Chapter 13

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Chapter 13

Mexico’s Middle Miocene Mammalian Assemblages: An Overview

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ABSTRACT

Information on Mexico’s middle Miocene mammal record improves understanding of the southern extent, makeup, and relationships of North American Tertiary faunas. The Hemingfordian–Barstovian combined assemblage (= HBCA) in Mexico records 6 orders, 17 families, and 35 genera, each represented probably by a single species known from sites in Baja California Norte and Sur (one each), Sonora (two), Aguascalientes (one), Oaxaca (three), and Chiapas (one). Barstovian diversity is nearly triple that of the Hemingfordian. The Barstovian Oaxacan subassemblage is by far the largest. This combined assemblage includes most of the orders and a little over a third of the families known to occur in North America for this interval. The better Tertiary post-Barstovian record does not include Clarendonian age sites, and has no representation in southern Mexico.

The HBCA consists mainly of herbivores and has very few carnivorans. The Barstovian equids from Southeastern Mexico include an ancestral merychippine coexisting with hipparionines and pliohippines. The coexistence of two derived lineages implies either repeated southward migration of equid species from temperate North America shortly after their origination or that some equid differentiation took place in tropical Middle America. Further work may clarify this issue. The HBCA shows strict North American affinities. Seven families and 16 genera have their southernmost occurrence in Mexico. The putative recent discovery in Peru of North American Clarendonian or older mammals may indicate that at least the southward migrating component of the Great American Faunal Interchange occurred earlier than currently thought. Three of the four families recorded in Peru occur in the Barstovian of Southeastern Mexico, thus lending support to this contention.

INTRODUCTION

The Cenozoic land mammal records of temperate North and South America largely show independent faunistic evolution, punctuated by a few migration events, which had far-reaching biotic consequences. These events in due time changed the taxonomic makeup and physiognomy of the continental mammal fauna, chiefly in the tropics and in temperate South America. Temperate North America was, by comparison, much less affected. The migration event documented best is the Late Tertiary Great American Faunal Interchange (Stehli and Webb, 1985). Other events in the early Paleogene (Simpson, 1948, 1967; Wood and Patterson, 1959; Patterson and Pascual, 1963; Patterson and Wood, 1982; Ferrusquía-Villafranca, 1989) and possibly the early Late Miocene (Campbell et al., 2000) have been proposed.

The inter-American overland migration routes must have included Mexico and Central America (and perhaps the Antilles to a lesser degree). Mexico and northern Central America form a peninsular extension of North America that narrows southward down to the Isthmus of Tehuantepec, then widens a little (Chiapas-Yucatán) and narrows again (Honduras–Nicaragua). Geographically it is quite complex, particularly south of the Trans-Mex-

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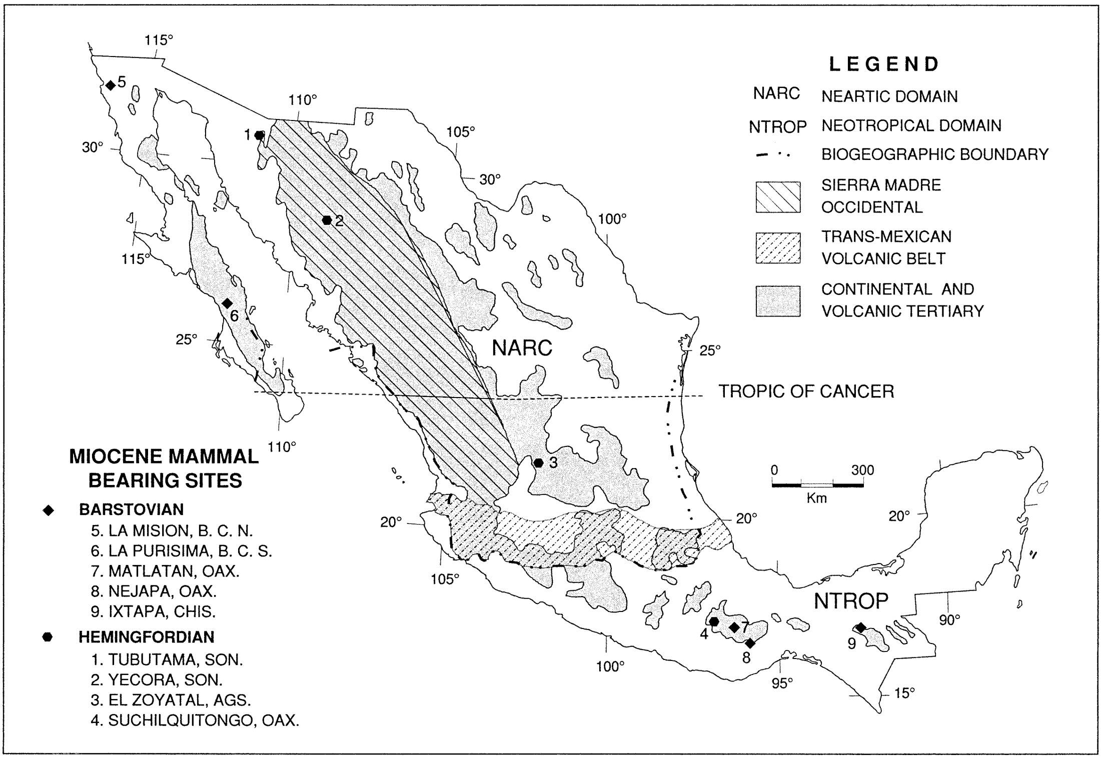

Fig. 13.1. Index map of Mexico showing location of areas mentioned in this study, the approximate extent of the continental sedimentary and volcanic Tertiary, two major geologic provinces, and present-day biogeographic domains.

ican Volcanic Belt (TMVB). Climatically, it grades from temperate/xeric conditions in the north to tropical in the south. However, south of the TMVB the broad climatic belts become a complex tapestry of irregular zones, closely related to the maze of lowlands and ranges present there. This in turn reflects an exceedingly complicated geologic makeup and evolution, which is still not well known chiefly due to insufficient detailed geologic/geophysical work. The key position of this region, where the North American, Caribbean, and Cocos Plates meet and interact, has led to proposals of a large number of geologic/tectonic models to explain its evolution (Anderson and Schmidt, 1983, review the models). Such models, though, are based on scarce factual evidence.

New World mammals living in the tropics were closest to participate in inter-American migration events. Therefore, the study of Middle America's Tertiary mammal record is critical to document and improve understanding of mammalian evolution in the tropics, as well as the faunal relationships between North and South America during this period. The Tertiary record in Mexico, although limited, improves significantly from the Miocene onward. Two or more faunas are known for each land mammal age other than the Clarendonian and Arikareean (Ferrusquía-Villafranca, 1990a, 1990b, 1990c, and references therein). Increasing the knowledge of this record is important. Accordingly, in the present contribution, the information on Mexico's middle Miocene mammals is reviewed and updated, emphasizing the advances made since 1990.

The location of the Hemingfordian and Barstovian sites is shown (fig. 13.1), and the taxonomic makeup of the respective mammalian assemblages is given in table 13.1. The Hemingfordian assemblage includes two single occurrences and two small local faunas from sites in Sonora, Aguascalientes, and Oaxaca (the only one south of the TMVB). The composite assemblage records an aggregate diversity of 3 orders, 7 families, and 11 genera each represented mainly by a single species. The Barstovian assemblage includes four local faunas and one fauna (collected at several localities), from Baja California Norte, Baja California Sur (both north of the TMVB), Oaxaca, and Chiapas (both in Southeastern Mexico). This composite assemblage has an aggregate diversity of 5 orders, 15 families, and 27 genera, each represented chiefly by a single species, and thus is more than double the Hemingfordian record, but much less diverse than the Barstovian mammalian assemblages of the United States and Canada. A brief description and discussion of the Mexican assemblages follows.

THE HEMINGFORDIAN MAMMALIAN ASSEMBLAGE

Tubutama Single Occurrence, Unnamed Formation, Northwestern Sonora

Geologic Setting: The area lies between 30°58′48″–31°01′12″ N Lat. and 111°40′20″–111°42′00″ W Long., some 20 km north of Tubutama (Ferrusquía-Villafranca, 1990a: figs. 2, 6), roughly midway between Caborca and Nogales. A Cretaceous granitic pluton and a clastic marine unit unconformably underlie the Tertiary sequence. The Tertiary is approximately 1050 m thick and consists of andesitic to rhyolitic volcanics, plus lacustrine and fluvial deposits, sparsely interbedded by lava flows and volcaniclastics, all unconformably overlain by Quaternary deposits (Salas, 1970; Gómez-Caballero et al., 1981; Arriaga-Meléndez et al., 1986). The basal volcanics are Early Oligocene, based on a K-Ar age of 33.4 ± 0.9 Ma. A basaltic lava flow intercalated between the lacustrine and the lower fluvial bodies has a K-Ar age of 22.3 ± 0.4 Ma. The flow, on this basis, is dated as early Middle Miocene; some 80 m above it, camelid remains were collected.

Paleontologic Remarks: The camelid remains consist of skull and jaw fragments belonging to juvenile and adult individuals of a new endemic species, *Stenomylus tubutamensis* (Ferrusquía-Villafranca, 1990a: pl. 2). It displays a combination of primitive and derived features that makes it not particularly close to any known species of *Stenomylus* (Frick and Taylor, 1968; Honey et al., 1998).

Given the isolation of the find, the precise age of *S. tubutamensis* remains problematic. The K-Ar 22.3 ± 0.4 Ma age of the underlying basalt flow indicates a maximum Late Arikareean age for this species. However, derived characters suggest an early Hemingfordian age, and it is regarded as such. *Stenomylus tubutamensis* extends the geographic range of the Stenomylinae from the southwestern United States to northwestern Mexico (Tedford et al., 1987; Honey et al., 1998).

Yécora Single Occurrence, Unnamed Formation, East-Central Sonora

Geologic Setting: The area lies in the Sierra Madre Occidental, between 28°15′–28°25′ N Lat. and 108°45′–109°00′ W Long., some 245 km east-southeast of Hermosillo (Ferrusquía-Villafranca, 1990a: figs. 2, 7). The relief is mountainous. The Upper Volcanic Complex crops out in the area (Bockoven, 1981; McDowell and Clabaugh, 1981). Here it includes Oligocene andesitic and basaltic lava flows and pyroclastics overlain by Miocene arkosic sandstones and volcaniclastics, in turn covered by Late Miocene volcanics and Quaternary deposits. About 3 km north of Yécora, a leporid mandible was collected from a sandstone body.

Paleontologic Remarks: The specimen was originally described by Alvarez-Solórzano (1963) under the name *Archaeolagus sonoranus*, and dated as Miocene–Pliocene. In a subsequent study this species was transferred to *Hypolagus* on the basis of overall tooth morphology (Ferrusquía-Villafranca, 1990a: fig. 8), which shows an intermediate to advanced stage within the *Archaeolagus–Hypolagus* lineage (Dawson, 1958). *H. sonoranus* appears to be a primitive species, comparable to other Hemingfordian ones.

