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The diversification of Nearctic mammals in the Mexican transition zone

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The boundary between the Nearctic and Neotropical regions has been delineated using different approaches, methods and taxa. Using a panbiogeographical approach, identification of nodes can help understand the dynamics and evolution of the boundary. We analysed the distribution patterns of 46 Mexican land mammal species belonging to the Nearctic biotic component and delineated generalized tracks and nodes, in order to determine the southernmost boundary of the Nearctic region in Mexico. We found six generalized tracks and nine nodes; the latter located largely in the Sierra Madre Oriental, Transmexican Volcanic Belt, Sierra Madre del Sur and Chiapas biogeographical provinces. The highlands of Chiapas were found to represent the southernmost area inhabited by Nearctic taxa. The other biogeographical provinces, together with the Sierra Madre Occidental and Balsas Basin provinces, represent the Mexican transition zone in the strict sense. Instead of a classic static boundary, this transition zone represents an evolutionarily 'active' zone, where several speciation events have taken place in the past. *Biological Journal of the Linnean Society*, 2004, **83**, 327–339.

ADDITIONAL KEYWORDS: land mammals – Nearctic region – Neotropical region – panbiogeography.

INTRODUCTION

'The most pervasive feature of geographical distributions is the fact that they have limits' (Brown & Lomolino, 1998: 295). These limits are repeated for many organisms and led to the earliest recognition of biogeographical regions. Modern biogeographical regionalizations of the world date from the 19th century; attempts to establish the precise boundary of the Nearctic and Neotropical regions have been made since then (Sclater, 1858; Rapoport, 1968; Cox, 2001; Morrone, 2002). Exploration of biotic transition zones is an essential part of the study of the processes that shape the distribution of biota (Ruggiero & Ezcurra, 2003), although parts of these transition zones may be arbitrary constructs (Williams, 1996). Halffter (1962, 1965, 1972, 1974, 1976, 1978, 1987) postulated the existence of a Mexican transition zone, which includes south-western USA, Mexico and a large part of Mesoamerica, extending to the Nicaraguan lowlands. In the last few years, there have been several biogeographical studies of this zone (Ortega & Arita, 1998; Marshall & Liebherr, 2000; Morrone & Márquez, 2001; Carleton, Sánchez & Urbano-Vidales, 2002), but none of these has analysed land mammals using a panbiogeographical approach.

Based on his premise 'life and earth evolve together', which means that geographical barriers and biotas coevolve, Léon Croizat (1894–1982) developed a new biogeographical approach termed panbiogeography. This is one of the most important research programmes in modern historical biogeography (Craw, Grehan & Heads, 1999; Morrone, 2000; Grehan, 2001). In simple terms, it consists of plotting the distributions of organisms on maps and connecting the disjunct collection localities together with lines called individual tracks. Croizat found that individual tracks for unrelated taxa were highly repetitive, and considered the resulting summary lines as generalized or

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standard tracks, which indicated the pre-existence of ancestral biotic components, subsequently fragmented by tectonic and/or climatic changes (Morrone & Crisci, 1995; Morrone, 2000). Nodes are the sites of intersection between two or more generalized tracks, and represent compound geobiotic areas (Craw *et al.*, 1999). According to Heads (1989), a node may be characterized as a locality where plant and animal taxa exhibit distributional boundaries, where taxa 'begin and end' both phylogenetically and geographically. Thus, nodes may help to delineate boundary zones, such as the Mexican transition zone.

The development of panbiogeography, as well as cladistic biogeography (a more recent approach that resulted from the 'hybridization' between panbiogeography and phylogenetic systematics; see Nelson & Platnick, 1981, and Humphries & Parenti, 1999), has had the consequence of traditional biogeographical classifications being questioned. Both newer approaches have shown that traditionally recognized biogeographical units may not represent natural units (Morrone, 2002). Furthermore, they have corroborated the finding that Mexico represents the area of contact between the Nearctic and Neotropical regions (Morrone, 2001).

The total number of mammal families in the Nearctic region is 37, although only Aplodontidae and Antilocapridae are endemic to it (Cole, Reeder & Wilson, 1994; Vaughan, Ryan & Czaplewski, 2000). Many mammal taxa are shared with the Palaearctic region, for example several genera and even species of Soricidae, Muridae, Canidae and Mustelidae (Vaughan *et al.*, 2000). In addition, the Nearctic region shares more than 80% of its families with the Neotropical region (Cole *et al.*, 1994). The mammal fauna of Mexico combines Neotropical and Nearctic biotic elements in almost equal proportions, as well as many species endemic to the country (Hall, 1981; Arita, 1993; Arita & Ceballos, 1997; Álvarez-Castañeda & Patton, 1999). Nearctic taxa are mainly represented by the orders Insectivora (families Soricidae and Talpidae), Rodentia (families Castoridae, Geomyidae, Heteromyidae, Muridae, and Sciuridae) and Lagomorpha (Fa & Morales, 1998), which usually have relatively low dispersal capacities and body mass.

In this paper, we apply the panbiogeographical method to distributional data of some Mexican land mammal representatives of the Nearctic biota, in order to delineate biogeographical nodes that allow us to analyse the dynamics of diversification of Nearctic mammals in the Mexican transition zone.

