

Chapter 15

The Evolution and Diversification of Neotropical Generalist Herbivores: The Evolutionary History of the Grasshopper Genus *Sphenarium* Charpentier, 1842



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Abstract We present the current understanding on the diversification of the Mesoamerican genus *Sphenarium*, a group of generalist-herbivorous grasshoppers that could play a major role on the evolution of defense mechanisms and life history traits of plants along to their distribution range. We discuss their phylogenetic relationships and how geological and climatic history, as well as environmental variation, could favor their expansion and diversification. Furthermore, in a phylogenetical framework, we considered future directions on the study of their interactions with the plants with which their populations have evolved.

Keywords Neotropical region · Diversification · Quaternary speciation · Cryptic diversity · Local adaptation

Introduction

The diversity of herbivores, their host plants, and the defensive adaptations of plants to herbivory are postulated to have arisen by a long history of coevolution that has affected the food web links between these trophic levels (Ehrlich and Raven 1964). The understanding of the macroevolutionary history of interactions requires the integration of ecology, evolution, and the role of history in shaping the diversification or decline of lineages (Futuyma and Agrawal 2009; Reznick and Ricklefs 2009). Phylogenies allow us to infer a major component of evolutionary history, namely, the sequence of divergence of lineages as portrayed in phylogenetic trees (Futuyma and Agrawal 2009). They play a fundamental role to understanding the

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dynamic of communities (Kraft et al. 2007; Buckley et al. 2010; Gerhold et al. 2015); the phylogenetic evidence allows us to examine the structure of community assemblages, exploring the basis of community niche structure and adding a community context to studies of trait evolution and biogeography (Webb et al. 2002; Cavender-Bares et al. 2012; Villalobos et al. 2016).

The Evolutionary History of the Genus *Sphenarium*

The Genus Sphenarium, Its Higher-Level Phylogenetic Relationships, and Biogeographic Origin

The genus *Sphenarium* Charpentier, 1842 comprises a monophyletic group of 17 fusiform flightless grasshopper species (Sanabria-Urbán et al. 2017). This genus belongs to the family Pyrgomorphidae (Orthoptera: Caelifera), an ancient lineage of grasshoppers of Gondwanan origin around 141 mya (Mariño-Pérez and Song 2019). This family comprises 482 extant species in 149 genera mainly distributed across the tropics of the world (Mariño-Pérez and Song 2018). However, most pyrgomorphs are found in the Old World (Africa, Asia and Australia), whereas only 41 species in 13 endemic genera are found in the New World, where *Sphenarium* is the most diverse genus (Cigliano et al. 2019).

Various phylogenetic and biogeographic hypotheses for the origin of the New World Pyrgomorphidae, including *Sphenarium*, have been proposed (Kevan 1977; Mariño-Pérez and Song 2019). However, only currently these hypotheses have been tested by Mariño-Pérez and Song (2019) using molecular information. They found that the New World Pyrgomorphidae consist of at least three separate clades spread throughout the phylogeny of the family. The first clade includes the genera in the South American endemic tribe Omurini and the genus *Jaragua* restricted to the Caribbean, the second clade comprises the genera in the Mexican endemic tribes Ichthiacridini and Ichthyotettigini, and the last clade includes the Mesoamerican genera *Sphenarium* and *Prospheana*. Interestingly, this last clade, *Sphenarium-Prospheana*, is more closely related to the African genera *Ochrophlegma* and *Tanita* than to other American pyrgomorphs. Moreover, these four genera (*Sphenarium-Prospheana-Ochrophlegma-Tanita*) are most closely related to the Mexican Ichthiacridini-Ichthyotettigini clade within the phylogeny of the family.