The precise age of *H. sonoranus* is unknown, because of its isolation and the lack of other objective time constraints. Its position within the *Archaeolagus–Hypolagus* lineage is suggestive of a Hemingfordian age, and it is regarded as such here. *Hypolagus* is a widespread and long-lived genus in North America (Hemingfordian to Blancan, and

TABLE 13.1

Middle Miocene Land Mammal Record of Mexico

	Hemingfordian				Barstovian				
	NMex		CMex	SEMex	NMex		SEMex		
Taxa	TB	YE	ZO	SU	LM	LP	MA	NE	IX
CARNIVORA									
1. Family Felidae									
Gen. & sp. Indet.							x		
2. Family Mustelidae									
cf. *Leptarctus* sp.							x		
Plionictis oaxacaensis								x	
3. Family Canidae									
Euoplocyon cf. *E. brachygnathus*						x			
Gen. & sp. Indet.								x	
RODENTIA									
4. Fam., Gen. & sp. Indet. A								x	
5. Fam., Gen. & sp. Indet. B							x		
LAGOMORPHA									
6. Family Leporidae									
Hypolagus sonoranus		x							
ARTIODACTYLA									
7. Family Tayassuidae									
"Prosthennops" xiphidonticus			x						
cf. *Prosthennops* sp.								x	
8. Family Merycoidodontidae									
Merychyus elegans			x						
Merychyus aff. *M. minimus*				x					
9. Family Camelidae									
Aguascalientia wilsoni			x						
cf. *Pliauchenia* sp.								x	
cf. *Procamelus* sp.								x	
cf. *Protolabis* sp.							x	x	
Stenomylus tubutamensis	x								
Gen. & sp. Indet.					x		x	x	
10. Family Protoceratidae									
cf. *Paratoceras* sp.				x					
Gen. & sp. nov.				x					
? Protoceratidae Gen. & sp. Indet							x	x	
11. Family Leptomerycidae									
?*Pseudoparablastomeryx* sp.							x		
12. Fam., Gen. & sp. Indet A							x	x	
13. Fam., Gen. & sp. Indet B							x	x	
14. Family Antilocapridae									
Merycodus sabulonis								x	
?Antilocapridae Gen. & sp. Indet.								x	

TABLE 13.1
Middle Miocene Land Mammal Record of Mexico
(*Continued*)

	Hemingfordian				Barstovian				
	NMex		CMex	SEMex	NMex		SEMex		
Taxa	TB	YE	ZO	SU	LM	LP	MA	NE	IX
PERISSODACTYLA									
15. Family Equidae									
Merychippus sp.				x				x	
Merychippus cf. *M. primus*							x	x	
Merychippus cf. *M. sejunctus*							x	x	
Merychippus cf. *M. californicus*								x	
Aff. *Cormohipparion* sp. n.									x
Neohipparion aff. *N. trampasense*								x	
Calippus sp.								x	
Pliohippus aff. *P. pernix*							x	x	
16. Family Rhinocerotidae									
cf. *Menoceras* sp.			x						
cf. *Teleoceras* sp.									x
Gen. & sp. Indet.				x			x	x	
PROBOSCIDEA									
17. Family Gomphotheriidae									
Gomphotherium sp.								x	x

SUMMARY

	Hemingfordian					Barstovian						M-Mioc
	TB	YE	ZO	SU	TD	LM	LP	MA	NE	IX	TD	GTD
ORDER	1	1	2	2	3	1	1	4	5	2	5	6
FAMILY	1	1	4	4	7	1	1	10(3)	12(3)	3	15(4)	17(4)
GENUS	1	1	4	5(1)	11(2)	1(1)	1	11(4)	19(8)	3	26(7)	35(8)
SPECIES	1	1	4	5(1)	12(2)	1(1)	1	12(4)	22(8)	3	29(7)	38(8)

Abbreviations: **CMex**, Central Mexico including the Trans-Mexican Volcanic Belt; **TD**, total different taxa recorded; **GTD**, grand total of different taxa for Hemingfordian plus Barstovian; **IX**, Ixtapa, Chiapas; **LM**, La Misión, Baja California Norte; **LP**, Baja California Sur; **MA**, Matatlán, Oaxaca; **NE**, Nejapa, Oaxaca; **NMex**, Northern Mexico; **SEMex**, Southeastern Mexico; **SU**, Suchilquitongo, Oaxaca; **TB**, Tubutama, Sonora; **YE,** Yécora, Sonora; **ZO**, Zoyatal, Aguascalientes.

Note: The numbers in parentheses indicate indeterminate taxa in that category.

possibly Irvingtonian; Tedford et al., 1987; White, 1987). In Mexico, *Hypolagus* has also been recovered from the much younger Hemphillian of Guanajuato (Miller and Carranza, 1982) and Blancan of Baja California Sur (Miller, 1980).

El Zoyatal Local Fauna, El Zoyatal Tuff, Southeastern Aguascalientes

Geologic Setting: The area lies between 21°46′–21°58′ N Lat., and 102°08′–102°20′ W Long. (Ferrusquía-Villafranca, 1990a: figs. 2, 9) and includes the state capital; relief is low and only the Cenozoic sequence crops out (Hernández-Láscares, 1981). The lower unit is the apparently Oligocene Ojo Caliente Rhyolite, which is unconformably overlain by a Middle Miocene rhyolitic, pyroclastic blanket named El Zoyatal Tuff, which in turn is overlain by Quaternary deposits. The tuff unit also includes interbeds of fine- to medium-grained, arkosic, fluvial sandstones. The namesake fauna was collected from these sandstone beds.

PALEONTOLOGIC REMARKS: El Zoyatal local fauna was initially described by Dalquest and Mooser (1974); subsequent revisions by Stevens (1977) and Ferrusquía-Villafranca (1990a) resulted in major changes pertaining to taxonomy and age. The cheek tooth originally referred to *Aphelops* sp. was reassigned to cf. *Menoceras* sp. on the basis of its size and morphology. Because of its unique features, the mandible referred to *Miotylopus wilsoni* (then described as a new species by Dalquest and Mooser, 1774: fig. 5) was renamed *Aguascalientia wilsoni*, the type species of a new floridatraguline genus (Stevens, 1977). The material referred to *Merychyus* cf. *M. elegans* (Dalquest and Mooser, 1974: fig. 4) can be assigned positively to this species. Wright (1998: 396), in his authoritative review of the Tayassuidae, regards *Dyseohyus stirtoni* Woodburne, 1969, as a junior synonym of ''*Prosthennops*'' *xiphidonticus* Barbour, 1925; in keeping with this nomenclature, *Dyseohyus* cf. *D. stirtoni* (Dalquest and Mooser, 1974: fig. 3) becomes ''*Prosthennops*'' cf. ''*P.*'' *xiphidonticus*.

Dalquest and Mooser (1974) regarded El Zoyatal local fauna as Barstovian, based on *Miotylopus wilsoni* and *Dyseohyus* cf. *D. stirtoni*. This is no longer tenable. The presence of *Merychyus elegans* and *Aguascalientia wilsoni*, a species more advanced than the Arikareean *Aguascalientia* sp. from Texas and less so than the Barstovian floridatragulines from the Gulf Coastal Plain (Stevens, 1977), suggests an (early?) Hemingfordian age as most probable for this fauna (Ferrusquía-Villafranca, 1990a).

SUCHILQUITONGO LOCAL FAUNA, SUCHILQUITONGO FORMATION, CENTRAL OAXACA

GEOLOGIC SETTING: The area lies between 17°10′–17°20′ N Lat. and 96°45′–97°00′ W Long.; the village of Suchilquitongo is located about 15 km north-northwest of Oaxaca City. The Tertiary sequence occurs in the northwest–southeast trending Valle de Oaxaca Graben, bounded to the west by a horst formed by the Late Proterozoic metamorphic Oaxacan Complex and by a Mid-Paleozoic granitoid pluton, and to the east by an unnamed Paleozoic metamorphic complex, partly covered by a continental Jurassic and two marine Cretaceous sedimentary units (Wilson and Clabaugh, 1970; Ortega-Gutiérrez, 1981; Ferrusquía-Villafranca, 1990d).

The Tertiary sequence consists (fig. 13.2) of pre-Miocene calcilithitic conglomerates, latite-andesite lava flows, the fluvio-lacustrine and volcaniclastic Miocene Suchilquitongo Formation, and the polymictic Telixtlahuaca Conglomerate, possibly Pliocene in age (Wilson and Clabaugh, 1970; Ferrusquía-Villafranca, 1990d). Quaternary deposits extensively cover the Tertiary units. The Etla Tuff Member of the Suchilquitongo Formation yielded biotite and plagioclase K-Ar ages of 19.3 ± 0.3 Ma and 20.6 ± 0.3 Ma, respectively (Ferrusquía-Villafranca, 1992), which date it as early Middle Miocene. Strata located some 80 m above the Tuff produced the Suchilquitongo local fauna.

PALEONTOLOGIC REMARKS: This local fauna includes the oreodont *Merychyus* aff. *M. minimus* (Ferrusquía-Villafranca, 1990b: pl. 1), the smallest species of this genus. When first reported (Ferrusquía-Villafranca et al., 1974), it was the second Miocene oreodont recorded in Middle America. Suchilquitongo roughly lies midway between the Hemingfordian localities of the southern United States and the Panama Canal Zone, where Miocene oreodonts were first collected outside North America (Whitmore and Stewart, 1965).

Two protoceratid species are present, one referred to cf. *Paratoceras* sp. (Ferrusquía-Villafranca, 1990b: pl. 1) on the basis of toothed mandibular fragments, and a new kyptoceratine genus and species, characterized among other features by its large size and extreme hypsodonty (fig. 13.3A–B). This species is much larger than *Syndioceras cooley*, the only other known Hemingfordian kyptoceratine (Webb, 1981; Tedford et al., 1987; Prothero, 1998a) and larger than *Kyptoceras amatorum* from the Hemphillian of Florida (Webb, 1981).

