Taraxella* Wanless, 1984\*  
*Veissella* Wanless, 1984  
*Wanlessia* Wijesinghe, 1992  
*Yaginumanis* Wanless, 1984

#### Tribe Spartaeini: Subtribe Holcolaetina (9 species in 2 genera)

*Holcolaetis* Simon, 1886\*

*Sonoita* Peckham & Peckham, 1903\*

#### Tribe Cocalodini (25 species in 6 genera)

*Allococalodes* Wanless, 1982\*  
*Cocalodes* Pocock, 1897\*

*Cucudeta* Maddison, 2009\*  
*Depreissia* Lessert, 1942\*

*Tabuina* Maddison, 2009\*  
*Yamangalea* Maddison, 2009\*

#### Tribe Lapsiini (20 species in 5 genera)

*Galianora* Maddison, 2006\*  
*Lapsamita* Ruiz, 2013

*Lapsias* Simon, 1900\*  
*Soesiladeepakius* Makhani, 2007\*

*Thrandina* Maddison, 2006\*

### Subfamily Eupoinae

(34 species in 3 genera)

*Eupoa* Žabka, 1985\*

*Corusca* Zhou & Li, 2013

*Sinoinsula* Zhou & Li, 2013

### Subfamily Hispaninae

(53 species in 9 genera)

†*Almolinus* Petrunkevitch, 1958  
†*Gorgopsina* Petrunkevitch, 1955  
*Hispo* Simon, 1886\*

*Jerzego* Maddison, 2014\*  
*Massagris* Simon, 1900\*  
†*Prolinus* Petrunkevitch, 1958

*Tomobella* Szűts & Scharff, 2009\*  
*Tomocyrra* Simon, 1900\*  
*Tomomingi* Szűts & Scharff, 2009\*

## Subfamily Salticinae

(5379 species in 538 genera)

### Salticinae: Clade Amycoida

(430 species in 63 genera)

#### Tribe Gophoiini (59 species in 8 genera)

*Banksetosa* Chickering, 1946  
*Carabella* Chickering, 1946\*  
*Ceriomura* Simon, 1901\*

*Colonus* F. O. P.-Cambridge, 1901\*  
*Cotinusa* Simon, 1900\*  
*Nilakantha* Peckham & Peckham, 1901\*

*Parathiodina* Bryant, 1943  
*Proctonemesia* Bauab & Soares, 1978

#### Tribe Sitticini (120 species in 10 genera)

*Aillutticus* Galiano, 1987\*  
*Amatorculus* Ruiz & Brescovit, 2005  
*Attulus* Simon, 1889\*  
*Capeta* Ruiz & Brescovit, 2005

*Gavarilla* Ruiz & Brescovit, 2006  
*Jollas* Simon, 1901\*  
*Nosferattus* Ruiz & Brescovit, 2005  
*Pseudattulus* Caporiacco, 1947

*Semiopyla* Simon, 1901  
*Sitticus* Simon, 1901\*

#### Tribe Bredini (14 species in 2 genera)

*Breda* Peckham & Peckham, 1894\*

*Druzia* Ruiz & Brescovit, 2013

#### Tribe Scopocirini (10 species in 2 genera)

*Gypogyna* Simon, 1900\*

*Scopocira* Simon, 1900\*

#### Tribe Thiodinini (24 species in 9 genera)

*Agelista* Simon, 1900\*  
*Arachnomura* Mello-Leitão, 1917\*  
*Atomosphyrus* Simon, 1902

*Bredana* Gertsch, 1936  
*Cylrodania* Simon, 1902\*  
*Hyetussa* Simon, 1902\*

*Micalula* Strand, 1932  
*Thiodina* Simon, 1900  
*Titanattus* Peckham & Peckham, 1885\*

#### Tribe Sarindini (36 species in 7 genera)

*Corcovetella* Galiano, 1975  
*Martella* Peckham & Peckham, 1892\*  
*Parafluda* Chickering, 1946

*Sarinda* Peckham & Peckham, 1892\*  
*Simprulla* Simon, 1901  
*Tanybelus* Simon, 1902

