Chapter 6
Biogeography of New World Tarantulas

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Abstract Biogeography is a multidisciplinary field that is concerned with delimiting and explaining the geographic distributions of organisms in space and time. Due to their distribution patterns and interesting biology (e.g., ancient lineage with a nearly cosmopolitan distribution, sedentary lifestyle with limited dispersal capabilities), tarantulas are an appealing taxonomic group for addressing a variety of biogeographic questions concerning the Earth's history. In this chapter, we discuss some biogeographic basic concepts, delve into the distribution patterns of New World tarantulas, and explore some of the historical explanations that may have led to these distributions. We mostly review and highlight the results of recent studies but also include personal observations and unpublished data. The distributions of higher-level taxonomic groups (subfamilies and tribes) are described and we detail their latitudinal and elevational limits. We also review the distributions of groups with unique insular habitats such as those found on islands surrounded by seas, forested "islands" surrounded by "seas" of deserts, and caves. Furthermore, we discuss the distribution of some unique morphological characters of taxonomic importance such as urticating setae. Finally, we review a handful of studies that have explicitly investigated the biogeography of New World tarantulas using a variety of different analytical methods.

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6.1 Introduction

In its simplest sense, the discipline of biogeography is concerned with delimiting and explaining the geographic distributions of organisms. In other words, biogeographers are engaged in answering three fundamental questions about organisms: What is it? Where is it found? and Why is it found there? The first two questions help identify and describe the *patterns* of organismal distributions whereas the third attempts to analyze and interpret the *processes* responsible for generating these patterns. Two conceptually different approaches have been developed to aid in the interpretation of organismal distributions: ecological biogeography and historical biogeography. The primary difference between both approaches is a matter of scale (i.e., ecological biogeography tends to be concerned with smaller spatial and shorter temporal scales than historical biogeography).

Ecological biogeography examines the role that biotic and abiotic environmental factors play in confining an organism to its *present-day* distribution. This field draws upon information from a variety of *ecological* disciplines including physical geography, climatology, community ecology, and physiology. Historical biogeography, on the other hand, examines the roles that dispersal and vicariance (Fig. 6.1) have played in shaping organismal distributions over *evolutionary time* and utilizes information from *historical* disciplines such as geology, paleontology, and phylogenetics to address its aims.

Despite most biogeographers falling into only one of the two camps, integration of the two fields is necessary in order to best understand *all* the processes that have shaped organismal distributions over ecological *and* evolutionary time (Crisci et al. 2006; Ricklefs and Jenkins 2011; Wiens et al. 2019). Biogeography is an exciting field of study and has experienced a revolution as of late due to many recent technical and analytical advancements (e.g., phylogenomics, molecular clocks, ecological niche modeling, etc.) and has moved from a largely descriptive discipline to one that is hypothesis-driven, complex, and challenging (Crisci 2001; Posadas et al. 2006).

6.1.1 Overview of New World Tarantula Biogeography

The "New World" is composed of three major biogeographical regions, characterized by their distinctive biotas: Nearctic, Neotropical and Andean (Morrone 2015a). The Neotropical region, in a broad sense, encompasses the entirety of Central and South America, southern Mexico, the Caribbean, and South Florida in the United States. The Nearctic region includes northern Mexico and the remainder of North America. Together, these two regions exhibit complex topography with elevations ranging from below sea level to above 6900 m and encompass an incredible diversity of biomes including some of the harshest deserts and most humid forests on Earth. The amazing biodiversity of the Neotropics in particular, as compared with the rest of the planet, is well illustrated by higher plants which have been considered

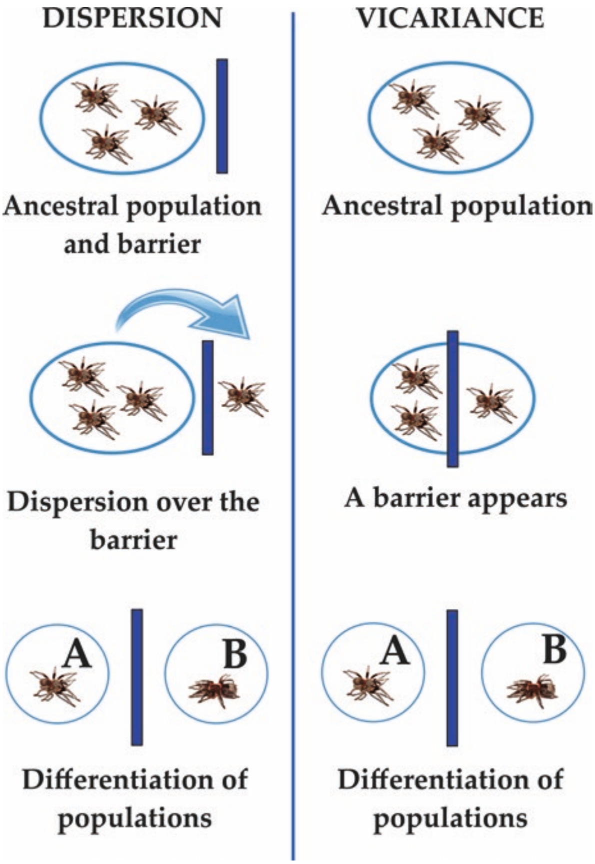

Fig. 6.1 Schematic representation of historical biogeographical explanations for disjunct distributions in closely related taxa. Vicariance describes the process by which a geographic barrier (e.g., a river, mountain range, arid valley) forms and isolates populations. Dispersal is the process by which organisms reach new regions by traversing a preexisting geographic barrier (e.g., transoceanic rafting). Vicariance is thought to be the most important explanation for disjunct distributions in tarantulas due to the spiders' sedentary habits and limited dispersal capabilities. Dispersal is probably rare for theraphosids but likely accounted for the distributions for at least some taxa

surrogates for estimating general biological diversity (Usinowicz et al. 2017). This pattern of rich Neotropical diversity is similar for many animal taxa including reptiles, amphibians, mammals, birds, butterflies and many others (Antonelli et al. 2015). Therefore, the Neotropics are generally considered the most biodiverse region of the world and provide a well-suited location to study the drivers, processes, and mechanisms involved in shaping the geographical distribution of organisms.

Tarantulas (family Theraphosidae) are the most diverse lineage of mygalomorph spiders and are particularly well represented in the New World (Table 6.1). They are found in a large variety of environments and inhabit all 10 biodiversity hotspots that

Table 6.1 Diversity and distribution of tarantulas in the New World organized by country based on data obtained from Kambas (2019) and World Spider Catalog (2019)

Region/Country	Subfamilies	Genera	Species
North America			
Mexico	2	15	101
United States	1	1	29
Central America			
Belize	3	5	5
Costa Rica	3	13	35
El Salvador	1	2	4
Guatemala	1	7	9
Honduras	1	2	2
Nicaragua	1	1	2
Panama	4	13	18
South America			
Argentina	2	15	45
Bolivia	3	12	19
Brazil	5	42	188
Caribbean Islands[a]	5	16	63
Chile	2	6	17
Colombia	4	19	32
Ecuador	3	12	19
French Guiana	3	6	7
Guyana	4	8	9
Paraguay	1	7	11
Peru	3	12	36
Suriname	2	2	2
Uruguay	2	7	16
Venezuela	5	20	37

Note: This table should only be used to identify general trends in diversity and distributions. Some values (especially number of species) are undoubtedly erroneous for some countries due to unpublished information (e.g., unpublished taxonomic data, incorrect taxonomic placements, etc.)

[a] For simplicity, all of the Caribbean Islands were grouped into a single category under South America

have been recognized in the New World (https://www.cepf.net/our-work/biodiversity-hotspots), threatened regions known for their exceptional biodiversity and high levels of endemism. But despite their diversity and abundance, potential relevance as top invertebrate predators in ecosystems (Sergio et al. 2008), importance to pharmacological and therapeutic research (Escoubas and Rash 2004; Cardoso et al. 2015), and conservation concern (Bertani and Fukushima 2009; Hendrixson et al. 2015; Mendoza and Francke 2017), theraphosids have been largely neglected in biological research and very little is known about their biogeography (Bertani 2012). But why is the group's biogeography so poorly understood?

The first questions that biogeographers seek to answer about organismal distributions ("What is it?" and "Where is it found?") appear straightforward but have been incredibly complicated for theraphosids. Species and higher-level taxa must be identified and defined to understand patterns of biodiversity. Biogeographical studies assume that the taxonomic entities in question have been accurately delimited and that their distributions have been carefully documented. Neither assumption can be taken lightly in the case of theraphosids. Tarantulas, like most mygalomorph taxa, appear very similar to each other and do not possess the complex and diverse structures found in araneomorph spiders. As a consequence, morphological homogeneity between closely related taxa and high levels of intraspecific variation have posed significant challenges for species delimitation (Prentice 1997; Hamilton et al. 2016) and higher-level classification (Raven 1985). The taxonomic problem is furthered complicated by the proliferation of monotypic genera (e.g., nearly 1 out of every 3 theraphosine genera are known from a single species, World Spider Catalog 2019) whose phylogenetic positions remain unknown.

In addition to inadequately defined taxa (genera and species) and our lack of phylogenetic data, the geographic distributions for most New World tarantulas are poorly known. Distribution records for most taxa are restricted to only a few sites or type localities. Moreover, researchers face a number of challenges when attempting to document the distribution of New World tarantulas. It is uncommon to find large series of theraphosids housed in scientific collections, due in part to the difficulty of finding and collecting these cryptic animals from their retreats (e.g., inside burrows, under rocks, etc.). Only under special conditions it is possible to collect more than a few individuals (Bertani 2001).