Another member of the fauna is *Merychippus* sp. (Ferrusquía-Villafranca, 1990b: pl. 1), which is fairly hypsodont for a Hemingfordian species, approaching the degree of hypsodonty seen in the Barstovian *M. seversus* and *M. californicus* from the western United States (Downs, 1961; MacFadden, 1984; Hulbert and MacFadden, 1991). An in-

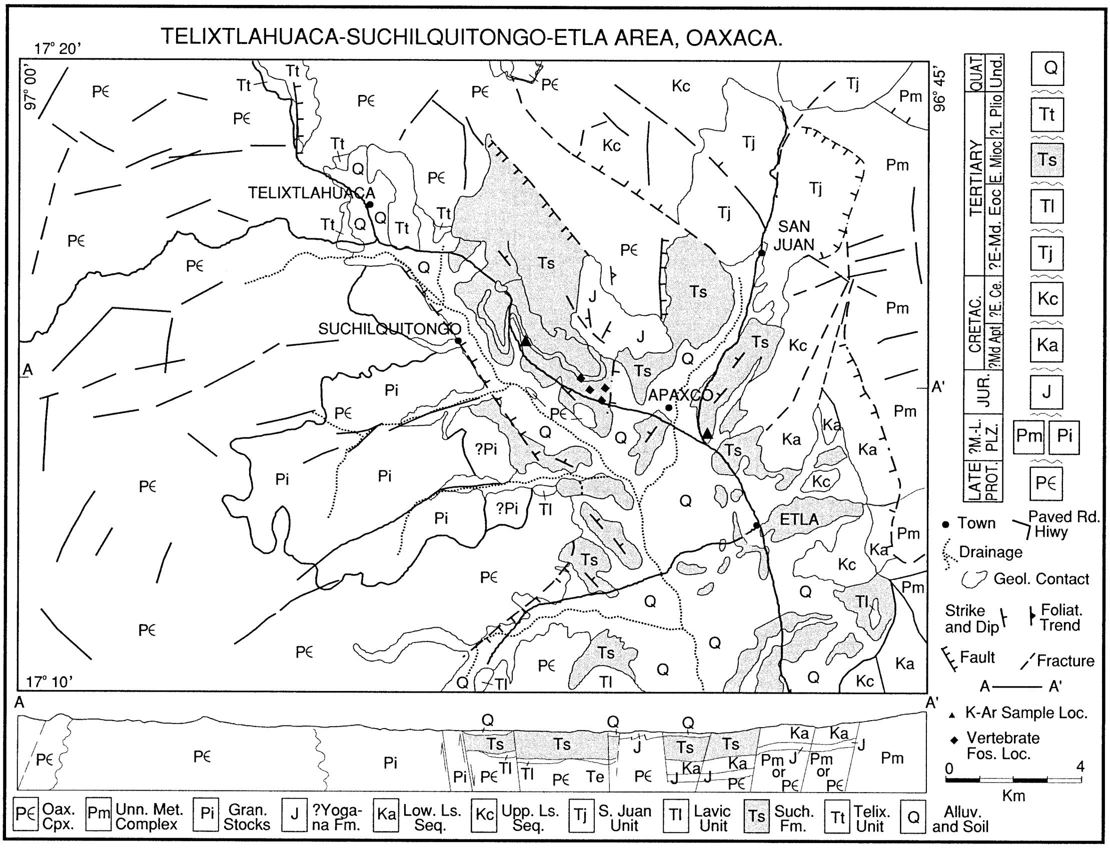

Fig. 13.2. Geologic map and generalized structural section of the Telixtlahuaca-Suchilquitongo-Etla Area, Central Oaxaca. Abbreviations: Alluv., alluvium; Gran., granitoid; Low Ls. Seq., Lower Carbonate Sequence; Oax. Cpx., Oaxacan Complex; S., San (= Saint); Such., Suchilquitongo; Telix., Telixtlahuaca; Unn. Met., Unnamed Metamorphic; Upp. Ls. Seq., Upper Carbonate Sequence.

determinate rhinocerotid completes the faunal list.

The precise age of the Suchilquitongo local fauna remains unknown; however, its makeup and stratigraphic position (the fossiliferous beds overlie 19.2–20 Ma dated tuffs), strongly suggests that it is Early Hemingfordian.

THE BARSTOVIAN MAMMALIAN ASSEMBLAGE

La Mision Local Fauna, Rosarito Beach Formation, Northern Baja Californa Norte

Geologic Setting: The area lies between 32°01′–32°10′ N Lat. and 116°45′–116°45′ W Long., that is, adjacent to the Pacific Ocean, some 40 km north of Ensenada (Ferrusquía-Villafranca, 1990a: figs. 2, 3). There the Tertiary sequence forms low mesas set over the pre-Cenozoic basement, which includes prebatholithic metamorphics intruded by Aptian-Albian quartz-diorite plutons, and small aprons of the Campanian-Maastrichtian transitional El Rosario Formation (Minch, 1967; Minch et al., 1970; Gastil et al., 1975). The Tertiary sequence includes the Rosarito Beach Formation, which consists of two basalt flow successions separated by a largely marine and transitional, fossiliferous, arkosic, sandstone body (Minch et al., 1970). The lower basalt flows have yielded a K-Ar age of 16.1 ± 2.1 Ma (Minch et al., 1984: 35). A seemingly Late Tertiary arkosic breccia unconformably overlies the Ro-

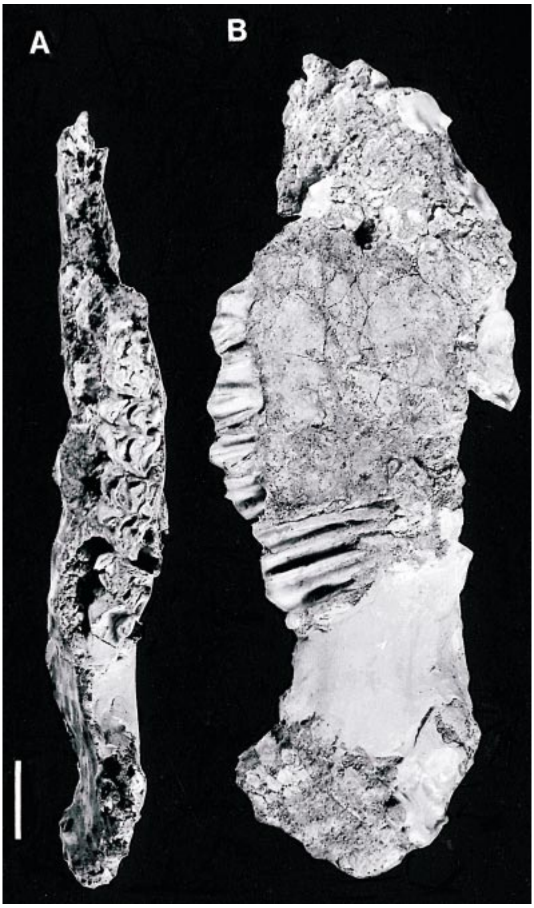

Fig. 13.3. Protoceratidae, gen. et sp. n. **A, B,** Occlusal and lateral views of partial left rostrum with P2–M2, IGM 7961, Suchilquitongo Formation (Hemingfordian), Municipio de San Pablo Etla, Oaxaca; white bar indicates 3 cm.

sarito Beach Formation. Finally, Quaternary deposits complete the roster of Cenozoic units.

PALEONTOLOGIC REMARKS: La Misión local fauna comes from the sandstone body, and is dominantly marine. The mammals include otariid carnivorans, cetaceans belonging to at least five families, dugongid sirenians, and desmostylids (Gascón-Romero, 1991, 1997; Gascón-Romero and Aranda-Manteca, 1992; Gascón-Romero et al., 1994; Barnes, 1998, and references therein). The only terrestrial mammal is a camel originally referred to *Oxydactylus longipes* (Minch et al., 1970), but the material is not diagnostic beyond family level (Ferrusquía-Villafranca, 1990a).

The presence of *O. longipes* was the basis for assigning the Rosarito Beach Formation and the fossils it bears to the Hemingfordian. However, given the above, the now well-known marine mammal fauna, and the mollusk assemblage, it is necessary to date this fauna as middle Miocene, correlative with the Temblor Provincial Stage (Addicott, 1972) and with the Barstovian (Barnes, 1998).

LA PURÍSIMA LOCAL FAUNA, ISIDRO FORMATION, CENTRAL BAJA CALIFORNIA SUR

GEOLOGIC SETTING: The area lies between 26°05′–26°15′ N Lat. and 112°00′–112°15′ W Long. (Ferrusquía-Villafranca, 1990a: figs. 2, 4), the relief is low, and only the Cenozoic sequence crops out (INEGI, 1982; McLean and Hausback, 1983; Hausback, 1984). The lowest unit is the Late Oligocene, marine San Gregorio Formation, which is unconformably overlain by the Miocene Isidro (also spelled Ysidro) and Comondú formations. The Isidro Formation is very fossiliferous and consists of shallow marine, fine to coarse clastics; the Comondú contains continental volcaniclastics and andesitic to basaltic lava flows. K-Ar ages from these flows are 17 to 23 Ma in the lower ones, and 11.5 to 15 Ma in the upper ones (McLean et al., 1987). The contact between the Isidro and Comondú formations is diachronous. Late Tertiary and Quaternary basalt flows and pyroclastics, as well as Quaternary sedimentary deposits, complete the Cenozoic sequence.

PALEONTOLOGIC REMARKS: The Isidro Formation has yielded La Purísima local fauna, which includes marine mammals referred to otariid carnivores, three families of cetaceans, dugongid sirenians, and desmostylids (Kilmer, 1965; Domning, 1972, 1978; Ferrusquía-Villafranca, 1990a; Barnes, 1998). The only terrestrial mammal fossil is an incomplete upper molar referred to the borophagine carnivore *Euoplocyon* cf. *E. praedator* (Ferrusquía-Villafranca, 1990a: pl. 1). Recently, Wang et al. (1999: 133) have placed *E. praedator* Matthew, 1924, as a junior synonym of *E. brachygnathus* (Douglas, 1903), which is followed here. *E. brachygnathus* is known from the Early Barstovian of Nebraska (Matthew, 1924; White, 1947; Tedford and Frailey, 1976; Wang et al., 1999).

The early Barstovian age of this fauna suggested by the *Euoplocyon* cf. *E. brachygnathus* record is further supported by the Isidro Formation mollusk fauna, which is transitional between that of the Vaqueros and Temblor Stages (Addicott, 1972), known to be correlative to the late Hemingfordian and early Barstovian land mammal ages. The stratigraphic ranges of the marine mammal taxa (Barnes, 1998, and references therein) lend additional support to this age assignment.

THE MATATLÁN FAUNA, MATATLÁN FORMATION, CENTRAL OAXACA

GEOLOGIC SETTING: The area lies between 16°50′–17°00′ N Lat. and 96°15′–96°30′ W Long. (fig. 13.4). The town of Matatlán is located some 40 km east-southeast of the city of Oaxaca (Ferrusquía-Villafranca, 1990a: fig. 2). The Tertiary sequence occurs in the Valle de Oaxaca Graben, which terminates in the area. The Pre-Cenozoic basement consists of ?Aptian and Cenomanian marine calcareous units that bound the graben to the south and east. The Cenozoic sequence includes a thick, felsic, pyroclastic pile, the Mitla Tuff, which makes up the mountains that surround Mitla (Ferrusquía-Villafranca, 1990d, 1995, 1996a). Biotite and plagioclase K-Ar ages of 15.3 ± 0.8 Ma and 16.0 ± 0.8 Ma, respectively (Ferrusquía-Villafranca, 1992), date this tuff as middle Miocene. It should be noted that the Mitla Tuff is 5 m.y. younger than the Etla Tuff from the Valle de Oaxaca at Suchilquitongo, about 40 km to the west-northwest. This is significant to understand the evolution of volcanism in Oaxaca (Ferrusquía-Villafranca, 1996a). The Matatlán Formation, a fluvio-lacustrine, largely tuffaceous, fine to course clastic unit, unconformably overlies the Mitla Tuff. The Matatlán fauna, a small but significant Barstovian mammal assemblage, was collected from several localities. An unfossiliferous, seemingly Late Tertiary conglomerate unit and Quaternary deposits complete the Cenozoic sequence.

