

The evolution of jumping spiders (Araneae: Salticidae): a review

David E. Hill¹ and David B. Richman²

¹ 213 Wild Horse Creek Drive, Simpsonville, South Carolina 29680

² Corresponding author: nmbugman@taipan.nmsu.edu Department of Entomology, Plant Pathology and Weed Science, New Mexico State University, Las Cruces, NM 88003

The following article was written as part of the yearlong celebration of the 200th birthday of Charles Darwin and the 150th Anniversary of the publication of his *Origin of Species*.

Abstract

The evolution of the family Salticidae (jumping spiders) has always puzzled arachnologists, but with modern DNA and morphological analysis, using cladistic techniques, a pattern is starting to emerge. The Salticidae apparently originated in the late Cretaceous and were derived from one of the other RTA dionychan clades, which include Philodromidae, Thomisidae, Miturgidae, Anyphaenidae, Gnaphosidae and related groups. Speciation appears to have been well along by the Oligocene–Miocene and may have been spurred on by the warm conditions of the late Paleocene–Eocene. At this point it seems wise to gather the current evidence and thinking on the origin and evolution of jumping spiders and the more “typical” Salticoida together and to give an overview of where the research currently stands. This is the main purpose of the current review.

Introduction

With more than 5,000 described species (Platnick 2009), the jumping spiders (Salticidae) arguably represent the most diverse family of modern spiders. Although we do not have any scientific standards for comparison of evolutionary diversity, those familiar with salticids might consider the group to be *at least* as diverse as the birds (Class Aves), and *perhaps* just as ancient in their origin.

The most remarkable and distinguishing characteristic of salticid spiders lies in their development of high visual acuity, particularly with respect to their large, tubular principal eyes (also known as anterior medial eyes, or AME) (Figure 1). Converging with vertebrates, these spiders use six different muscles to move each AME eye tube, through both translation and rotation (Land 1969a, 1969b), and they are also equipped with three different opsins, indicative of trichromatic color vision (Koyanagi *et al.* 2008). Visual acuity of these animals is far greater than that of any other terrestrial invertebrates (Blest 1985). Phylogenetic reconstruction of the evolution of these opsins suggests that UV receptors diverged from the visible light receptors of spiders long before the Chelicerata–Pancrustacea split, but that the subsequent evolution of two different visible light receptors (accounting for trichromatic vision in the Salticidae) took place much later (Koyanagi *et al.* 2008; see also Oakley 2003). Future study of the opsins of other chelicerates, and the Araneae in particular, will certainly help to clarify the relationship of salticids to other spider families.

Important recent work on the evolution of the Salticidae has been in the emerging arena of molecular phylogenetics, based upon the comparative study of gene sequences (Hedin and Maddison 2001, Maddison and Hedin 2003a, 2003b, Maddison and Needham 2006, Su *et al.* 2007, Maddison *et al.* 2007,



Figure 1. Face of adult male *Hentzia palmarum* (Hentz 1832) showing extreme enlargement of the principal or anterior medial eyes (AME) characteristic of the family Salticidae. Photo by Thomas Shahan.

2008, Maddison 2009). Although available work is still preliminary in many respects (the great majority of taxa have never been studied) we now have much more confidence in outlining major directions taken by the evolving salticids.

The unique development of vision in salticid spiders has supported their evolution of an extraordinarily diverse range of lifestyles, all associated with visually-mediated behavior. Morphology within this group varies wildly. A large number closely resemble, and behave like, ants, velvet ants or even beetles. Some are mantis-like, complete with the raptorial fore-legs. Many species exhibit brilliant coloring, often associated with the pigmented or structural (iridescent or metallic) colors of scales (modified setae). Colors vary from purples, through blues, reds, greens and yellows, as well as black, gray, brown and white. Their prey-capture strategies also vary greatly, ranging from a very cat-like visual stalking to web-making (*Portia* and some others), ambushing, and prey specialization (*Naphrys pulex* catches ants primarily and *Portia* prefers spiders). Their courtship displays (known for only a hundred or so species) are both visual and vibrational. Some engage in visual male-male agonistic displays (See Richman and Jackson 1992 for a review of jumping spider behavior).