*Zuniga* Peckham & Peckham, 1892\*

#### Tribe Simonellini (39 species in 4 genera)

*Cylistella* Simon, 1901\*  
*Erica* Peckham & Peckham, 1892\*

*Fluda* Peckham & Peckham, 1892\*  
*Synemosyna* Hentz, 1846\*

#### Tribe Huriini (16 species in 6 genera)

*Admesturius* Galiano, 1988  
*Atelurius* Simon, 1901

*Hurius* Simon, 1901\*  
*Scoturius* Simon, 1901

*Simonurius* Galiano, 1988  
*Uruguayu* Ruiz & Maddison, 2015\*

#### Tribe Amycini (110 species in 13 genera)

*Acragas* Simon, 1900\*  
*Amycus* C. L. Koch, 1846\*  
*Anaurus* Simon, 1900  
*Arnoliseus* Braul, 2002  
*Encolpius* Simon, 1900\*

*Frespera* Braul & Lise, 2002\*  
*Hypaeus* Simon, 1900\*  
*Letoia* Simon, 1900\*  
*Macutula* Ruiz, 2011  
*Maenola* Simon, 1900

*Mago* O. P.-Cambridge, 1882\*  
*Noegus* Simon, 1900\*  
*Vinnius* Simon, 1902

#### Amycoida incertae sedis (2 species in 2 genera)

*Orvilleus* Chickering, 1946

*Toloella* Chickering, 1946

### Salticinae: Clade Salticoida

(4825 species in 427 genera)