PALEONTOLOGIC REMARKS: Ferrusquía-Villafranca (1990b) reported the mammal record known at that time, which included a camelid, a protoceratid, a tylopod, a rhinocerotid, and *Merychippus* sp. (Ferrusquía-Villafranca, 1990b: pl. 2) Subsequent work by this writer and students, V. M. Bravo-Cuevas and E. Jiménez-Hidalgo, has greatly improved the record. Carnivorans were found for the first time in this area, and they include a large felid (*Pseudaelurus* size, fig. 13.5A–B), a canid (fig. 13.5E), and a mustelid cf. *Leptarctus* sp. (fig. 13.5C–D), the second Barstovian mustelid of Mexico. Rodents were evidenced by extensive gnaw-marks present on large mammal bones. New artiodactyls include the camelid cf. *Protolabis* sp., the leptomerycid cf. *Pseudoblastomeryx* sp., and two pecorans. The perissodactyl record adds *Merychyppus* cf. *M. sejunctus* (fig. 13.6), and *Pliohippus* aff. *P. pernix*.

Leptarctus, *Protolabis*, and *Pseudoparablastomeryx* are long-lived (Hemingfordian to Clarendonian), widespread North American genera (table 13.2; Baskin, 1998; Honey et al., 1998; Webb, 1998). *Merychippus sejunctus* is largely known from Barstovian strata in Colorado, California, and Florida (Hulbert and McFadden, 1991; MacFadden, 1998), whereas *Pliohippus pernix*, although known in the Barstovian, is better represented in the Clarendonian of the Central Great Plains and Texas (table 13.2; Quinn, 1955; Webb, 1969; MacFadden, 1998). There are also Hemphillian records of *P. pernix* in Central Mexico (Carranza-Castañeda and Espinosa Arrubarrena, 1994; Miller and Carranza-Castañeda, 1998).

The Barstovian age of the Matatlán fauna hinges upon the stratigraphic position of the fossil-bearing strata, derived from the underlying Mitla Tuff, and the geochronologic ranges of the taxa involved. The coexistence of seemingly less derived and more derived equid species suggests, among other things, the presence of factors that allowed the survival of the less derived species. All these records extend the known geographic range of the above-mentioned taxa southward, from temperate North America to northern Middle America (Oaxaca, Southeastern Mexico).

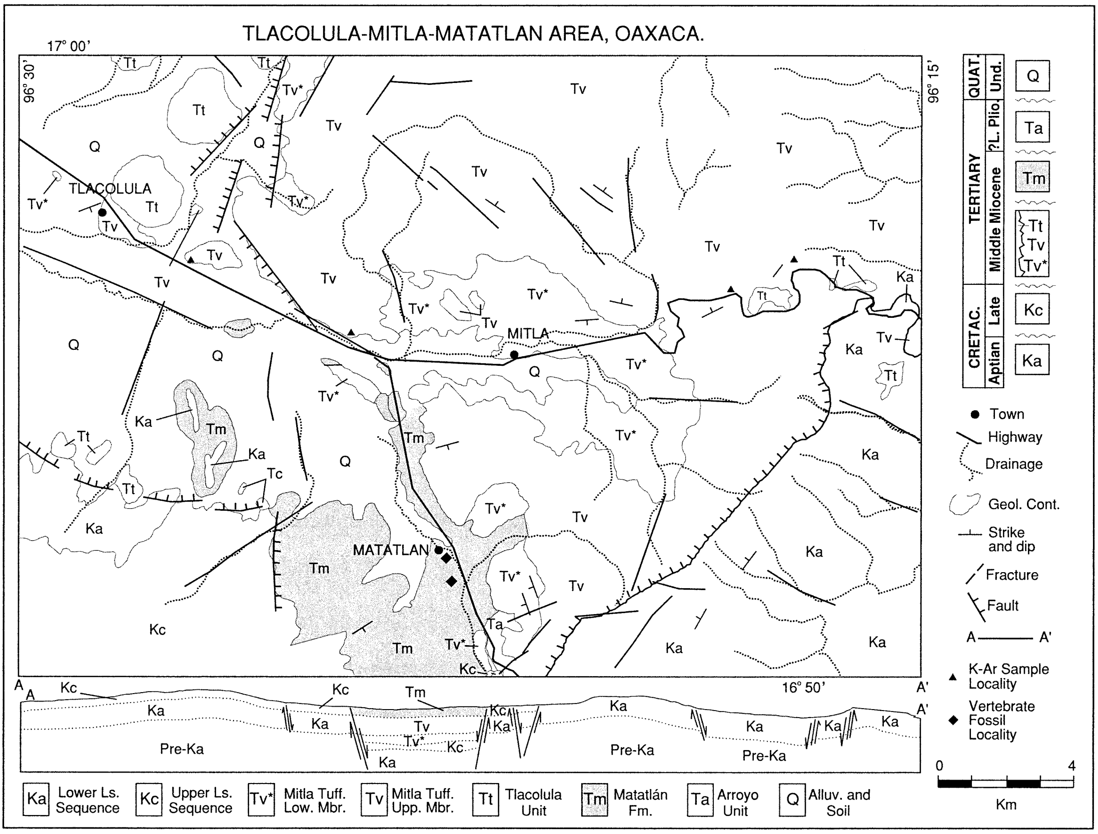

Fig. 13.4. Geologic map and generalized structural section of the Tlacolula-Mitla-Matatlán Area, Central Oaxaca.

The Nejapa Fauna, El Camarón Formation, Southeastern Oaxaca

Geologic Setting: The area lies between 16°30′–16°40′ N Lat. and 95°55′–96°10′ W Long.; the territory is very rugged (fig. 13.7). The Pre-Cenozoic basement, represented by an unnamed metamorphic unit, unconformably underlies the Cenozoic sequence. The basal unit is the Early Tertiary, red phyllarenitic Limón Conglomerate. An extensive Miocene pyroclastic succession, the Yautepec Tuff, blankets most of the area (Ferrusquía-Villafranca, 1990d). This Tuff has yielded biotite and plagioclase K-Ar ages, 15.0 ± 0.8 and 17.4 ± 0.8 Ma, respectively (Ferrusquía-Villafranca, 1992), that allow it to be dated as middle Miocene. The Tuff intertongues and partly underlies rhyolitic lava flows. The chief structure developed in this unit is a small, rectangular graben where the overlying El Camarón Formation is largely preserved (fig. 13.7). Evidence of intertonguing between these units is discernible in the western graben margin; therefore, El Camarón is syntectonic and largely coeval with the Yautepec Tuff. El Camarón Formation chiefly consists of fluvio-lacustrine, fine- to medium-grained tuffaceous clastics, and has yielded mammal remains (the Nejapa Fauna) at several localities, which allow it to be dated as early Barstovian. A thin Late Tertiary sandstone and Quaternary deposits complete the Cenozoic sequence.

Paleontologic Remarks: The Nejapa fauna includes El Gramal, El Camarón, and other local faunas collected from El Camarón Formation. The first two were the only ones known up to 1990. They include the mustelid *Plionictis oaxacaensis*, a rodent, a camelid, a protoceratid, an antilocaprid, *Merychippus*

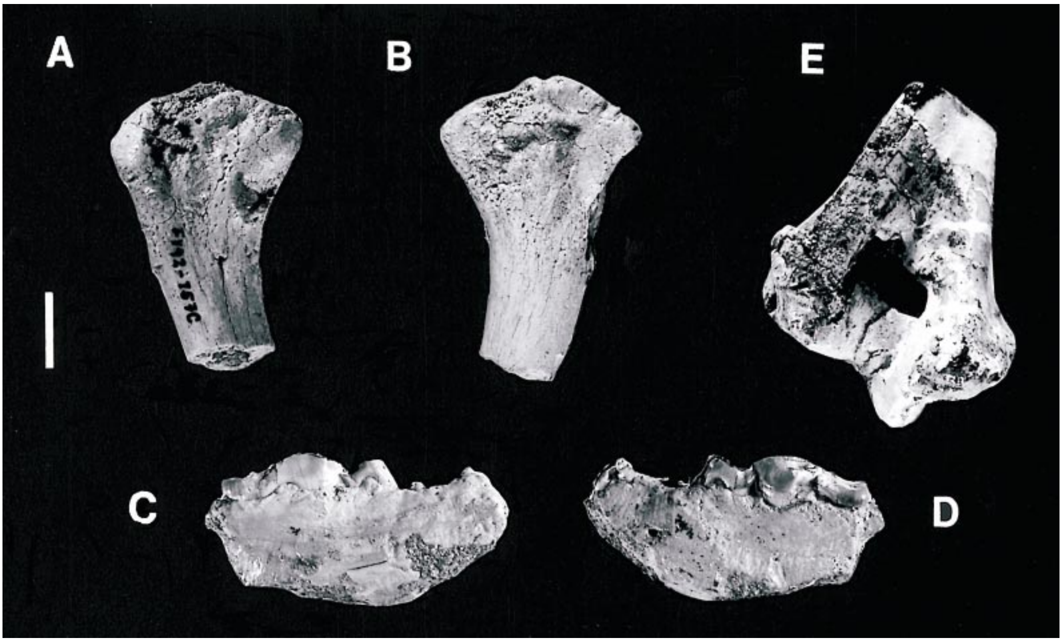

Fig. 13.5. Felidae, gen. et sp. indet.: **A, B,** Mesial and lateral views of proximal right metacarpal fragment, IGM 7962. Cf. *Leptarctus* sp.: **C, D,** Mesial and lateral views of a left ramus with p2–p3 roots and p4–m1, IGM 7963. Canidae, gen. et sp. indet.: **E,** Posterior view of distal left humerus fragment, IGM 7964. All Matatlán Formation (Barstovian), Municipio de Matatlán, Oaxaca; white bar indicates 1 cm.

sp., and *Gomphotherium* sp. (Ferrusquía-Villafranca, 1990b: fig. 5, pls. 3, 4). *Plionictis oaxacaensis* is the southernmost Tertiary carnivoran record in North America. *Merychippus* sp. has a complex occlusal pattern, similar to that of hipparionine horses. The camelid limb bone fragments, referred to *Oxydactylus* sp. by Stirton (1954), are indeterminate at the generic level.