MATERIAL AND METHODS

We studied several Mexican Nearctic species with small dispersal capacities, that are relatively well collected in comparison with other taxa. The geographical distribution of the species was reviewed according to Wilson & Reeder (1993), Ramírez-Pulido *et al.* (1996), and Nowak & Paradiso (1999). The following species were excluded, because they are not well collected or have very few (one or two) localities: *Cratogeomys fumosus* and *C. neglectus* (Rodentia: Geomyidae), *Cryptotis goodwini* (Insectivora: Soricidae), *Geomys tropicalis* (Rodentia: Geomyidae), *Lepus insularis* (Lagomorpha: Leporidae), *Microtus pennsylvanicus* (Rodentia: Muridae), *Orthogeomys cuniculus* and *O. lanius* (Rodentia: Geomyidae), *Pappogeomys alcorni* (Rodentia: Geomyidae), *Scapanus latimanus* (Insectivora: Talpidae), and *Sylvilagus mansuetus* and *S. graysoni* (Lagomorpha: Leporidae). Species localities were obtained from a database containing 56 859 specimen records from collections and literature (Ceballos & Arita, 1996; López-Wilchis, 1996; López-Wilchis & López-Jardinez, 1998; see Acknowledgements), that was transferred onto a map of Mexico using ARCVIEW v.3.2 Geographic Information System (GIS). Each locality was joined with the nearest locality via minimum distance lines, generating 46 individual tracks. In the areas where two or more individual tracks coincided, generalized tracks were delimited. Nodes were drawn where two or more generalized tracks converged. Nodes were represented on the maps following the conventions of Fortino & Morrone (1997), and superimposed onto a map of Mexican biogeographical provinces (Morrone, Espinosa-Organista & Llorente-Bousquets, 2002), showing elevational, climatic and geological features (INEGI, 1988a, b, c).

RESULTS AND DISCUSSION

Individual tracks were drawn for the following species: *Cratogeomys castanops*, *C. goldmani*, *C. gymnurus*, *C. merriami*, *C. tylorhinus* and *C. zinseri* (Rodentia: Geomyidae); *Cryptotis goldmani*, *C. magna*, *C. mexicana* and *C. parva* (Insectivora: Soricidae); *Geomys personatus*, *G. arenarius* (Rodentia: Geomyidae); *Lepus alleni*, *L. californicus*, *L. callotis* and *L. flavigularis* (Lagomorpha: Leporidae); *Megasorex gigas* (Insectivora: Soricidae); *Microtus californicus*, *M. guatemalensis*, *M. mexicanus*, *M. oaxacensis*, *M. quasiater* and *M. umbrosus* (Rodentia: Muridae); *Orthogeomys grandis* and *O. hispidus* (Rodentia: Geomyidae); *Pappogeomys bulleri* (Rodentia: Geomyidae); *Romerolagus diazi* (Lagomorpha: Leporidae); *Scalopus aquaticus* (Insectivora: Talpidae); *Sorex emarginatus*, *S. macrodon*, *S. milleri*, *S. monticolus*, *S. oreopolus*, *S. ornatus*, *S. saussurei*, *S. stizodon*, *S. ventralis* and *S. veraepacis* (Insectivora: Soricidae); *Sylvilagus audubonii, S. bachmani*, *S. brasiliensis*, *S. cunicularius* and *S. floridanus* (Lagomorpha: Leporidae); *Thomomys bottae* and *T. umbrinus* (Rodentia: Geomyidae); and *Zygogeomys trichopus* (Rodentia: Geomyidae).

We obtained six generalized tracks from 28 individual tracks (Figs 1–9), which are described in terms of the species assigned to them and the biogeographical provinces to which they belong (Table 1). The Califor-

Table 1. Description of generalized tracks in terms of mammal species and biogeographical provinces

Generalized tracks	Species	Biogeographical provinces
California	*Microtus californicus, Sorex ornatus* and *Sylvilagus bachmani*	Baja California and California
Centre-Gulf	*Cratogeomys merriami, Microtus oaxacensis, M. quasiater, Orthogeomys hispidus, Sorex macrodon* and *Sylvilagus brasiliensis*	Mexican Gulf, Transmexican Volcanic Belt and Sierra Madre Oriental
Centre-North Pacific	*Cratogeomys gymnurus*, *C. tylorhinus*, *Pappogepmys bulleri*, *Sorex emarginatus*, *S. oreopolus*, *S. monticolus* and *Zygogeomys trichopus*	Sierra Madre Occidental and Transmexican Volcanic Belt
Centre-South Pacific	*Cryptotis goldmani, Lepus callotis, Megasorex gigas, Sorex saussurei* and *Sylvilagus cunicularis*	Mexican Pacific Coast, Transmexican Volcanic Belt, Balsas Basin, Sierra Madre del Sur, Mexican Gulf and Chiapas
Chiapas	*Microtus guatemalensis* and *Sorex stizodon*	Chiapas
Isthmus of Tehuantepec	*Cryptotis magna, C. mexicana, Lepus flavigularis, Orthogeomys grandis* and *Sorex veraepacis*	Transmexican Volcanic Belt, Sierra Madre del Sur, Mexican Gulf and Chiapas

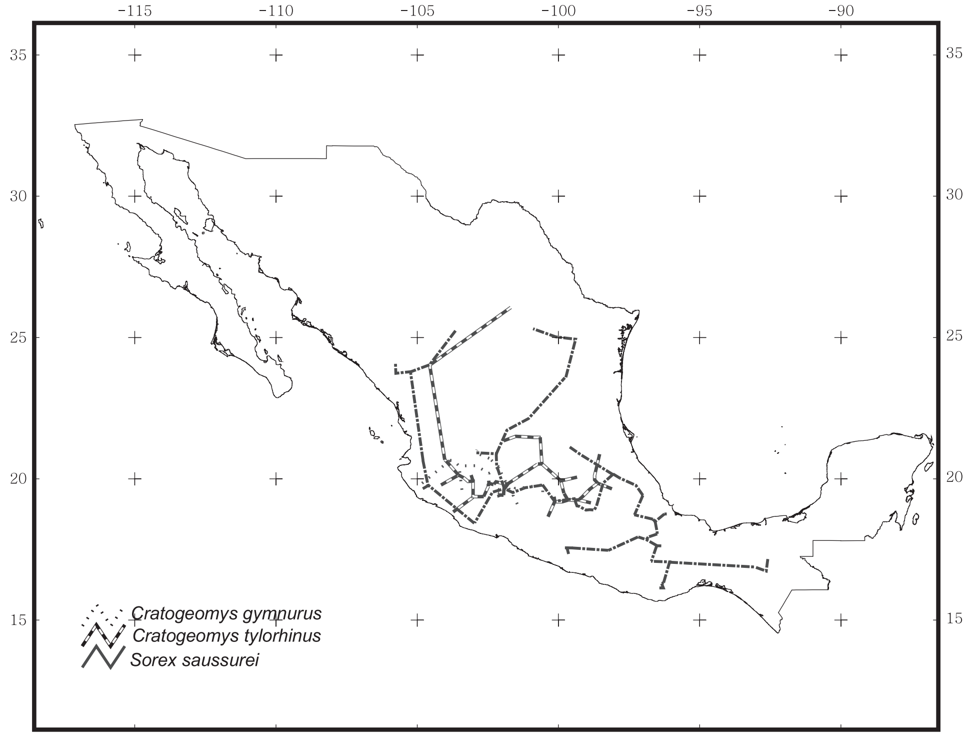

Figure 1. Individual tracks of *Cratogeomys gymnurus*, *C. tylorhinus* and *Sorex saussurei*.

