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Origins of the North American jumping spiders (Araneae: Salticidae)

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Abstract. The origin of every major group or clade of North American salticid spiders can be explained by its origin in, and subsequent introduction from, either the Neotropical or Palaearctic regions. Although the more ancient salticid fauna represented by Eocene fossils from the Baltic Amber of Europe (~45Ma) was probably present in North America, we have no record of a North American fauna predating that represented by Miocene fossils in the amber of Chiapas, Mexico (~23-15Ma). Before completion of the Panamanian Land Bridge (~2.5-2.3Ma), Antillean and Central American volcanic island arcs could have supported an early introduction of dendryphantine and marpissine ancestors from South America. Throughout the Cenozoic, the Beringia Land Bridge was generally available to support the introduction of the other important North American group, the pellenines, from Eurasia. Since the Pleistocene, cycles of glaciation have repeatedly altered the distribution of the North America fauna.

Introduction to an introduced fauna

Perhaps the most notable thing about the modern North American salticid fauna is that, although this fauna includes a handful of endemic and speciose genera (*e.g.*, the plexippoid *Habronattus* and the marpissoid *Phidippus*; Richman *et al.* 2012), above the level of genus all of the represented groups or subfamilies are much more diverse and almost certainly originated elsewhere (Figure 1).

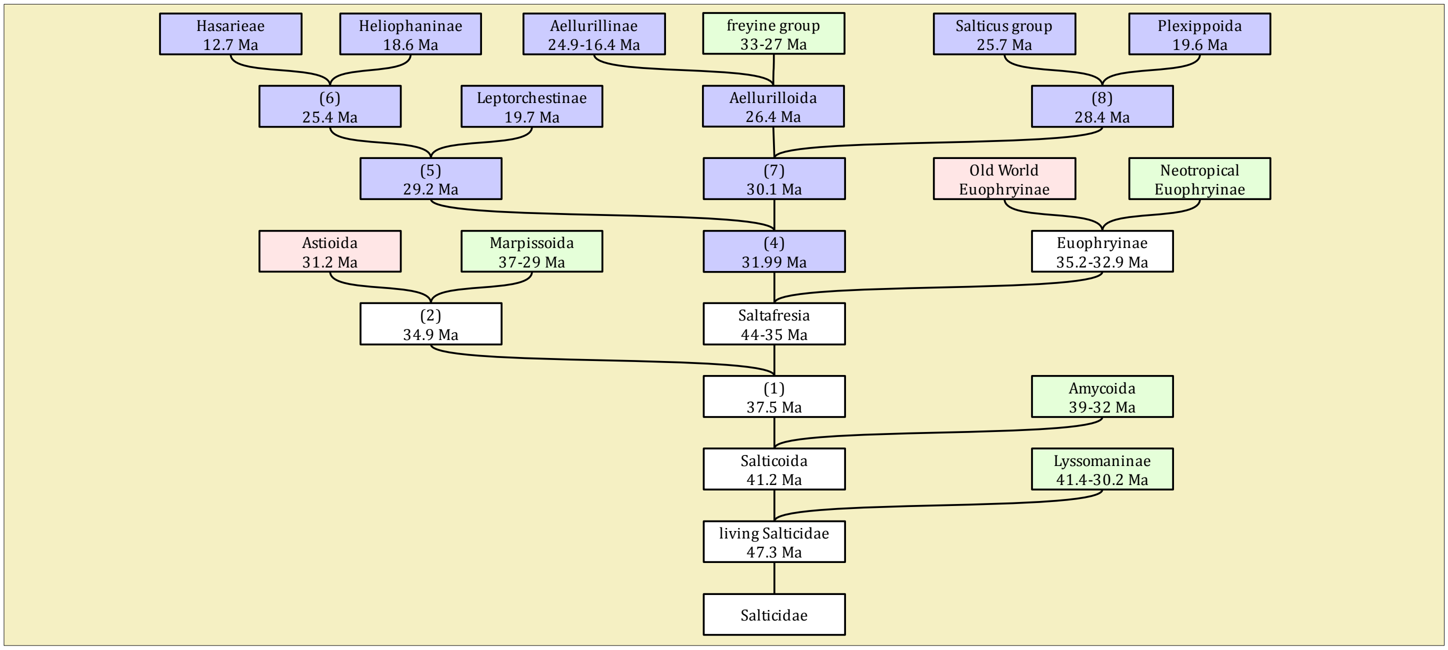


Figure 1. Hypothetical phylogeny of salticid clades represented in the modern North American fauna, with estimated time of origin for each clade, based on Bodner & Maddison (2012). All of these clades are most diverse in either Afro-Eurasia (purple), the Neotropics (green), or Australasia (pink). In North America, the most important modern genera are related to the Neotropical marpissoids and the Afro-Eurasian plexippoids.

A series of recent studies has greatly improved our understanding of the relationship of continental isolation to the diversification and evolution of the Salticidae during the Cenozoic era (Hedin & Maddison 2001a, Maddison & Hedin 2003a, Maddison & Needham 2006, Maddison *et al.* 2007, 2008, Zhang 2012, Bodner & Maddison 2012). We have previously reviewed evidence in support of a distinctive Australasian fauna, and the isolation of Neotropical marpissoids and euophryines from Australasian astioids and euophryines, respectively, by the loss of the Antarctic land bridge at the end of the Eocene (Hill 2009a, 2010). Given the proximity of North America to Neotropical and Palaearctic regions (Figure 2), there is little mystery regarding the ultimate source of the modern North American fauna. Here we will address the likely timing associated with the arrival of each North American group, and its subsequent history, in some detail. For purposes of this discussion, the North American *fauna* includes species presently found in Alaska, Canada, the continental United States, and Mexico (Richman *et al.* 2012). The Cenozoic North American *continent* also includes parts of Central America joined to Mexico.

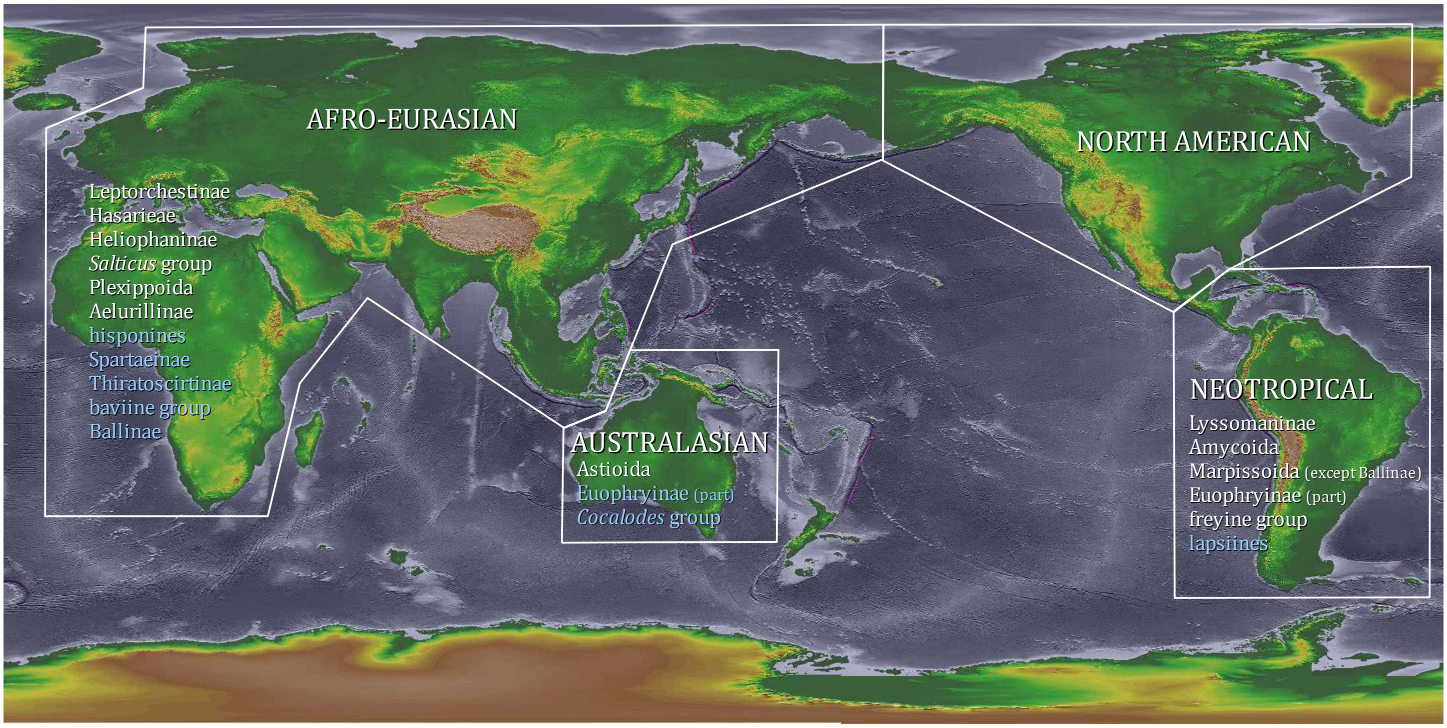


Figure 2. Global perspective on salticid clades represented in North America (white text). Important modern clades or subfamilies not represented in North America are also shown in blue. Each clade is shown in the major faunal region associated with its greatest number of genera and species. North America has endemic genera but no endemic subfamilies or major groups. Background image showing sea level at the last glacial maximum (LGM ~18-15Ka, shore line at 110m depth) courtesy of the NOAA National Geophysical Data Center.

If the North American fauna is now dominated by salticoids introduced since the Eocene, was there ever a more ancient fauna here and, if so, what became of it? Unfortunately, we have no fossils that can answer this question directly. However, the relationship of the early Cenozoic (~60-40Ma) Baltic Amber fauna to the modern European fauna gives us some important clues. As we will discuss below, for most of the Cenozoic, the Afro-Eurasian region has been joined to North America via a high-latitude land bridge called Beringia. In addition, for much of this time, the climate that prevailed across this connection was quite warm, even subtropical. The relationship of the Baltic Amber fauna to modern salticids is poorly understood, and many of the groups represented in that fauna may be extinct today. At the same time, we can say with assurance that this was already a very diverse fauna (Figure 3; Dunlop *et al.* 2013), the result of an ancient evolutionary history for which we have no fossil record at present. The modern European fauna is now dominated by salticoid groups with close affinity to Africa and Asia. It is thus likely that, as in Europe, in the absence of protective isolation North America lost this more ancient fauna as a result of climate change and the introduction of salticoids.

Figure 3. Four representative salticids from the Baltic amber. **1,** 'Bug-eyed' salticid from Yantarnyi village, Kalingrad (Eocene: Lutetian estimated age 48.6-40.4Ma, 54.9° N, 19.9° E, palaeocoordinates 52.1° N, 15.0° E). Photograph Copyright © Wolfgang Weitschat, used with permission. **2-6,** Salticids from the Eocene (~45Ma) of Palanga, Lithuania in the collection of D. E. Hill. **2,** Small salticid with relatively few setae. The PME of this specimen (arrow) are small and legs are relatively short, a pattern seen in many recent salticoid groups. **3,** Salticid with large, laterally-oriented PME. **4,** Detail from (3), showing well-preserved scales of the carapace. These long scales have a single shaft and regular lateral projections along their length, a pattern seen in many modern salticids, including spartaeines and many salticoids. **5-6,** Salticid with median carapacial stripe comprised of white setae and large PME with axis oriented in antero-lateral direction.

The earliest known salticid fauna in North America is represented by the Miocene (15-23Ma) Chiapas amber from the far south of Mexico. Until recently, only one named salticid specimen from this amber, a *Lyssomanes*, had been reported (García-Villafuerte & Penney 2003). The recent discovery of what appears to be a marpissine in Chiapas amber (Figure 4) suggests that a diverse salticid fauna with close ties to the South American fauna was already present in North America by the early to middle Miocene (23-13 Ma; Riquelme & Hill 2013). This fauna may have included the ancestors of the marpissoid genera that now dominate the salticid fauna of this continent, as well as those presently found in Eurasia. Other fossils found in the Chiapas amber suggest a close environmental affinity to the better-known *Dominican amber* from the Dominican Republic (Carbot-Chanona & Milani 2008), from which fossil *Corythalia*, *Lyssomanes*, and *Thiodina* have been reported (Cutler 1984, Dunlop *et al.* 2013).

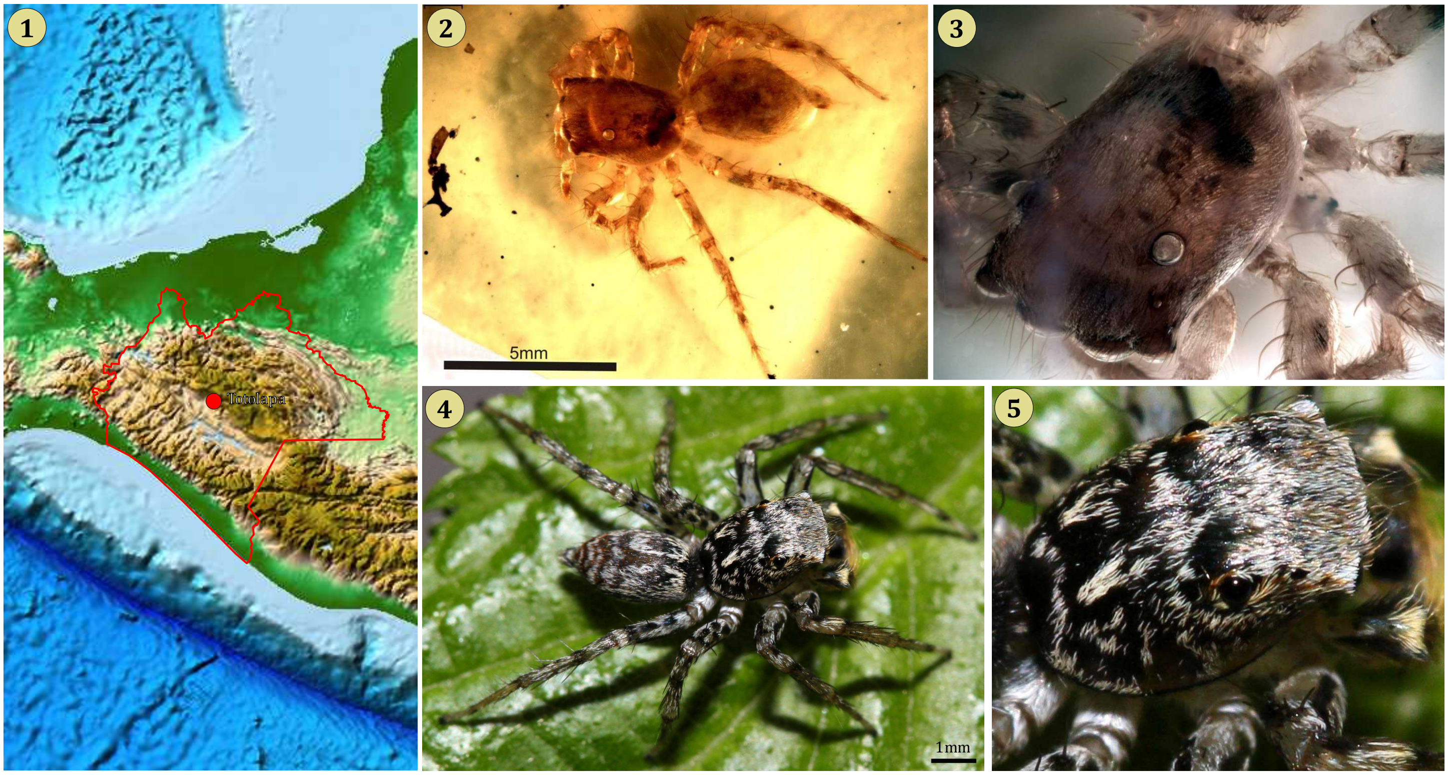


Figure 4. Comparison of a Miocene salticid from the Chiapas amber with a North American marpissine of the genus *Maevia*, after Riquelme & Hill (2013). **1,** Map of southern Mexico showing the site at which this fossil (2-3) was found in lignite sediment from the Mazantic Shale formation, Rio Salado, Totolapa, Chiapas, Mexico. **4-5,** ♂ *Maevia inclemens* (Walckenaer 1837), from southern Greenville County, South Carolina, 12 MAY 2012. Map image (1) courtesy of the NOAA Satellite and Information Service (Amante & Eakins 2009). Photos (2-3) by Francisco Riquelme, used with permission.

Before we discuss each of the North American salticid groups in detail, we will first review the geological history of land and island-chain connections between North America, Asia, and South America. We will then review the Cenozoic climate of North America, as well as important studies of other animals and plants that have crossed into North America.

Geological perspective on land and island chain routes to North America

The geological time line. Major geological events related to routes of species introduction to North America during the Cenozoic era are shown in Table 1. Species introductions associated with the modern salticid fauna of North America may date back no further than the late Oligocene-early Miocene. We have no evidence of an earlier salticid fauna that may have existed here.

Table 1. Status of routes of introduction to North America over geological time (Graham 1999, Iturralde-Vinent & MacPhee 1999, Gladenkov *et al.* 2002, Haug *et al.* 2005, Jahn 2005, Iturralde-Vinent 2006, Fiorello 2008, Clark *et al.* 2009, Lauver *et al.* 2010). Timeline based on the International Stratigraphic Chart of the International Commission on Stratigraphy for 2009 (ICS 2009).

Age				*Route of species introduction to North America*		
Period	Epoch	Age	Start (Ma)	Mexican to Panamanian	Antillean	Beringian
Quaternary	Holocene		00.012	Completion of Panamanian Land Bridge since ~2.5-2.3Ma	Larger islands of the Greater Antilles partly submerged and divided into smaller islands during glacial minima, growing much larger during glacial maxima	Present interglacial period
	Pleistocene	Upper Pleistocene	00.126			Start of last major glaciation ~120Ka, end of Last Glacial Maximum (LGM) ~20-19Ka, rise in sea level to flood Beringia ~14.5Ka
		“Ionian”	00.781			Longer glaciation cycles (~100Ky) of greater extent
		Calabrian	01.806			Shorter glacial cycles (~41Ky) of lesser extent
		Gelasian	02.588			
Neogene	Pliocene	Piacenzian	03.600	Shallow water ridge of Central American volcanic arc ~3Ma	Greater and Lesser Antilles near present day position	Onset of major North American glaciation ~2.7Ma
		Zanclean	05.332	Central American volcanic arc		First flooding of Bering Strait ~5.32Ma
	Miocene	Messinian	07.246			Beringia near present day position
		Tortonian	11.608	*Ephemeral precursor* of Panamanian Land Bridge ~8Ma?		
		Serravallian	13.820	Larger islands of Central American volcanic arc system	Islands of Greater Antilles growing, Lesser Antilles reduced, Aves Ridge submerged ~20-15Ma	
		Langhian	15.970			
		Burdigalian	20.430			
		Aquitanian	23.030			
Paleogene	Oligocene	Chattian	28.400	Elevated sea level and greater separation of smaller islands of the Antilles and the Aves Ridge to the west		
		Rupelian	33.900			
	Eocene	Priabonian	37.200	Antilles (*Gaarlandian Ridge*) may have joined South America to eastern Mexico by land for ~1My, but evidence for this is ambiguous		
		Bartonian	40.400	Deep marine separation of North and South America	Antilles arc, comprised of isolated deep water volcanos, growing	Southward drift of Beringia slows
		Lutetian	48.600			Southward drift of Beringia from 85° N after ~82Ma
		Ypresian	55.800			
	Paleocene	Thanetian	58.700	Movement of the Antilles volcanic arc system with the leading edge of the Caribbean plate to the northeast, increasing isolation of North and South America		
		Selandian	61.100			
		Danian	65.500			
Cretaceous	Upper Cretaceous	Maastrichtian	70.600	Antillean volcanic arc system, a chain of islands connected by shallow seas, between North and South America		

Beringian route. The North American plate actually extends well into Asia, where it is fused with the Eurasian plate (Figure 5). Part of the North American plate, the Bering Land Bridge (*Beringia*) is a high-latitude land connection between Eurasia and North America that has generally been available during the Cenozoic (Figure 6; Hopkins 1959, Fiorello 2008, Lauver *et al.* 2010). Since the Pliocene, however, intermittent flooding of the low-lying Bering Strait has often made that route impassable by land (Gladenkov *et al.* 2002, Haug *et al.* 2005, Jahn 2005, Clark *et al.* 2009).