Current research adds the following taxa: an *Aelurodon*-sized canid, the tayassuid cf. *Prosthennops* sp. (fig. 13.8A–B), the camelids cf. *Pliauchenia* sp. (fig. 13.8C–D), cf. *Procamelus* sp. (fig. 13.8E), and cf. *Protolabis* sp., two pecorans, the antilocaprid *Merycodus sabulonis* (fig. 13.9A–B), the equids *Merychippus* cf. *M. primus* (fig. 13.9C–D), *M.* cf. *M. sejunctus, M.* cf. *M. californicus* (fig. 13.10A–C), *Neohipparion* aff. *N. trampasense* (fig. 13.10D–E), *Calippus* sp. (fig. 13.11A–C), and *Pliohippus* aff. *P. pernix* (fig. 13.11D–F), and a rhinocerotid (fig. 13.12A–B).

Prosthenops, Procamelus, Pliauchenia, and *Protolabis* are long-lived (largely Barstovian to Hemphillian) and widespread genera in temperate North America (Honey et al., 1998; Wright, 1998). Elsewhere, these genera have been reported from the Hemphillian of Guanajuato and Hidalgo, Central Mexico (Miller and Carranza-Castañeda, 1984; Carranza-Castañeda and Miller, 2000), and of Honduras and El Salvador in Central America (see table 13.2; Olson and McGrew, 1941; Savage and Russell, 1983; Webb and Perrigo, 1984; Honey et al., 1998; Wright, 1998). It should be noted that the *Pliauchenia* from the Hemphillian of Guanajuato, Central Mexico (Dalquest and Mooser, 1980) is now assigned to *Alforjas* (Montellano-Ballesteros, 1989).

The equids show a diversity similar to that observed in faunas of the Great Plains and the Gulf Coastal Plain (Quinn, 1955; MacFadden, 1998). They include small and large horses with simple and complex occlusal patterns of the cheek teeth. These features indicate a fine partitioning of the adaptive

Fig. 13.6. *Merychippus* cf. *M. sejunctus*, palate with left and right P2–M2 and anterior half of RM3, IGM 7965, Matatlán Formation (Barstovian), Municipio de Matatlán, Oaxaca; white bar indicates 1 cm.

zone. The coexistence of merychippine, hipparionine, and equine species living around 15.5 Ma in the tropics of northern Middle America, as disclosed by the Nejapa record (table 13.2), poses evolutionary and biogeographic questions not fully addressable here (but see below). At least two hypotheses could be proposed: (a) Repeated migration events brought diversified equids from temperate North America to Middle America or (b) horses underwent extensive differentiation in Middle America during the Miocene, and spread to the north. Both hypotheses need testing.

THE IXTAPA LOCAL FAUNA, IXTAPA FORMATION, WEST CENTRAL CHIAPAS

GEOLOGIC SETTING: The rugged area located about 25 km east of Tuxtla Gutiérrez, the state capital, lies between 16°45′–16°55′ N Lat. and 92°50′–93°00′ W Long. (Ferrusquía-Villafranca, 1996b: fig. 1 and pl. I). The pre-Cenozoic basement includes the Aptian-Albian Sierra Madre Limestone and the Turonian-Campanian Angostura Formation, which constitute the horsts that bound the graben (seemingly a strike-slip basin) where the Tertiary sequence occurs. This is a very thick sedimentary pile consisting of the Soyaló (marine, Paleocene-Early Eocene), El Bosque (continental, Middle Eocene), San Juan (marine, Late Eocene), Masaniló (marine and transitional, Oligocene), Modelo (marine, Early Miocene), Río Hondo (marine and transitional, Early Middle Miocene), Coyolar (mostly transitional), and Ixtapa (continental, Middle Miocene) formations (Ferrusquía-Villafranca, 1996b). This sequence records transgressive and regressive events occurring in Chiapas during most of the Tertiary. The Quaternary Punta de Llano Formation and sedimentary deposits unconformably overlie the Tertiary sequence.

The fossil-mammal-bearing unit is the Ixtapa Formation, which consists of rhyolitic ashflow and ashfall tuffs interbedded by tuffaceous, fluvio-lacustrine clastics and calcilithitic conglomerates. Tuff strata located some 200 m above mammal horizons yielded biotite and plagioclase K-Ar ages of 15.2 ± 0.35 and 16.02 ± 0.53 Ma, respectively (Ferrusquía-Villafranca, 1996b, sample FV88–545), which permits them to be assigned to the middle Miocene.

PALEONTOLOGIC REMARKS: The Ixtapa local fauna includes a probably new species of *Cormohipparion* (Ferrusquía-Villafranca, 1990c: pl. 1), somewhat close in degree of hypsodonty and occlusal pattern to *C. occidentale*, from the Barstovian of the West Coast (MacFadden, 1998, and references therein). The other perissodactyl is the rhinocerotid cf. *Teleoceras* sp. This is a long-lived genus (late Hemingfordian to late Hemphillian) in temperate North American (Prothero, 1998b, and references therein). Elsewhere, *Teleoceras* is known from the Hemphillian of Guanajuato, Central Mexico (Carranza-Castañeda, 1988) and Honduras, Central America (Webb and Perrigo, 1984).

The Ixtapa record also includes the proboscidean *Gomphotherium* sp., which has a very simple molar occlusal pattern (Ferrusquía-Villafranca, 1990c: pl. 2) reminiscent of that seen in *G. obscurum*, the most primitive species of *Gomphotherium* (Osborn, 1936). Also a long-lived genus in temperate North America (Tedford et al., 1987; Lambert and Shoshani, 1998), *Gomphotherium* is known only from the Barstovian Nejapa Fauna of Oaxaca, Southeastern Mexico. Other gomphotheriids, though, are known from the Hemphillian of Central Mexico (Miller and Carranza-Castañeda, 1984) and Honduras, Central America (Frick, 1933; Olson and McGrew, 1941; Webb and Perrigo, 1984; Lambert and Shoshani, 1998), as well as from the Blancan of Mexico (Miller, 1980; Carranza-Castañeda and Miller, 1984).

The chronostratigraphic ranges of the Ixtapa mammal taxa fall within the Barstovian–Blancan interval. However, the K-Ar ~15.5 Ma age of tuffs overlying the fossiliferous strata permits the fauna to be dated as Early Barstovian. This is significant because (a) the Ixtapa aff. *Cormohipparion* record antedates by at least one million years that of the United States *C. sphenodus*, a North American candidate as sister species of the Old World hipparionine radiation (MacFadden, 1998), and (b) the Ixtapa gomphothere is practically coeval to the earliest record of *Gomphotherium* in the United States (Lambert and Shoshani, 1998). This suggests a rapid spread of gomphotheres during the early Barstovian, or perhaps that the arrival of gomphotheres in North America from the Old World took place earlier than currently thought.

COMMENTS ON DIVERSITY, FAUNAL SUCCESSION, ECOLOGY, EVOLUTIONARY SIGNIFICANCE, AND BIOGEOGRAPHY

DIVERSITY

The combined Hemingfordian–Barstovian land mammal assemblage of Mexico (table 13.1) includes 6 of the 9 orders and 13 of the 38 families known to occur in North America for this interval (Tedford et al., 1987; Janis et al., 1998). This is noteworthy, given the small number of localities and the limited resources devoted to paleontological work. Therefore, insufficient sampling needs to be considered in pondering the significance of this assemblage, particularly in regard to deficiencies of the record.

The Hemingfordian Assemblage is much less diverse than the Barstovian one: carnivorans, rodents, and proboscideans are altogether absent. Within the artyodactyls, only four of the eight families recorded in the combined Hemingfordian–Barstovian assemblage are present (Tayassuidae, Merycoidontidae, Camelidae, and Protoceratidae), and of these, only the merycoidodonts are not recorded in the Barstovian. Equids, rhinocerotids, and camelids are present in both the Hemingfordian and Barstovian assemblages, although the equids and camelids are much less diverse in the former.

FAUNAL SUCCESSION

The Tertiary post-Barstovian record of land mammal taxa in Mexico is significantly greater. It includes most of the families and many of the genera that make up the combined Hemingfordian–Barstovian assemblage, plus other taxa such as insectivorans, xenarthrans, and caviomorph rodents (Miller, 1980; Ferrusquía-Villafranca and Carranza-Castañeda, 1981; Miller and Carranza-Cas-

TABLE 13.2

Geographic Distribution and Biogeochronologic Occurrence of Selected Land Mammal Taxa of North and Middle America

	North America										Middle America			
	United States								Mexico					
				Southwest			Southeast							
	NW	West	CGPL	CA	AZ	NM	TX	AGF	NMex	CMex	SEMex	SAL	HON	PAN
CARNIVORA														
1. Family Felidae									**He**	**He, Bl**				
Gen. & sp. indet.											Ba			
2. Family Mustelidae									**He**	**He, Bl**				
cf. *Leptarctus* sp.	Hm, Ba Cl	Ba	Hm, Ba Cl, He	Hm, Cl			Cl	Hm, Ba Cl			Ba			
Plionictis oaxacaensis		**Ba**	**Ba, Cl**	**Cl**							Ba			
3. Family Canidae									**He, Bl**	**He, Bl**				
Euoplocyon cf. *E. brachygnathus*	Ba	Ba	Ba	Ba				Hm	Ba					
Gen. & sp. indet.											Ba			
LAGOMORPHA														
4. Family Leporidae										**He**				
Hypolagus sonoranus	**Hm, Ba, Cl, He**	**Hm, Ba, Cl He, Bl**	**Hm, Ba Cl, He**	**Hm, Ba, Cl He, Bl**		**Bl**	**Hm, Cl He, Bl**	**Hm, Cl He, Bl**	Hm, **Bl**	**He**				
ARTIODACTYLA														
5. Family Tayassuidae									**He**	**He, Bl**				
"Prosthennops" xiphidonticus		Ba	Ba				Ba			Hm				
cf. *Prosthennops* sp.	Ba, Cl, He		Ba, Cl				Cl, He, Bl		He	He	Ba		He	
6. Family Merycoidodontidae														
Merychyus elegans		Hm	Hm	Hm				Hm		Hm				
Merychyus aff. *M. minimus*		Hm	Hm	Ar, Hm			Hm				Hm			
Merycochoerus sp.		Ar, Hm	Ar, Ba											Hm
7. Family Camelidae									**He**	**He, Bl**				
Aguascalientia wilsoni							Ar, Hm			Hm				
cf. *Pliauchenia* sp.	Cl		Ba, Cl	Ba, Cl		Ba					Ba			
cf. *Procamelus* sp.	Ba, Cl, He	Ba	Ba, Cl, He	Cl		Ba, He	Cl, He	Cl, He		He	Ba	He	He	
cf. *Protolabis* sp.	Hm, Ba, Cl	Hm, Ba	Ba-Cl	Ar, Hm, Ba, Cl	Ba, Cl	Hm, Ba	Cl			Ba	He	He		
Stenomylus tubutamensis	**Ar, Hm**	**Ar**	**Ar, Hm**		**Hm**	**Ar**	**Ar**		Hm					
Gen. & sp. indet.									Ba		Ba			
8. Family Protoceratidae														
cf. *Paratoceras* sp.							Ba, Cl				Hm			Hm
Gen. & sp. nov.		**Ar**	**Ar, Hm**					**He**			Hm			
? Protoceratidae gen. & sp. indet											Ba			

TABLE 13.2
(*Continued*)

