THE EARLY-LATE HEMPHILLIAN (HH2) FAUNAL ASSEMBLAGE FROM JUCHIPILA BASIN, STATE OF ZACATECAS, MEXICO, AND ITS BIOCHRONOLOGICAL CORRELATION WITH OTHER HEMPHILLIAN FAUNAS IN CENTRAL MEXICO

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ABSTRACT. A fairly extensive fossil collection was recovered from the sediments in the central part of the Juchipila graben, which represents the oldest Hemphillian (HH2) mammalian faunal assemblage so far documented in central Mexico. A large number of fossils of the equid Calippus (Grammohippus) bondarensis were used to correlate the Juchipila local fauna with other isolated Hemphillian records in central Mexico. A skull fragment collected in Juchipila may be referred to Dinobippus mexicanus based on the dental structures; however, the fossil is significantly different from other samples of D. mexicanus of the late Hemphillian faunas of central Mexico, as it lacks a dorsal preorbital fossa in the facial region.

The discovery of Cosoryx in central Mexico extends the geographic distribution and stratigraphic range of a genus formerly regarded as characteristic of the Clarendonian faunas of California, Nebraska, and New Mexico. Cosoryx in Juchipila is clearly associated with an HH2 fauna. A partial skull of Plioceros found at the study area is the only HH2 fossil known in a site located 1000 miles south of the Great Plains. The presence of Alfhorias is the oldest in central Mexico. Likewise, a third metatarsal of Pliometanastes is the only record of this megahonychid in Mexico that has a well-documented stratigraphic position and locality.

A set of NNE-to NNW-trending major grabens and half-grabens occur at the southern end of the Sierra Madre Occidental in central Mexico. Our reconnaissance work has shown that at least three of the structures (Juchipila, Tlaltenango, and Jalostotitlan), graben-fill sedimentary sequences with late-early Hemphillian (HH2) vertebrate faunas exist. Zircon separated from ash-fall beds interlayered with the fluvi al and/or lake sediments, as well as the fossil faunas, indicate that during the late Miocene and early Pliocene (U-Pb, 6.95-5.59 Ma), the structural basins were partly occupied by extensive freshwater lakes that supported their shores a rich and diverse vertebrate fauna. A fairly extensive fossil collection recovered from the sediments in the easternmost structure, the Juchipila graben, represents the oldest Hemphillian (HH2) mammalian faunal assemblage so far documented in central Mexico. The Juchipila fauna is a key to establishing the biostratigraphic correlation of Hemphillian faunas of central Mexico.

RESUMEN. Se recolectó una abundante asociación de mamíferos fósiles en los sedimentos de la parte central del graben de Juchipila, que representa la fauna del Hemphílano (HH2) más antigua que hasta ahora se conoce en el centro de México. El material abundante recolectado del equido Calippus (Grammohippus) bondarensis fue primordial para correlacionar con los registros previos en faunas del centro de México. Un fragmento de cráneo fue colectado en la cuenca de Juchipila; con base en las estructuras de sus molares fue asignado a Dinobippus mexicanus. Sin embargo el especimen presenta importantes diferencias con otros ejemplares de D. mexicanus de faunas del Hemphílano tardío del centro de México como la ausencia de la DPOF en la región facial.

El descubrimiento de Cosoryx en el centro de México extiende la distribución geográfica y rango estratigráfico de éste género formalmente considerado extinto de las faunas del Clarendoniano de California, Nebraska y Nuevo México. Cosoryx en Juchipila está asociado con faunas referidas al lo más temprano del Hemphílano tardío (HH2). Un fragmento de cráneo referido a Plioceros fue recolectado en el área de estudios éste junto con un cuerno de Sphenophalos son los únicos registros que se conocen en una fauna que existió en un área ubicada a unos mil quilométros en la parte meridional de las Grandes Placencias. El registro de Alfhorias taylori es el más antiguo en el centro de México. Asimismo, un MTIII de Pliometanastes es el último registro de este megahonychido en México del cual se conoce su nivel estratigráfico y localidad.

Existe un sistema de cuencas tectónicas con dirección NNE a NNW en la parte sur de la Sierra Madre Occidental en el centro de México. Los trabajos de reconocimiento en la región han demostrado que en tres de estas estructuras (Juchipila, Tlaltenango, Jalostotitlan) hay secuencias sedimentarias que contienen faunas de vertebrados referidos a lo más temprano del Hemphílano tardío. Los zircos que se han separado de las cenizas volcánicas interestratificadas con los sedimentos fluvio-lacustres y la fauna de mamíferos contenida en esta secuencia, han demostrado que durante el Mioceno tardío y el Plioceno temprano (U-Pb, 6.95-5.59 Ma) estas cuencas fueron parcialmente ocupadas por lagos de agua dulce extensos en donde una gran diversidad de mamíferos encontraron el suministro para sus condiciones de vida. El descubrimiento de la fauna de Juchipila ha sido fundamental para establecer la correlación biostratigráfica de las faunas del Hemphílano del centro de México.

INTRODUCTION

Paleontological research conducted over the last 30 years in several late Cenozoic continental sedimentary basins of central Mexico has contributed to the understanding of important biological and geological events. Up to now, most of the published information has been derived from detailed studies of fossil vertebrate localities in the San Miguel de Allende Basin and, to a lesser extent, from the Tecolutlán Basin (Carranza-Castañeda, 2006; Fig. 1). Together, these basins have produced
Figure 1  Mexican localities of Hemphillian age.

The largest and most diverse vertebrate faunas from the late Hemphillian and early Blancan North American land mammal ages (NALMAs) in Mexico. One of the most significant facts derived from these mammal assemblages is the presence of South American immigrants that are more than 1 million years older than similar occurrences elsewhere in North America (Carranza-Castañeda and Miller, 2004). The occurrence of the hog-nosed skunk Conepatus, an immediate ancestor of skunks that dispersed to South America (Wang and Carranza-Castañeda, 2008), and the presence of Blancan camelids from the San Miguel de Allende Basin suggest that diversification in several mammalian lineages took place in central Mexico (Ferrusquia-Villafranca, 2003; Woodburne et al., 2006; Woodburne, 2010; Jimenez-Hidalgo and Carranza-Castañeda, 2010). These contributions to the knowledge of the evolution and migration of the mammals during the Hemphillian and Blancan NALMAs reveal the importance of research in the late Cenozoic continental sedimentary basins of central Mexico.

On the other hand, there are a few reports of older faunal assemblages (early-late Hemphillian [Hh2]) discovered in isolated areas during reconnaissance work, such as Zietla in the Zacualtipan Basin of the state of Hidalgo (Carranza-Castañeda, 1994), Landa de Matamoros in the state of Queretaro (Miller and Carranza-Castañeda, 1998b; Carranza-Castañeda, 2006), and Santo Domingo in the Tlaltenango-Colorlan Basin at the border of Jalisco and Zacatecas states (Carranza-Castañeda, 2006; Miller and Carranza-Castañeda, 2001; Fig. 1). All of these local faunas were referred to Hh2 mainly because of the presence of the equid Calippus. However, until now, these faunas have remained isolated, lacking clear biostratigraphic correlations among them.

One of the most important paleontological events in the late Cenozoic history of America is the Great American Biotic Interchange (GABl), an intense faunal exchange following geographic connection of the previously isolated North and South American continents. The GABl occurred after the formation of the Panamanian Isthmus, which acted as a land bridge allowing dispersal of terrestrial mammals in both directions. This phenomenon was recognized based on the fossil records of mid-latitude of North America in the southern Great Plains and West Coast of the United States (Stehli and Webb, 1985). Based on these findings, it has been proposed that the Panamanian land bridge became permanently established in the period between 2.4 (Webb, 1997) and 3.0 million years ago (e.g. Marshall, 1985), although the initial closing of the Central American Seaway was mediated by other minor exchanges of faunal elements. Thus, in the view of Woodburne (2010), the records of South American immigrants recovered in central Mexico must be considered as evidence that this region acted as a holding pen for the earlier waves of immigrants. It must be pointed out that while the holding pen concept construes the age difference among the first arrivals in central Mexico and southern United States, it does not offer a satisfactory explanation as to why the early immigrants stopped in central Mexico as to our knowledge there was no topographic or ecologic barriers between these regions.

In the context of the GABl, in addition to establishing the isotopic ages of the first immigrants, it is important to search for
evidence about the routes followed by migrating South American mammals across the highlands of central Mexico (i.e., the Trans Mexican Volcanic Belt, the Mesa Central, and the southern ends of the Sierra Madre Occidental and Oriental, respectively; Fig. 2A and B) in order to reach and colonize as far north as the southern Great Plains of North America as well as Florida and southern California. The details of this interchange, which profoundly modified faunas and environments in both North and South America as well as the geographic distribution of Neotropical immigrants in central Mexico, are still largely unknown, as there are at least 1000 miles between central Mexico and the southern Great Plains that are paleontologically unexplored. Notable exceptions are an isolated report of Hemphillian remains found at Rancho Santa Rosa, state of Sinaloa (Maldonado-Koerrell, 1954), and the classic Mexican late Hemphillian fauna of Yopemora in northwest Chihuahua (Fig. 1). Thus, to fill these gaps in our knowledge, it is necessary to extend research efforts to other late Cenozoic continental basins in the states of Tamaulipas, Coahuila, Durango, Chihuahua, Sonora, and Baja California (Fig. 1).