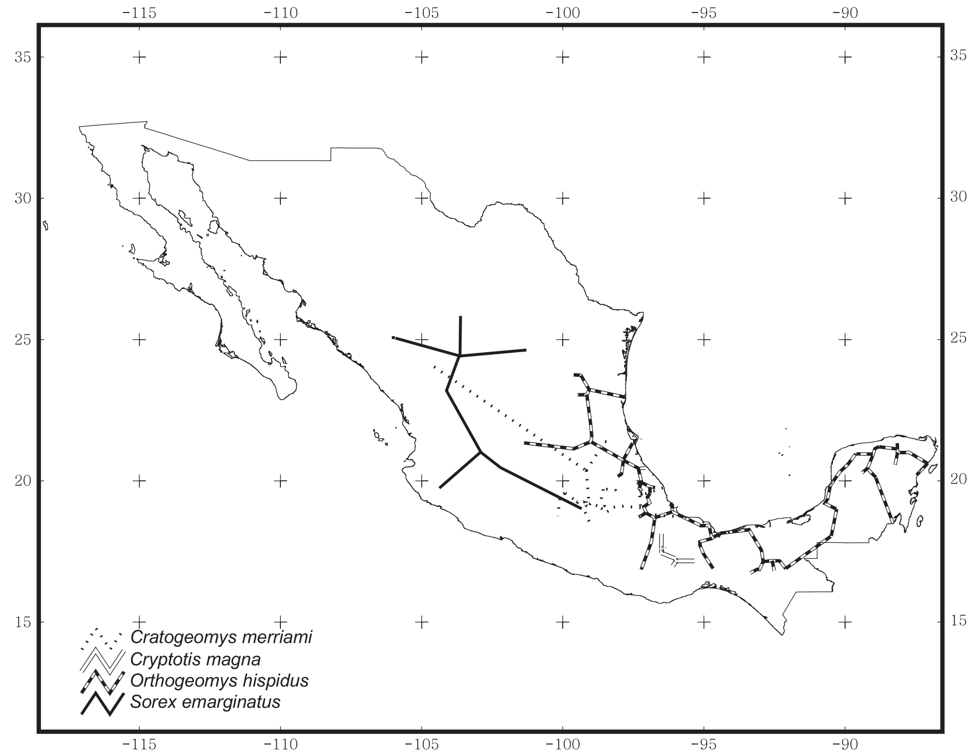

Figure 2. Individual tracks of *Cratogeomys merriami*, *Cryptotis magna*, *Orthogeomys hispidus* and *Sorex emarginatus*.

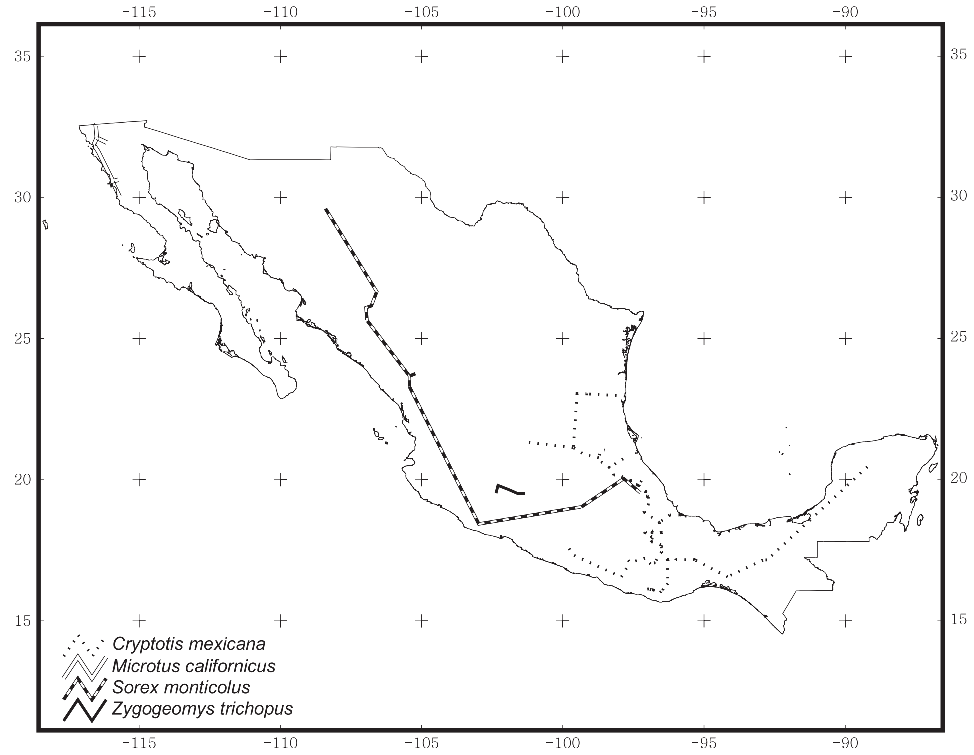

Figure 3. Individual tracks of *Cryptotis mexicana*, *Microtus californicus*, *Sorex monticolus* and *Zygogeomys trichopus*.