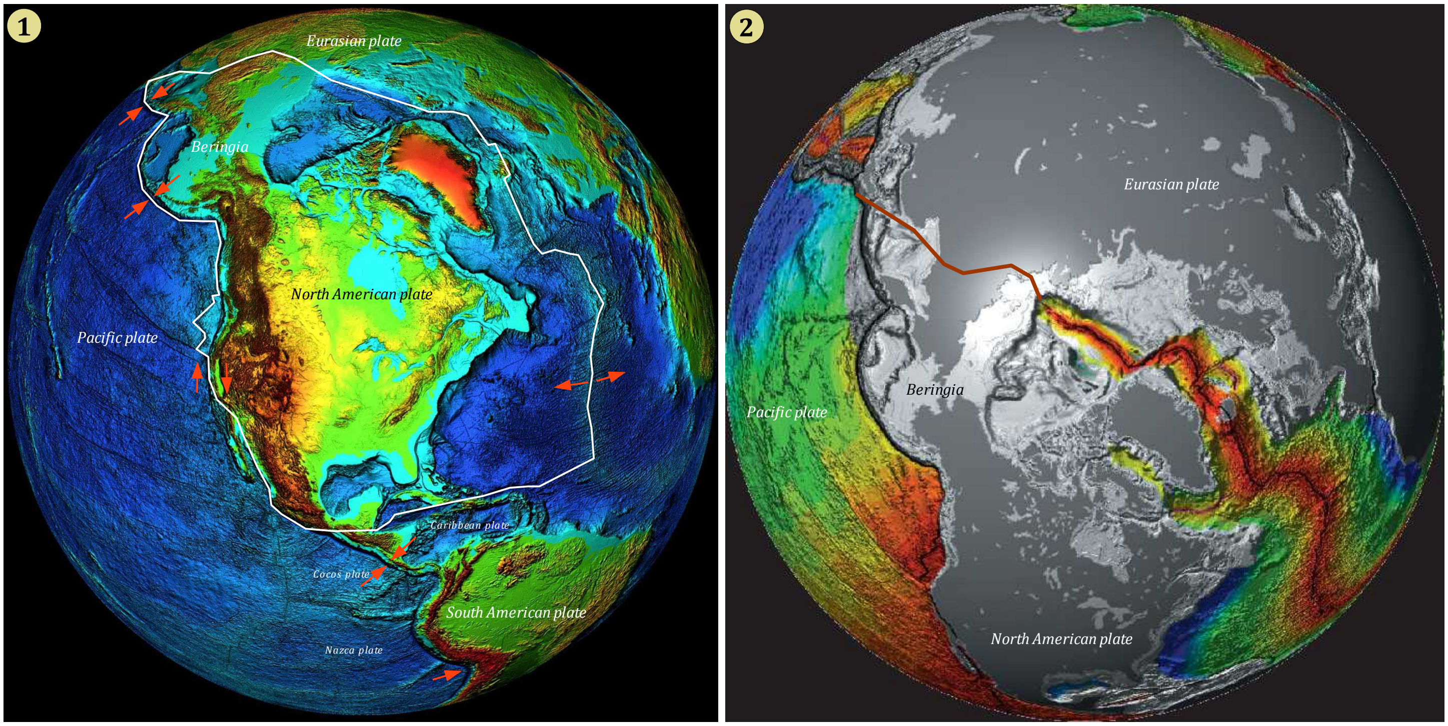


Figure 5. Global views of North American plate. **1,** In this vertical view the approximate plate boundary, extending from the mid-Atlantic ridge to northeastern Asia, is outlined in white. Red arrows show relative movement of this plate to adjacent plates. **2,** North polar view showing long boundary between North American and Eurasian plates. The age of the ocean bottom is color-coded, with the youngest rocks at the red end of the spectrum. Plate boundaries and relative movement based on USGS Moving Slabs chart (http://pubs.usgs.gov/gip/dynamic/slabs.html). Image (1), centered on 45° N, 90° W, courtesy of NOAA (http://www.ngdc.noaa.gov/mgg/global/relief/SLIDES/JPEGfull/Slide01.jpg). Image (2) by R. D. Müller and P. W. Sloss, NOAA-NESDIS-NGDC, available from http://www.ngdc.noaa.gov/mgg/. Data Source Müller *et al.* (2008).

Figure 6. Reconstruction of the North American continent during the Cenozoic era, showing continuity of the Beringian land bridge between North America and Asia. Copyright © Ron Blakley, NAU Geology, used with permission.

Southern routes. Species introductions from South America to North America after the Eocene (since 33.9Ma), and before the completion of the Panamanian land bridge (2.5-2.3Ma) would have required 'island hopping' between impermanent volcanic islands of either the Antillean or Central American volcanic arc systems (Figure 7; Iturralde-Vinent 2006). If a temporary precursor of the Panamanian land bridge was present ~8Ma, that may also have been used as a direct pathway. The Antillean volcanic arc system was comprised of a series of isolated, deep water volcanos in the early Eocene (~55Ma). This arc may have formed a direct land connection (the *Gaarlandian ridge*) from South America to what are now the Lesser and Greater Antilles at the Eocene-Oligocene boundary (35-33Ma). By the late Oligocene (29-27Ma) this ridge was reduced to a series of smaller islands extending from western Cuba to the Lesser

Antilles and, to the west of these, the Aves Ridge. By the middle Miocene (15Ma) the islands of the Aves Ridge were submerged, the remaining Lesser Antillean islands were much reduced in size, and the larger islands of the Greater Antilles were growing. During the Pleistocene and Holocene (since ~2.6Ma), larger islands of the Greater Antilles have been separated into smaller islands separated by shallow seas when sea level rose during glacial minima (interglacial periods), and these islands were much larger than at present when sea level fell during glacial maxima (Figure 8).

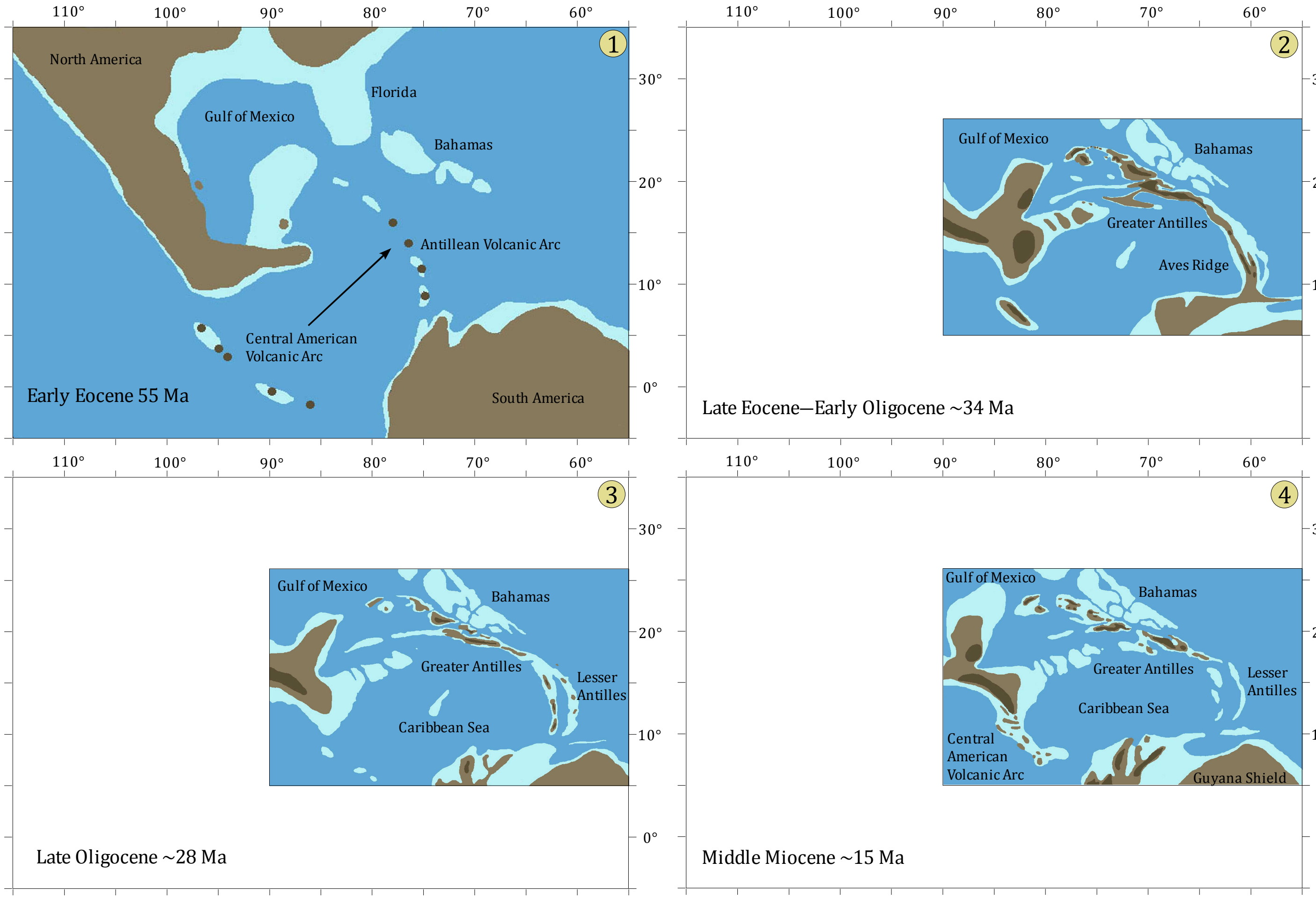


Figure 7. Reconstructions of land area in the Caribbean region during the Cenozic (based on Iturralde-Vinent 2006 and Iturralde-Vinent & MacPhee 1999). **1,** Early Eocene. Moving to the northeast (arrow) relative to North and South America, the Central American plate was (and is now) bounded by the Central American Volcanic Arc to the west, and the Antillean Volcanic Arc to the East. **2,** By the early Oligocene, the Antilles may have formed an almost continuous link between South America and the Greater Antilles. **3,** By the late Oligocene much of the Antillean island chain was submerged. **4,** The Central American Volcanic Arc, ultimately forming the Panamanian land bridge (2.5-2.3Ma), continued to develop in the Miocene.

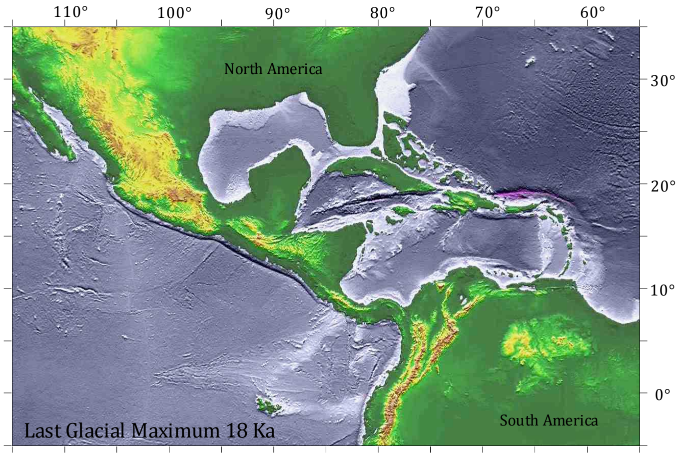


Figure 8. Connections between North and South America during the last glacial maximum (LGM, 18Ka). At this time the Florida and Yucatan peninsulas were much larger, and the distance between islands of the Greater Antilles and the North American continent much smaller. At this time the Panamanian land bridge, including a much larger area of Nicaraguan lowlands, formed a much wider connection than it does at present. Background image courtesy of the NOAA National Geophysical Data Center.

With a complex plate structure (Figure 9), the Antillean and Central American boundaries of the present-day Caribbean are still areas of active volcanism, seismic activity, and the resultant mountainous terrain. The continuity of the Panamanian land bridge to the west contrasts with the relative isolation of the islands associated with the Antillean arc to the east. This isolation has led to the development of a distinctly Antillean fauna, and allows us to consider the possibility of separate (1) 'Antillean' and (2) 'Panamanian' routes, and species introductions, to North America during the Pleistocene. We will treat much earlier (perhaps Miocene) introductions, whether across the Antillean or the Central American island arc, as (3) Mexican.

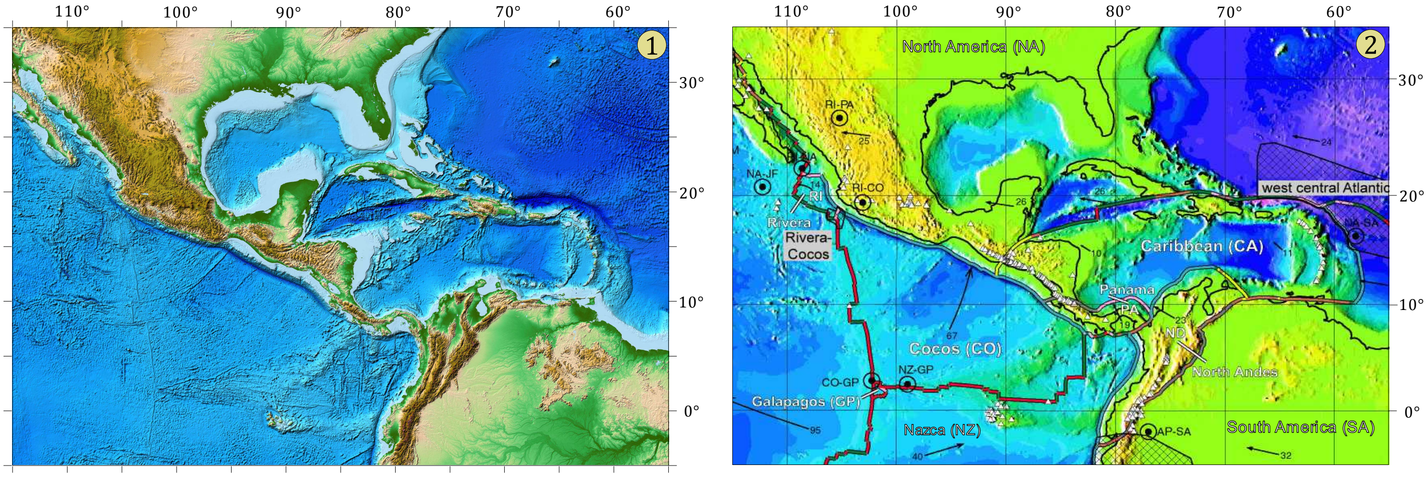


Figure 9. Present day maps of the Carribean and Central American regions. **1,** Relief map, showing the mountainous terrain of both Antillean and Panamanian routes between South and North America. Background data and imaging courtesy of NOAA Satellite and Information Service (Amante & Eakins 2009). **2,** Detailed plate structure associated with this topography based the *Plate Boundary Model PB2002* (Bird 2003). Courtesy of Peter Bird.

Cenozoic climate and vegetation of North America

Eocene to Pliocene (33.9-2.588Ma). Before the onset of Pleistocene glaciation, the climate of North America was at times warm and humid. Retallack (2007) studied carbonate nodules in paleosols deposited over the last 40My in the Western United States, and identified a number of warm-wet climatic intervals (late Eocene 35Ma, middle Miocene 16Ma, late Miocene 7Ma, and early Pliocene 4Ma).

A more comprehensive view of the timing of global climate change during the Cenozoic is based on a compiliation of global stable isotope data, based on sea-bottom core samples of foraminifers of known genus and species (Zachos *et al.* 2001, 2008). Charts based on the relative level of a heavy oxygen isotope [$\delta^{18}O$ (‰)] in these samples are shown in Figure 10. As noted by Zachos *et al.* (2001), cyclic changes in global temperature can be associated with cyclic (~10-100Ky) changes in the Earth's orbit and the longer term effects of plate tectonics which have radically altered the pattern of ocean circulation. After an even warmer Mesozoic followed by cooling, temperatures began to rise in the Paleocene, peaking in the early Eocene, and than dropping. There was a precipitous temperature drop at the end of the Eocene, followed by late Oligocene and middle Miocene peaks. Since that time temperatures have gradually dropped, but the shorter (~40Ky) and less extreme cycles of the Pliocene have now been replaced with the longer (~100Ky) and more extreme cycles of the Pleistocene and Holocene. This change coincides with the completion of the Panamanian land bridge (~2.5-2.3Ma). It is important to realize that the temperature changes that have moved us from a global 'hot house' to an 'ice box' climate do not represent a steady transition, but rather a series of temperature cycles of variable magnitude and duration. At times during the early Pliocene (5-4Ma), for example, Arctic temperatures were 14.2°C warmer than they are today (Ballantyne *et al.* 2006).

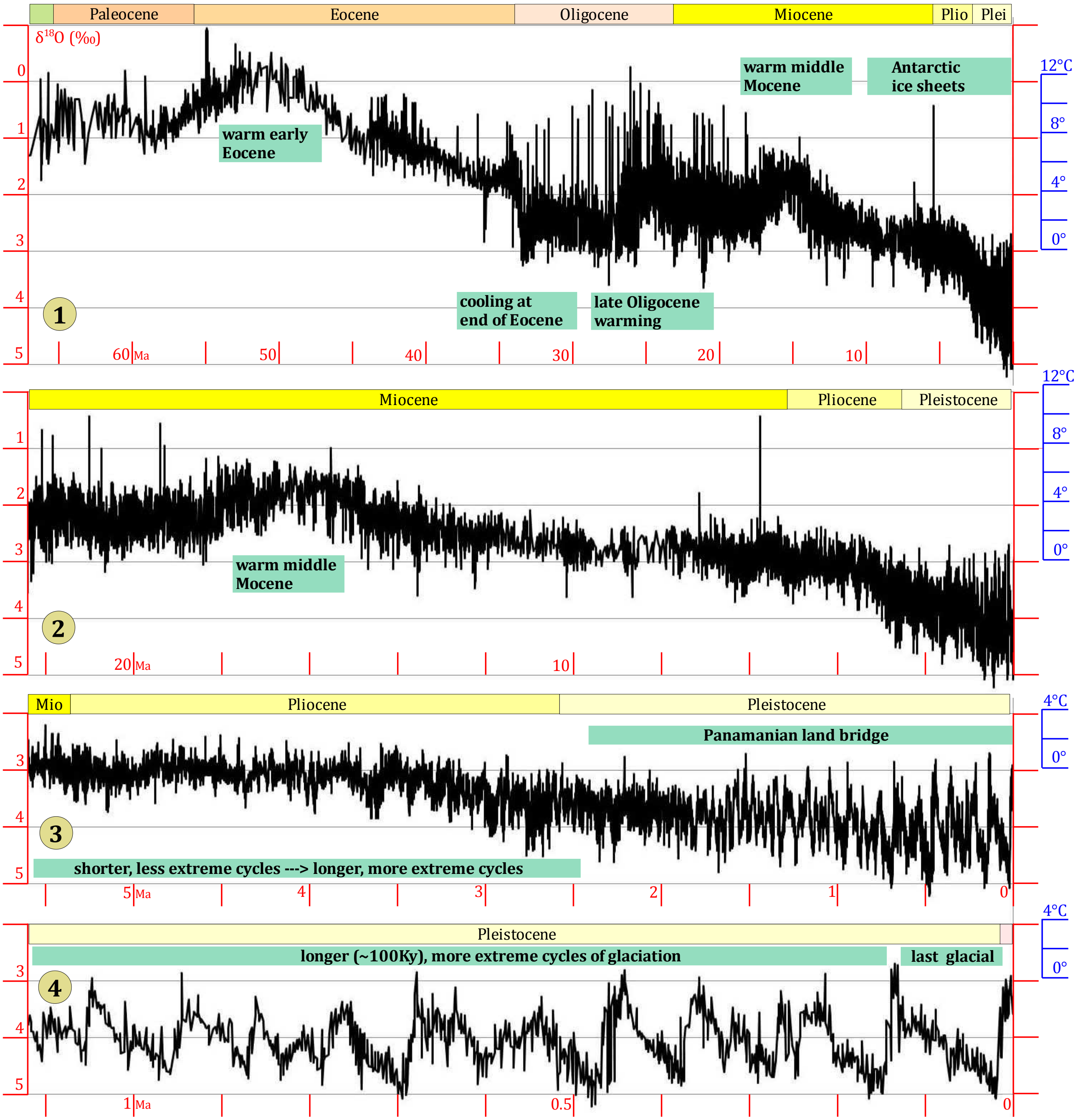


Figure 10. Cyclic warming and cooling during the Cenozoic, based on δ^{18}O levels associated with foraminifers in carbonate-rich deep-sea core samples, after Zachos *et al.* (2001). Original data contributed by Jim Zachos (14,888 data points from 40 localities; Zachos *et al.* 2008) was used to generate these charts. Measured δ^{18}O level is shown to the left of each chart, and the corresponding benthic temperature anomaly (relative to present) is shown at the right (blue axis). This estimate of relative benthic temperature is based on an ice-free ocean, and is only accurate for periods when Antarctica was not covered by large glaciers. **1,** Cenozoic era. After a warm interval in the early Eocene, temperatures declined steadily until a sudden drop at the end of the Eocene, associated with the isolation of Antarctica from South America and Australia, and the isolation of that continent by circum-Antarctic currents. The late Oligocene and middle Miocene were also periods of relative warming, but with much more variation or cycling from warm to cool periods. After the middle Miocene average temperatures continued to cool at a more rapid rate, associated with formation of polar ice sheets. **2,** Neogene (Miocene to present). This shows the global temperature drop after the late Miocene, again with many cycles of warming and cooling. **3,** Pliocene and Pleistocene. Shorter (~40Ky) and less extreme temperature cycles of the Pliocene were followed by longer (~100Ky) and more extreme cycles of Pleistocene. **4,** Detail of the last 1M years of the Pleistocene, showing regular temperature cycles (~100Ky).