#### Tribe Agoriini (45 species in 2 genera)

*Agorius* Thorell, 1877\*

*Synagelides* Strand, 1906\*

#### Tribe Baviini (26 species in 3 genera)

*Bavia* Simon, 1877\*

*Piranthus* Thorell, 1895<sup>2</sup>

*Stagetillus* Simon, 1885

**Salticoida: Astioida***(584 species in 55 genera)***Tribe Myrmarachnini** (246 species in 7 genera)*Belippo* Simon, 1910\**Bocus* Peckham & Peckham, 1892*Damoetas* Peckham & Peckham, 1886*Judalana* Rix, 1999*Ligonipes* Karsch, 1878\**Myrmarachne* MacLeay, 1839\**Rhombonotus* L. Koch, 1879**Tribe Neonini** (27 species in 1 genus)*Neon* Simon, 1876\***Tribe Astiini** (54 species in 11 genera)*Arasia* Simon, 1901\**Astia* L. Koch, 1879*Astilodes* Żabka, 2009<sup>?</sup>*Helpis* Simon, 1901\**Jacksonoides* Wanless, 1988\**Katya* Prószyński & Deeleman-Reinhold,  
2010<sup>?</sup>*Megaloastia* Żabka, 1995*Orthrus* Simon, 1900\**Parahelpis* Gardzińska & Żabka, 2010*Sondra* Wanless, 1988\**Tauala* Wanless, 1988\***Tribe Mopsini** (12 species in 3 genera)*Mopsolodes* Żabka, 1991*Mopsus* Karsch, 1878\**Sandalodes* Keyserling, 1883\***Tribe Vicirini (other than Simaethina)** (176 species in 20 genera)*Abracadabrella* Żabka, 1991<sup>?</sup>*Avarua* Marples, 1955*Clynotis* Simon, 1901\**Corambis* Simon, 1901\**Holoplatys* Simon, 1885\**Huntiglennia* Żabka & Gray, 2004*Lystrocteisa* Simon, 1884<sup>?</sup>*Nungia* Żabka, 1985\**Ocrisiona* Simon, 1901\**Opisthonus* L. Koch, 1880\**Paraphilaeus* Żabka, 2003<sup>?</sup>*Paraplatoides* Żabka, 1992*Penionomus* Simon, 1903\**Pungalina* Richardson, 2013<sup>?</sup>*Rhondes* Simon, 1901\**Rogmocrypta* Simon, 1900<sup>?</sup>*Tara* Peckham & Peckham, 1886*Trite* Simon, 1885\**Viciria* Thorell, 1877\**Zebraplatys* Żabka, 1992**Tribe Vicirini: Subtribe Simaethina** (69 species in 13 genera)*Heratemita* Strand, 1932\**Iona* Peckham & Peckham, 1886*Irura* Peckham & Peckham, 1901\**Ligurra* Simon, 1903\**Mantius* Thorell, 1891*Phyaces* Simon, 1902*Poecilorchestes* Simon, 1901*Porius* Thorell, 1892*Simaetha* Thorell, 1881\**Simaethula* Simon, 1902*Stertinius* Simon, 1890<sup>?</sup>*Uroballus* Simon, 1902\**Urogelides* Żabka, 2009**Salticoida: Marpissoida***(840 species in 90 genera)***Tribe Ballini** (85 species in 15 genera)*Afromarengo* Benjamin, 2004\**Ballus* C. L. Koch, 1850\**Colaxes* Simon, 1900*Copocrossa* Simon, 1901*Cynapes* Simon, 1900*Goleta* Peckham & Peckham, 1894*Indomarengo* Benjamin, 2004*Leikung* Benjamin, 2004\**Mantisatta* Warburton, 1900\**Marengo* Peckham & Peckham, 1892\**Pachyballus* Simon, 1900\**Padilla* Peckham & Peckham, 1894\**Peplometus* Simon, 1900\**Philates* Simon, 1900*Sadies* Wanless, 1984**Tribe Tisanibini** (6 species in 2 genera)*Saaristattus* Logunov & Azarkina, 2008<sup>?