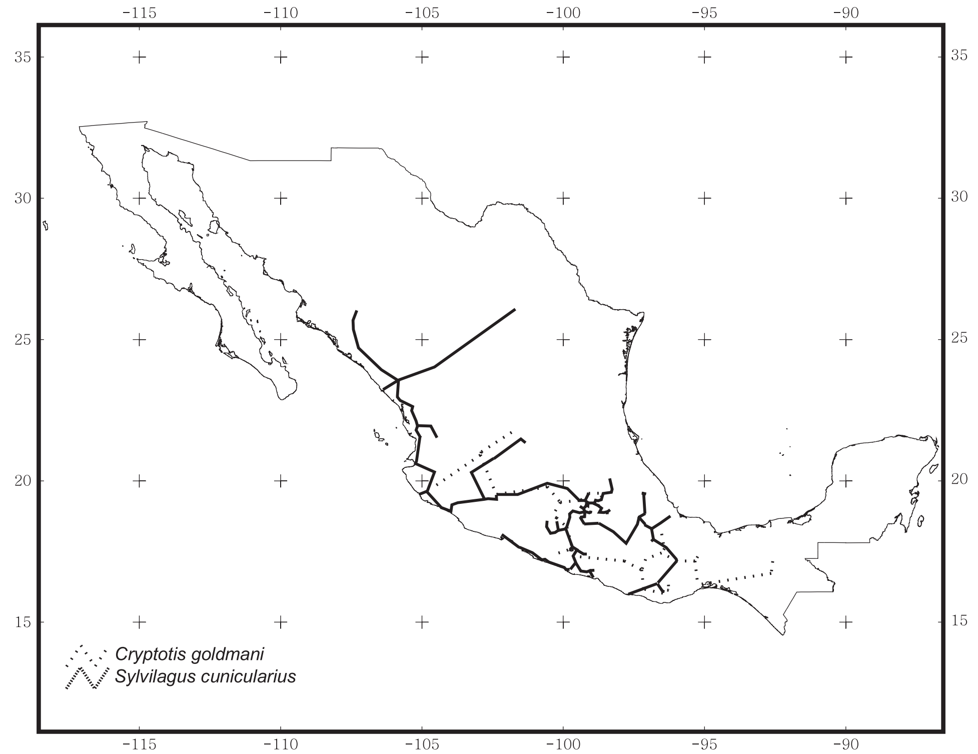

Figure 4. Individual tracks of *Cryptotis goldmani* and *Sylvilagus cunicularius*.

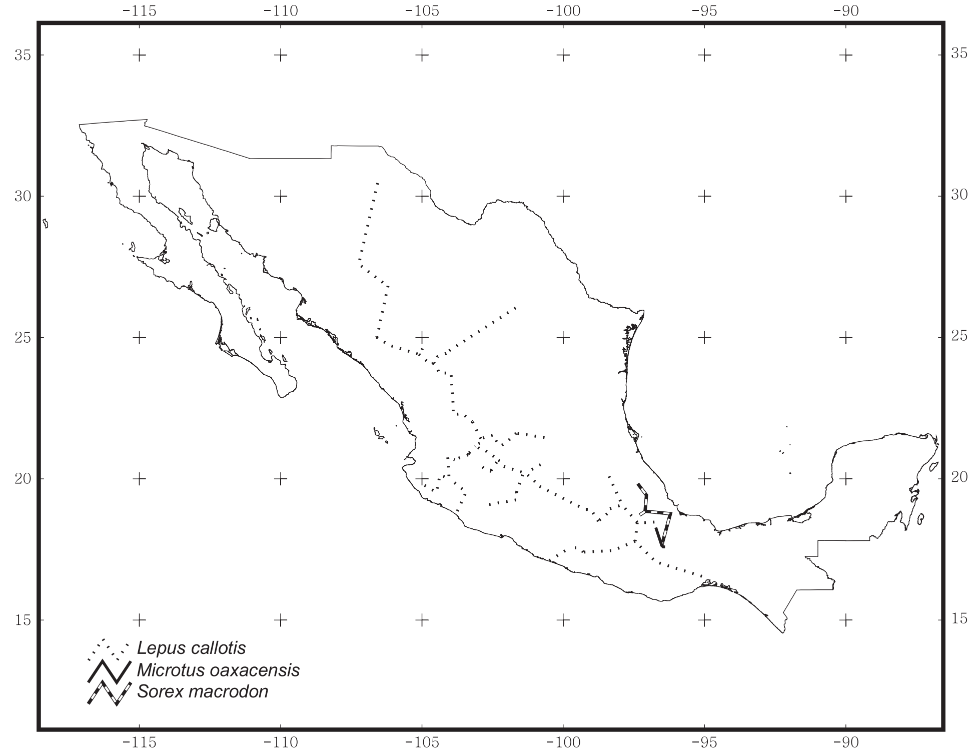

Figure 5. Individual tracks of *Lepus callotis*, *Microtus oaxacensis* and *Sorex macrodon*.

