

# **Chapter 3**

## **Quaternary Mammals, People, and Climate Change: A View from Southern North America**

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**Abstract** The Pleistocene and modern mammal faunas of southern North America strongly differ in taxonomic makeup, distribution, and physiognomy. The former faunal complexes are part of the ancient landscape in which early peoples may have interacted. Customarily, differences between the Pleistocene and modern faunas have been attributed to climate change or human-impact driven extinctions. Mexico's Pleistocene mammal record is analyzed in time and space, emphasizing the study of the Rancholabrean Chronofauna, which is the most recent North American Land Mammal Age fauna. Palynological and paleosol records are reviewed as an independent check of the interpretation derived from mammals. The integration of the information provides the basis for a proposal regarding Late Pleistocene climate change trends across the country, and whether people were involved in the mammalian community response to climate change in terms of extinction or biogeographic shifting within and outside the country. This approach supports an explanation of the differences between southern North America's Pleistocene and modern mammal faunas.

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### **Introduction**

Climate change is a world-wide phenomenon that has affected, and is affecting, biodiversity. Currently, that change may be driven largely by human activities (Kellogg 1978; Schneider and Temkin 1978; AIMES 2010; Caballero-Miranda et al. 2010). Changes, however, have taken place episodically during the Quaternary, i.e., the last 2.6 million years (Wright et al. 1993; Barnosky 2008; Gibbard et al. 2010), and have occurred many times in the history of the Earth. Nonetheless, given their recent nature, Pleistocene climatic oscillations are understood better than those of previous geologic epochs because their records are well documented and dated. Their impact on the constitution, structure, and distribution of the biota can be assessed more easily because many species involved are extant (Barnosky et al. 2011).

The North American Quaternary mammal record is very extensive, but that of its southern part (meaning Mexico) is comparatively less well known. Mexico's record is crucial for adequately understanding the impact of climate change that affected continental taxonomic makeup, community structure, and biogeography. Mexico's Quaternary mammal record is enormous, and its modern and Pleistocene components show important differences.

The modern terrestrial mammal fauna consists of 11 orders, 36 families, 168 genera, and 496 species (Ramírez-Pulido et al. 2014). The Pleistocene fauna retrieved from more than 15,000 mammal records consists at present of 13 orders (if the questionable Litoptern record is corroborated), 43 families, 146 genera, and 297 species. Thus, the Pleistocene record is more diverse at ordinal and family levels. It includes both extinct and extant taxa, and some of the latter

were wider-ranging than today's distribution. As in the present, the order with the highest number of fossil species is Rodentia, followed by Chiroptera and Carnivora (Wilson and Reeder 2005). All terrestrial extant orders and families also are recorded as fossils, but only 197 (approximately 2/5) of the 496 modern species are found in the Pleistocene record (Arroyo-Cabralles et al. 2007, 2010; Ferrusquía-Villafranca et al. 2010).

On the other hand, 3 orders, 10 families, 38 genera, and 86 species that existed in the Pleistocene are no longer present in the modern fauna. The Orders Notoungulata and Litopterna are extinct world-wide, and the Proboscidea no longer occur in the Americas. Five families are extinct (Gomphotheriidae, Mammutidae, Glyptodontidae, Megatheriidae, and Mylodontidae), whereas the families Herpestidae, Equidae, Hydrochoeridae, Camelidae, and Megalonychidae have been extirpated from North America. Twenty-nine (20%) of the 146 genera recorded in the Pleistocene are now extinct, and nine (6%) have been extirpated. At the species level, 77 are extinct (26%) and nine (3%) are extirpated from Mexico (Ferrusquía-Villafranca et al. 2010).

Although the Laurentide Glacier did not reach Mexico, its advances and retreats in the Pleistocene most likely affected its climate and influenced its landscape (Caballero et al. 2010). A wide variety of environmental conditions existed, such as low lake levels and a downward displacement of ~1000 m for the limit of pine forests with alpine vegetation, as well as changes in vegetation composition and distribution. This variety, in turn, allowed co-occurrence of very diverse mammalian taxa, including megaherbivores and megacarnivores that functioned as community-dominant or keystone species. For example, during the Pleistocene, the Central Plateau was covered by grassland, and mammoth coexisted with camel, bison, horses, pronghorns, saber-toothed cat, Pleistocene lion, short-faced bear, dire wolf, skunks, hares, rabbits, capybaras, voles, rats, mice, and bats. At that time, the forested areas on the mountain slopes of the contiguous Sierras Madres Occidental and Oriental, and the Trans-Mexican Volcanic Belt were the roaming grounds of mastodon, gomphotheres, ground sloths, toxodonts, deer, spectacled bear, mountain lion, weasel, otter, raccoon, forest rodents, lagomorphs, and shrews. Early peoples may have coexisted in some of those areas, with the earliest record of human occupation in Mexico dating to around 11.0  $^{14}\text{C}$  kBP (Sánchez 2001; Gonzalez and Huddart 2008; Sánchez et al. 2009).

Geographically, Mexico has an important role in regard to current discussion about the First Americans. It has been considered a large biogeographic corridor (after Simpson 1940; Martin and Harrell 1957) for the first human groups coming from north to south. Few data are available, however, regarding the interactions of these early peoples and large Pleistocene mammals in Mexico (e.g., Arroyo-Cabralles et al. 2006; Johnson et al. 2006). Data equally are limited on the relationship, if any, between the extinction of those large mammals and early peoples in southern North America (Sanchez 2001; González and Huddart 2008).

Changes in the biota's physiognomy have been invoked as instances of extinction/migration processes (ultimately) driven by climate change (Barnosky 2008; Ceballos et al. 2010b). For example, a comparison of Mexico's Pleistocene and modern mammal faunas indicates the latter has very few large species. Extinct taxa include among others, Notoungulata, Mammutidae, Gomphotheriidae, *Smilodon*, *Glossotherium*, and *Neotoma magnodonta*. On the other hand, Elephantidae, Camelidae, Equidae, Hydrochoeridae, and *Neotoma floridana* are extant but extirpated from the country. Finally, the present distribution of some mammal species may be due to their movements during glacial times, with vestigial or relict distributions in those areas that they were able to reach, e.g., *Sorex milleri* and *Lepus flavigularis*. Changes in biodiversity and geographic range seem to be greater in temperate than tropical areas. In the former, a southward shift is apparent, such as with Felidae and Ursidae.

Summing up, extinction, extirpation, and the fauna's physiognomic change related to individual species body size may be linked directly to resource depletion. Resources are distributed differently over the landscape, affected by environmental and geologic conditions, and forming part of the ecosystem (Forman and Godron 1986). In depletion, the type, quality, or quantity of a resource is no longer available or at an adequate level to maintain the population. That depletion could have been induced by shrinking and/or loss of primary plant food-source areas, replacement by less nutritional plants, large herbivore density decrease and/or extinction, as well as possible competition by humans for food. The cause(s) may be different for each species, yet they all seem related primarily to climate and ecosystem changes (Koch and Barnosky 2006). This overview provides a synthesis of the Quaternary Mexican mammalian faunas, their geographic and chronologic distribution, and climatic

implications. It creates a foundation from which to explore possible causes for extinctions and extirpations, including human influence.

## Methods

The Quaternary mammal record of southern North America has been examined in an attempt to characterize the impact of climate change in the fauna's makeup, structure, and distribution. Comparisons are made between the Pleistocene (Table 3.1) and modern faunas, using the mammal species of the latter as environmental indicators. Their presence/absence in particular times and/or places may disclose differences that may be linked to or explained by climate change. Corroborative evidence from other indicators such as Pleistocene palynological assemblages (regarded as flora surrogates) and paleosol (buried soils) records where available also are used (see Ferrusquía-Villafranca et al. 2010).

For the Pleistocene mammal record analysis, the chronological framework used by Bell et al. (2004) is followed. In Mexico, the Rancholabrean Chronofauna is the best represented. Most local faunas are of Late Rancholabrean age (Quaternary Mexican Mammalian Database, QMMDB; Arroyo-Cabral et al. 2002). Dating is largely biochronological, i.e., commonly based on a few age-diagnostic taxa. Thus, their position within the Rancholabrean North American Land Mammal Age (NALMA; roughly between 200 to 150 ka and 11 ka; Bell et al. 2004) is approximate. Furthermore, less than 30 local faunas have radiocarbon ages (Arroyo-Cabral et al. 2002, 2007; Ferrusquía-Villafranca 2010), all Late Rancholabrean. In some instances, the faunas, palynological assemblages, and paleosol records can be placed within the 40–11  $^{14}\text{C}$  kBP interval. In most cases, the environmental comparisons of the fossil and modern mammal faunas largely involve Late Rancholabrean local faunas.

Discussion and comparison of results from segments of a territory as large as Mexico ( $\sim 2,000,000 \text{ km}^2$ ), with a bewildering geomorphic and geologic diversity, calls for reference to an ecologically/geologically meaningful spatial framework. That framework must have equally meaningful spatial units in order to promote precision, clarity, and reproducibility of results. Scientific comparisons based on such vaguely bounded territorial segments as central Mexico, northern Mexico, or the state boundaries would render nearly meaningless such comparisons. Hence, the spatial framework used here (Table 3.2 and Fig. 3.1) is based on the morphotectonic province concept (Ferrusquía-Villafranca 1993; Ferrusquía-Villafranca et al. 2010).

**Table 3.1** Pleistocene fossil mammals of Mexico, extant species also included. Main sources: Alvarez (1965), Barrios Rivera (1985), QMMDB (Arroyo-Cabral et al. 2002), Arroyo-Cabral et al. (2007); and Ferrusquía-Villafranca et al. (2010)

	Body size	Diet
<b>DIDELPHIMORPHIA</b>		
<b>Didelphidae</b>		
<i>Caluromys derbianus</i>	S	O
<i>Didelphis marsupialis</i>	S	O
<i>Didelphis virginiana</i>	S	O
<i>Marmosa canescens</i>	S	O
<i>Marmosa lorenzo<sup>a</sup></i>	S	O
<i>Marmosa mexicana</i>	S	O
<i>Philander opossum</i>	S	O
<b>XENARTHRA sensu lato</b>		
<b>Dasypodidae</b>		
<i>Cabassous centralis<sup>d</sup></i>	S	O
<i>Dasypus novemcinctus</i>	S	O
<i>Holmesina septentrionalis<sup>a</sup></i>	L	O
<i>Pampatherium mexicanum<sup>a</sup></i>	L	O
<b>Glyptodontidae<sup>a</sup></b>		
<i>Glyptotherium cylindricum<sup>a</sup></i>	L	H
<i>Glyptotherium floridanum<sup>a</sup></i>	L	H
<i>Glyptotherium mexicanum<sup>a</sup></i>	L	H
<b>Megalonychidae<sup>a</sup></b>		
<i>Megalonyx jeffersoni<sup>a</sup></i>	L	H
<i>Megalonyx wheatleyi<sup>a</sup></i>	L	H
<b>Megatheriidae<sup>a</sup></b>		
<i>Eremotherium laurillardii<sup>a</sup></i>	L	H
<i>Nothrotheriops mexicanum<sup>a</sup></i>	L	H
<i>Nothrotheriops shastensis<sup>a</sup></i>	L	H
<b>Mylodontidae<sup>a</sup></b>		
<i>Paramylodon harlani<sup>a</sup></i>	L	H
<b>Myrmecophagidae</b>		
<i>Myrmecophaga tridactyla<sup>d</sup></i>	M	C
<i>Tamandua mexicana</i>	S	C
<b>SORICOMORPHA</b>		
<b>Soricidae</b>		
<i>Cryptotis mayensis</i>	S	C
<i>Cryptotis mexicana</i>	S	C
<i>Cryptotis parva</i>	S	C
<i>Notiosorex crawfordi</i>	S	C
<i>Sorex cinereus</i>	S	C
<i>Sorex milleri</i>	S	C
<i>Sorex oreopolus</i>	S	C
<i>Sorex saussurei</i>	S	C
<b>CHIROPTERA</b>		
<b>Antrozoidae</b>		
<i>Antrozous pallidus<sup>d</sup></i>	S	C
<b>Emballonuridae</b>		
<i>Balantiopteryx io<sup>d</sup></i>	S	C
<i>Peropteryx macrotis</i>	S	C
<i>Saccopteryx bilineata</i>	S	C
<b>Molossidae</b>		
<i>Eumops bonariensis</i>	S	C
<i>Eumops perotis<sup>d</sup></i>	S	C

(continued)

**Table 3.1** (continued)

	Body size	Diet
<i>Eumops underwoodi</i> <sup>d</sup>	S	C
<i>Molossus rufus</i>	S	C
<i>Nyctinomops aurispinosus</i>	S	C
<i>Nyctinomops laticaudatus</i>	S	C
<i>Promops centralis</i>	S	C
<i>Tadarida brasiliensis</i>	S	C
<b>Mormoopidae</b>		
<i>Mormoops megalophylla</i>	S	C
<i>Pteronotus davyi</i>	S	C
<i>Pteronotus parnellii</i>	S	C
<b>Natalidae</b>		
<i>Natalus stramineus</i>	S	C
<b>Phyllostomidae</b>		
<i>Artibeus jamaicensis</i>	S	H
<i>Artibeus lituratus</i>	S	H
<i>Carollia brevicauda</i>	S	H
<i>Carollia perspicillata</i>	S	H
<i>Carollia sowelli</i>	S	H
<i>Centurio senex</i>	S	H
<i>Chiroderma villosum</i>	S	H
<i>Choeronycteris mexicana</i>	S	H
<i>Chrotopterus auritus</i>	S	C
<i>Dermanura Phaeotis</i>	S	H
<i>Desmodus cf. D. draculae</i> <sup>a</sup>	S	B
<i>Desmodus rotundus</i>	S	B
<i>Desmodus stocki</i> <sup>a</sup>	S	B
<i>Diphylla ecaudata</i>	S	B
<i>Enchisthenes hartii</i>	S	H
<i>Glossophaga soricina</i>	S	H
<i>Leptonycteris curasoae</i>	S	H
<i>Leptonycteris nivalis</i>	S	H
<i>Macrotus californicus</i> <sup>d</sup>	S	C
<i>Micronycteris microtis</i>	S	C
<i>Mimon bennettii</i>	S	C
<i>Sturnira lilium</i>	S	H
<i>Tonatia evotis</i>	S	C
<b>Vespertilionidae</b>		
<i>Corynorhinus townsendii</i>	S	C
<i>Eptesicus brasiliensis</i>	S	C
<i>Eptesicus furinalis</i>	S	C
<i>Eptesicus fuscus</i>	S	C
<i>Lasionycteris noctivagans</i>	S	C
<i>Lasiurus cinereus</i>	S	C
<i>Lasiurus ega</i>	S	C
<i>Lasiurus intermedius</i>	S	C
<i>Myotis californicus</i>	S	C
<i>Myotis keaysi</i>	S	C
<i>Myotis thysanodes</i>	S	C
<b>PRIMATES</b>		
<b>Cebidae</b>		
<i>Alouatta palliata</i> <sup>d</sup>	S	O
<i>Alouatta pigra</i>	S	O
<i>Ateles geoffroyi</i> <sup>d</sup>	S	O