Given these phylogenetic relationships Mariño-Pérez and Song (2019) have inferred a complex biogeographic history for the New World Pyrgomorphidae that implicate at least two colonization events to America. The first and oldest event could involve vicariance or dispersal from Africa of the common ancestor of the South American and Caribbean lineage (Omurini-*Jaragua*) during the Cretaceous (112–81 mya). In both cases a subsequent dispersal event from South America to the Caribbean in the late Cretaceous (~68 mya) is also inferred. The second wave of colonization came by dispersal from West Africa to northern South America and

then to North America and Africa, when the continents were already separated. The common ancestor that colonized South America for the second time in the late Cretaceous (~69 mya) gave rise over there to the clades *Sphenarium-Prospheia*, *Ochrophlegma-Tanita*, and Ichthiacridini-Ichthyotettigini. The common ancestors of these clades then dispersed to North America (*Sphenarium-Prospheia* and Ichthiacridini-Ichthyotettigini) and back to Africa (*Ochrophlegma-Tanita*), before the entire lineage became extinct in South America during the early Paleogene (60–50 mya). According with this scenario, the ancestors of *Sphenarium* could establish in North America since the Eocene (~ 50–40 mya), which may imply a relatively long history of evolution of *Sphenarium* grasshoppers in this region.

Ecology and Natural History of the Genus Sphenarium

The species of *Sphenarium* are distributed from central Mexico to northwestern Guatemala (Fig. 15.1), where the major mountain ranges delimit their parapatric distribution (Sanabria-Urbán et al. 2017). *Sphenarium* grasshoppers are found in a wide variety of plant communities, including xerophytic, temperate, tropical deciduous, and rain forests. These insects are mainly found in the border vegetation and in sunny areas, where they feed on weeds, shrubs, and even trees of a wide variety of seasonal and perennial plants species. At least 47 species in 25 families of vascular plants and ferns are known to be eaten by *S. purpurascens* (Table 15.1) (Cano-Santana and Castellanos-Vargas 2009; and references therein).

The diet breadth of the other species of *Sphenarium* has remained unstudied. However, these other species are commonly found in the same plant species and/or families in nature (Márquez 1962, 1965a, b; Descamps 1975; Oyama et al. 1994; Sanabria-Urbán, *pers. obs.*), suggesting that in general these insects are polyphagous herbivories.

The diet composition of the grasshoppers of *Sphenarium* could be determined by a mix of their food preferences and the encounter probability with their host plants. Moreover, the population densities of these insects can modulate their diet breadth. For instance, in low population densities, their diet breadth can be narrow, tending to feed mostly on soft tissue plants (e.g., seasonal Asteraceae), whereas when they reach high densities, their diet breadth can expand to include plants species with harder tissues, such as cactus (e.g., *Opuntia* sp.) (Cueva del Castillo, *pers. obs.*). Similar behaviors have been documented in other grasshoppers (Otte and Joern 1976; Bernays and Chapman 1977; Joern 1979), which can be explained by the quality and quantity of nutriments and the difficulty to obtain them from these types of plants.

Besides being polyphagous herbivorous, the species of *Sphenarium* can be very abundant and even show populations outbreaks (Kevan 1977). For instance, *S. purpurascens* can represent up to 95% of the dry biomass of the epiphytic arthropods in xerophytic habitats in central Mexico (Ríos-Casanova and Cano-Santana 1994). During their populations outbreaks, these insects can infest several crop plant