Pleistocene to Holocene (2.588Ma to present). During the Pleistocene, both the severity and duration of glacial cycles has increased, from about 40Ky to 130Ky (Figure 9:3-4). At present we are at the warm end of the Wisconsin glacial cycle, a cycle that began about 130Ka. The peak of glaciation (last glacial maximum, or LGM) took place 22-15Ka, and warming has been relatively rapid since that time. But even this transition from the cool LGM (estimated 4-7°C temperature depression over tropical landmasses; Bush & Philander 1999) to the present has been interrupted by cooler episodes of shorter duration. The best known of these episodes, the *Younger Dryas event* (~12.9-11.6Ka), is associated with abrupt cooling over a span of at most several decades, followed by gradual warming over the next millennium. The actual cause of this cooling has not been resolved (Wunsch 2005, Brunelle 2007, Colman 2007, Firestone *et al.* 2007, Haynes Jr. 2008, Bakke *et al.* 2009, Surovell *et al.* 2009, Carlson 2010, Murton *et al.* 2010). These drastic climate changes must play a very important role in the distribution and evolution of North American Salticidae. Genera that have survived on this continent for 1My or longer have experienced many glacial cycles and thus many radical changes in the geographical extent of their optimal habitat.

Analysis of pollen deposits (Table 2) indicates that, from ~30Ka to the most recent flooding associated with rising sea level (late Wisconsin to present), the vegetation of Beringia was primarily cold and arid, a graminoid-herb tundra with some small woody plants (*Salix*, *Betula*, Ericales).

Table 2. Pollen deposits indicate that since about 30Ka, Beringia has been cold and arid (Ager 2003).

~30-26Ka	late middle Wisconsin interstadial	graminoid herb tundra, willows (*Salix*), dwarf birch (*Betula nana*), Ericales
26-15Ka	late Wisconsin glacial	graminoid herb tundra, willows, fewer dwarf birch, fewer Ericales, grasses (Poaceae) dominant
15-13Ka	current interglacial	spreading birch shrub-Ericales-sedge-moss tundra
11-9.5Ka	Younger Dryas interval	invasion of poplar and aspen (*Populus*)
9.5-0Ka	latest Wisconsion to present	Beringia flooded by rising seas, boreal forests dominated by spruce (*Picea*) in unflooded areas

^{14}C-dated pollen deposits from many localities in North America indicate that cool but unglaciated areas of Alaska and Beringia were dominated at the LGM (21Ka) by tundra species similar to those presently found in Alaska and northern Canada. The cool boreal forest (Taiga) that now dominates much of Canada extended as far south as central Missouri and North Carolina during the LGM (Figure 11).

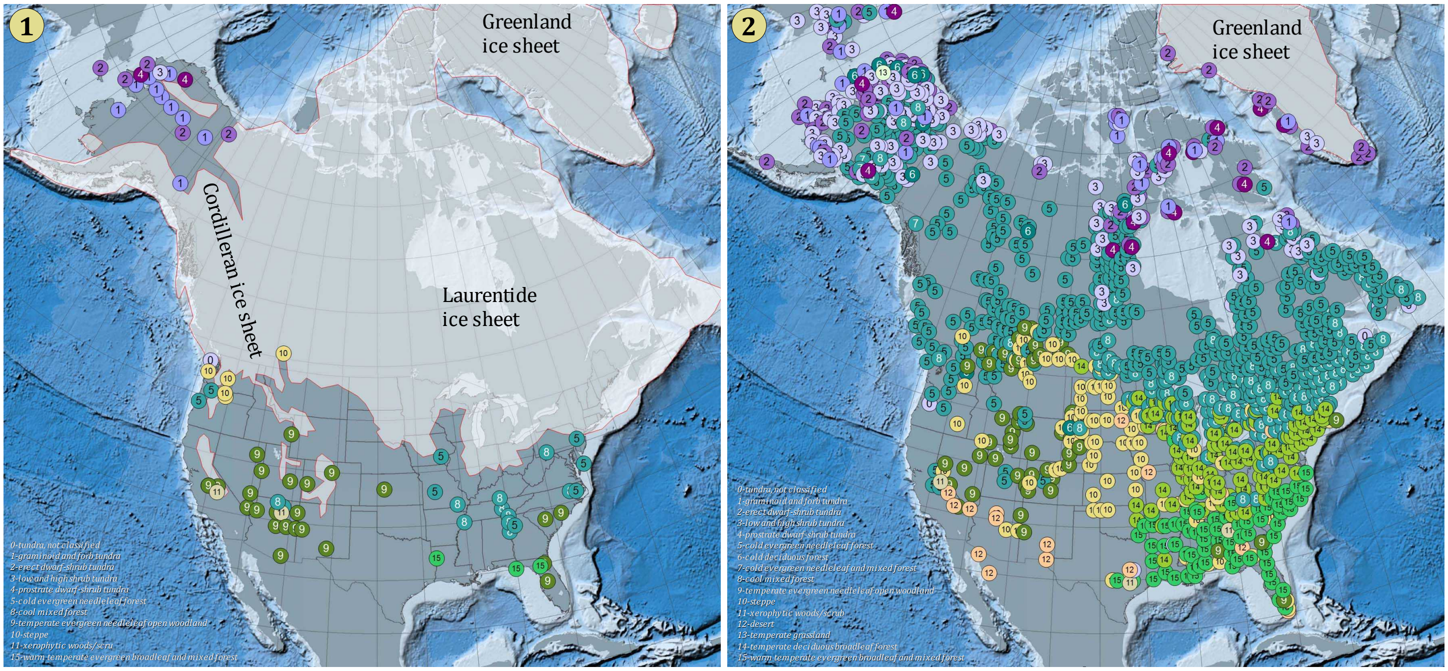


Figure 11. Plotted North American biomes by locality based on ^{14}C-dated pollen samples collected by the BIOME 6000 project (Prentice & Webb 1998, Edwards *et al.* 2000, Prentice *et al.* 2000, Thompson & Anderson 2000, Williams *et al.* 2000, Kaplan *et al.* 2003, BRIDGE 2012). **1,** LGM (21Ka) biomes. Unglaciated land area at this time included continental shelf areas. **2,** Present day biomes. Background maps were generated with the online mapmaker of the National Atlas of the USA.

The warmer eastern and southeastern forests that now figure greatly in the distribution of North American salticid species were relegated to a relatively narrow strip extending from a much wider Florida peninsula west toward Mexico along the northern shore of the Gulf of Mexico during the LGM. Jackson *et al.* (2000) characterized the forests of southern Florida of 21Ka as open conifer forest dominated by a mixture of warm to temperate species of *Pinus*. The Holocene (12-0Ka) should be viewed as an epoch of fairly rapid range expansion as entire biomes shifted to the north, following the melting of the continental glaciers (Overpeck *et al.* 1992, Prentice *et al.* 2000, Williams *et al.* 2004).

A growing human population continues to change the land cover of North America (Figure 12). All biomes are affected by this change, but the most drastic change has been the replacement of almost all of the tallgrass or eastern prairie lands by intensively cultivated croplands in the midwest, and by a combination of croplands and forest in other areas where grasslands are no longer maintained by grazers and natural fires (Smith 2001). For salticid species associated with either the tallgrass prairies, or with prairie-forest margins, the loss of this important habitat may have a profound impact on distribution. In addition, a warming trend in our climate continues to alter plant hardiness zones, and this can also be expected to have a major impact on the distribution of both native and introduced plants (McKenney *et al.* 2007).

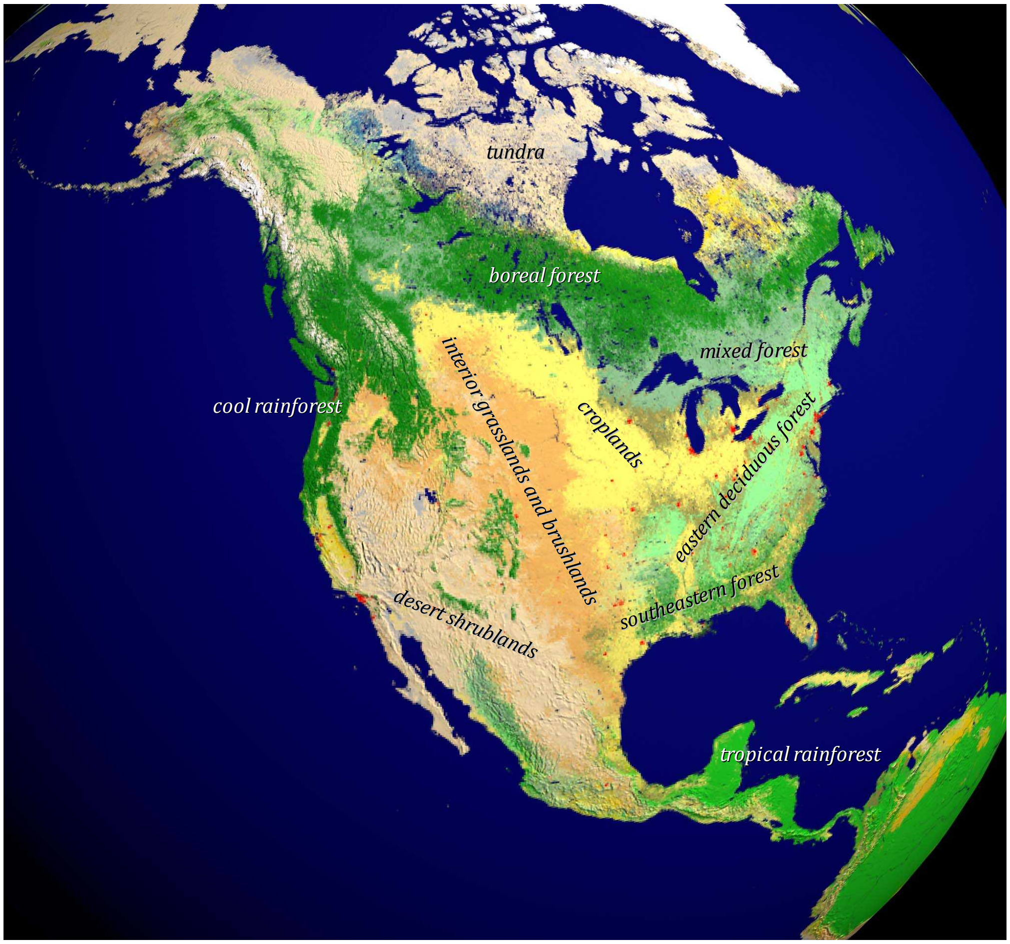


Figure 12. Current land cover of North America, showing major biomes. Croplands (light yellow) have almost entirely replaced the tallgrass prairies of this continent over the last 200 years. Many areas of drier shortgrass prairie (*interior grasslands and brushlands*) have also been replaced more recently through the use of well-water irrigation to support croplands. The color-keyed land cover map shown here was developed at Boston University with data supplied by the MODIS instrument on NASA's Terra satellite, collected NOV 2000-OCT 2001 (NASA Earth Observatory 2012).

Other relevant biogeographical studies

Paleocene-Eocene links between Neotropical, North American and Eurasian biota. Based on the estimated dates of origin for modern North American salticids (Figure 1), we have not looked closely at the early Cenozoic. There is good evidence for the successful movement of many species between South America, North America, and Eurasia at this earlier time, and these include many important ancestors of the modern flora and fauna of North America (Table 3). In the early Cenozoic, there may also have been a direct land route between Europe and North America. At the end of the Cretaceous, the continental shelves of North America and Europe were contiguous, but have been moving apart ever since (Torsvik *et al.* 2001). Graham (1999) placed the opening of a seaway between Norway and Greenland at 55Ma. If there was a salticid or proto-salticid fauna in the Paleocene and Eocene of Eurasia, there was no barrier to movement of this fauna between Eurasia and North America at that time. As noted previously, if this earlier fauna did live in North America at one time, we find no evidence of it now.

Table 3. Studies related to species introductions between the Americas and Eurasia in the Paleocene-Eocene.

Timeframe	Hypothetical events	References
~60 and 34-31Ma	Divergence of tropical Malpighiaceae with South American origin (~68Ma) after migration to North America and then to Europe over a *boreotropical* North Atlantic Land Bridge	Davis *et al.* 2002, 2004, Zhou *et al.* 2006
~57Ma	First introduction of leptodactylid frogs (*Eleutherodactylus*) from South to North America	Crawford & Smith 2005
~55.8Ma	Movement of primate *Teilhardina* between Asia, North America and Europe	Smith *et al.* 2006, Beard 2008
~51Ma	*Eomerope* (Mecoptera) crossed Beringia between northeastern Asia and western North America in either direction	Archibald *et al.* 2005
~50.9Ma	*Alligator* diverged from Neotropical *Caiman* ~74.9Ma, followed by divergence of American and Chinese *Alligator* species ~50.9Ma	Wu *et al.* 2003
49-47Ma	Two introductions of land-breeding eleutherodactyline frogs from South to North America	Heinike *et al.* 2007
~45Ma	Second introduction of leptodactylid frogs (*Eleutherodactylus*) from South to North America	Crawford & Smith 2005
42-36Ma	High latitude divergence of Asian and North American Magnoliaceae	Azuma *et al.* 2001
40-32 Ma	Overland dispersal of lizards (*Ctenonotus, Deiroptyx, Xiphosaurus*) across a fused North Antillean land mass (Cuba + Hispaniola + Puerto Rico)	Nicholson *et al.* 2012
35-33Ma	Introduction of a single species of *Selenops* (Selenopidae) from South America to the Antilles	Crews & Gillespie 2010

Oligocene-Pliocene introductions. Many species moved between Eurasia and North America, and between North and South America, at this time. Published plant and animal studies based on current distribution and estimated 'molecular clocks' (Table 4) point to the importance of species introductions during the warm middle Miocene (18-15Ma) when the east Asian and North American biota were very similar.

Table 4. Studies related to species introductions between the Americas and Eurasia in the Oligocene-Pliocene.

Timeframe	Hypothetical events	References
32.9-32.3Ma	Divergence of Asian *Sabacon* from sister group in western North America, and divergence of European *Sabacon* from sister group in eastern North America (Arachnida: Opiliones: Dyspnoi)	Schönhofer *et al.* 2013
30-20Ma	Divergence of eastern Asian (Japanese) and North American clades of *Hamamelistes* and *Hormaphis* (Hemiptera: Aphididae)	von Dohlen *et al.* 2002
27Ma	Dispersal of natricine snakes from Eurasia into North America via Beringia	Guo *et al.* 2012
25.2Ma	Divergence of North American *Calocedrus decurrens* (Cupressaceae) from Eurasian members of this genus	Chen *et al.* 2009
25-20Ma	Single introduction of North American rat snakes (monophyletic northwestern Lampropeltini) from Asia through Beringia	Burbrink & Lawson 2007
Miocene	Introduction of *Eumeces* and *Scincella* (Scincidae), *Ophisaurus* (Anguidae), and *Rana* (Ranidae) into North America from Asia through Beringia	Macey *et al.* 2006
16-12Ma	Divergence of Eurasian (four other pteromyid genera) and New World (*Glaucomys*) flying squirrels (Sciuridae: Pteromyinae)	Mercer & Roth 2003, Arbogast 2007
16-10Ma	Divergence of east Asian *Liriodendron chinense* from eastern North American *L. tulipifera* (Magnoliaceae)	Parks & Wendel 1990, Xiang *et al.* 2000
20-5Ma	Divergence of 7 different North American *Bombus*-group (bumblebees, Bombini) clades from ancestral Eurasian groups	Hines 2008
15-7Ma	Divergence of 2 different South American *Bombus*-group (bumblebees, Bombini) clades from ancestral North American groups	Hines 2008
~14Ma	Introduction of dipsadoid snakes (Dipsadidae, Xenodontidae) into North America through Beringia	Pinou *et al.* 2004
mostly since 10Ma (18-0.3Ma)	Divergence of many east Asian and eastern North American flowering plants (*Campsis, Caulophyllum, Cornus, Decumaria, Menispermum, Mitchella, Pachysandra, Pethorum, Podophyllum*)	Xiang *et al.* 2000
13-10Ma	Divergence of Chinese *Castanea mollissima* and American Chestnut *C. dentata*	Dane *et al.* 2003
7-2Ma	Divergence of 4 different South American *Bombus*-group (bumblebees, Bombini) clades from ancestral North American groups	Hines 2008
7-2.5Ma	Divergence of Central American subclade (*mermeria* group) of *Taygetina* from South American species (Nymphalidae: Satyrinae: Euptychiina)	Matos-Maraví *et al.* 2013

~6.73Ma	Divergence of Central and South American *Crotalus* rattlesnakes from ancestral North American *Crotalus* species	Wüster *et al.* 2005
6.6-1.4Ma	Divergence of east Asian and eastern North American *Phryma* (Phrymaceae), after a North American origin of the genus	Xiang *et al.* 2000, Nie *et al.* 2006
~5Ma	Introduction of odocoileine deer into North America via Beringia after Eurasian origin of this group 12.4-9.3Ma	Miyamoto *et al.* 1990
4-0Ma	Divergence of 3 different Eurasian *Bombus*-group (bumblebees, Bombini) clades from ancestral North American groups	Hines 2008
~3.74Ma	Divergence of three eastern North American *Zizania* species from one eastern Asian species associated with migration through Beringia	Xu *et al.* 2010
~3Ma	Divergence of new howler monkey species in Yucatan (*Alouetta pigra*) from the South American *A. palliata*	Cortés-Ortiz 2003

Impact of land bridges on Pleistocene-Holocene biota. The study of marine fauna complements geological studies of the age of the land bridges that have connected North America to other continents. Late Cenozoic deposits indicate the migration of molluscs between the Arctic and Pacific Oceans at times when Beringia was submerged in the late Miocene and Pliocene (5.5-4.8, 4.0, 3.5, and 2.7-2.14Ma), and the absence of marine mollusc migration when sea levels fell in the late Pleistocene (Taldenkova 2000). The divergence of marine gastropods (*Conus*) in the Western Atlantic and Eastern Pacific can be correlated with the emergence of the Isthmus of Panama (Duda & Kohn 2005). Completion of the Panamanian Land Bridge has also closed off westward circulation of warm water from the Atlantic into the Pacific via a north circumtropical current, converting this to a Caribbean Current that feeds the Gulf Stream flowing northward along the eastern coast of North America (Figure 13; Iturralde-Vinent & MacPhee 1999). This circulation of water and overlying air masses is responsible for the relatively high humidity and rainfall of eastern North America, and it also moderates the cold continental winter climate in coastal areas. In addition, it provides a vehicle for the air-borne and water-borne transport of biota from South America through the Caribbean to the shores of North America.

