**PECKHAMIA 76.1**, 7 October 2009, 1—14 ISSN 1944—8120

# Salticidae of the Antarctic land bridge

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## Introduction

At the breakup of Gondwanaland (~130—110 Ma), Africa, India, and Madagascar moved away from South America and Antarctica, with Australia still firmly conjoined to the latter (Figure 1). This movement left South America connected to Antarctica—Australia by a long isthmus (*Ithmus of Scotia*) of the southern Andes, at least from the Late Cretaceous (Campanian) through the Eocene (Yanbin 1998, Lawver *et al.* 1999, Sanmartín 2002). This *Antarctic land bridge* remained in place from the late Cretaceous through the Paleocene (65.5 ± 0.3 Ma to 55.8 ± 0.2 Ma) and Eocene (55.8 ± 0.2 to 33.9 ± 0.1 Ma) epochs. At times it may have included short island arcs at either the Australian (Tasmanian) or South American ends. This land bridge, associated with a tropical to temperate Antarctic climate (Francis *et al.* 2008), was thus available to support the dispersal of plant and animal species for about 75 to 95 million years after the separation of Africa, a very long time. One very interesting aspect about this interval is that it also brackets the mass extinction event at the end of the Cretaceous. According to Penney *et al.* (2003), however, that event did nothing to reduce the diversity of spiders as a group.

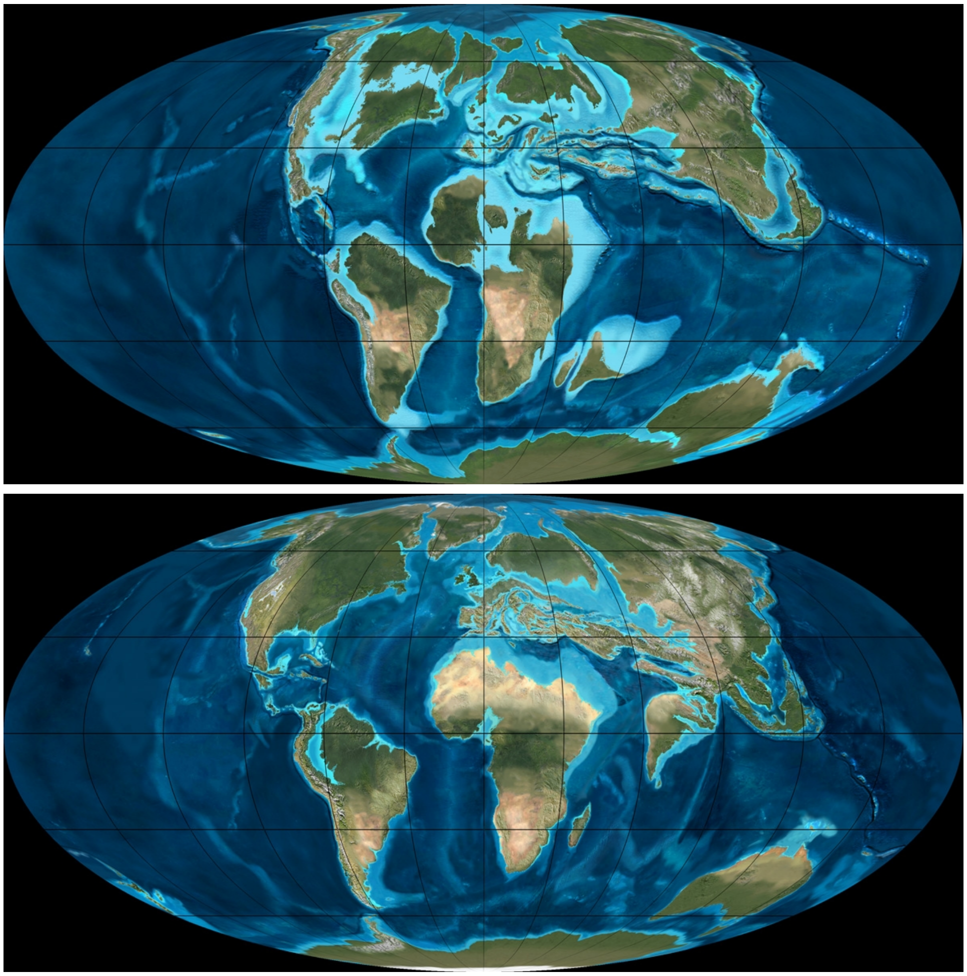

Figure 1. Cretaceous (top) and Eocene (bottom) reconstructions of Earth topography and bathymetry. Although these reconstructions provide a good view of the separation of Africa, Madagascar, and India from the rest of Gondwanaland, they do not depict the land connections beween Antarctica and either South America, or Australia, respectively, that are thought to have persisted well into the Eocene (Yanbin 1998, Lawver et al. 1999, Sanmartín 2002, Francis et al. 2008, and others). © by Ron Blakely, NAU Geology. Noncommercial use with attribution permitted.