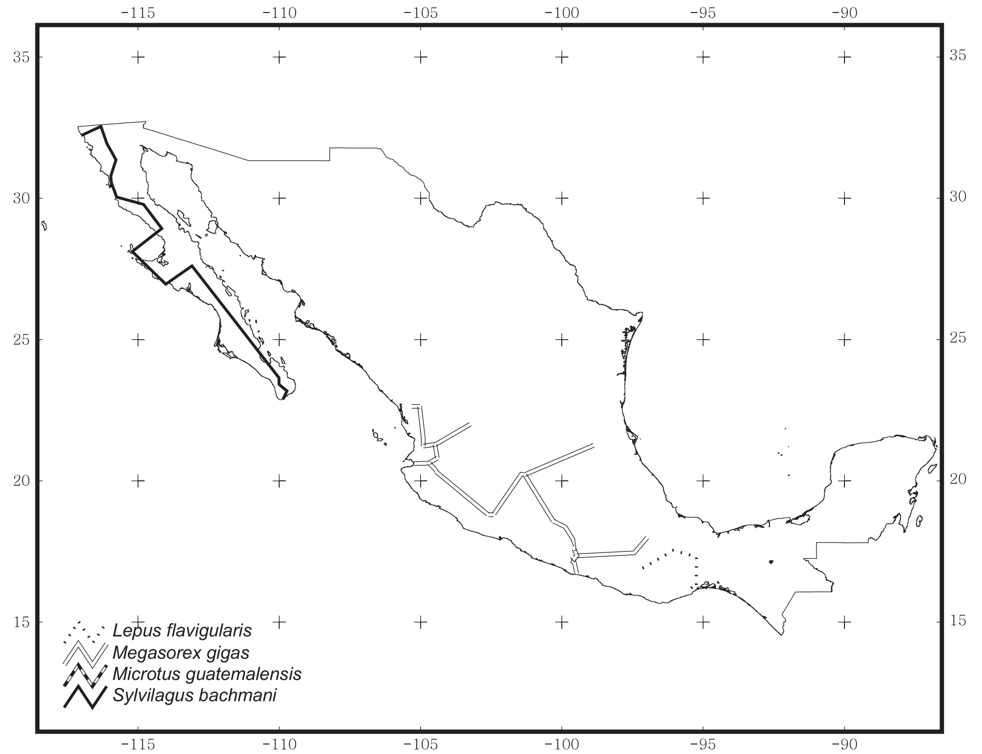

Figure 6. Individual tracks of *Lepus flavigularis*, *Megasorex gigas*, *Microtus guatemalensis* and *Sylvilagus bachmani*.

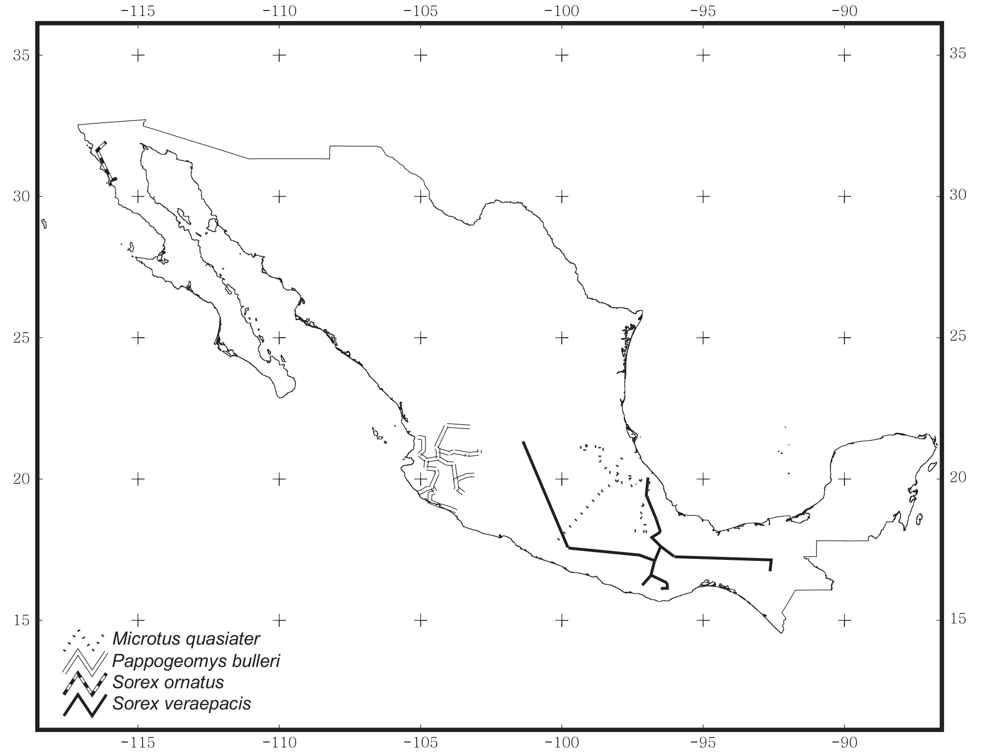

Figure 7. Individual tracks of *Microtus quasiater*, *Pappogeomys bulleri*, *Sorex ornatus* and *Sorex veraepacis*.

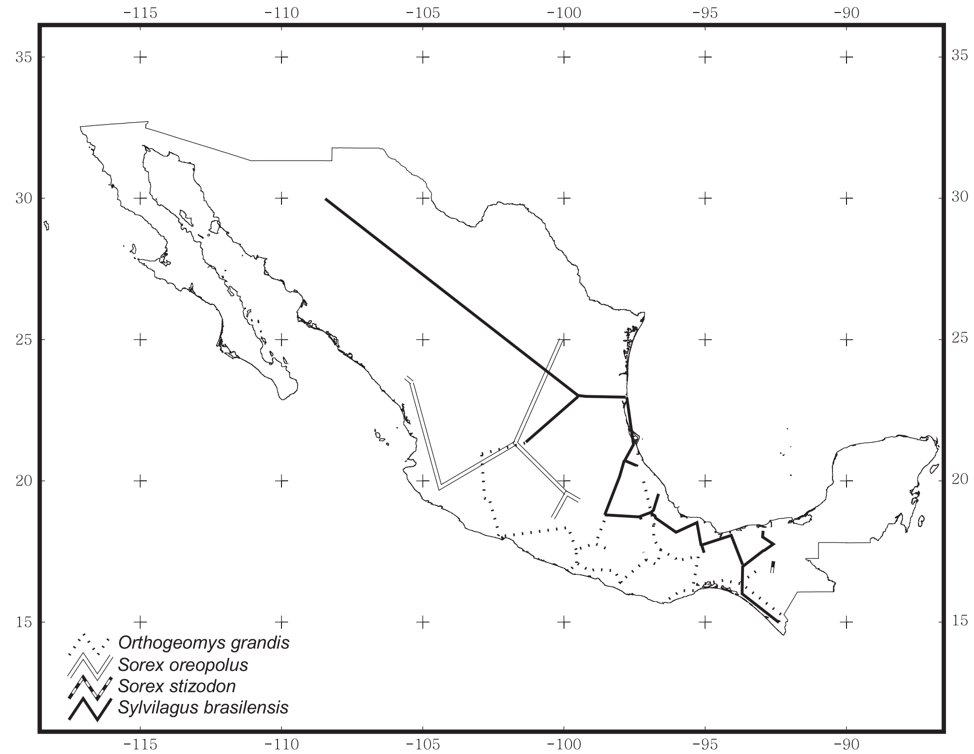

Figure 8. Individual tracks of *Orthogeomys grandis*, *Sorex oreopolus*, *Sorex stizodon* and *Sylvilagus brasiliensis*.