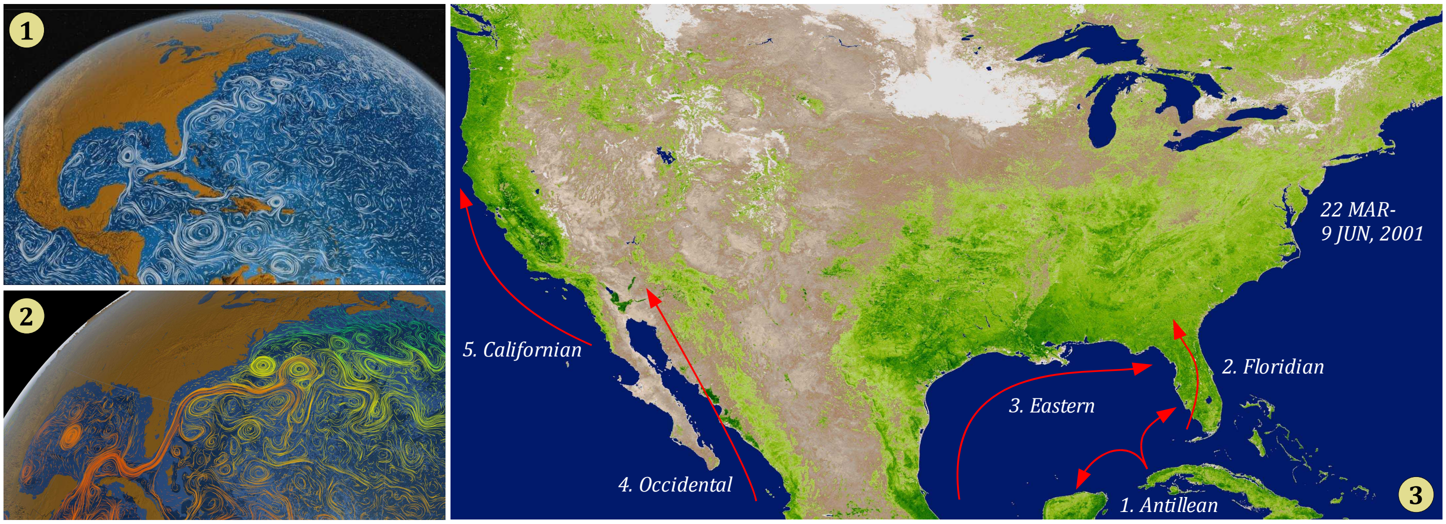


Figure 13. Physical factors affecting present-day climate of North America. **1,** White lines show the complex circulation of the Caribbean, with many clockwise gyres, moving westward along the northern coast of South America toward Yucatan. **2,** Color-coded (orange is warmer) view of circulation in the northwestern Atlantic, showing the powerful Gulf Stream that carries warm, tropical surface water along the eastern coast of North America. **3,** *Enhanced Vegetation Index* satellite image of temperate North America near the spring equinox, with concentration of chlorophyll indicated by the intensity of green. Western forests, high-altitude mountain forests in the west, and boreal forests to the north are predominantly comprised of needle-leaved evergreens. Five possible routes of post-glacial repopulation of North American fauna from warmer areas to the south through areas of persistent vegetation are labeled: 1) an over-water *Antillean* route, with much smaller gaps at the glacial maximum (Figure 7), 2) a *Floridian* route, 3) an *Eastern* route connecting the tropical rainforests of southern Mexico and Central America directly to eastern forests, 4) an *Occidental* route connecting the west coast of Mexico to the vegetation of the Sonoran and Chihuahan 'deserts', and 5) a *Californian* route along the west coast. Background images (1-2) taken from NASA Perpetual Ocean video frames, satellite background image (3) generated by the NASA Earth Observatory.

Since the early Pleistocene (2.588-0Ma), Beringia (except during glacial minima and maxima) and the Panamanian Land Bridge have provided almost continuous land routes from North America to South America and Eurasia. The massive biotic upheaval or *great American biotic exchange* associated with migration of terrestrial species in both directions across the Panamanian Land Bridge is well known (Stehli & Webb 1985, Downes and Kavanaugh 1988). The major barrier to intercontinental dispersal at this time has been based on climate, which is presently about as warm as it has ever been during the Pleistocene. Successful entry of tropical species into North America from the south has required that they either adapt to extremely arid conditions, or to high latitude variations in day-length and seasonal temperature, or to both. To the north, a much poorer salticid fauna is present, providing fewer opportunities for introduction in either direction between North America and Asia. Pleistocene-Holocene continuity of Beringia has also resulted in a Holarctic distribution for many recent mammalian species (*e.g.*, *Canis lupus*, *Vulpes vulpes*, *Castor fiber*, *Microtus gregalis*, *Cervus elaphus*; Rausch 1963).

Distribution and origin of the North American salticid clades

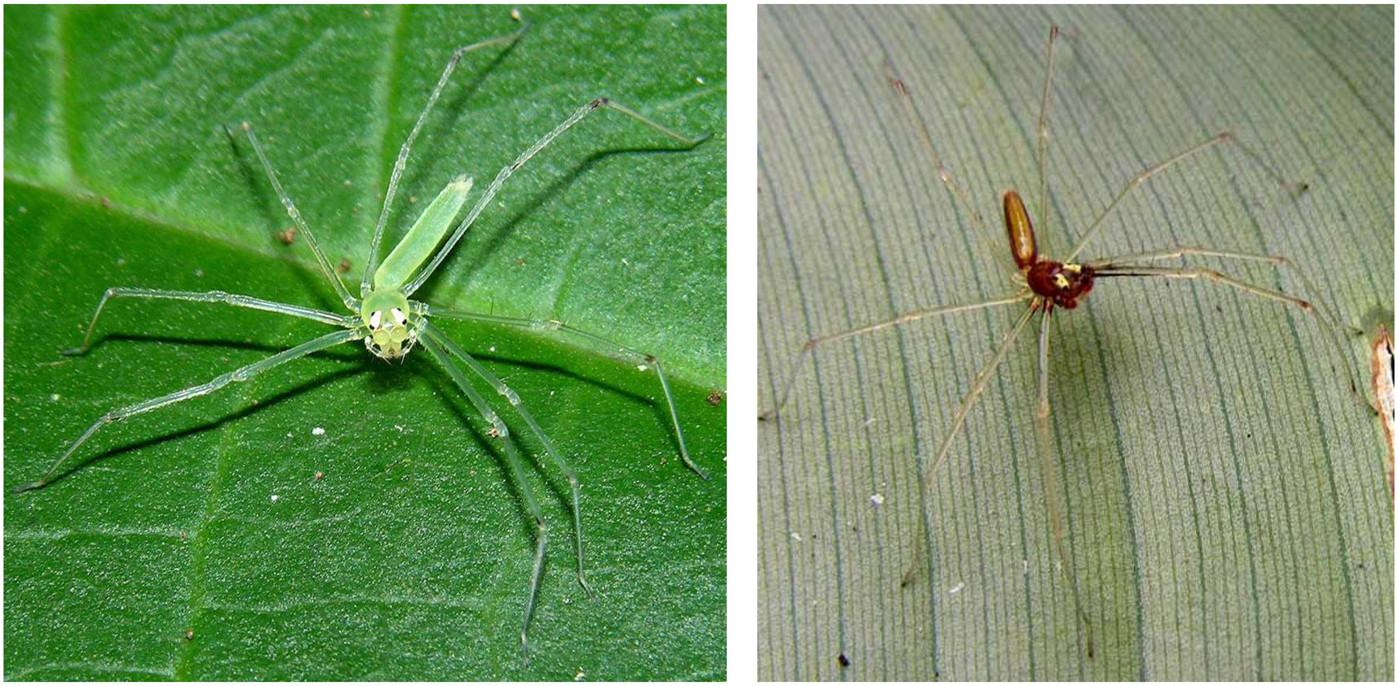
In the tables presented in this section, species found in more than one area are included in the tally for both areas. Counts are based on species listed in Platnick (2012) and Richman et al. (2012), modified in some cases by unpublished data available to the authors. Subgroups which are part of the North American fauna are included in individual tables. An asterisk precedes recently introduced species, not native to the region, followed by the number of species in that genus that are introduced. Some genera with uncertain placement have been omitted from this review.

Lyssomaninae. Despite a superficial resemblance to the *Asemonea-Goleba* clade, previously thought to be Old World lyssomanines, it is now thought that the New World Lyssomaninae are more closely related to other non-salticoid basal groups (Bodner & Maddison 2012). Only one genus, *Lyssomanes* (Table 5), has been found in North America. The greatest diversity of lyssomanines in general and *Lyssomanes* in particular is found in tropical South America, indicating a probable Neotropical origin for this group. The diversity of *Lyssomanes* (11 species) in Mexico is relatively high, although only 6 known species are actually endemic to that area, and a number of 'Mexican' species range well into South America. There are relatively few species known from the Caribbean. This genus has a long history in southern Mexico, dating back at least 23-15Ma (Oligocene-Miocene) in Chiapas (García-Villafuerte & Penney 2003), but only one subtropical species, *Lyssomanes viridis* (Walckenaer 1837), has extended its range into temperate North America. Based on the fossil record and a published estimate of the age of this group (41.4-31.2Ma; Bodner & Maddison 2012) we can hypothesize a late Eocene to early Oligocene (40-20Ma) introduction of *Lyssomanes* into North America from South America, by way of either the Antilles or the Central American Volcanic Arc. If the group proves to be older than this estimate, it could have crossed the Antillean Volcanic Arc when it was positioned to the west relative to its current position. There is also a possibility that the recent North American species are more closely related to recent South American species than to fossils from *Chiapas*, and in this case their introduction may have taken place at a much later time.

Table 5. Genera of Lyssomaninae. In this and in subsequent tables of genera, counts of species are given by region, with the regions of highest diversity highlighted (Palaearctic in purple, North America in yellow, Neotropical regions in green).

Lyssomaninae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Chinoscopus Simon 1901			1		4
Lyssomanes Hentz 1845		12	19	4	52

Both *Chinoscopus* (endemic to South America) and *Lyssomanes* are long-legged, with the ALE positioned well behind the AME (Figures 14-15).



1, ♀ *Chinoscopus flavus* (Peckham, Peckham & Wheeler 1889), Panama.

2, ♂ *Chinoscopus flavus*, Panama. Note the relatively small pedipalps.

3, ♂ *Chinoscopus* sp. (Panama?).

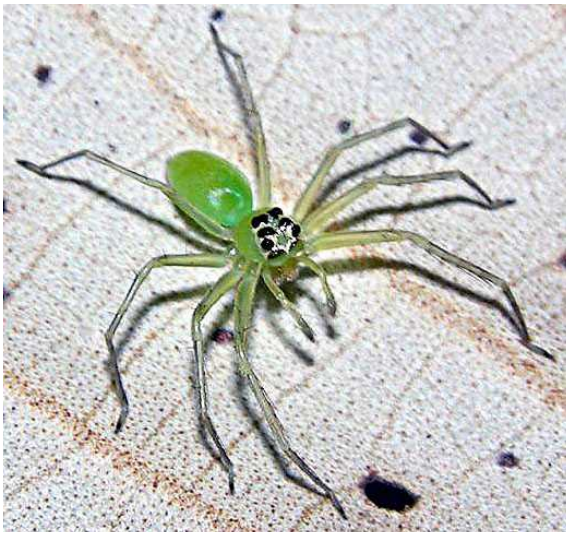
4, ♀ *Lyssomanes* sp, Copan, Honduras.

5-6, ♂ *Lyssomanes* sp. (Ecuador?) with ant-like abdomen and relatively large PME.

Figure 14. Neotropical Lyssomaninae. *Chinoscopus* (1-3) have very long, thin legs and males have small pedipalps. Photos by Dr. Arthur Anker, Florida Museum of Natural History, used with permission.

1, ♀ *Lyssomanes viridis* (Walckenaer 1837), southern Greenville County, South Carolina, 26 MAY 2011.

2, ♂ *L. viridis*, southern Greenville County, South Carolina, 20 MAY 2011.



3, *Lyssomanes* sp., Rio Urubu, Brazil.

4, ♀ *Lyssomanes* sp., Panama.

5, ♂ *Lyssomanes* sp., Copan, Honduras.

6, ♂ *Lyssomanes* sp., Cenote Xbatun near Merida, Yucatan.

Figure 15. More *Lyssomanes*. The type species of this genus, *L. viridis* (1-2), is atypical in that it has a subtropical to mild temperate distribution in the southeastern United States. Photos (3-6) by Dr. Arthur Anker, Florida Museum of Natural History, used with permission.

Amycoida. This is a large clade that represents a sister group to all other Salticoida. All amycoid groups are either confined to or most diverse in South America, with a few exceptions, so that a Neotropical origin of the group is quite likely. Here we treat the Sitticinae, Synemosyninae, Thiodininae, and remaining amycoid genera separately.

Sitticinae. Most sitticine genera are South American. Of the two genera found in North America, only *Sitticus* Simon 1901 is important in terms of distribution and number of species (Table 6). The greatest modern diversity of this group is Palaearctic. In fact, almost half of the North American species (7) are also found in the Palaearctic, and more are closely related to Palaearctic species. Although the sitticines almost certainly originated in South America where their diversity is greatest, an ancestor of *Sitticus* may have traversed North America en route to Asia, where the genus may have originated. In this case, the modern North American species would represent one or more groups with an Asian origin, the ancestors of which crossed back over Beringia to North America, and possibly later into South America (although there is some question as to the proper generic placement of the South American species).

Table 6. Genera of Sitticinae. The North American fauna includes 3 species of *Sitticus* recently introduced from Eurasia (indicated as **3* here).

Amycoida: Sitticinae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Aillutticus Galiano 1987					8
Amatorculus Ruiz & Brescovit 2005					2
Attulus Simon 1889	1				
Capeta Ruiz & Brescovit 2005					2
Gavarilla Ruiz & Brescovit 2006					2
Jollas Simon 1901			2	4	7
Nosferattus Ruiz & Brescovit 2005					5
Pseudattulus Caporiacco 1947					2
Semiopyla Simon 1901		1	1		3
Sitticus Simon 1901	60	17 *3			6

A South American origin of this genus is also possible. Bodner & Maddison (2012) estimated the divergence of *Jollas* from *Sitticus* at 17.1Ma, and the divergence of *S. floricola palustris* (Peckham & Peckham 1883) from a South American (Ecuadorean) *Sitticus* at 12.6Ma. These estimates are consistent with a mid-Miocene origin of *Sitticus* in South America, followed by a later Miocene introduction of the genus into North America. Subsequently, there have been many opportunities for species to move in either direction between Eurasia and North America. A more detailed study of the molecular phylogeny of the genus should be able to resolve many related questions.

The only North American species of *Semiopyla* (*S. cataphracta* Simon 1901) ranges from the extreme south of Mexico into South America (Richman *et al.* 2012, Platnick 2012). This genus and species are clearly Neotropical, and the movement of this single species into southern Mexico may have taken place long after the closing of the Panamanian Land Bridge (2.5-2.3 Ma).

Sitticus (Figure 16) are compact spiders with many setae and generally cryptic coloration; the Neotropical sitticines are much more diverse in form and many resemble other amycines with relatively longer legs and fewer setae.

1, ♀ *Sittius pubescens* (Fabricius 1775), Concord, Massachusetts.

2, ♀ *S.* cf. *floricola* (C. L. Koch 1837), 22 JUN 2011, between Faversham and Whitstable, England.

Figure 16. *Sitticus* (Sitticinae) from North America and Europe. Most *Sitticus* are Palearctic, but *S. pubescens* and *S. floricola* are both Holarctic. Photo credits: (1) by Dick Walton, (2) by Phil Warner, both used with permission.

Synemosyninae. These ant-like amycoids are also mostly confined to the Neotropics, where all genera are most diverse (Table 7, Figure 17). *Martella lineatipes* F. O. Pickard-Cambridge 1900 has only been found in extreme southern Mexico (Tabasco) and ranges into Central America (Richman *et al.* 2012, Platnick 2012), so this appears to be a recent arrival. Two species of the related *Sarinda* occur in North America, the widespread *S. hentzi* (Banks 1913) and the western *S. cutleri* (Richman 1965). *Synemosyna* is the only diverse genus from the group in North America, but only one species (*S. formica* Hentz 1846) is widely distributed in eastern North America, and the rest are primarily confined to southernmost Mexico. With this lack of diversity, it is possible that the first crossing of this group into North America came after the closing of the Panamanian Land Bridge (2.5-2.3 Ma). One species, *S. petrunkevitchi* (Chapin 1922) is found only in Florida and the Greater Antilles.

Table 7. Genera of Synemosyninae. All are primarily Neotropical in distribution.

Amycoida: Synemosyninae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Corcovetella Galiano 1975					1
Erica Peckham & Peckham 1892			1		1
Fluda Peckham & Peckham 1892			1		10
Martella Peckham & Peckham 1892		1	4		9
Parafluda Chickering 1946			1		1
Pseudofluda Mello-Leitão 1928					1
Sarinda Peckham & Peckham 1892		2	5	1	12
Simprulla Simon 1901			1		1
Synemosyna Hentz 1846		6	6	2	12
Zuniga Peckham & Peckham 1892			1		2

1-2, Feeding ♀ *Sarinda hentzi* (Banks 1913), southern Greenville County, South Carolina, (1) 10 JUL 2010, (2) 8 JUL 2010. Scale = 1.0 mm.

3-4, *Synemosyna* sp. (3) and similar ant from same locality (4, *Pseudomyrmex* cf. *gracilis*), Costa Rica.

Figure 17. Synemosyninae. Photos (3-4) by Bernhard Jacobi, used with permission.

Thiodininae. Only one species of *Cotinusa* occurs in southern Mexico, and three species of *Thiodina* are widespread (two in the east, one in the west) in southern North America (Richman *et al.* 2012, Hill 2012). All represent more diverse Neotropical genera (Table 8). Bodner & Maddison (2012) estimated divergence of *Thiodina* from another genus in this subfamily at 19.9Ma. The three North American species are widely distributed in warmer parts of the continent, and are similar to Neotropical species (Hill 2012). With three Caribbean species, over-water introduction from South to North America as early as the Miocene is possible, but a more recent introduction of modern species over the Panamanian Land Bridge is supported by the similarity of North and South American species of *Thiodina.* (Figures 18-19).

Table 8. Genera of Thiodininae.

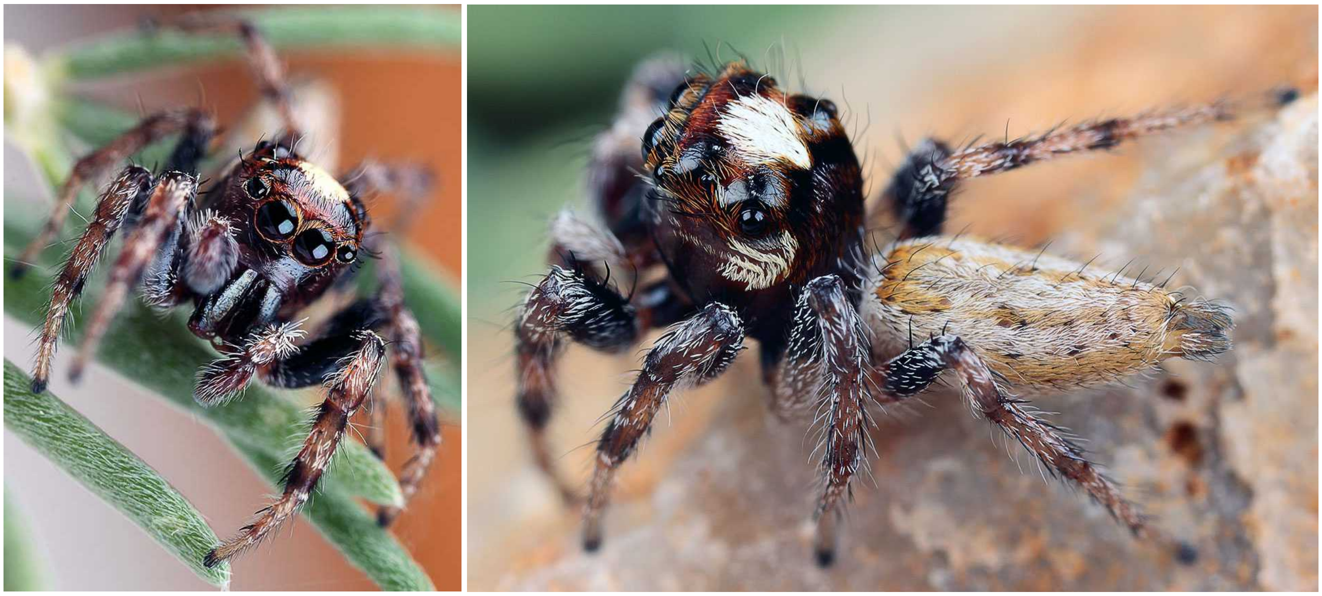
Amycoida: Thiodininae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Banksetosa Chickering 1946			2		
Carabella Chickering 1946			2		
Cotinusa Simon 1900		1	3		27
Parathiodina Bryant 1943				1	
Thiodina Simon 1900		3	3	3	12

1, ♂ *Thiodina sylvana* (Hentz 1846), southern Greenville County, South Carolina, 4 OCT 2012.