Near the end of the Eocene, at the Eocene—Oligocene boundary, the Australian plate, including New Guinea, separated from Antarctica and began its long journey toward the north. This opened up the *Tasmanian Seaway*, allowing the cold Antarctic Circumpolar Current to isolate Antarctica, leading to the formation of a permanent ice sheet over that continent by ~33.5 Ma (Exon *et al.* 2000, 2004, Pollard and DeConto 2005). Whether this opening, and the subsequent opening of the *Drake Passage* between South America and Antarctica (Bohoyo *et al.* 2007, Maldonado *et al.* 2007, Miller 2007, Smalley *et al.* 2007, Eagles *et al.* 2009), can fully account for the rapid cooling of Antarctica at the end of the Eocene is still an open question, and the decline in atmospheric $CO_2$ at that time may have been more important (DeConto and Pollard 2003, Huber *et al.* 2004, Barker and Thomas 2004, Livermore *et al.* 2004, Barker *et al.* 2006). Ocean floor presently separating South America and Tasmania, respectively, from Antarctica was deposited after this time, beginning at the Eocene—Oligocene boundary (Torsvik et al., 2008). In any case, rapid cooling did follow the end of the *Antarctic land bridge* between Australia and South America, and contributed to the subsequent isolation of the two great continental faunas. The Eocene was followed by more extensive cooling and the growth of ice sheets in the Oligocene (Miller *et al.* 2008). For reference, Lawver *et al.* (1999) provide a useful animated reconstruction of the breakup of Gondwanaland, and both Brown *et al.* (2006) and Torsvik *et al.* (2008) have published plate tectonic reconstructions (maps) of the entire Cenozoic transition around Antarctica. The age of the oceanic lithosphere (Figure 2) provides a concise graphic overview of the timing of separation of the continents since the break-up of Pangaea (~175 Ma).

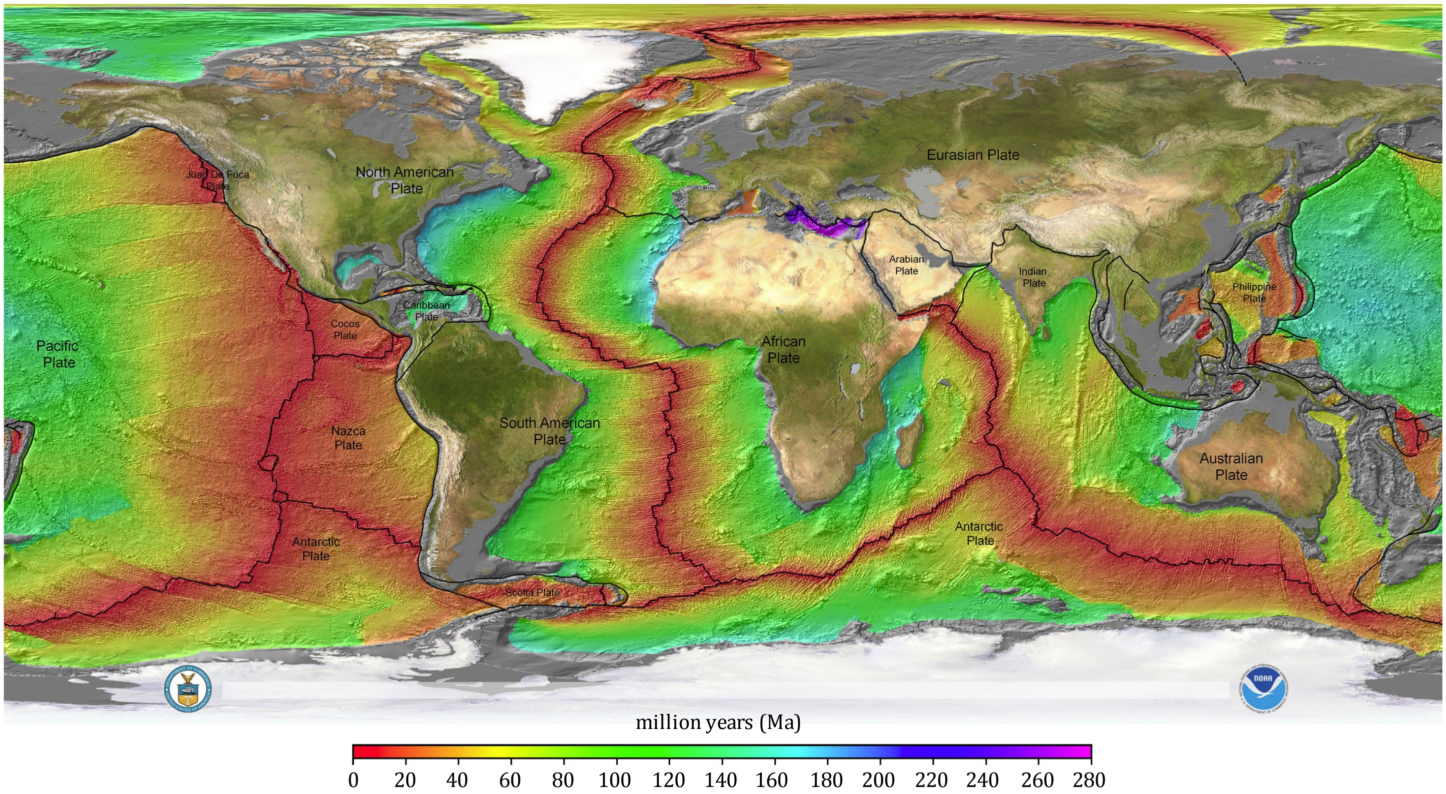

Figure 2. Age of the ocean lithosphere (Ma). Image created by Elliot Lim, Cooperative Institute for Research in Environmental Sciences, NOAA National Geophysical Data Center (NGDC) Marine Geology and Geophysics Division. Data and images available from http://www.ngdc.noaa.gov/mgg/. Data Source Müller *et al.* (2008).