Our recent research focused on the Juchipila Basin, one of the largest and most prominent tectonic features in the southern end of the Sierra Madre Occidental, just north of the Trans Mexican Volcanic Belt (Fig. 2C). The goals of our work were to 1) discuss in broad terms the geological setting of the area, 2) document the diversity of the local mammalian fauna, 3) determine the local biostratigraphy, and 4) establish the biochronologic correlation between the local faunas and other Neogene faunas known from central Mexico, particularly from the San Miguel de Allende and Tecolutlan basins (Fig. 1).

PREVIOUS WORK

The first geological and paleontological investigations in the Juchipila Basin were performed by two graduate students of the University of New Orleans. Both of them, Lahiere (1982) and López (1991), described in their master’s theses the stratigraphy and petrology of lacustrine and associated fluvial sediments accumulated in a thick continental succession that they informally named the “Juchipila Formation” (Fig. 3). López (1991) reported a great diversity of fossils in the lacustrine facies of the Juchipila Formation, including diatoms, ostracods, and mollusks, as well as plant remains and abundant pollen. The occurrence of mammal bones in alluvial and floodplain sediments interbedded with the lacustrine deposits in the Juchipila quadrangle was also reported by López (1991), but he commented that the remains were generally not diagnostic. The only vertebrate fossils collected complete enough for identification were a pecary tooth of *Platygonus rex*, collected at the base of the Amoxochitl section (Fig. 3), and well-preserved cyprinodont fishes collected in lacustrine sediments close to the Atemajac section (Fig. 3).

Based on the occurrence of *P. rex*, a late Hemphillian age was assigned to the sedimentary succession in the Juchipila graben. After this initial fossil discovery, no additional information was available until now. In a short visit to the Atemajac section, we found tracks of small mammals and fossil bones of birds.

During our reconnaissance in the grabens at the southern end of the Sierra Madre Occidental, we found new localities yielding an important and diverse assemblage of mammals in the Juchipila graben. The relationships of these important localities to the geological framework of the basin were briefly discussed by Aranda-Gómez et al. (2008).

Our field research focused on collecting mammal fossils preserved in fluvial deposits exposed on the western side of the Juchipila Basin, mainly in an area near El Mixtión (Carranza-Castañeda et al., 2008), Coñadria, La Copa y El Resbalón, close by the Juchipila city, and to a lesser extent localities at the northern part of the graben, near the Huamusco and Tabasco villages (Fig. 3), where fluvial deposits contain fairly abundant mammal remains. The fossil assemblage from Juchipila, constrained by radiometric ages (U-Pb, in zircon) obtained from ash-fall layers intercalated with the fossil-bearing sediments, gave us the opportunity to establish biochronologic correlations of Hemphillian mammal faunas throughout central Mexico.

MATERIALS AND METHODS

All fossil materials described in this article were collected in localities within the Juchipila Basin. Only maximum measurements are provided. However, because of the state of preservation in some fossils, it is not always possible to take accurate measurements, especially of teeth, in which cases the ratio between the anteroposterior length and protocone length is approximate. All measurements are in millimeters. The wear stage (age) is deduced from the height of the tooth from the base of the crown to the tip of the mesostyle.

INSTITUTIONAL, ANATOMICAL, AND LOCALITY ABBREVIATIONS

| Code | Description |
|------|-------------|
| APL  | Anteroposterior |
| apl  | Maximum anteroposterior length, excluding the ecctoloph and hypocone |
| atw  | Anterior width from metaconid to protoconid length |
| EW   | EarthWatch |
| GABI | Great American Biotic Interchange |
| IGM  | Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City |
| JAL  | Jalisco Teocolotlán |
| LACM | Natural History Museum of Los Angeles County |
| MC   | Metacarpal |
| MPGJ | Museo de Paleontología Geocienciás Juriquilla |
| MSCH | Maximum crown height from the occlusal surface along the mesostyle |
| mt   | Metacristid-metastyloid length |
| MT   | Metatarsal |
| NALMA| North American Land Mammal Age |
| PRL  | Maximum protocone length |
| pw   | Posterior width from metastylid to hypoconid |
| TMM  | Texas Memorial Museum, University of Texas at Austin |
| TRW  | Transverse width from the mesostyle to lingual-most part of the protocone |
| TR   | Transverse axis |
| UNAM | Universidad Nacional Autónoma de México |
| ZJ   | Zacatecas-Juchipila |
| ZT   | Zacatecas-Tabasco |
| ~    | Approximately |

Each specimen is matched by state, locality, and catalog number. Some specimens also include a site number (e.g., ZJ 30-10 Zacatecas-Juchipila locality) The site number denotes the exact place where a fossil was collected, and UTM coordinates of this strict locality are included in the MPGJ Catalogue. The locations of the fossil discussed in this article are marked in Figure 3.

STRATIGRAPHY OF THE JUCHIPILA GRABEN-FILL DEPOSITS

The Juchipila graben is a large NNE-trending topographic depression, approximately 165 km long and 15 km wide (Fig. 3). It extends from Villanueva to Moyahua de Estrada (Fig. 2C). At both ends, the valley disappears, presumably because the master faults of the graben gradually die out. The Juchipila River is the main drain of the hydrological basin within the graben, and it joins the Rio Grande de Santiago. The floodplain of the Juchipila River becomes increasingly narrow south of the town of Jalpa, until eventually disappears south of Moyahua de Estrada (Figs. 2C and 3).
Figure 2. A. Location of study area and distribution of mid-Tertiary subduction related volcanic rocks in central and northwest Mexico. Those outcrops east of the Gulf of California are considered as part of the Upper Volcanic Supergroup (see text) of the Sierra Madre Occidental. Key: A = Aguascalientes, CH = Chihuahua, D = Durango, G = Guanajuato, Gdl = Guadalajara, LP = La Paz, M = Mazatlán, SLP = San Luis Potosí, SMA = San Miguel Allende. B. The volcanic pile associated with the Sierra Madre Occidental activity was profoundly modified by normal faulting and erosion during mid- and late Cenozoic times. Extensional deformation left a large, nearly unfaulted block at the core of the Sierra Madre Occidental physiographic province. The studied area is located in an area characterized by large grabens that at certain times acted as continental sedimentary basins. C. The southern end of the Sierra Madre Occidental is characterized by several (1–9) elongated NNE-to-NNW topographic depressions. These grabens and semgrabens are in places partially filled with clastic sediments that locally contain vertebrate fossils. Key to localities mentioned in the text:
Figure 3 Geology of the Juchipila graben (modified after Servicio Geológico Mexicano, 1988). Areas where vertebrate fossils occur are shown with rectangles; size of the rectangle is proportional to their extension, and areas are labeled with fossil catalog keys (see text). Locations of fossil-bearing stratigraphic sections described by López (1991) are shown with white circles.

Part of the continental deposits inside the southern and central parts of the Juchipila graben (Fig. 3) have been informally described as the Juchipila formation by Lahiere (1982) and López (1991). This formation is a late Miocene–early Pliocene sedimentary succession composed of interlayered beds of freshwater limestone, claystone, epiclastic-volcanic sandstone, and ash-fall tuffs. Facies in the formation are of lacustrine, alluvial, fluvial, floodplain, and pyroclastic origin (Fig. 4). Grain size and facies variations documented by Lahiere (1982) and López (1991) between Santa Rosa (Fig. 3) and San Miguel (Fig. 2C) may be interpreted as the product of four long-lived sedimentary cycles that were associated with transgressions and regressions of the shoreline of a freshwater lake. These facies changes are related with two periods of regional faulting that alternated with an equal number of periods of relative tectonic stability that occurred while the Juchipila formation was being accumulated (López, 1991).

In addition to the outcrops of the Juchipila formation documented by Lahiere (1982) and López (1991), there is an extensive region north of Apozol (Fig. 3) where the Juchipila formation is exposed. West of the Achoquén dam (Fig. 3), in an area that we refer to as El Mixtón, is exposed a >80-m-thick fossil-bearing stratigraphic succession that begins close to the bottom of an arroyo, where massive (1–5 m thick) beds of green tuffaceous claystone are interlayered with thinner, more indurated strata of calcareous claystone with abundant ostracods and gastropods (Fig. 4). Resting atop this shallow lacustrine succession is a thin bed of unconsolidated white ash-fall material composed of felsic glass shards and small, rounded grains of black obsidian. In this part of the succession, camélid and proboscidean footprints were found. Moving up the section, the green tuffaceous claystone beds alternate with pale red, sometimes with irregular green spots, tuffaceous mudstone, and rare layers of epiclastic-volcanic, fine- to medium-grained, distinctly laminated sandstone that in places displays convoluted and/or graded bedding. The clastic succession above the first sandstone layer in the section lacks beds with olistrocks and gastropods, and the proportion of reddish claystone and mudstone steadily increases upward. Higher up in the section exists an approximately 12-m-thick succession composed of several erosion-resistant beds of medium- to coarse-grained, slightly conglomeratic (clasts up to 1 cm) epiclastic-volcanic sandstone that in places displays structures such as convoluted bedding, bioturbation, normal graded bedding, cross bedding, and shallow channels (several meters wide and tens of centimeters deep). Associated with these sandstone beds are thin, clay-rich, unconsolidated horizons that are interpreted as paleosols. Both the cemented conglomeratic sandstone beds and loose paleosols contain mammal fossils. Without any apparent break, this coarse-grained interval is followed by ~10 m of finer sediments (mudstones and sandy clays) in thick, massive beds with alternating green and red colors. Near the top of the exposed section, the proportion of conglomeratic sandstone and fine-grained conglomerate notably increases, as does the maximum clast size (up to 5 cm), while the finer-grained, reddish mudstone layers decrease. Close to a dirt road that leads from the paved road (Mexico 54) to this locality and up to a cliff-forming outcrop of felsic ignimbrite, the Pliocene sedimentary succession is covered by talus deposits derived from the Oligocene ignimbrite.