**Table 3.1** (continued)

	Body size	Diet
<b>CARNIVORA</b>		
<b>Canidae</b>		
<i>Canis cedazoensis</i> <sup>a</sup>	M	C
<i>Canis dirus</i> <sup>a</sup>	M	C
<i>Canis edwardii</i> <sup>a</sup>	M	C
<i>Canis familiaris</i>	M	C
<i>Canis latrans</i>	M	C
<i>Canis lupus</i>	M	C
<i>Canis rufus</i> <sup>c</sup>	M	C
<i>Cuon alpinus</i> <sup>c</sup>	M	C
<i>Urocyon cinereoargenteus</i>	S	C
<b>Felidae</b>		
<i>Herpailurus yagouaroundi</i>	S	C
<i>Leopardus pardalis</i>	M	C
<i>Leopardus wiedii</i>	S	C
<i>Lynx rufus</i>	S	C
<i>Panthera atrox</i> <sup>a</sup>	L	C
<i>Panthera onca</i>	L	C
<i>Puma concolor</i>	M	C
<i>Smilodon californicus</i>	L	C
<i>Smilodon fatalis</i> <sup>a</sup>	L	C
<i>Smilodon gracilis</i> <sup>a</sup>	L	C
<b>Hyaenidae</b> <sup>b</sup>		
<i>Chasmaporthetes johnstoni</i> <sup>a</sup>	M	C
<b>Mustelidae</b>		
<i>Conepatus leuconotus</i>	S	O
<i>Conepatus mesoleucus</i>	S	O
<i>Lontra longicaudis</i>	S	C
<i>Mephitis macroura</i>	S	O
<i>Mephitis mephitis</i>	S	O
<i>Mustela frenata</i>	S	C
<i>Mustela nigripes</i> <sup>d</sup>	S	C
<i>Spilogale putorius</i> <sup>d</sup>	S	O
<i>Taxidea taxus</i>	S	C
<b>Procyonidae</b>		
<i>Bassariscus astutus</i>	S	O
<i>Bassariscus sumichrasti</i>	S	O
<i>Bassariscus tigrinus</i> <sup>a</sup>	S	O
<i>Nasua narica</i>	M	O
<i>Potos flavus</i>	S	H
<i>Procyon lotor</i>	M	O
<i>Procyon pygmaeus</i>	M	O
<b>Ursidae</b>		
<i>Arctodus pristinus</i> <sup>a</sup>	L	C
<i>Arctodus simus</i> <sup>a</sup>	L	C
<i>Tremarctos floridanus</i> <sup>a</sup>	L	O
<i>Ursus americanus</i> <sup>d</sup>	L	O
<b>RODENTIA</b>		
<b>Castoridae</b>		
<i>Castor cf. C. californicus</i>	M	H
<b>Cuniculidae</b>		
<i>Cuniculus paca</i>	M	H

(continued)

(continued)

**Table 3.1** (continued)

	Body size	Diet
<b>Dasyproctidae</b>		
<i>Dasyprocta mexicana</i>	M	H
<i>Dasyprocta punctata</i>	M	H
<b>Erethizontidae</b>		
<i>Erethizon dorsatum<sup>d</sup></i>	M	H
<i>Coendou mexicanus</i>	M	H
<b>Geomysidae</b>		
<i>Cratogeomys bensoni<sup>a</sup></i>	S	H
<i>Cratogeomys castanops</i>	S	H
<i>Cratogeomys gymnurus</i>	S	H
<i>Cratogeomys merriami</i>	S	H
<i>Cratogeomys tylorrhinus</i>	S	H
<i>Orthogeomys grandis</i>	S	H
<i>Orthogeomys hispidus</i>	S	H
<i>Orthogeomys onerous<sup>a</sup></i>	S	H
<i>Thomomys bottae</i>	S	H
<i>Thomomys umbrinus</i>	S	H
<b>Heteromyidae</b>		
<i>Chaetodipus hispidus</i>	S	H
<i>Chaetodipus huastecensis<sup>a</sup></i>	S	H
<i>Chaetodipus nelsoni</i>	S	H
<i>Chaetodipus penicillatus<sup>d</sup></i>	S	H
<i>Dipodomys nelsoni</i>	S	H
<i>Dipodomys phillipsii</i>	S	H
<i>Dipodomys spectabilis</i>	S	H
<i>Heteromys desmarestianus</i>	S	H
<i>Heteromys gaumeri</i>	S	H
<i>Liomys irroratus</i>	S	H
<i>Perognathus flavus</i>	S	H
<b>Hydrochaeridae<sup>b</sup></b>		
<i>Neochoerus aesop<sup>a</sup></i>	M	H
<b>Muridae</b>		
<i>Baiomys intermedius<sup>a</sup></i>	S	H
<i>Baiomys musculus</i>	S	H
<i>Baiomys taylori</i>	S	H
<i>Hodomys alleni<sup>d</sup></i>	S	H
<i>Hodomys sp. nov.<sup>a</sup></i>	S	H
<i>Microtus californicus<sup>d</sup></i>	S	H
<i>Microtus guatemalensis</i>	S	H
<i>Microtus meadensis<sup>a</sup></i>	S	H
<i>Microtus mexicanus</i>	S	H
<i>Microtus oaxacensis</i>	S	H
<i>Microtus pennsylvanicus<sup>d</sup></i>	S	H
<i>Microtus quasater</i>	S	H
<i>Microtus umbrosus</i>	S	H
<i>Neotoma albicula<sup>d</sup></i>	S	H
<i>Neotoma angustapalata</i>	S	H
<i>Neotoma anomala<sup>a</sup></i>	S	H
<i>Neotoma cinerea<sup>c</sup></i>	S	H
<i>Neotoma floridana<sup>c</sup></i>	S	H
<i>Neotoma lepida</i>	S	H
<i>Neotoma magnodonta<sup>a</sup></i>	S	H

(continued)

**Table 3.1** (continued)

	Body size	Diet
<i>Neotoma mexicana</i>	S	H
<i>Neotoma micropus</i>	S	H
<i>Neotoma palatina</i>	S	H
<i>Neotoma phenax<sup>d</sup></i>	S	H
<i>Neotoma tlapacoyana<sup>a</sup></i>	S	H
<i>Neotomodon alstoni</i>	S	H
<i>Nyctomyssumichrasti</i>	S	H
<i>Oligoryzomys fulvescens</i>	S	H
<i>Ondatra nebrascensis<sup>a</sup></i>	S	H
<i>Onychomys leucogaster</i>	S	H
<i>Oryzomys alfaroi</i>	S	H
<i>Oryzomys couesi</i>	S	H
<i>Oryzomys melanotis</i>	S	H
<i>Otonyctomys hatti</i>	S	H
<i>Ototylomysphyllotis</i>	S	H
<i>Peromyscus boylii</i>	S	H
<i>Peromyscus difcili</i>	S	H
<i>Peromyscus eremicus</i>	S	H
<i>Peromyscus leucopus</i>	S	H
<i>Peromyscus levipes</i>	S	H
<i>Peromyscus maldonadoi<sup>a</sup></i>	S	H
<i>Peromyscus maniculatus</i>	S	H
<i>Peromyscus melanophrys</i>	S	H
<i>Peromyscus melanotis<sup>d</sup></i>	S	H
<i>Peromyscus mexicanus</i>	S	H
<i>Peromyscus ochraventer</i>	S	H
<i>Peromyscus pectoralis</i>	S	H
<i>Peromyscus truei<sup>d</sup></i>	S	H
<i>Peromyscus yucatanicus</i>	S	H
<i>Reithrodontomys fulvescens</i>	S	H
<i>Reithrodontomys megalotis</i>	S	H
<i>Reithrodontomys mexicanus</i>	S	H
<i>Reithrodontomys montanus</i>	S	H
<i>Sigmodon alleni</i>	S	H
<i>Sigmodon arizonae</i>	S	H
<i>Sigmodon curtisi<sup>a</sup></i>	S	H
<i>Sigmodon fulviventer</i>	S	H
<i>Sigmodon hispidus</i>	S	H
<i>Sigmodon leucotis</i>	S	O
<i>Sigmodon toltecus</i>	S	H
<i>Synaptomys cooperi<sup>d</sup></i>	S	H
<i>Tylomys nudicaudus</i>	S	H
<b>Sciuridae</b>		
<i>Ammospermophilus interpres</i>	S	H
<i>Cynomys ludovicianus<sup>d</sup></i>	S	H
<i>Cynomys mexicanus</i>	S	H
<i>Glaucomys volans</i>	S	H
<i>Marmota flaviventris<sup>d</sup></i>	S	H
<i>Sciurus allenii</i>	S	H
<i>Sciurus aureogaster</i>	S	H
<i>Sciurus deppei</i>	S	H
<i>Sciurus nayaritensis</i>	S	H

(continued)

**Table 3.1** (continued)

	Body size	Diet
<i>Sciurus variegatoides</i> <sup>d</sup>	S	H
<i>Sciurus yucatanensis</i>	S	H
<i>Spermophilus mexicanus</i>	S	H
<i>Spermophilus spilosoma</i>	S	H
<i>Spermophilus variegatus</i>	S	H
<b>LAGOMORPHA</b>		
<b>Leporidae</b>		
<i>Aluragus</i> sp. <sup>a</sup>	S	H
<i>Aztlanolagus agilis</i> <sup>a</sup>	S	H
<i>Lepus alleni</i>	S	H
<i>Lepus californicus</i>	S	H
<i>Lepus callotis</i>	S	H
<i>Romerolagus diazii</i>	S	H
<i>Sylvilagus audubonii</i>	S	H
<i>Sylvilagus bachmani</i>	S	H
<i>Sylvilagus brasiliensis</i>	S	H
<i>Sylvilagus cunicularius</i>	S	H
<i>Sylvilagus floridanus</i>	S	H
<i>Sylvilagus hibbardi</i> <sup>a</sup>	S	H
<i>Sylvilagus leonensis</i> <sup>a</sup>	S	H
<b>PERISSODACTYLA</b>		
<b>Equidae</b> <sup>b</sup>		
<i>Equus alaskae</i> <sup>a</sup>	L	H
<i>Equus calobatus</i> <sup>a</sup>	L	H
<i>Equus conversidens</i> <sup>a</sup>	L	H
<i>Equus excelsus</i> <sup>a</sup>	L	H
<i>Equus ferus</i> <sup>a</sup>	L	H
<i>Equus cf. E. francisci</i>	L	H
<i>Equus giganteus</i> <sup>a</sup>	L	H
<i>Equus mexicanus</i> <sup>a</sup>	L	H
<i>Equus pacificus</i> <sup>a</sup>	L	H
<i>Equus parastylidens</i> <sup>a</sup>	L	H
<i>Equus simplicidens</i> <sup>a</sup>	L	H
<i>Equus tau</i> <sup>a</sup>	L	H
<b>Tapiridae</b>		
<i>Tapirus bairdii</i> <sup>d</sup>	L	H
<i>Tapirus haysii</i> <sup>a</sup>	L	H
<b>ARTIODACTYLA</b>		
<b>Antilocapridae</b>		
<i>Antilocapra americana</i>	L	H
<i>Capromeryx mexicana</i> <sup>a</sup>	L	H
<i>Capromeryx minor</i> <sup>a</sup>	L	H
<i>Stockoceros conklingi</i> <sup>a</sup>	L	H
<i>Tetrameryx mooseri</i> <sup>a</sup>	L	H
<i>Tetrameryx shuleri</i> <sup>a</sup>	L	H
<i>Tetrameryx tacubayensis</i> <sup>a</sup>	L	H
<b>Bovidae</b>		
<i>Bison alaskensis</i> <sup>a</sup>	L	H
<i>Bison antiquus</i> <sup>a</sup>	L	H
<i>Bison bison</i> <sup>d</sup>	L	H
<i>Bison latifrons</i> <sup>a</sup>	L	H
<i>Bison priscus</i> <sup>a</sup>	L	H
<i>Euceratherium collinum</i> <sup>a</sup>	L	H

**Table 3.1** (continued)

	Body size	Diet
<i>Oreamnos harringtoni</i> <sup>a</sup>	L	H
<i>Ovis canadensis</i> <sup>d</sup>	L	H
<b>Camelidae</b> <sup>b</sup>		
<i>Camelops hesternus</i> <sup>a</sup>	L	H
<i>Camelops mexicanus</i> <sup>a</sup>	L	H
<i>Camelops minidokae</i> <sup>a</sup>	L	H
<i>Camelops traviswhitei</i> <sup>a</sup>	L	H
<i>Eschatius conidens</i> <sup>a</sup>	L	H
<i>Hemiauchenia blancoensis</i> <sup>a</sup>	L	H
<i>Hemiauchenia macrocephala</i> <sup>a</sup>	L	H
<i>Hemiauchenia vera</i> <sup>a</sup>	L	H
<i>Procamelops minimus</i> <sup>a</sup>	L	H
<b>Cervidae</b>		
<i>Cervus elaphus</i> <sup>c</sup>	L	H
<i>Mazama americana</i>	M	H
<i>Navahoceros fricki</i> <sup>a</sup>	L	H
<i>Odocoileus halli</i> <sup>a</sup>	L	H
<i>Odocoileus hemionus</i>	L	H
<i>Odocoileus lucasi</i> <sup>a</sup>	L	H
<i>Odocoileus virginianus</i>	L	H
<b>Tayassuidae</b>		
<i>Platygonus alemanii</i> <sup>a</sup>	M	H
<i>Platygonus compressus</i> <sup>a</sup>	M	H
<i>Platygonus tictuli</i> <sup>a</sup>	M	H
<i>Tayassu tajacu</i>	M	H
<i>Tayassu pecari</i>	M	H
<b>PROBOSCIDEA</b>		
<b>Elephantidae</b> <sup>b</sup>		
<i>Mammuthus columbi</i> <sup>a</sup>	L	H
<i>Mammuthus primigenius</i> <sup>a</sup>	L	H
<b>Gomphotheriidae</b> <sup>a</sup>		
<i>Cuvieronioides tropicus</i> <sup>a</sup>	L	H
<i>Stegomastodon mirificus</i> <sup>a</sup>	L	H
<b>Mammutidae</b> <sup>a</sup>		
<i>Mammut americanum</i> <sup>a</sup>	L	H
<b>NOTONGULATA<sup>a</sup></b>		
<b>Toxodontidae</b> <sup>a</sup>		
<i>Myxotodon</i> cf. <i>M. larensis</i> <sup>a</sup>	L	H
<b>LITOPTERNA<sup>a</sup></b>		
<b>Macrauchenidae</b> <sup>a</sup>		
Gen. et sp. indet. <sup>a</sup>	L	H

**Summary:** 13 Orders, 43 Families, 146 Genera, and 297 Species

Notes and abbreviations: Marine taxa excluded. References to taxa identified only at generic level are not included, but Litopterna

<sup>a</sup>Extinct taxon

<sup>b</sup>Suprageneric taxon extinct in Mexico, but extant outside Mexico

<sup>c</sup>Species extinct in Mexico, but extant outside this country

<sup>d</sup>Species extinct in the morphotectonic province(s) bearing the fossil locality (ies), but extant elsewhere in Mexico. Body mass: L, large. M, medium. S, small. Diet: H, herbivore. B, hematophagous. C, carnivore. O, omnivore. Further information in the text

(continued)

**Table 3.2** Location and basic features of the Morphotectonic Provinces of Mexico. Main sources: Ferrusquía-Villafranca (1993)