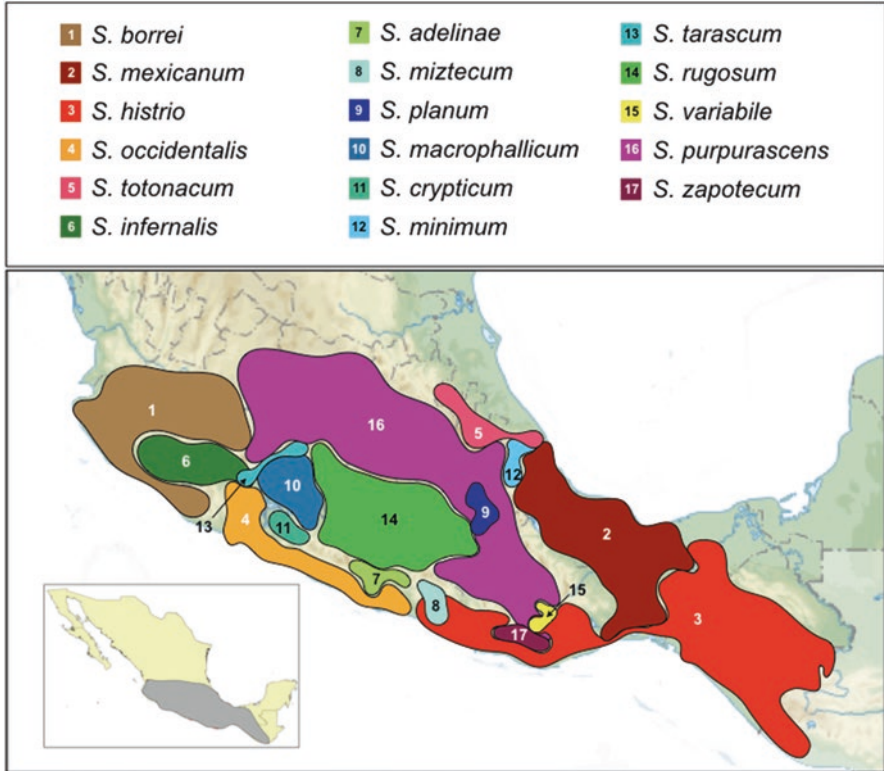


Fig. 15.1 Geographic distribution ranges of the species of *Sphenarium*. (After Sanabria-Urbán et al. 2017)

species. Indeed, *Sphenarium* grasshoppers have long been regarded as one of the most severe agricultural pests of corn and beans in central Mexico (Cerritos and Cano-Santana 2008). But at the same time, they have been used as food since pre-Colombian times for Mexican people (Ramos-Elorduy and Moreno 1989). Other crop pest species are also recognized in at least ten genera of Pyrgomorphidae, but all of them in the Old World, mainly in Africa and Asia (Table 15.2).

Even though studies on the phenology of *Sphenarium* grasshoppers have focused mainly in one species, *S. purpurascens* (Cano-Santana and Castellanos-Vargas 2009; and the references therein), several lines of evidence suggest that all species in the genus are phenologically similar (Márquez 1962, 1965a, b; Descamps 1975; Sanabria-Urbán et al. 2015, 2017). These grasshoppers are univoltine. Their nymphs emerge mainly in the beginning of the rainy season (June–July), and they become adults and reproduce mainly during the fall (from mid-September to mid-December). After reproduction the oviposition and the highest adult mortality occur during the winter (approximately from mid-December to mid-February) (Sanabria-Urbán et al. 2015, 2017). However, the species of *Sphenarium* show extensive variation at inter- and intraspecific levels on body size and life history traits (Kevan 1977;

Table 15.1 Plant families and species known to be eaten by *Sphenarium purpurascens*

Family	Plant species	Family	Plant species
Amaranthaceae	<i>Amaranthus</i> sp.	Hydrophyllaceae	<i>Wigandia urens</i>
	<i>Iresine calea</i>	Hypoxidaceae	<i>Hypoxis decumberus</i>
	<i>Iresine celosa</i>	Lamiaceae	<i>Salvia mexicana</i>
Anacardiaceae	<i>Schinus molle</i>	Leguminosae	<i>Cologania</i> sp.
Asparagaceae	<i>Manfreda brachystachya</i>	Loasaceae	<i>Eysenhardtia polystachya</i>
Begoniaceae	<i>Begonia gracilis</i>		<i>Gliricidia sepium</i>
Burceraceae	<i>Bursera</i> sp.		<i>Phaseolus heterophyllus</i>
Commelinaceae	<i>Tradescantia crassifolia</i>		<i>Mentzelia hispida</i>
Compositae	<i>Baccharis ramulosa</i>	Loganiaceae	<i>Buddleja cortada</i>
	<i>Dahlia coccinea</i>		<i>Buddleja parviflora</i>
	<i>Eupatorium petiolare</i>	Nyctaginaceae	<i>Mirabilis jalapa</i>
	<i>Gnaphalium canescens</i>	Plantaginaceae	<i>Penstemon campanulatus</i>
	<i>Helianthus annuus</i>	Poaceae	<i>Plantago major</i>
	<i>Lagascea rigida</i>		<i>Melinis repens</i>
	<i>Montanoa tomentosa</i>	Poaceae	<i>Tripsacum lanceolatum</i>
	<i>Piqueria trinervia</i>	Polygonaceae	<i>Rumex obtusifolius</i>
	<i>Senecio praecox</i>	Polypodiaceae	<i>Polypodium</i> sp.
	<i>Stevia ovata</i>	Rubiaceae	<i>Bouvardia ternifolia</i>
	<i>Stevia salicifolia</i>	Sapindaceae	<i>Cardiospermum halicacabum</i>
	<i>Tagetes micrantha</i>	Solanaceae	<i>Datura stramonium</i>
	<i>Tithonia</i> sp.		<i>Nicotiana glauca</i>
<i>Verbesina virgata</i>		<i>Physalis</i> sp.	
Crassulaceae	<i>Echeveria gibbiflora</i>		<i>Solanum</i> sp.
Dioscoreaceae	<i>Dioscorea galeottiana</i>	Vitaceae	<i>Cissus sicyoides</i>
Euphorbiaceae	<i>Acalypha indica</i>		