	North America										Middle America			
	United States								Mexico					
				Southwest			Southeast							
	NW	West	CGPL	CA	AZ	NM	TX	AGF	NMex	CMex	SEMex	SAL	HON	PAN
ARTIODACTYLA (Continued)														
9. Family Leptomerycidae														
?*Pseudoparablastomeryx* sp.			?Hm, Ba,He			Ba	Ba				Ba			
10. Family Antilocapridae									**He**	**He, Bl**				
Merycodus sabulonis		Hm, Ba, Cl	Hm, Ba, Cl			Cl					Ba			
?Antilocapridae gen. & sp. indet.											Ba			
ORDER PERISSODACTYLA														
11. Family Equidae									**He**	**He, Bl**				
Archaeohippus sp.	Ba		Hm				Ar, Hm	Hm, Ba, Cl						Hm
Kalobatippus sp.	Ar	Ar	Ar, Hm				Ar, Hm	Hm, Ba						Hm
Merychippus cf. *M. primus*		Hm	Hm					Hm, Ba			Ba			
Merychippus cf. *M. sejunctus*		Ba					Ba				Ba			
Merychippus cf. *M. californicus*	Ba			Ar, Hm, Ba				Ba, Cl			Ba			
aff. *Cormohipparion* undescr.	Cl	Ba, He	Ba, Cl, He	Ba, Cl, He		Cl	Cl, He	Ba, Cl, He			Ba	**He**	**He**	
Neohipparion aff. *N. trampasense*	Cl		Hm, Ba, Cl	Cl			Cl, He	He	**He**	**He**	Ba			
Calippus sp.		Ba	Ba, Cl, He				Ba, Cl	Ba,Cl, He		**Bl**, He	Ba	He	He	
Pliohippus aff. *P. pernix*			Ba-Cl			Cl	Cl		**He**	**He**	Ba			
12. Family Rhinocerotidae									**He**	**He**				
Diceratherium sp.		Ar	Ar	Ar										**Hm**
cf. *Menoceras* sp.		Ar, Hm, Ba	Ar, Hm			Hm	Ar, Hm	A, Hm		Hm				
cf. *Teleoceras* sp.	He	Ba, Cl, Hb	Ba, Cl, He			Cl,He	Cl, He	He	Bl	He	Ba		He	
Gen. & sp. indet.											Ba			
ORDER PROBOSCIDEA														
13. Family Gomphotheriidae									**He, Bl**	**He, Bl**			**He**	
Gomphotherium sp.	Ba, Cl	Ba, Cl	Ba, Cl, He	Ba, Cl, He		Ba, Cl, He	Ba, Cl, He	Ba, Cl, He		He?	Ba			

Abbreviations: AGF, Alabama-Georgia-Florida; Ar, Arikareean; AZ, Arizona; Ba, Barstovian; Bl, Blancan; CA, California; CGPL, Central Great Plains; Cl, Clarendonian; CMEX, Central Mexico and the Trans-Mexican Volcanic Belt; He, Hemphillian; Hm, Hemingfordian; HON, Honduras; NM, New Mexico; NMEX, Northwestern and Northern Mexico; NW, The Northwest; PAN, Panama; SAL, El Salvador; SEMEX, Southeastern Mexico; TX, Texas. Boldface indicates that in the stated region, either (1) genus or species differs from the one listed in the taxa column, or (2) family includes genera not listed there.

Sources: (1) North America: Savage and Russell, 1983; Tedford et al., 1987; Baskin, 1998; Honey et al., 1998; Janis and Manning, 1998; Lambert and Shoshani, 1998; Lander, 1998; McFadden, 1998; Prothero, 1998a-1998b; Webb, 1998; and Wright, 1998. (2) Mexico: Bravo-Cuevas, 2000; Carranza-Castañeda, 1988; Carranza-Castañeda and Espinoza Arrubarrena, 1994; Carranza-Castañeda and Miller, 2000; Ferrusquía-Villafranca, 1990a, 1990b, 1990c; Jimenez-Hidalgo, 2000; Miller, 1980; Miller and Carranza-Castañeda 1982, 1984, 1998; Montellano-Ballesteros, 1989, 1997. (3) Central America: Olson and McGrew, 1941; Whitmore and Stewart, 1965; Webb and Perrigo, 1984.

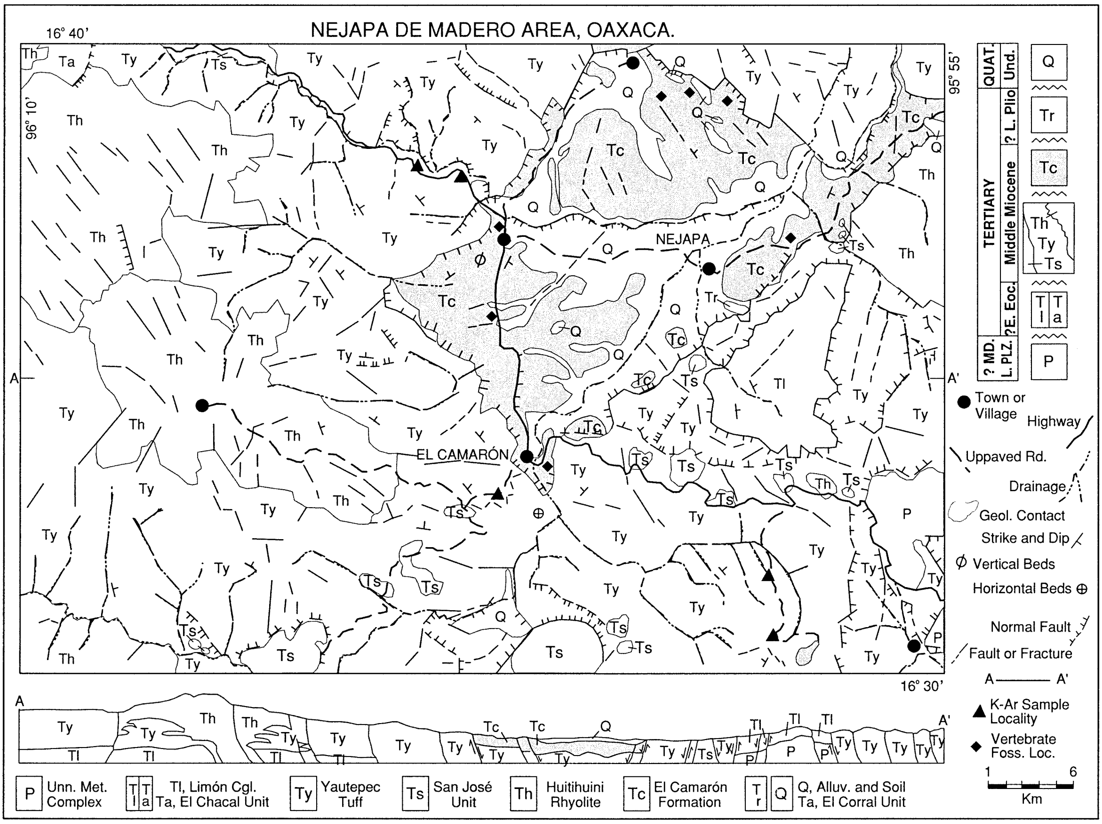

Fig. 13.7. Geologic map and generalized structural section of the Nejapa de Madero Area, Southeastern Oaxaca. Abbreviations as in figure 13.2.

tañeda, 1982, 1984, 1998; Carranza and Miller, 1988, 2000, and references therein). The relatively archaic taxa did not survive beyond the Barstovian.

A major gap in the Mexican record is the lack of Clarendonian land mammals. The scarce stratigraphic differentiation and limited paleontologic reconnaissance of Mexico's continental Tertiary may account for this absence. However, the lithostratigraphic information in the best known fossiliferous areas discloses the lack of demonstrably post-Barstovian, pre-Hemphillian strata there (Minch, 1967, Gastil et al., 1975, Miller, 1980, and Frizzel, 1984 for areas in Baja California; Lance, 1950, and Lindsay and Jacobs, 1984 for areas in Chihuahua; Carranza-Castañeda et al., 1994 for areas in Guanajuato; Wilson and Clabaugh, 1970, and Ferrusquía-Villafranca, 1990d for areas in Oaxaca; and Frost and Langenheim, 1974, Ferrusquía-Villafranca, 1996b, and Ferrusquía-Villafranca et al., 2000 for areas in Chiapas). Additional geologic and paleontologic work is needed to fill or explain the Clarendonian gap.

ECOLOGY

Southeastern Mexico's Barstovian, the richest middle Miocene record in Mexico, shows that mammals of this age and region belonged to an ecologically balanced community that included carnivores (at least one large felid, a medium-size canid, and medium to small mustelids) and a large assortment of browsers, grazers, and mixed-feeders, chiefly of medium to large size, belonging to no less than 10 families (table 13.1). This in turn is evidence of a fine partitioning of food resources and a wide variety of them. A scenario of juxtaposed areas with diverse

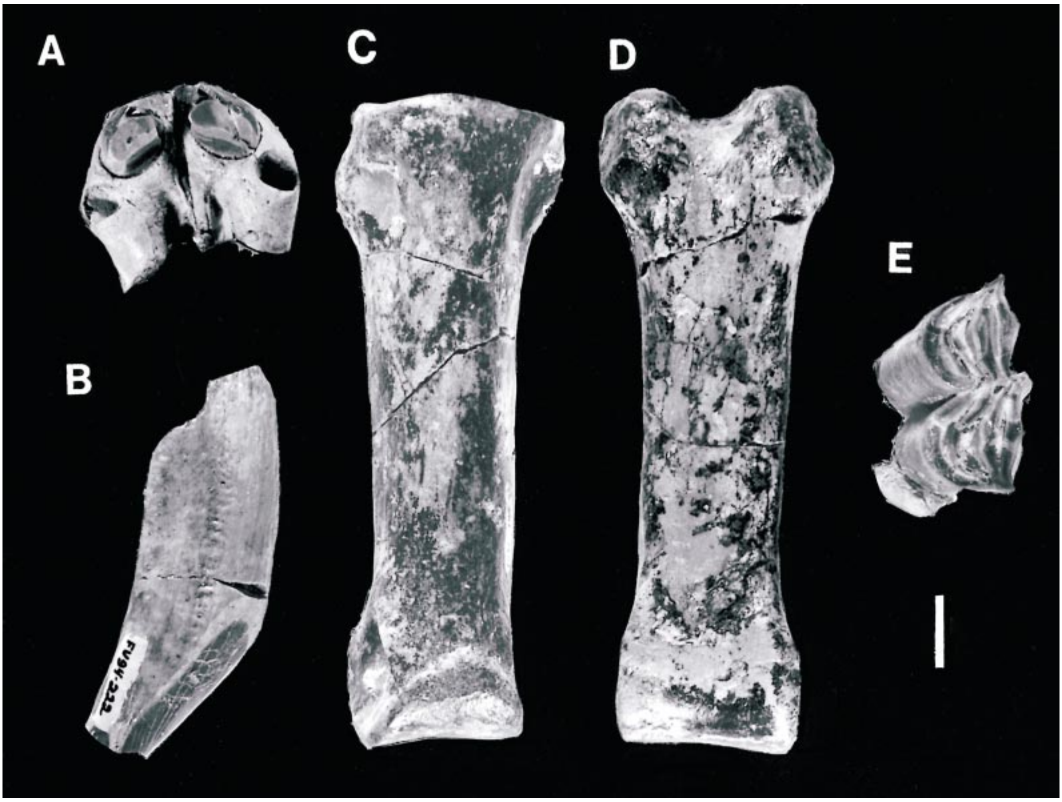

Fig. 13.8. Cf. *Prosthennops* sp.: **A,** Occlusal view of rostral tip with left and right I1, IGM 7966. **B,** Lateral view of a right upper canine, IGM 7967. Cf. *Pliauchenia* sp.: **C, D,** Anterior and posterior views of phalanx I, IGM 7968. Cf. *Procamelus* sp.: **E,** Occlusal view of left M2, IGM 7969. All El Camarón Formation (Barstovian), Municipio de San Carlos Yautepec, Oaxaca; white bar indicates 1 cm.

physical-geographic conditions could best provide the needed diversity of ecological factors (including food resources). Present-day Southeastern Mexico, with its complex geologic makeup and physiographic features as well as a tapestry of climatic zones broadly set within the tropics, fits this scenario. A similar setting could confidently be inferred as prevailing during the middle Miocene (Morán-Zenteno, 1984; Sedlock et al., 1993).