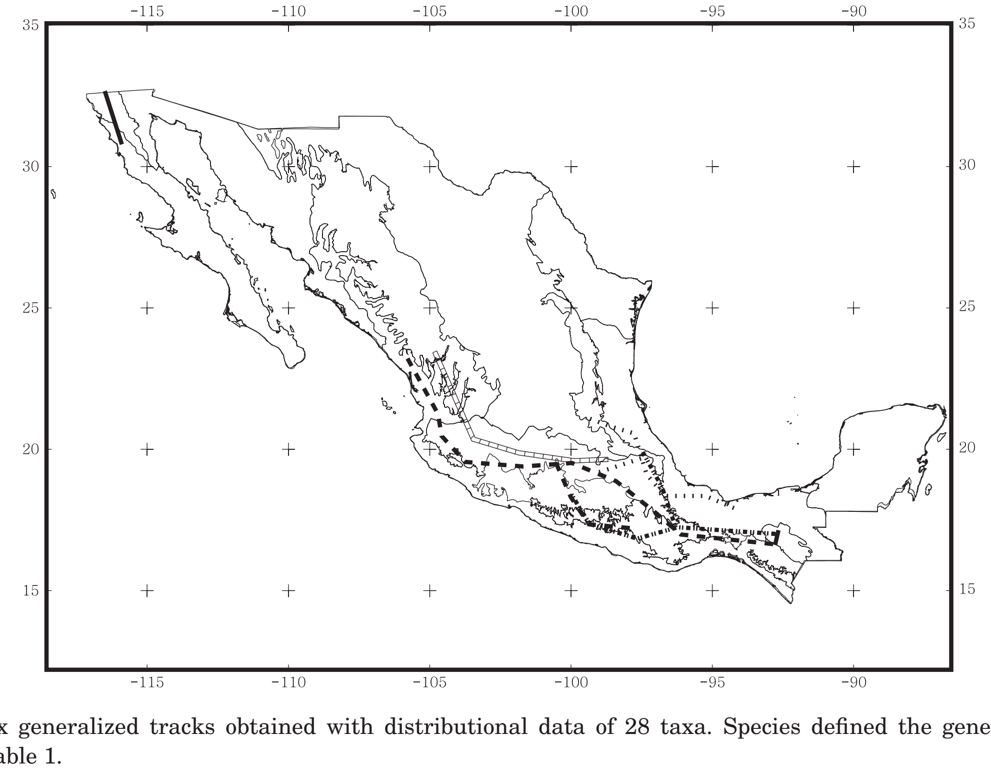

Figure 9. Six generalized tracks obtained with distributional data of 28 taxa. Species defined the generalized tracks detailed in Table 1.

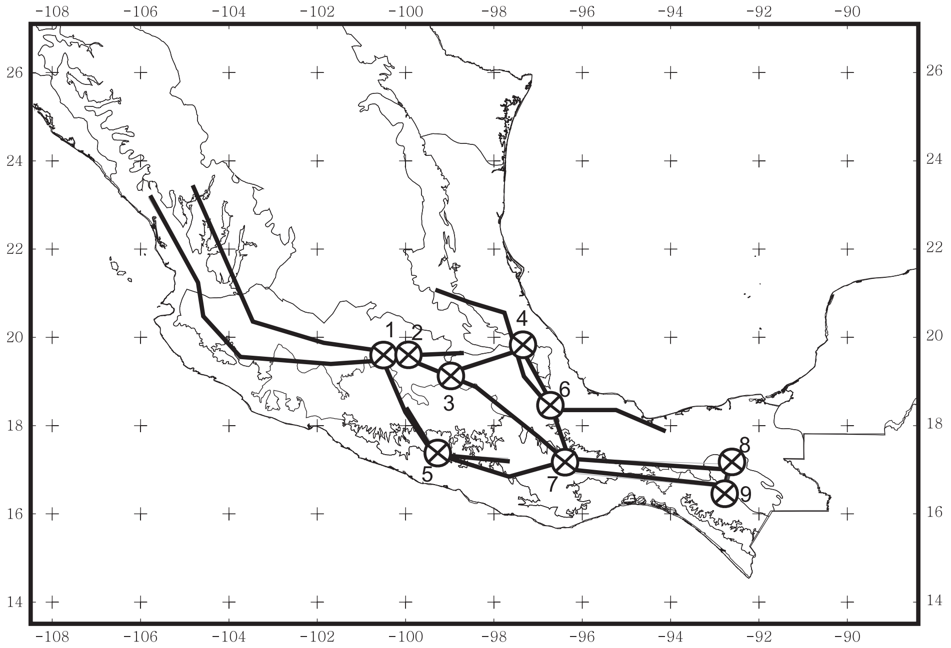

Figure 10. Nine panbiogeographical nodes for taxa of Nearctic mammals of Mexico. Details of these nodes are given in Table 2.

nia generalized track lies in the northern part of the California Peninsula, in Baja California state, occupying the northern Sierras of Baja California, in the Sierra de San Pedro Mártir, Sierra de Juárez and the north-western coastal chaparral (Arriaga *et al*., 1997). This pattern was also detected for other taxa (Rojas-Soto, Alcántara-Ayala & Navarro, 2003), and recognized as the Nearctic Californian dominion (Morrone & Márquez, 2003), an important area of endemism for land mammals (Escalante, Espinosa & Morrone, 2003). The Centre-Gulf generalized track crosses from northern Hidalgo and Veracruz, to southern Veracruz, bifurcates in Puebla and Tlaxcala, and ends in the state of Mexico. The Centre-North Pacific generalized track is represented by species distributed on the Sierra Madre Occidental and the Transmexican Volcanic Belt, crossing Durango, Jalisco, Michoacán and the state of Mexico; this track is part of the Mexican Mountain dominion (Morrone & Márquez, 2003). The Centre-South Pacific generalized track begins in southern Sinaloa, crosses Nayarit and Jalisco and bifurcates in Michoacán: one part crosses the states of Mexico, Puebla and Oaxaca, and ends in Chiapas; the other part crosses the south-western portion of the states of Mexico and Guerrero, ending in western Oaxaca. The Isthmus of Tehuantepec generalized track begins in Guerrero and Veracruz, in both the Pacific and Gulf coasts; both parts join in Oaxaca and then continue to Chiapas. The Centre-South Pacific and Isthmus of Tehuantepec generalized tracks belong to the Mesoamerican dominion (Morrone & Márquez, 2003). The Chiapas generalized track lies in the Altos de Chiapas pine–oak and tropical montane cloud forests (Arriaga *et al*., 1997).