Only within the last few decades have New World tarantulas received any significant attention from the scientific community in the form of taxonomic revisions and phylogenetic analyses, constituting a starting point for future biogeographical studies (e.g., Raven 1985; Pérez-Miles et al. 1996; Bertani 2001, 2012; Guadanucci 2014; Perafán and Pérez-Miles 2014; Ferretti 2015; Hamilton et al. 2016; Fukushima and Bertani 2017). The adoption of integrative taxonomy has greatly improved our understanding of species boundaries and distributions in some New World taxa (e.g., Hendrixson et al. 2013, 2015; Hamilton et al. 2011, 2014, 2016; Mendoza and Francke 2017; Montes de Oca et al. 2016; Ortiz and Francke 2016, 2017) and provides a robust methodological approach for future taxonomic revisions. Likewise, advances in molecular systematics and phylogenomics should complement recent phylogenetic treatments of Theraphosidae (Lüddecke et al. 2018; Turner et al. 2018; Foley et al. 2019; see discuss in Chap. 2) and provide the phylogenetic framework required for addressing the family's historical biogeography.

6.2 Biogeography of the Infraorder Mygalomorphae

The spider infraorder Mygalomorphae is fascinating because it possesses numerous characteristics that make it an excellent model for biogeographical research at various spatial and temporal scales. The group is distributed on every continent (except Antarctica), has an ancient origin dating back to the Carboniferous

(Ayoub et al. 2007; Opatova et al. 2019), has a largely sedentary lifestyle, exhibits high habitat fidelity (e.g., Pétillon et al. 2012), and generally has limited dispersal abilities (i.e., most mygalomorphs are restricted to terrestrial locomotion).

Pocock's (1903) seminal paper "On the Geographical Distribution of Spiders of the Order Mygalomorphae" was the first to shed light on some aspects of the biogeography of mygalomorphs. He discussed different dispersal mechanisms in spiders and noted the relevance of limited vagility in Mygalomorphae from a geographical standpoint. He also provided a detailed description of mygalomorph spider distributions (for families, subfamilies, and genera), spearheading subsequent biogeographical research on the group. In the 1970s and 1980s, numerous researchers began investigating the biogeography of Mygalomorphae in more depth. There was also a shift from producing largely descriptive works detailing distributional patterns to testing specific biogeographical hypotheses. Coyle (1971) analyzed the distributions of Antrodiaetidae in the United States and Japan, and proposed a sequence of geological and climatic events that may have shaped their distribution. Raven (1980, 1984a) did the same for Hexathelidae and Migidae in Australia, and for Dipluridae and Barychelidae (Raven 1984b, 1986). Main (1981a, b) presented some biogeographical considerations for these spiders in New Guinea and discussed the eco-evolutionary radiation of mygalomorphs in Australia. These early contributions used a cladistic or phylogenetic biogeographic approach to unveil and explain the geographical patterns of these spiders.

Cladistic or phylogenetic biogeography is an "area biogeography" approach whose aim is to identify patterns in the relationships among areas of endemism that arise repeatedly in the phylogenies for different taxa, which may correspond to shared events in Earth's history (Crisci et al. 2003). Areas of endemism are understood to be biogeographical units that can be described as geographic areas that are defined by the spatial congruence of two or more taxa. Spatial congruence between taxa implies a shared history in space and time (Morrone 1994; Noguera-Urbano 2016) and suggests the same historical process(es) may be responsible for shaping their shared distributions.

More recently, advances in molecular phylogenetics (see Opatova et al. 2019) and the founding of phylogeography (Avise et al. 1987) have had an enormous impact on our understanding of mygalomorph biogeography. Molecular-based phylogenies provide the evolutionary framework for historical biogeographic methods and the incorporation of molecular clocks provide the temporal context for testing specific hypotheses and inferring causal biogeographic events. For example, if a defined tectonic event is hypothesized as the causal explanation for a taxon's disjunct distribution, molecular clock analyses can provide evidence that supports or rejects such a hypothesis (Posadas et al. 2006). If a molecular clock analysis indicates that sister taxa diverged well after the last known connection between two currently isolated regions, a dispersal event—rather than vicariance—can be implicated.

Several phylogenetic and phylogeographic studies of Mygalomorphae (especially non-theraphosid taxa)—with an explicit biogeographic component—have been published during the last two decades. Some of them cover the phylogenetic and geographic breadth of the infraorder (e.g., Bond et al. 2001; Cooper et al. 2011;

Godwin et al. 2018; Hedin et al. 2013, 2015, 2019; Hendrixson and Bond 2007; Opatova and Arnedo 2014a, b; Opatova et al. 2013, 2016, 2019; Rix et al. 2017; Starrett and Hedin 2007; Starrett et al. 2013, 2018). As expected, most studies demonstrate that vicariance has played an important role in shaping the distributions of mygalomorph taxa at all spatial scales (i.e., from local to continental). Phylogeographic research has revealed several important trends consistent with a history of vicariance: (1) long-term persistence of populations; (2) deep phylogenetic divergence between populations; (3) and short-range endemism. Drifting continents, extensional tectonics, submersion of land bridges, climate change, and other phenomena have all been hypothesized to have led to vicariance in mygalomorphs. However, some mygalomorphs are able to passively disperse by ballooning (Coyle et al. 1985; Bell et al. 2005; Ferretti et al. 2013) and other means including short-range (e.g., Hedin et al. 2013; Opatova and Arnedo 2014b) and even trans-oceanic rafting (Harrison et al. 2017).

Non-phylogenetic methods have also been developed for the study of historical biogeography. Such methods only consider the distributions of taxa and are primarily focused on analyzing patterns of endemism. Some of these methods (such as panbiogeography) have been criticized for lacking a phylogenetic framework but they do provide evidence of change in distributions over time and identify hypotheses of primary biogeographical homology, including identifying the geographic origins of entire biotas (Rosen 1988; Nihei 2006; Casazza and Minuto 2009; Morrone 2011, 2014a, 2015b). There are only a few studies that utilize these approaches in mygalomorphs and some concerning theraphosids will be discussed later in the chapter.

6.3 Distribution of New World Tarantulas

The New World is particularly rich in theraphosid spiders [more than half of all described species are reported from there (World Spider Catalog 2019)], comprising representatives of five currently recognized subfamilies: Aviculariinae, Ischnocolinae, Psalmopoeinae, Schismatothelinae, and Theraphosinae (Raven 1985; West et al. 2008; Guadanucci 2014; Lüddecke et al. 2018; Foley et al. 2019). Tarantula diversity is highest in the Neotropics but considerable species-level diversity is also known from the Nearctic region in northern Mexico and the southwestern United States (Table 6.1).

6.3.1 Geographical Distribution of Theraphosidae Subfamilies

The monophyly and composition of Aviculariinae have been widely investigated in recent years (West et al. 2008; Bertani 2012; Fukushima and Bertani 2017; Lüddecke et al. 2018; Turner et al. 2018; Hüsser 2018; Foley et al. 2019). According to the

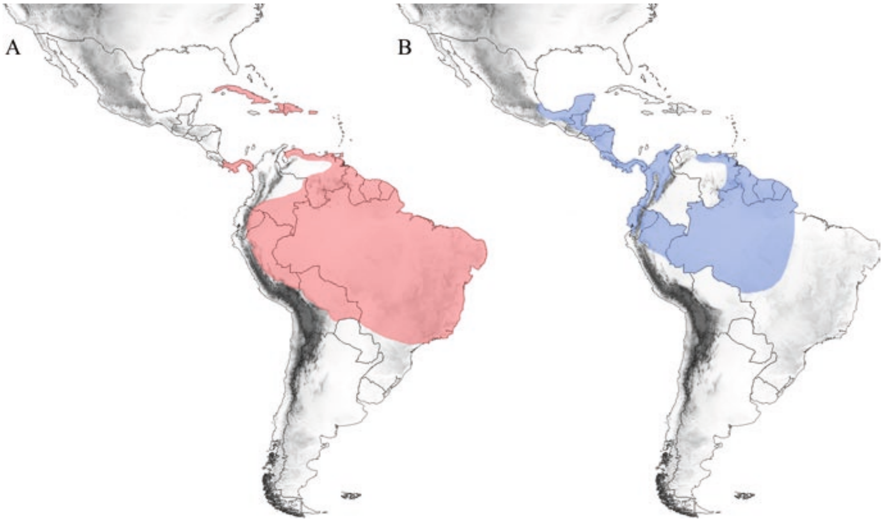

Fig. 6.2 Approximate distribution area of the subfamilies (**a**) Aviculariinae and (**b**) Psalmopoeinae

latest molecular phylogenetic evidence, Aviculariinae is endemic to the Neotropics and comprises the genera *Antillena*, *Avicularia*, *Caribena*, *Iridopelma*, *Pachistopelma*, *Typhochlaena*, and *Ybirapora* (see discuss in Chap. 4). The subfamily is distributed from Central America, north to central South America, and is present on some Caribbean islands (Fig. 6.2a; Bertani 2012; Fukushima and Bertani 2017). Aviculariine species have mainly arboreal habits and predominantly inhabit tropical rainforests, although *Iridopelma*, *Pachistopelma*, and *Typhochalena* are principally distributed in Atlantic forests of northern and northeastern Brazil (Bertani 2012). The genus *Avicularia* has the widest distribution and can be found throughout Costa Rica, Panama, Trinidad and Tobago, Venezuela, Guyana, Suriname, French Guiana, Colombia, Ecuador, Peru, Bolivia, and Brazil. Conversely, the genera *Antillena* and *Caribena* have limited distributions restricted to various Caribbean islands (Fig. 6.2a; Fukushima and Bertani 2017).