2, ♀ *T. sylvana* feeding on young mantid, southern Greenville County, South Carolina, 3 MAY 2011.

3, ♂ *T. puerpera* (Hentz 1846), southern Greenville County, South Carolina, 17 OCT 2011.

4, ♀ *T. puerpera* feeding on spider, southern Greenville County, South Carolina, 10 MAY 2011.



5-6, ♂ *T. hespera* Richman & Vetter 2004, Arizona.

Figure 18. North American *Thiodina* species. Although similar in appearance, *T. sylvana* is an inhabitant of the forest understory and forest margins, while *T. puerpera* lives in mixed grass/herbaceous old field or tallgrass prairie. *T. hespera* is found in the southwest. Scale bars = 1.0 mm. Photos (5-6) by Gerardine Vargas, used with permission.

1, ♂ *Thiodina* cf. *sylvana*, Panama, rainforest.

2, ♂ *Thiodina* cf. *sylvana*, Copan, Honduras.

Figure 19. *Thiodina* species from Central America. Many Neotropical *Thiodina* species are similar to the three North American species, and these males closely resemble the widely distributed *T. sylvana*. Photos by Dr. Arthur Anker, Florida Museum of Natural History, used with permission,

Other amycoids. All of the remaining amycoid genera are Neotropical, with the exception of *Bredana* Gertsch 1936 (Table 9). The two known species of *Bredana* (*B. alternata* Gertsch 1936, *B. complicata* Gertsch 1936) have been found only in Texas. *Bredana* is very close to, and most likely synonymous with, a different South American genus (Edwards unpubl.). Thus all of the North American species shown here are probably the result of introductions from South America over the Panamanian Land Bridge. These include two species of *Acragas*, two species of *Cylistella*, one species of *Hypaeus* that ranges from South or Central America to the extreme south of Mexico, one Mexican *Amycus* from an unknown locality, and an undescribed species of *Cyllodania* from southern Arizona (U. S.).

Table 9. Other amycoid genera. Many of these have been placed in their own subfamily, the Amycinae.

Amycoida: others					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Acragas Simon 1900		2	9		13
Admesturius Galiano 1988					2
Agelista Simon 1900					1
Aillutticus Galiano 1987					8
Albionella Chickering 1946			1		
Amycus C. L. Koch 1846		1			10
Anaurus Simon 1900					1
Arachnomura Mello-Leitão 1917					2
Arnoliseus Braul 2002					2
Atelurius Simon 1901					2
Atomosphyrus Simon 1902					2
Breda Peckham & Peckham 1894			2		12
Bredana Gertsch 1936		2			
Ceriomura Simon 1901					2
Cylistella Simon 1901		2	4		3
Cyllodania Simon 1902		1	1		2
Encolpius Simon 1900					3
Frespera Braul & Lise 2002					2
Hurius Simon 1901					4
Hyetussa Simon 1902					6
Hypaeus Simon 1900		1	1		19

GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Macutula Ruiz 2011					3
Maenola Simon 1900					3
Mago O. Pickard-Cambridge 1882					14
Noegus Simon 1900			1		23
Scopocira Simon 1900			1		8
Scoturius Simon 1901					1
Simonurius Galiano 1988					4
Tanybelus Simon 1902					1
Titanattus Peckham & Peckham 1885			3		4
Toloella Chickering 1946			1		
Vinnius Simon 1902					4

The Amycoida is a very large and diverse Neotropical group (Figure 20). This is presently recognized as the sister group to all other Salticoida, with divergence estimated at 41.2Ma (mid-Eocene; Bodner & Maddison 2012). Given this long time line, the fact that this group is still almost entirely tropical with relatively few representatives in temperate North America is hard to explain. Even the highly successful North American *Thiodina* species are restricted to warmer or subtropical areas.

1, ♂ *Cotinusa* sp. (Thiodininae), Panama, rainforest.

2, ♂ *Amycus* sp., Ecuador, Amazon rainforest.

3, ♂ *Amycus* sp., Ecuador.

4, ♂ *Hypaeus* cf. *benignus* (Peckham & Peckham 1885), Panama, rainforest.

5, ♂ *Hypaeus* cf. *benignus*, Costa Rica.

Figure 20. Neotropical Amycoida. Photo credits: (1-4) by Dr. Arthur Anker, Florida Museum of Natural History, (5) by Bernhard Jacobi, all used with permission.

Marpissoida. We will consider the three major North American divisions of the Marpissoida (Dendryphantinae, Marpissinae, and Synagelinae) separately. The greater marpissoid clade (<2> in Figure 21) appears to have diverged from the Australasian Astioida near the end of the Eocene (~33.9Ma after Bodner & Maddison 2012). This may have occurred just before the breaking of the land bridges that spanned what is now the Southern Ocean to connect South America with Antarctica and Australasia (Hill 2009). The origin of the baviines, now found in southeast Asia and to a lesser extent in Australasia, is more problematic. These could represent the descendents of a marpissoid-like species (<2> in Figure 21) that lived in Australasia prior to the opening of the Southern Ocean. The Ballinae, now widely distributed with genera that are either primarily African or primarily south Asian, could represent the descendents of an early marpissoid species that was able to move from South America to Afro-Eurasia in the Oligocene. Either a trans-Atlantic or a trans-North American route of introduction could have been used by this balline ancestor. Although the greatest diversity and most likely origin of marpissoid groups is Neotropical, all are well-represented in North America, and there are several genera that have also diversified in the Palaearctic. This pattern suggests at least several early island arc or oceanic crossings of marpissoids from the Neotropics into North America, and then across Beringia into the Palaearctic region. In North America species derived from these introductions represent the most important part of the indigenous salticid fauna.

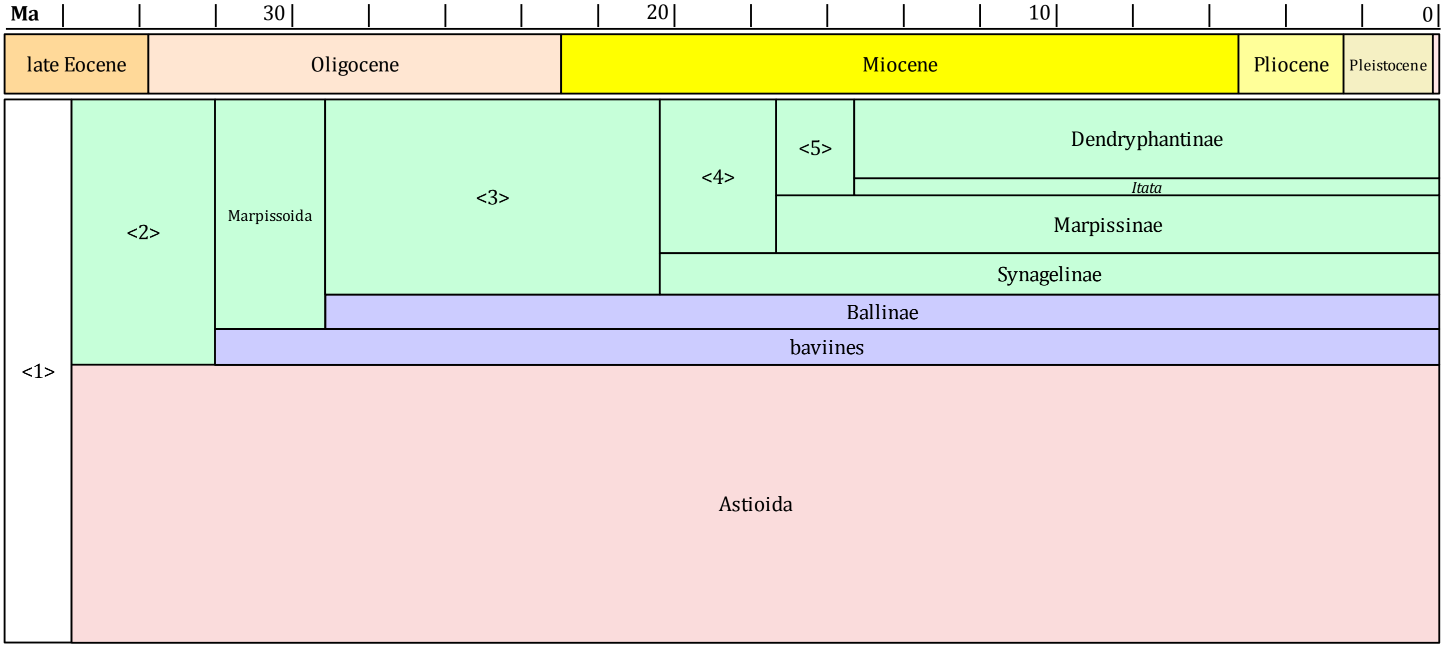


Figure 21. Later Cenozoic timeline showing the phylogenetic relationship of the Marpissoida and related groups to the Australasian Astioida (after Benjamin 2004, Fig. 8 in Bodner & Maddison 2012). Unnamed clades are indicated with numbers, thus <2> represents the sister group of the Astioida. According to Bodner & Maddison, divergence of the major marpissoid subfamilies in the Americas (shaded in green) probably took place during the Miocene after the earlier, Oligocene divergence of several smaller, presently Afro-Eurasian groups (baviines, Ballinae).

Dendryphantinae. With this subfamily we encounter many distinctly North American genera (Table 10). The greatest dendryphantine diversity is still Neotropical, in agreement with their likely origin in South America. Of the few Palaearctic genera, only *Dendryphantes*, with a disjunct presence in South America (probably species misplaced to genus) but only one North American species, poses a question of North American origin. Here we also exclude *D. pugnax* (C. L. Koch 1846), *D. strenuous* (C. L. Koch 1846) and *D. zygoballoides* Chamberlin 1924 which do not belong in this genus (Richman *et al.* 2012). It is also unlikely that the one species reported from the Caribbean region, *D. mendicus* (C. L. Koch 1846), belongs in this genus. The one North American species, *D. nigromaculatus* (Keyserling 1885), is found in alpine and boreal areas, a distribution that suggests a close affinity to the Palaearctic, and a relatively recent crossing into North America via the Bering Land Bridge (Beringia).

Table 10. Dendryphantine genera. This includes two new species of Central American *Bagheera* (Ruiz & Edwards 2013).

Marpissoida: Dendryphantinae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Alcmena C. L. Koch 1846		1			3
Anicius Chamberlin 1925		1			
Ashtabula Peckham & Peckham 1894		1	2		6
Avitus Peckham & Peckham 1896			1	1	4
Bagheera Peckham & Peckham 1896		2	3		
Beata Peckham & Peckham 1895		1	9	2	10
Bellota Peckham & Peckham 1892		2	1		4
Bryantella Chickering 1946			2		2
Chirothecia Taczanowski 1878					13
Dendryphantes C. L. Koch 1837	18	1			22
Donaldius Chickering 1946			1		
Eris C. L. Koch 1846		7	3	2	1
Gastromicans Mello-Leitão 1917			2		4
Ghelna Maddison 1996		4			
Hentzia Marx 1883		9	2	14	3
Lurio Simon 1901					4
Mabellina Chickering 1946			1		
Macaroeris Wunderlich 1992	5				
Mburuvicha Scioscia 1993					1
Messua Peckham & Peckham 1896		3	8		1
Metaphidippus F. O. Pickard-Cambridge 1901		15	22		11
Monaga Chickering 1946			1		
Nagaina Peckham & Peckham 1896		1	1		3
Naubolus Simon 1901					9
Osericta Simon 1901					2
Paradamoetas Peckham & Peckham 1885		3	3		
Paraphidippus F. O. Pickard-Cambridge 1901		12	7	1	
Parnaenus Peckham & Peckham 1896			2		2
Pelegrina Franganillo 1930		36	7	1	
Phanias F. O. Pickard-Cambridge 1901		10	1		
Phidippus C. L. Koch 1846		60	3		
Poultonella Peckham & Peckham 1909		2			
Rhene Thorell 1869	12				1
Rhetenor Simon 1902		1			1
Rudra Peckham & Peckham 1885			2		8
Sassacus Peckham & Peckham 1895		9	4		12
Sebastira Simon 1901			1		1
Selimus Peckham & Peckham 1901					1
Semora Peckham & Peckham 1892					4
Semorina Simon 1901					5
Tacuna Peckham & Peckham 1901					4
Terralonus Maddison 1996		7			
Thammaca Simon 1902					2
Tulpius Peckham & Peckham 1896			1		1
Tutelina Simon 1901		4			2
Tuvaphantes Logunov 1993	2				
Uluella Chickering			1		
Zeuxippus Thorell 1891	3				
Zygoballus Peckham & Peckham 1885		3	9	2	6

We can separate the North American dendryphantines into two groups: those that are widely distributed and relatively speciose in North America, indicative of an earlier or Miocene origin (Table 11), and those with a limited presence in North America and a modern distribution that is compatible with a recent crossing over the Panamanian Land Bridge from South America (Table 12). If we follow Richman's (2008) hypothesis that the *Sassacus arcuatus* group of South America may belong in a separate genus, then we can consider *Sassacus* to be a predominantly North American genus.

Table 11. Dendryphantine genera with a major presence in North America.

Eris C. L. Koch 1846	Four widely distributed species in North America.
Ghelna Maddison 1996	Four species endemic to eastern North America.
Hentzia Marx 1883	Seven species with two widely distributed in eastern North America. Diversity of this genus is centered in the Caribbean region.
Metaphidippus F. O. Pickard-Cambridge 1901	Clearly a Neotropical genus but with 15 species (likely misplaced) in North America, primarily in the southwest.
Paraphidippus F. O. Pickard-Cambridge 1901	Only one species of this Neotropical genus has a wide distribution in North America, *P. aurantius* (Lucas 1833). *P. basalis* (Banks 1904) is found in the southwest. Others are either Mexican with locality unknown, or from southern Mexico, except for one that ranges into southern Arizona.
Pelegrina Franganillo 1930	One of the most important North American genera, with 36 known species and a wide distribution.
Phanias F. O. Pickard-Cambridge 1901	Ten known species, largely confined to western North America.
Phidippus C. L. Koch 1846	One of the most important North American genera, with 60 known species (plus 9 other species misplaced here) and a wide distribution.
Poultonella Peckham & Peckham 1909	Only two species, one of which is widely distributed in southern North America.
Sassacus Peckham & Peckham 1895	Only nine species, but widely distributed.
Terralonus Maddison 1996	Known only from localities in central and western North America.
Tutelina Simon 1901	The four known species are widely distributed, from the southern United States into Southern Canada.
Zygoballus Peckham & Peckham 1885	The three North American species are widely distributed in eastern North America.

Table 12. Neotropical dendryphantine genera with a limited presence in North America

Alcmena C. L. Koch 1846	A single Mexican species, *A. amabilis* C. L. Koch 1846, Mexican locality unknown.
Anicius Chamberlin 1925	A single species in southern Mexico, *A. dolius* Chamberlin 1925.
Bagheera Peckham & Peckham 1896	Two species, one in Texas and both in southern Mexico.
Beata Peckham & Peckham 1895	A single species, *B. hispida* (Peckham & Peckham 1901) from Quintana Roo in extreme southeastern Mexico. *B. wickhami* (Peckham & Peckham 1894) belongs in a different genus (Richman *et al.* 2012)
Bellota Peckham & Peckham 1892	The two North American species are known only from Texas.
Messua Peckham & Peckham 1896	Two of the three North American species are from southwestern border states, the third from southern Mexico.
Nagaina Peckham & Peckham 1896	The single North American species is from southeastern Mexico.
Paradamoetas Peckham & Peckham 1885	Two species in southern Mexico and one in the Great Lakes region.

Representative dendryphantines are shown in Figures 22-33.

1-2, ♂ *Eris militaris*, southern Greenville County, South Carolina, 18 SEP 2009. Each scale = 1.0 mm.

Figure 22. Male *Eris militaris* (Hentz 1845), a widely distributed North American species.

1-2, ♀ *Eris militaris*, southern Greenville County, South Carolina, 01 APR 2011.

3, ♀ *Eris militaris*, southern Greenville County, South Carolina, 13 APR 2012.

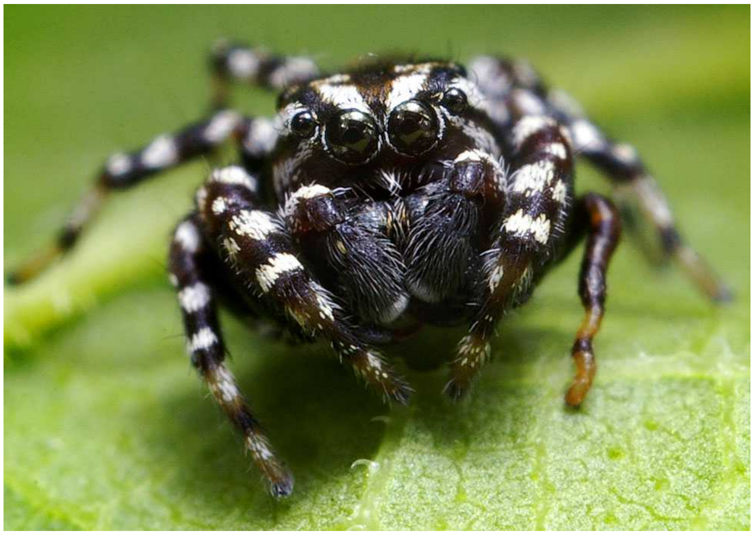
4, ♀ *Eris floridana* (Banks 1904), Concord, Massachusetts.

5, ♂ *Metaphidippus chera* Chamberlin 1924, Tucson, Arizona.

6, ♂ *Pelegrina pervaga* (Peckham & Peckham 1909), Norman, Oklahoma, 3 APR 2009.

Figure 23. North American *Eris*, *Metaphidippus* and *Pelegrina*. The wide distribution of *E. militaris* may be a result of the extensive use of 'ballooning' on draglines by this spider, even as an adult (Hill 1978, 2008). Maddison (1986) described several differences between *E. militaris* and *E. flava* (Peckham & Peckham 1888), but in practice it may still be difficult to distinguish between the two species. Each scale bar = 1.0 mm. Photo credits: (4) by Dick Walton, (5) by Gerardine Vargas, (6) by Thomas Shahan, all used with permission.

1, ♂ *Pelegrina galathea* (Walckenaer 1837), s. Greenville County, South Carolina, 7 JUL 2012.



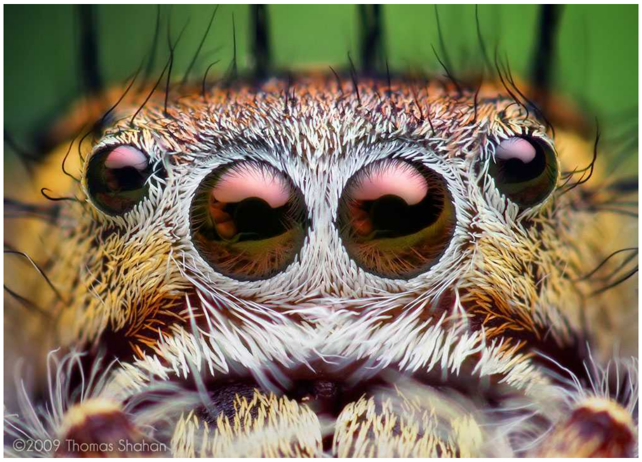
2, ♂ *Pelegrina galathea*, Oklahoma, 22 SEP 2005.

3, ♀ *Pelegrina galathea* (Walckenaer 1837), southern Greenville County, South Carolina, 7 JUL 2012.

4, ♂ *Paraphidippus aurantius* (Lucas 1833), Red Bud Valley Nature Preserve, Caloosa, Oklahoma, 22 JUL 2009.

5-6, ♂ *Paraphidippus aurantius*, southern Greenville County, South Carolina, 8 JUN 2008.

Figure 24. North American *Pelegrina* and *Paraphidippus*. Each scale bar = 1.0 mm. Photos (2, 4) by Thomas Shahan, used with permission.