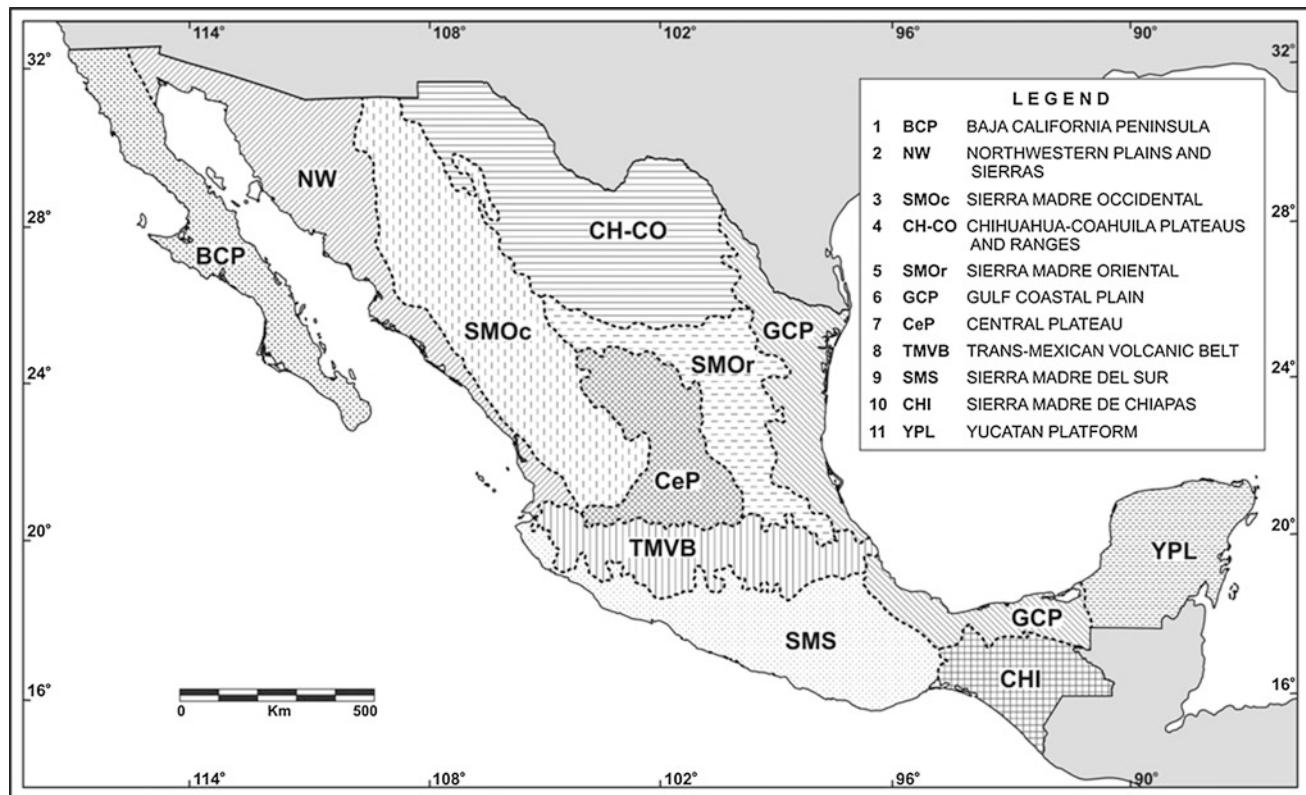
Province <sup>a</sup>	Location	Surface in km <sup>2</sup> and percentage <sup>b</sup>	Altitude ranges (m) <sup>c</sup>	Climate <sup>d</sup>	Chief land form
1	Northwestern Mexico 109°30'–117°00' WL 23°00'–32°30' NL	144,000 ~ 7.34%	0–2,130 0–1,000	BWh, BShs, Csa	Sierras and plains
2	Northwestern Mexico 107°00'–116°00' WL 23°00'–32°30' NL	236,800 ~ 12.02%	0–2,200 200–1,000	BWh, BSh	Sierras and plains
3	Western and northwestern Mexico 102°20'–109°40' WL 20°30'–31°20' NL	289,000 ~ 14.68%	200–3,000 2,000–3,000	Cfb, Aw	Sierras and plateaus
4	Northern Mexico 101°31'–110°31' WL 26°00'–31°45' NL	255,900 ~ 12.52%	200–2,000 800–1,200	BShw, BWh, BSk	Sierras and plateaus
5	Northeastern and northcentral Mexico Transverse sector 100°00'–105°00' WL 24°30'–26°00' NL Eastern sector 97°30'–101°20' WL 19°40'–26°00' NL	145,500 ~ 7.54%	200–3,000 1,000–2,000	Transverse sector BWh, BSk Eastern sector Cla, Cwa, BSh	Sierras
6	Eastern Mexico Northern sector 96°30'–100°20' WL 20°00'–26°00' NL Southern sector 91°15'–96°46' WL 17°10'–19°20' NL	170,600 ~ 8.66%	0–200	Northern sector Aw', Cw, Cx'w' Southern sector Afw', Amw'	Plains
7	Central Mexico 100°00'–104°00' WL 21°00'–24°00' NL	85,300 ~ 4.33%	1,000–3,300 2,000–3,000	BSh	Plateaus
8	Central Mexico 96°20'–105°20' WL 17°30'–20°25' NL Main sector 19°00'–21°00' N L	175,700 ~ 9.17%	1,000–5,000 1,000–2,000	Aw', Cfa, Cwa BSh, Cw, Cfbb, Aw	Peaks and plateaus
9	Southern Mexico 94°45'–104°40' WL 15°40'–19°40' NL	195,700 ~ 9.93%	0–3,500 1,200–1,800	Aw', Aw, BShw, Cwa, Cfa	Sierras and depressions
10	Southeastern Mexico 90°30'–95°00' WL 14°30'–17°40' NL	105,400 ~ 5.35%	0–2,500 200–1,000	Aw, Cw, Cf	Sierras, depressions, and plains
11	Eastern Mexico 87°00'–91°00' WL 17°50'–21°30' NL	167,600 ~ 8.46%	0–200	BShw, Amw	Plains and karst topography

<sup>a</sup>These numbers correspond to those on the map in Figure 1. Baja California morphotectonic province (mp). 2. Northwestern Plains and Sierras mp. 3. Sierra Madre Occidental mp. 4. Chihuahuan-Coahuilan Plateaus and Ranges mp. 5. Sierra Madre Oriental mp. 6. Gulf Coast Plain mp. 7. Central Plateau mp. 8. Trans-Mexican Volcanic Belt mp. 9. Sierra Madre del Sur mp. 10. Sierra Madre de Chiapas mp. 11. Yucatan Platform mp

<sup>b</sup>Percentage = ratio of mp to total surface area of Mexico

<sup>c</sup>First entry = total range, second entry = dominant range

<sup>d</sup>BWh, desert-like, Mat > 18°C; BShs, Csa, temperate with dry winter; BSh, dry Mat > 18°C; Cfb, temperate humid with no dry season; BShw, steppe-like, winter dry season, Mat > 18°C; BSk, steppe-like, Mat > 18°C; Cfa, temperate, no defined dry season; Cwa, temperate with dry winter; Aw', tropical with dry winter and rainy fall; Cw, temperate with dry winter; Cx'w', temperate with little rain throughout the year; Afw', tropical rainy with no defined dry season; Cf, temperate with no defined dry season. The key to the letter symbology is: A, warm humid and subhumid Climate Group (lack of a well-defined dry season); m, rainy season restricted to the summer; w, dry winter and warm season from April to September; w', less rainy summer with a short dry season. B, warm to cold and very arid to semiarid Climate Group; BS, warm to semicold and arid to semiarid Climate Subgroup; BW, warm to semicold and very arid Climate Subgroup; h, semiwarm with cool winter; k, temperate with a warm summer; s, rainy winter. C, temperate to semicold and humid to semihumid Climate Group; a, warm summer; b, cool and long summer; x', rainy fall. Source: García (1988)



**Fig. 3.1** Morphotectonic provinces of Mexico (modified from Ferrusquía-Villafranca 1993, 1998)

## Results

### The Mammal Record

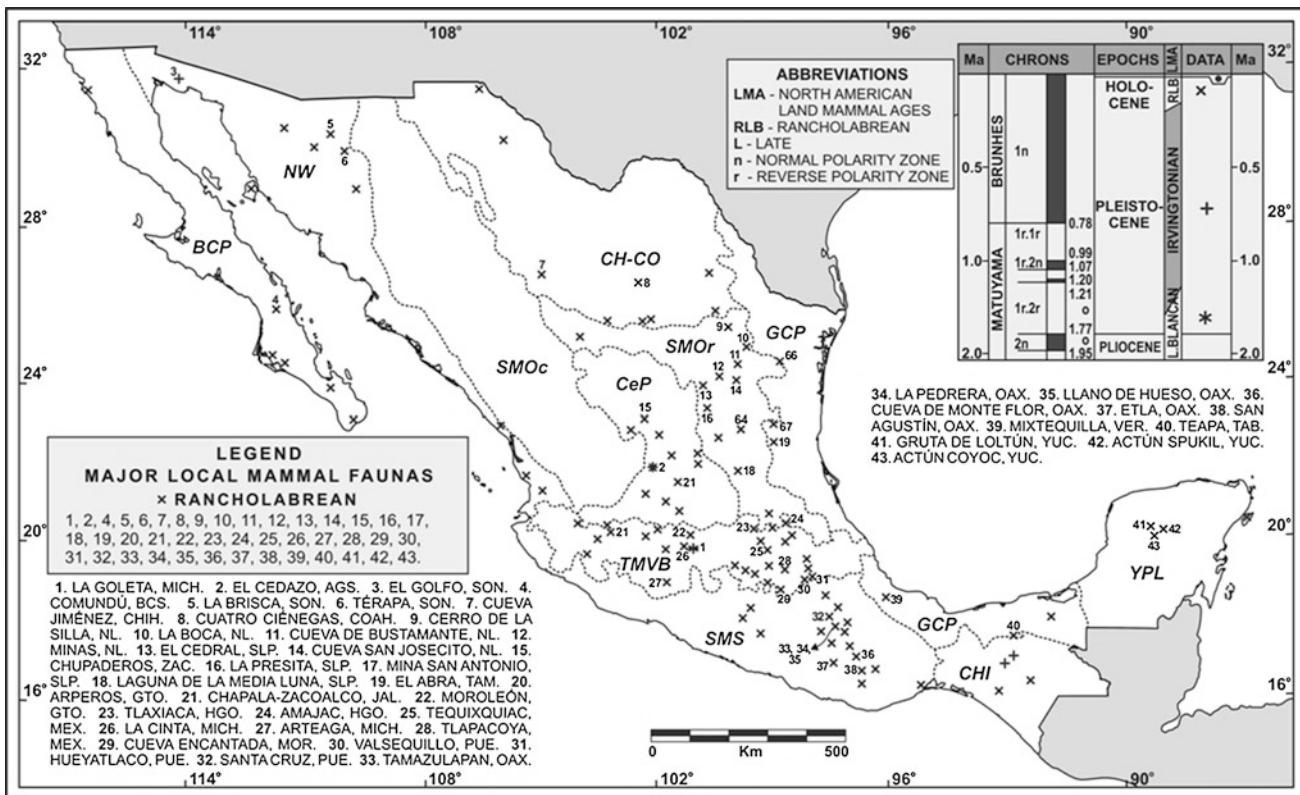
Mexico's Pleistocene mammal record consists of 297 species, belonging to 146 genera, 43 families, and 13 orders (including Litopterna; Table 3.1), largely drawn from the QMMDB (Arroyo-Cabral et al. 2002), and supplemented by recent literature (modified from Ferrusquía-Villafranca et al. 2010). This record has been retrieved from ~ 800 localities unevenly distributed across the country, primarily from the last 100 years (cf. Arroyo-Cabral et al. 2002). In order to furnish a representative sample of such localities, the 120 most significant ones are plotted on a morphotectonic province template, including those having major local faunas (Fig. 3.2) and listed in Table 3.3; also, those major local faunas are plotted on a modern potential vegetation map (Fig. 3.3) to disclose their ecological congruency (or lack thereof) with their Holocene setting. Due to space limitations, 25 major local faunas (Table 3.4) have been selected and arranged by their morphotectonic province occurrence. This procedure allows assessment of the climate change impact on mammal faunas of

particular provinces or groups and detection of major patterns of climate change in space and time across Mexico.

### Northern Provinces

The Baja California Peninsula, Northwestern Plains and Sierras, Sierra Madre Occidental, and the Chihuahua-Coahuila plateaus and ranges comprise this morphotectonic province (Fig. 3.1). Only the Northwestern Plains and Sierras and Chihuahua-Coahuila Plateaus and Ranges provinces have yielded major local faunas (Table 3.4 and Fig. 3.2), palynofloras (Fig. 3.4), and paleosol localities (Fig. 3.5). The Northwestern Plains and Sierras have yielded Mexico's only Irvingtonian fauna, El Golfo Local Fauna (l.f.) (Shaw 1981; Croxen et al. 2007), as well as the earliest Rancholabrean fauna, Térapa l.f. (Mead et al. 2006), both in Sonora.

These faunas indicated a more humid climate regime that allowed the presence of a subtropical biota during the Irvingtonian and Early Rancholabrean. The Sierra Madre Occidental paleosol record and the Chihuahua-Coahuila



**Fig. 3.2** Selected Rancholabrean terrestrial mammal localities of Mexico mapped on the morphotectonic provinces template. Time frame adapted from Bell et al. (2004). The geographic position of the localities is approximated. Main sources: Alvarez (1965), Barrios-Rivera (1985), QMMDB (Arroyo-Cabral et al. 2002), and Arroyo-Cabral et al. (2007)

**Table 3.3** Selected Pleistocene mammal bearing localities of Mexico. Num. is the locality number shown at Figs. 3.2 and 3.3. The locality names correspond to the nearest town/village or topographic feature. Main sources: Alvarez (1965), Barrios-Rivera (1985), and QMMDB (Arroyo-Cabral et al. 2002)

Num.	Locality	State	Morphotectonic province	Age
1	La Goleta	Mich	TMBV	Late Blancan/Irvingtonian/Rancholabrean
2	El Cedazo	Ags	CeP	Late Blancan/Irvingtonian/Rancholabrean
3	El Golfo	Son	NW	Irvingtonian
4	Comondú	BCS	BCP	Rancholabrean
5	La Brisca	Son	NW	Rancholabrean
6	Terapa	Son	NW	Early Rancholabrean
7	Cueva Jiménez	Chih	CH-CO	Rancholabrean
8	Cuatro Ciénelas	Coah	CH-CO	Rancholabrean
9	Cerro de la Silla	NL	SMOr	Rancholabrean
10	La Boca	NL	SMOr	Rancholabrean
11	Cueva de Bustamante	NL	SMOr	Rancholabrean
12	Minas	NL	SMOr	Rancholabrean
13	El Cedral	SLP	SMOr	Rancholabrean
14	San Josecito	NL	SMOr	Rancholabrean
15	Chupaderos	Zac	CeP	Rancholabrean
16	La Presita	SLP	SMOr	Rancholabrean
17	Mina San Antonio	SLP	SMOr	Rancholabrean
18	Laguna de la Media Luna	SLP	SMOr	Rancholabrean
19	El Abra	Tam	SMOr	Rancholabrean

(continued)