The geographic distribution of Aviculariinae in tropical rainforest areas and with few representatives in northern Caatinga and Cerrado provinces (Brazil) could be interpreted as that the group was ancestrally widely distributed before vicariance of the Antilles, Early Jurassic-Early Cretaceous (Morrone 2014b). In this sense, the currently restricted distribution in the open environments of Caatinga and Cerrado would be explained by the later paleoecological changes which turning them to open areas; that is to say, that the presence of only a few species in Caatinga and Cerrado could be a relic (Pérez-Miles and Perafán 2015). In agreement with this hypothesis, vicariance events during the Miocene-Pliocene were used to explain endemism for species of *Iridopelma* and *Pachistopelma* (Bertani 2012). The distribution of aviculariines is also consistent with the Neotropical region proposed by

Morrone (2014b, c) in his biogeographical regionalization, and could constitute additional evidence of the naturalness of this region (Pérez-Miles and Perafán 2015). According to Morrone (2014b, c) the Neotropical region corresponds to the tropical areas of the New World. On the other hand, and interestingly, the subfamily Aviculariinae is not present in the Andes Mountains or other mountain ranges in Central America.

The subfamily Psalmopoeinae (validated by Hüsser 2018) consists of four Neotropical genera including *Ephebopus*, *Psalmopoeus*, *Pseudoclamoris*, and *Tapinauchenius* (see Chap. 4), distributed throughout Central America and northern South America (Fig. 6.2b). Of these, *Ephebopus* is the only fossorial genus (Marshall and West 2008) in an otherwise arboreal subfamily. *Ephebopus* is distributed in northern Brazil, French Guiana, Suriname, and Guyana where they can be found in lowland and upland rainforests and fringing grasslands (West et al. 2008). *Psalmopoeus* is known from northern South America (including Trinidad), Central America, and southern Mexico (Mendoza-Marroquín 2014b); in South America it inhabits mainly in wet Andean forests. *Pseudoclamoris* has an apparent disjunct distribution with some members in Ecuador, Peru, and Colombia and others in French Guiana (Hüsser 2018). *Tapinauchenius* is more broadly distributed throughout northern South America with some species on various Caribbean islands (Hüsser 2018).

The subfamily Ischnocolinae is an enigmatic group with a problematic taxonomic history and there remains considerable confusion regarding its generic composition (Raven 1985; Guadanucci 2014; Lüddecke et al. 2018; Foley et al. 2019). It has the widest distribution among theraphosid subfamilies with species located in the Americas, Asia, Africa, and Europe. A systematic revision of the group is badly needed and recent phylogenetic analyses suggest that the subfamily is not monophyletic (Guadanucci 2014; Foley et al. 2019). Despite this confusion, five ischnocoline genera (which themselves probably do not form a monophyletic group; see Hüsser 2018; Foley et al. 2019) are reported from the New World including *Catumiri*, *Dolichothele*, *Holothele*, *Reichlingia*, and *Trichopelma* (see discuss in Chap. 3). Most species are distributed in tropical areas of central and northern South America, Central America, and some Caribbean islands (Fig. 6.3b). Only *Catumiri* inhabits more temperate zones in South America. A few *Dolichothele*, *Holothele* and *Trichopelma* species inhabit cave environments (Bloom et al. 2014; Fonseca-Ferreira et al. 2017; Guadanucci et al. 2017). Interestingly (and strangely for theraphosids), *Holothele longipes* occupies a very large range in northern South America. It is reported from Bolivia, Peru, Brazil, Colombia, Venezuela, Suriname, and Trinidad and Tobago where it can be found from sea level along the Caribbean and Atlantic coasts to above 2000 m in Colombia's Eastern Range (Guadanucci et al. 2017).

The subfamily Schismatothelinae comprises five Neotropical genera including *Euthycaelus*, *Guyruita*, *Neoholothele*, *Schismatothele*, and *Sickius* (see Chap. 3). This group of taxa formerly placed in Ischnocolinae may not be monophyletic (Guadanucci 2014) but recent phylogenetic analyses suggest a close relationship to

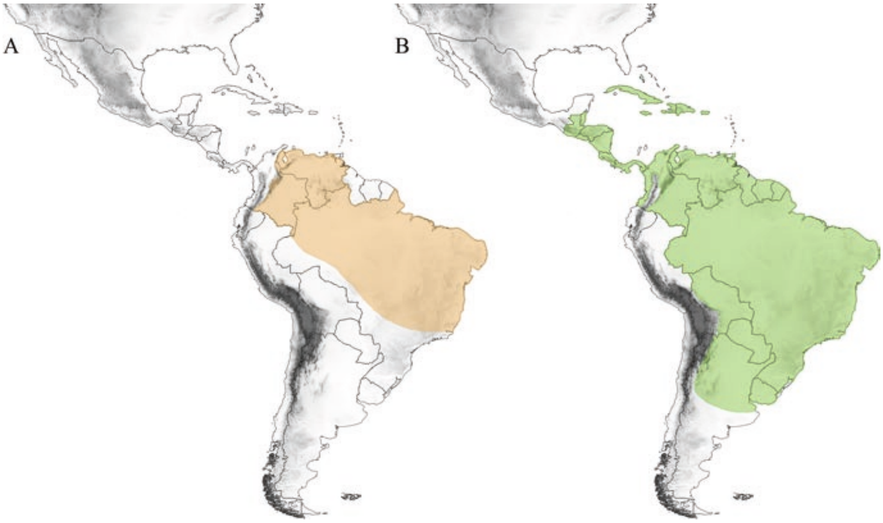

Fig. 6.3 Approximate distribution area of the subfamilies (**a**) Schismatothelinae and (**b**) Ischnocolinae (Neotropical)

Psalmopoeinae (Hüsser 2018; Lüddecke et al. 2018; Foley et al. 2019). With the exception of *Guyruita*, the other genera have very restricted distributions (Fig. 6.3a). *Guyruita* is distributed in Brazilian Cerrado and Atlantic Rainforest areas, and in the Amazon region of Venezuela and northern Brazil (Guadanucci et al. 2007; Fukushima and Bertani 2018). *Neoholothele*, *Euthycaelus*, and *Schismatothele* are distributed in northeastern South America. *Euthycaelus* and *Schismatothele* have a cis-Andean distribution along the Colombia's Eastern Range and Venezuela's Mérida Range and can also be found in northeastern Venezuela, from sea level to about 1700 m (Guadanucci and Weinmann 2014; Valencia-Cuéllar et al. 2019). Likewise, *Neoholothele* is distributed in northeastern Venezuela, Trinidad and Tobago, and central Colombia east of the Eastern Range (Guadanucci and Weinmann 2015). The monotypic genus *Sickius* is distributed in Brazil in the eastern State of Mato Grosso to the Distrito Federal, and south to the States of Mato Grosso do Sul, São Paulo, and western Paraná (Bertani and da Silva 2002).

Theraphosinae is the most diverse theraphosid subfamily and currently comprises 68 genera and more than 500 species (World Spider Catalog 2019; Kambas 2019) including the only species found in the Nearctic. These tarantulas are mainly found in tropical regions of Central and South America, southern Mexico, and some Caribbean islands, but many species inhabit more temperate climates found in the southwestern United States, northern Mexico, Chile, Argentina, and Uruguay (Fig. 6.4). Theraphosines inhabit a great diversity of environments, from tropical wet forests, cloud forests, montane forests, and alpine tundra to sea coastlines, savannas, and deserts.

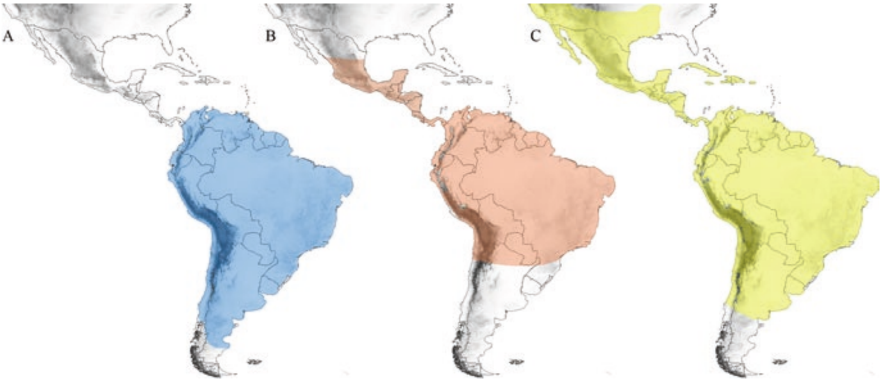

Fig. 6.4 Approximate distribution area of the Theraphosinae tribes (**a**) Gramostolini, (**b**) Hapalopini, and (**c**) Theraphosini

6.3.2 Geographical Distribution of Urticating Setae Types

While not all tarantulas in the New World possess urticating setae (*Psalmopoeus*, *Pseudoclamoris*, *Tapinauchenius*, some troglobitic *Hemirrhagus* species, and the ischnocoline/schismatotheline genera lack them), the presence of these interesting structures is unique to New World tarantulas. Seven different types of urticating setae have been described (reviewed by Bertani and Guadanucci 2013, see also Perafán et al. 2016, and Chap. 9) and some interesting biogeographic patterns have emerged from their distributions. These setae are most diverse in the Theraphosinae (including Types I, III, IV, VI, and VII) but unique types are found in a handful of non-theraphosine taxa including Type II in Aviculariinae and Type V in the psalmopoeine genus *Ephebopus*.