1, ♀ *Phidippus putnami* (Hentz 1845) Oklahoma, 24 JUL 2009.

2, ♂ *P. putnami* (Peckham & Peckham 1883), Tulsa, Oklahoma, 3 AUG 2010.

3, ♂ *P. putnami*, s. Greenville County, South Carolina, 28 JUN 2012.

4, ♂ *P. mystaceus* (Hentz 1846), Oklahoma, 30 OCT 2011.

5-6, ♀ *P. mystaceus*, northern Laurens County, South Carolina, 24-25 OCT 2011.

Figure 25. North American *Phidippus* of the *putnami* and *mystaceus* groups (after Edwards 2004). Each scale bar = 1.0 mm. Photos (1-2, 4) by Thomas Shahan, used with permission.

1-2, ♀ *Phidippus cardinalis* (Hentz 1845), 9 OCT 2011.

3, ♂ *P. cardinalis*, 9 OCT 2011

4, ♂ *P. pius* Scheffer 1905, 5 JUN 2011.

5-6, ♀ *P. pius*, 4 JUN 2011.

Figure 26. Red *Phidippus* species from old fields in southern Greenville County, South Carolina. Both *P. cardinalis* and *P. pius* have dark iridescent blue to blue-green distal chelicerae. Edwards (2004) included *P. pius* in the *otiosus* group of this genus, and suggested that *P. cardinalis* was more closely related to *P. clarus*, the females of which also have dark pigmented bands on each leg segment. The two species shown here alternate generations in the same habitat in South Carolina, with *P. pius* maturing in the late spring, and *P. cardinalis* maturing in the fall. Scale = 1.0 mm.

1-2, Two different ♀ *Phidippus clarus* Keyserling 1885, southern Greenville County, South Carolina, (1) 6 AUG 2011, (2) 6 AUG 2012.

3, ♀ (left) with a grooming ♂ *P. clarus* after mating, southern Greenville County, South Carolina, 8 AUG 2011.

4, ♂ *P. whitmani* Peckham & Peckham 1909, Concord, Massachusetts.

5-6, ♀ *P. whitmani* (5) with female mutillid wasp (6, *Dasymutilla* sp.), leaf litter in forest understory near Rocky Creek, southern Greenville County, South Carolina, (5) 1 SEP 2011, (6) 2 SEP 2011.

Figure 27. North American *Phidippus*. *P. clarus* is perhaps the most widely distributed member of the genus. Females are quite variable in color, some with the male color pattern shown in (3). *P. whitmani* is a leaf-litter inhabitant and eastern representative of the *johnsoni* group (Edwards 2004), and like many *Phidippus* has the aposematic or warning coloration of mutillid wasps that share its habitat (Edwards 1984). Each scale bar = 1.0 mm. Photo (4) by Dick Walton, used with permission.

1, ♀ *Phidippus princeps* (Peckham & Peckham 1883), southern Greenville County, South Carolina, 17 SEP 2012.

2, ♀ *P. princeps* feeding on *Oxyopes salticus*, southern Greenville County, South Carolina, 15 SEP 2012.

3, ♂ *P. princeps*, northern Laurens County, South Carolina, 6 NOV 2011.

4, ♂ *P. pulcherrimus* Keyserling 1885, Screven County, Georgia, 28 OCT 2011.

5, ♀ *P. pulcherrimus*, Screven County, Georgia.

6, ♀ *P. pulcherrimus*, Screven County, Georgia.

Figure 28. Two closely related *Phidippus* (from the *audax* group of that genus after Edwards 2004) from the eastern United States. *P. pulcherrimus* is restricted to Florida and the southern parts of Alabama, Georgia and South Carolina. The allopatric *P. princeps* is widely distributed north of this range, in a region corresponding to the historical extent of the eastern deciduous forest. Each scale bar = 1.0 mm.

1, ♀ *Phidippus audax* (Hentz 1845) feeding on lycosid, Paris Mountain, Greenville County, South Carolina, 1 MAY 2011.

2, ♀ *P. audax*, southern Greenville County, South Carolina, 9 NOV 2011.

3, ♂ *P. audax*, northern Laurens County, South Carolina, 7 OCT 2012.

4, ♀ *Phidippus* sp., Tucson, Arizona.

5-6, ♂ *Phidippus* cf. *morpheus* Edwards 2004, Arizona.

7, ♀ *P. workmani* (Peckham & Peckham 1901), Archbold, Florida, 25 AUG 2012.

Figure 29. North American *Phidippus*. *P. audax*, the type species for the genus, is widely distributed in eastern to central North America. *P. workmani*, restricted to a few localities in the southeast, is also a member of the *audax* group within this genus (Edwards 2004). Photo credits: (4-6) by Gerardine Vargas, used with permission, (7) by Thomas Shahan, used with permission. Each scale bar = 1.0 mm.

1-2, ♂ *Hentzia palmarum* (Hentz 1832), Texas.

3, ♂ *H. mitrata* (Hentz 1846), Bixby, Oklahoma, 9 JUL 2009.

4, ♂ *H. mitrata*, southern Greenville County, South Carolina, 8 APR 2011.

5-6, Two different ♀ *H. mitrata*, southern Greenville County, South Carolina, 11 APR 2011 (5), 28 APR 2011 (6).

Figure 30. North American *Hentzia*. Photo credits: (1-2) by Gerardine Vargas, used with permission, (3) by Thomas Shahan, used with permission. Each scale bar = 1.0 mm.

1, ♀ *Tutelina elegans* (Hentz 1846), southern Greenville County, South Carolina, 29 JUN 2012.

2, ♂ *Tutelina elegans*, southern Greenville County, South Carolina, 30 JUN 2011.

3, ♂ *Tutelina elegans* feeding on mite, Oklahoma, 5 JUN 2010.

4, ♀ *Sassacus cyaneus* (Hentz 1846), s. Greenville Cty,, S. Carolina, 31 AUG 2011.

5, ♀ *Sassacus papenhoei* Peckham & Peckham 1895, s. Greenville Cty,, S. Carolina, 8 JUN 2012.

6-7, ♂ *Sassacus papenhoei*, southern Greenville County, South Carolina, 5 JUN 2012.

Figure 31. North American *Tutelina* and *Sassacus*. Richman recently (2008) transfered *S. cyaneus* to *Sassacus*. Each scale bar = 1.0 mm. Photo (3) by Thomas Shahan, used with permission.

1, ♂ *Zygoballus rufipes* Peckham & Peckham 1885, southern Greenville County, South Carolina, 20 AUG 2012.

2, ♂ *Z. rufipes*, Reimers Ranch Park, Travis County, Texas, 29 AUG 2010.

3-4, ♀ *Z. rufipes*, northern Laurens County, South Carolina, 21 AUG 2012.

5-6, ♂ *Z. sexpunctatus* (Hentz 1845), southern Greenville County, South Carolina, 9 SEP 2012.

7, ♀ *Z. sexpunctatus*, southern Greenville County, South Carolina, 24 JUL 2012.

Figure 32. North American *Zygoballus*. The male in (6) was displaying to another male. Each scale bar = 1.0 mm. Photos (2-4, 7) by Ryan Kaldari, released to Public Domain (CC0 1.0).

1-2, ♀ *Parnaenus* sp., Iwokrama Rainforest, Guyana.

3, *Parnaenus* or *Paraphidippus* sp., Panama.

4, "*Sassacus*" sp. near entrance to shelter, Amazon forest, Bolivia.

Figure 33. Neotropical dendryphantines. There are no systematic comparisons of shelter construction across salticid groups, but many dendryphantines build lined shelters with more than one door that can be opened and closed. Photos by Dr. Arthur Anker, Florida Museum of Natural History, used with permission.

In reviewing the origin of the most important dendryphantine genera of North America (Table 11), we must first consider what is known of the phylogeny of this group. The four publications dealing with the molecular phylogeny of dendryphantines (Hedin & Maddison 2001a, Maddison & Hedin 2003a, Maddison *et al.* 2008, Bodner & Maddison 2012) include representatives of the most important North American genera, but few from the Neotropical region (Table 13).

Table 13. Hypothetical dendryphantine clades published in four different papers dealing with their molecular phylogeny (2001-2012), with a *consistent hypothesis* (at right) based on the most recent proposals from these papers. The degree of confidence expressed in these relationships varies. Neotropical groups are highlighted in green, and the single Palaearctic genus *Dendryphantes* is highlighted in violet. The remaining genera are Nearctic.

Hedin & Maddison 2001a (fig. 12)	**Maddison & Hedin 2003a (fig. 5)**	**Maddison *et al.* 2008 (fig. 8)**	**Bodner & Maddison 2012 (fig. 8)**	**consistent hypothesis**
Group 1	Group 1	*Phanias*	*Phanias* ~11.6 Ma	Group 1
Mabellina	*Rudra*	Group 2	Group 3	*Hentzia*
Rudra	*Phanias*	*Mabellina*	Group 4	*Phanias*
Group 2	Group 2	*Rudra*	*Ghelna*	Group 2
Hentzia	Group 3	Group 3	*G. canadensis*	*Mabellina*
Phanias	*Terralonus*	Group 4	*Zygoballus*	*Rudra*
Group 3	*Zygoballus*	*Ghelna*	*Z. rufipes*	Group 3
Group 4	Group 4	*Zygoballus*	Group 6	Group 4
Rhetenor	Group 5	Group 5	*Terralonus*	*Ghelna*
Zygoballus	*Bellota*	*Eris militaris*	*T. mylothrus*	Group 5
Group 5	*Mabellina*	Group 6	Group 9	*Rhetenor*
Beata	Group 6	Group 7	*Pelegrina*	*Zygoballus*
Group 6	*Beata*	*Dendryphantes*	Group 11	Group 6
Eris	Group 7	*D. hastatus*	*Eris*	*Messua*
Pelegrina	*Phidippus*	*Terralonus*	*Phidippus*	*Sassacus*
Terralonus	Group 8	*T. mylothrus*		Group 7
Group 7	*Eris*	Group 9		*Dendryphantes*
Tutelina	*Pelegrina*	Group 10		*Terralonus*
Poultonella		*Beata*		Group 8
Sassacus		*Pelegrina*		*Tutelina*
S. papenhoei		Group 11		*Poultonella*
S. vitis		*Bellota*		Group 9
Group 8		*Phidippus*		Group 10
Phidippus				*Beata*
Paraphidippus				*Pelegrina*
Messua				Group 11
				Eris
				Group 12
				Bellota
				Group 13
				Paraphidippus
				Phidippus

Based on the *consistent hypothesis* of phylogeny shown here (right column in Table 13), we can account for the presence of dendryphantines in North America by a single Miocene (~10Ma, *Group 6*) introduction, preceding the completion of the Panamanian Land Bridge (2.5-2.3 Ma), followed by a series of later introductions. This early introduction could represent the ancestor of *Dendryphantes* (later to diversify in the Palaearctic), *Eris*, *Paraphidippus*, *Pelegrina*, *Phidippus*, *Poultonella*, *Sassacus*, *Terralonus*, and *Tutelina*. This group clearly includes the most diverse Nearctic dendryphantine genera. The Neotropical genera *Beata*, *Bellota* and *Messua* also fall within this group. *Beata* and *Messua* are both diverse in Central America and may also represent a later introduction from the North. *Hentzia*, with many Caribbean species, was most likely introduced from that region. The first introduction of *Hentzia* may be late Miocene, as both widely-distributed temperate and western species are known from North America.

Phidippus, with 60 known species, represents the largest genus of North American dendryphantines (Edwards 2004, Richman et al. 2012). This genus also includes many of the largest known jumping spiders (Figures 25-29). With few exceptions, species can be separated into distinct groups according to their distribution: *west coast, western interior, south central, eastern, southeastern, boreal, and tropical*. In Figure 34 we map the present distribution of these species back to the location of their biomes at the Last Glacial Maximum (LGM; Figures 11-12). This should be viewed only as a *working hypothesis* for the movement of these species from the southern-most parts of North America toward the north over the last 20Ka, and more detailed studies of population genetics will be necessary to increase our confidence in these proposals. Detailed studies of subfossil insects have shown that many modern species predate the Pleistocene, and their movement has in fact correlated with movement of biomes (Downes & Kavanaugh 1988). Repeated cycles of glaciation may however be associated with the isolation of populations and the generation of some closely related species pairs recognized previously by Edwards (2004).

Figure 34. Hypothetical movement of the 60 known *Phidippus* species since the Last Glacial Maximum (LGM; ~20Ka), based on movement of associated biomes toward the north as continental glaciers retreated. At the time of the LGM, terrestrial habitats extended over the continental shelves, and those in the Gulf of Mexico were particularly important (Yucatan peninsula, northwestern Gulf coast, Florida peninsula). Eastern and western faunas continue to be isolated by extensive mountain ranges extending from the south of Mexico north to Alaska. Even today, the greatest diversity in this genus can be found to the south, and only two species can be considered to be boreal. There are also few species in the northwest. Some of the species presently found at higher altitudes in the west may have simply moved up from lower elevations occupied during the LGM. The divided distribution of likely sister-species groups (*e.g.*, *ardens+purpuratus+texanus*, *princeps+pulcherrimus*, *putnami+richmani*; Edwards 2004) supports the hypothesis that at least some of the speciation in this genus has resulted from intermittent isolation of populations during glaciation events in the Pleistocene. Background courtesy of NASA Worldwind project.

Marpissinae. Like the Dendryphantinae, the Marpissinae comprise one of the most important North American groups, but they are not as diverse here. As with other marpissoids, they are most diverse in the Neotropics (Table 14), so a Neotropical origin is likely. The important North American genera are *Maevia*, *Marpissa* (also diverse in the Palaearctic, most likely the result of introduction from North America over Beringia), *Metacyrba*, and *Platycryptus*. Of these, the only really diverse genus, based on described species, is *Marpissa*. The relationship of Palaearctic *Marpissa* species to those of North America is not known, but it is significant that none of the North American species are found in the Palaearctic, and none are associated with boreal forests. Thus these may have been isolated since the late Miocene (10-6Ma). North American marpissines tend to be cryptic in coloration. Representatives of the major North American genera, and some related neotropical species, are shown in Figures 35-38.

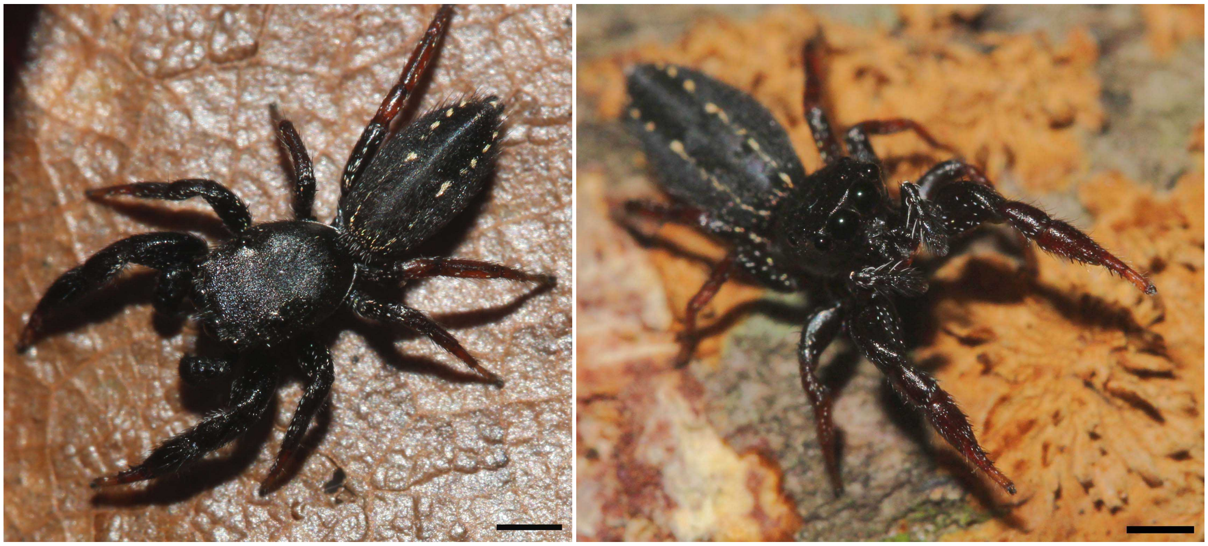
Table 14. Marpissine genera.

Marpissoida: Marpissinae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Balmaceda Peckham & Peckham 1894			4		5
Fritzia O. Pickard-Cambridge 1879					1
Fuentes Peckham & Peckham 1894		1	2		
Maevia C. L. Koch 1846		6			3
Marpissa C. L. Koch 1846	15	11	1	1	5
Metacyrba F. O. Pickard-Cambridge 1901		4	2	1	2
Platycryptus Hill 1979		4	3		1
Psecas C. L. Koch 1850			2		13

1-2, ♂ *Marpissa lineata* (C. L. Koch 1846), southern Greenville County, South Carolina, 4 MAY 2012.

Figure 35. North American *Marpissa lineata.* These have the rounded, 'pom-pom' pedipalps characteristic of male *Marpissa*. Each scale bar = 1.0 mm.

1-2, ♀ *Marpissa muscosa* (Clerck 1757), Schlesswig Holstein, Germany.



3-4, ♀ *Metacyrba taeniola* (Hentz 1846), southern Greenville County, South Carolina, 17 MAY 2012.

5-6, ♂ *Metacyrba taeniola* , southern Greenville County, South Carolina, 27 MAY 2012 (5), 28 MAY 2012 (6).

Figure 36. European *Marpissa* and North American *Metacyrba*. Each scale bar = 1.0 mm. Photos (1-2) by Bernhard Jacobi, used with permission.

1-2, ♀ *Platycryptus undatus* (DeGeer 1778), southern Greenville County, South Carolina, 3 MAY 2012 (1), 29 NOV 2012 (2).

3, ♂ *P. undatus*, southern Greenville County, South Carolina, 11 APR 2011.

4, ♂ *Platycryptus* cf. *magnus*, Amazon rainforest, Ecuador.

5, ♀ *Psecas* sp., Amazon rainforest, Peru.

6, ♂ *Psecas* sp., Yasuni National Park, Ecuador.

Figure 37. Large marpissines. Each scale bar = 1.0 mm. Photos (4-6) by Dr. Arthur Anker of the Florida Museum of Natural History, used with permission.

1,♀ *Maevia inclemens* (Walckenaer 1837), southern Greenville County, South Carolina, broadleaf forest understory, 7 MAY 2013

2, ♂ *M. inclemens*, southern Greenville County, South Carolina, 22 OCT 2011.

3-4, ♂ *M. inclemens*, southern Greenville County, South Carolina, 14 NOV 2011.

5-6, ♂ *Maevia* sp., Pleasant Ridge County Park, northern Greenville County, South Carolina, 25 MAY 2011.

Figure 38. *Maevia* from the broadleaf deciduous forests of eastern North America. Each scale bar = 1.0 mm.

The three dark 'pencils' of setae emerging from the top of the carapace of some *Maevia inclemens* (Figure 38:2) are not present in all males of this form. Barnes (1955) first called this species *M. inclemens*, and others have since followed suit (Edwards 1977, Edwards *et al.* 1978). Because this species has two different male forms, each with its own display behavior, it has been called the 'Dimorphic Jumping Spider', the subject of many behavioral studies (Clark & Uetz 1992, 1993, Clark 1994, Clark & Biesiadecki 2002).

When we look at published charts of the molecular phylogeny of this group (Table 15), we have information on few genera, but these include the most important marpissines in North America. Assuming that *Marpissa* originated in North America, then crossed Beringia to diversify in the Palaearctic, we can hypothesize a single early *marpissine introduction* (Miocene, ~12.5Ma if not earlier) from South America to account for the major North American genera (Figure 2, *consistent hypothesis, Group 1*): *Maevia*, *Marpissa*, *Metacyrba* and *Platycryptus*. *Marpissa* species may have moved into Eurasia via Beringia in the Miocene, soon after this genus diverged from *Platycryptus* (~9Ma). Although we still have much to learn about *Platycryptus* in South America (Figure 26:8), this genus may have migrated back to that continent at a much later time, over the Panamanian Land Bridge.

Table 15. Hypothetical marpissine clades published in three different papers dealing with their molecular phylogeny (2003-2012), with a *consistent hypothesis* (at right) based on the most recent proposals from these papers. As with dendryphantines, the degree of confidence expressed in these relationships varies. The Neotropical genus *Psecas* is highlighted in green, and the single Palaearctic genus *Marpissa* is highlighted in violet. The remaining genera are Nearctic.