We will consider only three of the central issues related to the world-wide evolution of the Salticidae. The first is the origin of the group. Where did the first salticid come from? Second, we will consider the origin and radiation of the most successful group of salticids, the Salticoida, constituting the great majority of modern salticid species. Finally, we will examine available evidence related to the biogeography and timeline for this evolution. We will then consider the biogeographic evidence for the origin of the North American fauna, with special emphasis on the southwestern fauna in the United States and adjacent northern Mexico.

Origin of the Salticidae

The Salticidae is a member of the RTA (for retrolateral tibial apophysis of males) clade, which includes at least half of all known spiders (Blackledge *et al.* 2009), and (with a few exceptions) the family is among those members of the clade that apparently lost the ability to build webs (web-building RTA clade

members include dictynids, agelenids, and amaurobiids) (Blackledge *et al.* 2009). This loss is also true for the apparently related RTA families in the “clubionoid,” thomisid and philodromid groups. The origin of the Salticidae itself within the RTA clade must be closely linked to the evolution of their remarkable, tubular, and telescopic principal eyes (Williams and McIntyre 1980, Blest *et al.* 1981, 1988, Hill 2007). Other spider families also have the capability to move the retinæ of these eyes, but to the best of our knowledge none have a comparable size, degree of visual acuity, or more than two muscles per eye (Land 1969a, 1969b). Because of the relatively large size of these eyes, a salticid is immediately recognizable. Unfortunately, meaningful comparative study of the evolution of the principal eyes of related spider families may have to wait for a renaissance in the discipline of functional morphology. The few studies that have been published (Blest and O'Carroll 1990, Dacke *et al.* 2001) have described a localized receptor bilayer in the principal eyes of some lycosids, pisaurids, oxyopids, and thomisids, but nothing close to the four-tiered retinæ of salticids.

The Salticidae are presently grouped with a number of somewhat similar families into the Dionycha, an assemblage of two-clawed hunting spiders (Coddington 2005). Further insight into phylogenetic relationships within this assemblage, for the present, will have to come from a handful of published studies of *intra-familial* molecular phylogeny, where representatives of related dionychan families were used as out-groups. A recent study of thomisid relationships (Benjamin *et al.* 2008) placed the Philodromidae into a basal position relative to the Salticidae and a sister group of families including the Corinnidae, Miturgidae, Gnaphosidae, Anyphaenidae, and Thomisidae. This study suggested that some philodromids (*Philodromus*) were actually more closely related to the latter families (including the Salticidae), than they were to other philodromids (*Pagiopalus*, *Proernus*). The enlargement of the anterior medial eyes in *Ebo* (Philodromidae) and related genera is well illustrated by Muster (2009). Studies of Salticidae by Maddison and Hedin (2003a) and Maddison and Needham (2006) were consistent with respect to the grouping of Gnaphosidae, Miturgidae, and Thomisidae into a sister clade with respect to the Salticidae. A more recent salticid study by Maddison *et al.* (2008), however, placed a clade containing the Thomisidae, Salticidae, Corinnidae, and Miturgidae into a sister relationship with Gnaphosidae and Anyphaenidae. Within this clade, Thomisidae was basal to other three families, and Salticidae was a sister group to a clade containing the Corinnidae and the Miturgidae. Vink *et al.* (2008) attempted with some success to use the nuclear gene Actin 5C to compare with analyses based on mitochondrial and/or nuclear ribosomal genes. They did not include thomisids or philodromids in their initial trees (Vink *et al.* 2008, Figure 1, p. 380) and only the thomisid *Xysticus* sp. is included in the Actin 5C cladogram (Vink *et al.* 2008, Figure 2, p. 381). The first figures did appear to show a fairly close relationship of salticids to the RTA clade members *Syspira* (Miturgidae) and possibly *Homalonychus* (Homalonychidae). The Actin 5C analysis seems to indicate that *Xysticus* splits out with *Lyssomanes* and *Portia*, among others, while the Salticoidea forms a separate clade! Further work with Actin 5C, mitochondrial DNA and nuclear ribosomal DNA may eventually give a better resolution of the RTA clade, but we are still at an early stage of our understanding. None of these salticid studies considered the relative position of the Philodromidae. It is of interest to note that certain philodromids (notably *Ebo*, Sauer and Platnick 1972) share one important and uncommon feature with the Salticidae: *enlargement* of the principal eyes. Careful behavioral studies of *Ebo* and other non-salticid spiders with relatively large principal eyes would certainly shed some light on evolution of the Salticidae, even if these groups are not closely related. If *Ebo* is any indicator, then it *may* be likely that advantages associated with a detailed visual evaluation of sighted prey played a major role in the evolution of the salticid principal eye. Prior to those behavioral studies, this is only conjecture.