Recently, Turner et al. (2018) investigated the phylogenetic relationships of some theraphosine genera and proposed three tribes for the subfamily including the Grammostolini, Hapalopini, and Theraphosini. The tribes are distinguished primarily by the types and combinations of abdominal urticating setae present in each group, confirming that the different setal conditions are closely linked to deeper-level relationships in the group (Pérez-Miles et al. 1996; Bertani and Guadanucci 2013; Pérez-Miles and Perafán 2015; Ortiz et al. 2018). Turner et al. (2018) also discussed that the tribes are largely congruent with distinct geographic regions, in agreement with Pérez-Miles and Perafán et al. (2015) who studied the geographic distribution of theraphosid abdominal urticating setae types and combinations. It should be noted that some theraphosine genera with unique urticating setae types [Type VI in *Hemirrhagus* (Pérez-Miles 1998) and Type VII in *Kankuamo* (Perafán et al. 2016)] could not be assigned to a tribe (Turner et al. 2018).

Grammostolini is characterized by taxa that possess both Types III and IV urticating setae but never Type I (Turner et al. 2018). The tribe is predominantly distributed in southern South America in temperate countries such as Chile, Argentina, and Uruguay, but also ranges into Paraguay, Bolivia, Amazonian Brazil, and Colombia (Perez-Miles et al. 1996; Perafán and Pérez-Miles 2014; Pérez-Miles and Perafán 2015; Turner et al. 2018). The northern limit of Type IV setae (and therefore the northern limit of Grammostolini) is represented by the Colombian genus *Aguapanela* (Perafán et al. 2015). Consequently, Grammostolini and Type IV setae are restricted to South America (Fig. 6.4a).

Members of the tribe Hapalopini possess Type III urticating setae but never Type I; a few genera also possess Type IV but there is some confusion in the literature regarding how to distinguish among the two types in some genera (Turner et al. 2018). Hapalopini primarily occurs in South America with some genera (e.g., *Cyriocosmus* and *Hapalopus*) widespread throughout the Amazonian and Andean regions, but the tribe also extends northward into Central America and Mexico (Fig. 6.4b). The northern limit of Hapalopini is represented by the Mexican genus *Magnacarina* in the Pacific coast states of Sinaloa and Nayarit (Mendoza et al. 2016).

Finally, members of the tribe Theraphosini uniquely possess Type I urticating setae (except for the genus *Theraphosa*) and most genera have Type I in combination with Type III; Type IV is conspicuously absent in this tribe (Turner et al. 2018). Theraphosini is most diverse in tropical regions of South America but numerous genera are distributed throughout Central America, some Caribbean islands, Mexico, and northward into the southwestern United States (Fig. 6.4c; Turner et al. 2018).

Pérez-Miles and Perafán (2015) concluded that the genera that only possess Type III urticating setae (but without type I or IV) are widely distributed throughout most of the Neotropics with the exception of the Antillean subregion and the Southeastern Amazonian dominion (Morrone 2014c). On the other hand, the co-occurrence of types I and III urticating setae (which is the most common combination in Theraphosinae) is widespread throughout the Neotropics (Morrone 2014c) and into the Neartic (Morrone 2014c).

The widespread distribution of type III setae occurring alone or in combination with other types of urticating setae supports the hypothesis that type III is the ancestral condition for Theraphosinae (Pérez-Miles et al. 1996; Bertani and Guadanucci 2013; Turner et al. 2018). The unique presence of type I (without co-occurrence of type III) is interpreted as a secondary loss of type III setae (Pérez-Miles et al. 1996; Bertani and Guadanucci 2013; Turner et al. 2018) and mainly occurs in northern South America, Central America, and North America. This pattern could reflect differential ecological pressures between these areas given that type I setae are used more in passive defense (Pérez-Miles and Perafán 2015). Moreover, the presence of type III setae in Mexico (e.g., *Brachypelma*) supports the hypothesis that portions of the Neotropical entomofauna migrated into the Nearctic (Halffter 1987; Morrone 2005).

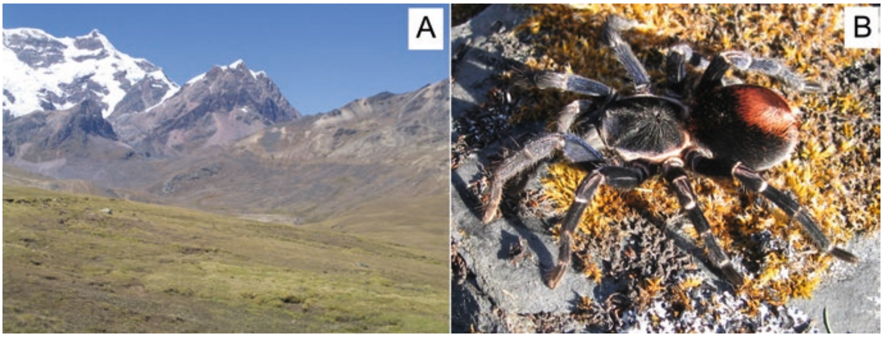

Fig. 6.5 (**a**) High altitude habitat of *Hapalotremus* species at Cordillera Vilcanota in Peru, at about 4000 m high, (**b**) *Hapalotremus carabaya*, habitus. Photos: Tracie Seimon

6.3.3 Elevational and Latitudinal Limits for New World Tarantulas

There are relatively few tarantula species found living at high elevations (most species are distributed below 1600 m) but particularly two genera (*Bistriopelma* and *Hapalotremus*) have been documented from 4000–4500 m high up in the Peruvian Andes (Kaderka 2015; Ferretti et al. 2018), and represent the highest elevations reported for theraphosid spiders (Fig. 6.5). Other genera with at least some high-elevation members include *Euathlus* in Chile and Argentina (up to 3200 m, Perafán and Pérez-Miles 2014; Ferretti 2015), *Cyclosternum* in Ecuador (around 3000 m, Perafán 2017), *Hemirrhagus* in Mexico (around 3000 m, Mendoza-Marroquín 2014a), *Cyriocosmus* in Peru (up to 3000 m, Pérez-Miles and Weinmann 2009), *Aphonopelma* in the United States (up to 2850 m, Hamilton et al. 2016; Hendrixson personal observation), *Bonnetina* in Mexico (around 2700 m, Ortiz and Francke 2017), and from Colombia *Agnostopelma* (up to 3000 m, Pérez-Miles and Weinmann 2010), *Aguapanela* (up to 2400 m, Perafán et al. 2015), and *Neischnocolus* (up to 2400 m, Perafán 2017).

In the United States, the theraphosine *Aphonopelma iodius* appears to reach the northernmost latitudinal limit for tarantulas (near 42°N) in the state of Utah (Hamilton et al. 2016). Interestingly, there are no reliable observations of this species in southern Idaho despite its close proximity (<40 km) to the border. The southern latitudinal limit for theraphosids (near 47°S) is reached by the theraphosine *Euathlus* sp. at the province of Santa Cruz in Argentina (Ferretti personal observation).

6.3.4 Islands

Insularity is one of the most interesting and important concepts for students of biogeography to understand in that it can reveal the evolutionary processes involved in generating and maintaining biodiversity. Islands tend to be less biologically complex than their continental counterparts and therefore provide the ideal geographical and historical settings for studying these phenomena. If the timing of an island's formation is known, such studies can be conducted within a well-defined time frame. Moreover, if an island is part of an archipelago, each island represents a natural repeated experiment and therefore provides increased statistical power for testing ideas related to the patterns and processes of island biogeography (Parent et al. 2008).

MacArthur and Wilson (1967) famously proposed their "Theory of Island Biogeography" and surmised that the number of species on an island is in a dynamic equilibrium between immigration and extinction (Fig. 6.6). They also considered how an island's size and distance from the mainland affect these two parameters (Fig. 6.6). Island size largely affects extinction rate (i.e., small islands have higher extinction rates compared to larger islands) whereas distance from the mainland primarily affects immigration rate (i.e., close islands have higher immigration rates compared to islands further away). In this way, a large island that is close to the mainland is predicted to harbor more species than a small island that is far from the mainland due to a combination of its higher immigration and lower extinction rates. This model remains fundamentally important in biogeography but downplays the importance of in situ speciation and diversification. Species arriving at oceanic islands may undergo speciation and adaptive radiations (Schluter 2000; Ricklefs and Bermingham 2008) such that species richness may not entirely depend on successful immigration and colonization. Doubtless, one reason why the species richness-area relationship has been so well established in different models without consideration of speciation is that the impact of speciation on species richness can be expected to be in the same direction as the impacts of colonization and extinction.

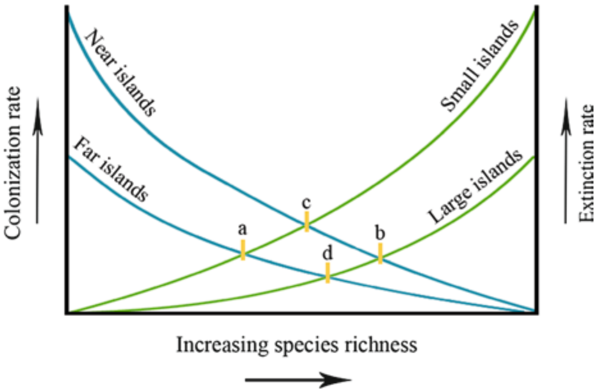

Fig. 6.6 The number of species on an island is set by equilibrium between colonization rates and extinction rates. (**a**) Small far islands have few species in the equilibrium state, (**b**) Large near islands have many species in equilibrium, (**c**) Small and near islands, and (**d**) Large and far islands have an intermediate number of species. Modified version of the island biogeography model proposed by MacArthur and Wilson (1967); taken from: http://www.islandbiogeography.org/

Spiders have figured prominently in studies of island biogeography (e.g., see http://www.islandbiogeography.org, Gillespie 2002; Pugh 2004; Kuntner and Agnarsson 2011; Agnarsson et al. 2018, and many others) but no such studies exist for New World theraphosids despite their occurrence on several Caribbean islands. For those taxa that inhabit these islands, some genera are endemic whereas others include congeners that can also be found on the mainland. The monotypic genera *Antillena*, *Cubanana*, and *Nesipelma* are endemic to specific islands including Hispaniola (Dominican Republic), Cuba, and Nevis Island (Saint Kitts and Nevis), respectively. The genera *Caribena* and *Cyrtopholis* are likewise endemic to various Caribbean islands but are more broadly distributed among them. Genera that occur on Caribbean islands and the mainland include *Acanthoscurria*, *Avicularia*, *Citharacanthus*, *Holothele*, *Neoholothele*, *Phormictopus*, *Psalmopoeus*, *Tapinauchenius*, and *Trichopelma* (World Spider Catalog 2019).