A south-polar view of this chart (Figure 3) also depicts the relatively recent (since the Eocene ~33 Ma) separation of Antarctica from Australia (upper right, Tasmania) and South America (lower left, Andes to Transantarctic Range). Also note the extensive sea-floor spreading (green areas) to the left, between Antarctica and Africa (upper left), and between South America and Africa, associated with the early break-up of Gondwana (~130—110 Ma).

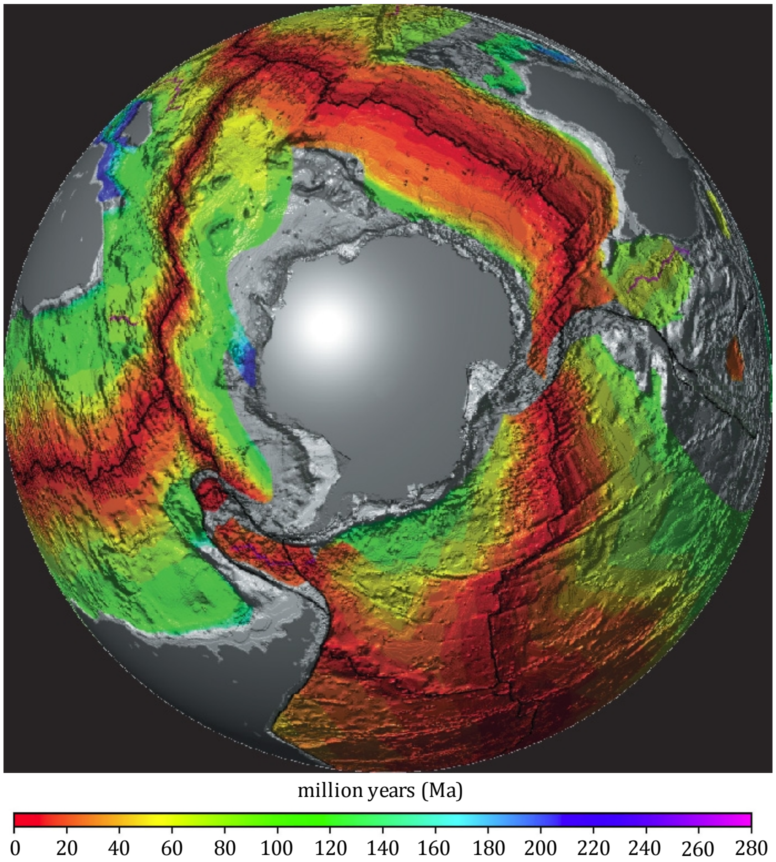

Figure 3. Age of the ocean lithosphere, from a south polar view with Antarctica at the center. Australia is to the upper right, South America to the lower left, and Africa to the upper left. Sea-floor spreading in green is primarily associated with the break-up of Gondwana. Note the presence of an earlier rift to the south of Australia, before later sea-floor spreading separated Tasmania from Antarctica. Sea-floor spreading between the southern Andes of South America and the Transantarctic Range also took place primarily in the post-Eocene timeframe. Images by R. D. Müller and P. W. Sloss, NOAA-NESDIS-NGDC. Data and images available from [http://www.ngdc.noaa.gov/mgg/](http://www.ngdc.noaa.gov/mgg/). Data Source Müller *et al.* (2008).

Although much of present-day Antarctica. particularly in the West (Western Hemisphere), is below sea-level (Figure 4), models of the Eocene—Oligocene transition that have been corrected for *thermal contraction resulting from tectonic extension and for erosion and sedimentation since 34 Ma* indicate that most of Western Antarctica was actually above sea level at that time (Wilson and Luyendyk 2009). Even after more extensive glaciation in the Miocene (Jamieson and Sugden 2008), a tundra habitat persisted in Antarctica as recently as 14.1—13.8 Ma (Lewis *et al.* 2008).

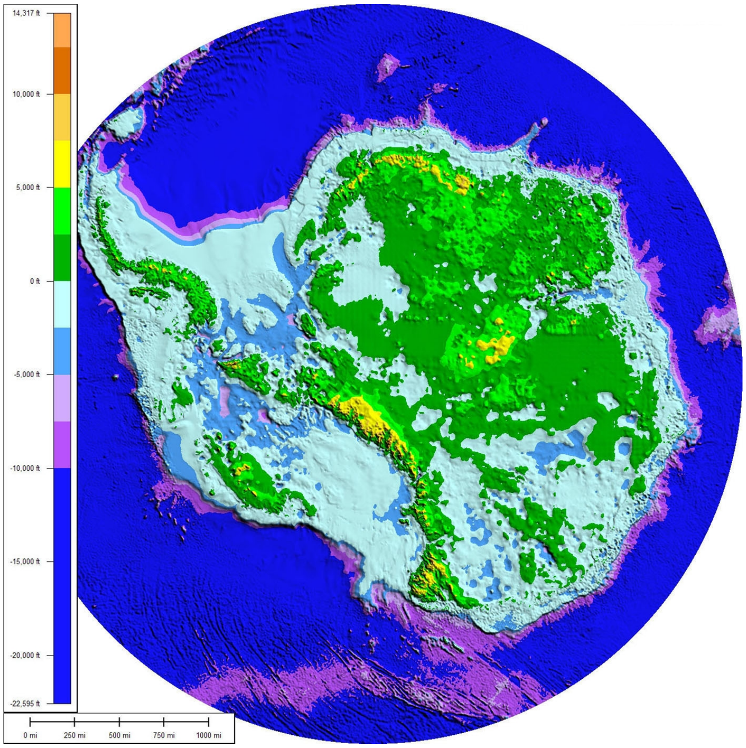

Figure 4. Subglacial topography and bathymetry of Antarctica. Although much of Western (*Western Hemphere*, to the left) Antarctica is now below sea level, corrected models now indicate that most of this area was above sea level in the Eocene (Wilson and Luyendyk 2009). At upper left, the long Transantarctic Mountain Range approaches the southern Andes of South America. © by Paul V. Heinrich. Use subject to Creative Commons Attribution 3.0 Unported License.