Sanabria-Urbán et al. 2015, 2017). These traits are common targets of natural selection, and their geographic variation suggest high levels of adaptation to environmental heterogeneity across their distribution (Sanabria-Urbán et al. 2015). Moreover, morphological and behavioral traits appear to be under strong sexual selection (Cueva del Castillo and Nunez-Farfan 1999, 2002; Cueva del Castillo et al. 1999). For instance, in *S. purpurascens*, larger males have advantage in accessing females (Cueva del Castillo et al. 1999) and show prolonged female guarding behavior (spending up to 22 days mounted on females) that may suggest strong sperm competition (Cueva del Castillo 2003).

Most *Sphenarium* species exhibit apparently cryptic coloration patterns, but in some species (e.g., *S. purpurascens*, *S. histrio*, *S. mexicanum*, and *S. mixtecum*) brightly colorations are relatively common (Sanabria-Urbán et al. 2017), resembling aposematic pyrgomorphs from the Old World (Mariño-Pérez and Song 2018). Aposematism and the ability to sequester secondary compounds from toxic plant have been documented in about 10% of the species of Pyrgomorphidae (Mariño-Pérez and Song 2018). However, it seems that these traits have not evolved

Table 15.2 Grasshopper species of the family Pyrgomorphidae from Africa and Asia that have been recognized as crop pest

Species	Region	Country	Attacked crops	References
<i>Atractomorpha burri</i>	Asia	India, Filipinas	Rise	Ane and Hussain (2015)
<i>Atractomorpha crenaticeps</i>	Asia	Indonesia (Java)	Sugarcane	Jarvis (1927)
<i>Atractomorpha crenulata</i>	Asia	India	Cotton, sugarcane, cauliflower, chickpea, paddy, maize, milch, millet, jute, gram, oat, cow pea, tobacco, oriental pickling melon	Jago (1998), Thakur and Thakur (2011), Gupta and Chandra (2013), Patra et al. (2013), and Debbarna et al. (2017)
<i>Atractomorpha lata</i>	Africa, Asia	Cameroon, Japan, Korea	Rice, and it is also pest to over 132 medicinal plant species	Kobayashi et al. (1972), Lee et al. (2007), and Seino and Njoya (2018)
<i>Atractomorpha sinensis</i>	Asia	China, Taiwan, Mongolia, Vietnam	Ornamental plants, rice paddy, cotton, sugarcane, pineapple	Kevan and Hsiung (1985)
<i>Aularches miliaris</i>	Asia	India	Jack fruit, coconut, <i>Pinus</i> , <i>Shorea robusta</i> , coppica shoots, banana, beans, betel nut, cocoa, cardamom, cashew, chili, <i>Cinchona</i> , cotton, millet, guava, jute, maize, mango, rice, rubber, sugarcane, tobacco	Gupta and Chandra (2013)
<i>Chrotogonus oxypterus</i>	Asia	India	Cotton, sorghum, maize, wheat, groundnut	Tandon (1986) and Gupta and Chandra (2013)
<i>Chrotogonus trachypterus</i>	Asia	India Filipinas	Rise, cauliflower, minor pests of cotton, sorghum, maize, wheat, groundnut, tobacco, and paddy	Mahabir (1980), Thakur and Thakur (2011), and Ane and Hussain (2015)
<i>Colemania sphenaroides</i>	Asia	India	Jowar, bajra, sugarcane, and millets	Gupta and Chandra (2013)
<i>Hieroglyphus banian</i>	Asia	India, Pakistan	Rice, maize, cotton	Gupta and Chandra (2013)
<i>Neorthacris acuticeps</i>	Asia	India	Minor damage the tea plantation; low growing crops	Gupta and Chandra (2013)
<i>Neorthacris simulans</i>	Asia	India	<i>Rauwolfia serpentina</i>	Gupta and Chandra (2013)
<i>Neorthacris acuticeps</i>	Asia	India	<i>Costus speciosus</i>	Swamy et al. (1993)