As a whole, the El Mixtón early–late Hemphillian fossiferous section displays a coarsening upward pattern, where a thick succession of lake beds is covered by relatively coarse-grained subaerial sediments interlayered with green or red mudstones. Facies variations suggest the presence of four long-period sedimentary cycles. It remains to be established whether these cycles correspond with those documented by López (1991) farther south in the basin where the paleolake was deeper. The cycles recognized at El Mixtón section indicate two periods when alluvial fans were prograding, probably as the result of syn-sedimentary faulting. Facies observed at El Mixtón section suggest distal alluvial fans and high mudflat and mudflat-lagoon environments.
Figure 4 Strigraphic columns of Juchipila Basin.
Table 1  U(Th)-Pb zircon data for volcanic ash layers analyzed by LA-Q-ICP-MS at the Centro de Geociencias, Universidad Nacional Autónoma de México, Mexico.

| Sample   | U* (ppm)  | Th* (ppm) | Th/U | 206Pb/238U ± error (%) | 207Pb/235U ± error (%) | Corr. error (Ma) ± error (1σ) |
|----------|------------|------------|------|-------------------------|-------------------------|-------------------------------|
| M6-11    | 1967       | 750        | 0.35 | 0.00545 ± 3.3           | 0.00086 ± 1.2           | 0.240                        |
| M6-24    | 2437       | 920        | 0.47 | 0.00566 ± 4.6           | 0.00085 ± 1.2           | 0.310                        |
| M6-3     | 3163       | 1054       | 0.35 | 0.00533 ± 3.8           | 0.00080 ± 1.2           | 0.310                        |
| M6-20    | 2014       | 1044       | 0.48 | 0.00544 ± 1.3           | 0.00083 ± 1.2           | 0.320                        |
| M6-35    | 1601       | 1002       | 0.55 | 0.00559 ± 1.8           | 0.00086 ± 1.2           | 0.260                        |
| M6-9     | 2521       | 1936       | 0.46 | 0.00531 ± 3.1           | 0.00085 ± 1.2           | 0.270                        |
| M6-2     | 1605       | 738        | 0.42 | 0.00558 ± 2.9           | 0.00087 ± 1.1           | 0.360                        |
| M6-15    | 1087       | 636        | 0.54 | 0.00601 ± 2.2           | 0.00094 ± 1.1           | 0.240                        |
| M6-14    | 1074       | 492        | 0.74 | 0.00614 ± 3.7           | 0.00096 ± 1.1           | 0.230                        |
| M6-10    | 619        | 291        | 0.43 | 0.00290 ± 3.8           | 0.00334 ± 1.2           | 0.280                        |
| M6-12    | 2142       | 1564       | 0.67 | 0.02141 ± 3.4           | 0.00329 ± 0.9           | 0.330                        |
| M6-27    | 325        | 153        | 0.43 | 0.02347 ± 3.4           | 0.00369 ± 1.4           | 0.290                        |
| M6-43    | 487        | 712        | 1.35 | 0.02467 ± 4.8           | 0.00388 ± 1.0           | 0.240                        |
| M6-31    | 555        | 563        | 0.36 | 0.02592 ± 1.5           | 0.00399 ± 0.8           | 0.490                        |
| Weighted mean | 231       | 123        | 0.56 | 0.06491 ± 3.4           | 0.00686 ± 1.6           | 0.460                        |

* ±0.10 Ma. Numbers are in ppm.

* Coordinates: 2,365,629 mN-694,048 e (Zone 13Q DATUM WSG-84); MSWD = 1.8 (8 of 17).

* * Coordinates: 2,383,571 mN-703,214 m (Zone 13Q DATUM WSG-84); MSWD = 0.33 (3 of 15).

MEXICO LAB: Centro de Geociencias, Universidad Nacional Autónoma de México. U-Pb analytical techniques are discussed in Solari et al. (2010) and Solari and Tanner (2011).

* U and Th concentrations (ppm) are calculated relative to analyses of trace-element glass standard NIST 612.

* Isotopic ratios are corrected relative to data for single zircon for mass bias and down-hole fractionation (PFL, Plešovec = ~337 Ma; Sláma et al., 2008).

All errors in isotopic ratios and ages are absolute and given at the 1-sigma level except for the weighted mean ±0.10 Ma, which is reported at the 2-sigma level.

Fossils were also found in the Cofradía, La Copa, and El Resbalón sites, where lithofacies, broadly similar to those described at El Mirón, are found (Fig. 4). Despite the fact that ash-fall layers are relatively common in all the sites depicted in Figure 4, only a few of the samples studied yielded isotopic ages that are consistent with the NALMA of the fossils. Although several ash samples were collected in each site from layers in different stratigraphic positions that potentially could yield age brackets for the local fauna, most samples contained significantly older zircons that were interpreted as accidental and were probably derived from the wall rocks of the volcanic conduit or, more likely, from reworking of the ash and mixing with detrital material derived from the mid-Tertiary ash flow tuffs exposed on the footwall blocks around the graben.

U-PB ZIRCON GEOCHRONOLOGY OF VOLCANIC ASHES

In an attempt to temporarily bracket faunas from different areas in the Juchipila Basin, we have undertaken extensive U-Pb zircon geochronology of a dozen intercalated volcanic ashes. A laser ablation single-crystal approach was followed, and abundant older, xenocrystic, Miocene and Oligocene grains were detected.
in many of those ashes. In some samples, all of the zircons were interpreted as xenocrystic grains and were discarded for age calculations; however, four of the ash beds had zircons that represent the time of ash formation (igneous crystallization). We used three different geochronology laboratories in Mexico and the United States to undertake the U-Pb studies using both quadrupole and multicolonector instrumentation (inductively coupled plasma-mass spectrometry [ICP-MS]). The data from the different labs are presented in Tables 1 to 3 and illustrated in age probability diagrams in Figure 5. We calculated weighted mean 206Pb/238U ages for four samples, using the youngest and most concordant zircon populations, which we interpret as representing the time of crystallization of the different volcanic ashes present in the Juchipila Basin.

### SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Xenarthra Cope, 1889
Family Megalonychidae Gervais, 1855
Genus aff. Pliometaenastes Hirschfeld and Webb, 1968

**REFERRED SPECIMEN AND LOCALITY.** ZJ 30-10 El Mixtón, MPJG 1630, left metatarsal III; ZJ 47 El Resbalón, MPJG 1929, fragment of first molariform tooth; MPJG 1930, fragment of second molariform tooth.

**DESCRIPTION.** MPJG 1929 exhibits a squared crown; the anterior side is convex all along, while the posterior side is slightly concave. The AP crown measured is ~9.3 mm, and the TR is ~12 mm. In MPJG 1930, the crown is triangular, the anterior border is convex, and the posterior is concave with the channel situated in the labial border; AP ~8 mm and TR ~12 mm. The MT III is broken ventrally as well as almost the entire ectocuneiform surface. The length is slightly longer than the width. The ectocuneiform facet is partially broken, but it is nevertheless clear that the surface is concave with a faint ridge present in the middle. The external part of the ectocuneiform facet where it contacts the upper part of the facet for the articulation of MT IV forms a conspicuous sharp triangular structure in the proximal-dorsal end of the shaft that resembles the MT III of Hapalops. The facet for articulation of MT II is convex and smaller than that for MT IV (Fig. 6A). The facet for the articulation of MT IV is large, family concave in the middle with subrounded shape, and the main axis is in proximal-distal direction (Fig. 6B). The distal end is stout, and the carina is long and well developed.

**DISCUSSION.** In order to assign the specimen MPJG 1630, it is important to mention that its relationship between length and breadth corresponds to what has been reported in Hemphillian megalonychids (length always larger than breadth), a condition that has been demonstrated completely opposite in Megalonyx leptostomus and other megalonychids from Pleistocene faunas (Scott, 1903; Stock, 1925; Hirschfeld and Webb, 1968).

In comparison with the MT III of megalonychid from the Mulholland fauna (early-late Hemphillian), the main differences from the Mexican specimen are its longer shaft and the concave facet for MT II (Stafford, 1939). Compared with Pliometaenastes protistus from McGehee Farm, MPJG 1630 is generally similar, especially in relation to the elliptical and concave outline of the MT IV articulation. Nevertheless, when examined in detail, the facet of the MT II is slightly convex (Hirschfeld and Webb, 1968). Another comparison was made with a picture of MT III of P. protistus (UF 95400) from Moss Acres Race Track locality, early
Hemphillian (lateral external and internal view). The size is comparable; the inner facet of MT II has a similarly convex structure in terms of position, shape, and size. On the external side, the facet for MT IV is large, elongate, and concave; both facets are similar to the Mexican specimen. However, because of the incompleteness of the anterior lateral part of the MT III, it is not possible to establish the real contact between the facet for MT IV and the ectocuneiform surface. Regardless of its fragmentary nature, the Mexican material adds to the very few detailed descriptions reported for megalonychid metatarsals. Our specimen is not sufficient to permit more accurate comparisons or to assign more precise value to the characters.

The structures of the MT III and the dental fragments from Juchipila match those of the Pliometanastes description (Hirschfeld and Webb, 1968; Hirschfeld, 1981; Table 4).