To date, these family-outgroup studies of molecular phylogeny have been generally consistent with the view that the Salticidae is a monophyletic group, when compared to related spider families. Studies that compare a range of key genera in each of these families, based on comparison of gene sequences relevant to this level of comparison, can be expected to clear up our clouded picture of the Dionycha in the future.

Origin of the Salticoida

Maddison and Hedin (2003a) excluded several basal salticids (lyssomanines and spartaeines) from a clade they named the *Salticoida*, containing the great majority of all salticid species. In addition to support for this clade from their gene sequencing, they identified a number of key synaptomorphies. With respect to the evolution of salticid vision, these included a major reduction in the size of the posterior medial eyes (PME), the presence of six arms of pigmented glia around each lateral eye receptor (Blest and Sigmund 1984), and displacement of the cell bodies of the anterior and posterior lateral eyes (ALE and PLE, or *secondary eyes*), from a position in front of the retinae, to a position outside of the eye capsule (Blest 1983, Hill 2006). The retina of the principal eyes of salticoids is also sharply curved (Blest and Sigmund 1984). In addition to other structural changes identified by Maddison and Hedin, a number of physiological, neurological, or behavioral changes may also be associated with the emergence of the Salticoida as the most successful salticid group. At the present time, comparative studies relating the Salticoida to other salticids in these respects are lacking.

Nonetheless, the known changes with respect to the vision and visual acuity of this group, affecting both principal *and* secondary eyes, indicate that improvement of vision and visual resolution played a major role in its emergence. Reduction of the PME was apparently associated with increased size, resolution, and field of vision of the other secondary eyes.

Our understanding of the subsequent radiation of the salticoids is now based primarily on a series of recent papers on salticid phylogeny, including the identification of major subfamilies within the Salticoida (Hedin and Maddison 2001, Maddison and Hedin 2003a, 2003b, Maddison and Needham 2006, Su *et al.* 2007, Maddison *et al.* 2007, 2008, Maddison 2009). This work has also identified additional non-salticoid groups within the Salticidae (cocalodines, lapsiines, hisponines, *Eupoa*, *Goleba*). There is a suggestion that some salticid genera (*Hispo*, *Massagris*, *Tomocyrrba*) are closer to the Salticoida than they are to either *Lyssomanes* or the Spartaeineae as a group, but additional work will be required to give us confidence here.