Camelids and equids are the most diverse herbivorous mammals. The number of coexisting equid species in the Barstovian of Oaxaca (table 13.1) is similar to that recorded in Clarendonian faunas from the Central Great Plains and the Texas Gulf Coastal Plain (Quinn, 1955; Webb, 1969; Savage and Russell, 1983; Tedford et al., 1987; MacFadden, 1998), and is somewhat larger than that of Barstovian faunas from these and other regions in North America (MacFadden, 1984, 1998). Differences in overall individual size and in cheek-tooth features would diminish competition for food resources, thus allowing the coexistence of several equid species in Southeastern Mexico. The Barstovian equid record of Oaxaca is evidence of these characters.

EVOLUTIONARY SIGNIFICANCE

The coexistence in Southeastern Mexico of Barstovian merychippine, hipparionine, and equine horses (tables 13.1, 13.2) is paradoxical to say the least. *Merychippus* cf. *M. primus*, a taxon closely related to the ancestry of the Hipparionini and Equini (Stirton, 1940; MacFadden, 1984, 1998; Hulbert, 1987, 1988, 1989; Hulbert and MacFadden, 1991), would have roamed Southeastern

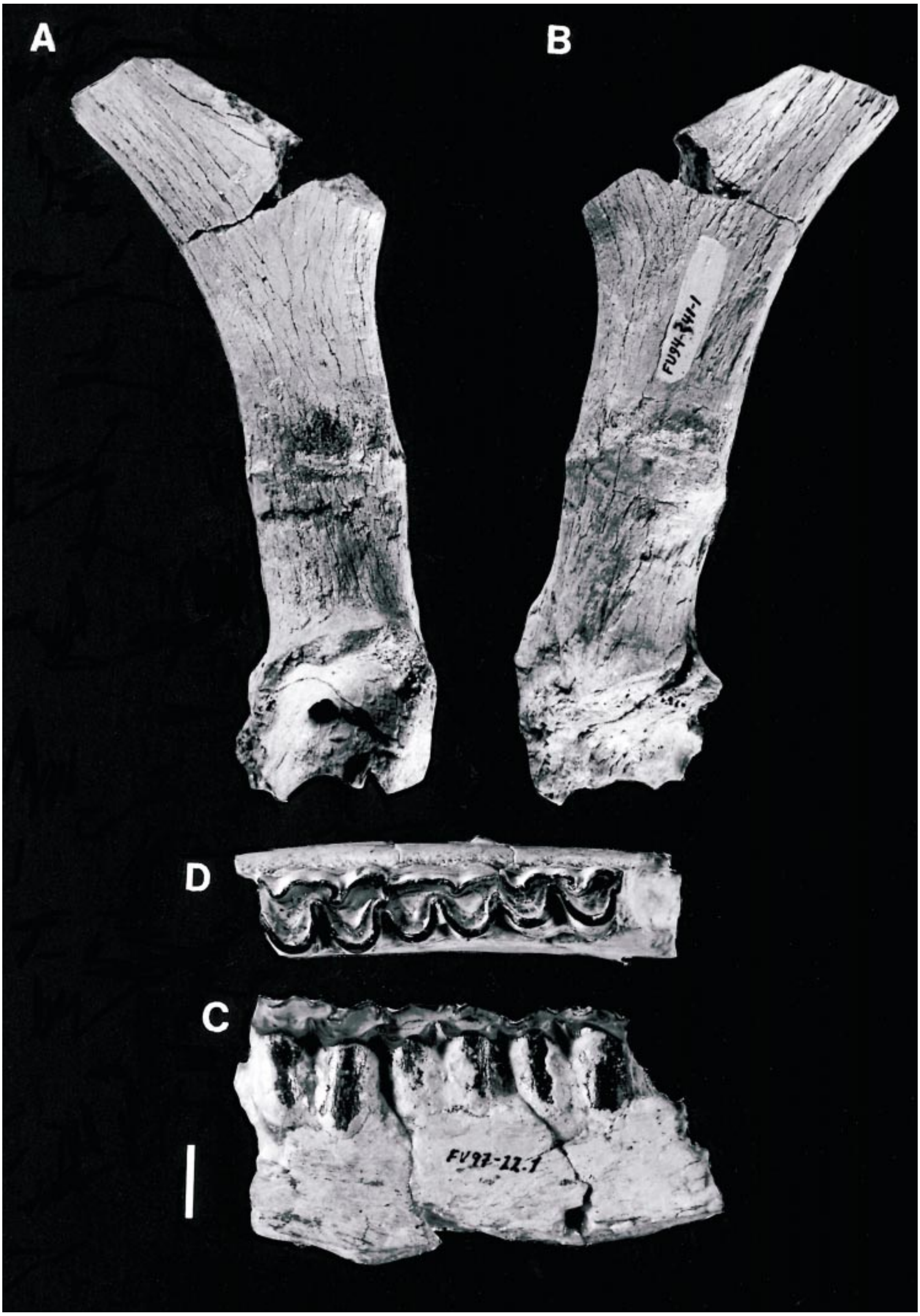

Fig. 13.9. *Merycodus sabulonis*: **A, B,** Lateral and mesial views of basal right horn core fragment, IGM 7970. *Merychippus* cf. *M. primus*: **C, D,** Lateral and occlusal views of left ramus fragment with p4–m2, IGM 7971. All from El Camarón Formation (Barstovian), Municipio de San Carlos Yautepec, Oaxaca; white bar indicates 1 cm.

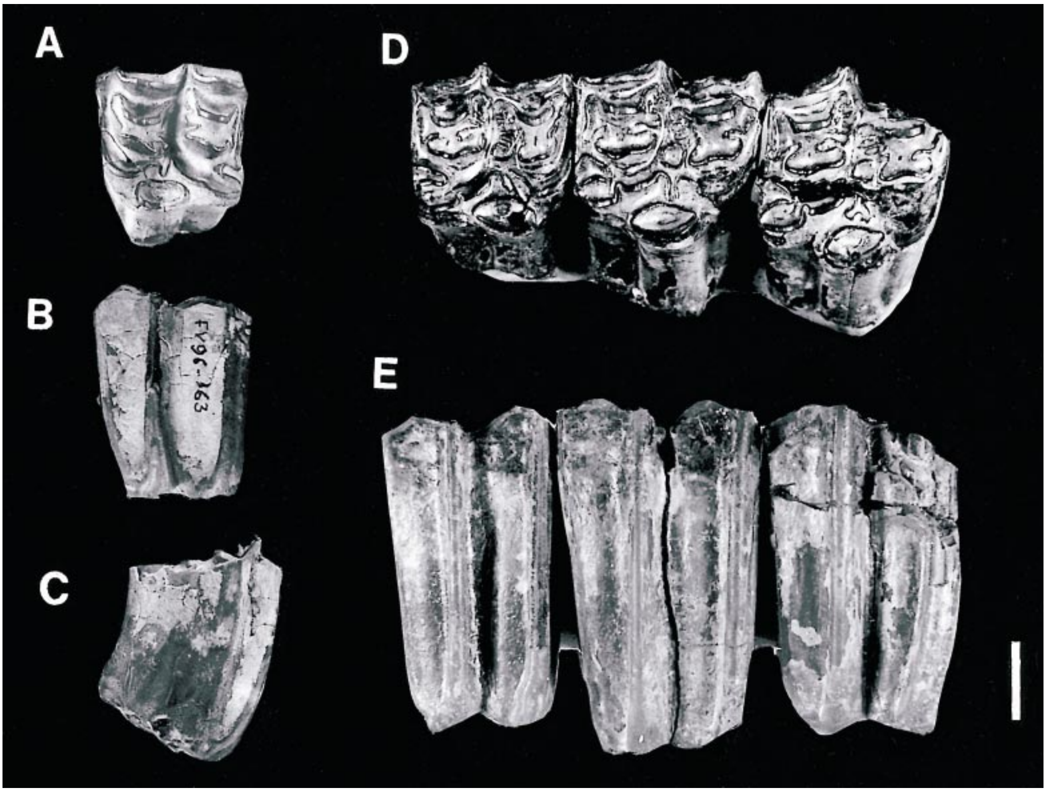

Fig. 13.10. *Merychippus* cf. *M. californicus*: **A–C,** Occlusal, labial, and posterior views of left M1 (medium wear), IGM 7972. *Neohipparion* aff. *N trampasense*: **D, E,** Occlusal and labial views of a putative P3–M1 series; (D) is a real left image and (B) is a virtual right image, IGM 7973. All El Camarón Formation (Barstovian), Municipio de San Carlos Yautepec, Oaxaca; white bar indicates 1 cm.

Mexico during the Barstovian (ca. 15.5 Ma), sharing the region with derived hipparionines (cf. *M. sejunctus*, cf. *M. californicus*, aff. *Cormohipparion* sp., *Neohipparion* cf. *N. trampasense*) and equines (*Calippus* sp. and *Pliohippus* aff. *P. pernix*).

It appears that this combination of equid species is not present in any Barstovian local or regional fauna from temperate North America (table 13.2; MacFadden, 1998, and references therein). *Merychippus primus* for instance, is only known from the Hemingfordian of the Great Basin and the Central Great Plains, and from the Hemingfordian and Barstovian of the Gulf Coastal Plain. Some of the same or closely related hipparionine and equine species are known from Barstovian, Clarendonian, and Hemphillian faunas from several regions of temperate North America. *Neohipparion*, *Calippus*, and *Pliohipus* are also known from the Hemphillian of Mexico (table 13.2; Miller and Carranza-Castañeda, 1998).