**DISTRIBUTION IN MEXICO.** There are few records of megalonychids in Hemphillian faunas of the Transmexican Volcanic Belt. Two megalonychid teeth were recently collected at the Zetla locality in the Tehuichila area in Zacualtipán Basin (Fig. 1). That fauna was assigned to the early-late Hemphillian NALMA (Carranza-Castañeda, 1994; Carranza-Castañeda and Miller, 2002). Two fragments of teeth were collected from the Rhino layer of Rancho El Ocone locality in the San Miguel de Allende Basin (Fig. 1). A tooth fragment of Megalonyx from La Plegaria locality (Fig. 1) was described and assigned to late Hemphillian age by Padilla-Gutiérrez (2004). Two phalanges and several teeth of Megalonyx were discovered at La Hacienda and Santa María localities dated to 4.8 Ma in the Tecolotlán Basin (Fig. 1), state of Jalisco (Carranza-Castañeda, 2006).

A previously known record of Pliometanastes occurs from an uncertain locality located near Rio Virgenes at the border between the states of Tamaulipas and Nuevo León. That fossil is housed at LACM in Los Angeles, California (McDonald, 2002). Up to now, the megalonychid from Juchipila is the oldest (isotopically dated) occurrence among the Mexican Hemphillian faunas with a well-documented location and stratigraphic position.

Order Carnivora Bowdich, 1821
Family Canidae Fischer de Waldheim, 1817
Genus Borophagus Cope, 1892
Borophagus secundus (Matthew and Cook, 1909)

**REFERRED SPECIMEN AND LOCALITY.** ZJ 30-3 El Mixtón locality, fragments of left maxillary with broken P4, incomplete M1, and alveolus of M2.

**DESCRIPTION.** The M1 is roughly rectangular in outline; the lingual border is rounded by the hypcone, posteriorly slightly skewed. The P4 is incomplete, and only the lower part of the blade of the metacone is preserved; a strong labial cingulum and a much weaker one on the lingual side are present. In M1 the paracone is broken, and the paracone is preserved only on the internal half of the cusp. The metacone is also cracked. The protocone is rounded, twice as big as the metacoonule. The hypocone is complete and rounded with a weak cingulum on the anterior lingual side. The alveolus for M2 is well preserved; it is double rooted anteriorly, and the posterior root is long.

**DISCUSSION.** Comparisons between the Juchipila specimen and those described from the Rinconada (IGM 6669, left P4-M2, and IGM 6671, right M1) and a left M1 (IGM 6670) from Rancho El Ocone fauna (Carranza-Castañeda, 1992; Miller and Carranza-Castañeda, 1998b) indicate that structures of the occlusal surface are similar. The main difference is the size of the Rinconada M1, which is a little larger, and its cingulum is
Figure 5  Age probability histograms and weighted mean $^{206}\text{Pb}/^{238}\text{U}$ age diagrams of single-crystal zircons for volcanic ashes in the Juchipila Basin. Insets show age probability diagrams that include older xenocrystic zircons that were not included in the U-Pb age calculations.
more prominent. The M1s from Juchipila and Rancho El Ocote are similar in size.

**GEOGRAPHIC DISTRIBUTION IN CENTRAL MEXICO.** *Borophagus secundus* has been collected in all Hemphillian localities in the San Miguel de Allende Basin, in La Plegaria locality in the state of Hidalgo, in several sites in the Santa Maria area, in La Hacienda locality in the Tecolotlan Basin, and in the Teocaltiche Basin in the state of Jalisco.

Family Felidae Fischer von Waldheim 1817  
Subfamily Machairodontinae Gill, 1872  
Gen. and sp. indet.

**REFERRED SPECIMEN AND LOCALITY.** ZJ 30-3 El Mixtón locality, MPGJ 1685, proximal end of right MC IV.  
**DESCRIPTION.** MPGJ 1685 has an almost complete proximal end. The shaft is straight, and the distal end is missing. The lateral facets for the metacarpal V are complete, the proximal end with the medial surface is partially damaged, the surface for the unicompact curve posteriorly, and the medial side preserves a small surface for the metacarpal III that is convex.  
**DISCUSSION.** The shaft of MPGJ 1685 is straight and not curved as in *Smilodon* or other more derived cats (Dalquest, 1969). In cross section, the shaft is oval, not subtriangular as in *Homoatherium* (Dundas, 1992). In size, the proximal end is similar to those of *Machairodus catacopis* from Coffee Ranch (Dalquest, 1969) and *Machairodus coloradensis* from Edson fauna (Harrison, 1983) and is smaller than *Smilodon* (Merriam and Stock, 1932; Table 5).

**GEOGRAPHIC DISTRIBUTION IN CENTRAL MEXICO.** Remains of *Machairodus* have been collected at Rancho El Ocote, Rinconada, and Arroyo Tepalcati localities in San Miguel de Allende Basin, state of Guanajuato. The genus also occurs at the La Plegaria locality, state of Hidalgo, and at La Hacienda and Hilda's localities in the Tecolotlán Basin, state of Jalisco.

Order Perissodactyla Owen, 1848  
Family Equidae Gray, 1821  
Genus *Calippus* Matthew and Stirton, 1930  
*Calippus* (Grammohippus) bonarensis (Olson and McGrew, 1941)

**REFERRED SPECIMEN AND LOCALITY.** Upper dentition: locality ZJ 30 El Mixtón MPGJ 1704, palate with left P1-M3, right P1-P4 and M2, left C, and II-3 and right I2-1. Locality ZJ 30-3: MPGJ 1309, left M1; MPGJ 1311, right M3; MPGJ 1324, unworn left P3; MPGJ 1326, left M1; MPGJ 1327, right P4; MPGJ 1639, right P4; MPGJ 1625, left M1; MPGJ 1629, left M1; MPGJ 1640, left P4; MPGJ 1642, left M1. Locality ZT 32, La Escaleria: MPGJ 1606, left P4; MPGJ 1607, right P2; MPGJ 1609, right M3. Locality ZJ 42 Cofradia: MPGJ 1645, right M1. Locality ZJ 48 La Copa: MPGJ 1973, palate with left dp2-P3 and right dp3-4.

Table 4  
Measurements (in mm) of the MT III of aff. *Pliometanastes* from ZJ 30 El Mixtón locality, Juchipila Basin, Zacatecas, and comparison with *P. protistus* from Florida. ~ indicates estimates.

| Aff. *Pliometanastes* | *P. protistus*, UF95400 Moss Acres S. Racetrack |
|------------------------|---------------------------------------------|
| ZJ 30-10               |                                              |
| Max. length through the facet MT II to the middle distal carina | 45.8 | ~44.0 |
| Max. length through the facet MT IV to the middle distal carina | 55.7 | ~48.0 |
| Max. breadth through the facet MT II to MT IV | 34.3 |               |
| Max. breadth dorsoventral of distal end above the carina | 32.4 |               |
| Max. length of the carina | 46.3 | ~44.0 |
Isolated upper teeth represent all stages of wear from very young to old individuals. All defining characters of the upper cheek teeth of the genus *Calippus* are well represented in the teeth of younger individuals. The teeth are strongly curved, even in old individuals. In MPGJ 1629 (M1) and MPGJ 1640 (P4), which represent young adults, as well as MPGJ 1606 (P4), the oldest individual (Fig. 8A-D), the strong curvature is evident. The plications in the pre- and postfossette in early stages are more evident, becoming less well defined with wear. The pli caballin is regular in younger individuals and disappears in different stages of abrasion; it is well developed in MPGJ 1625 (P4) and MPGJ 1609 (M3) with very little wear; in MPGJ 1639 (P4), with moderate wear, it is represented by small folds of the enamel (Fig. 8C).

The protocone has considerable variation. In teeth with very little wear, the shape varies from large with a pointed end to rounded and lenticular in older individuals; however, it is always connected to the protoselene by a small isthmus, and the preprotoconal groove is open and present in all specimens even in advanced phases of abrasion (Fig. 8A–C).

The hypocone shows high variability as well. In MPGJ 1625 (M1), which exhibits very little wear, this structure is large and the hypoconal groove very wide; in MPGJ 1640 (M2), which represents an adult individual, the hypocone is rounded, and the hypoconal groove is deep. In MPGJ 1639, which shows advanced wear, the same structure is reduced, while in MPGJ 1309, from a senescent individual, the hypocone disappears.

In the lower dentition of MPGJ 1735, all teeth are well preserved; the p2 metaconid is tiny, and its metastylid is rounded. In p3-m3, the metaconids are elongated and rounded, and the metastylids are rounded, almost the same size as the metaconid. In premolars and molars, the paralophids are the same height as the metaconids. All the teeth lack the protostylids; the lingual flexids are shallow in premolars and slightly V shaped in molars. The protoconids and hypoconids are moderately rounded; the ectolophids are deeper in molars, not crossing the isthmus. Hypoconulids are present in p3-4 and m2. The mental foramen is
Figure 8. Lateral and occlusal views of isolated teeth of *Calippus* (*Grammohippus*) *hondurensis* in different stage of abrasion. A, B. Young adults. C. Adult with small P1 caballin. D. Old individual. Juchipila, Zacatecas.

just in front of p2; the tooth row (p2-m3) is ~109 mm in length (Fig. 9A). In MPGJ 2044, p2-m3, the lingual flexid, is open and faintly V shaped. The metaconids and metastylids are almost the same rounded shape, with the metastylids in all the teeth slightly smaller. The ectoflexids are slightly deeper in the molars. The protoconid and hypaconid in molars and premolars are roughly rounded. The paralophids are well developed in premolars and molars (Fig. 9B).

The isolated premolars and molars from Juchipila represent individuals of different ontogenetic ages; their occlusal morphology therefore varies widely with wear. The lower teeth fall within the variability of *Calippus* (*Grammohippus*) *hondurensis* (Olson and McGrew, 1941; Hulbert, 1988).