Timeline and biogeography

Presently no molecular clock has been proposed in association with the molecular phylogeny of either the Salticidae, or the larger group of dionychan families, as we have seen for the Insecta (Gaunt and Miles 2002). Penney *et al.* (2003, Fig. 2) did produce a preliminary timeline for the emergence of many modern araneomorph families, and this assumed an early Cenozoic emergence of the Salticidae. Recent evidence for the origin of the Araneidae, Linyphiidae, Tetragnathidae, and Uloboridae by the Lower Cretaceous (Penney and Selden 2002, Penney and Ortuño 2006) has greatly extended our timeline for the emergence of modern entelegyne spider families. As noted by Penney and Selden (2002), current evidence, which suggests the higher araneoids did not radiate and diversify until after the end of Cretaceous mass extinction event, may be an artifact of sample size. A thomisid has been reported from Cretaceous amber in Myanmar (Burma) (Grimaldi *et al.* 2002). Then, after a considerably gap in the fossil record, a relatively modern salticid fauna, including modern salticoid genera, emerged in association with late Eocene–Oligocene–Miocene (“Baltic” to “Dominican,” spanning ~45 to ~10 MYA) amber (Prószyński and Żabka 1980, Cutler 1984, Żabka 1995, Garcia-Villafuerte and Penney 2003, Wunderlich 2004). Some earlier specimens within this time-frame exhibited non-salticoid characteristics, including larger PME. At the present time, however this fossil record is too fragmentary to draw any firm conclusions with respect to the origin of existing salticid groups.

Although many basal salticid groups are found in the Old World tropics, and in the East Indies in particular, others, including many lyssomanines and lapsiines, are widely distributed in the New World tropics. It is quite possible that the earliest salticids predated the lower Cretaceous breakup of Pangaea,

and were widely distributed over this land mass. At this time we cannot say whether or not surviving non-salticoid groups from the Old World tropics also had New World representatives that became extinct, or were replaced by derivative forms. Even salticoids could have emerged by the lower Cretaceous but, as noted by Maddison and Hedin (2003a), the distribution of major clades within the Salticoida has been constrained by modern continental boundaries and undoubtedly followed the breakup of Pangaea during the Cretaceous. The Amycoidea and Marpissoida (Marpissinae and Dendryphantinae) are almost exclusively New World in distribution, whereas the Heliophaninae, Aelurillinae, and Plexippoida are largely old world in distribution. Recently, Maddison *et al.* (2008) identified a large group of salticoids (Astioda) that may comprise an exclusively Australasian sister group to the New World marpissoids. Continental separation has not *absolutely* restricted the diversification and distribution of major salticoid groups, however. For example, the essentially Old World group of plexippoids has successfully diversified within North America, with the emergence of a large number of species of *Habronattus*. euophryines, also salticoids, are diverse in both hemispheres. The divergence and rapid speciation of the salticids probably took off in the Paleocene–Miocene, especially during the late Paleocene through the Eocene global warming period (Scotese 2003). Recent research indicates that rapid speciation is based on high metabolic rates and may thus occur in warm localities, such as the tropics (Allen *et al.* 2006). This seems to explain the high diversity of the tropics and suggests that the early tertiary global warming event may have increased speciation of clades, such as the salticoid clade, able to take advantage of new niche opportunities.

The southwestern United States (including southern California, Nevada, Utah, Arizona, New Mexico and western Texas) has a fairly large fauna—probably well over 150 species (145 known from Arizona, New Mexico and Trans-Pecos Texas—Richman *et al.* 2005). The fauna is probably primarily derived from the genera that developed within North America, although some genera (e.g. *Salticus*, *Pellenes*, and a few others) are apparently Eurasian in origin, with some individual species of several genera obviously introduced since the European colonization. Our largest genera (e. g. *Pelegrina*, *Phidippus* and *Habronattus*) seem to be primarily North American in origin, although *Habronattus* is a member of the primarily Old World Plexippoida and is apparently derived from *Pellenes*, a widespread genus (at least as now delineated) (Maddison and Hedin 2003b). It is likely that *Pellenes* was already established in the New World before the continents drifted apart as far as they are now. However this is complicated by the existence of a genus, *Havaika*, which is closely related to both genera, but is restricted totally to the Hawaiian Islands (Prószyński, 2002, 2008; Arnedo and Gillespie 2006)! Richman (unpublished) has specimens of a plexippoid from Puerto Rico that is also apparently related to both.

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