</sup>*Tisaniba* Zhang & Maddison, 2014\***Tribe Dendryphantini: Subtribe Synagelina** (48 species in 6 genera)*Admestina* Peckham & Peckham, 1888\**Attidops* Banks, 1905\**Cheliferooides* F. O. P.-Cambridge, 1901\**Descanso* Peckham & Peckham, 1892*Peckhamia* Simon, 1901\**Synageles* Simon, 1876\***Tribe Dendryphantini: Subtribe Itatina** (5 species in 1 genus)*Itata* Peckham & Peckham, 1894\***Tribe Dendryphantini: Subtribe Marpissina** (110 species in 9 genera)*Balmaceda* Peckham & Peckham, 1894\**Empanda* Simon, 1903*Fuentes* Peckham & Peckham, 1894*Maevia* C. L. Koch, 1846\**Marpissa* C. L. Koch, 1846\**Mendoza* Peckham & Peckham, 1894*Metacyrba* F. O. P.-Cambridge, 1901\**Platycriptus* Hill, 1979\**Psecas* C. L. Koch, 1850\*

**Tribe Dendryphantini: Subtribe Dendryphantina** (581 species in 56 genera)

- Alcmena* C. L. Koch, 1846  
*Anokopsis* Bauab & Soares, 1980  
*Anicius* Chamberlin, 1925  
*Ashtabula* Peckham & Peckham, 1894\*  
*Avitus* Peckham & Peckham, 1896  
*Bagheera* Peckham & Peckham, 1896  
*Beata* Peckham & Peckham, 1895\*  
*Bellota* Peckham & Peckham, 1892\*  
*Bryantella* Chickering, 1946\*  
*Cerionesta* Simon, 1901  
*Chirothecia* Taczanowski, 1878\*  
*Dendryphantes* C. L. Koch, 1837\*  
*Donaldius* Chickering, 1946  
*Eris* C. L. Koch, 1846\*  
*Fritzia* O. P.-Cambridge, 1879\*  
*Gastromicans* Mello-Leitão, 1917\*  
*Ghelna* Maddison, 1996\*  
*Hentzia* Marx, 1883\*  
*Lurio* Simon, 1901  
*Mabellina* Chickering, 1946\*  
*Macaroeris* Wunderlich, 1992  
*Mburuvicha* Scioscia, 1993  
*Messua* Peckham & Peckham, 1896\*  
*Metaphidippus* F. O. P.-Cambridge, 1901  
*Mirandia* Badcock, 1932?  
*Monaga* Chickering, 1946  
*Nagaina* Peckham & Peckham, 1896  
*Naubolus* Simon, 1901  
*Osericta* Simon, 1901  
*Paradamoetas* Peckham & Peckham, 1885  
*Paraphidippus* F. O. P.-Cambridge, 1901\*  
*Parnaenus* Peckham & Peckham, 1896  
*Pelegrina* Franganillo, 1930\*  
*Phanias* F. O. P.-Cambridge, 1901\*  
*Phidippus* C. L. Koch, 1846\*  
*Planiemen* Wesolowska & van Harten, 2007?  
*Poultonella* Peckham & Peckham, 1909\*  
*Pseudofluda* Mello-Leitão, 1928  
*Pseudopartona* Caporiacco, 1954  
*Rhene* Thorell, 1869\*  
*Rhetenor* Simon, 1902\*  
*Rudra* Peckham & Peckham, 1885\*  
*Sassacus* Peckham & Peckham, 1895\*  
*Sebastira* Simon, 1901  
*Selimus* Peckham & Peckham, 1901  
*Semora* Peckham & Peckham, 1892  
*Tacuna* Peckham & Peckham, 1901  
*Terralonus* Maddison, 1996\*  
*Thammaca* Simon, 1902  
*Tulpus* Peckham & Peckham, 1896  
*Tutelina* Simon, 1901\*  
*Tuvaphantes* Logunov, 1993  
*Uluella* Chickering, 1946  
*Xuriella* Wesolowska & Russell-Smith, 2000?  
*Zeuxippus* Thorell, 1891  
*Zygoballus* Peckham & Peckham, 1885\*

