

IMPORTANCE OF LATE TERTIARY CARNIVORES AND EQUIDS FROM THE TRANSMEXICAN VOLCANIC BELT

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ABSTRACT

Intensive field work in central Mexico over the past two decades has resulted in the discovery of many hundreds of Blancan and Hemphillian age mammalian fossils. Among the most interesting and useful of the taxa recovered are the carnivores and equids. Both have proven valuable as chronologic indicators. The equids especially provide information allowing a reasonable determination of environmental conditions throughout central Mexico for the late Tertiary. Sites producing both mammalian carnivores and equids extend from southernmost Baja California Sur to eastern Hidalgo, and mark the most southern localities in North America known to produce most of them. Carnivora genera thus far identified are *Osteoborus*, *Canis*, *Agriotherium*, *Machairodus*, *Pseudaelurus* (Hemphillian), and *Borophagus*, *Cerdocyon*, cf. *Trigonictis*, cf. *Mustela*, and *Felis* (Blancan). Equid genera recognized include *Calippus*, *Dinohippus*, *Neohipparion*, *Nannippus* and *Astrohippus* (Hemphillian), and *Nannippus*, *Equus* (Blancan). Both earliest and latest occurrences of taxa within each of the two groups can possibly be found in Mexico. *Canis* and *Equus* probably have their earliest records here. The latest occurrences of *Osteoborus*, *Agriotherium*, *Machairodus*, *Pseudaelurus*, *Calippus*, *Dinohippus*, and *Astrohippus* seem to be in central Mexico.

Key words: Carnivore, equid, Blancan, Hemphillian, Guanajuato, Mexico.

RESUMEN

En los últimos veinte años, se ha realizado un intenso trabajo de campo en las cuencas sedimentarias del centro de México. El resultado, es el descubrimiento de cientos de fósiles de mamíferos que representan las dos edades de mamíferos, Henfiliano y Blancano. De los taxa descubiertos, los más importantes y útiles como índices estratigráficos son los carnívoros y los équidos. Especialmente, los équidos proporcionan una razonable información de las condiciones ambientales durante el Terciario tardío en el centro de México. Las localidades que contienen los dos grupos, carnívoros y équidos, se encuentran desde la parte meridional de Baja California Sur hasta el estado de Hidalgo, y representan las localidades más meridionales en América del Norte que contienen estos taxa.

Los géneros de carnívoros determinados hasta ahora para el Henfiliano son: *Osteoborus*, *Canis*, *Agriotherium*, *Machairodus*, *Pseudaelurus*. En las localidades del Blancano, *Borophagus*, *Cerdocyon*, cf. *Trigonictis*, cf. *Mustela*, y *Felis* (Blancano).

Los équidos que han sido descritos para el Henfiliano de México son *Calippus*, *Dinohippus*, *Neohipparion*, *Astrohippus* y *Nannippus*. En las localidades del Blancano, se han determinado *Nannippus* y *Equus*.

Es posible encontrar en el centro de México, el primer y último registro de estos taxa. *Canis* y *Equus* probablemente tienen sus primeros registros en estas localidades. Los últimos registros en América del Norte de *Osteoborus*, *Agriotherium*, *Machairodus*, *Pseudaelurus*, *Calippus*, *Dinohippus* y *Astrohippus*, provienen del centro de México.

Palabras clave: Carnívoros, équidos, Blancano, Hemphilliano, Guanajuato, México.

INTRODUCTION

Central Mexico, as defined here, covers an east-west belt from about 19–22° north latitude. While southernmost Baja California Sur presently lies slightly north of this zone, during the late Tertiary it was situated within it (Smith, 1991).

With the exception of Baja California Sur, the late Tertiary mammalian carnivores and equids listed in this paper were mostly recovered within the above defined belt between the Sierra Madre Occidental and Sierra Madre Oriental in the Cen-

tral Mexican Highlands (Figure 1). These fossils, along with other vertebrates of this age, come primarily from alluvial sediments. Recent field work has demonstrated that the Hemphillian and Blancan fossil-bearing deposits occur in north-south trending grabens that apparently extend across central Mexico from the state of Hidalgo west to Baja California Sur (Carranza-Castañeda *et al.*, 1994; Carranza-Castañeda and Miller, 1996a,b). This graben complex is situated in mid-Tertiary andesites and is part of the Transmexican Volcanic Belt. Following Woodburne (1987), the chronologic range of the Hemphillian runs from 8.2 to 4.6 Ma, and that of the Blancan 4.6 to 1.8 Ma.