The Antarctic climate during this transition is of great interest. Studies of plant fossils indicate that a tropical to subtropical climate dominated during the late Cretaceous (85 Ma), with a mean summer temperature of about 20ºC (Francis *et al.* 2008). After some cooling, a generally warm, ice-free period continued through the Paleocene, with some warming in the early Eocene. By the late Eocene, the climate was much cooler, and temperate forests were dominated by Southern Beech (*Nothofagus*, with living species in Australia, Tasmania, New Guinea, New Caledonia, New Zealand, Chile and Argentina), and monkey puzzle trees similar to living *Araucaria araucama* (Cantrill and Poole 2005, Poole and Cantrill 2006, Francis *et al.* 2008, Jamieson and Sugden 2008). *Araucaria* species are now found in New Caledonia, Norfolk Island, Australia, New Guinea, Argentina, Chile, and southern Brazil. Fossil marsupials, related to those presently found in South America, have recently been reported from Antarctic rocks of Eocene age (Woodburne and Zinsmeister 1982, Goin et al. 1999, 2007, Beck et al. 2008). There is even good reason to believe that at least four endemic species of Antarctic springtails (Collembola) represent a continuous Gondwanan line of descent that diversified in Antarctica during the mid- to late Miocene, 21—11 Ma (Stevens et al. 2006). Based on the requirements of modern salticids, we can safely say that the Antarctic land bridge could have easily supported a diverse array of salticids during its long existence, particularly up to the late Eocene.

For ease of reference, I will refer to the joined continents of Australia, Antarctica, and South America collectively as *Australamerica* (*late Gondwana*). To find *Australamerican* clades that used the Antarctic land bridge, we can look for groups that meet the following conditions: 1, The clade had to originate in Australamerica, during the long time period of its existence (~130—34 Ma). 2, Sister groups within the clade can now be found in both Australia and South America (at least in fossil form). 3, The presence of members of the clade in other areas, if applicable, can be explained by secondary migration from either Australia or South America.

The relationship of the Australian to the South American fauna, particularly with respect to the distribution of marsupial mammals, has been long recognized. Most early explanations for this relationship, before the current acceptance of *continental drift* and *plate tectonics*, were awkward, and have little or no support today. As early as 1924, however, Launcelot Harris presented a very bold and determined argument in support of the migration of marsupials directly over an Antarctic land bridge. Several other groups of animals that, based on criteria 1—3, above, may be characterized as native Australamericans, are identified in Table 1.

Table 1. Some clades of apparent Australamerican origin that appear to have migrated across the Antarctic land bridge before their more recent diversification within continental boundaries.

| *Clade* | *Australian sister group* | *South American sister group* | *Gondwanan outgroup (more ancient clade)* | *References* |
|---|---|---|---|---|
| Mammalia: Marsupalia (part) | all Australian marsupials | all South American marsupials | Mammalia: Marsupalia | Woodburne and Zinsmeister 1982, Goin *et al.* 1999, Luo *et al.* 2003, Nilsson *et al.* 2004, Goin *et al.* 2007, Beck *et al.* 2008 |
| Aves: Struthioniformes (part) | Emu (*Dromaius*), Cassowary (*Casuarius*), Kiwi (*Apteryx*) | Tinamiformes: *Crypturellus*, *Eudromia*, *Nothoprocta*, *Tinamus* | Struthioniformes, including African Ostrich (*Struthio*) | van Tuinen *et al.* 1998, Cooper *et al.* 2001, Gibb *et al.* 2007, Hackett *et al.* 2008, Harshman *et al.* 2008 |
| Testudines: Chelidae | all Australian chelids | all South American chelids | Pleurodira, including Podocnemidae and Pelomedusidae | Gaffney 1977, Fujita *et al.* 2004, Krenz *et al.* 2005 |
| Anura: Hylidae (part) | all Pelodryadinae | all Phyllomedusinae | Hylidae, including Hylinae (*Hyla*) | Faivovich *et al.* 2005, Frost *et al.* 2006, Zeisset and Beebee 2008 |

Of these groups, the timing of the diversification of the Marsupalia (late Cretaceous to early Cenozoic) has received the most attention, and is fully in line with the hypothesis of Australamerican origin for the *living* species (Nilsson *et al.* 2004). This does not require that the *first* marsupial was Australamerican, however (Luo *et al.* 2003). Recent work (Hackett *et al.* 2008, Harshman *et al.* 2008) places the *flying* neotropical Tinamous (Tinamiformes) as a sister group to living flightless birds of Australia, New Guinea, and New Zealand. South American Rheas (*Rhea* and *Pterocnemia*) are more closely related to this group than the Ostrich (*Struthio*), and at least one view (Harshman *et al.* 2008, Fig. 2) supports the possibility of a closer relationship between the Rheas and the Tinamiformes. The Kiwi (*Apteryx*) appears to have arrived in New Zealand later than the extinct Moas, and is not closely related (Cooper *et al.* 2001). Chelid fossils have never been found outside of Australamerica.