**Dendryphantini incertae sedis** (5 species in 1 genus)

*Semorina* Simon, 1901

**Salticoida: Saltafresia**

(3330 species in 277 genera)

**Tribe Nannenini** (8 species in 3 genera)

*Idastrandia* Strand, 1929\* *Langerra* Żabka, 1985\*? *Nannenus* Simon, 1902\*

**Tribe Hasariini** (116 species in 15 genera)

*Bristowia* Reimoser, 1934\*  
*Cheliceroides* Żabka, 1985\*  
*Chinattus* Logunov, 1999\*  
*Curubis* Simon, 1902  
*Diplocanthopoda* Abraham, 1925\*  
*Echeclus* Thorell, 1890\*  
*Gede* Simon, 1902\*  
*Habrocestoides* Prószyński, 1992  
*Habrocestum* Simon, 1876\*  
*Hasarina* Schenkel, 1963  
*Hasarius* Simon, 1871\*  
*Imperceptus* Prószyński, 1992?  
*Madhyattus* Prószyński, 1992?  
*Mikrus* Wesolowska, 2001  
*Uxuma* Simon, 1902?

**Tribe Chrysellini** (599 species in 31 genera)

*Afraflacilla* Berland & Millot, 1941  
*Augustaea* Szombathy, 1915  
*Chryzilla* Thorell, 1887  
*Cosmophasis* Simon, 1901\*  
*Echinussa* Simon, 1901  
*Epocilla* Thorell, 1887\*  
*Festucula* Simon, 1901  
*Hakka* Berry & Prószyński, 2001  
*Helicius* Żabka, 1981  
*Heliophanillus* Prószyński, 1989  
*Heliophanus* C. L. Koch, 1833\*  
*Helvetia* Peckham & Peckham, 1894\*  
*Icius* Simon, 1876\*  
*Jaluiticola* Roewer, 1944  
*Kupiuka* Ruiz, 2010  
*Marchena* Peckham & Peckham, 1909\*  
*Matagaia* Ruiz, Brescovit & Freitas, 2007  
*Menemerus* Simon, 1868\*  
*Mexcala* Peckham & Peckham, 1902\*  
*Natta* Karsch, 1879  
*Ogdenia* Peckham & Peckham, 1908  
*Orsima* Simon, 1901\*  
*Paraheliophanus* Clark & Benoit, 1977  
*Phintella* Strand, 1906\*  
*Plesiopiuka* Ruiz, 2010  
*Pseudicius* Simon, 1885\*  
*Siler* Simon, 1889\*  
*Tasa* Wesolowska, 1981  
*Theriella* Bräul & Lise, 1996  
*Wesolowskana* Koçak & Kemal, 2008  
*Yepoella* Galiano, 1970\*