These facts suggest at least two biogeographic hypotheses: (a) Merychippini–Hipparionini–Equini cladogenetic differentiation took place in temperate North America–Old World, some of the resulting lineages nearly instantaneously dispersing southward to reach Middle America very soon after origination, or (b) at least part of this differentiation occurred in (tropical) Middle America, with the resulting lineages migrating northward. The physiographic complexity of Southeastern Mexico could have provided enough diversity and local isolation to allow survival of ancestral species and coexistence with derived ones.

The new kyptoceratine genus and species from the Hemingfordian of Southeastern

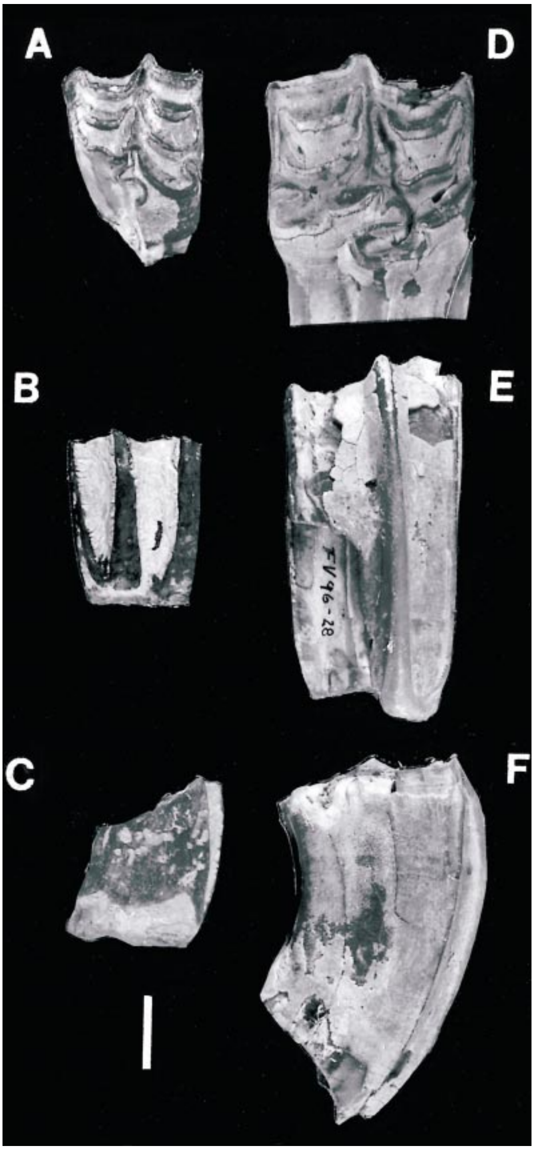

Fig. 13.11. *Calippus* sp.: **A–C,** Occlusal, labial, and posterior views of left M1 (medium wear), IGM 7974. *Pliohippus* aff. *P. pernix*: **D–F,** Occlusal, labial, and posterior views of right P4, IGM 7975. All El Camarón Formation (Barstovian), Municipio de San Carlos Yautepec, Oaxaca; white bar indicates 1 cm.

Mexico, and the floridatraguline *Aguascalientia wilsoni*, from the Hemingfordian of Central Mexico, strongly suggest that some mammalian lineages evolved in southern North America, perhaps in Middle America as well, migrating from there northward to temperate North America. This was proposed independently by Stevens (1977) and Webb (1981).

BIOGEOGRAPHY

Table 13.2 summarizes the biogoechronologic and geographic occurrence of selected land mammal taxa known to be present in temperate North America (represented by the United States) and either Mexico, Central America, or both. The purpose is to detect patterns of occurrence and to assess the biogeographic significance of the Mexican Hemingfordian and Barstovian assemblages. Seven orders of land mammals are recorded in the Middle Miocene of Middle America. However, carnivorans, rodents, lagomorphs, and proboscideans are absent, not only from the Miocene, but from the whole Tertiary of Central America. Seven of the 13 named families known to occur in the Miocene of Middle America (Felidae, Mustelidae, Canidae, Leporidae, Leptomerycidae, Antilocapridae, and Gomphotheriidae), have their southernmost North American record in Mexico; the others extend their geographic range to Central America (Merycoidontidae and Protoceratidae, Hemingfordian; Equidae and Rhinocerotidae, Hemingfordian and Hemphillian; Tayassuidae and Camelidae, Hemphillian).

Sixteen of the 27 named genera present in the middle American Miocene have their southernmost American record in Mexico (table 13.2); 11 extend their geographic range to Central America: *Merycochoerus* and *Paratoceras*, the first records of oreodonts and protoceratids outside the United States and Canada; the browsing equids *Archaeohippus* and *Kalobatippus* (formerly *Anchitherium*, Whitemore and Stewart, 1965) and the rhinocerotid *Diceratherium*, all three from the Hemingfordian of Panama; and the tayassuid *Prosthennops*, the camelids *Procamelus* and *Protolabis*, the grazing equids *Calippus* and *Pliohippus*, and the rhinocerotid *Teleoceras*, all from the Hemphillian of Honduras and El Salvador.

Although *Anchitherium* and *Kalobatippus* are morphologically close, there are enough differences in the skeleton, precise age oc-

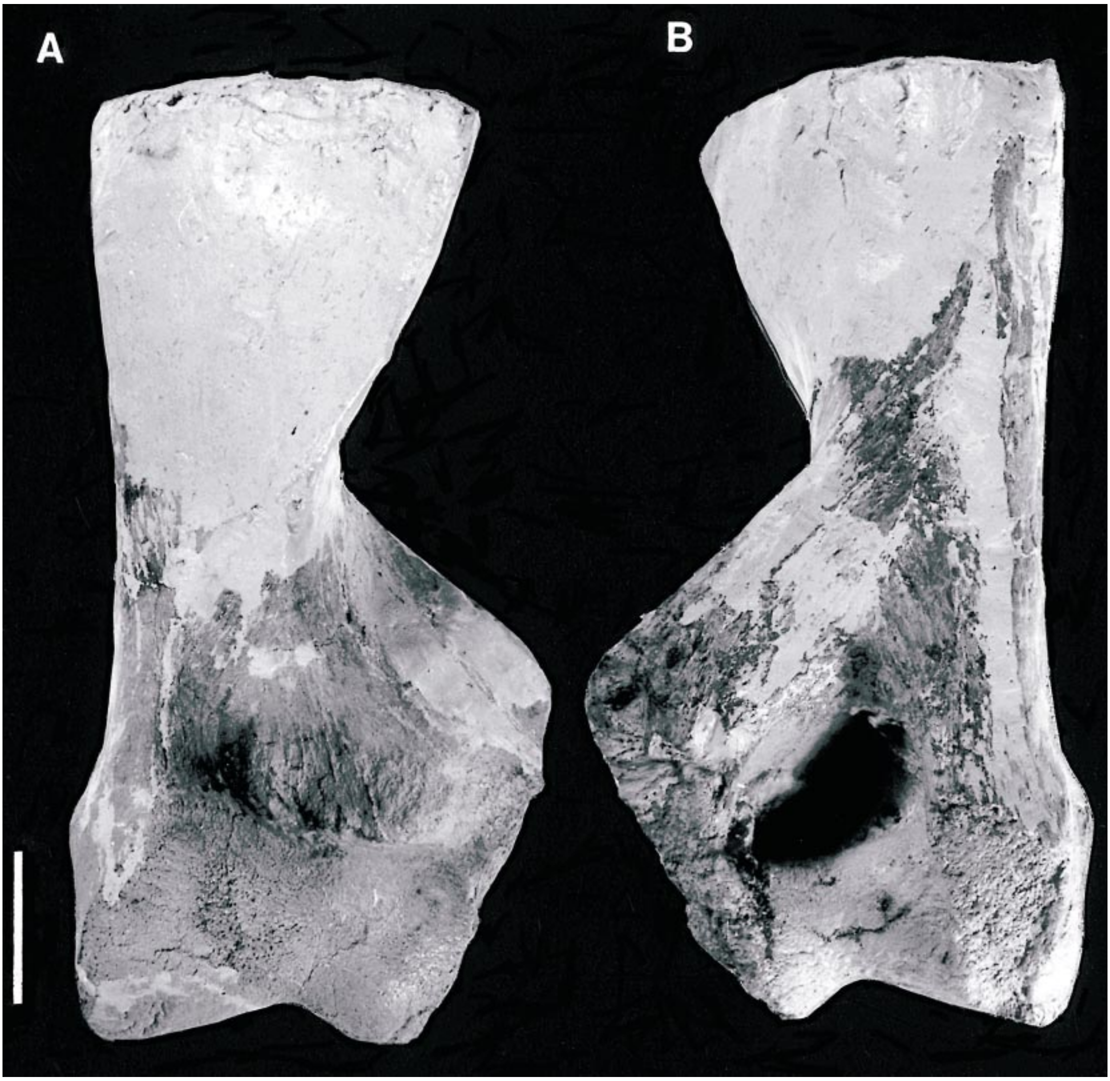

Fig. 13.12. Rhinocerotidae, gen. et sp. indet.: **A, B,** Anterior and posterior views of distal left humerus fragment, IGM 7976, El Camarón Formation (Barstovian), Municipio de San Carlos Yautepec, Oaxaca; white bar indicates 3.1 cm.

currence, and geographic distribution to warrant their taxonomic distinction (Abusch-Siewert, 1983; MacFadden, 1998). Under this interpretation, *Kalobatippus* is regarded as the Early Miocene primitive anchithere of the American Continent (see table 13.2).

The known middle and late Miocene (Hemingfordian–Hemphillian) land mammal assemblage from Mexico–Middle America consists wholly of North American taxa. Not even the Hemingfordian fauna from Panama includes a single taxon from South America. This indicates that a biogeographic barrier (probably marine), effectively prevented migration between Middle and South America during the Tertiary, up to the very Late Miocene (latest Hemphillian), when it was no longer effective, allowing the beginning of the Great American Faunal Interchange (Patterson and Pascual, 1972; Ferrusquía-Villafranca, 1977; Marshall, 1985, 1988; Kowallis et al., 1998).

However, the recent discovery in Amazonian Peru of gomphotheriids, tayassuids, tapirids, and camelids from strata below a pyroclastic bed Ar-Ar dated as 9.01 ± 0.28 Ma (Campbell et al., 2000, and oral commun.), demands the presence of these families in Clarendonian age or older deposits of Middle America. All but the tapirids have already been recognized in the Barstovian of Southeastern Mexico (i.e., in northern Middle America), which is consistent with this contention. The presence of such taxa further south in Central America during the Barstovian and later is quite possible, as attested by the Hemphillian tayassuid and camelid records from Honduras and El Salvador. The Peruvian discovery, once fully documented, would establish a much earlier age for the beginning of at least the southward component of the Great American Faunal Interchange, and it already provides an important additional stimulus to continue paleontological work in Middle America.

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