I know of no salticid spiders, living or fossil, that have ever been found in Antarctica. Yet it is quite possible that a diverse population of salticids, ancestral to at least some of those that we can find today in Australia and the Americas, did live in Australamerica, and were of Australamerican origin. Assuming that Australasian ancestors (or clades based on these ancestors and their descendents) did exist, our challenge lies in finding the corresponding clades among the known Salticidae.

## Prehistory of the Salticidae

As noted by Hill and Richman (2009), the fossil record for the Salticidae is indeed sparse, and is limited to the Cenozoic. Some of the fossils that have been found are reviewed in Table 2.

Table 2. Some fossil salticid genera. Under each description, similar recent salticids are identified in some cases in parentheses.

| *Era/Epoch* | *Locality and Source* | *Description* | *References* |
|---|---|---|---|
| Eocene ~54—42 Ma | Baltic Sea: Baltic Amber | *Gorgopsina (~hisponine), Prolinus (~hisponine), Eolinus* (~*Cyrba, Portia*), *Paralinus (~spartaeine?), Almolinus, Cenattus, Distanilinus* | Prószyński and Żabka 1980, Keiser and Weitschat 2006, Maddison and Zhang 2006, Dunlop *et al.* 2009, Wolfe *et al.* 2009 |
| Oligocene to Miocene ~30—20 Ma | Chiapas, Mexico: Chiapas Amber | *Lyssomanes* | García-Villafuerte and Penney 2003 |
| Miocene ~20—15 Ma | Dominican Republic: Dominican Amber | *Lyssomanes, Nebridia, Thiodina, Corythalia, Descangeles, Descanso, Pensacolatus* | Cutler 1984, Iturralde-Vinet and MacPhee 1996, Dunlop *et al.* 2009 |

Given our necessary reliance on fossil amber, we need to recognize that the absence of a group from that record does not establish the fact that this group did not exist. It may simply mean that members of this group did not live on the trunks of trees that produced that amber, or that, for behavioral reasons, that group was not likely to be captured in amber. For example, Penney (2007) has reported an unusual lack of *any* salticid fossils from a deposit of lower Eocene amber in the Paris Basin (France). Although this finding is *consistent* with the hypothesis that salticids did not occur in Europe until later in the Eocene, it does little to establish that hypothesis as credible. In addition, we have not found *any* definitive intermediate fossils, or *proto-salticids*, to clarify the evolution of the family.

Żabka (1995) referred to the major influence of continental isolation in the distribution of major salticid groups that appeared to become highly diversified in the late Cretaceous to Eocene period. However, we have no Cretaceous or Paleocene fossils from this group to support any hypotheses related to their radiation. From the few available records (Table 2), we may assume that a diverse group that included hisponines and *possibly* spartaeines (or their close relatives), not greatly different from existing species in Africa or Asia, could be found in a much warmer northern Europe during the Eocene. For much of this time the climate there was *paratropical* (Andreasson and Schmitz 2000, Harrington 2001, Kvaček 2002, Huber and Caballero 2003). About 20 My later, by the early Miocene, we find an essentially modern fauna on a Caribbean island. We have no transitional records to explain the emergence of diversity in either area. With few fossil records, however, *hypotheses* relative to the Salticidae of Australamerica will have to rely primarily on the current distribution of salticids, and their known (or *supported*) phylogeny. For example, with the current center of hisponine diversity in Africa (Maddison and Needham 2006, Maddison and Zhang 2006), the presence of Eocene hisponine fossils in Europe, and the lack of hisponines in Australia and the Americas, it is possible that this group evolved in the Laurasia-African supercontinent in a post-Gondwana time frame. Given the diversity of spartaeines in Southeast Asia (Wijesinghe 1990), it is likewise tempting to think that this group also evolved in Laurasia-Africa. However, as we will discuss below, there is also some evidence for a post-Australamerican origin for this group, from Australasian ancestors. It is important to note that all living salticids, whether *basal* or *salticoid* (Maddison and Hedin 2006), still represent modern groups. Within the Salticidae, although some groups have been termed *primitive*, evolution proceeds in many directions, and there has been more than one line of descent leading to either an increase in the acuity of the anterior medial eyes, or to reduction of the posterior medial eyes (Blest 1983, Blest and Sigmund 1984, 1985, Blest *et al.* 1990, Hill and Richman 2009).

It has been notoriously difficult to pinpoint the time of emergence of *any* major group from the fossil record. Even well-known groups can turn out to be much more ancient than previously assumed (Table 3).