**Salticoida: Saltafresia: Simonida**

(2607 species in 228 genera)

**Tribe Leptorchestini** (92 species in 7 genera)

*Araegeus* Simon, 1901  
*Enoplomischus* Giltay, 1931\*  
*Kima* Peckham & Peckham, 1902  
*Leptorchestes* Thorell, 1870\*  
*Paramarpissa* F. O. P.-Cambridge, 1901\*  
*Ugandinella* Wesolowska, 2006  
*Yllenus* Simon, 1868\*

**Tribe Euophryini** (1087 species in 116 genera)

- Agobardus* Keyserling, 1885\*  
*Allodecta* Bryant, 1950  
*Amphidraus* Simon, 1900\*  
*Anasaitis* Bryant, 1950\*  
*Antillattus* Bryant, 1943\*  
*Araneotanna* Özdikmen & Kury, 2006  
*Aruattus* Logunov & Azarkina, 2008  
*Ascyltus* Karsch, 1878  
*Athamas* O. P.-Cambridge, 1877\*  
*Barraina* Richardson, 2013  
*Bathippus* Thorell, 1892\*  
*Baviola* Simon, 1898<sup>?</sup>  
*Bellienna* Simon, 1902\*  
*Bindax* Thorell, 1892  
*Bulolia* Żabka, 1996\*  
*Bythocrotus* Simon, 1903\*  
*Canama* Simon, 1903\*  
*Caribattus* Bryant, 1950  
*Chalcolecta* Simon, 1884\*  
*Chalcolemia* Zhang & Maddison, 2012\*  
*Chalcoscirtus* Bertkau, 1880\*  
*Chalcotropis* Simon, 1902\*  
*Chapoda* Peckham & Peckham, 1896\*  
*Charippus* Thorell, 1895  
*Chinophrys* Zhang & Maddison, 2012\*  
*Coccorchestes* Thorell, 1881\*  
*Colyttus* Thorell, 1891\*  
*Commoris* Simon, 1902  
*Compsodecta* Simon, 1903\*  
*Corticattus* Zhang & Maddison, 2012\*  
*Coryphasia* Simon, 1902\*  
*Corythalia* C. L. Koch, 1850\*  
*Cytaea* Keyserling, 1882\*  
*Darwinneon* Cutler, 1971  
*Diolenius* Thorell, 1870\*  
*Ecuadattus* Zhang & Maddison, 2012\*  
*Efate* Berland, 1938\*  
*Emathis* Simon, 1899\*  
*Ergane* L. Koch, 1881  
*Euophrys* C. L. Koch, 1834\*  
*Euryattus* Thorell, 1881\*  
*Featheroides* Peng, Ying & Kim, 1994  
*Foliabitus* Zhang & Maddison, 2012\*  
*Frewena* Richardson, 2013  
*Furculattus* Balogh, 1980  
*Gorgasella* Chickering, 1946<sup>?</sup>  
*Hypoblemum* Peckham & Peckham, 1886\*  
*Ilargus* Simon, 1901\*  
*Jotus* L. Koch, 1881\*  
*Lagnus* L. Koch, 1879\*  
*Lakarobius* Berry, Beatty & Prószyński, 1998  
*Laufeia* Simon, 1889\*  
*Lauharulla* Keyserling, 1889<sup>?</sup>  
*Lepidemathis* Simon, 1883\*  
*Leptathamus* Balogh, 1980\*  
*Lophostica* Simon, 1902  
*Maeota* Simon, 1901\*  
*Magyarus* Żabka, 1985  
*Maileus* Peckham & Peckham, 1907\*  
*Maratus* Karsch, 1878\*  
*Margaromma* Keyserling, 1882  
*Marma* Simon, 1902\*  
*Mexigonus* Edwards, 2003\*  
*Mopiopia* Simon, 1902\*  
*Naphrys* Edwards, 2003\*  
*Neonella* Gertsch, 1936\*  
*Ohilimia* Strand, 1911\*  
*Omoedus* Thorell, 1881\*  
*Opisthoncana* Strand, 1913  
*Parabathippus* Zhang & Maddison, 2012\*  
*Paraharmochirus* Szombathy, 1915\*  
*Parasaitis* Bryant, 1950  
*Parvattus* Zhang & Maddison, 2012\*  
*Pensacola* Peckham & Peckham, 1885\*  
†*Pensacolatus* Wunderlich, 1988  
*Pensacolops* Bauab, 1983  
*Petemathis* Prószyński & Deeleman-Reinhold, 2012\*  
*Phasmolia* Zhang & Maddison, 2012\*  
*Philaeus* Thorell, 1869\*  
*Pignus* Wesolowska, 2000\*  
*Salticus* Latreille, 1804\*  
*Platypsecas* Caporiacco, 1955<sup>?</sup>  
*Popcornella* Zhang & Maddison, 2012\*  
*Pristobaeus* Simon, 1902\*  
*Prostheclina* Keyserling, 1882\*  
*Pseudemathis* Simon, 1902  
*Pseudeuophrys* Dahl, 1912\*  
*Pseudocorythalia* Caporiacco, 1938  
*Rarahu* Berland, 1929<sup>?</sup>  
*Rhyphelia* Simon, 1902  
*Rumburak* Wesolowska, Azarkina & Russell-Smith, 2014\*  
*Saitidops* Simon, 1901  
*Saitis* Simon, 1876\*  
*Saitissus* Roewer, 1938  
*Saphrys* Zhang & Maddison, 2015\*  
*Semnolius* Simon, 1902  
*Servaea* Simon, 1888\*  
*Sidusa* Peckham & Peckham, 1895\*  
*Sigytes* Simon, 1902  
*Sobasina* Simon, 1898\*  
*Soesilarishius* Makhan, 2007\*  
*Spilargis* Simon, 1902  
*Stoidis* Simon, 1901  
*Talavera* Peckham & Peckham, 1909\*  
*Tanzania* Koçak & Kemal, 2008  
*Tarodes* Pocock, 1899  
*Thiania* C. L. Koch, 1846\*  
*Thorelliola* Strand, 1942\*  
*Thyenula* Simon, 1902\*  
*Truncattus* Zhang & Maddison, 2012\*  
*Tylogonus* Simon, 1902\*  
*Udvardya* Prószyński, 1992  
*Variratina* Zhang & Maddison, 2012\*  
*Viribestus* Zhang & Maddison, 2012\*  
*Viroqua* Peckham & Peckham, 1901  
*Xenocytaea* Berry, 1998\*  
*Yacuitella* Galiano, 1999<sup>?</sup>  
*Yimbulunga* Wesolowska, Azarkina & Russell-Smith, 2014  
*Zabkattus* Zhang & Maddison, 2012\*  
*Tusitala* Peckham & Peckham, 1902\*  
*Phlegra* Simon, 1876\*  
*Proszynskiana* Logunov, 1996  
*Rafalus* Prószyński, 1999  
*Stenaehurillus* Simon, 1886\*  
*Rishaschia* Makhan, 2006\*  
*Sumampattus* Galiano, 1983  
*Tarkas* Edwards, 2015  
*Triggella* Edwards, 2015  
*Trydarssus* Galiano, 1995\*  
*Tullgrenella* Mello-Leitão, 1941  
*Wedoquella* Galiano, 1984  
*Xanthofreya* Edwards, 2015