Presently the fossiliferous areas throughout central Mexico are mostly in Sonoran desert. However, the late Tertiary fauna from this region generally reflects warm, humid conditions in a savanna setting (Miller and Carranza-Castañeda, 1984). This

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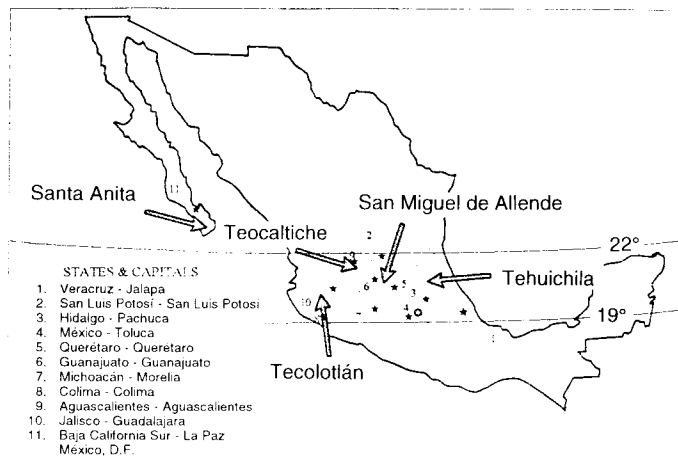


Figure 1. Index map showing states and localities discussed in this paper.

differs from the conditions set forth by Webb (1976, 1978) for regions above 30° north latitude. In these articles evidence was presented to show that a previous woodland savanna biota changed to one of steppe or grassland conditions by late Hemphillian time. If fossil floras could be found in late Tertiary deposits of central Mexico, especially those containing vertebrates, a more accurate climatic picture could be obtained.

Northern as well as central Mexico contains numerous exposures of potentially fossil-bearing deposits of late Tertiary age. Paleontological field work in these regions is still in a beginning stage. The central states of Aguascalientes, Querétaro and San Luis Potosí, while capable of producing significant numbers of fossils, have not yet received in-depth attention. South of central Mexico, the vegetative cover effectively prohibits extensive collecting, even though late Tertiary strata may exist at the surface. Hidalgo has yielded few fossils due to such cover. In the more heavily vegetated eastern state of Veracruz only one taxon has been found to our knowledge, an unreported find of *Teleoceras* (Applegate, personal communication).

HISTORY OF PALEONTOLOGICAL STUDIES

The vast majority of articles pertaining to late Cenozoic mammals from central Mexico includes descriptions and/or discussions relating to the Pleistocene. Articles providing information on late Tertiary mammalian faunas from this region are rare prior to the last two decades. Even more rare are those in which mammalian carnivores of this age have been described or discussed. One of the earliest descriptions of a late Tertiary mammal from Mexico appears to be that of Falconer (1863 in Osborn, 1936), wherein he described a new species of *Rhynchotherium*, *R. tlascalae*. A few other mammals of this age, including equids, were reported by various authors (e.g., Leidy, 1882; Cope, 1884, 1886) who had specimens sent to them, but did not examine the sites from which they came. Not until Freudenberg (1910) described a lower first molar of a bear, *Hyaenarctos* (= *Agriotherium*) from Tehuichila was a late Tertiary mammalian carnivore reported from Mexico.

By the mid 1900's coordinated collecting of late Cenozoic mammals from Mexico was underway (e.g., Stock, 1948). Much of this work was done through the California Institute of Technology (C.I.T.) in the northern part of the country. These collections are now housed at the Natural History Museum of Los Angeles County. The most productive late Tertiary sites explored were in Chihuahua, and constitute the taxonomically diverse and abundant *Yepómera* fauna (s.l.) of late Hemphillian age. This fauna is especially rich in horses. While some carnivore taxa were recovered, very little information about them has been published (Drescher, 1939; Lance, 1950). Lindsay (1984) provided a table listing late Tertiary faunas, including carnivores and equids from northern Mexico. Because of their much greater abundance as well as their importance, many more articles have been written about equids (e.g., Arellano and Azcon, 1949; Carranza-Castañeda, 1991, 1992, 1994; Carranza-Castañeda and Espinosa-Arrubarrena, 1994; Carranza-Castañeda and Ferrusquía, 1979; Lance, 1950; Leidy, 1882; Miller, 1980; Miller and Carranza-Castañeda, 1984; Mooser and Dalquest, 1975).