Very little is known about New World theraphosids on islands outside of the Caribbean region. In the United States, *Aphonopelma anax* has been observed on South Padre Island (Hamilton et al. 2016), a narrow barrier island located in the Gulf of Mexico near the main coastline of Texas. Theraphosids are conspicuously absent from California's Channel Islands despite the occurrence of other dispersal-limited arachnids there (e.g., Bryson et al. 2013b). In Mexico, reliable records of tarantulas have been reported from several islands in the Gulf of California, on Isla María Madre off the coast of Nayarit, and on Islas Coronado off the Pacific coast of northern Baja California (see https://www.inaturalist.org/observations?place_id=6793&taxon_id=47424).

There are few islands in the Tropical Eastern Pacific and most of them are located far from the mainland so it is not surprising that there are very few records of theraphosids (and mygalomorphs in general) on these islands. Nevertheless, a species of *Neischnocolus* and an unidentified ischnocoline have been confirmed on Isla Gorgona off the coast of Colombia (Rico-G et al. 2005; Perafán personal observations).

6.3.5 Caves

Caves are natural cavities on the Earth's surface that extend to depths where sunlight is unable to penetrate. They are generally formed through mechanical or chemical weathering processes but other types of caves such as lava tubes and talus caves are formed through different geological processes (e.g., volcanic activity and rockfalls, respectively). Most cave systems consist of surface-subsurface hydrological connections within a drainage basin, but lithological and tectonic constraints often limit connectivity of passages across drainage basins. As a consequence, most cave systems are discontinuous and can be considered biogeographic islands (Romero 2009).

Cave-adapted organisms generally have small distributions and exhibit high levels of endemism, with many species restricted to single caves (Christman et al. 2005). These distinctive geographic patterns have led researchers to investigate a variety of questions regarding how organisms colonize, adapt, and persist in subterranean environments (Romero 2009). It is largely recognized that the distributions of cave-adapted organisms can be explained by a combination of both dispersal and vicariance events, reflecting the processes that likely occurred in ancestral surface populations before they colonized the subsurface (Porter 2007).

Although the environmental conditions inside caves remain fairly stable over time (e.g., constant temperature, high humidity), cave-adapted organisms face many unique challenges. In addition to living in a world of total darkness, these organisms must also deal with limited food availability and access to mating partners. Consequently, cave-adapted fauna often present a unique suite of regressive (e.g., reduction or loss of eyes and pigment, thinning of the cuticle) and/or progressive (e.g., appendage elongation, enhanced sensitivity to non-visual stimuli) traits known as troglomorphies (Christiansen 1962). Many studies have thus focused on answering the following question: "Was the ability to live in subsurface habitats derived from preadaptive metabolic, behavioral, or even genetic traits of ancestral individuals, or was it from genetic modification or phenotypic plasticity of individuals over countless generations?" (Romero 2009).

Not all animals associated with cave environments have such adaptations, however. As such, cave fauna can be placed into three categories based on the amount of time they spend in caves. Trogloxenes are temporary cave residents which freely move in and out of caves but never spend their entire life cycle inside them. Troglophiles can spend their entire life cycle in the dark zones of a cave but can also survive outside of caves. Troglobites are the "true cave dwellers" (with troglomorphies) that spend their entire life cycle in the dark zone of caves and cannot survive on the surface (Trajano 2012).

Even though Theraphosidae comprises mostly sedentary spiders (as is the case for mygalomorphs in general), only a few species have been observed associated with caves. *Dolichothele tucuruiense*, *Hapalopus aymara*, *Acanthoscurria geniculata*, *Theraphosa blondi*, *Nhandu coloratovillosus*, *Guyruita metallophila*, *Hapalopus serrapelada*, and *Holothele longipes* have been observed in cave environments but are considered trogloxenes or troglophiles (Fonseca-Ferreira et al. 2017; Guadanucci et al. 2017). The only described troglobitic theraphosids include *Tmesiphantes hypogeus* from two caves in Bahia State, Brazil; *Trichopelma maddeni* (originally placed in Barychelidae but subsequently transferred to Theraphosidae by Guadanucci 2014) from Cueva Seibo in Altagracia Province, Dominican Republic (Bloom et al. 2014); and *Hemirrhagus* spp. in Mexico (see below). An undescribed species that has been discovered from a cave in Colombia is the only theraphosid known that lacks scopulae on all of its tarsi (the presence of claw tuft and Type IV urticating setae confirm its placement in Theraphosidae) (Perafán personal observations). We interpret the loss of scopulae in this specimen as an adaptation for living in caves. The unique presence of claw tufts in the absence of scopulae in Mygalomorphae has only been reported in a species of the paratropidid genus *Melloina* which interestingly also inhabits caves (Bertani 2013; Perafán personal observations).

The genus *Hemirrhagus* is fascinating from a biogeographic and evolutionary standpoint. More than half of the 27 described species have been collected from inside caves (Mendoza-Marroquín 2014a; Mendoza and Francke 2018) and in at least one case, two species (*H. grieta* and *H. billsteelei*) occupy different depths within the same cave (Cueva de la Grieta in Oaxaca). Several cave-dwelling species are bona fide troglobites that possess well-defined troglomorphies (e.g., reduction in size or complete loss of eyes, reduction of ocular pigmentation, elongation of appendages, loss of urticating setae). Future phylogenetic work (also see Pérez-Miles and Locht 2003) should help elucidate a variety of interesting biogeographic phenomena in this captivating genus.

6.3.6 Exotic Species Introductions

The native range of tarantulas in the United States (genus *Aphonopelma*) is bound longitudinally by the Pacific Ocean to the west and the Mississippi River Embayment to the east (Hamilton et al. 2016). However, *Tliltocatl vagans* (native to Central America and southern Mexico) has reportedly become established in South Florida (Edwards and Hibbard 1999). The exact origin of the Florida population is unknown but it is suspected to be from exotic pet trade specimens that were released or escaped from captivity. There have been no follow-up studies on this introduced population so it is unclear if these tarantulas have become invasive.

6.4 Historical Events Affecting the Distributional Patterns of New World Theraphosids

The mygalomorph fossil record extends as far back as the Triassic (Selden and Gall 1992; Dalla Vecchia and Selden 2013) but recent phylogenetic and molecular clock analyses suggest that the group is considerably older, placing the root node of Mygalomorphae in the Permian (Garrison et al. 2016), Carboniferous (Opatova et al. 2019), or even the Devonian (Hedin et al. 2019). The oldest mygalomorph known to date is *Rosamygale rauvogeli*, found at the Triassic locality in the Vosges, France (Selden and Gall 1992) and was provisionally assigned to the family Hexathelidae. A Triassic atypoid was described from Italy (Dalla Vecchia and Selden 2013) while other Mesozoic mygalomorphs include members of "Dipluridae" found in Brazil dating from 115 Ma (Selden et al. 2006) and a representative of "Nemesiidae" found in the United Kingdom dating from 90 Ma (Selden 2002). A particular rich mygalomorph fauna was described from the Cretaceous (Eskov and Zonshtein 1990), including representatives of the family Atypidae, Antrodiaetidae and Mecicobothriidae. Those authors proposed with their findings that could be related with an "age of mygalomorphs" during the Mesozoic when mygalomorphs could be the predominant spiders.

But what about the age of Theraphosidae? Despite being the most diverse mygalomorph family with approximately 1000 described extant species, only three fossils have been convincingly assigned to the group [all of Neogene (Miocene) age]: *Ischnocolinopsis acutus* from Dominican amber (Wunderlich 1988) and two species (*Hemirrhagus* sp. and an unidentified genus) from Chiapas amber (García-Villafuerte 2008; Dunlop et al. 2008). Two recent studies (Ortiz et al. 2018; Opatova et al. 2019), however, place the root node of Theraphosidae in the Cretaceous (discussed in more detail in the next section).

Below, we summarize the main paleoenvironmental changes of the New World from the Cretaceous to the present (with some earlier historical context), emphasizing the relationships between biomes and the geological forces that, through different climatic-environmental factors, could have driven the evolution and distribution of the New World tarantula fauna. Because Theraphosidae likely originated in Gondwana (see Opatova et al. 2019), much of the following review concerns the history of South America.

6.4.1 Origin and Diversification of the New World Theraphosid Fauna

The most significant events concerning the origin and diversification of the New World tarantula fauna are related to the isolation of South America from Gondwana, dramatic changes in land-sea geographical patterns (e.g., continental drift, changes in sea level, formation of dispersal corridors), uplift and deformation events of the American Cordillera, additional consequences of plate tectonics during the Cenozoic, and climatic variations during the Pleistocene (Gentry 1982; Palminteri and Powell 2001; Rull 2018).

North and South America (as parts of Laurasia and Gondwana, respectively) were joined together as part of the supercontinent Pangea during the Carboniferous up until their initial separation in the early Jurassic ca. 185 Ma (Veevers 2004). From then, Gondwana continued fragmenting and South America began separating from Africa in the early Cretaceous (ca. 130–110 Ma). The South America-Australia connection (via Antarctica) occurred up until at least the late Cretaceous (ca. 80 Ma). During the Oligocene (ca. 30 Ma) South America completed its transformation into an island continent after its definitive separation from Antarctica and the opening of Drake Passage or Sea of Hoces.