(continued)

Table 15.2 (continued)

Species	Region	Country	Attacked crops	References
<i>Poekilocerus pictus</i>	Asia	India	Alfalfa, crop, citrus, melon, papaya, chili, cucurbit, orchards, betel, creepers, forest trees, trees of jasmine, mulberry	Soomro et al. (2014)
<i>Pyrgomorpha granulata</i>	Africa		It sometimes attacks cotton and other crops	Ferdio and Cardoso (1972); Mason (1979), Kevan and Chia-Chi Hsiung (1985)
<i>Pyrgomorpha vigneaudi</i>	Africa	Nigeria	Cowpea, soya bean, rice, <i>Ceratotheca sesamoides</i> , millet, amaranth, green gram	IITA (1984), Fassakin (1991), Heinrichs and Barrion (2004), Adamu et al. (1999), Paraíso et al. (2012), and Kekeunou et al. (2006)
<i>Taphronota thaelephora</i>	Africa	Cameron	Coffee	Seino et al. (2013)
<i>Zonocerus elegans</i>	Africa	Kenia	Sunflower	Khaemba and Mutinga (1982)
<i>Zonocerus variegatus</i>	Africa	Nigeria	Cassava, coffee	Page et al. (1980) and Jago (1998)

in the group. For instance, morphological and molecular specializations related with aposematism in pyrgomorphs have not been observed in *Sphenarium* grasshoppers (Mariño-Pérez and Song 2018; Yang et al. 2019). In fact, these grasshoppers are heavily predated by multiple species of arthropods, lizards, birds, and mammals, including humans (Cano-Santana and Castellanos-Vargas 2009; Sanabria-Urbán, *pers. obs.*). Thus, it seems unlikely that these grasshoppers are toxic for their predators. Nevertheless, some species in the genus (e.g., *S. purpurascens* and *S. rugosum*) can feed on toxic plants, such as *Datura stramonium* (Castillo et al. 2014; Sanabria-Urbán, *pers. obs.*), and generate enormous damage to them (Núñez-Farfán and Dirzo 1994; Fornoni et al. 2003; Castillo et al. 2014), despite of *D. stramonium* has well-known defense mechanisms against herbivores (e.g., tropane alkaloids and trichomes) (Valverde et al. 2001). So far, it remains largely unknown what are the mechanisms that have allowed *Sphenarium* species to feed on their multiple host plant species.

The Phylogenetic Relationships Among the Species of *Sphenarium*

The most comprehensive phylogenetic study on *Sphenarium* until now was conducted by Sanabria-Urban et al. (2017). They found that after the divergence from its sister genus *Prospheana*, the common ancestor of *Sphenarium* gave rise to three major clades that diversified subsequently (Fig. 15.2). These clades are geographically restricted to particular regions across the distribution of the genus. The first and most basal clade is just composed by the species *S. borrei*, which is restricted to the inner highlands of western-central Mexico. The second clade is composed by the species *S. totonacum*, *S. occidentalis*, *S. mexicanum*, and *S. histrio* that are distributed in the costal lowlands and the highlands of southern Mexico and