Maddison & Hedin 2003a (fig. 5)	Maddison *et al.* 2008 (fig. 8)	Bodner & Maddison 2012 (fig. 8)		consistent hypothesis
Group 1	*Psecas*	*Psecas*	~13.2 Ma	*Psecas*
Maevia	Group 1	Group 1		Group 1
Marpissa	*Platycryptus*	*Maevia intermedia*	~11.4 Ma	Group 2
Group 2	Group 2	Group 2		*Maevia*
Psecas	*Marpissa pikei*	*Marpissa pikei*	~9 Ma	*Metacyrba*
Group 3	Group 3	*Platycryptus undatus*		Group 3
Metacyrba	*Maevia intermedia*			*Marpissa*
Platycryptus	*Metacyrba taeniola*			*Platycryptus*

Synagelinae. Synageline genera are shown in Table 16. The diversity of Holarctic *Synageles* and the endemic North American genera *Admestina* and *Attidops* support the hypothesis of at least one earlier *synageline introduction* into North America from South America, possibly Miocene. Bodner & Maddison (2012) estimate the divergence of *Attidops* and *Peckhamia* at ~16.6Ma. This divergence may have taken place after the arrival of a common ancestor in North America. We still have much to learn about the South American and Caribbean members of this group of spiders. The ancestor of *Synageles* may have originated in either North America or the Palaearctic, and species of this genus may have subsequently moved in either direction over Beringia. Ant mimics of the genus *Peckhamia* are shown in Figure 39.

Table 16. Synageline genera.

Marpissoida: Synagelinae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Admestina Peckham & Peckham 1888		3			
Attidops Banks 1905		4			
Cheliferoides F. O. Pickard-Cambridge 1901		2	2		
Consingis Simon 1900					1
Descanso Peckham & Peckham 1892			2	3	5
Paradescanso Vellard 1924					1
Peckhamia Simon 1901		4	2	1	2
Synageles Simon 1876	11	8	1		

1-2, ♂ *Peckhamia* sp., southern Greenville County, South Carolina, 26 MAY 2011 (1), 27 MAY 2011 (2).

3-4, ♀ *Peckhamia* sp., southern Greenville County, South Carolina, 31 MAY 2011 (3), 24 MAY 2012 (4).

Figure 39. North American *Peckhamia*. Spiders of this genus have thick, short legs I, and thin, long legs II. The latter are raised and waved in the air like antennae. They live in areas frequented by ants of similar size and are alert to their presence, but feed on smaller insects as shown here (3). Like ants, they also take fluid at the extrafloral nectaries of plants like the *Prunus* shown here (4). Durkee *et al.* recently (2011) published evidence that these are Batesian ant mimics, based on their observation that the salticid *Thiodina puerpera* did not feed on them. *T. puerpera* is however a specialist at feeding on mostly stationary prey, so it would not tend to pursue a rapidly moving arthropod in any case (Hill 2012). Each scale bar = 1.0 mm.

Other marpissoids. The Neotropical genus *Itata* (Table 17, Figure 40) has not been associated with one of the three marpissoid subfamilies. It is listed here to highlight the greater diversity of Marpissoida in the Neotropics, not represented in the North American fauna.

Table 17. Other marpissoids not included in the Dendryphantinae or Marpissinae.

Marpissoida: other					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Itata Peckham & Peckham 1894			1		4


1, ♂ *Itata completa* (Banks 1929), Barro Colorado Island, Panama.
1, Penultimate ♂ *Itata completa* , Panama, rainforest.

Figure 40. Neotropical marpissoids of the genus *Itata*. Photos by Dr. Arthur Anker, Florida Museum of Natural History, used with permission.

Astioida. This is a large clade of primarily Australasian salticids (Maddison *et al.* 2008, Hill 2010). There is strong evidence that a common ancestor of the the Astioida and Marpissoida lived on a great southern continent (*Australamerica*) comprised of South America, Antarctica and Australia, in the Eocene after the breakup of Gondwanaland (Hill 2009b). According to this hypothesis, the marpissoids and astioids would represent parallel lines of descent from this common ancestor, after the separation of Antarctica at the end of the Eocene. The two genera with a significant presence in North America (*Myrmarachne* and *Neon*) are both much more diverse in the Old World (Table 18, Figure 41). *Myrmarachne* is most diverse in Africa and southern Asia and is certainly a recent introduction to North America. *M. centralis* (Peckham & Peckham 1892) is a Central American species found only in the extreme south of Mexico, and *M. formicaria* is a Palaearctic species that has been recently introduced to New York, Ohio and Pennsylvania (Bradley *et al.* 2006, Richman *et al.* 2012), apparently as a result of human activity.

The North American species of *Neon* are most likely the result of at least one earlier introduction from the Palaearctic over the Bering land bridge (Beringia). Bodner & Maddison (2012) estimate the divergence of *Neon* from other astioids at 29.6Ma, so an early Oligocene to Miocene introduction of this genus to North America over Beringia is possible, although not required to explain its present distribution. One species, *N. reticulatus* (Blackwall 1853), is widely distributed from the Palaearctic to Alaska and south along the west coast of North America to Arizona and New Mexico (Richman *et al.* 2012). The other North American species are endemic.

Table 18. Astioid genera with Nearctic, Neotropical or Palaearctic representatives.

Astioida					
GENUS	Palaearctic	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Arachnotermes Mello-Leitão 1928					1
Myrmarachne MacLeay 1839	22	2*1	4		6
Neon Simon 1876	14	6		1	1

1, ♂ *Myrmarachne formicaria* (DeGeer 1778), Nordrheinwestfalen, Germany.

2, *Myrmarachne* sp., Chaffey Dam near Tamworth, New South Wales.

Figure 41. Astioid spiders of the genus *Myrmarachne*. *M. formicaria* (1) was recently introduced into the northeastern United States. Although this large cosmopolitan genus has many species, only two are found in North America. Photo credits: (1) by Berhard Jacobi, (2) by Jürgen Otto, both used with permission.

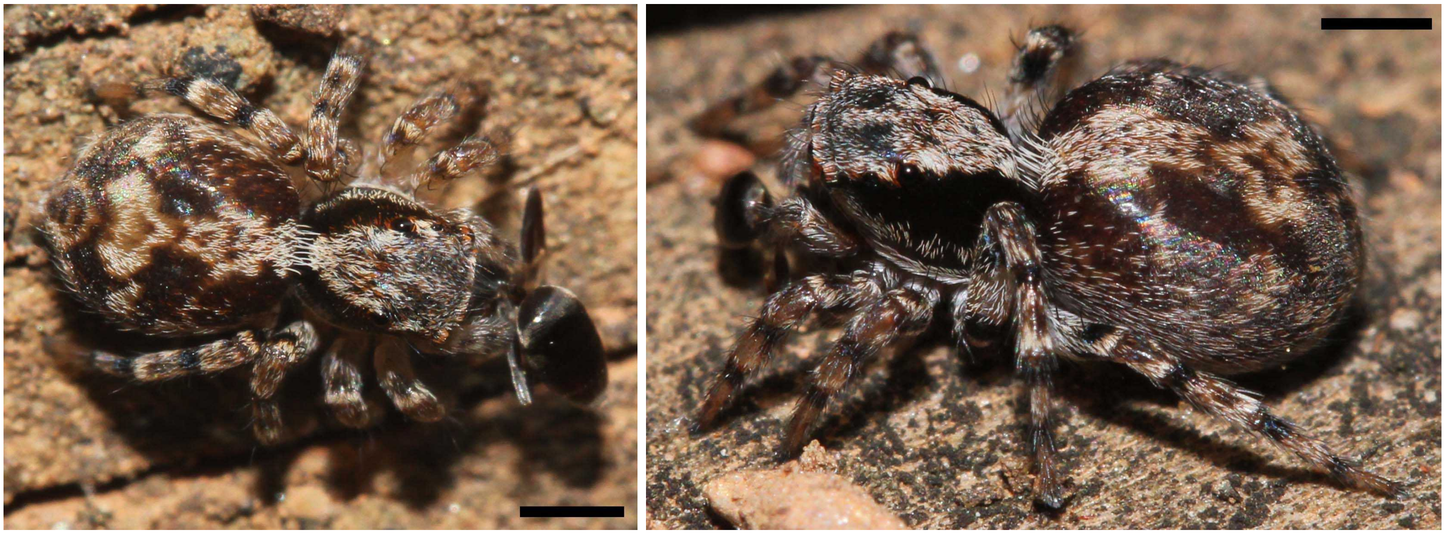
Euophryinae. This is a large group with two primary centers of diversity, one Neotropical, where they are particularly diverse in the Caribbean (making up the majority of the salticid fauna), and the other Australasian (Hill 2009a, 2010, Zhang 2012, Zhang & Maddison 2012a, 2012b). This distribution suggests that the 'first' euophryine lived in Australamerica after the breakup of Gondwana (Hill 2009b).

Given the importance of this group to the Neotropical fauna, the presence of only two small endemic genera in North America is surprising. Most species found in North America (Table 19, Figures 42-43) have either an obvious Palaearctic affinity (*e.g.*, *Chalcoscirtus*, *Euophrys*, *Pseudeuophrys*, *Talavera*) or an obvious Neotropical affinity (*e.g.*, *Anasaitis*, *Corythalia*, *Naphrys*, *Neonella*). The Palaearctic group of genera are all closely related members of the *Euophrys* clade (Zhang 2012, Zhang & Maddison 2013), and almost certainly represent fairly recent introductions over Beringia. Likewise, the Neotropical group can be accounted for by recent introductions from either Central America (*Corythalia*, *Neonella*) or the Caribbean (*Anasaitis*). A single species of *Anasaitis*, *A. canosa* (Walckenaer 1837), can be found in the leaf-litter of the southeastern United States and adjacent parts of Mexico (Richman *et al.* 2012).

Table 19. Euophryine genera with Nearctic, Neotropical or Palaearctic representatives. This list includes new genera described by Zhang & Maddison (2012a, 2012b).

Euophryinae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Agobardus Keyserling 1885				17	
Allodecta Bryant 1950				1	
Amphidraus Simon 1900					4
Anasaitis Bryant 1950		1		9	
Antillattus Bryant 1943				2	
Asaphobelis Simon 1902					1
Belliena Simon 1902					4
Bythocrotus Simon 1903				3	
Caribattus Bryant 1950				1	
Chalcoscirtus Bertkau 1880	45	4			
Chapoda Peckham & Peckham 1896		1	4		1
Chloridusa Simon 1902					1
Cobanus F. O. Pickard-Cambridge 1900		1	12		2
Commoris Simon 1902				3	
Compsodecta Simon 1903			2	4	
Corticattus Zhang & Maddison 2012a				2	
Coryphasia Simon 1902					10
Corythalia C. L. Koch 1850		9	33	17	24

GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Dinattus Bryant 1943				3	
Ecuadattus Zhang & Maddison 2012b					2
Euophrys C. L. Koch 1834	46	1	1	2	27
Featheroides Peng et al. 1994	2				
Laufeia Simon 1889	4				
Marma Simon 1902					3
Mexigonus Edwards 2003		4			
Micalula Strand 1932			1		
Mirandia Badcock 1932					1
Mopiopia Simon 1902					3
Naphrys Edwards 2003		4			
Nebridia Simon 1902				2	2
Neonella Gertsch 1936		2		2	8
Ocnotelus Simon 1902					3
Paradecta Bryant 1950				4	
Parasaitis Bryant 1950				1	
Pensacola Peckham & Peckham 1885		1	3	6	6
Pensacolops Bauab 1983					1
Petemathis Prószyński & Deeleman-Reinhold 2012				5	
Popcornella Zhang & Maddison 2012a				4	
Pseudeuophrys Dahl 1912	8	1 *1			
Pseudocorythalia Caporiacco 1938			1		
Rhyphelia Simon 1902					2
Saitidops Simon 1901				1	1
Saitis Simon 1876	6			1	6
Semnolius Simon 1902					3
Sidusa Peckham & Peckham 1895		1	8	6	2
Siloca Simon 1902				5	4
Soesilarishius Makhan 2007					9
Stoidis Simon 1901				2	1
Talavera Peckham & Peckham 1909	16	1			
Tariona Simon 1902				1	4
Thiania C. L. Koch 1846	4				
Truncattus Zhang & Maddison 2012a				3	
Tylogonus Simon 1902				1	8
Wallaba Mello-Leitão 1940					1



1-2, Two different ♀*Naphrys pulex* (Hentz 1846) feeding on ants, southern Greenville County, South Carolina, 15 APR 2012 (1), 30 APR 2012 (2).

Figure 42. Female *Naphrys pulex* from the eastern United States. Each scale bar = 1.0 mm.

1-2, ♂ *Naphrys pulex*, southern Greenville County, South Carolina, 1 MAY 2011 (1), 2 MAY 2012 (2).

3-4, ♀ *Anasaitis canosa* (Walckenaer 1837) feeding on ant (*Camponotus*), s. Greenville County, South Carolina, 29 APR 2012.

5-6, ♂ *Anasaitis canosa*, southern Greenville County, South Carolina, 10 MAR 2012.

Figure 43. *Naphrys pulex* and *Anasaitis canosa* from southern Greenville County, South Carolina. These two skilled ant-eating species (Edwards *et al.* 1974, Li *et al.* 1996, Hill 2006) are widely distributed and can occur in very high density populations in leaf litter and on fallen trees and branches in the forest understory. Both are also synanthropic. *A. canosa* is restricted to the warm forests of the southeastern United States, and *N. pulex* occupies most of the eastern part of the continent, from Florida to the mixed and boreal forests of southeastern Canada. As shown in (5), their diet is not restricted to ants. Each scale bar = 1.0 mm.

The two endemic North American genera *Mexigonus* and *Naphrys* were named by Edwards (2003). *Mexigonus* is found only in Mexico and the southwestern United States, whereas *Naphrys* is mostly restricted to the south, with a single species, *Naphrys pulex* (Hentz 1846), widely distributed in the deciduous forest understory of the eastern United States. *Mexigonus* is related to the Neotropical genus *Pensacola* (*Pensacola-Mexigonus* clade) and *Naphrys* is most closely related to the Caribbean genera *Corticattus* and *Popcornella* (Zhang & Maddison 2012a), but these appear to have diverged at least 20Ma (Zhang 2012).

Three fossil *Corythalia* have been reported from the Dominican Amber (Wunderlich 1982, 1988) and represent an earlier presence of the *Anasaitis-Corythalia* clade (Zhang 2012, Zhang & Maddison 2013) in the Greater Antilles. However, the North American *Corythalia* are almost all confined to the southern part of Mexico, and a more recent dispersal from a much more diverse Neotropical fauna (Figure 44) can explain their recent presence here.

1-2, Two *Corythalia* sp., Trinidad, (1) feeding on a leafcutter ant (*Atta cephalotes*).

3, *Anasaitis* sp., Costa Rica.

4, cf. *Corythalia* Costa Rica.

5, ♂ *Corythalia opima* (Peckham & Peckham 1885) feeding on ant, Bocas del Toro, Panama.

6, ♂ *Cobanus* sp., Panama.

7, ♀ cf. *Cobanus*, Panama.

8, ♀ *Sidusa recondita* Peckham & Peckham 1896, Panama.

Figure 44. Some representative Neotropical euophryines. Photo credits: (1-3) by Bryan Reynolds, (4) by Bernhard Jacobi, (5-8) by Dr. Arthur Anker, Florida Museum of Natural History, all used with permission.

Hasarieae. This is an old-world group closely related to the Heliophaninae (Bodner & Maddison 2012). There are only two genera, each with a single species, in North America (Table 20). *Chinattus parvulus* (Banks 1895), widely distributed in eastern North America, is the singular representative here of a Palaearctic genus that is primarily known from China. *Chinattus* is closely related to *Habrocestoides*, an Asian genus prevalent in India, and *Habrocestum*, a much larger genus ranging from Eurasia to Africa. Thus a relatively recent introduction through Beringia is likely. The cosmopolitan species *Hasarius adansoni* (Audouin 1825) has only been found at a few localities in the northeastern United States, southern Texas, and southwestern Mexico (Richman *et al.* 2012, R. K. Walton 2012), and its distribution is clearly associated with recent human activity.

Table 20. Genera of the Hasarieae with a Nearctic, Neotropical or Palaearctic presence.

Hasarieae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Chinattus Logunov 1999	9	1			
Habrocestoides Prószyński 1992	6				
Habrocestum Simon 1876	10				
Hasarius Simon 1871	3*1	1*1	2*1	3*1	2*1

Heliophaninae. This is a predominantly Eurasian group (Hill 2010), related to the Hasarieae and Leptorchestinae (Bodner & Maddison 2012). There are many Palaearctic representatives of this group, but only four species from three different genera in North America (Table 21). *Hakka himeshimensis* (Dönitz & Strand, in Bösenberg & Strand, 1906), from the Far East and Hawaii, is a recent introduction to seaports in Massachusetts and New Jersey (Kaldari et al. 2011). *Marchena minuta* Peckham & Peckham 1909 is found only in the temperate far west (Maddison 1987, Richman *et al.* 2012), a distribution that suggests fairly recent migration of an ancestor from Asia via Beringia. The cosmotropical and synanthropic *Menemerus bivittatus* (Dufour 1831) has become established in the southern part of North America, most likely as a result of recent human activity. More recently, a second introduced species, *Menemerus semilimbatus* (Hahn 1829), was discovered in California (Manolis & Carmichael 2010). The two Neotropical *Icius* listed in Table 21 are almost certainly misplaced to genus. The relationship of the larger Palaearctic fauna to the South American 'heliophanine' genera shown here, unrelated to the North America fauna, needs more study. Bodner & Maddison (2012) estimated the divergence of *Helvetia* from its old world relatives at about 18.6Ma.

Table 21. Genera of the Heliophaninae with a Nearctic, Neotropical or Palaearctic presence.

Heliophaninae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Afraflacilla Berland & Millot 1941	2				
Hakka Berry & Prószyński 2001	1	1 *1			
Helicius Żabka 1981	4				
Heliophanillus Prószyński 1989	1				
Heliophanus C. L. Koch 1833	48				
Helvetia Peckham & Peckham 1894					11
Icius Simon 1876	13			1	1
Kupiuka Ruiz 2010					8
Marchena Peckham & Peckham 1909		1			
Matagaia Ruiz & Bescovit & Freitas 2007					1
Menemerus Simon 1868	12	2*2	2*1	1*1	3*1
Phintella Strand in Bösenberg & Strand 1906	13				
Plesiopiuka Ruiz 2010					1
Pseudicius Simon 1885	36				
Siler Simon 1889	4				
Tasa Wesolowska 1981	2				
Theriella Braul & Lise 1996					3
Yepoella Galiano 1970					1

Leptorchestinae. The sole North American genus of this group, *Paramarpissa* (Table 22), is related to the large and diverse Palaearctic genus *Yllenus*. The Leptorchestinae is also closely allied to both the Hasarieae and Heliophaninae, as part of a larger clade of African-Eurasian spiders (Bodner & Maddison 2012). *Paramarpissa* is found only in the southwestern United States and Mexico, and appears to represent a radiation of 6 species in that area from a single leptorchestine introduction over Beringia at an earlier time. The estimated divergence of *Paramarpissa* and *Yllenus* at 13.8Ma (Bodner & Maddison 2012) suggests that this took place during the Miocene. If this had been a recent introduction, we would expect to see temperate species, but instead the genus is limited to subtropical areas, with a center of diversity in Mexico (Richman *et al.* 2012). Both *Paramarpissa* and *Yllenus* are quite different from the more distantly related, ant-like *Leptochestes*.

Table 22. Genera of the Leptochestinae with a Nearctic, Neotropical or Palaearctic presence.

Leptorchestinae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Leptorchestes Thorell 1870	4				
Paramarpissa F. O. Pickard-Cambridge 1901		6			
Yllenus Simon 1868	61				

Salticus and related genera. These species comprise a sister group to the Plexippoida (Pelleninae+ Plexippinae), based on relationships charted by Bodner and Maddison (2102). This is an important Palaearctic group, with only four species from one genus (*Salticus*) occuring in North America (Table 23, Figure 45). Thus, there can be little doubt of a Palaearctic origin. The estimated divergence of *Salticus* from the other genera shown here is 25.7Ma (Bodner & Maddison 2012), and a single Miocene introduction over Beringia is a plausible origin for the three species that are endemic to southwestern United States, with a nearly allopatric distribution from California and Arizona (*S. palpalis* (Banks 1904)) to New Mexico and Texas (*S. peckhamae* (Cockerell 1897)) to the southern Great Plains (*S. austinensis* Gertsch 1936). The fourth species is the cosmopolitan, synanthropic *Salticus scenicus* (Clerck 1757), and its current distribution is almost certainly the result of recent human activity.