The composition of South America's biota was and is very much dependent upon those periods of connection and fragmentation. Until the early Cretaceous, the flora and fauna of South America were connected to the remainder of Gondwana through a system of corridors. The eventual separation and isolation of South America ultimately resulted in the evolution of the continent's unique biota (Smith and Klicka 2010). At the beginning of the Cenozoic, however, occasional long-distance dispersal events and temporary corridors (e.g., land bridges, island arcs) created opportunities for organisms to colonize South America after its split. The organisms that utilized these corridors became an integral part of the South American biota (Simpson 1980; Oliveira et al. 2009; Chávez Hoffmeister 2016).

When the biotic exchanges between South America and the remainder of Gondwana began to decline, they increased between South America and North America. It is generally accepted that North and South America remained separated until the Pliocene but the closure of the Isthmus of Panama may have been completed as early as the Miocene (Coates and Stallard 2013; Montes et al. 2015, but see O'Dea et al. 2016). Regardless, numerous trans-oceanic corridors permitted biotic exchanges between the two continents—albeit sporadically (Woodburne et al. 2006; Woodburne 2010)—prior to the Pliocene (Chávez Hoffmeister 2016). But during the Pliocene, following the *definitive* closure of the Isthmus, there were no longer any major barriers blocking the passage of biotas between North and South America; Central America became a terrestrial bridge linking the two continents. This newly formed corridor permitted mass migration of continental faunas between North and South America, particularly during the late Neogene and early Quaternary, and is known as the Great American Biotic Interchange (GABI) (Woodburne 2010). GABI is considered one of the most important biogeographical events that has shaped the composition of the modern fauna on both continents (Chávez Hoffmeister 2016).

Although GABI is considered to have been a bidirectional process, it appears that movement mostly occurred in the north to south direction, at least initially (Chávez Hoffmeister 2016). The evidence for theraphosids, however, suggests that the migration mainly occurred in the south to north direction. This hypothesis is supported by the presumed Gondwanide origin of the family, the group's high diversity (including endemics) in South America, and recent molecular phylogenetic analyses (Opatova et al. 2019).

As noted above, theraphosids occupy several Caribbean Islands. As is the case for many island biotas, over-water dispersal has been evoked to explain the origin of the Caribbean fauna (e.g., Hedges et al. 1992). However, some researchers think that a land bridge may have also played a role. This idea, known as the GAARlandia hypothesis (Iturralde-Vinent and MacPhee 1999), suggests that a terrestrial connection between South America and the Greater Antilles existed for one- to two million years during the mid-Cenozoic (ca. 34 Ma). GAARlandia has been criticized by some authors (e.g., Ali 2012) but a few recent studies (including some on araneomorph spiders) show evidence in support of it (e.g., Chamberland et al. 2018; Tong et al. 2019). Future biogeographical research on Caribbean theraphosids may provide additional insight on the GAARlandia hypothesis.

The uplift of the Andes during the Mesozoic produced a diverse number of new environments and brought with it a profound impact on the history of the continent's biota (Palminteri and Powell 2001). In the late Eocene, the northern Andes were isolated by a Pacific marine incursion known as the "Western Andean Portal" or "Guayaquil Gap" (Antonelli et al. 2009). Subsequently, with the closure of this marine incursion and the gradual uplift of the Eastern Range, the Andes played an important role that can be summarized by three main points: (1) they have acted as an important dispersal route throughout South America (Antonelli et al. 2009); (2) they represent the most recent separation between the Amazonian and western biotas (Hernández-Camacho et al. 1992); and (3) they have formed a major barrier between the crossing American biota. Their formation has also led to rapid diversification through allopatric fragmentation and ecological specialization in the highlands (Antonelli et al. 2009).

During the Paleocene–Oligocene (ca. 65–55 Ma) in southern South America, the sequences of the Andean dominion showed considerable variation in depositional regimes from north to south, and consequently volcanic rocks were deposited from southwestern Peru to Puna latitudes (Pascual et al. 1996; Ortíz-Jaureguizar and Cladera 2006). The absence of large continental topographic barriers allowed a widespread Atlantic marine incursion during the late Cretaceous and early Paleocene. This seaway covered most of southern South America from Patagonia to Bolivia and Peru. Consequently, the continent was divided into northeastern and southeastern sections (Pascual et al. 1996; Ortíz-Jaureguizar and Cladera 2006). During much of the Paleocene, the Atlantic incursion was transformed into a series of broad alluvial plains and large lake basins (Ortíz-Jaureguizar and Cladera 2006).

During much of the Eocene (ca. 55–33 Ma), the geological characteristics were largely similar to that of the Paleocene. Toward the end of the Eocene, however, tectonic deformation in the Andean basin of Bolivia, Peru, and southern Argentina/Chile occurred (Salfity and Marquillas 1999). This reactivation and uplift of the southern Andes correlated with a sharp marine regression (Haq et al. 1987). By the late Oligocene and early Miocene (ca. 26–20 Ma), the present structural configuration of the Andes began to develop and as a consequence, a new Atlantic marine incursion occurred as well as a Pacific incursion along the west margin of South America (Malumián 1999).

During the mid-Miocene (ca. 17 Ma), landscapes in the southern Neotropics were dominated by the processes that led to the present configuration of the Andes (Uliana and Biddle 1988). Successive Atlantic incursions separated terrestrial environments and spread over virtually all of eastern Argentina, western Uruguay, southern Paraguay, and southeastern Bolivia (Pascual et al. 1996). The northwestern part of this incursion covered widespread areas among the Andean chain and the Guayanian and Brazilian bedrocks (see Rässänen et al. 1995; Webb 1995; Ortíz-Jaureguizar and Cladera 2006). At this time, a significantly higher equator-to-pole thermal gradient developed (Ortíz-Jaureguizar and Cladera 2006). During the late Miocene and early Pliocene (ca. 11–3 Ma), the widespread marine incursions were succeeded by the spread of vast plains, extending from northern Patagonia to central and northern Argentina, Uruguay, along the eastern slopes of the Andes in northern Bolivia, southern Peru, Venezuela, and into the upper Amazon Basin (Pascual et al. 1996; Ortíz-Jaureguizar and Cladera 2006). This event was correlated with a new uplift in the main Andean chain ca. 14–10 Ma that progressively produced a major barrier to moisture-laden south Pacific winds (Riccardi and Rolleri 1980; Ortíz-Jaureguizar and Cladera 2006). This produced a rain shadow in the eastern

Patagonian landscapes that led to the first stages on the differentiation of the present biogeographic subregions in southern South America (Pascual et al. 1996).

The modern Amazon Basin was formed during the Miocene when the Andean uplift caused a major shift in the drainage patterns of northern South America. Up until the early Miocene, most drainages of the western Amazon region were directed to the north. By the late Miocene, the Andean uplift drastically changed this pattern and formed the huge Amazon and Orinoco River systems that drain eastward into the Atlantic Ocean (Hoorn et al. 1995; Rull 2018). During the Pliocene (ca. 5–2 Ma), a new orogenic phase uplifted the Southern Andes in Argentina and Chile, the eastern orographic systems in Argentina, and the Mesopotamia region (Ortíz-Jaureguizar and Cladera 2006). This event resulted in a series of drastic climatic and ecological changes to the region including the extreme aridity and climatic conditions of the Puna (e.g., Atacama Desert) we see today.

The "Tertiary" (Paleogene and Neogene) and Quaternary periods can largely be differentiated on the basis of the amplitude and frequency of environmental changes that occurred during those times. As Ortíz-Jaureguizar and Cladera (2006) stated: "*During the Tertiary, the geologic and biotic records apparently show long periods of uniform environmental conditions, sporadically interrupted by geologically short but highly disruptive periods of change. Contrarily, the climatic changes that occurred during the Quaternary had larger amplitude and frequency.*" As a consequence, the biotic composition (both taxonomic and ecological) largely changed by means of cladogenesis, extinction, and migration during Paleogene and Neogene whereas distributional shifts (e.g., contractions and expansions) occurred more during the Quaternary. During the Pleistocene (2.5–0.01 Ma), the South American fauna was primarily affected by periods of glaciation and the arrival of North American immigrants (Pascual et al. 1996; Ortíz-Jaureguizar and Cladera 2006). Glacial cycles caused the expansion and contraction of arid (e.g., savannas, steppes) and humid (e.g., tropical and subtropical forests) biomes. During cold and dry climates, humid biomes contracted and a savanna corridor formed along the eastern Andes, linking the steppes and grasslands of southern Argentina with those of Colombia. These biomes continued northward across the Panamanian land bridge into southeastern North America (Webb and Rancy 1996). Conversely, when open areas retreated during interglacial periods, rainforest biomes were uniformly distributed throughout the North and South American tropics (Webb and Rancy 1996).

Orogenic and tectonic activity, marine incursions, and climatic fluctuations during Cenozoic Era played similarly important roles in shaping North America's biota. Many of the continent's mountain ranges were uplifted during this time providing the impetus for the origin and spread of several unique biomes (e.g., North American deserts, Madrean pine-oak woodlands) that harbor tarantulas today. The separation of Baja California from mainland Mexico during the Miocene-Pliocene along with its significant latitudinal coverage and diversity of habitats has resulted in the evolution of numerous endemic taxa along the peninsula, especially arthropods (e.g., Johnson and Ward 2002; Williams 1980). In addition, extensional tectonics in the Basin and Range Physiographic Province of northern Mexico and the western United States has presumably isolated some montane biotas through the creation of low-elevation barriers (e.g., Bryson et al. 2013a, b; Graham et al. 2015).