In 1951 Arellano made a brief report of several late Cenozoic fossiliferous deposits in central Mexico. In this article he mentioned his making a collection of Hemphillian mammalian fossils at El Ocote in the San Miguel Allende district within the state of Guanajuato. Three equid genera were identified: *Neohipparion*, *Nannippus*, and *Pliohippus*. Two carnivores were listed, an unidentified canid and saber-toothed cat. This appears to be the first indication of late Tertiary carnivores from central Mexico since Freudenberg's (1910) report. It was not until the 1970s that what might be considered the modern era of vertebrate paleontological research in Mexico got underway. It began with a systematic study of Cenozoic vertebrate sites in central Mexico by scientific personnel from the Instituto de Geología at the Universidad Nacional Autónoma de México. This work received its initial impetus by Ismael Ferrusquía-Villafranca and those influenced by him. He wrote what can be considered a landmark paper (Ferrusquía-Villafranca, 1978) in his compilation of known Cenozoic vertebrate localities.

In 1974 a project was initiated under the auspices of the above named Instituto wherein Oscar Carranza-Castañeda began a thorough paleontological as well as stratigraphic study of late Cenozoic, mostly Hemphillian and Blancan, strata in the state of Guanajuato. With the assistance of various students and technicians from the Instituto de Geología, and Harley Garbani (affiliated with the Natural History Museum of Los Angeles County), this work intensified and expanded. After his study of a Blancan age vertebrate locality in southern Baja California Sur in the mid 1970s, the first author of this paper joined the above personnel in the aforementioned project. This project has now grown to include numerous late Tertiary vertebrate localities in the states of Baja California Sur, Jalisco, Michoacán, Guanajuato, and Hidalgo. Attention also has been directed to the stratigraphic context in which all fossils are recorded, something rarely done prior to the 1970s.

LATE TERTIARY CARNIVORES

BLANCAN

Prior to 1980 there were no unequivocal descriptions of Blancan age terrestrial vertebrate faunas in Mexico (Miller, 1980). However, Freudenberg (1910) discussed a canid, *Hyaenognathus* (= *Borophagus*) from near Tequixquiac in the state of Mexico, where both Pliocene and Pleistocene mammals had been collected. A giant ground squirrel, *Paemarmota*, from near the village of La Goleta in northern Michoacán was described by Repenning (1962). He said that it might be either Blancan or Hemphillian in age, but that the undescribed La Goleta fauna was tentatively assignable to the Hemphillian. Of the animals listed, none were carnivores.

In the earliest description of a Blancan age fauna from Mexico, Miller (1980) discussed the paleontology and geology of a locality near the town of Santa Anita in southernmost Baja California Sur. A moderately diverse fauna, the Las Tunas local fauna, was described. It consists of 20 vertebrate taxa including three mammalian carnivore species: *Borophagus*, ?*B. diversidens*, ?*Machairodus* sp., and *Felis*, ?*F. lacustris*. Torres-Roldán (1980) reported a new species of canid, *Cerdocyon avius*, from Blancan deposits near those previously yielding the Las Tunas local fauna. He considered this species as ancestral to the living South American form. Field work in southern Baja California Sur by the present authors has uncovered additional Blancan age terrestrial vertebrate sites several kilometers north of the Las Tunas site. While negligible collecting has yet been done here, the likelihood of some mammalian carnivores being found is very promising.

During the past two years the current authors with the assistance of others have been doing field work in the state of Jalisco, especially near the town of Tecolotlán. Although several sites have produced late Tertiary vertebrates, only one is tentatively identified as Blancan; the others are Hemphillian. Of the meager ?Blancan fauna recovered to date, no carnivores exist.

While many hundred Blancan age mammals have been recovered from the state of Guanajuato, surprisingly few are carnivores. Only four taxa thus far occur. Two of these have been formally described: *Felis* cf. *F. studeri* (Carranza-Castañeda and Miller, 1996b) and *Borophagus diversidens* (Miller and Carranza-Castañeda, in press). The other two have yet to be described and consist only of isolated teeth. Tentative identifications ascribed to these are cf. *Mustela* and cf. *Trigonictis* (Table 1). Given the wealth of other species identified from many productive localities in Guanajuato, additional carnivores should soon be added as collecting continues.