**Tribe Salticini** (134 species in 7 genera)

- Carrhotus* Thorell, 1891\*  
*Mogrus* Simon, 1882\*  
*Phaulostylus* Simon, 1902\*  
*Mashonarus* Wesolowska & Cumming, 2002  
*Microheros* Wesolowska & Cumming, 1999  
*Phanuelus* Caleb & Mathai, 2015

**Tribe Aelurillini: Subtribe Aelurillina** (262 species in 11 genera)

- Aelurillus* Simon, 1884\*  
*Asianellus* Logunov & Heciak, 1996\*  
*Langelurillus* Próchniewicz, 1994\*  
*Langona* Simon, 1901

**Tribe Aelurillini: Subtribe Freyina** (192 species in 26 genera)

- Akela* Peckham & Peckham, 1896\*  
*Aphirape* C. L. Koch, 1850\*  
*Asaracus* C. L. Koch, 1846\*  
*Capidava* Simon, 1902  
*Chira* Peckham & Peckham, 1896\*  
*Drizttius* Edwards, 2015\*  
*Edilemma* Ruiz & Brescovit, 2006  
*Eustromastix* Simon, 1902\*  
*Freya* C. L. Koch, 1850\*  
*Frigga* C. L. Koch, 1850\*  
*Kalcerrytus* Galiano, 2000\*  
*Leptofreya* Edwards, 2015  
*Megafreya* Edwards, 2015  
*Nycerella* Galiano, 1982\*  
*Onofre* Ruiz & Brescovit, 2007  
*Pachomius* Peckham & Peckham, 1896\*  
*Phiale* C. L. Koch, 1846\*  
*Philira* Edwards, 2015

**Tribe Aelurillini: Subtribe Thiratoscirtina** (60 species in 14 genera)

*Ajaraneola* Wesolowska & A. Russell-Smith, 2011<sup>?</sup>  
*Alfenus* Simon, 1902\*  
*Bacelarella* Berland & Millot, 1941\*  
*Cembalea* Wesolowska, 1993<sup>?</sup>

*Gramenca* Rollard & Wesolowska, 2002<sup>?</sup>  
*Lamottella* Rollard & Wesolowska, 2002<sup>?</sup>  
*Longarenius* Simon, 1903\*  
*Malloneta* Simon, 1902\*  
*Nimbarus* Rollard & Wesolowska, 2002<sup>?</sup>

*Pochyta* Simon, 1901\*  
*Saraina* Wanless & Clark, 1975\*  
*Tarne* Simon, 1886\*  
*Thiratoscirtus* Simon, 1886\*  
*Ureta* Wesolowska & Haddad, 2013<sup>?</sup>

**Tribe Plexippini: Subtribe Plexippina** (493 species in 32 genera)

*Afrobeata* Caporiacco, 1941  
*Anarrhotus* Simon, 1902\*  
*Artabrus* Simon, 1902  
*Baryphas* Simon, 1902\*  
*Brancus* Simon, 1902\*  
*Burmattus* Prószyński, 1992\*  
*Dasycyptus* Simon, 1902<sup>?</sup>  
*Dexippus* Thorell, 1891  
*Encymachus* Simon, 1902<sup>?</sup>  
*Epeus* Peckham & Peckham, 1886\*  
*Erasinus* Simon, 1899

*Evarcha* Simon, 1902\*  
*Hermotimus* Simon, 1903\*  
*Hyllus* C. L. Koch, 1846\*  
*Nigorella* Wesolowska & Tomasiewicz, 2008\*  
*Pachyonomastus* Caporiacco, 1947  
*Pancorius* Simon, 1902\*  
*Parajotus* Peckham & Peckham, 1903<sup>?</sup>  
*Paraplexippus* Franganillo, 1930<sup>?</sup>  
*Pharacocerus* Simon, 1902<sup>?</sup>  
*Plexippoides* Prószyński, 1984\*

*Plexippus* C. L. Koch, 1846\*  
*Polemus* Simon, 1902\*  
*Pseudamycus* Simon, 1885  
*Pseudoplexippus* Caporiacco, 1947  
*Ptocasius* Simon, 1885\*  
*Schenkelia* Lessert, 1927\*  
*Taivala* Peckham & Peckham, 1907  
*Telamonia* Thorell, 1887\*  
*Thyene* Simon, 1885\*  
*Vailimia* Kammerer, 2006  
*Yaginumaella* Prószyński, 1979\*

**Tribe Plexippini: Subtribe Harmochirina** (287 species in 15 genera)

*Bianor* Peckham & Peckham, 1886\*  
*Eburneana* Wesolowska & Szűts, 2001\*  
*Habronattus* F. O. P.-Cambridge, 1901\*  
*Harmochirus* Simon, 1885\*  
*Havaika* Prószyński, 2002\*

*Iranattus* Prószyński, 1992  
*Microbianor* Logunov, 2000  
*Modunda* Simon, 1901  
*Monomotapa* Wesolowska, 2000  
*Napoca* Simon, 1901