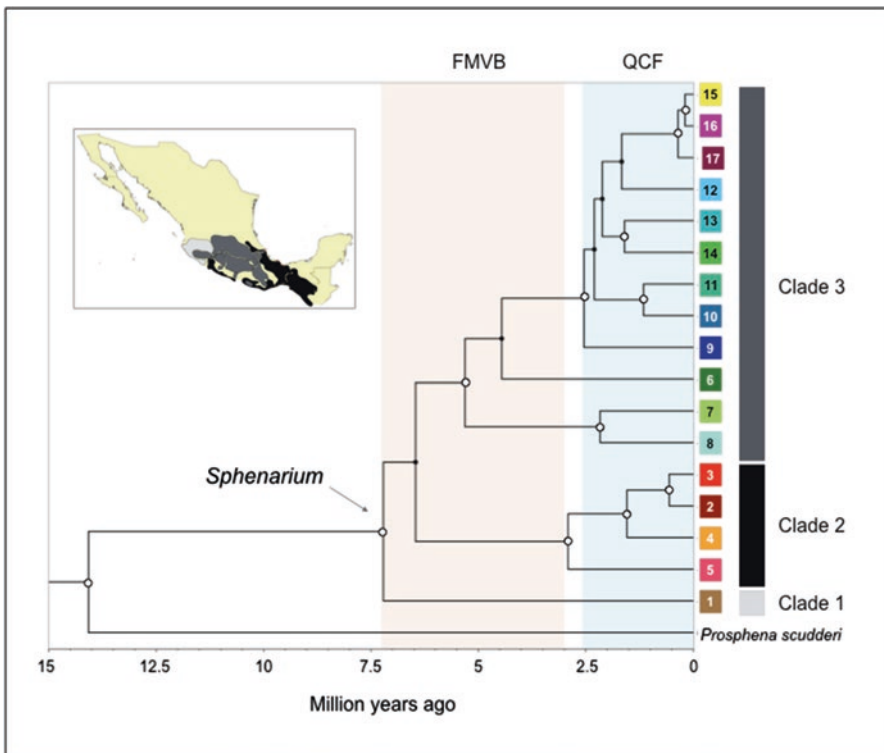


Fig. 15.2 Phylogenetic relationships and mean divergence times between the species of *Sphenarium* based on a Bayesian species tree analysis of the genus (after Sanabria-Urban et al. 2017). The geographic distribution and species within the three major clades of *Sphenarium* are represented by the gray shapes and rectangles. Each species is represented by different colored squares (same as in Fig. 15.1). Nodes with posterior probability values ≥ 0.8 are indicated with open circles. The temporal occurrence of the second major formation of the Mexican Volcanic Belt (FMVB) and Quaternary climatic fluctuations (QCF) is denoted by the light-colored areas on the chronogram

northwestern Guatemala. The third clade comprises all the species distributed in the inner basins and highlands of central Mexico: *S. infernalis*, *S. adelinae*, *S. mixtecum*, *S. planum*, *S. minimum*, *S. macrophallicum*, *S. crypticum*, *S. rugosum*, *S. tarascum*, *S. zapotecum*, *S. variabile*, and *S. purpurascens* (Fig. 15.2). A closer phylogenetic relationship is recovered between the last two clades but with poor support.

The species within the last two clades integrate into different nested monophyletic groups. In the second clade, the basal position is occupied by *S. totonacum*, followed by *S. occidentalis*, which is closely related to *S. mexicanum* and *S. histrio*. In the third clade, sister relationships were recovered between *S. adelinae* and *S. mixtecum*, *S. crypticum* and *S. macrophallicum*, and *S. rugosum* and *S. tarascum*, and between *S. purpurascens*, *S. variabile*, and *S. zapotecum*. The last seven species conform a monophyletic group along with *S. minimum* and *S. planum*. Nonetheless, the phylogenetic relationships between these groups of species and the other species in the clade are poorly supported. The basal positions in this last monophyletic group are occupied by the species in the western range of the clade (*S. adelinae*, *S. mixtecum*, and *S. infernalis*), followed by the species distributed in the Tehuacan Valley (*S. planum*), the Balsas River Basin (*S. crypticum*, *S. macrophallicum*, *S. rugosum*, and *S. tarascum*), and in the southern Sierra Madre Oriental (*S. minimum*), whereas the most recently derived species are those distributed in the highlands of central and southern Mexico (*S. purpurascens*, *S. variabile*, and *S. zapotecum*) (Fig. 15.2). The low phylogenetic resolution of some of the basal divergences, as well as the fact that some morphologically different sister species were found to be paraphyletic in their genetic lineages (*S. histrio*-*S. mexicanum*; *S. macrophallicum*-*S. crypticum*; *S. rugosum*-*S. tarascum*; and *S. purpurascens*-*S. variabile*-*S. zapotecum*), can be explained by incomplete lineage sorting associated with relatively rapid and/or simultaneous cladogenetic events.