**Table 3.3** (continued)

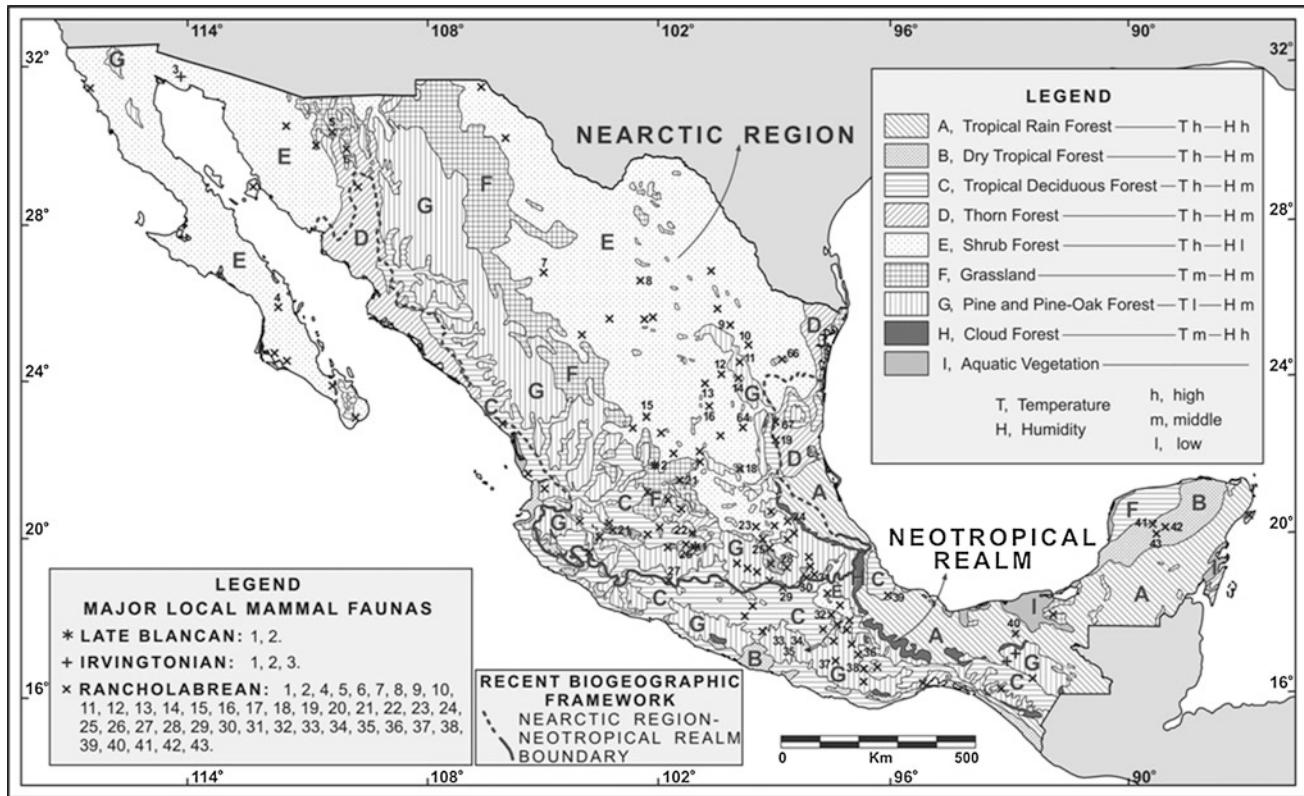
Num.	Locality	State	Morphotectonic province	Age
20	Arperos	Gto	CeP	Rancholabrean
21	Chapala-Zacoalco	Jal	TMBV	Rancholabrean
22	Moroleón	Gto	TMBV	Rancholabrean
23	Tlaxiaca	Hgo	TMBV	Rancholabrean
24	Amajac	Hgo	TMBV	Pleistocene (?Middle-Late)
25	Tequixquiac	Mex	TMBV	Rancholabrean
26	La Cinta	Mich	TMBV	Rancholabrean
27	Arteaga	Mich	TMBV	Rancholabrean
28	Tlapacoya	Mex	TMBV	Rancholabrean
29	Cueva Encantada	Mor	TMBV	Rancholabrean
30	Valsequillo	Pue	TMBV	Rancholabrean
31	Hueyatlaco	Pue	TMBV	Rancholabrean
32	Santa Cruz	Pue	SMS	Rancholabrean
33	Tamazulapan	Oax	SMS	Rancholabrean
34	La Pedrera	Oax	SMS	Rancholabrean
35	Llano de Hueso	Oax	SMS	Rancholabrean
36	Cueva de Monte Flor	Oax	SMS	Rancholabrean
37	Etla	Oax	SMS	Rancholabrean
38	San Agustín	Oax	SMS	Rancholabrean
39	Mixtequila	Ver	GCP	Rancholabrean
40	Teapa	Tab	GCP	Rancholabrean
41	Gruta de Loltún	Yuc	YPL	Rancholabrean
42	Actún Spukil	Yuc	YPL	Rancholabrean
43	Actún Coyoc	Yuc	YPL	Rancholabrean
44	Punta San José	BC	BCP	Pleistocene
45	Bahía Magdalena	BCS	BCP	Late Pleistocene
46	Santa Rita	BCS	BCP	Rancholabrean
47	El Carrizal	BCS	BCP	Rancholabrean
48	Santa Anita	BCS	BCP	?Early Pleistocene
49	La Playa	Son	NW	Rancholabrean
50	Arizpe	Son	NW	Pleistocene
51	Isla Tiburón	Son	NW	Pleistocene
52	La Guitarra	Son	NW	Pleistocene
53	El Rosario	Sin	NW	Pleistocene
54	San Blas	Nay	NW	Pleistocene
55	El Pantanal	Nay	NW	Pleistocene
56	Samalayuca	Chih	CH-CO	Pleistocene
57	La Erupción	Chih	CH-CO	Pleistocene
58	La Candela	Coah	CH-CO	Pleistocene
59	Torreón	Coah	CH-CO	Pleistocene
60	Arroyo del Arenal	Coah	CH-CO	Pleistocene
61	Arroyo Ojuelo	Coah	CH-CO	Pleistocene
62	Cuevas del Padre	NL	CH-CO	Pleistocene
63	Cuevas de las Iglesias	Dgo	SMOr	Pleistocene
64	Tula	Tams	SMOr	Pleistocene
65	Mezquital	Hgo	SMOr	Pleistocene
66	San Lázaro	Tams	GCP	Rancholabrean
67	El Salitrillo	Tams	GCP	Pleistocene
68	Zacatecas	Zac	CeP	Pleistocene
69	Laguna de las Tres Cruces	SLP	CeP	Pleistocene
70	Laguna del Salitrillo	Zac	CeP	Pleistocene
71	Brechas Coloradas	SLP	CeP	Pleistocene
72	Rancho Peotillos	SLP	CeP	Pleistocene

(continued)

**Table 3.3** (continued)

Num.	Locality	State	Morphotectonic province	Age
73	Rancho la Verdolaga	Jal	Cep	Pleistocene
74	León	Gto	Cep	Pleistocene
75	Guanajuato	Gto	Cep	Pleistocene
76	Ameca	Jal	TMBV	Pleistocene
77	El Salto	Jal	TMBV	Rancholabrean
78	Atotonilco-Zacoalco	Jal	TMBV	Rancholabrean
79	Venustiano Carranza	Jal	TMBV	Pleistocene
80	Ario de Rayón	Mich	TMBV	Pleistocene
81	La Piedad-Santa Ana	Mich-Jal	TMBV	Rancholabrean
82	Zacapú	Mich	TMBV	Rancholabrean
83	Portalitos	Gto	TMBV	Rancholabrean
84	Cuitzeo	Mich	TMBV	Rancholabrean
85	Uruétaro	Mich	TMBV	Rancholabrean
86	Actopan	Hgo	TMBV	Rancholabrean
87	Real del Monte	Hgo	TMBV	Pleistocene
88	Pachuca	Hgo	TMBV	Pleistocene
89	Villa de Tezontepec	Hgo	TMBV	Rancholabrean
90	Huitexcalco	Hgo	TMBV	Rancholabrean
91	Amanalco de Becerra	Mex	TMBV	Pleistocene
92	Tacubaya	DF	TMVB	Rancholabrean
93	Valle de Toluca	Mex	TMBV	Rancholabrean
94	Lerma	Mex	TMBV	Rancholabrean
95	Palpan	Mor	TMBV	Pleistocene
96	Tetela	Mor	TMBV	Rancholabrean
97	Apizaco	Tlax	TMBV	Pleistocene
98	Atlihuetzia	Tlax	TMBV	Pleistocene (?Middle-Late)
99	Nanacatla	Gro	SMS	Pleistocene (?Middle)
100	Huixtac	Gro	SMS	Rancholabrean
101	Tepecoacuilco	Gro	SMS	Rancholabrean
102	Apaxtla	Gro	SMS	Rancholabrean
103	Chichihualco	Gro	SMS	Pleistocene
104	San Pedro Tecamachalco	Pue	SMS	Pleistocene
105	Tehuacan	Pue	SMS	Rancholabrean
106	Tepelmemé	Oax	SMS	Pleistocene
107	Coixtlahuaca	Oax	SMS	Pleistocene
108	Huajuapan de León	Oax	SMS	Pleistocene
109	Yolomecatl	Oax	SMS	Late Pleistocene
110	Nochixtlan	Oax	SMS	Pleistocene
111	La Salina	Oax	SMS	Rancholabrean
112	Santa Marta Ejutla	Oax	SMS	Pleistocene
113	Tehuantepec	Oax	SMS	Pleistocene
114	Villa Corzo	Chis	CHI	Late Pleistocene
115	Aguacatenango	Chis	CHI	Pleistocene
116	Chiapa de Corzo	Chis	CHI	Irvingtonian/Rancholabrean
117	Ixtapa	Chis	CHI	Irvingtonian/Rancholabrean
118	El Ocotlán	Camp	GCP	Pleistocene
119	Actun Lara	Yuc	YPL	Rancholabrean
120	Cozumel	QRoo	YPL	Pleistocene

**Abbreviations:** **BCP**, Baja California Península. **NW**, Northwestern Plains and Sierras. **CH-CO**, Chihuahuan-Coahuilan Plateaus and Ranges. **SMOr**, Sierra Madre Oriental. **CeP**, Central Plateau. **GCP**, Gulf Coastal Plain. **TMVB**, Trans-Mexican Volcanic Belt. **SMS**, Sierra Madre del Sur. **YPL**, Yucatan Platform



**Fig. 3.3** Mexico's chief Pleistocene terrestrial mammal-bearing localities mapped on a modern natural vegetation template (adapted from Rzedowski and Reyna-Trujillo 1990, and Challenger 1998); additionally, the Nearctic Region/Neotropical Realm boundary is plotted. Main sources: Alvarez (1965), Barrios-Rivera (1985), QMMDB (Arroyo-Cabralles et al. 2002), and Arroyo-Cabralles et al. (2007)

Plateaus and Ranges paleo-vegetation record (Betancourt et al. 1990) indicated a cooler and moister climate regime for the latest Rancholabrean ( $\sim 25$ – $11$  kyr). This regime made possible a biotic diversity unparalleled anywhere in Mexico at present. Mammals with diverse ecological requirements coexisted within short distances of each other.

The biota became depleted and modified compositionally as the climate regime changed by the earliest Holocene. Increasing aridity caused xerophilous species largely to replace the former inhabitants. Many mammal taxa, ranging from medium-sized animals weighting between 10 and 100 kg (mesobaric) to large-sized animals weighting over 100 kg (megabaric) (Ferrusquía-Villafranca et al. 2010), became extinct (Table 3.4). Others, depending on their climatic tolerances, experienced major range contractions either northward, e.g., the temperate rodents *Castor* and *Marmota* and the carnivore *Canis rufus*, or southward, e.g., the tropical capybara *Hydrochoerus*. The extent of this biogeographic shift was such that the extant taxa no longer

inhabit Mexico, i.e., they are extirpated. In other instances, some taxa became extirpated from their Rancholabrean morphotectonic province but persist at present elsewhere in the country, e.g., the rodent *Hodomys allenii* and perissodactyl *Tapirus*, currently living in the tropics (Ceballos and Oliva 2005). *Cynomys ludovicianus*, the black-tailed prairie dog, known from the La Playa local fauna (Mead et al. 2010), retreated at least 150 km ENE from its Rancholabrean grounds to easternmost Sonora and adjacent Arizona. The Late Wisconsinan climate regime allowed the existence of these herbivores in northern Sonora, whereas the current climate prevents their presence.

### Central and Eastern Provinces

These morphotectonic provinces include the Central Plateau Sierra Madre Oriental and Gulf Coastal Plain. They have yielded eight major local faunas (Table 3.4 and Figs. 3.2 and

**Table 3.4** Selected main Pleistocene local mammal faunas of Mexico. Main sources: Alvarez (1965); Barrios-Rivera (1985); QMMDB; Arroyo-Cabral et al. (2002), and Arroyo-Cabral et al. (2007). Symbols: <sup>a</sup>Extinct taxon everywhere in the world. <sup>b</sup>Species extinct in Mexico, but still extant outside this country. <sup>c</sup>Species extinct in the morphotectonic province(s) bearing the fossil locality(ies), but extant elsewhere in Mexico

		NW			CH-CO			SMOr			Cep			GCP			TMVB			SMS			YPL			
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
<b>DIDELPHIMORPHIA</b>																										
<b>Didelphidae</b>																										
<i>Didelphis marsupialis</i>																										
<i>Didelphis virginiana</i>											X															X
<i>Marmosa canescens</i>																										X
<i>Marmosa lorenzi</i> <sup>a</sup>																										X
<i>Marmosa mexicana</i>																										X
<b>XENARTHRA sensu lato</b>																										
<b>Dasyproctidae</b>																										
<i>Cabassous centralis</i> <sup>c</sup>																										X
<i>Dasyprocta novemcinctus</i>																										
<i>Holmesina septentrionalis</i> <sup>a</sup>											X															
<i>Pampatherium mexicanum</i> <sup>a</sup>											X															
<b>Glyptodontidae</b> <sup>a</sup>																										
<i>Glyptotherium cylindricum</i> <sup>a</sup>											X															
<i>Glyptotherium floridanum</i> <sup>a</sup>																										
<i>Glyptotherium mexicanum</i> <sup>a</sup>												X														
<b>Megalonychidae</b> <sup>a</sup>																										
<i>Megalonyx jeffersoni</i> <sup>a</sup>											X															
<i>Megalonyx wheateyae</i> <sup>a</sup>											X															
<b>Megatheriidae</b> <sup>a</sup>																										
<i>Eremotherium laurillardi</i> <sup>a</sup>											X															
<i>Nothrotheriops shastensis</i> <sup>a</sup>												X														
<b>Mylodonidae</b> <sup>a</sup>																										
<i>Paramylodon harlani</i> <sup>a</sup>												X														
<i>Paramylodon</i> sp. <sup>a</sup>												sp														
<b>Myrmecophagidae</b>																										X
<i>Myrmecophaga tridactyla</i> <sup>c</sup>												X														

(continued)

Table 3.4 (continued)

		NW				CH-CO				SMOr				CeP				GCP				TMVB				SMS				YPL			
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z						
<b>SORICOMORPHA</b>																																	
Soricidae																																	
<i>Cryptotis maysensis</i>																																	
<i>Cryptotis mexicana</i>																																	
<i>Cryptotis parva</i>																																	
<i>Neotomodex crawfordi</i>																																	
<i>Sorex cinereus</i>																																	
<i>Sorex milleri</i>																																	
<i>Sorex saussurei</i>																																	
<b>CHIROPTERA</b>																																	
Antrozoidae																																	
<i>Antrozous pallidus</i> <sup>c</sup>																																	
Emballonuridae																																	
<i>Peropteryx macrotis</i>																																	
Molossidae																																	
<i>Eumops bonariensis</i>																																	
<i>Eumops perotis</i> <sup>c</sup>																																	
<i>Eumops underwoodi</i> <sup>c</sup>																																	
<i>Molossus rufus</i>																																	
<i>Nyctinomops leucinus</i>																																	
<i>Promops centralis</i>																																	
<i>Tadarida brasiliensis</i>																																	
Mormoopidae																																	
<i>Mormoops megalophylla</i>																																	
<i>Pteronotus davyi</i>																																	
<i>Pteronotus parnellii</i>																																	
Natalidae																																	
<i>Natalus stramineus</i>																																	
Phyllostomidae																																	
<i>Artibeus jamaicensis</i>																																	
<i>Artibeus lituratus</i>																																	
<i>Carollia brevicauda</i>																																	
<i>Centurio senex</i>																																	

(continued)

Table 3.4 (continued)

		NW			CH-CO			SMOr			CeP			GCP			TMVB			SMS			YPL				
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	
<i>Chiroderma villosum</i>																											
<i>Choeronycteris mexicana</i>																											
<i>Chrotopterus auritus</i>																											
<i>Desmodus cf. D. draculae<sup>a</sup></i>																											
<i>Desmodus rotundus</i>																											
<i>Desmodus stocki<sup>a</sup></i>																											
<i>Diphylla ecaudata</i>																											
<i>Glossophaga soricina</i>																											
<i>Leptonycteris curasoae</i>																											
<i>Leptonycteris nivalis</i>																											
<i>Macrotis californicus<sup>c</sup></i>																											
<i>Minon bennettii</i>																											
<i>Starnira lilium</i>																											
<b>Vespertilionidae</b>																											
<i>Corynorhinus townsendii</i>																											
<i>Eptesicus brasiliensis</i>																											
<i>Eptesicus furinalis</i>																											
<i>Eptesicus fuscus</i>																											
<i>Lasiorus cinereus</i>																											
<i>Lasiorus ega</i>																											
<i>Lasiorus intermedius</i>																											
<i>Myotis californicus</i>																											
<i>Myotis keenayi</i>																											
<i>Myotis thysanodes</i>																											
<b>CARNIVORA</b>																											
<b>Canidae</b>																											
<i>Canis cedazoensis<sup>a</sup></i>																											
<i>Canis dirus<sup>a</sup></i>																											
<i>Canis familiaris</i>																											
<i>Canis latrans</i>																											
<i>Canis lupus</i>																											
<i>Canis rufus<sup>b</sup></i>																											
<i>Cyon alpinus<sup>b</sup></i>																											
<i>Urocyon cinereoargenteus</i>																											

(continued)

Table 3.4 (continued)

	NW			CH-CO			SMOr			CeP			GCP			TMVB			SMS			YPL			
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
<b>Felidae</b>																									
<i>Herpailurus yagouaroundi</i>																									
<i>Leopardus pardalis</i>																									
<i>Leopardus wiedii</i>																									
<i>Lynx rufus</i>	X			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
<i>Panthera atrox</i> <sup>a</sup>	X			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
<i>Panthera onca</i>	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
<i>Puma concolor</i>				X	X	X																			
<i>Smilodon fatalis</i> <sup>a</sup>				X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
<i>Smilodon gracilis</i> <sup>a</sup>																									
<i>Smilodon californicus</i>																									
<b>Hyenidae *</b>																									
<i>Chasmaporthetes johnstoni</i> <sup>a</sup>	X																								
<b>Mustelidae</b>																									
<i>Conepatus leuconotus</i>																									
<i>Conepatus mesoleucus</i>				X	X	X																			
<i>Lontra longicaudis</i>																									
<i>Mephitis macroura</i>																									
<i>Mephitis mephitis</i>	X	X	X																						
<i>Mustela frenata</i>																									
<i>Mustela nigripes</i> <sup>c</sup>																									
<i>Spilogale putorius</i> <sup>c</sup>	X	X	X																						
<i>Taxidea taxus</i>				X	X	X																			
<b>Procyonidae</b>																									
<i>Bassaris astutus</i>	X	X	X																						
<i>Bassaris sumichrasti</i>																									
<i>Bassaris fuscus</i> <sup>a</sup>																									
<i>Nasua narica</i>																									
<i>Procyon lotor</i>	X																								
<b>Ursidae</b>																									
<i>Arcodus pristinus</i> <sup>a</sup>																									
<i>Arcodus simus</i> <sup>a</sup>																									
<i>Tremarctos floridanus</i> <sup>a</sup>	X																								
<i>Ursus americanus</i> <sup>c</sup>		X	X	X	X	X																			