Table 23. *Salticus* and related genera with a Nearctic, Neotropical or Palaearctic presence.

***Salticus* and related genera**					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Carrhotus Thorell 1891	1				
Mogrus Simon 1882	11				
Philaeus Thorell 1869	7				
Salticus Latreille 1804	30	4 *1			

1-2, ♀ *Salticus palpalis* (Banks 1904), Arizona.

Figure 45. Iridescent *Salticus* from the southwest. Photos by Gerardine Vargas, used with permission.

Plexippoida. The Plexippoida, comprised of the clades Plexippinae and Pelleninae, is a large and almost exclusively African and Eurasian group (Maddison & Hedin 2003a, Hill 2010, Bodner & Maddison 2012).

Plexippinae. There are only two genera from this large Afro-Eurasian group that occur in North America, both associated with a much greater diversity of Palaearctic species (Table 24, Figure 46). There are many African-Eurasian species of *Evarcha*, including one of the two North American species, *E. proszynskii* Marusik & Logunov, 1998. The distribution of *E. proszynskii* in North America, from Alaska south into the higher elevations of the western United States, and east across the boreal areas of southern Canada, is clearly indicative of a recent crossing from Asia via Beringia. *E. hoyi* (Peckham & Peckham 1883), largely confined to the northeastern United States and adjacent parts of Canada, may represent a somewhat earlier crossing via Beringia. Two of the three *Plexippus* species are from 'Mexico' but they are only known from Koch's original (1846) description. One, *P. paykulli* (Audouin 1826), is a well-known synanthropic, cosmotropical species that is widely distributed in subtropical areas of the United States, and in Mexico. Its distribution is thought to be the result of recent human activity.

Table 24. Genera of the Plexippinae with a Nearctic, Neotropical or Palaearctic presence.

Plexippoida: Plexippinae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Evarcha Simon 1902	34	2			
Pancorius Simon 1902	4				
Paraplexippus Franganillo 1930				2	
Plexippoides Prószyński 1984	20				
Plexippus C. L. Koch 1846	11	3*1	2*1	1*1	3*1
Ptocasius Simon 1885	8				
Telamonia Thorell 1887	3				
Thyene Simon 1885	7				
Yaginumaella Prószyński 1979	38				

1, ♂ *Evarcha hoyi* (Peckham & Peckham 1883), Concord, Massachusetts.

2, ♂ *Plexippus paykulli* (Audouin 1826), Barro Colorado Island, Panama.

Figure 46. Plexippines found in North America. Photo credits: (1) by Dick Walton, (2) by Dr. Arthur Anker, Florida Museum of Natural History, both used by permission.

Pelleninae. By far the largest genera in this group are the closely related Holarctic *Pellenes* and the Nearctic *Habronattus* (Table 25, Figures 47-50). As a branch of the Plexippoida, we have good reason to view the Pelleninae as a group with a Eurasian origin from which a single older introduction over Beringia gave rise to the many species of *Habronattus* now found in North America. Based on an estimated 9.3-4.8Ma divergence of *Habronattus* and *Pellenes* (Bodner & Maddison 2012), this introduction may have taken place in the late Miocene to Pliocene. With its many widely-distributed species, *Habronattus* now represents one the best groups of salticids to study from the perspective of recent geological history, distribution, and speciation. Although *Pellenes* is more diverse in the Palaearctic, there are several North American species, including those found only in the arid southwest. Some of these may be the result of a single earlier introduction from Asia, but others with a Holarctic distribution (*P. ignifrons* (Grube 1861), *P. lapponicus* (Sundevall 1833)) most certainly crossed recently. This crossing could have been in either direction. The single North American species of *Sibianor*, *S. aemulus* (Gertsch 1934), is primarily found across southern Canada and very likely represents a relatively recent introduction from Asia by way of Beringia.

Table 25. Genera of the Pelleninae with a Nearctic, Neotropical or Palaearctic presence.

Plexippoida: Pelleninae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Habronattus F. O. Pickard-Cambridge 1901		92	8	7	1
Harmochirus Simon 1885	2				
Neaetha Simon 1884	4				
Pellenes Simon 1876	43	14			
Sibianor Logunov 2001	12	1			

1-4, *Habronattus viridipes* (Hentz 1846), Concord, Massachusetts, (1-2) ♂, (3-4) ♂ (upper right) courting ♀.

5, ♂ *Habronattus* sp., New Mexico.

6, ♀ *Habronattus* sp., Tucson, Arizona.

Figure 47. North American *Habronattus*. Male displays in this genus can include flexion (3) and extension (4) of metatarsi I., and elevation of the patellae of legs III. Photo credits: (1-4) by Dick Walton, used with permission, (5) by Bryan Reynolds, used with permission, (6) by Ryan Kaldari, released to Public Domain (CC0 1.0).

1-2, ♂ *Habronattus coecatus* (Hentz 1846), 31 JUL 2010.

3-4, ♂ *H. coecatus*, Lexington County, South Carolina, OCT 2011.

5-6, ♀ *H. coecatus*, southern Greenville County, South Carolina, 21 JUL 2012.

Figure 48. *Habronattus coecatus*. Note the elaborate decoration of the distal femur, patella and tibia of leg III of the male (4). Each scale bar = 1.0 mm. Photos (1-2) by Jeremy Royall, used with permission.

1-2, ♂ *Habronattus virgulatus* Griswold 1987, Santa Rita Mountains, Arizona.

3, ♂ *H. virgulatus*, south of Tucson, Arizona, 22 JUN 2012.

4, ♂ *H. mexicanus* (Peckham & Peckham 1896), Stann Creek District, Belize, 2 FEB 2011.

5, ♂ *Habronattus* sp., southern Arizona,22 JUN 2012.

6, ♂ *H. hallani* (Richman 1973), Coronado National Forest near Tucson, Arizona, 23 JUN 2012.

Figure 49. North American *Habronattus*. *H. virgulatus* and *H. mexicanus* (type species for *Habronattus*) are in the *coecatus* group of this genus. Photo credits: (1-2, 4) by Ryan Kaldari, released to Public Domain (CC0 1.0), (3, 5-6) by Thomas Shahan, used with permission.

1-2, ♂ *Habronattus peckhami* (Banks 1921), Point Reyes National Seashore, Marin County, California.

3, ♂ *H.cognatus* (Peckham & Peckham 1901), Goldsby, Oklahoma, 5 MAY 2010.

4, ♂ *H.pugillus* Griswold 1987, Santa Rita Mountains, Arizona, 23 JUN 2012.

5-6, ♂ *H. dossenus* Griswold 1987, Santa Rita Mountains, Arizona.

Figure 50. North American *Habronattus*. Photo credits: (1-2, 5-6) by Ryan Kaldari, released to Public Domain (CC0 1.0), (3-4) by Thomas Shahan, used with permission.

If we look at the distribution of one clade within *Habronattus*, the *coecatus* group (Figure 51), we can see the same combination of latitudinal (or biome) and east to west segregation of related species that we saw in the genus *Phidippus* (Figure 34). For the most part, *coecatus* group species are allopatric.

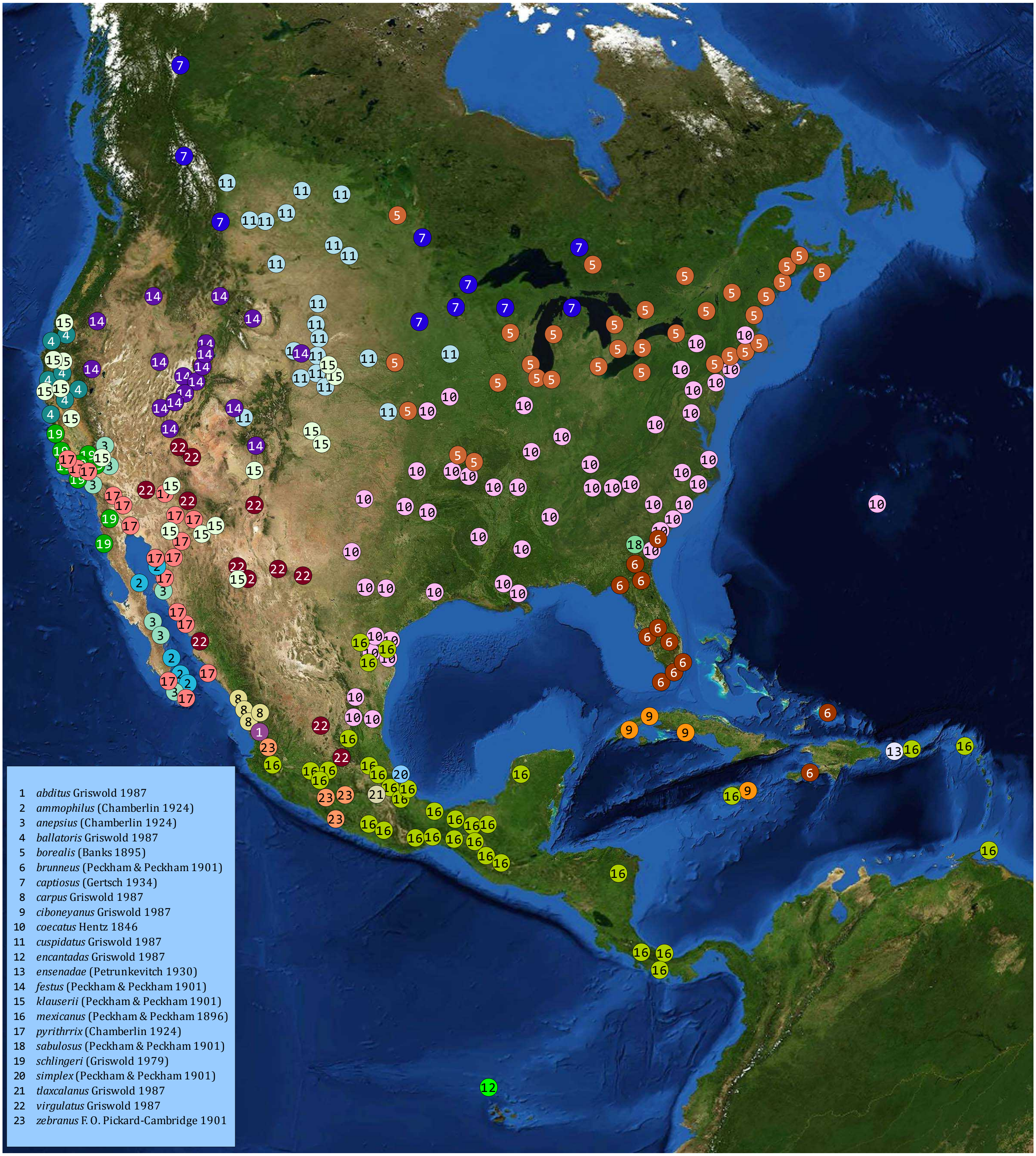


Figure 51. Modern distribution of 23 species associated with the *coecatus* group of the genus *Habronattus* (Griswold 1987, Maddison & Hedin 2003b, Richman *et al.* 2012, Cutler pers. comm.; see also Figures 38, 39:1-4). Map background courtesy of NASA.

As with *Phidippus*, populations of *Habronattus* species must have been pushed to the south and then north again many times during glacial cycles of the Pleistocene and Holocene, producing complex and changing patterns of intermittent isolation that have probably contributed much to diversity within the genus. There are many published studies of population genetics and comparative courtship behavior of species and isolated populations of species within this genus (Richman & Cutler 1998, Maddison & McMahon 2000, Masta 2000, Hedin & Maddison 2001b, Masta & Maddison 2002, Maddison & Hedin 2003b, Masta & Boore 2004, Hebets & Maddison 2005, Elias *et al.* 2006, 2012, Hedin & Lowder 2009). During each glaciation cycle, biomes associated with the range of montane *Habronattus* species in western North America shift by altitude as much as by latitude (DeChaine & Martin 2004, Ni *et al.* 2010). This can result in many generations of relatively high isolation between populations (*fragmentation*) alternating by many generations of contact between these populations (*expansion*).

Aelurilloida. The Aelurillinae and the Neotropical 'freyine group' fall within the Aelurilloida (Maddison *et al.* 2008, Bodner & Maddison 2012), a large clade that also includes the African thiratoscirtines.

Aelurillinae. This Old World subfamily has little relevance for the fauna of North America, and only one species, *Phlegra hentzi* (Marx 1890), associated with a large and important African-Eurasian genus (Table 26, Figure 52). Our only species, *P. hentzi*, is widely distributed in association with the temperate forest areas of eastern North America, usually found on or near the ground. This may be the result of a fairly recent introduction from Asia via Beringia.

Table 26. Genera of the Aelurillinae with a Nearctic, Neotropical or Palaearctic presence.

Aelurillinae					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Aelurillus Simon 1884	48				
Asianellus Logunov & Heciak 1996	5				
Langona Simon 1901	9				
Phlegra Simon 1876	32	1			
Proszynskiana Logunov 1996	5				
Rafalus Prószyński 1999	4				
Stenaelurillus Simon 1886	3				

1, ♂ *Phlegra fasciata* (Hahn 1826), Italy.

2, ♂ *P. hentzi* (Marx 1890), Massachusetts.

Figure 52. Closely related *Phlegra* species from Europe and North America. Logunov & Koponen (2002) redescribed and separated *P. hentzi*, the only North American representative of this genus, from *P. fasciata*. Photo credits: (1) by Jari Segreto, used under CC BY 2.0 license, (2) by Dick Walton, used with permission.

Freyine group. The few North American representatives of this diverse Neotropical group (Table 27, Figures 53-54) are largely confined to southern Mexico (Richman *et al.* 2012). Since none of these has a significant Caribbean presence, their current distribution in North America is consistent with recent introduction over the Panamanian land bridge. Two of the *Freya* species, and the single *Frigga*, *Nycerella* and *Pachomius* species from North America also range well into Neotropical areas of Central and South America. One *Freya*, *F. ambigua* (C. L. Koch), is introduced from northern South America (Edwards & Ruiz 2013). Three of the four North American *Phiale* species are also found in Central America.

Table 27. Genera of the freyine group with a Nearctic, Neotropical or Palaearctic presence.

freyine group					
GENUS	PALAEARCTIC	NORTH AMERICA	CENTRAL AMERICA	CARIBBEAN	SOUTH AMERICA
Akela Peckham & Peckham 1896			1		1
Aphirape C. L. Koch 1850					8
Capidava Simon 1902					7
Chira Peckham & Peckham 1896			1		15
Edilemma Ruiz & Brescovit 2006					1
Eustiromastix Simon 1902				2	9
Freya C. L. Koch 1850		4*1	17		11
Frigga C. L. Koch 1850		1	2		9
Kalcerrytus Galiano 2000					15
Nycerella Galiano 1982		1	6	1	5
Pachomius Peckham & Peckham 1896		1	3		5
Phiale C. L. Koch 1846		4	15	2	19
Sumampattus Galiano 1983					3
Trydarssus Galiano 1995					2
Tullgrenella Mello-Leitão 1941					13
Wedoquella Galiano 1984					3

1, ♀ *Phiale guttata* (C. L. Koch 1846), Trinidad.

2, ♀ *Phiale guttata*, Costa Rica.

Figure 53. Two different female color forms of the large neotropical freyine *Phiale guttata*. *Phiale* species are boldly patterned. Photo credits: (1) by Bryan Reynolds, (2) by Bernhard Jacobi, both used with permission.


1, ♀ *Phiale* sp., Panama.


2, ♀ *Phiale* sp., Panama, with platystomid fly.


3, ♀ *Freya* sp., Amazon forest, Peru.


4, ♀ cf. *Frigga pratensis* (Peckham & Peckham 1885), Palo Verde, Costa Rica

Figure 54. Other Neotropical freyines. Photo credits: (1-3) by Dr. Arthur Anker, Florida Museum of Natural History, (4) by Bernhard Jacobi, all used with permission.

Pathways of introduction

Major pathways for the introduction of salticid groups into North America are summarized in Tables 28-29. Cenozoic introductions from South America prior to completion of the Panamanian Land Bridge were either trans-oceanic, or followed the transient islands of one of two (Antillean, Central American) volcanic arcs on the eastern or western margin of the Caribbean plate (1). Later Neotropical introductions could take an Antillean route (3), via the Greater Antilles, or a direct Panamanian route (5). During periods of Pleistocene glaciation, the distance between the large islands of the Greater Antilles and Florida was greatly reduced. Beringian access has been generally available during the Cenozoic, but only the Early Beringian route (2) allowed direct access to North America by a temperate or even subtropical fauna. Use of the Later Beringian route (4) during the Pleistocene required an ability to survive in a very cold climate with a short growing season, and even this would only have been available during interglacial periods. At our current position in the post-Wisconsin interglacial, this route now lies partly beneath the Bering Sea.

Table 28. Hypothetical origins of the North American Salticidae: older pathways available prior to the Pleistocene.

1. Mexican	Ancestors of these genera came from South America to North America via a transoceanic route or an island arc (Antillean or Central American) that preceded completion of the Panamanian Land Bridge (2.5-2.3Ma), surviving in southern refugia during episodes of glaciation	Lyssomaninae: *Lyssomanes*
		Dendryphantinae: *Eris, Paraphidippus, Pelegrina, Phanias, Phidippus, Poultonella, Sassacus, Terralonus, Tutelina*
		Marpissinae: *Maevia, Marpissa, Metacyrba, Platycryptus*
		Synagelinae: *Admestina, Attidops, Peckhamia, Synageles*
		Euophryinae: *Mexigonus*, *Naphrys*
2. Early Beringian	Ancestors came from northern Asia during periods of warm climate before the Pleistocene and were able to speciate in North America, surviving in southern refugia during episodes of glaciation	Leptochestinae: *Paramarpissa*
		Salticus group: *Salticus* (except *S. scenicus*)
		Pelleninae: *Habronattus*

Table 29. Hypothetical origins of the North American Salticidae: later pathways available since the Pleistocene.

3. Antillean	Descended from South American ancestors that became well-established on Caribbean islands; more recent introduction to North America of these species is also a possibility.	Dendryphantinae: *Hentzia*
		Euophryinae: *Anasaitis canosa*
4. Later Beringian	Mostly isolated representatives of genera that are speciose and widely distributed in the Palaearctic, including a number of Holarctic species that probably crossed over from Asia during a recent glacial episode; ancestor of the amycoid *Sitticus* probably came from South America to Asia via Beringia	Sitticinae: *Sitticus*
		Dendryphantinae: *Dendryphantes nigromaculatus*
		Astioida: *Neon*
		Euophryinae: *Euophrys* clade: *Chalcoscirtus, Euophrys,, Talavera*
		Hasarieae: *Chinattus parvulus*
		Heliophaninae: *Marchena minuta*
		Pelleninae: *Pellenes, Sibianor*
		Plexippinae: *Evarcha*
		Aellurillinae: *Phlegra*
5. Panamanian	Mostly isolated representatives of Neotropical genera introduced via the Panamanian Land Bridge with limited speciation in North America and usually greater diversity in South and Central America	Amycoida: all except *Sitticus*
		Dendryphantinae: *Alcmena, Anicius, Bagheera, Beata, Bellota, Ghelna, Messua, Nagaina, Paradamoetas, Parnaenus, Zygoballus*
		Marpissinae: *Fuentes*
		Synagelinae: *Cheliferoides*
		Astioida: *Myrmarachne centralis*
		Euophryinae: *Corythalia, Neonella*
		freyine group
6. Anthropic	Includes a limited number of cosmopolitan or synanthropic species and two quite recent introductions as a result of human activity, all representing Old World salticid groups	Astioida: *Myrmarachne formicaria*
		Euophryinae: *Pseudeuophrys erratica*
		Heliophaninae: *Hakka himeshimensis, Menemerus bivittatus, Menemerus semilimbatus*
		Salticus group: *Salticus scenicus*
		Plexippinae: *Plexippus paykulli*
		Hasarieae: *Hasarius adansoni*
		freyine: *Freya ambigua*

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