**COMPARISONS WITH CALIPPUS IN OTHER MEXICAN FAUNAS**

*Calippus* was described from La Presa fauna in the San Miguel de Allende Basin and from the Zietla locality in the Zacualtipán Basin. These materials were assigned to the species *Calippus* (*Grammohippus*) *castilli* (Carranza-Castaneda, 1994; Carranza-Castaneda and Espinoza-Arrubarena, 1994). The isolated teeth of *Calippus* from the La Presa fauna were compared with the Juchipila materials. All the structures of the occlusal surface show the same range of variability in the metaconid-metastylid shape and size, the ectoflexid, and other features.

Complete jaws (MPGJ 1644) from the Jalostotitlán area, about 200 km southeast of the Juchipila Basin, has 11-2 and p2-m3 in both sides and belong to a young-adult individual. The characters of the dentition and the jaw are comparable with those described as *C. (Grammohippus) hondurensis* (Olson and McGrew, 1941; Hulbert, 1988; Montellano-Ballesteros, 1997). Differences from the Juchipila jaws are insignificant and interpreted as individual variation. In the Jalostotitlán jaw, the length from the anterior part of p2 to the base of i3 is ~30 mm, tooth row length (p2-m3) at the base of the teeth is 110 mm.

In conclusion, all the specimens of *Calippus* from Juchipila, La Presa, Zietla and Jalostotitlán are similar and interpreted to be different populations of the same species; displaying few differences in dental morphology are attributed to discrepancies in age and wear (Olson and McGrew, 1941; Hulbert, 1988).
COMPARISON WITH CALIPPUS FOUND OUTSIDE OF MEXICO

The main difference between the Mexican material and the fossils from Honduras and Florida is the relationship of the length of the protocone and the APL in the upper teeth. In the Juchipila assemblage, the relationship between the APL and PRL is 31-35% larger than Calippus from Florida described by Hulbert (1988). In comparison with Calippus (Grammobippus) cerasius, the most important difference is the preprotoconal groove being more evident in C. (Grammobippus) hondurensis than in C. (Grammobippus) cerasius; however, the great variability in the shape and size of the protocone and other structures of the occlusal surface makes it difficult to identify objective differences between these two species. According to Hulbert (1988:271), “The two species are inseparable on the basis of the size.” Consequently, the relative differences in the measurements of the Juchipila assemblage fall within the variability of the two populations separated geographically. In addition, the crown heights of premolars (P3-4) and molar (M1-2) in all the samples described in this article are less than 55 mm, similar to that in the materials from Honduras and Florida. The small differences documented in the material from Juchipila may not be significant, as the number of specimens is rather small and the materials come from individuals of different ages. The MSCH measurements from the Juchipila samples are summarized in Table 6.

GEOGRAPHIC DISTRIBUTION IN MEXICO. Calippus (Grammobippus) hondurensis was reported from 1) the Zietia locality in lower section of the Zacaúlén Basin, state of Hidalgo; 2) La Presa locality in the lower part of the stratigraphic sequence of the Rancho Viejo and Coecillos area, San Miguel de Allende Basin (Carranza-Castañeda, 1994; Carranza-Castañeda and Espinosa-Arribabena, 1994); 3) the Tlatenango, Santo Domingo in Colorado basin; and 4) Jalostotitlán and Teocaltiche basins (Carranza-Castañeda, 2006, 2009). Ferrusquia Villafranca (1990) mentioned a record of (?) Calippus from the El Gramal Fauna, in state of Oaxaca.

Neohipparion Gidley, 1903

Neohipparion eurystyle (Cope, 1893)

REFERRED SPECIMEN AND LOCALITY. Locality ZJ 30 Mixtitlán: MPGJ 1970, left and right fragments of maxillary of the same individual with pP2-PP4; MPGJ 1308, left M3 fragment; MPGJ 1641, right M1; MPGJ 1623, dM3. Locality ZT 32 La Escalerita: MPGJ 1301 left M3; MPGJ 1590 left M3. Locality ZJ 47 El Resbalón: MPGJ 1996 left P2.

DESCRIPTION. The Juchipila assemblage represents individuals in different wear stages. On the P2 of MPGJ 1970, the anterostyle is broken but was small, the parastyl is small and rounded; a well-developed mesostyle and weak metastyle are present; P3-4 have complex plications in fossettes; anterior half of prefossette has a deep pli protoloph; the posterior border has

Figure 9  MPGJ 1735, Calippus (Grammobippus) hondurensis. A. Left mandible with p2-3. B. MPGJ 2044, right jaw with p2-3 and m1-3 and left jaw with p3-m3, belonging to the same individual. Locality ZJ 47 El Resbalón, Juchipila, Zacatecas.
complex and deeply bifurcate prefossette loop, postfossette with simpler plications; p1 caballin in dp2 has four small branches; in dp3 and dp4 it is bifurcate; the protocone is rounded and isolated with flat lingual border and pinched in the anterior labial part; the hypoconal groove is open with a well-developed, pointed hypocone. The left P2 in MPGJ 1996 is from a very young individual; the anterostyle is short and pointed; the protocone is small and rounded; the hypocone is triangular and hypoconal groove open; p1 caballin is bifid, and fossettes are very complex; the posterior border of the postfossette has multiple plications, the larger is the bifurcate protofossette loop; the post fossette in the anterior border has multiple plications, simpler in the posterior border line. In MPGJ 1623, dp3-4 are in early stages of wear and present the same features described above; the most significant is the fish pattern of the protocone, described previously for Neohippotherium from Rancho El Ocote (Carranza-Castañeda and Ferrusquia-Villafranca, 1979).

Specimens MPGJ 1590 and MPGJ 1308 belong to mature individuals. The most diagnostic structures are isolated protocone, hypocone and hypoconal groove, and bifid p1 caballin, and the pre fossette loop is large, reaching the lingual line of the post fossette. All these characters are diagnostic of Neohippotherium eurystyle from the late Hemphillian faunas of Tecolutlán and San Miguel de Allende basins (Carranza-Castañeda and Ferrusquia-Villafranca, 1979).

MPGJ 1301 and MPGJ 1641 exhibit advanced wear and represent senescent individuals. In each the most diagnostic features are preserved, that is, the isolated protocone, open hypoconal groove, pre fossette loop, and p1 caballin.

**DISCUSSION AND COMPARISON.** The Juchipila teeth were compared with specimens from the Rancho El Ocote and Rinoconada localities. In the Juchipila assemblage, the M3s are the most commonly represented teeth, but unfortunately M3s are highly variable. However, when compared with M3s from Rancho El Ocote (MPGJ 249, left M3) and Tecolutlán (MPGJ 343) that are comparably worn, the features of the occlusal surface are similar: isolated large protocone as well as flat lingual border, hypocone and hypoconal groove similar and constant until last stages of wear, pre fossette loop and p1 caballin always present, branched or single even in the old teeth.

The young maxillary in MPGJ 1970 (Fig. 10) was compared with illustrations of Neohippotherium transpanense (Hulbert, 1987). Some differences are evident: in P2, the anterostyle is clearly longer, the para styline is more developed and recurved posteriorly, and metastyle is evident; all these features set apart this specimen from the Mexican Neohippotherium, but they share the complicated posterior half of the pre fossette, with the complex pre fossette loop and bifurcate p1 caballin.

Specimens of Neohippotherium from Juchipila, including deciduous premolars, possess all the diagnostic features reported by previous authors (e.g., MacFadden, 1984; Hulbert, 1987) and were widely discussed in the revision of the neohippotheriids from Mexico (Carranza-Castañeda and Ferrusquia-Villafranca, 1979). The differences observed in the Juchipila teeth fall in the variation of the characters that the above-cited authors recognize for N. eurystyle from central Mexico. Thus, the Juchipila material must be referred to the same species recognized in other Hemphillian faunas of Mexico.

**DISTRIBUTION IN MEXICO.** Neohippotherium had a wide distribution in Mexico. The species is recognized in all of the late Hemphillian faunas. Since the report fromYepomera fauna (Stirton, 1955), it has been recovered from the late Hemphillian localities such as 1) the Rhino layer of Rancho El Ocote (Carranza-Castañeda, 1989), Rinoconada, Arroyo Tepalcates, and Coecillos areas in the San Miguel de Allende Basin, state of Guanajuato; 2) all the late Hemphillian sites in the Tecolutlán Basin, state of Jalisco; 3) the Zierta fauna in the Zaculipitan Basin and in La Plegaria locality; and 4) El Gigante and El Trapiche localities in the state of Nayarit (Carranza-Castañeda, 2006). It is also present in all localities assigned to the earliest late Hemphillian: 1) Los Velis area and Santo Domingo locality from the Tlatenango-Colorlan Basin, at the border between the states of Jalisco and Zacatecas, and 2) in the Chiqua locality in the state of Michoacan (Fig. 1).

**Genus Astrohippus** Stirton, 1940

*Astrohippus anste* (Matthew and Stirton, 1930)

REFERRED SPECIMEN AND LOCALITY. Locality ZJ 48 La Copa, MPGJ 1997, fragment of left jaw with p2-m2; locality ZJ 47 El Resbalón, MPGJ 1755, right m2.