(continued)

Table 3.4 (continued)

		NW			CH-CO			SMOR			Cep			GCP			TMVB			SMS			YPL			
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
<b>RODENTIA</b>																										
<b>Castoridae</b>																										
<i>Castor</i> cf. <i>C. californicus</i>																										
<b>Cuniculidae</b>																										
<i>Canis lupus pacas</i>																										
<b>Dasyproctidae</b>																										
<i>Dasyprocta mexicana</i>																										
<i>Dasyprocta punctata</i>																										
<b>Erethizontidae</b>																										
<i>Erethizon dorsatum</i> <sup>c</sup>																										
<i>Ctenomys mexicanus</i>																										
<b>Geomysidae</b>																										
<i>Cratogeomys bensonii</i> <sup>a</sup>																										
<i>Cratogeomys castanops</i>																										
<i>Cratogeomys gymnurus</i>																										
<i>Cratogeomys merriami</i>																										
<i>Cratogeomys tylocephalus</i>																										
<i>Geomys</i> sp.																										
<i>Orthogeomys grandis</i>																										
<i>Orthogeomys hispidus</i>																										
<i>Orthogeomys onerous</i> <sup>a</sup>																										
<i>Thomomys bottae</i>																										
<i>Thomomys umbrinus</i>																										
<b>Heteromysidae</b>																										
<i>Chaetodipus hispidus</i>																										
<i>Chaetodipus houstoni</i> <sup>a</sup>																										
<i>Chaetodipus nelsoni</i>																										
<i>Chaetodipus penicillatus</i> <sup>c</sup>																										
<i>Dipodomys nelsoni</i>																										
<i>Dipodomys phillipsii</i>																										
<i>Dipodomys spectabilis</i>																										
<i>Heteromys desmarestianus</i>																										
<i>Heteromys gaumeri</i>																										

(continued)

Table 3.4 (continued)

	NW				CH-CO				SMOr				cEP				GCP				TMVB				SMS				
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y				
<i>Lionys irratus</i>			sp			X												X											
<i>Perognathus flavus</i>					sp		X																						
<b>Hydrochoeridae*</b>																													
<i>Hydrochoerus sp.</i>		X																											
<i>Neochaoeris aesop*</i> <sup>a</sup>			sp																										
<b>Cricetidae</b>																													
<i>Baiomys intermedius</i> <sup>a</sup>																													
<i>Baiomys musculus</i>																													
<i>Baiomys taylori</i>			X																										
<i>Hodomys allen</i> <sup>c</sup>				sp																									
<i>Hodomys sp. nov</i> <sup>a</sup>																													
<i>Micromys californicus</i> <sup>c</sup>																													
<i>Micromys guatemalensis</i>																													
<i>Micromys meadensis</i> <sup>a</sup>																													
<i>Micromys mexicanus</i>																													
<i>Micromys oaxacensis</i>																													
<i>Micromys pennsylvanicus</i> <sup>c</sup>																													
<i>Micromys quasitater</i>																													
<i>Micromys umbrinus</i>																													
<i>Neotoma albigena</i> <sup>c</sup>		sp	sp	X	X	X	X	sp																					
<i>Neotoma angustapalata</i>																													
<i>Neotoma anomala</i> <sup>a</sup>																													
<i>Neotoma cinerea</i> <sup>b</sup>																													
<i>Neotoma floridana</i> <sup>b</sup>																													
<i>Neotoma lepida</i>			X																										
<i>Neotoma magnodonta</i> <sup>a</sup>																													
<i>Neotoma mexicana</i>			X																										
<i>Neotoma micropus</i>			X																										
<i>Neotoma pallatina</i>																													
<i>Neotoma phenax</i> <sup>c</sup>																													
<i>Neotoma tlapacoyana</i> <sup>a</sup>																													
<i>Neotomodon alstoni</i>																													

(continued)

Table 3.4 (continued)

	NW				CH-CO				SMOr				CeP				GCP				TMVB				SMS				YPL			
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y							
<i>Nyctomyssumichrasti</i>																																
<i>Oligoryzomysfulvescens</i>																																
<i>Ondatranebracensis</i> <sup>a</sup>																																
<i>Onychomysleucogaster</i>	sp																															
<i>Oryzomysaffaroi</i>																																
<i>Oryzomyscouesi</i>																																
<i>Oryzomysmelanotis</i>																																
<i>Otomyzomyshatti</i>																																
<i>Ototylomysphyllotis</i>																																
<i>Peromyscusboylii</i>																																
<i>Peromyscusdifficilis</i>																																
<i>Peromyscuseremicus</i>																																
<i>Peromyscusleucopus</i>																																
<i>Peromyscuslevipes</i>																																
<i>Peromyscusmaldonadoi</i> <sup>a</sup>																																
<i>Peromyscusmaniculatus</i>																																
<i>Peromyscusmelanophrys</i>																																
<i>Peromyscusmelanotis</i> <sup>c</sup>																																
<i>Peromyscusmexicanus</i>																																
<i>Peromyscusochraventer</i>																																
<i>Peromyscuspectoralis</i>																																
<i>Peromyscustruei</i> <sup>c</sup>																																
<i>Peromyscusyucatanicus</i>																																
<i>Reithrodontomysfulvescens</i>																																
<i>Reithrodontomysmegadon</i>																																
<i>Reithrodontomysmexicanus</i>																																
<i>Reithrodontomysmontanus</i>																																
<i>Sigmodonalleni</i>																																
<i>Sigmodonarizoneae</i>																																
<i>Sigmodoncaristii</i> <sup>a</sup>	sp	sp	sp	sp																												
<i>Sigmodonfulviventer</i>																																
<i>Sigmodonhirsidus</i>																																
<i>Sigmodonleucotis</i>																																

(continued)

Table 3.4 (continued)

	NW				CH-CO				SMOR				CeP				GCP				TMVB				SMS				YPL			
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y							
<i>Sigmodon toltecus</i>																																
<i>Synaptomyss cooperi</i> <sup>c</sup>																																
<i>Tylomys mazatlanus</i>																																
<b>Sciuridae</b>																																
<i>Ammospermophilus interpres</i>			X																													
<i>Cynomys ludovicianus</i> <sup>c</sup>																																
<i>Cynomys mexicanus</i>																																
<i>Glaucomys volans</i>																																
<i>Marmota flaviventris</i> <sup>c</sup>																																
<i>Sciurus albieri</i>																																
<i>Sciurus aureogaster</i>																																
<i>Sciurus leucurus</i>																																
<i>Sciurus nayaritensis</i>																																
<i>Sciurus variegatoides</i> <sup>c</sup>																																
<i>Sciurus yucatanensis</i>																																
<i>Spermophilus mexicanus</i>																																
<i>Spermophilus spilogaster</i>																																
<i>Spermophilus variegatus</i>																																
<b>LAGOMORPHA</b>																																
<b>Leporidae</b>																																
<i>Aztlanolagus agilis</i> <sup>a</sup>																																
<i>Lepus alleni</i>																																
<i>Lepus californicus</i>																																
<i>Lepus callotis</i>																																
<i>Sylvilagus auduboni</i>																																
<i>Sylvilagus brasiliensis</i>																																
<i>Sylvilagus cunicularius</i>																																
<i>Sylvilagus floridanus</i>																																
<i>Sylvilagus hibbardii</i> <sup>a</sup>																																
<i>Sylvilagus leonensis</i> <sup>b</sup>																																

(continued)

Table 3.4 (continued)

	NW				CH-CO				SMOR				CeP				GCP				TMVB				SMS				YPL.			
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y							
<b>PERISSODACTyla</b>																																
<b>Equidae</b>																																
<i>Equus dasydactylus</i> <sup>a</sup>	sp																															
<i>Equus calobatus</i> <sup>a</sup>																																
<i>Equus complicatus</i> <sup>a</sup>			X																													
<i>Equus conversidens</i> <sup>a</sup>	sp	X																														
<i>Equus exelstus</i> <sup>a</sup>																																
<i>Equus ferus</i> <sup>a</sup>																																
<i>Equus giganteus</i> <sup>a</sup>																																
<i>Equus mexicanus</i> <sup>a</sup>																																
<i>Equus occidentalis</i> <sup>a</sup>																																
<i>Equus pacificus</i> <sup>a</sup>																																
<i>Equus parvulus</i> <sup>a</sup>																																
<i>Equus simplicidens</i> <sup>a</sup>																																
<i>Equus zancalus</i> <sup>a</sup>			X																													
<b>Tapiroidea</b>																																
<i>Tapirus bairdii</i> <sup>c</sup>	sp		sp																													
<i>Tapirus hayasi</i> <sup>a</sup>																																
<b>ARTIODACTyla</b>																																
<b>Antilocapridae</b>																																
<i>Antilocapra americana</i>			X	X																												
<i>Capromeryx mexicana</i> <sup>a</sup>	sp																															
<i>Capromeryx minor</i> <sup>a</sup>	X																															
<i>Stockoceros conklingi</i> <sup>a</sup>	sp																															
<i>Tetrameryx mooseri</i> <sup>a</sup>	sp	sp																														
<i>Tetrameryx shaleri</i> <sup>a</sup>																																
<i>Tetrameryx tacubayensis</i> <sup>a</sup>																																
<b>Bovidae</b>																																
<i>Bison alascensis</i> <sup>a</sup>	sp	sp																														
<i>Bison antiquus</i> <sup>a</sup>																																
<i>Bison bison</i> <sup>c</sup>																																
<i>Bison latifrons</i> <sup>a</sup>																																
<i>Bison priscus</i> <sup>a</sup>																																

(continued)

Table 3.4 (continued)

		NW				CH-CO				SMOr				CeP				GCP				TMVB				SMS			
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y			
	<i>Eucraterium collinum</i> <sup>a</sup>						X	X											X										
	<i>Oreamnos harringtoni</i> <sup>a</sup>						X																						
	<i>Ovis canadensis</i> <sup>s</sup>	sp	X																										
<b>Camelidae*</b>																													
	<i>Camelops hesternus</i> <sup>a</sup>	sp	X						X	X					X	X	X	X	X										
	<i>Camelops mexicanus</i> <sup>a</sup>	sp																											
	<i>Camelops minimokiae</i> <sup>a</sup>																												
	<i>Camelops traviswhiteli</i> <sup>a</sup>								X										X										
	<i>Eschatus conidens</i> <sup>a</sup>														X														
	<i>Hemiauchenia blanconensis</i> <sup>a</sup>	X					sp								sp														
	<i>Hemiauchenia macrocephala</i> <sup>a</sup>							X	X						X		X												
	<i>Hemiauchenia vera</i> <sup>a</sup>								X																				
	<i>Procamelops minimus</i> <sup>a</sup>																		X										
	<i>Paleolama</i> sp. ???	sp																											
	<i>Titanotylops</i> sp. ???	sp																											
<b>Cervidae</b>																													
	<i>Cervus elaphus</i> <sup>b</sup>		X												X														
	<i>Mazama americana</i>																										X		
	<i>Navahoceros fricki</i> <sup>a</sup>						X								X														
	<i>Odocoileus halli</i> <sup>a</sup>	sp						sp							X												sp		
	<i>Odocoileus hemionus</i>		X		X										X														
	<i>Odocoileus lucasi</i>							X		X				X															
	<i>Odocoileus virginianus</i>						X			X				X			X		M		X								
<b>Tayassuidae</b>																													
	<i>Platygonus alemanii</i> <sup>a</sup>	sp												sp													X		
	<i>Platygonus compressus</i> <sup>a</sup>															X		X											
	<i>Platygonus tictul</i> <sup>a</sup>															X													
	<i>Tayassu tajacu</i>																		sp								X		
<b>PROROSCIDEA</b>																													
<b>Elephantidae*</b>																													
	<i>Mammuthus columbi</i> <sup>a</sup>	sp	sp	sp																									
	<i>Mammuthus primigenius</i> <sup>a</sup>																												

(continued)

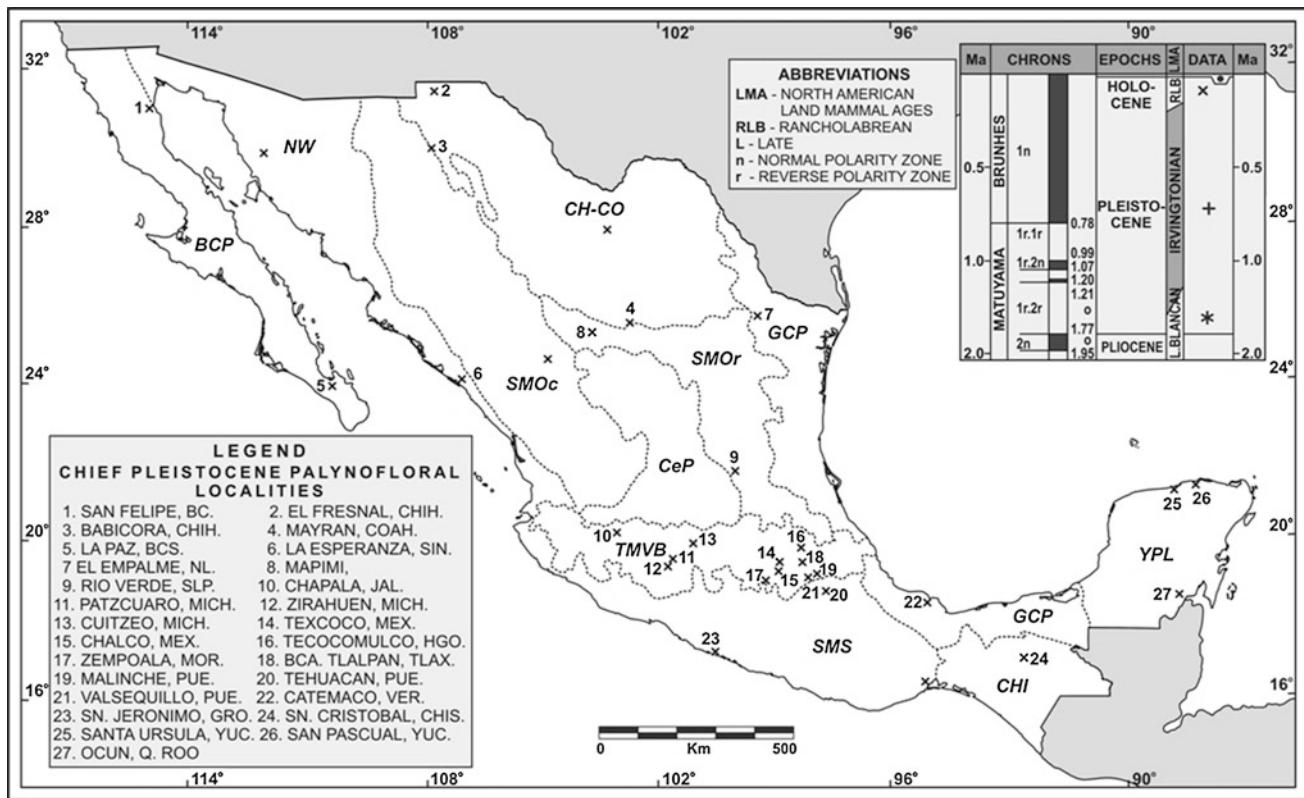
Table 3.4 (continued)

	NW				CH-CO				SMOr				CeP				GCP				TMVB				SMS			
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y			
<b>Gomphotheriidae<sup>a</sup></b>																												
<i>Caviatorius tropicus</i> <sup>a</sup>	sp	sp												sp	X	sp							sp					
<i>Stegomastodon</i> cf. <i>S. mirificus</i> <sup>a</sup>														X	X													
<b>Mammuthidae<sup>a</sup></b>																												
<i>Mammuth americanum</i> <sup>a</sup>									X	sp	X			sp	X	X												
<b>NOTONGULATA<sup>a</sup></b>																												
<b>Toxodontidae<sup>a</sup></b>																												
<i>Mylodonodon</i> cf. <i>M..latreensis</i> <sup>a</sup>																												
<b>?LITOPTERNA<sup>a</sup></b>																												
<b>?Macrauchenidae<sup>a</sup></b>																												
Gen. et sp. indet. <sup>a</sup>																												

**Morphotectonic Provinces:** NW, Northwestern Plains and Sierras; CH-CO, Chihuahuan-Coahuilan Plateaus and Ranges; SMOr, Sierra Madre Oriental; CeP, Central Plateau; GCP, Gulf Coast Plain; TMVB, Trans-Mexican Volcanic Belt; SMS, Sierra Madre del Sur; YPL, Yucatan Platform

**Local Faunas:** A, Terapa; Son. B, La Brisca; Son. C, El Golfo; Son. D, Cuatro Ciénegas; Coah. E, Cueva Jiménez, Chih. F, San Josecito, NL. G, La Presita, SLP. H, El Cedral, SLP. I, Minas, NL. J, Mina San Antonio, SLP. K, El Cedazo, Ags. L, Chupaderos, Zac. M, La Mixtequilla, N, Chapala-Zacatlán, Jal. O, Tequixquiac, Mex. P, Tlapacoya, Mex. Q, Valsequillo, Pue. R, Hueyatlaco, Pue. S, La Cinta, Mich. T, San Agustín Tlaxiaca, Hgo. U, Amajac, Hgo. V, San Agustín, Oax. W, Planicie de Tamazulapan, Oax. X, Gruta de Lolotún, Yuc. Y, Actún Sputul, Yuc.