Vegetative cover in Hidalgo as mentioned above restricts fossil recovery there. Nevertheless, some of the earliest discoveries of late Tertiary fossils from Mexico have come from this state. Recovery of fossils here was due to development of coal mines and prospects near the villages of Tehuichila and Zietla in the 1800s. Limited collecting has produced a few Blancan as

well as Hemphillian age mammals. The only Blancan carnivores thus far recognized are questionably identified, a bear, *Tremarctos*, and a canid, *Borophagus*. More extensive collecting is planned, and should result in a more diverse fauna, including additional carnivores.

HEMPHILLIAN

Mammalian carnivores from Mexico of Hemphillian age, like those of the Blancan, are only very poorly known. Exceptionally few descriptions and/or discussions can be found in the literature for those of either age. Aside from Freudenberg's 1910 report of *Hyaenarctos*, Hemphillian age Carnivora from central Mexico were not adequately discussed before the 1980s (Miller and Carranza-Castañeda, 1984). Not until the 1970s was collecting of late Tertiary terrestrial vertebrates done using meaningful stratigraphic controls.

To date four central Mexican states have yielded Hemphillian mammalian carnivores: Jalisco, Aguascalientes, Guanajuato, and Hidalgo. Recent collecting in the central part of Jalisco has produced a small but significant fauna of this age. However, only two carnivores occur in it thus far, a bear questionably assigned to the genus *Agriotherium*, and *Osteoborus cyonoides*. The latter was described by Montellano-Ballesteros (in press). Current and anticipated field work in the productive areas identified in Jalisco should soon add to the diversity of this fauna.

Only a few late Tertiary vertebrates have been collected in the state of Aguascalientes to our knowledge. *Osteoborus* cf. *O. cyonoides* represents the only carnivore. It exists in a private collection, and so far has not been made available for study. The specimen consists of a partial skull and right dentary both with full dentition. It was viewed by one of us (Carranza-Castañeda).

Most of the Hemphillian carnivore specimens from central Mexico have been collected in Guanajuato. The earliest discussions of those known at the time were made by Dalquest and Mooser (1980). However, the discussions were very brief and no stratigraphic positions were given. In this report *Osteoborus*, cf. *O. Cyonoides*, ?*Indarctos*, and *Machairodus* sp. were identified from El Ocote. Additional material collected here and at several other Hemphillian sites in Guanajuato using stratigraphic controls has been added to the carnivore fauna. Also, subsequent finds indicate that the bear listed above is probably *Agriotherium* and not *Indarctos*. A site 10 km west of El Ocote produced a partial upper and lower dentition of *Agriotherium schneideri*, a Hemphillian index fossil (Miller and Carranza-Castañeda, 1996). A few additional specimens of *Osteoborus cyonoides* also come from Guanajuato sites (Miller and Carranza-Castañeda, in press). Hemphillian felids from this state thus far identified are *Machairodus*, cf. *M. coloradensis*, and *Pseudaelurus*, ?*P. intrepidus* (Table 1). Based on the numbers of Hemphillian age mammals recovered from many localities in Guanajuato, and their diversity, additional carnivore taxa should occur.

Table 1. Faunal listing of late Tertiary Carnivora from Central Mexico (largely the Transmexican Volcanic Belt).