**DESCRIPTION.** The specimen MPGJ 1997 belongs to an adult judged by the teeth abrasion. The main characters to justify referral of the specimen to *Astrohippus* are the ectoflexid that never reaches the enamel of the isthmus and the premolars that are short and slightly wider and just longer than the molars. The lingual folds are V shaped, splitting the metaconid-metastylid structures, which are of different size and shape. The isthmus is larger in premolars; the posterior column of the shaft in p2-m4 and m2 is straight and higher in the area where it is in contact with the enamel of the lingual fold, forming a lobular and closed metastylid except in m4; the anterior column of the isthmus are shorter and curved, leaving the metaconid larger, roughly flattened, and open as is typical in *Astrohippus*. The entoconid is rounded with well-developed hypoconulid; the stout parallophids has the same height as the metaconid. The protoconids and hypoconids are slightly rounded. There is definitely no evidence of the p1 caballin in the Juchipila jaw (Fig. 11). The length of p2-m2 is 119 mm, p3-4 is 48.7 mm, and m1-2 is 44.5 mm.
COMPARISON. In general, some of the characters discussed by Dalquest (1988) for Astrohippus ansae are comparable with the fossils from Juchipila; however, several differences can be established between the Juchipila specimen and Astrohippus stockii from Rancho El Ocote and Rinconada localities (Carranza-Castañeda, 1992).

The teeth represented A. stockii are smaller in the AP and TR axis; the metaconids and metastylids are flared, almost the same shape and size; and the lingualesflexids are wider and barely U shaped, only in the specimen MPGJ 254 (m1), the metastylid is almost closed, resembling the specimen from Juchipila. The paralophids in all the specimens from Rancho El Ocote and Rinconada are thinner and shorter and situated below the metaconids in comparison with the Juchipila material, in which the paralophids are in the same plane as the metaconids although more stout, similar to the illustrated specimen by Matthew and Stirton (1930:pl. 54; Fig. 1). This structure is not referred by Dalquest (1983) in the Coffee Ranch material. The ectolophids in both species are similar: short and never touching the enamel of the isthmus.

The size of the Juchipila jaw is comparable to the measurements of A. ansae from Coffee Ranch (Dalquest 1983; Table 7).

DISTRIBUTION IN MEXICO. This is the first record in the Hemphillian faunas from central Mexico.

**Dinohippus Quinn, 1955**

*Dinohippus mexicanus* (Lance, 1950)

REFERRED SPECIMEN AND LOCALITY. Upper dentition: locality El Mixtón, ZJ 30-3, MPGJ 1682, partial skull with posterior half of right P2 and P3-M3. Locality Wang ZJ 34: MPGJ 1593, left P2-3; MPGJ 1688, left 11-3. Lower dentition: locality Wang ZJ 34, MPGJ 1683, jaw fragment with right p2-p3-m3, c, and right and left 13-1; MPGJ 1635, right p3-m2 and associated right m3.

DESCRIPTION. MPGJ 1682 is a nearly complete skull, slightly crushed in the facial region, and the left side is almost destroyed, although the structures of the dorsal preorbital fossa (DPOF) and the infraorbital foramen are not deformed. In the right side the preservation is much better and complete, and all the dentition, the malar crest, the zygomatic arch, part of the occipital crest, the condyle, and the paramastoid process are well preserved.

The basilar portion of the skull from the right condyle to the anterior part of the P3 is complete. The nasal bones are broken, so that the end of the nasal notch is difficult to differentiate; it is estimated to be located above the P2. The infraorbital foramen is positioned in the middle part of P4, and the end of the malar crest is placed between the mesostyle and metastyle of the same premolar. The only evidence of the malar fossa is a shallow and
smooth depression. The facial region is narrow, especially in the nasal bones (47 mm), and wider in the maxillary region above M2.

The DPOF is present on both sides of the rostrum, but sutures cannot be observed; it appears as a faint, shallow depression with very slight, barely defined margins. The DPOF is oriented to the anterior part of the nasal and maxillary bones (~78 mm length) and ends ahead of the infraorbital foramen. The posterior margin is weak; there is a large preorbital bar (~63 mm; Fig. 12).

The cheek teeth of the left side are lost; on the right side the P2 is partially destroyed, and only part of the postfossette remains; P3-M3 are surrounded by thick cement. The postfo settes in P3 and M1 are almost worn, suggesting that the specimen belonged to a mature individual. The fossettes are very small; the posterior part of the postfossette shows tiny folds, the largest being located in the lingual border. The postfos sette has one small fold in the anterior border, and only M3 shows another small fold in the posterior border. The protocones in P3-M1 have an evident anterior heel, and they are markedly longer in M2-3. The lingual borders are flat in M2-3 and P3; it is slightly concave in M1, and that in P4 is clearly concave; in both teeth the protocone form a wooden-shape shoe. The postprotoconal grooves are always open and have almost the same size across in all the teeth. The hypocone is lobular pointed, and the hypoconal groove is of nearly similar size in all of the cheek teeth (Fig. 13).

MPGJ 1593 consists of two isolated left teeth from the same old individual; their most important characteristic is the protocone: the lingual border of P2 is flat, whereas in P3 it is weakly concave. The postprotoconal groove is always open, the hypocone is rounded, and the hypoconal groove small but open.

Judging by the wear, the fragment of right 11-3 arcade in MPGJ 1688 belonged to a young individual; it is smoothly curved, and its shape suggests that the complete palate was rounded. The 11-2 present a thin and large infundibulum, the enamel in the labial side being thicker; the 13 enamel is thinner and open and runs toward the posterolateral side; in all incisors the infundibula are filled with cement.

The jaw of MPGJ 1683, judging by the wear, belonged to an adult individual. The incisors are complete with 1-3 in both sides, all with wide infundibula; a small canine is present in the right side. The diastema between c and the p2 is 77 mm. The teeth row p2-m3 is well preserved 151 mm; the linguaflexid is widely U shaped in the premolars and reduced in the molars. The metaconid and metastylid of P2 are rounded in shape; in p3-p4 they are bigger but with the same rounded shape. In the molars the metaconid is lobular and the metastylid smaller and slightly pointed in the lingual direction. The paralophid in premolars and molars is high like the metaconid. The metaflexid in the premolars has two folds; the encondid has a well-developed hypoconulid. The ectoflexid is short in the premolars and deep in the molars, passing the isthms almost in contact with the internal border of the linguaflexid. The protoconid and hypoconid are faintly rounded (Fig. 14).

MPGJ 1635 (right p3-m2), judging by the wear, corresponds to an old individual. The linguaflexid in the premolars is deep with a V outline, and it is wider in the molars. The shapes of metaconid-metastylid in p3-4 are lobular, and they are similar in size. The metastylid in the molars is smaller than the metaconid, and it is pointed in the lingual direction. Ectoflexid in premolars reach the isthms; it is deeper in molars, reaching the internal border of the linguaflexid.

COMPARISON. The faint DPOF and the postprotoconal groove of the protocone, which is always open even in the last stages of wear, make the Juchipila skull easily separated from any species of Pliobippus. A cast of Dinobippus leidyanus (FAM 87201) mentioned by Azzaroli (1988), housed in the collection of University of Texas at Austin (TMM 41478-1), shows similarities with the skull from Juchipila, such as the absence of malar fosse, the malar crest ending behind the P4, the lachrymal foramen located above the middle of P4, and the posterior end of DPOF located above the middle of M2. The main differences are the well-developed DPOF with rounded borders and the smaller and more rounded protocones, with heels considerably smaller or absent in comparison with the Mexican specimen.

Comparison between the skull of Dinobippus mexicanus and illustrations of Dinobippus interolatus by Matthew and Stirton (1930) show significant differences in the protocone and the fossettes. In D. interolatus, the protocone is smaller, without or

| Table 7 | Comparative measurements (in mm) of the lower teeth of Astrohippus ainsae from Coffee Ranch and the Juchipila jaw. |
|---------|---------------------------------------------------|
|         | p3-4  | p2    | p3    | p4    | m1    | m2    |
| Coffee Ranch | 49.2  | 22.5  | 23.6  | 23   | 20.5  | 20.9 |
| Juchipila Jaw | 49.0  | 23.5  | 24.8  | 24.0 | 21.6  | 22.3 |
| Depth under p2 | 47.0  |       |       |      |       |      |
| Depth under the ectoflexid of p2 | 46   |       |       |      |       |      |
with very small heel and simple fossettes; these characters contrast with those already mentioned for the Juchipila specimen.

The dentition in the Juchipila skull shows diagnostic characters that can be assigned to D. mexicanus; however, the facial region, in particular the DPOF, is different from other skulls referred to the same species, which were collected in the late Hemphillian localities in the San Miguel de Allende and Tecolotlán basins (Table 8).

In a skull from Rancho El Ocate, the DPOF is noticeably developed with well-defined edges (MacFadden and Carranza-Castañeda, 2002), whereas the Juchipila specimen has a shallow DPOF with faint borders. Both specimens share the absence of malar fossa, a character that has been mentioned in the partial skull from Yepomera described by MacFadden (1984). Likewise, the end of the malar crest and infraorbital foramene are located in the same position. All the features in the occlusal surface demonstrate the similarity of the dentition in both specimens, including the wooden-shoe shape of the protocone (Fig. 13).

Other specimens from the late Hemphillian faunas of central Mexico also assigned to D. mexicanus display important similarities in the DPOF and upper teeth with the Rancho El Ocate specimen (MacFadden and Carranza-Castañeda, 2002). MPGJ 1686 from locality JAL TECO 35 is an incomplete skull of a young individual with P4 and M3 partially erupted and M1-2 in the early stages of wear. These specimens show more similarities in the DPOF with the skull from Rancho El Ocate than the Juchipila skull. The DPOF is situated above the anterior half of M2, and the borders are well defined and rounded; the posterior part is pocketed, ~6 mm deep and ~23 mm wide. The length of the preorbital bar is only ~58 mm; the malar bar ends in the posterior part of P4. On the other hand, the dentition is comparable in both specimens from the El Ocate and Juchipila, as it has simple fossettes, only two small folds in the posterior half of the prefossette in M1 but not in M2, a well-developed heel in the protocone, and an open postprotoconal groove, large hypococone and open hypocoanal groove.