**Sources for the local faunas:** A: (Paz-Morano et al. 2003; Bell et al. 2004; Mead et al. 2006, 2007; Carranza-Castañeda and Roldán-Quintana 2007; Hodnett et al. 2009; Núñez et al. 2010; White et al. 2010). B: (Van Devender et al. 1990; White et al. 2010). C: (Shaw 1981; Shaw and McDonald 1987; Jefferson 1989; Shaw et al. 2005; White et al. 2010). D: (Gilmore 1947; Lundelius 1980; Fraizer 1981; QMMDB Arroyo-Cabralles et al. 2002). E: (Messing 1986; Russell and Harris 1986). F: (Furlong 1943; Cushing 1945; Findley 1953; Jackway 1958; Russell 1960; Kurtén 1975; Nowak 1979; Kurtén and Anderson 1980; Alvarez and Polaco 1981; Barrios-Rivera 1985; Arroyo-Cabralles and Johnson 1995, 1998, 2008; Arroyo-Cabralles and Alvarez 1997; Arroyo-Cabralles and Polaco 2003; Esteve et al. 2005). G: (Polaco and Butron-M. 1997; Arroyo-Cabralles et al. 2004). H: (Nowak 1979; Alvarez and Polaco 1981; Polaco 1986; Arroyo-Cabralles et al. 1996; Polaco and Butron-M. 1997; Alberdi et al. 2003; Perez-Crespo et al. 2011). I: (Franzen 1994; Arroyo-Cabralles et al. 1996). J: (Furlong 1943; Torres-Martínez 1995; Arroyo-Cabralles and Johnson 1998; Ferrusquia-Villafanca and de Anda-Hurtado 2008; de Anda-Hurtado 2009). K: (Mooser 1958; Hibbard and Mooser 1963; Dalquest 1974; Mooser and Dalquest 1975a; Frazier 1981; Barrios-Rivera 1985; Montellano-Ballesteros 1992; Reynoso-Rosales and Montellano-Ballesteros 1994; Churcher et al. 1996; QMMDB, Arroyo-Cabralles and Alvarez 2003). L: (Barroñ-Ortiz et al. 2009). M: (Polaco (1995). N: (Furlong 1925; Hibbard 1955; Downs 1958; Álvarez and Ferrusquia 1967; Guenther 1968; Aviña 1969; Silva-Barcenas 1969; Alvarez 1971, 1983, 1986; Mones 1973b; Kurtén 1974; Nowak 1979; Berta 1988; Churcher et al. 1996; Edmund 1996; Pichardo 1999; QMMDB Arroyo-Cabralles et al. 2002; McDonald 2002; Alberdi et al. 2004; Lucas 2008; Guznán Gutierrez et al. 2009). O: (Cuatlaparo and Ramírez 1875; Cope 1884; Freudentenberg 1921; Furlong 1925; Hibbard and Villa-Ramírez 1950; Hibbard 1955; Downs 1958; Álvarez and Berta 1968; Aviña 1969; Von Thenuis 1970; Guenther and Bunde 1973; Nowak 1979; Guenther 1968; Aviña 1969; Von Thenuis 1970; Guenther and Bunde 1973; Nowak 1979; Berta 1988; Churcher et al. 1996; Pichardo 1997, 1999; Arroyo-Cabralles et al. 2002; McDonald 2002; QMMDB Arroyo-Cabralles et al. 2002; Alberdi and Corona 2005; Lucas 2008; Edmund 1996; Pichardo-García et al. 2011; Melgarjo-Meraz et al. 2011; Morena-Fernández et al. 2011; Cruz-Muñoz et al. 2009). P: (Hibbard and Villa-Ramírez, 1950; Hibbard, 1955; Downs, 1958; Álvarez, 1969, 1986; Aviña, 1969, 1986; Kurtén, 1969, 1974; Nowak, 1979; Berta, 1988; Alvarez and Hernández-Chávez, 1994; Pichardo 1999; González et al. 2003; Lucas, 2008). Q: (Freudentenberg 1921; Furlong 1925; Hibbard and Villa-Ramírez 1950; Hibbard 1955; Downs 1958; Álvarez and Bunda 1973; Nowak 1979; Berta 1988; Churcher et al. 1996; Pichardo 1997, 1999; Arroyo-Cabralles et al. 2002; McDonald 2002; QMMDB Arroyo-Cabralles et al. 2002; Alberdi and Corona 2005; Lucas 2008; Edmund 1996; Pichardo-García et al. 2011; Melgarjo-Meraz et al. 2011; Morena-Fernández et al. 2011; Cruz-Muñoz et al. 2009). R: (Aviña 1982; Jiménez-Hidalgo et al. 2011). S: (García-Zepeda 1983; Jiménez-Hidalgo et al. 2011). T: (Bravo Cuevas et al. 2009; Marin-Leyva et al. 2009). U: Palma-Ramírez et al. 2009). V: (Ferrusquia-Villafanca 1975; Jiménez-Hidalgo et al. 2011). W: (Ferrusquia-Villafanca 1976; Jiménez-Hidalgo et al. 2011). X: (Aviña 1982, 1983; Arroyo-Cabralles and Alvarez-Cabralles 2003; Morales-Mejía and Arroyo-Cabralles 2009). Y: Arroyo-Cabralles and Alvarez 2003)



**Fig. 3.4** Mexico's chief Pleistocene palynofloral localities mapped on the morphotectonic provinces template. Time frame adapted from Bell et al. (2004). Main sources: (Foreman 1955; Clisby and Sears 1955; Sears and Clisby 1955; Ohngemach 1973, 1977; Bradbury 1971, 1989; Meyer 1973; Brown 1984; González-Quintero 1986; Straka and Ohngemach 1989; Metcalfe 1992; Leyden et al. 1994, 1996; Lozano-García and Ortega-Guerrero 1994, 1997; Anderson and Van Devender 1995; Ortega-Ramírez et al. 1998; Caballero-Miranda et al. 1999; Canul-Montañez 2008; Vázquez et al. 2010; Israde-Alcántara et al. 2010; Caballero-Miranda et al. 2010; Ortega et al. 2010; and Martínez-Hernández, E., unpublished data)

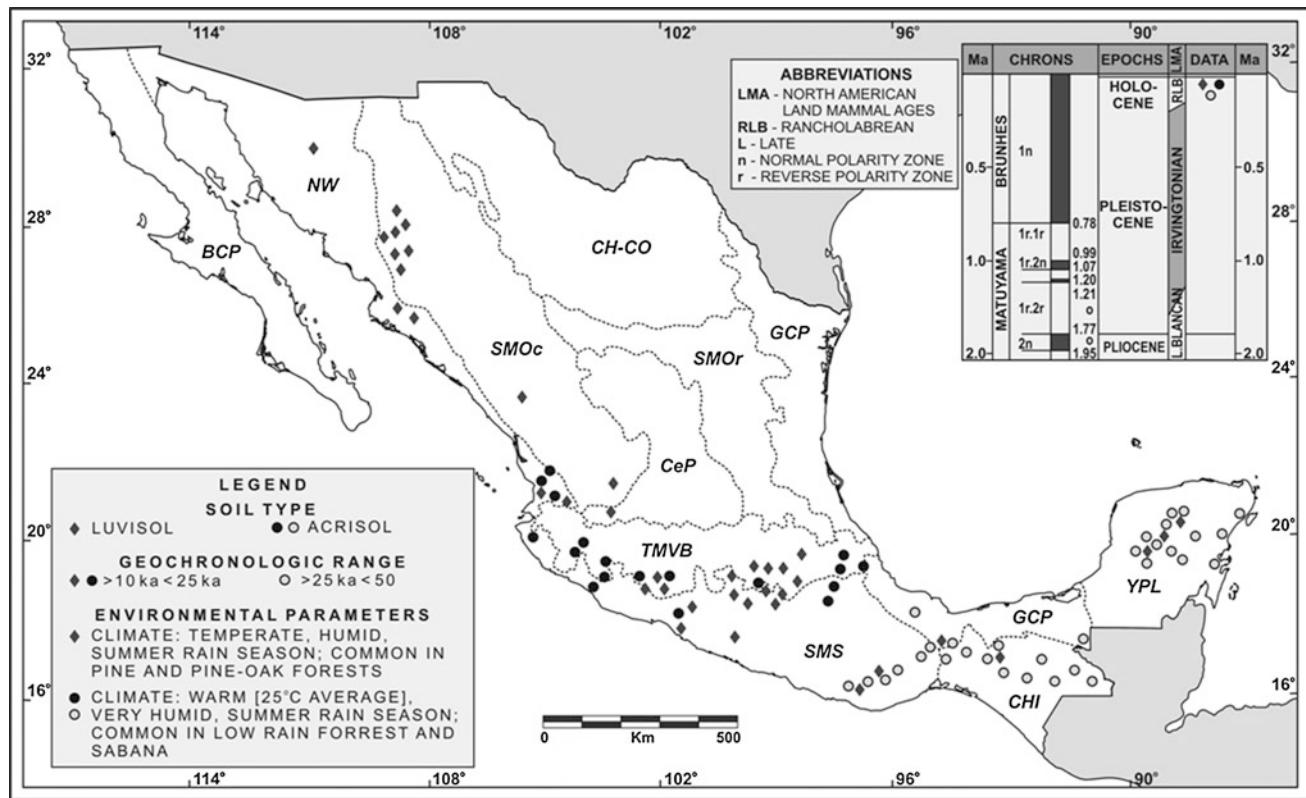
3.3), a few palynofloras (Table 3.5 and Fig. 3.4), and a few paleosol localities, chiefly in the Sierra Madre Oriental province (Fig. 3.5). The Central Plateau province has yielded a biochronologically mixed mammal assemblage including taxa of apparently Late Blancan to Rancholabrean age (Montellano-Ballesteros 1992; Bell et al. 2004) whose time relations are not well understood. Nevertheless, the better part of the assemblage, El Cedazo l.f., is Rancholabrean (Ferrusquía-Villafranca et al. 2010).

By and large, what was inferred from the Northern provinces applies as well to these provinces. The Sierra Madre Oriental and Central Plateau local faunas include tropical/subtropical, temperate, and even xeric species. This combination suggests a variety of ecological settings not extant at present. These provinces would have had a quite different climate during the Rancholabrean, marked by thermal (warm/cold) and humidity/rain (moist/dry) oscillations. These oscillations ultimately were related to advances and retreats of the Laurentide Glacier, as it responded to global climate pattern changes (Broecker 2003). Such climate oscillations also were affected by altitude and latitude,

and did not occur in a fixed fashion, i.e., warm with either moist or dry conditions, or cold with moist or dry conditions.

The mammalian and palynological records indicated a latest Rancholabrean (~25–11 ka) cooler and moister climate regime than that of today. The disharmonious character of the mammal fauna, i.e., the non-analogous mammal fauna (Semken 1966), was much more diverse and ecologically varied than today's, involving at least the better part of the Pleistocene. During that longer timeframe, a complex shifting of species distribution, i.e., biogeographic range expansion, contraction, displacement, and/or colonization of new habitats, within relatively short time intervals, as well as extinction, would have taken place. By the end of the Pleistocene, the climate became warmer and drier in general, perhaps to such an extent or intensity that many taxa became extinct.

Medium to large mammals fared the worst, with a major portion of them becoming extinct (Table 3.4). Other species reduced their biogeographic range and currently live outside Mexico, e.g., the carnivore *Cuon alpinus* and the rodent *Marmota flaviventris* (Hall 2001; Nowak 1991). Others were



**Fig. 3.5** Mexico's chief Pleistocene paleosol localities mapped on the morphotectonic provinces template. Time frame adapted from Bell et al. (2004). Main source: INEGI 2006. Other sources: (Cervantez-Borja et al. 1997; Sedov et al. 2001, 2007, 2008, 2009, 2011; Gama-Castro et al. 2004, 2005; Ortega-Guerrero, et al. 2004; Solleiro-Rebolledo et al. 2003, 2004, 2006; McClung et al. 2005; Jasso-Castañeda et al. 2006, 2007, 2012; Díaz-Ortega et al. 2010; Cruz y Cruz 2011; González-Arqueros et al. 2011; Solis et al. 2011; and Tovar and Sedov 2011)

extirpated from their Rancholabrean morphotectonic province, but survived elsewhere within Mexico. For example, the rodent *Hodomys alleni* currently thrives in the tropics. Other rodents such as *Erethizon dorsatum*, *Microtus pennsylvanicus*, *Neotoma albiventer*, *Sigmodon arizonae*, and *Synaptomys cooperi* now live in the Northern provinces (Ceballos and Oliva 2005). Finally, rodents such as *Sigmodon alleni* now live in provinces of the southern Northwestern Plains and Sierras, western Trans-Mexican Volcanic Belt, and the Pacific part of Sierra Madre del Sur. While *S. fulviventer* thrives in the Sierra Madre Occidental, small portions of northwestern and southwestern Central Plateau, and a small area in western Trans-Mexican Volcanic Belt (Ceballos and Oliva 2005).

### Trans-Mexican Volcanic Belt

This morphotectonic province has a greater number of palynofloral, paleosol, and fossil mammal localities than any of the others (Figs. 3.2, 3.3, 3.4 and 3.5); major local faunas are listed in Table 3.4. Some of the earliest described Pleistocene mammal specials are from the Mexican Basin (Owen 1869). The sampling, however, is biased both

geographically (eastern part is more dense) and diachronically (Late Rancholabrean faunas are over-represented, including those few where radiocarbon dating placed them in the ~40–11 ka interval).

The diversity of the Trans-Mexican Volcanic Belt Late Rancholabrean mammal fauna is far greater than that of today. It includes modern taxa of different ecological requirements that are sympatric at the time, e.g., *Neococherus*, *Platygonus*, *Odocoileus hemionus*, and *Bison*. This association indicates a correspondingly diverse setting, where different vegetation types were either intermixed or separated over short distances. Pleistocene climatic fluctuations acting on a complexly rugged territory such as that of the Trans-Mexican Volcanic Belt could have promoted the large vegetation diversity implied by the diverse mammal record. The pollen record seems to support this contention.