Taxon	Age	Type of Material	Locality	Selected Published References
Family Ursidae				
<i>Agriotherium</i> cf. <i>schneideri</i>	Hemphillian	lower first molar	Tehuichila, Hidalgo	Freudenberg, 1910
? <i>Agriotherium</i> sp.	Hemphillian	upper canine	El Ocote, Guanajuato	Dalquest and Mooser, 1980
<i>Agriotherium schneideri</i>	Hemphillian	partial maxilla and dentary	Northeastern Guanajuato	Miller and Carranza-Castañeda, 1996; Carranza-Castañeda, 1992
? <i>Agriotherium</i> sp.	Hemphillian	partial canine	Tecolotlán, Jalisco	unpublished
Family Canidae				
<i>Osteoborus cyonoides</i>	Hemphillian	dentary with partial dentition	Teocaltiche, Jalisco	Montellano-Ballesteros, in press
<i>Osteoborus</i> cf. <i>cyonoides</i>	Hemphillian	partial skull and dentary with dentition	Aguascalientes	unpublished
<i>Osteoborus</i> cf. <i>cyonoides</i>	Hemphillian	P ⁴ , M ₁	El Ocote, Guanajuato	Dalquest and Mooser, 1980
<i>Osteoborus cyonoides</i>	Hemphillian	maxillary fragment with P ⁴ -M ² , two M's, incomplete dentary with P ₄ -M ₃	El Ocote and Rinconada,	Miller and Carranza-Castañeda, in press
<i>Canis ferrox</i>	Hemphillian	Skull and dentary with incomplete dentition, and several postcranial bones	Northeastern Guanajuato	Miller and Carranza-Castañeda, in press
Family Felidae				
<i>Machairodus</i> sp.	Hemphillian	M ₁	El Ocote, Guanajuato	Dalquest and Mooser, 1980
<i>Machairodus</i> cf. <i>coloradensis</i>	Hemphillian	canine, P ⁴ and two dentaries with dentitions	Northeastern Guanajuato	Carranza-Castañeda and Miller, 1996b
<i>Pseudaelurus ?intrepidus</i>	Hemphillian	maxilla with P ^{3,4} , and an isolated P ⁴	El Ocote, Guanajuato	Carranza-Castañeda and Miller, 1996b
Family Canidae				
<i>Borophagus matthewi</i>	Blancan	incomplete palate with dentition	Near Tequixquiác, Mexico	Freudenberg, 1910
<i>Borophagus ?diversidens</i>	Blancan	jaw fragment with M ₁ and incomplete dentary with P ₃ -M ₂	Near Santa Anita, Baja California Sur, Mexico	Miller, 1980
<i>Borophagus diversidens</i>	Blancan	incomplete dentary with P ₃ -M ₁	Northeastern Guanajuato	Miller and Carranza-Castañeda, in press
<i>Cerdocyon avius</i>	Blancan	M ¹ , nearly complete dentary with dentition and several postcranial bones	Near Santa Anita, Baja California Sur, Mexico	Torres-Roldán, 1980
Family Mustelidae				
cf. <i>Mustela</i> sp.	Blancan	P ⁴	Northeastern Guanajuato	unpublished
cf. <i>Trigonictis</i> sp.	Blancan	right and left M ¹	Northeastern Guanajuato	unpublished
Family Felidae				
<i>Felis ?lacustris</i>	Blancan	P ³ , partial P ⁴ , incomplete femur and tibia	Near Santa Anita, Baja California Sur, Mexico	Miller, 1980
<i>Felis</i> cf. <i>studerii</i>	Blancan	anterior rostrum with partial dentition and isolated P ³	Northeastern Guanajuato	Miller and Carranza-Castañeda, 1996

LATE TERTIARY EQUIDS

BLANCAN

Apparently, the first record of a fossil horse was made in 1882 by Leidy; wherein he briefly described *Hippotherium montezuma* (= *Nannippus peninsulatus*) from a site near the village of Tehuichila in the state of Hidalgo. Carranza-Castañeda and Espinosa-Arrubarrena (1994) indicated that *Nannippus montezuma* might be a separate species, but that the evidence suggests a strong possibility that *N. montezuma* could be a synonym of *N. peninsulatus*. MacFadden (1984a) considered that this species was restricted to the Blancan and hence an index fossil for this age. *N. peninsulatus* specimens, although not common, occur at several localities in central Mexico. Most of the known material has been recovered from the states of Hidalgo and Guanajuato, with rare specimens coming from Michoacán and Jalisco.

The genus *Equus*, as generally agreed upon by most researchers on late Cenozoic equids (e.g., Lindsay *et al.*, 1980; MacFadden, 1984b; Dalquest, 1988; Hulbert, 1993), evolved from *Dinohippus mexicanus*. In 1980 Miller reported *E. simplicidens* from southernmost Baja California Sur, which presumably is one of the oldest records of this genus (Azzaroli and Voorhies, 1993). More recently, specimens collected from different localities on the Mexican mainland appear intermediate in their characters between these two taxa. All equid fossils assignable to *Equus* from Blancan age deposits have been referred to *E. (Dolichohippus) simplicidens*. And, according to Azzaroli and Voorhies (1993), *E. simplicidens* may be assumed to be the common ancestor of all later species of *Equus*. This of course includes all the living horses. Fossils of this taxon are more abundant in central Mexico than those of *Nannippus peninsulatus*. Most have been collected in the state of Guanajuato, but specimens have also been found in Michoacán, and Baja California Sur as mentioned above.