Nine nodes were delineated at the intersections between these generalized tracks (Fig. 10). The nodes are characterized in terms of the biogeographical provinces where they are found, as well as their elevational, climatic and geological features in Table 2. Most of the nodes are in areas with A and C Köppen climatic types, i.e. tropical humid and subtropical climates. Furthermore, they are located mostly in highlands composed of rocks of Tertiary and Quaternary ages. Three nodes lie on the Transmexican Volcanic Belt, one in southern Sierra Madre Oriental, one in eastern Sierra Madre del Sur, one in the highlands of Chiapas, and three between the boundaries of two provinces. Two generalized tracks cross Jalisco state, both beginning near the Sierra Madre Occidental. Iñiguez & Santana (1993) postulated that the state of Jalisco harbours the highest number of species that reach their limit of distribution, indicating the existence of an abrupt biogeographical transitional zone in central Mexico.

Nodes reveal boundaries of Nearctic taxa. According to Halffter (1976), mammals exhibit a divisionary line between the Nearctic and Neotropical regions, geographically defined by the Sierra Madre Occiden-

Table 2. Characterization of the biogeographical nodes generated from intersections of generalized tracks from mammal distribution data

Nodes	Provinces	Climate	Elevation (m a.s.l.)	Geology	Localization
1	Transmexican Volcanic Belt	C(w$_2$)(w) and C(E) (w$_2$)(w)	3000	Tertiary gritty-tufa and extrusive igneous rocks	North Angangueo, San José and San Ramon river
2	Transmexican Volcanic Belt	C(w$_2$)(w), Aw$_0$(w) and (A)C(w$_1$)(w)	3020	Tertiary extrusive igneous rocks	North-west Toluca to Oro de Hidalgo, west Atlacomulco. El Salto river
3	Transmexican Volcanic Belt	(A)C(w$_1$)(w), C(w$_2$)(w), and Aw$_0$(w)	2500	Tertiary and Quaternary extrusive igneous rocks	South Mexico City, near Tlaloc volcano, between Mexico City and Parque Nacional Zoquiapan
4	Sierra Madre Oriental	C(fm) (A)C(fm), C(m) and (A)C(m)	1000	Cretaceous limestone and shale, and Jurassic gritty and sandy rocks	South Poza Rica, between Cuetzalan del Progreso and Mazatepec, near Chichical river
5	Mexican Pacific Coast–Sierra Madre del Sur	BS$_1$ (h)w(w), Aw$_0$(w), A(C)w$_0$(w) and C(w$_1$)(w)	800	Cretaceous shale-gritty and limestone, Upper Tertiary extrusive igneous, and Quaternary soil rocks	South Iguala, near Barranca Tejopilco, Barranca Tijeras and Cañada San Marcos. Cross Mezcala river
6	Mexican Gulf–Transmexican Volcanic Belt	Aw$_2$(w)	0–1500	Tertiary gneiss, and Quaternary extrusive igneous rocks	South-west Veracruz, near Paso Grande river
7	Santa María del Sur	(A)C(m)(w), C(m)(w), A(C)(w$_1$)(w), C(w$_2$)(w) and Am(w)	1500	Palaeozoic schist, and Tertiary–Jurassic and Cretaceous rocks	Cempoaltepetl, Sierra de Juárez. South-west Sierra Madre Jacatepec
8	Chiapas	Aw$_1$(w) (A)C(w$_2$)(w), C(w$_2$)(w), and Aw$_0$(w)	500–2000	Oligocene shale-gritty, Miocene gritty, and Quaternary soil rocks	Near Usumacinta river and Jonuta river. North Pom and Atasta lagoons
9	Chiapas–Mexican Pacific Coast	Aw$_1$(w) and Aw$_2$(w)	1000	Tertiary and Mesozoic extrusive igneous rocks	North-east Nezahualcoyotl dike, between Tapilula and Nuevo Jolistahuacan. Jobo and Sidna rivers

tal, the Transmexican Volcanic Belt and the Sierra Madre Oriental. The Sierra Madre Occidental dates from the Miocene, the Transmexican Volcanic Belt from the Tertiary (although its formation was more intense during the Quaternary), and the Sierra Madre Oriental developed during Cretaceous to Palaeocene times (Viniegra, 1992; Graham, 1998). At the end of the Tertiary and early Quaternary (Eocene–Pleistocene) periods, when the climate was cooler, southern Mexico received Nearctic temperate biotic elements (Graham, 1998). The occurrence of isolated or semi-isolated populations of northern mammals on mountain ranges at low latitudes is the result of Pleistocene southward migration of Nearctic elements (Vaughan, Ryan & Czaplewski, 2000). Taxa isolated in the highlands of Chiapas (as well as Guatemala) at the end of the Pleistocene may represent the southernmost Nearctic relicts in Mesoamerica (Conroy *et al*., 2001).