*Neaetha* Simon, 1884  
*Paranaetha* Denis, 1947  
*Pellenes* Simon, 1876\*  
*Pellolessertia* Strand, 1929  
*Sibianor* Logunov, 2001

**Salticinae incertae sedis** (124 species in 48 genera)**Africa**

*Bokokius* Roewer, 1942  
*Cavillator* Wesolowska, 2000  
*Giuiria* Strand, 1906  
*Hasarinella* Wesolowska, 2012  
*Homalattus* White, 1841  
*Maltecora* Simon, 1910  
*Pachypoessa* Simon, 1902  
*Poessa* Simon, 1902  
*Salpesia* Simon, 1901  
*Simaethulina* Wesolowska, 2012  
*Thyenillus* Simon, 1910  
*Toticoryx* Rollard & Wesolowska, 2002  
*Yogetor* Wesolowska & Russell-Smith, 2000  
*Zulunigma* Wesolowska & Cumming, 2011

**Asia**

*Epidelaxia* Simon, 1902  
*Flacillula* Strand, 1932  
*Gambaquezonia* Barrion & Litsinger, 1995  
*Ghumattus* Prószyński, 1992  
*Heliophanoides* Prószyński, 1992  
*Jajpurattus* Prószyński, 1992  
*Lechia* Żabka, 1985  
*Leuserattus* Prószyński & Deeleman-Reinhold, 2012  
*Ligdus* Thorell, 1895  
*Microhasarius* Simon, 1902  
*Necatia* Özdikmen, 2007  
*Panysinus* Simon, 1901  
*Phausina* Simon, 1902  
*Pilia* Simon, 1902  
*Similaria* Prószyński, 1992  
*Stichius* Thorell, 1890  
*Tamigalesus* Żabka, 1988

**Australasia/Oceania**

*Adoxotoma* Simon, 1909  
*Ananeon* Richardson, 2013  
*Aruana* Strand, 1911  
*Grayenulla* Żabka, 1992  
*Hinewaia* Żabka & Pollard, 2002  
*Maddisonia* Żabka, 2014  
*Muziris* Simon, 1901  
*Proszynellus* Patoleta & Żabka, 2015  
*Pseudomaevia* Rainbow, 1920  
*Pseudosynagelides* Żabka, 1991  
*Stergusa* Simon, 1889  
*Tatari* Berland, 1938

**Americas**

*Albionella* Chickering, 1946  
*Haplopsecas* Caporiacco, 1955  
*Hisukattus* Galiano, 1987  
*Sarindoides* Mello-Leitão, 1922  
*Udalmella* Galiano, 1994

**Salticidae incertae sedis** (13 extant species in 9 genera; 28 fossil species in 13 genera)**Africa**

*Vatovia* Caporiacco, 1940

**Australasia/Oceania**

*Hyciotea* Strand, 1911

**Fossil Salticidae incertae sedis** (8 species in 6 genera)

†*Attoides* Brongniart, 1877  
 †*Descangeles* Wunderlich, 1988

**Asia**

*Ballognatha* Caporiacco, 1935  
*Ceglusa* Thorell, 1895  
*Dolichoneon* Caporiacco, 1935  
*Thianella* Strand, 1907

†*Eoatopsis* Gourret, 1887  
 †*Evagoratus* Zhang, Sun & Zhang, 1994

**Americas**

*Arachnotermes* Mello-Leitão, 1928  
*Clynotooides* Mello-Leitão, 1944  
*Stenodeza* Simon, 1900

†*Phlegrata* Wunderlich, 1988  
 †*Steneattus* Bronn, 1856

**Fossil Salticidae incertae sedis, not in the Salticinae** (20 species in 7 genera)

†*Calilinus* Wunderlich, 2004  
 †*Cenattus* Petrunkevitch, 1942  
 †*Distanilinus* Wunderlich, 2004

†*Eolinus* Petrunkevitch, 1942  
 †*Gorgopsidis* Wunderlich, 2004  
 †*Microlinus* Wunderlich, 2004

†*Paralimus* Petrunkevitch, 1942

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