HEMPHILLIAN

Both diversity and abundance of equids are much greater in the Hemphillian than in the Blancan for central Mexico, as well as elsewhere in North America. The least well represented genus in Hemphillian age deposits of central Mexico is *Calippus*. *C. castilli* (new combination of names; Carranza-Castañeda and Espinosa-Arrubarrena, 1994) apparently is the only species present. To date only a few teeth have been discovered from the states of Guanajuato and Hidalgo. *Calippus* importance lies in its being one of the two earliest equids known from central Mexico (*Dinohippus interpolatus* is the other), occurring in lower Hemphillian sediments.

In 1886 Cope described *Hippotherium rectidens* on the basis of a single cheek tooth from the Tehuichila local fauna. After a series of nomenclatural changes, this taxon is now regarded as *Neohipparion eurystyle* (Carranza-Castañeda and Espinosa-Ar-

rubarrena, 1994). Basically, this species is recognized from late Hemphillian age deposits on relatively numerous specimens from sites in Hidalgo and Guanajuato. It may have replaced *Calippus* as it appears in faunas immediately after *Calippus* disappears.

Astrohippus stockii, the forerunner of the ass according to Dalquest (1988), is an abundant equid in Hemphillian sediments of central Mexico (and in the Yepómera fauna; Lance, [1950]). It constitutes the most numerous horse taxon by far in Mexico during the late Hemphillian. And it also surpasses all nonequid species in numbers of specimens. In the El Ocote local fauna of Guanajuato, the most abundant Hemphillian fauna known from central Mexico, *Astrohippus* fossils account for more than 60% of the equid material collected. *A. stockii* is a constituent of all significant Hemphillian sites throughout the central states. According to Baskin (1991), *Astrohippus* is restricted to the late Hemphillian.

Nanippus minor, unlike *Astrohippus*, is uncommon in Hemphillian age strata of central Mexico. Even in the rich El Ocote local fauna where it is best known, fossils of this species comprise only about 5% of the equids present. Thus far *N. minor* is unknown outside the state of Guanajuato in central Mexico. It may be that the southern portion of central Mexico was the southernmost limit of this species. *N. minor* has only been found in late Hemphillian age deposits to date, and apparently became extinct at the end of this time.

A rare equid taxon in central Mexico is *Dinohippus interpolatus*. However, the scarcity of this early *Dinohippus* species may be mostly the result of few early Hemphillian age exposures in central Mexico. Thus far *D. interpolatus* has only been recovered at one site in Guanajuato (La Presa) and one site in Hidalgo (Zietla). Whether *D. interpolatus* is ancestral to *D. mexicanus*, or even should belong to this genus (MacFadden, 1984b), has yet to be determined. Nevertheless, its joint occurrence with *Calippus* in central Mexico reasonably defines an early Hemphillian age.

Dinohippus mexicanus, while best represented anywhere in the Yepómera fauna of northern Mexico, is well represented in central Mexico, mostly occurring at several sites in Guanajuato. Chief among these is the Rancho El Ocote locality. *D. mexicanus* has also been recovered from Jalisco near Tecolotlán (Carranza-Castañeda and Miller, 1996a), but has thus far not been recognized in other central Mexican states. It is a biochronologically important species, known only to occur in late to latest Hemphillian age deposits. Phylogenetically, it has great importance as the probable ancestor of the genus *Equus*.

CONCLUSIONS

Analyses of late Tertiary mammalian faunas from central Mexican states indicates that carnivores are decidedly under represented as a group; both as to numbers and diversity. This is despite the fact that collecting of late Cenozoic vertebrates has taken place for about two centuries. The paucity of some faunas logically provides but few or no carnivores. However, the rea-

sonably well sampled Guanajuato faunas should contain more than have been collected. We know of no reason for such limited numbers considering the care taken in collecting. Undoubtedly, planned extensive collecting in Baja California Sur, Jalisco, Guanajuato, and Hidalgo should significantly increase the number of mammalian carnivore specimens as well as other late Tertiary taxa.

During Blancan time in Mexico, as in other parts of the world, equids show a pronounced diminution of species and presumably of numbers. This must reflect significant environmental changes that were transpiring in most global regions. A conservative estimate is that at least six species of horses lived in central Mexico within the Hemphillian age interval as opposed to just two for the Blancan. Unlike carnivores, equids are well represented at many late Tertiary localities in central Mexico. In some instances they constitute over 75% of the recovered fauna. These equids make excellent biochronological indicators for both Hemphillian and Blancan age deposits.

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