Historical Biogeography of the Genus

According with Sanabria-Urbán et al. (2017), the initial divergences in *Sphenarium* (between the clades and the basal lineages within them) occurred between 2.91 and 7.22 mya, whereas most of the cladogenetic events within the clades occurred between 0.19 and 2.51 mya (Fig. 15.2). These two major episodes of diversification correlate temporally and spatially with the third major formation of the Mexican Volcanic Belt (MVB), around 3–7.5 mya (Ferrari et al. 2012), and the Quaternary climatic fluctuations around 0.01–2.6 mya. These historic events are recognized as some of the most important drivers of lineage diversification in other co-distributed taxa in Mexico (Bryson et al. 2011, 2012; Duennes et al. 2012; Mastretta-Yanes et al. 2015).

The several volcanic episodes during the formation of the MVB (Ferrari et al. 2012) probably sundered ancestral populations of *Sphenarium*, causing to the divergences between the three major clades, whereas Quaternary climatic changes

probably caused several vicariance events within the clades by promoting recurrent distribution shifts of the ancestral populations across the mountain ranges and the coastal lowlands of Mexico. In addition, the fact that strongly supported monophyletic groups of *Sphenarium* are geographically restricted to well-defined biogeographic provinces (Figs. 15.1 and 15.2) indicates that vicariance events could have played a fundamental role on the diversification of the group. Therefore, the current parapatric distribution of the species, along with their narrow sympatric zones, has probably resulted from secondary dispersal events. Moreover, the phylogenetic relationships among the lineages of *Sphenarium* suggest that probably the common ancestor of the group occupied initially the outer lowlands and that younger lineages have more recently colonized inner basins and highlands of central Mexico.

The Mechanisms of Differentiation Among the Species

The genus *Sphenarium* is an assemblage of lineages with different levels of morphological and genetic divergence suggesting a complex interplay between evolutionary forces during the evolution of the genus. There are three broad patterns of differentiation that reflect the relative importance of evolutionary forces on the diversification of *Sphenarium* (Sanabria-Urbán et al. 2017). Firstly, despite some species pairs are very close genetically (e.g., *S. histrio*-*S. mexicanum*; *S. macrophallicum*-*S. crypticum*; *S. rugosum*-*S. tarascum*; and *S. purpurascens*-*S. variabile*), they strongly differ from each other by male genital morphology. Because male genitalia are known to be under strong sexual selection (Eberhard 2010), and sexually selected characters tend to diverge very rapidly (Hosken and Stockley 2004), sexual selection may have played a major role in the divergence among these *Sphenarium* species. A second pattern is found among species that are morphologically similar (e.g., *S. miztecum*-*S. adelinae*; *S. histrio*-*S. occidentalis*; and *S. infernalis*-*S. rugosum*) but strongly differ genetically, revealing cryptic diversity in the genus. In these cases, evolutionary processes different from sexual selection on male genitalia could have played an important role in the divergence of lineages. Recurrent isolation events and genetic drift in ancestral populations could have generated genetic rather than morphological divergence. The last pattern involves species that differ both morphologically and genetically (e.g., *S. borrei* and *S. totonacum*), which suggest an interplay between different evolutionary forces (e.g., drift and sexual selection) in driving the species differentiation. In addition, Sanabria-Urbán et al. (2015) found correlative evidence suggesting that natural selection on body size in response to altitudinal climatic variation could have also promoted the diversification of the genus *Sphenarium*. Despite phylogenetic relationships have heavily affected the body size and the climatic niche of *Sphenarium* species, they have diverged considerably in size, and large species are associated with high temperatures during the winter (Sanabria-Urbán et al. 2015). This climatic body size cline probably reflects the life history adaptability of *Sphenarium* grasshoppers. In lowlands, during benign winters, the window for development and