Ortega & Arita (1998) used a biogeographical index to analyse bat distributional data in order to delineate the boundary between the Neotropical and Nearctic regions. They distinguished three zones: Nearctic, Transitional and Neotropical. Based on our analysis, the Nearctic region occupies northern Mexico; the transitional zone comprises the Sierra Madre

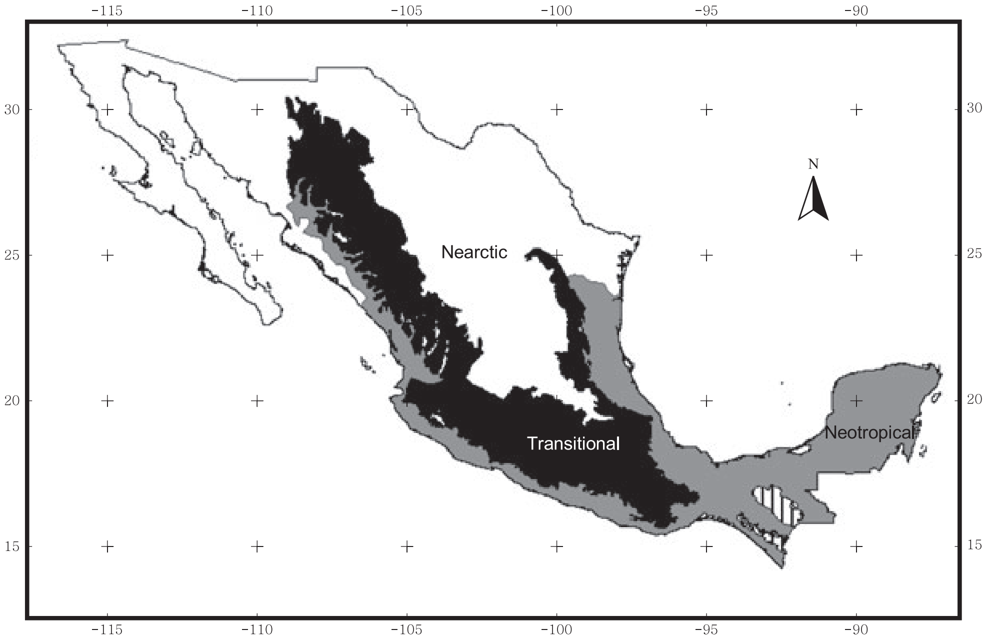

Figure 11. Transitional, Nearctic and Neotropical regions delimited based on mammal species analysed in this study. The highlands of Chiapas are in the Neotropical region, although they harbour some relictual Nearctic species.

Oriental, Transmexican Volcanic Belt, Sierra Madre del Sur and probably Sierra Madre Occidental provinces; and the Neotropical region is restricted to the southern part of the country (Fig. 11). Our results are similar to those of Ortega & Arita (1998), but we assigned the highlands of Chiapas to the Neotropical region.

The Isthmus of Tehuantepec has been postulated as a conspicuous boundary between the Nearctic and Neotropical biotas. Cole *et al.* (1994) ended the Nearctic region in the Mexican border with Guatemala. Carleton *et al.* (2002) undertook a parsimony analysis of endemicity for 76 species of small mammals, postulating that the Isthmus of Tehuantepec may be a barrier for distributional limits of *Habromys* species. Leopold (1983) mentioned that the Isthmus of Tehuantepec acts as a bridge naturally linking the biotas of the eastern and west coastal regions. Marshall & Liebherr (2000) undertook a cladistic biogeographical analysis based on insect, fish, reptile and vascular plant taxa, and found two clades: the northern one includes the Sierra Madre Occidental, the Mexican Plateau, the Sonoran Desert, and the Sierra Madre Oriental; whereas the southern one comprises the southern Sierra Madre Occidental, the Chiapas Highlands, the Transmexican Volcanic Belt and the Sierra Madre del Sur. According to Marshall & Liebherr (2000), the boundary between the Nearctic and Neotropical regions lies in the Transmexican Volcanic Belt, not in the Isthmus of Tehuantepec.

Although boundaries between regions may differ for animals and plants (Cox, 2001), it is possible to postulate a single model for all organisms (Morrone, 2002). Track analyses for our nodes coincide partially with those of other taxa (vascular plants, Luna-Vega *et al*., 2000; land birds, Álvarez Mondragón, 2001; gymnosperms, vertebrates and insects, Contreras-Medina & Eliosa, 2001). Morrone & Márquez (2001) used a parsimony analysis of endemicity to analyse several beetle (Coleoptera) taxa and found two generalized tracks: the northern one includes the Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Balsas Basin and Sierra Madre del Sur provinces; and the southern one includes the Chiapas, Mexican Gulf, Mexican Pacific Coast and Western Panamanian Isthmus provinces. The former generalized track occupies the areas where the majority of our nodes are located, which agrees with the hypothesis of a transition zone between the Nearctic and Neotropical regions. Luna-Vega *et al*. (2001) also found two generalized tracks based on vascular plant taxa, which agree with Morrone & Márquez's (2001) hypothesis.

The majority of our nodes are located on the Sierra Madre Oriental, Transmexican Volcanic Belt and Sierra Madre del Sur biogeographical provinces, which together with the Sierra Madre Occidental largely constitute the main mountain systems of Mexico; however, several Nearctic taxa continue their distribution into the montane areas of the Chiapas biogeographical province. Fa & Morales (1998) considered that these places were likely sites for dispersion of mammals, e.g. for species of *Sorex* and *Microtus*, in the Quaternary. The Cenozoic was the period when the most important climatic changes occurred (Graham, 1998), and it is possible that the southern mountains of Mexico acted as relict areas of cool periods during the Pleistocene, as has been discussed for *Microtus* species by Conroy *et al*. (2001). Ceballos, Arroyo-Cabrales & Medellín (2002) also mentioned that the presence of these relict species supported the hypothesis of big biogeographical filters, which allowed differential dispersal of species, in the Sierra Madre Oriental, Sierra Madre Occidental, northern Mexico, Transmexican Volcanic Belt and Sierra Madre del Sur (Ceballos *et al.*, 2002).

The Nearctic region has been delimited by distributional data of different taxa, but the main barriers to expansion indicated by previous authors, namely the major mountain systems of the Mexican transition zone, also constitute an evolutionarily ‘active’ zone, supported by the presence of nodes in the Sierra Madre Oriental, Sierra Madre Occidental, Sierra Madre del Sur and Transmexican Volcanic Belt, which are evidence of several speciation events in the past. According to our analysis, the southernmost influence of the Nearctic land mammals in Mexico lies on the highlands of Chiapas.

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