The climate regime changed by the early Holocene, becoming warmer and drier. As in other provinces, most medium to large species became extinct (Table 3.4). Other species became extirpated from Mexico and currently live outside the country, e.g., the carnivore *Canis rufus* now living in temperate North America (Hall 2001). Others disappeared from their Rancholabrean morphotectonic province but survived elsewhere within Mexico. For example, the

**Table 3.5** Late Pleistocene (Rancholabrean) Trans-Mexican Volcanic Belt flora identified from its palynological record. Taxonomical arrangement sensu Cronquist 1981; ranks employed (from higher to lower): Division, Class, Order, Family and Genus. Main sources: (Foreman 1955; Clisby and Sears 1955; Sears and Clisby 1955; Bradbury 1971, 1989, 2000; Ohngemach 1973, 1977; Meyer 1973; Brown 1984; González-Quintero 1986; Straka and Ohngemach 1989; Metcalfe 1992; Lozano García et al. 1993; Lozano-García and Ortega-Guerrero 1994; Caballero-Miranda et al. 1999; Canul-Montañez 2008; Vázquez et al. 2010; Israde-Alcantara et al. 2010; Caballero-Miranda et al. 2010; Ortega et al. 2010; and Martínez-Hernández, E. unpublished data)

<b>BRYOPHYTA</b>	
<b>SPHAGNOPSIDA</b>	
Sphagnales	
Sphagnaceae	<i>Sphagnum</i>
<b>LYCOPODIOPHYTA</b>	
<b>ISOETOPSIDA</b>	
Isoetales	
Isoetaceae	<i>Isoetes</i>
<b>SELAGINELLOPSIDA</b>	
Selaginellales	
Selaginellaceae	<i>Selaginella</i>
<b>PTERIDOPHYTA</b>	
<b>POLYPODIOPSIDA</b>	
Filicales	
Aspleniaceae	<i>Asplenium</i>
<b>PINOPHYTA</b>	
<b>CONIFEROPSIDA</b>	
Coniferales	
Cupressaceae	
<i>Juniperus</i>	
<i>Taxodium</i>	
<i>Cupressus</i>	
Pinaceae	
<i>Abies</i>	
<i>Picea</i>	
<i>Pinus</i>	
<i>Tsuga</i>	
Podocarpaceae	
<i>Podocarpus</i>	
<b>MAGNOLIOPHYTA</b>	
<b>MAGNOLIOPSIDA</b>	
Apiales	
Araliaceae	
<i>Hydrocotyle</i>	
Asterales	
Asteraceae	
Capparales	
Brassicaceae	
<i>Rorippa</i>	
Caryophyllales	
Amaranthaceae - Chenopodiaceae	
Caryophyllaceae	
Celastrales	
Aquifoliaceae	
<i>Ilex</i>	
Dipsacales	
Adoxaceae	
<i>Viburnum</i>	
Caprifoliaceae	

**Table 3.5 (continued)**

Valerianaceae	
<i>Valeriana</i>	
Ericales	
Ericaceae	
Fabales	
Fabaceae	
<i>Piscidia</i>	
<i>Prosopis</i>	
Fagales	
Betulaceae	
<i>Alnus</i>	
<i>Betula</i>	
Fagaceae	
<i>Fagus</i>	
Gentianales	
Loganiaceae	
<i>Buddleja</i>	
Hamamelidales	
Hamamelidaceae	
<i>Liquidambar</i>	
Juglandales	
Juglandaceae	
<i>Carya</i>	
<i>Engelhardtia</i>	
<i>Juglans</i>	
Lamiales	
Lamiaceae	
Magnoliales	
Magnoliaceae	
<i>Drymyrs</i>	
Malpighiales	
Hypericaceae	
<i>Hypericum</i>	
Malvales	
Malvaceae	
Tiliaceae	
Myrales	
Myricaceae	
<i>Myrica</i>	
Myrtales	
Melastomataceae	
Myrtaceae	
Onagraceae	
<i>Ludwigia</i>	
Nymphaeales	
Nymphaeaceae	
<i>Nuphar</i>	
<i>Nymphaea</i>	
Piperales	
Chloranthaceae	
<i>Hedyosmum</i>	
Plantaginales	
Plantaginaceae	
Polygonales	
Polygonaceae	
<i>Polygonum</i>	
Ranunculales	
Ranunculaceae	
<i>Ranunculus</i>	
Thalictrum	
Rosales	
Rosaceae	
<i>Holodiscus</i>	
Salicales	

(continued)

(continued)

**Table 3.5** (continued)

Southern Provinces	
Salicaceae	
<i>Populus</i>	
<i>Salix</i>	
Santalales	
Santalaceae	
<i>Arceuthobium</i>	
Sapindales	
Burseraceae	
<i>Bursera</i>	
Saxifragales	
Haloragidaceae	
Scrophulariales	
Lentibulariaceae	
<i>Utricularia</i>	
Oleaceae	
<i>Fraxinus</i>	
Solanales	
Solanaceae	
<i>Datura</i>	
Urticales	
Moraceae	
Ulmaceae	
<i>Celtis</i>	
Urticaceae	
LILIOPSIDA	
Alismatales	
Alismataceae	
<i>Sagittaria</i>	
Poramogetonaceae	
<i>Potamogeton</i>	
Ruppiaceae	
<i>Ruppia</i>	
Cyperales	
Cyperaceae	
<i>Eleocharis</i>	
<i>Schoenoplectus</i>	
Poaceae	
Eriocalulales	
Eriocaulaceae	
<i>Eriocaulon</i>	
Juncales	
Juncaceae	
<i>Luzula</i>	
Liliales	
Pontederiaceae	
<i>Heteranthera</i>	
Typhales	
Typhaceae	
<i>Typha</i>	

rodent *Cynomys mexicanus* now lives in a narrow and elongated area located in easternmost Chihuahua-Coahuila Plateaus and Ranges and a small portion of northern Sierra Madre Oriental provinces. The rodent *Microtus californicus* now is restricted to the northern Baja California Peninsula province. The rodent *Neotoma albigena* now thrives in the Northwestern Plains and Sierras province, with *N. palatina* restricted at present to a small area in the southeastern Sierra Madre Occidental province and *N. phenax* to the southern Northwestern Plains and Sierras province. The perissodactyl *Tapirus bairdii* now is restricted to the tropics (Ceballos and Oliva 2005).

These provinces include the Sierra Madre del Sur Sierra Madre de Chiapas the southern part of the Gulf Coastal Plain, and the Yucatan Platform (Fig. 3.1). They have yielded four major local faunas (Table 3.4, and Figs. 3.3 and 3.6), along with a few important palynofloras (Fig. 3.4), and relatively numerous paleosol localities (Fig. 3.5). Sampling again is strongly biased toward the Late Pleistocene (Rancholabrean NALMA). The paleosol (Acrisol) record points to an equable, largely tropical climate regime for the last 40–50 kyr. The palynological record, particularly that of Tehuacán, Puebla (northeastern Sierra Madre del Sur just south of the Trans-Mexican Volcanic Belt), indicates moister and cooler conditions in the latest Pleistocene (Canul-Montañez 2008). The now prevailing xeric vegetation is a Holocene phenomenon.

The mammal record (Table 3.4; Figs. 3.2 and 3.3) largely includes tropical taxa. Temperate and cosmopolitan taxa are less frequent, but not uncommon. The latter taxa include *Ursus americanus*, *Eumops perotis*, and *Spilogale putorius*. This composition indicates that during the Late Rancholabrean, the climate regime, although warm and moist in general, probably was punctuated at least locally, by cooler and/or drier episodes that allowed temperate taxa to expand their range southward or to occupy parts of southern habitats in a discontinuous manner. This region's geomorphic complexity, as well as limited sampling both in space and time, does not permit recognition of a particular pattern of climate changes, only delineation of broad climate change trends.

Nevertheless, as in the other provinces, important mammal composition changes took place at the end of the Rancholabrean. Several medium and large taxa became extinct, such as the carnivore *Canis dirus*, the perissodactyl *Equus*, the artiodactyls *Navahoceros fricki*, *Odocoileus lucasi*, and *Hemiauchenia*, as well as the proboscideans. Other largely cosmopolitan or temperate taxa survived farther north in temperate habitats, e.g., the chiropterans *Eptesicus fuscus* and *Eumops underwoodi*; carnivore *Ursus americanus*; and artiodactyl *Bison* (Hall 2001; Ceballos and Oliva 2005), perhaps returning to their primary range.

### A Summary of Early Peoples in Mexico

In the last 20 years, studies referring to the early peopling of the Americas have increased, especially those for western North America, e.g., Bonnichsen 1999; Bonnichsen and Turnmire 1999; Parfit 2000; Haynes 2002; Bonnichsen et al. 2005; Jiménez López et al. 2006a,b; Meltzer 2009. In Mexico, interest in early peopling has existed for over a century, e.g., Reyes 1881; Mercer 1896). Research has not yet been able to define when and where the earliest people came into Mexico (see Lorenzo and Mirambell 1999 vs. Dixon 1999). Recent

reports on previously known localities (González et al. 2006), however, have enhanced the development of predictive models that assist with the search for new sites.

Much of the controversy about the early peopling of the Americas deals with the value that is given to the indirect evidence of human presence when human skeletal remains are lacking in the sites. Such evidence may include lithics, hearths, and culturally modified bone. Indirect evidence requires further detailed analyses that distinguish between natural processes the materials may have undergone and those processes that are signatures of human intervention. The following brief synthesis of current knowledge regarding early peoples in the Mexican Late Pleistocene underscores the very limited data available.

In northern Mexico, several North American Late Pleistocene Clovis sites now are known. More than a dozen sites have been found in Sonora, some of which have stratigraphically-controlled excavations such as at El Fin del Mundo (Sanchez 2001; Gaines and Sanchez 2009; Sanchez et al. 2014). At this site, possible interaction between people and gomphotheres indicates either hunting or scavenging activities (Sanchez et al. 2014). To the south, evidence for the presence of Clovis peoples greatly diminishes. A few Clovis points have been recovered from Baja California to Costa Rica (Sanchez 2001). Other sites with evidence of Clovis culture are found in the State of Hidalgo in eastern Mexico (Sanchez 2001). These occurrences may be explained by Clovis groups moving along the Gulf Coast from Texas.

Central Mexico is the most explored area in the country. The enormous amount of construction that continues to occur in the Basin of Mexico has resulted in the discovery of numerous paleontological localities and archaeological sites. These occurrences indicate that early peoples were in the area by  $11.0\ ^{14}\text{C kBP}$ , exemplified by Peñón woman dating to  $10,755 \pm 75\ ^{14}\text{C BP}$  (González et al. 2003; González and Huddart 2008). This early age indicates that Peñón woman is one of the oldest human skeletal remains in the Americas (Dillehay 2000; Meltzer 2009). Sites contain hearths or lithics, e.g., El Cedral San Luis Potosí; Tlapacoya, State of Mexico (Lorenzo and Mirambell 1999), or human-modified bone, e.g., Santa Isabel Ixtapa or Tocuila State of Mexico (Arroyo-Cabral et al. 2006; Johnson et al. 2012). The Late Pleistocene Basin of Mexico is a highly rich environment that supported a large Columbian mammoth (*Mammuthus columbi*) population. Over 100 mammoth localities are known for the area, yet very few show evidence of human interaction with the carcass (Arroyo-Cabral et al. 2006).

One of the most controversial sites in the Americas regarding early peopling is the basin of Valsequillo near the capital city of the state of Puebla, east of Mexico City. Several

archaeological excavations since the late 1950s and early 1960s have provided inconclusive evidence about the presence of the earliest people in the area. Occupation as early as the Sangamonian interglacial, between 132 and 119 ka, (González et al. 2006) has been proposed, with the latest hypothesis about human footprints having been questioned and recently rejected (Feinberg et al. 2009; Mark et al. 2010). Further research is warranted. Access, however, is prohibited by the pollution in the reservoir dam, where some of the specific sites like Hueyatlaco or Los Hornos are located (Gonzalez et al. 2006). Private settlements now extend along and over the edge of the dam means that expectations of being able to conduct excavations in the near future are minimal (Patricia Ochoa-Castillo 2011: personal communication).

Further south, Guila Naquitz is a small shelter near the Valley of Oaxaca, in central Oaxaca. Flannery's (1986) excavation has yielded both seeds and peduncles of squash (*Cucurbita pepo*) with indications of domestication as early as  $9.0\ ^{14}\text{C kBP}$  (Smith 1997). This date coincides with views about the earliest Naquitz phase being attributed to the early Archaic period (Flannery 1986). Nearby, within the Tlacolula Valley, a few Paleoindian projectile points have been found on the surface (Marcus Winter 2008: personal communication).

In southern Mexico, research seems to indicate the presence of the Americas' two early cultural traditions, North American Clovis from Oaxaca and Chiapas, and Fish-tail fluted points from Central and South America (Santamaría and García-Bárcena 1989). Recent studies from rock-shelters nearby Ocozocuautla, Chiapas, have provided strong evidence of human presence in the state around  $11.0\text{--}10.0\ ^{14}\text{C kBP}$ . These sites have yielded lithics reflecting expedient technology and also milling stones and botanical samples that may indicate incipient horticulture starting at the end of the Pleistocene to early Holocene. Small and medium-sized animals such as deer, peccary, and rabbit are the most hunted prey, while megafaunal remains were not found (Acosta 2010).

Finally, submerged caves near Tulum in the state of Quintana Roo, on the Yucatan Peninsula, contain a diverse megafaunal assemblage of latest Pleistocene age, along with hearths with burned bones, artifacts, and human skeletal remains that date between  $11.6$  and  $8.0\ ^{14}\text{C kBP}$  (González-González et al. 2008).

Most recently, a remarkable finding of a human female was reported from Hoyo Negro cenote. The skeleton dates to between 13,000 and 12,000 calendar years ago. She has Paleoamerican craniofacial characteristics and a Beringian-derived mitochondrial DNA (mtDNA) haplogroup (D1), meaning that differences between Paleoamericans and Native Americans probably resulted from in situ evolution rather than separate ancestry (Chatters et al. 2014).

## Discussion

The pollen record in Mexico is greatly biased towards the Trans-Mexican Volcanic Belt province in central Mexico and dominated by the Basin of Mexico. Half the records lie in the Trans-Mexican Volcanic Belt and two-thirds of the localities are in or north of the Trans-Mexican Volcanic Belt province. During the latter part of the Rancholabrean, the Basin of Mexico had a cooler, more humid climate regime that allowed the development of numerous freshwater lakes in low-lying areas. Vegetational changes involve altitudinal timberline shifts more than latitudinal displacements (Bradbury 1989; Metcalfe 1992; Caballero-Miranda et al. 2010). This general pattern can be discerned with greater or lesser similarity in other morphotectonic provinces studied.

In the northern part of the Sierra Madre del Sur province, a more humid flora existed at the end of the Pleistocene and was replaced by a xeric flora between 12.0 and 10.0  $^{14}\text{C}$  kBP (Canul-Montañez 2008). To the north in the Chihuahua-Coahuila Plateaus and Ranges province, a more equable, humid climate regime was in place from  $\sim$  22.0 to 11.0  $^{14}\text{C}$  kBP. A longitudinal east-west expansion of grassland and shrub forest occurred at the expense of pine and pine-oak forest (Van Devender et al. 1987; Betancourt et al. 1990; Van Devender 1990a, b; Van Devender and Bradley 1990).

The Late Pleistocene paleosol record indicates two major contrasting types occurring in different parts of Mexico. Luvisols are found in the Trans-Mexican Volcanic Belt and Sierra Madre Occidental provinces. They have developed within silicic pyroclastic sediments around 20.0–18.0  $^{14}\text{C}$  kBP under humid to subhumid conditions and moderate temperature (Solleiro-Rebolledo et al. 1999, 2003, 2006; Cabadas-Báez 2007; Cabadas-Báez et al. 2010). Acrisols occur in the Sierra Madre del Sur province. They have developed within heterogeneous sediments around 50.0–25.0  $^{14}\text{C}$  kBP under hot and humid conditions within a forested environment (Ispphording 1974; Bautista et al. 2003).