Table 3. Some new fossil discoveries that have pushed back the timeframe for emergence of respective animal groups.

| *Group* | *Previous discoveries* | | *New discovery* | | *Reference* |
|---|---|---|---|---|---|
| | *Age* | *Formation* | *Age* | *Formation* | |
| Mammalia: Metatheria or near-marsupials | ~75 Ma (skeletal) | | ~125 Ma | Lower Cretaceous Yixian Formation, China. | Luo *et al.* 2003 |
| Sauria: feathered theropod | ~150—145 Ma | Jurassic Solnhofen Limestone in Bavaria (*Archaeopteryx*) | ~160 Ma | Earliest Late Jurassic Tiaojishan Formation of western Liaoning, China | Hu *et al.* 2009 |
| Testudines: Chelidae | ~23—5 Ma | Miocene (?) and later fossils from Australia and South America | ~105 Ma | Lower Cretaceous (Lower Albian), Patagonia | Lapparent de Broin and de la Fuente 2001; see also de la Fuente 2003 |
| Squamata: Gekkonidae | ~54—42 Ma | Eocene Baltic amber | 110—97 Ma | Lower Cretaceous (Albian) amber from Myanmar | Bauer *et al.* 2005, Arnold and Poinar 2008 |
| Araneae: Araneidae | ~45 Ma | Middle Eocene oil shales of the Messel pit, Hesse, Germany | 121—115 Ma | Lower Cretaceous (Aptian) amber from Alava, Spain | Penney 2003, Penney and Ortuño 2006; see also Peñalver *et al.* 2006, 2007 |
| Araneae: Dipluridae | ~54—42 Ma | Eocene Baltic amber | 125—112 Ma | Lower Cretaceous (Aptian) Crato Lagerstätte of Cearà Province, north-east Brazil | Seldon *et al.* 2006 |
| Araneae: Linyphiidae | ~54—42 Ma | Eocene Baltic amber | 135—125 Ma | Lower Cretaceous (Upper Neocomian–basal Lower Aptian) amber, Kdeirji/ Hammana outcrop, Lebanon | Penney and Selden 2002 |
| Araneae: Mecysmaucheniidae | Recent | Living species found in southern South America and New Zealand | ~100 Ma | Lower Cretaceous (Late Albian) amber of Charente-Maritime, France | Saupe and Seldon 2009 |
| Araneae: Pisauridae | ~54—42 Ma | Eocene Baltic amber | 107—100 Ma | Lower Cretaceous (Albian) amber from Myanmar | Penney 2004 |

As noted by Seldon *et al*. (2009), *almost every new specimen of spider from the Palaeozoic and Mesozoic eras . . . can drastically alter our perception of spider phylogeny*. Proposed *molecular clocks* for evolutionary sequences are often based on synchronization with the fossil record, and these have to be reset when discoveries of earlier forms upset the underlying assumptions. The lack of fossil markers for salticids, in particular, makes this task even more challenging. When we examine the fossil record for emergence of a clade, we need to be cautious, given the fact that one or several uncommon, early representatives of that clade may have been evolving in relative isolation, or in a different area for a long time. Thus available fossils only set an *upper* bound for emergence, and with new fossil discoveries we can only expect that this bound will move *lower*, to an earlier time.

Some hypotheses related to the origin of the Salticidae, and the large salticoid clade, are outlined in Table 4.

Table 4. Some major, alternative hypotheses and associated predictions related to the origin of major salticid clades. All are *consistent* with the fossil record. Hypotheses 1—5 relate to origin of the Salticidae, 6—10 to the origin of the Salticoida).

| | *Hypothesis* | *Predicted fossils* | *Predicted faunal distribution* |
|---|---|---|---|
| 1 | Salticidae originated before the break-up of Pangaea into Gondwana and Laurasia ~150—175 Ma | Basal Pangaean lineages in Gondwanan and Laurasian fossils. | Major salticid lineages, except for relict groups, divided across Gondwana and Laurasia, and subsequently divided between Africa and Australamerica. Later lineages divided between Australia and South America. |
| 2 | Salticidae originated in Laurasia after the break-up of Pangaea ~150—175 Ma and before the initial break-up of Gondwana ~130—110 Ma | Laurasian fossils predate Gondwanan fossils. | Basal lineages found in many non-glaciated Laurasian areas as relict groups. |
| 3 | Salticidae originated in Gondwana after the break-up of Pangaea ~150—175 Ma and before the initial break-up of Gondwana ~130—110 Ma | Gondwanan fossils predate Laurasian fossils. | Basal lineages found in many non-glaciated Gonwanan areas as relict groups. |
| 4 | Salticidae originated in Laurasia after the initial break-up of Gondwana ~130—110 Ma, but before the break-up of Australasia ~35 Ma | Laurasian fossils predate Gondwanan fossils. | Basal lineages found in many non-glaciated Laurasian areas as relict groups. Relict groups should also appear in Africa. No endemic relict groups in Australamerica. |
| 5 | Salticidae originated in Australasia after the initial break-up of Gondwana ~130—110 Ma, but before the break-up of Australasia ~35 Ma | Australasian fossils predate any other fossils. | Basal, relict groups primarily found in Australasia, in both South America and Greater Australia. Most lineages in Laurasia appear in post-Australasian timeframe, after Australia and New Guinea approach Southeast Asia, or through Central America-Caribbean archipelago migration. |
| 6 | Salticoida originated before the break-up of Pangaea ~150—175 Ma | Diverse, Pangaean salticoid lineages in both Gondwanan and Laurasian fossils. | Major salticoid lineages, except for relict groups, divided across Gondwana and Laurasia, and subsequently divided between Africa and Australamerica. Later lineages divided between Australia and South America. |
| 7 | Salticoida originated in Laurasia after the break-up of Pangaea ~150—175 Ma and before the initial break-up of Gondwana ~130—110 Ma | Laurasian fossils predate Gondwanan fossils. | Each major Gondwanan salticoid lineage traced back to more basal Laurasian groups. |
| 8 | Salticoida originated in Gondwana after the break-up of Pangaea ~150—175 Ma and before the initial break-up of Gondwana ~130—110 Ma | Gonwanan fossils predate Laurasia fossils. | Multiple Gondwanan lineages diverge in Africa and Australamerica. these lineages diverge later between Australia and South America. |
| 9 | Salticoida originated in Laurasia after the initial break-up of Gondwana ~130—110 Ma, but before the break-up of Australasia ~35 Ma | Laurasian fossils predate Gondwanan fossils. | Multiple salticoid lineages can be traced from Laurasian groups to groups in either Africa or Australasia. More early salticoid lineages, and earlier fossils, in Africa than in Australamerica. |
| 10 | Salticoida originated in Australasia after the initial break-up of Gondwana ~130—110 Ma, but before the break-up of Australasia ~35 Ma | Australasian fossils predate any other fossils. | Multiple salticoid lineages can be traced from Australasian origins, with primary branches split between South America and Greater Australia. |