The Pleistocene glaciations had a tremendous impact on the North American fauna, especially those taxa found in more northern latitudes (e.g., the southwestern United States). The rapidly changing climate during glacial periods affected organisms by shifting their distributions, habitats, and population sizes, causing frequent and repeated extinctions. As a consequence, large numbers of organisms are thought to have experienced a general shift to more southern latitudes and lower elevations during glacial maxima, and often occupying a distributional range very different than the one in which they are found today (Hamilton et al. 2011). During interglacial periods, the opposite trends are expected and these predictions have been supported by numerous phylogeographic studies. Southern populations often exhibit relatively high amounts of genetic variation whereas their northern counterparts tend to possess much lower amounts of variation. It is hypothesized that the greater diversity of alleles found in southern populations is the result of their persistence in refugia which allowed them to accumulate genetic variation during the glacial-interglacial cycles. Conversely, the lack of diversity in northern populations is thought to be due to "founder effects" caused by rapid post-glacial expansion into more northern latitudes (Hewitt 1999, 2004).

6.5 Published and Ongoing Research on the Biogeography of New World Tarantulas

Despite a growing body of literature on the biogeography of mygalomorphs, only a handful of studies have explicitly examined or discussed the biogeography of New World theraphosids. Below, we review some of these studies and also include a brief discussion of ongoing research on the biogeography of North American tarantulas.

6.5.1 Divergence Dating

Very few researchers have investigated phylogenetic relationships involving Theraphosidae but even fewer have incorporated molecular divergence dating analyses into their studies. Recent higher-level research on Mygalomorphae places the divergence between Theraphosidae and Barychelidae in the Cretaceous (Ayoub et al. 2007; Bond et al. 2014; Garrison et al. 2016; Ortiz et al. 2018; Opatova et al. 2019) but only two studies have investigated the timing of divergence between multiple New World genera (Note: Hamilton et al. (2011) and Graham et al. (2015) also employed molecular clocks in their studies but focused on the North American genus *Aphonopelma*, see below for details). Ortiz et al. (2018) included *Hemirrhagus eros* and several theraphosine genera in their investigation of *Bonnetina*. They noted that Theraphosinae exhibits a relatively deep history and rapidly diversified into its three main lineages at a time when South America was isolated. The subfamily remained confined in South America for millions of years before expanding to Central and North America and the Caribbean islands. Interestingly, Ortiz et al. (2018) also suggested that the colonization of Central America and Mexico by Hapalopini may have occurred as a single event during the Oligocene (ca. 30 Ma), long before the rise of the Isthmus of Panama. Dispersal across such a formidable barrier seems unlikely for tarantulas but similar patterns have been observed in other mygalomorphs with limited dispersal capabilities (Opatova and Arnedo 2014b; Harrison et al. 2017). Opatova et al. (2019) included nine tarantulas in their study of mygalomorph phylogeny, six of which were from the New World. The ischnocoline *Catumiri parvum* diverged from the remaining theraphosids during the Cretaceous and several theraphosine genera from Central and North America diverged from each other during the Neogene.

The molecular phylogenies presented by Lüddecke et al. (2018) and Foley et al. (2019) have improved higher-level sampling for Theraphosidae but neither study included divergence dating analyses.

6.5.2 South America

Bertani (2001) was among the first to explicitly investigate the biogeography of New World theraphosids. He used cladistic biogeography to investigate patterns of endemism and identified a few biogeographical patterns, including a disjunction between a larger northwestern track and smaller southeastern track (Bertani 2001). The proposed northwestern track included Central America, the northwestern part of South America, and the eastern part of the Amazon. This is supported by the geographical distribution of the genera *Theraphosa*, *Pamphobeteus*, *Xenesthis*, *Brachypelma*, *Megaphobema*, and *Sericopelma*. A probable vicariant event related to the division of the Amazon by a lake along the Amazonas, Madeira and Mamoré Rivers during the Late Cretaceous (Amorim and Pires 1996) was considered responsible for the separation (Bertani 2001).

A southeastern track was found to be correlated with the geographical distributions of *Nhandu* and *Vitalius* which are primarily found in the Atlantic Forest of southeastern Brazil (Bertani 2001). It was presumed that their distributions could be related to historical geological events that took place in the region. For example, the formation of the Serra do Mar and Serra da Mantiqueira mountain systems (Oligocene to Pleistocene) and the peripherial depression along the eastern boundary of Paraná Basin (Cenozoic Era) are congruent with the observed distributions (Ross 1996; Bertani 2001).

Bertani (2001) also found that *Proshapalopus amazonicus* was separated from its sister group (formed by *P. anomalus* and *P. multicuspidatus*) by a region characterized by more open vegetation. A possible explanation for the absence of *Proshapalopus* in this area could be due to an extinction event that resulted from environmental changes associated with the Quaternary glacial cycles (Vivo 1997).

Recently, *P. marimbai* was described from the Chocó Region of western Colombia, greatly expanding the known distribution of the genus (Perafán and Valencia-Cuellar 2018). Even though the authors warn about the inclusion of this species within *Proshapalopus* due to a lack of taxonomic studies in the region, they argued that if the species does indeed belong to genus, it suggests a highly fragmented evolutionary history between the Amazon Forest, Atlantic Forest, and Chocó Region. The environments where these species are currently distributed have similar characteristics: dense vegetation, high temperature, and high humidity with significant amounts of rain. This provides additional evidence of the connections between the eastern and western biota of northern South America, since separated by the uplift of the northern Andes (Antonelli et al. 2009; Perafán and Valencia-Cuellar 2018).

Guadanucci (2011) constructed an area cladogram from a cladistic analysis of the genus *Oligoxystre* (since synonymized with *Dolichothele*) and provided a discussion related to the origin of the group. Based on the cladogram, he concluded that the monophyly of species distributed in the northeastern Brazilian Cerrado (*D. bolivianum*, *D. dominguense*, and *D. diamantinensis*) suggests a single diversification event within the region as well as a historical relationship between the Cerrado and Caatinga plus Amazonia. On the other hand, observed sympatry between two distantly related species in Caatinga (*D. caatinga* and *D. rufoniger*) suggested the lineages diverged allopatrically but one may have dispersed after its original location. Finally, Guadanucci (2011) highlighted the importance of the Serra do Espinhaco and its role in shaping distribution patterns of *Dolichothele*. It represents the longest pre-Cambrian orogenic belt of the Brazilian territory (ca. 1200 km) and is composed of a series of hills and tablelands that vary between 900 and 2000 m in elevation. The range separates three major river basins (Bacia do Rio São Francisco, Rio Jequitinhonha, and Rio Doce) and represents the limit for the three major biomes in Brazil (Caatinga, Cerrado, and Atlantic Forest) (Almeida-Abreu and Renger 1998; Guadanucci 2011). Not surprisingly, the mountain range has been recognized for its high levels of endemism.

Ferretti et al. (2012) took a formal approach to understanding the historical biogeography of the genus *Cyriocosmus* in the Neotropics. The authors proposed that the genus could have originated in the areas of Amazonian and Paramo-Punan. During the late Oligocene and early Miocene, those areas could be considered a single unit due to their homogeneous climates (Donato 2006; Ortíz-Jaureguizar and Cladera 2006), and in the pre-Quaternary, the South American Neotropical biota expanded northward to Central America and Mexico and southward to Paramo-Punan and the Andean region (Ferretti et al. 2012). Some of the vicariant events identified that could have shaped the present geographical distribution of *Cyriocosmus* species appear related to geological changes during the Miocene. For example, the separation of an Amazonian clade (formed by *C. fasciatus* and *C. fernandoi*) from the Caribbean clade (*C. elegans* and *C. leetzi*) could be the result of the Atlantic marine transgression and a new phase of Andean orogenesis during the Middle and Late Miocene (Ferretti et al. 2012). In addition, the equator-to-pole thermal gradient registered during the Middle Miocene could have acted as a barrier that split *Cyriocosmus bertae* in the north from *C. versicolor* in the south (Ferretti et al. 2012).

Bertani (2012) discussed the biogeography of the aviculariine genera *Typhochlaena*, *Pachistopelma*, and *Iridopelma* in northeastern Brazil. He noted that the distributions of congeners never overlapped and most of the identified areas of endemism were concordant with river systems as has been proposed for Atlantic rainforest in northeastern and southeastern Brazil (Pellegrino et al. 2005; Bertani 2012). One of these endemic regions (occupied by *Iridopelma hirsutum*, *Pachistopelma rufonigrum*, and *Typhochlaena curumim*) is located from the State of Ceará–Río Grande do Norte southward to the State of Alagoas (Bertani 2012). To the south, a second area of endemism (occupied by *Iridopelma zorodes*, *Pachistopelma bromelicola*, and *Typhochlaena seladonia*) was identified between Rio São Francisco and Rio Paraguaçú. An additional area of endemism (occupied by *Typhochlaena pschoali*, *Avicularia diversipes* and *A. gamba*) from Rio Paraguaçú south to Rio Jequitinhonha was proposed. Finally, the southernmost area of endemism for aviculariines was recognized between Rio Doce and Rio Paraíba do Sul with *Typhochlaena amma* as the species endemic to this region (Bertani 2012).

At least two hypotheses have been proposed to explain the existence of regional endemism within the Atlantic forest of northeastern and southeastern Brazil (Pellegrino et al. 2005). The first states that the region experienced a semiarid climate through the late Miocene and early Pliocene. Later in the Pliocene, however, the region experienced higher humidity and rainfall resulting in the formation of the major river systems that are observed today. These rivers bisected deposits of the Barreiras Formation (Suguio and Nogueira 1999) and ultimately isolated the interriverine regions from each other. Other authors (e.g., Carnaval and Mortiz 2008) provide evidence for the existence of forest refugia during the Quaternary that are congruent with areas of endemism known for Atlantic Forest in northeastern Brazil.