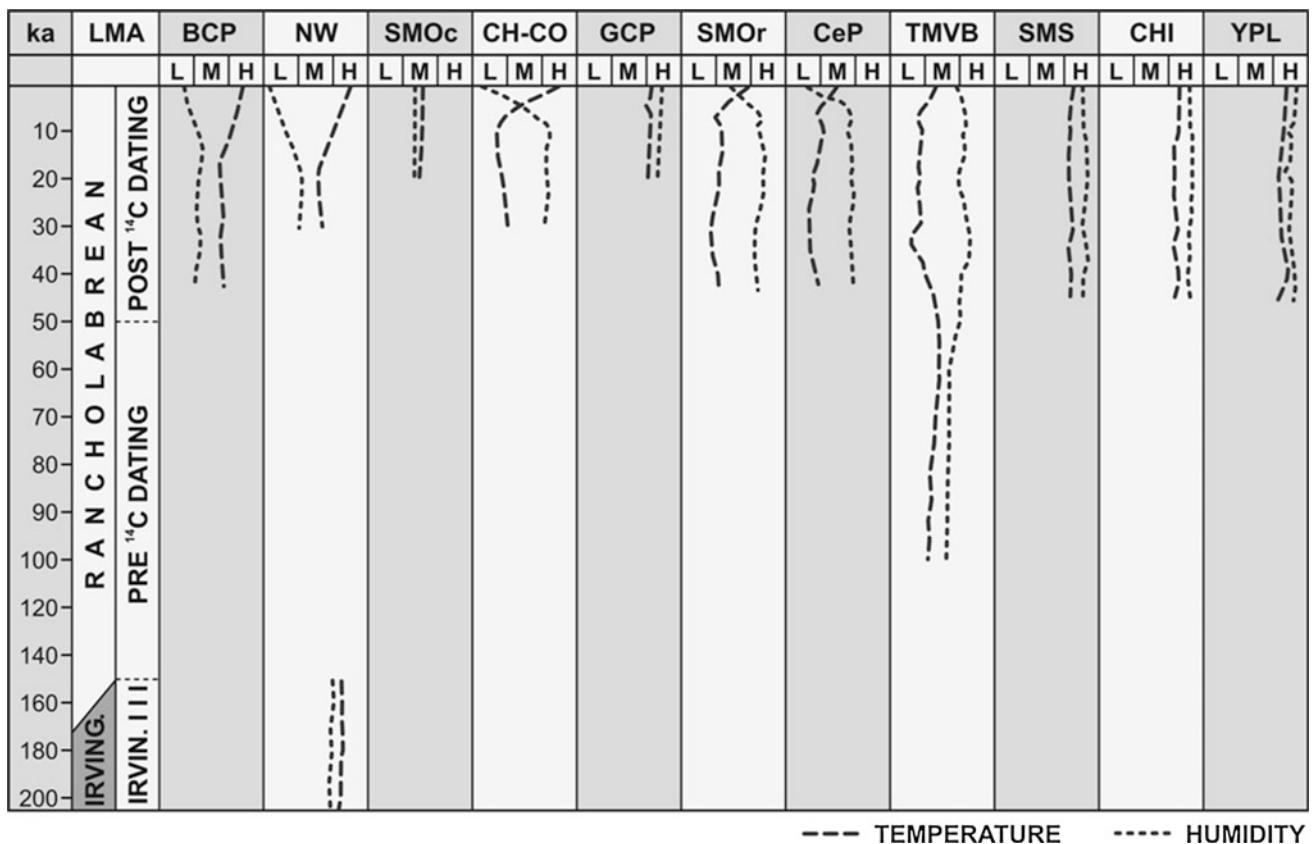
The mammal, palynological, and paleosol records (Figs. 3.3, 3.4, 3.5 and 3.6) show time and space biases; the temporal bias favors the Late Pleistocene, and the space bias favors the Trans-Mexican Volcanic Belt province. Both the palynological and paleosol records are sparse north of this province. On the other hand, the mammal record is relatively dense in the Sierra Madre Oriental and Sierra Madre del Sur provinces, yielding some major local faunas (Table 3.4). Interpretation of each data set from the provinces may differ. The environmental sensitivity of components from the individual records varies, indicating different conditions in a given place. For example, the Loltún local fauna includes temperate (ursid) and tropical (dasyproctid and xenarthran) taxa. Not surprisingly, the environmental information obtained from one data set coincides only in general with

that of another. In addition, the records disclose important gaps in space and time that must be filled to gain a better understanding of climate change across the country.

Biological communities in Mexico experienced profound changes in species composition (species that are represented) and structure (relationships among those species present) as a consequence of the environmental fluctuations during the Pleistocene. Comparison of Pleistocene and Holocene zoogeographic ranges disclosed different patterns. Many species expanded their distribution to different latitudes or higher/lower altitudes or moved further north/south during the Pleistocene. Also detected were the presence of biogeographic corridors, refugia, and centers of speciation in isolated regions (Caballero-Miranda et al. 2010).

The general situation for mammals is mirrored partially by human populations. Central Mexico is the region where the earliest archaeological sites are located, clearly pointing to their presence at around 11.0  $^{14}\text{C}$  kBP based on dating of human skeletal remains. Evidence for the utilization of faunal resources, however, is very limited (Arroyo-Cabralles et al. 2006; Johnson et al. 2006). For Mexico in general, modern taphonomic studies of Late Pleistocene faunal remains are lacking except for a few cases (Polaco and Heredia-C. 1988; Polaco et al. 1989; Solórzano 1989; Johnson et al. 2012). Although more than 270 mammoth localities are known throughout the country, only six have modified mammoth bone. Of these six, only three have good potential for demonstrating human involvement with mammoth, and those three are located in the Basin of Mexico (Arroyo-Cabralles et al. 2006).

To the northwest and differing from the faunal pattern, evidence is growing for a large presence of early sites that demonstrate a relationship with cultures in the southwestern U.S. Overall for northern Mexico, evidence of early peoples being hunter-gatherers is slowly accumulating (Sanchez 2001), but further discussion on climate change and human response are warranted because the possible questions about such relationships are not yet formulated (see Pilaar Birch and Miracle 2017). To the south, few localities have provided strong evidence for early peoples, most likely due to the poor preservation conditions in tropical soils and the emphasis of current research on advanced cultures. The finding of domesticated squash around 9.0  $^{14}\text{C}$  kBP may indicate that decreasing mobility began very early in the human occupation of Mexico (Sanchez 2001). In general, then, what influence early peoples may have had on medium and large size mammal populations at the end of the Pleistocene cannot be addressed. Using the very limited mammoth data as a potential indication, however, early peoples' hunting activities would not seem to have been the cause of extinctions. A similar situation appears to be the case for South America. Although extinctions may have been more common after early peoples arrived, some medium and large



**Fig. 3.6** Late Pleistocene probable climate trends in Mexico's morphotectonic provinces (sensu Ferrusquía-Villafranca 1993, 1998). Time frame adapted from Bell et al. (2004). The reviewed palynologic, paleosol, lake sediment, and mammal records were used to assess the trends. Abbreviations (from left to right): **LMA**, North American Land Mammal Ages. **BCP**, Baja California Peninsula. **NW**, Northwestern Plains and Sierras. **SMOc**, Sierra Madre Occidental. **CH-CO**, Chihuahuan-Coahuilan Plateaus and Ranges. **GCP**, Gulf Coastal Plain. **SMOr**, Sierra Madre Oriental. **CeP**, Central Plateau. **TMVB**, Trans-Mexican Volcanic Belt. **SMS**, Sierra Madre del Sur. **CHI**, Sierra Madre de Chiapas. **YPL**, Yucatan Platform

sized taxa persist for up to several thousand years after human arrival (Barnosky and Lindsey 2010). Australia is another case in which humans have always been implicated in megafaunal extinction. Nevertheless, it seems today that the problem was more complex, and the coexistence interval for human and megafauna remains imprecise (Brooks and Bowman 2002; Johnson and Brook 2011). Humans in Mexico coexist with medium and large sized animals rather than being the cause of their extinctions. The lack of genetic signature or any distinctive range dynamics that would distinguish the potential for extinction or survival emphasizes the challenges associated with predicting future responses of extant mammals to climate and human-mediated habitat change (Lorenzen et al. 2011; Ochoa and Piper 2017).

An initial conservative integration of data from the different sets for each province provides the basis for pattern recognition (Fig. 3.6). Modern average climate conditions for each morphotectonic province have been taken from García (1990), Hernández (1990), and Vidal-Zepeda (1990a, b). The general Wisconsinan fluctuating climate pattern and

timing have been recognized broadly long ago (Flint 1947), and those of Mexico shortly thereafter (Foreman 1955; Clisby and Sears 1955; Sears and Clisby 1955; Heine 1984). Currently available information, however, does not yet allow the establishment across the country of detailed climatic changes for the whole Wisconsinan, let alone the Pleistocene. For now, only trends can be portrayed.

The coexistence in Mexico of a highly diverse group of mammals during the Late Rancholabrean (and the entire Pleistocene for that matter), as shown by the fossil record, indicated environmental conditions quite different from those of today. Such conditions, among other things, allowed stenotopic species (restricted tolerance to a narrow range of environmental conditions) to extend their range beyond narrow parameters, and eurytopic ones (broad tolerance to a wide range of environmental conditions) to thrive extensively across the country. This situation underscored the fact that the shifting of ecological and climatic zones, at least during the Late Pleistocene, was not a simple matter of displacement or range reduction/extension. New ecological

conditions were created as zones overlapped and new and different faunal and floral communities emerged. In other words, Mexico's Pleistocene biome tapestry dynamically adjusted to environmental changes acting on a territory of quite complex relief. The net result was that by Late Rancholabrean, mammal fauna diversity (and by extension biotic diversity as well) was greater than that of today. Community structure, therefore, would have been organized differently to facilitate the complex relationships engendered by shifting and overlapping ecological zones.

The biotic response to these environmental conditions may have involved extinction. Extinctions are common throughout the Pleistocene (Kurtén and Anderson 1980; Bell et al. 2004), with most extinct mammals being medium and large species. The extent of extinctions and the complex of environmental changes involved point to a variety of causes that induced Pleistocene extinctions. The two main causes proposed are climate change in terms of geological-biological impacts or human-driven impacts (Koch and Barnosky 2006).

One such cause could have been disruption of biotic interactions creating a coevolutionary disequilibrium (Graham and Lundelius 1984). Coevolution is the common evolution of multiple taxa (plants and animals) that share close ecological relationships. Through reciprocal selective forces, the evolution of one taxon may be somewhat dependant on the other (Graham and Lundelius 1984:227). Taxa are not isolated on a landscape or in an ecosystem. Coevolution, then, is the interdependent interaction of taxa acting at the evolutionary level. The destabilization of the coevolutionary relationship through various types of disruptions (such as habitat destruction, climatic change, extinctions, extirpations) affects the balance and creates a breakdown in the structure and relationships (disequilibrium). Following that reasoning, the rapid decrease in size and eventual extinction of caballoid horses in Alaska has been linked to climatic shift, changing vegetation, and the collapse of the ecosystem at the end of the Pleistocene (Guthrie 2003). Similarly, the decline in genetic diversity in North American bison appears to be linked to environmental changes with the onset of the last Laurentide Glacial Maximum (Shapiro et al. 2004). The temporal mode of extinction (gradual through a long time span or sudden, nearly instantaneous) has received much attention and is the subject of ongoing debate (Martin and Klein 1989; Bell et al. 2004).

Recently, Faith and Surovell (2009) argued for the possibility of the second alternative, i.e., human driven impacts. They suggest the absence of extinct genera from the fossil record is a result of sampling error. The analysis of Mexico's record, incomplete and biased as the record may be, seems not to bear out this contention. By arguing on negative evidence, the hypothesis lacks evidence for testing its validity.

One other hypothesis that has been contentious over the past 10 years has been the possible meteorite airburst, similar to the famous K-T impact, and how that event could cause the extinction of megafauna and strong cultural changes and population decline in Paleoindian populations (Firestone et al. 2007). Most recently, evidence for such an airburst has been proposed at several Mexican sites where megafauna were found (Gonzalez et al. 2014). For at least one of those sites, a claim has been made that the dating procedures were compromised, and, because of that, the isochrony of the events cannot be confirmed (Meltzer et al. 2014).

Finally, the available information on Mexico's Pleistocene mammals allows only rough discriminations of a few of the many environmental factors involved in this complex environment/biota interplay. Under these circumstances, inferring Pleistocene climate in southern North America from bioevents alone, i.e., the fossil record and actualistic comparisons thereof, allows at best the tracing of broad qualitative patterns for each morphotectonic province. Nonetheless, the environmental factors contribute to a better understanding of the mammalian response, expressed in extinctions, biogeographic shifts, and extirpations that significantly change Pleistocene and Holocene mammal physiognomy. Furthermore, the temporal and spatial gaps of the mammal, paleontological, and paleosol records must be filled before a more complete understanding of the Quaternary climate and its changes can be gained in this part of the Americas.

## Concluding Remarks

The Holocene and Late Pleistocene Mexican faunas are quite different. This difference is the combined results of individual species extinctions and range modifications that affected and changed the vertebrate biota physiognomy and taxonomic makeup.. The available fossil record, however, does not portray this major biogeographic shifting of species in detail due to the lack of associated chronometric data. The analysis of disjunct (i.e., separated from the main range) and of demonstrably relict species may be an alternative to providing greater detail and understanding about the response of individual species to climate change during the Late Pleistocene. The following summary points are made to illuminate what is known from the Pleistocene record and directions for further research.

The Late Pleistocene mammal record was analyzed by morphotectonic provinces ( $n = 11$ ) that were grouped into four larger geographic units to examine zoogeographic distribution, any variance in distribution (extinctions,

extirpations), and environmental conditions inferred from that distribution and variance.

#### Northern provinces

- Biotic diversity unparalleled anywhere in Mexico today
- Both extinctions and extirpations (northward and southward) occurred that shaped the modern fauna
- More humid climatic regime during the Irvingtonian and early Rancholabrean than that of today that allowed a subtropical biota
- A cooler and moister regime during the latest Rancholabrean than that of today with a non-analogous fauna and expansion of grassland and shrub forest

#### Central and Eastern provinces

- Thermal (warm/cold) and humidity/rain (moist/dry) oscillations during the Rancholabrean with a non-analogous fauna
- Both extinctions and extirpations (northward, southward, and westward) occurred that shaped the modern fauna
- A cooler and moister regime during the latest Rancholabrean than that of today with a non-analogous fauna and flora

#### Trans-Mexican Volcanic Belt

- Mammalian diversity during late Rancholabrean far greater than that of today
- Both extinctions and extirpations (northward, southward, and westward) occurred that shaped the modern fauna
- A cooler and moister regime during the late Rancholabrean than that of today with a non-analogous fauna
- Numerous freshwater lakes developed in low-lying areas and vegetation experienced altitudinal timberline shifts

#### Southern provinces

- Equable, tropical climate regime during Rancholabrean with a largely tropical fauna and humid flora
- General tropical climate punctuated by cooler and drier episodes during the late Rancholabrean with a non-analogous fauna
- Both extinctions and extirpations (northward) occurred that shaped the modern fauna

#### Early peoples

- arrived in Mexico by the latest Pleistocene ( $\sim 11$   $^{14}\text{C}$  kBP)
- Growing evidence for a strong presence of Clovis culture in the Northern provinces and Gulf Coastal Plain of Eastern provinces
- Most of the known early sites are concentrated in the Basin of Mexico

- Both Clovis (North American tradition) and Fish-tail fluted points (Central and South American tradition) are found in southern Mexico, perhaps representing a cultural transitional zone
- A lack of taphonomic studies coupled with only a very few early sites having a solid association between medium to large animals and humans suggests that human impact on the Late Pleistocene populations appears to have been negligible and was not a cause for extinctions.

Time and space biases exist, with records favoring the Late Pleistocene (Rancholabrean) and the Trans-Mexican Volcanic Belt, particularly the Basin of Mexico. Nevertheless, biological communities throughout the country experience profound changes in species composition and structure. Such a pattern was due not to direct human impact but to the consequences of environmental changes throughout and particularly at the end of the Pleistocene. The shifting of ecological and climatic zones was not a simple matter of displacement and range adjustments. The coexistence of a highly diverse group of mammals indicates a community structure organized differently than that of today in order to facilitate the complex relationships that coexistence would have required. The disruption of these biotic interactions would have created a coevolutionary disequilibrium situation.

The available information on Mexico's Pleistocene mammal, palynological, and paleosol records allows only broad trends to be discerned in the complex environmental-biota interplay and what role, if any, early peoples played in extinction. A critical need exists to fill in the time and space gaps in these records. Solid radiocarbon chronologies need to be developed that can anchor the various records and provide the framework for more in-depth analyses of environmental changes and individual species response. In a focused radiocarbon dating program, the Trans-Mexican Volcanic Belt province and mammoth would be a reasonable target. The most concentrated research has been in this province (particularly the Basin of Mexico) and mammoth is the most ubiquitous Late Pleistocene mammal. Research needs to continue and expand in the other provinces in order to have a representative sample across the country. While research in the Northern provinces has been most fruitful in terms of mammal-human interactions during the latest Pleistocene, the Gulf Coastal Plains (Eastern province) has great potential in illuminating that interaction as well. Mexico's record is critical in understanding the continent-wide affects of Pleistocene climatic changes on plants, animals, and humans. This initial synthesis forms a first-order interpretation and basis for future research directions.

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