reproduction may increase, allowing grasshoppers to achieve larger body sizes. Conversely, when mean temperatures are lower, body sizes become smaller. Similar body size clines associated with decreasing temperatures have been observed in other insects at higher latitudes (Roff 1980; Dingle et al. 1990; Berner et al. 2004). Smaller body sizes at low temperatures are commonly explained by natural selection favoring faster development by decreasing development time (reducing the number of nymphal instars or diapause (Dingle et al. 1990) or increasing growth rates (Hodkinson 2005). However, decreasing the time to maturity at low temperatures may have negative effects on the fitness of individuals by reducing reproductive success via small body sizes (Mousseau and Roff 1987; Abrams et al. 1996; Morbey 2013). Therefore, the smallest species of *Sphenarium* (*S. purpurascens*, *S. minimum*, *S. planum*, *S. variabile*, and *S. tarascum*) probably have lower fecundity than larger species, but they have been able to colonize highlands.

The geologic and climatic events over the last 10 mya in Mexico had a profound impact on the diversification of the genus *Sphenarium* causing the vicariance of the ancestral lineages within this genus along their distribution. These historic events also determinate in great extent the complex mosaic of environmental heterogeneity to which *Sphenarium* species have adapted. The low mobility of these univoltine and flightless grasshoppers, plus the combination of strong natural selection on adult body size and maturation times, could enhance the genetic isolation and consequently the speciation of these Neotropical grasshoppers.

Perspectives

The current understanding of the evolutionary history of *Sphenarium* grasshoppers provides the opportunity to investigate many aspects of the interaction between these grasshoppers and their host plant species. Given that the species of *Sphenarium* are polyphagous insects that can reach high population densities; they can represent a strong selective force for several plant species across their distribution range. However, the strength of their selective pressure on their host plants might differ geographically and temporally depending on both, the variation in their own populations' densities and the variation on the composition and abundance of the plant in their communities. In those areas where these grasshoppers are more abundant, they might impose a stronger selective pressure on the plants. On the other hand, the distribution and abundances of their different host plant species also vary geographically and temporally. Thus, for some plant species and in some of their populations, these insects can be a more important selective factor than in others. Even though *Sphenarium* are generalist herbivorous, perhaps they have evolved in a complex mosaic of ecological interactions, generating places with high and low levels of coadaptation between them and their host plants. A recent study has depicted part of this complexity detecting geographic variation in defensive characteristics of the toxic plant *D. stramonium* associated with the abundance of *S. purpurascens* (Castillo et al. 2014). In some areas this grasshopper species exerts a strong

selective pressure in *D. stramonium* toward reduction of the alkaloid atropine, whereas in other populations, a more derived alkaloid confers a greater defense. These results are congruent with geographic mosaic of adaptation in *D. stramonium*, in which *Sphenarium* grasshoppers are involved. Similar studies in other plant species could reveal similar responses, adding to our understanding of the relative importance that these grasshoppers have had on the evolution of defense mechanisms in plants. In this context, it should be considered the biogeographic history of the genus *Sphenarium*, and how it has influenced the geographic distribution of its host plant species. The distribution of *Sphenarium* species can generate geographic variation on the levels of herbivory which could explain the geographic distribution of some plant species. For instance, the sunflower (*Helianthus annuus*) reaches its southern distribution limit in the Mexican tropics, where *Sphenarium* species and other herbivores exert a tremendous herbivory pressure on the species (Lentz et al. 2008). The plants' ability to colonize a new area can be constrained by its native generalist herbivores because the foreign plants may be poorly adapted to defend themselves against them (Avanesyan and Culley 2015). However, coadaptation to these herbivores may eventually happen allowing the foreign plants to expand their distribution ranges in the new areas (Schaffner et al. 2011). Therefore, dominant generalist herbivores, such as *Sphenarium* grasshoppers, might restrict more strongly the distribution of recently established plant lineages, in comparison with older clades that have coexisted with these insects during their evolution. These predictions can be tested by obtaining phylogenetic and biogeographic reconstructions of the different host plant lineages of *Sphenarium*. On the other hand, phylogenetic and biogeographic reconstructions of both, *Sphenarium* grasshoppers and their host plants, would allow to infer how old the interactions between *Sphenarium* species and their host plants are. In addition, the phylogenetic information would provide the bases to search for common adaptations among different host plants on defense and/or tolerance against these generalist grasshoppers. Finally, this would help to better understand how the evolutionary history of *Sphenarium* has been influenced by the diversification of their host plants and vice versa.

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