Unless many more fossils are discovered, any testing of these hypotheses must be based on the biogeography and phylogeny of recent species. The great diversity of lineages crossing the *Wallace Line* (Southeast Asia into the East Indies to New Guinea) is particularly problematic for this purpose, as these may have originated from either the north (Laurasia) or from the south (Australamerica). A number of groups that are basal to *both* the spartaeines and the salticoids (*Tomocyrba*, *Massagris*, hisponines, and perhaps *Goleba*; Maddison and Needham 2006, Maddison *et al.* 2008) in the recent Madagascar to East Africa fauna may support either a Pangaean (hypothesis 1, above) or a Gondwanan (3) origin for the Salticidae. With respect to the origin of the Salticoida, hypothesis (10) gets some support from the fact that one of the two major branches of the Salticoida, the almost exclusively neotropical Amycoida (Maddison and Hedin 2003, Maddison *et al.* 2008), almost certainly has a South American origin. The apparent failure of Amycoida to cross to Australia may be related to the fact that these are primarily *tropical* salticids. The other major branch divided many times, and includes several major groups that may have crossed the Antarctic land bridge (see below). The failure to find many salticids in early Eocene Europe (Penney 2007), and no salticoids in later Eocene Europe (Table 2) is *consistent* with this hypothesis. The Salticoida may have been largely confined to Australamerica in the Eocene, but we have no salticid fossils of any kind with which to establish their presence. Again, we need to be very cautious in our interpretation of a very fragmented, incomplete fossil record. We also must remember that even as diverse a group as the Salticoida at one time consisted of a single species, a species that may have been neither widely distributed nor abundant. It is almost certain that any important ancestor species like this would be missing altogether from the fossil record. Only at a much later date, after it had diversified into a number of competitive species, would there be any probability of a fossil presence. The relatively short interval (~13—18 My) between the end of the Eocene and the emergence of modern neotropical genera, as well the enormous diversity found within the major clades of modern salticoids, suggest that that there were a number of salticoid species alive during the Eocene. These would include the ancestral species for the major salticoid clades that we see today.

## Tentative identification of some trans-Antarctic salticid clades

Some local or *relatively endemic* salticid groups from Greater Australia (including New Guinea) have been matched with possible South American sister groups in Table 5.

Table 5. Some endemic or near-endemic salticid genera from greater Australia (including New Guinea) matched with possible South American sister groups.

| *Clade* | *Australian sister group* | *South American sister group* | *References* |
|---|---|---|---|
| Spartaeinae + lapsiines | Spartaeinae: *Mintonia*, *Portia* | lapsiines: *Gallianora*, *Lapsias*, *Thrandina* | Maddison and Needham 2006, Richardson 2006, Żabka 1994 |
| Astioida + Marpissoida | Astioida: *Adoxotoma, Arasia, Astia, Damoetas, Helpis, Holoplatys, Jacksonoides, Ligonipes, Megaloastia, Mopsolodes, Mopsus, Myrmarachne, Ocrisiona, Opisthoncus, Rhombonotus, Sandalodes, Simaetha, Simaethula, Sondra, Tara, Tauala, Zebraplatys* | Marpissoida: *Beata, Bellota, Eris, Hentzia, Itata, Maevia, Metacyrba, Peckhamia, Psecas, Rhetenor, Rudra, Sassacus, Tutelina, Zygoballus* | Wanless 1988, Hedin and Maddison 2001, Maddison and Hedin 2003, Richardson *et al.* 2006, Maddison *et al.* 2008 |
| Euophryinae | Euophryinae (part): *Ascyltus, Athamas, Bathippus, Canama, Cytaea, Ergane, Euryattus, Hypoblemum, Jotus, Lauharulla, Lycidas, Maratus, Margaromma, Prostheclina, Servaea, Spilargus, Udvardya, Zenodorus* | Euophryinae (part): *Amphidraus, Anasaitis, Asaphobelis, Belliena, Chapoda, Chloridusa, Cobanus, Commoris, Coryphasia, Corythalia, Ilargus, Maeota, Mopiopia, Neonella, Ocnotelus, Pensacola, Semnolius, Sidusa, Siloca, Stoidis, Tariona, Tylogonus* | Maddison and Hedin 2003, Richardson *et al.* 2006, Maddison *et al.* 2008, Hill 2009 |
| *Grayenulla* + *Hisukattus* | *Grayenulla* Żabka 1992: seven species from Australia | *Hisukattus* Galiano 1987: four species from Argentina, Brazil, and Paraguay | Galiano 1987, Żabka 1992, Żabka 2002, Żabka and Gray 2002, Richardson *et al.* 2006 |