Another specimen, MPGJ 856, consists of two maxillaries with left P1-M3, right P3-M3, and fragments of the nasal bones with part of the DPOF, all collected in the same site (GTO 56) and belonging to the same old individual. The major difference is found in the fragment of the rostrum with part of the DPOF: posteriorly pocketed with rounded edges, the groove of the DPOF being more horizontal as well as narrow and deep, similar to the Rancho El Ocate and the Tecolotlán specimens. The teeth show advanced wear but are similar to any other specimens from the late Hemphillian faunas.

Comparison of the lower teeth. The Juchipila specimen was compared with material of D. mexicanus from the late Hemphillian faunas from central Mexico, such as MPGJ 311 (p2-m3) from locality Jal Teco-8, state of Jalisco (Fig. 1) and MPGJ 310 (p2-m3) from GTO 30 Coecillos locality, state of Guanajuato (Fig. 1, Table 9). Teeth in both specimens are exceptionally preserved and in a similar stage of wear. In the jaw MPGJ 310, the metaconid of p2 is smaller and sharp, but in p3-4 the metaconid and metastylyl are the same size and shape; the metastylyl is pointed lingually. In the lower molars, the metastylyl is lobular, smaller, and pointed. The linguaflexid is in V shape in premolars and shallow in molars, and the ectoflexid is deeper in molars, resembling the Juchipila specimen. The
protoconid and hypoconid are barely rounded. The main difference is the short paralophid in all the teeth. In MPGJ 311 from Tecolotlán Basin, all the features of the occlusal surface match up with MPGJ 310 from Coecillos except the high paralophid, which is similar to the Juchipila specimen. Variation in the structures of the occlusal surface of the lower teeth of the *D. mexicanus* from Juchipila and specimens of late Hemphillian faunas of Coecillos of the San Miguel de Allende Basin and Santa Maria in the Tecolotlán Basin should be considered as individual variation within the population.

When compared with the figures of *D. interpolatus*, such as plates 50 and 51 in Matthew and Stirton (1930) and plate 8, figure 12, of Quinn (1955), the main dissimilarities are in premolars; in particular, the reduced metastyloid and the protoconid and hypoconid are strongly rounded in comparison with the Juchipila jaw. However, in MPGJ 311 from Santa Maria in the Tecolotlán Basin should be considered as individual variation within the population.

Figure 13 MPGJ 1682, *Dinohippus mexicanus*, skull fragment, in occlusal view, showing partially broken P2, P3 with protocone with well-developed heel, P4 with a wooden-shoe shape and open postprotoconal groove. Locality ZJ 30 Mixton, Juchipila, Zacatecas.

Figure 14 MPGJ 1683, *Dinohippus mexicanus*, jaw fragment with right and left 1-3, lower canine and right p2-m3. Locality ZJ 34 Wang, Juchipila locality Zacatecas.
Maria, both structures are rounded, similar to *D. interpolatus* illustrated by Matthew and Stirton (1930).

In conclusion, the dental differences between the jaws in MPGJ 1983 and MPGJ 1635, both from the Juchipila Basin, are attributed to the wear (= age) and individual variations of the population, similar to those observed in the jaws assigned to *D. mexicanus* from other Hemphillian faunas in central Mexico.

**DISCUSSION.** The most important difference that occurs in the skull from the Juchipila specimen is the absence of DPOF, represented only by a weak, almost imperceptible depression, which contrasts with the other Mexican specimens that have been referred to as *D. mexicanus*, reported from Rancho El Ocote (MacFadden and Carranza-Castañeda, 2004) in addition to the materials from Tecolotlán and San Miguel de Allende locality that have been discussed in this article. The structures of the teeth of the Juchipila skull are different from other specimens referred to as *D. mexicanus*. The observed differences in the upper and lower molars, protocone, hypocone, fossettes, metaconid-metastylid, ectoflexid, and so on are similar to the observed differences that correspond to variations in the natural wear of the molars.

In comparison with *D. leidyamts* and *D. interpolatus*, the main differences are the well-developed DPOF and the features of the occlusal surfaces. The protocormes of the Juchipila teeth are more advanced, as indicated by the very well developed heel and elongated posterior border and concave lingual margin (wooden-shoe shape), features not observed in *D. leidyamts* and *D. interpolatus*.

Although the Juchipila specimens show important characteristics that shed light on the evolutionary trend of *Dinohippus*, this topic is beyond the scope of this article. All Juchipila horse materials are used because of their importance in the biostratigraphy and correlations to late Tertiary faunas in central Mexico; however, it is important to point out that the skull from Juchipila reveals new information about the genus *Dinohippus*. The skull from Juchipila is not *D. interpolatus* because in that species the DPOF is complex and the molar fossa is a constant structure in the facial region (Kelly, 1998). An additional criterion related to the identification of *D. interpolatus* is the strong curvature of the teeth documented by several researchers (Matthew and Stirton, 1930; MacFadden, 1984; Kelly, 1995; Azzaroli, 1988). However, the curvature of the teeth of *Dinohippus* from Juchipila is not so different from that of teeth of other late Hemphillian faunas in central Mexico. In addition, the curvature criterion cannot be used in the isolated teeth from Juchipila, as these specimens represent an individual and so are worn very low. The molar fossa is absent in all of the Mexican skulls.

The DPOF in the skulls from central Mexico present a wide range of shape and depth. Thus, the taxonomic value of this feature is reduced even for horses from a restricted geographic area like Guanajuato, Jalisco, and Zacatecas, which are Hemphillian in age.

We have demonstrated that the Juchipila skull, based on the structures of the occlusal surface of the teeth, corresponds to *Dinohippus*. The most critical characteristics include protocones with flat lingual borders and a wooden-shoe shape in P4-M1. Likewise, preprotoconal grooves are consistent, and the postprotoconal grooves are open even in old teeth; the hypocones and hypoconal grooves are moderately developed, and the fossette borders are very simple. Finally, the protoconids and hypoconids are faintly flat. In addition, other criteria employed are the shape and depth of the ectoflexid in molars and premolars. The lower teeth illustrate the most significant dental features that show similarities between Juchipila *D. mexicanus* with those of other late Hemphillian localities in central Mexico.

| Table 8 | Comparative measurements (in mm) of the upper dentition of *Dinohippus mexicanus* from Juchipila Basin and other maxillaries from late Hemphillian faunas of central Mexico. |
|---------|-------------------------------------------------|
| MP Dj 1682 | P2 | P3 | P4 | M1 | M2 | M3 |
| L APL | 27.2 | 24.5 | 24.3 | 22.5 | 25.2 |
| L TRW | 26.8 | 25.7 | 25.8 | 24.0 | 22.3 |
| MP Dj 856, San Miguel de Allende Basin | | | | | | |
| R APL | 25.3 | 23.4 | 21.3 | 22.4 | 25.3 |
| R TRW | 27.4 | 27.2 | 25.2 | 24.8 | 22.6 |
| L APL | 33.6 | 26.2 | 23.6 | 20.8 | 24.8 |
| L TRW | 24.3 | 27.2 | 26.7 | 24.5 | 23.8 |
| MP Dj 1686, Tecolotlán Basin | | | | | | |
| L APL | 26.6 | 24.7 | | | |
| L TRW | 25.2 | 22.4 | | | |

| Table 9 | Occusal view of *Dinohippus mexicanus* from Juchipila Basin and comparative measurements of lower teeth with specimens from Coecillos and Tecolotlán areas in late Hemphillian faunas of central Mexico. |
|---------|-------------------------------------------------|
| Juchipila | Tecolotlán | Coecillos |
| MP Dj 1683 | MP Dj 1635 | MP Dj 311 | MP Dj 310 |
| APL p2-m3 | 149 | 159 | 160 |
| APL p3-4 | 51 | 45 | 53 | 52 |
| APL m1-2 | 47 | 44 | 49 | 47 |
| Diastema | | | | |
| Artw | | | | |
| p3 | 15 | 15 | 14 | 15 |
| p4 | 15 | 15 | 14 | 15 |
| m1 | 14 | 14 | 12 | 13 |
| m2 | 12 | 12 | 12 | 12 |
| Btw | | | | |
| p3 | 14 | 14 | 14 | 15 |
| p4 | 14 | 14 | 14 | 15 |
| m1 | 11 | 12 | 10 | 12 |
| m2 | 11 | 12 | 10 | 12 |
| mnl | | | | |
| p3 | 17 | 15 | 16 | 16 |
| p4 | 16 | 16 | 14 | 15 |
| m1 | 16 | 15 | 13 | 14 |
| m2 | 15 | 15 | 12 | 12 |
Distribution. Dinohippus mexicanus is present in all the late Hemphillian faunas so far known in Mexico.

Family Rhinocerotidae Owen, 1845
Rhinocerotidae, indet.

REFERRED SPECIMEN AND LOCALITY. ZJ 30 El Mixtón locality 30, MPGJ 1630, metacarpal I; locality ZT 32 La Escalera locality, MPGJ 1673, upper molar fragments.

DESCRIPTION. The only structures that can be recognized on MPGJ 1673 are the middle part of the tooth, where the medial sinus presents part of the pre fossette and medifossette. Likewise, the specimens show enamel and dentine characteristic of rhinoceroses.