In the same region of the Brazilian Atlantic Forest, Fabiano-da-Silva et al. (2015) provided notes on the biogeography of some species of *Tmesiphantes*. They argued that the occurrence of four sympatric species (three of which are endemic to the southern Bahia) supports the hypothesis that the forests remained relatively stable and served as refugia throughout the Quaternary (Carnaval and Mortiz 2008). The region has also been recognized as relevant area of endemism in the Atlantic Forest (DaSilva and Pinto-da-Rocha 2011; Fabiano-da-Silva et al. 2015).

Perafán (2017) used panbiogeographic analyses to study the distribution and patterns of endemicity of mygalomorph spiders in the Northern Andes, one of the most biodiverse regions of the world (Cuesta et al. 2009). Results from this research suggest that the Northern Andes do not represent a single biogeographical unit, but instead, comprises two distinct units (i.e., a northern and southern section) that were historically separated and isolated during gradual uplift of the range. The northern unit corresponds to the northern portion of the Central and Western Ranges (Colombia), the Eastern Range (Colombia), and the Mérida Range (Venezuela) whereas the southern unit includes the Ecuadorian Andes and southern portion of the Colombian Andes. The northern unit is supported by the distributions of *Aguapanela arvi*, *Cyriocosmus leetzi*, *Euthycaelus amandae*, *E. norae*, *Hapalopus triseriatus*, *Holothele longipes*, *Neischnocolus weinmanni, Pamphobeteus fortis*, *P. nigricolor*, *P. verdolaga*, *Psalmopoeus emeraldus*, *Pseudhapalopus* *spinulopalpus*, *Schismatothele olsoni*, *S. weinmanni*, *Xenesthis immanis*, and *X. intermedia*. The southern unit is supported by *Avicularia purpurea*, *Cyclosternum schmardae*, *Megaphobema velvetosoma*, *Pamphobeteus augusti*, *P. insignis*, *P. vespertinus* and *Psalmopoeus ecclesiasticus*.

The northern section of the Northern Andes also suggests a historical connection between the Magdalena Valley and northern part of the Cauca valley (both in Colombia) (Perafán 2017). Additionally, there is evidence for a historical connection between the Mérida Range and Cordillera de la Costa (Venezuela). The latter region is a major center of endemism for mygalomorphs, harboring approximately one-third of the species known from the country. The distribution patterns of the mygalomorphs also allowed Perafán (2017) to infer different areas of endemism and other biogeographical units of unique co-occurrence of species (Crother and Murray 2011), which are related to historical and current biogeographic processes. These areas were mainly found in the foothills and the inter-Andean valleys, to the north of Ecuador and in the center of Colombia.

6.5.3 Mexico

The theraphosid fauna of Mexico is quite diverse (Table 6.1) and interest in the group has been revitalized in the past decade. Even though few studies have explicitly discussed biogeographical patterns or processes in Mexico, several recent taxonomic revisions and species delimitation accounts have been published that provide the foundation for future biogeographic research (e.g., Mendoza-Marroquín 2014a; Ortiz and Francke 2016, 2017; Candia-Ramírez and Francke 2017; Mendoza et al. 2016; Mendoza and Francke 2017, 2018; Ortiz et al. 2018). In their taxonomic revision of the red-kneed species of *Brachypelma* in Mexico, Mendoza and Francke (2017) noted that the Balsas River Basin acts as a geographic barrier between the morphologically similar species *B. smithi* and *B. hamorii*. Ortiz and Francke (2017) suggested that the surprisingly high diversity of *Bonnetina* in central and southern Mexico can be attributed to the region's geological and ecological complexity as well as its proximity to five biotic provinces. Diversification within *Bonnetina* appears to have largely taken place during the Miocene (Ortiz et al. 2018), a period of intense geological activity in Mexico (e.g., Gans 1997; Molina-Garza et al. 2015).

6.5.4 United States

Although there are some questions regarding the generic placement of tarantulas in the United States (see Turner et al. 2018), the diversity and distribution of these spiders is fairly well understood (Hamilton et al. 2011, 2014, 2016; Hendrixson et al. 2013, 2015; Graham et al. 2015). Biogeographic research on the group has proceeded more slowly, however, because we know so little about related tarantulas in northern Mexico. The origin of the US fauna (1 genus with 29 species) is certainly due to northward dispersal from Mexico but it is unclear *when* or *how many times* this happened. Despite our meager knowledge regarding the biogeography of US theraphosids, two recent phylogeographic studies have helped set the foundation.

Hamilton et al. (2011) investigated phylogeographical patterns in the widely distributed species *Aphonopelma hentzi*. Divergence dating analyses and patterns of mitochondrial haplotype diversity led the authors to suggest that *A. hentzi* likely persisted in southern refugia during the Last Glacial Maximum (LGM) but rapidly expanded northward following the LGM. They concluded that climatic fluctuations in the Pleistocene likely led to habitat retraction and fragmentation during glacial periods and to habitat expansion during interglacial periods for a number of species in the US. This prediction has been confirmed for widespread desert-dwelling species such as *A. gabeli*, and *A. vorhiesi* (Hendrixson unpublished data), can be inferred for some members of the *A. iodius* species group (see Hamilton et al. 2016), and has been documented within various lineages of the *Aphonopelma mojave* group (Graham et al. 2015).

Graham et al. (2015) investigated patterns of diversification in turret-building tarantulas belonging to the *Aphonopelma mojave* group (Hendrixson et al. 2013) in the Mojave and Sonoran Deserts. They identified six major clades within the group that originated during the Miocene with subsequent lineage diversification during the Pleistocene (see above paragraph). Interestingly, the patterns of lineage formation during the Miocene were concordant with the time frame when tectonic activity was known to have displaced regional mountain ranges in the southwestern US (McQuarrie and Wernicke 2005). As a result, Graham et al. (2015) hypothesized that the six clades were the products of vicariance as populations became isolated when displaced mountain ranges formed low-elevation valleys that operated as barriers to dispersal. The authors argued that Miocene extensional tectonics played an important role in the assembly of desert biota in the southwestern US, a hypothesis that had not received much serious attention prior.

Much work remains to be done on the biogeography of US tarantulas. Current research is focused on the assembly and diversification of *Aphonopelma* in the Madrean Archipelago Ecoregion near the US-Mexico border in southeastern Arizona and the “bootheel” of New Mexico. This region is of great biogeographical interest due to its location at the intersection of five major biotic provinces and is renowned for its exceptional biodiversity. Many taxa (including tarantulas) reach their distributional limits here (Hamilton et al. 2016), adding to the region’s biogeographic intrigue. Of particular interest are tarantulas distributed in the Madrean woodlands (Hendrixson et al. 2015; Hamilton et al. 2016), a unique habitat consisting of various pines and/or oaks that is only found at higher elevations or in cool/moist canyons associated with the numerous mountain ranges (commonly referred to as the “Madrean Sky Islands”) that span the “cordilleran gap” between the Rocky Mountains/Colorado Plateau and Sierra Madre Occidental (Mexico). These mountain ranges are separated from each other by valleys consisting of arid grassland and desert scrub habitat.

As a consequence, the Madrean woodlands where tarantulas are found are also isolated (hence the term “sky island”). Previous research indicates that the Madrean tarantula fauna is monophyletic and that individual mountain ranges are also monophyletic (Hendrixson et al. 2015, Hamilton et al. 2016). These phylogeographic patterns are consistent with a history of vicariance (rather than dispersal) in the group but neither study proposed a biogeographic explanation for these patterns. Based on information that is available for co-distributed organisms, two hypotheses that may account for this pattern of lineage diversification should be tested: climate change (e.g., Wiens et al. 2019) or extensional tectonics (e.g., Bryson et al. 2013a, b). Under the first scenario, Madrean tarantulas may have been widespread at lower elevations when climates were cooler and subsequently became isolated through local extinction when temperatures warmed. Alternatively, Madrean tarantulas may have persisted in contiguous highlands and became isolated when the highlands fragmented and rifted due to extensional tectonics. Additional sampling throughout the Madrean Sky Islands along with divergence dating analyses should resolve this matter.

6.6 Final Comments

Tarantulas are a diverse and ancient lineage that likely originated during the Cretaceous. They have cosmopolitan distribution and have adapted to living in nearly every conceivable terrestrial ecosystem, except Antarctica, from the most humid rainforests and most arid deserts to the harshest andine environments and even deep inside caves. They are long-lived, sedentary animals with limited dispersal capabilities and high levels of endemism, and have embraced fossorial, arboreal, and other lifestyles. It is no coincidence that these remarkable animals are so appealing to biogeographers; they make excellent models for understanding the ecological, evolutionary, and biogeographical processes that have helped shape the planet’s terrestrial biota. Insights gained from such studies will also facilitate our understanding of tarantula conservation, especially for imperiled groups that are at risk of extinction due to habitat destruction, climate change, and illegal trade.

Our knowledge of tarantula biogeography is still in its infancy and we are far from understanding these spiders’ full potential for biogeographical research. The most daunting challenge is simply being able to answer the questions “What is it?” and “Where is it?” The family’s problematic taxonomy and lack of collections have slowed progress in being able to define the fundamental units for biogeographical studies. Despite these issues, recent advances in molecular systematics (including species delimitation), improved analytical methods, and new international collaborations have helped accelerate progress in this field. There are so many interesting questions and it is an incredibly exciting time to be a tarantula biogeographer!

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