To identify clades that *may* have crossed the Antarctic land bridge, I began with an examination of the Australian genera that do not appear to have migrated to that continent at a later time from southeast Asia. Many of these genera are also endemic to New Zealand and can be grouped into two larger clades, the Astioida (Maddison *et al.* 2008) and the Euophryinae (Prószyński 1976). Note that the clades divided into Australian and South American groups here range in nominal size from a small group of genera to major divisions of the Salticidae as a whole. Given the long interval over which the Australian land bridge was in place, and our present uncertainty with respect to a timeline for the evolution of salticid groups, this can be expected. Although modern genera are given as examples of the respective clades, it can be expected that unknown, now extinct members of these clades actually participated in any actual migration across Antarctica.

The modern distribution of spartaeines, with only a few known species from Australia and a center of diversity in the East Indies, provides little support for the division of spartaeines and lapsiines across Australamerica. One *pre-spartaeine* species may have migrated out of Greater Australia, however, and subsequently diversified in the tropical West Indies and Southeast Asia. This division is included for consideration because of recent evidence from gene sequencing (molecular phylogeny) that spartaeines and lapsiines are sister groups (Maddison and Needham 2006).

The second division, between the large groups *Astioida* (Maddison *et al.* 2008) and *Marpissoida* (Maddison and Hedin 2003), reflects the relatively close relationship between these groups that has been suggested through comparative gene sequencing (Maddison *et al.* 2008). Both groups are now greatly diversified, the former in the greater Australian area (including New Zealand) and the latter in both North and South America. Both groups include a variety of convergent forms that range from the largest of salticids (e.g., *Mopsus* and *Phidippus*), to flattened, cryptic forms (e.g., *Holoplatys* and *Platycryptus*), to ant mimics (e.g., *Myrmarachne* and *Peckhamia*). Given the size, diversity, and regional importance of these groups, the hypothesis that they diversified to current forms after the closing of the Antarctic land bridge (after the Eocene) appears to be most consistent with the fact that no astioids are found in South America, and marpissoids (while having a subsequent, smaller dispersal to the Palaearctic) are essentially American.

The third division (suggested by Hill 2009) of the Euophryinae is based on the fact that this group has two current centers of diversity, one in the Americas, and one that appears to radiate out of Australia, including many endemic species in that area. Comparative gene sequencing (Maddison and Hedin 2003, Maddison *et al.* 2008) has indicated a close relationship between euophryines in both areas, but the detailed phylogeny of existing genera will require more study to determine if a single, or if multiple divisions of the Euophryinae, can be associated with the closing of the Antarctic land bridge. Timing of diversification in this group is also of great interest. As noted above, Australamerica was around for a long time.

In addition to species with an affinity to either Asia or Australia, some very unusual endemic salticids can be found in the vicinity of New Guinea. These include the basal cocalodines (Maddison 2009), as well as highly unusual forms like *Coccorchestes*, *Diolenius*, and *Furculatus* (Balogh 1981, Żabka, 1994, Szűts 2003, Gardzińska and Żabka 2006). Many of the endemics, and almost all of the genera shared with Australia, can be placed in either the Astioda (e.g., *Opisthoncus* and *Sandalodes*) or the Euophryinae (e.g., *Bathippus* and *Euryattus*). More than 200 widely distributed species, most from the tropics of Africa or the East Indies, have been placed in the antlike genus *Myrmarachne*. Recently (Maddison *et al.* 2008) included this large genus with the related *Ligonipes* in the Astioida. Almost all of the other Astioda are Australasian in distribution, and this exception by a widely distributed genus that has also made its way to many tropical islands (including Madagascar) should not affect our hypothesis with respect to an older Australamerican origin for the Astioida as a group.

Finally, based on the suggestion (Żabka and Gray 2002) that distinctive Australian endemics of the genus *Grayenulla* Żabka 1992 resembled the South American *Hisukattus* Galiano 1987, I have added this division to Table 5 for consideration. In both genera the bulb of the male pedipalp is distinctively angulate or bears unusual protuberances, and and a heavy, curved ebolus emerges laterally (Galiano 1987, Żabka 1992).

Between the astioids, the endemic euophryines, and *Grayenulla*, this brief review has thus treated most of the endemic salticids in Australia, and supports the view (Richardson *et al.* 2006) that a significant number of endemic species *not closely related to the Asian fauna* remain to be discovered with further exploration of the Salticidae of that continent.

It is important to note that, although continental boundaries often appear to determine the distribution of major groups of salticids (Żabka 1995, Maddison et al. 2008), these spiders are also capable of dispersal over the ocean (e.g., Żabka and Nentwig 2002, Arnedo and Gillespie 2006). Successful transport of a single female spider, or a small number of spiders, *might* result in their colonization and diversification in a new area, particularly if they were not faced with serious competition. Statistically, the sheer number of dispersal opportunities across a direct physical connection would appear to drive the larger picture, but not the complete picture. The introduction of even one species *with novel or innovative features*, however improbable, could lead to the radiation of many descendent species over time.

## Acknowledgments

I would like to thank Drs. G. B. Edwards, Wayne P. Maddison, Jerzy Prószyński, and David B. Richman for their respective reviews and meaningful feedback.

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