DISTRIBUTION IN MEXICO. Rhinocerotidae remains have been collected in all late Hemphillian faunas of central Mexico and have been assigned to Teleoceras fossiger (= T. hicki).

Order Artiodactyla Owen, 1848
Family Antilocapridae Gray, 1866
Subfamily Merocodontinae Brooke, 1876
Genus Cosoryx Leidy, 1869
cf. Cosoryx sp.

REFERRED SPECIMEN AND LOCALITY. ZJ 42 Puente de Cofradia, MPGJ 1633, skull fragment with parts of the horns. ZJ 30-3 El Mixtón locality, MPGJ 1762, mandible fragment with m3-2 and part of m1 and the alveolus for p4; MPGJ 1596, mandible fragment with part of m1, alveolus of p4 and p3 complete; ZJ 41 La Pitahaya locality, MPGJ 1634, fragment of horn.

DESCRIPTION. The skull of MPGJ 1633 from the Mixtón locality is slightly damaged; the braincase is smashed dorsoventrally. Nevertheless, this specimen is otherwise excellently preserved, especially in the occipital area, where the paramastoid processes are largely complete. The braincase is almost flat and wide with a feeble parietal crest, and no sutures can be distinguished. A tiny fracture in the braincase shows the sutures between the squamosal and parietal bones. Two slight depressions are present in the anterior part of the frontal between the horns. The left side preserves the zygomatic arch.

The left horn-pedicle is in place, located above the orbit, and the suture between the horn and the orbit is rounded. The cross sections of the horns are almost rounded with longitudinal grooves in the back. The shaft of each is short and broken at the same height, suggesting the possibility that both were broken below the burr, as they are preserved, no burr is present (Fig. 15A). The occipital area is almost flat and wide surrounded by the lambdoidal crest, which is complete; a small external occipital protuberance interrupts the occipital bone medially in the upper part and does not reach the foramen magnum. The mastoid area is especially wide, almost the same size as the occipital bone; the paramastoid process is partially broken. The condyles are big and well preserved and joined to the mastoid process (Fig. 15B). On the ventral surface, the left side preserves the auditory bulla; the basioccipital and basisphenoid are well preserved, as are part of the pterygoid region.

MPGJ 1634 is a large and straight fragment of the horn, which is very badly preserved; however it is clearly rounded in cross section, pointed in the end and not twisted. We tentatively assign it to Cosoryx.

In the jaw fragment of MPGJ 1762, only the anterior lobe of the m3 is complete, and it is low. The middle column has the half left, and the posterior column is broken in the middle part; however, the accessory column is evident. The m2 is complete; m1 preserves only the posterior column, and p4 is represented by
the alveolus with the roots in place, and the size can be distinguished, being equivalent to half of m1. In MPGJ 1596, the p3 is smaller than the alveolus of p4, and both premolars are smaller than half of the m1.

**DISCUSSION.** The specimen is assigned to Cosoryx on the basis of the horns being almost round in cross section with a small shaft and no evidence of a burr. The left horn that is in place is tilted slightly to the front and outside. The absence of the burr suggests a young individual; however, there is no evidence of sutures in the skull. It is possible that the horns were broken below the burr. It is important to point out that the premolars are extremely reduced; the size is almost half of that of m1. All these features have been described by different authors in the genus Cosoryx (Frick, 1937; Skinner and Taylor, 1967; Janis and Manning, 1998).

**DISTRIBUTION IN MEXICO.** In addition to those described Juchipila materials, Ismael Ferrusquia-Villafranca (personal communication, 2011) collected indeterminate, poorly preserved merodontid remains associated with a Miocene fauna of Cucatlán, state of Oaxaca, in southern Mexico.

Subfamily Antilocaprinae Gray 1866
Genus Plioceros Frick, 1937

cf. Plioceros sp.

**REFERRED SPECIMEN AND LOCALITY.** ZJ 30-10 El Mixtón locality, MPGJ 1627, well-preserved skull fragment without horns.

**DESCRIPTION.** In MPGJ 1627, fragment of a skull, the braincase is flat, almost having an angle of 90° with the occipital bone. The parietal ridges are weakly developed; two thin and shallow grooves are present in the middle. The supraorbital areas in both sides show a compressed large suture back to the orbital; these positions of the sutures suggest the base of wide horns being planted behind the orbits (Fig. 16A). The occipital area is trapezoidal and narrow in the upper part and wide toward the bottom. It is interrupted in the middle by a strong convex occipital protuberance that ends in the foramen magnum. The lambdoidal crest is narrow. The condyles are big, separated from the upper part of the paramastoid process by a deep groove. The basioccipital and basisphenoid are well preserved, including the auditory bulla, and the almost circular auditory meatus is in the right side (Fig. 14B).

**DISCUSSION.** The main character used to assign MPGJ 1627 to Plioceros is the remarkably large, flat suture of the horn behind the orbit, which suggests a compressed horn (Frick, 1937; Webb, 1969) different from Cosoryx, which has a rounded cross section. In addition, the paramastoid region is different, as the condyles are slightly smaller and separated from the paramastoid process by a deep groove. The isolated horn of MPGJ 1754 agrees with descriptions of Plioceros by different authors (Frick, 1937; Webb, 1969; Janis and Manning, 1998), and it is the most important evidence to document the existence of these two genera of antilocaprids in the Juchipila fauna.

**COMPARISON OF THE JUCHIPIA ANTILOCAPRIDS.** The two skulls from Juchipila belong to different genera because the shapes of the horn bases and their structure are different. In Cosoryx, the horns are rounded in cross section and located above the orbit, whereas in Plioceros there is no evidence of a supraorbital, rounded horn (Frick, 1937; Webb, 1969; Janis and Manning, 1998; Prothero and Foss, 2007). In the Cosoryx skull, the shaft is broken in both horns at the same height, without evidence of a burr. This suggests that the specimen may correspond to a young individual, even though no sutures can be observed to prove this interpretation. Another important difference between Juchipila skulls is in the occipital area; the occipital bone in Cosoryx is flat, interrupted only by a small and

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Figure 16 MPGJ 1627, cf. Plioceros sp., skull fragment. A. Dorsal view with large horn sutures above the orbits. B. Occipital view. Locality ZJ 30 Mixtón, Juchipila, Zacatecas.
narrow external occipital protuberance that is joined with the lambdoidal crest but does not reach the foramen magnum. In *Plioceros* the large horn sutures are completely different from those of *Cosoryx*, the condyles and lambdoidal crest are almost straight, and the occipital area is interrupted by a convex occipital protuberance that separates slightly concave valleys on both sides of the occipital area (Table 10).

**DISTRIBUTION IN MEXICO.** These skulls represent the first record of *Cosoryx* and *Plioceros* in the Hemphillian faunas of Mexico.

Genus *Sphenopalos* Merriam, 1909

**REFERRED SPECIMEN AND LOCALITY.** ZJ 47 El Resbalón, MPGJ 2042, left horn.

**DESCRIPTION.** The specimen is a well-preserved left horn, complete from the base to the top. The distal end is bifurcate in two small prongs and twisted. The anterior tine is small and twists laterally with a small anterior flange, and the posterior prong is orientated mediadly and is more heavy and rounded (Fig. 17). All these characters had been mentioned previously (Frick, 1937; Barbour and Schultz, 1941; Janis and Manning, 1998). This horn is completely different from other specimen of antilocaprids collected in the Juchipila Basin.

**DISTRIBUTION IN MEXICO.** This is the first record of *Sphenopalos* in the Hemphillian faunas of central Mexico.

Family Camelidae Gray, 1821

Subfamily Camelinae Gray, 1821

Genus *Alforjas* Harrison, 1979

*Alforjas taylori* Harrison, 1979

**REFERRED SPECIMEN AND LOCALITY.** The specimen is an almost complete mandible from locality ZJ 48 La Copa, MPGJ 1998.

**DESCRIPTION.** MPGJ 1998, by its dental wear, belongs to an adult individual. The left side is broken in the diastema close to the mental foramen and has two rooted alveoli of p3. The right side comprises the diastema, c1 and p1, and complete dentition of p3-m3. The ascending rami are almost complete in both sides; the coronoid process and the condyle are partially broken. The jaw is deep; the symphysis is narrow and concave in the ventral side. The right c1 is partially broken; the inner side is flat, and the external side is slightly convex, showing a blade shape. The p1 is almost rounded and single rooted, located slightly anterior to the mental foramen. The diastema of c1-p1 is ~18.8 mm and between p1-p3 is ~51.6 mm. Its ventral border is concave and ~42.4 mm deep from the dorsal diastema border. The dorsal crest of mandibular symphysis is sharp and narrow. The horizontal ramus is convex below the p3-m3 until the thin and strong angular process. This structure ascends posteriorly and ends in an evident hook, separated from the condyle by a concave surface. The right condyle is largely complete and massive and is convex in the top. The coronoid process is long and complete in the left side, ending in a flat surface oriented backward.

The anteroposterior distance of the angular process to the hypoconulid is 103 mm, the distance across of the ascendant ramus below the condyle is 68 mm, and the length from the ventral part of the angular process to the condyle is 132 mm. The depth of the jaw from the ventral part to the base to the m3 hypoconid is 68.6 mm, and the depth in the anterior part of m1 is 49.6 mm (Fig. 18).

The cheek teeth are hypsodont; p3 is double rooted, with a height of 14.4 mm, nearly the same as in p4, and the occlusal surface is without evidence of an open fossettid in the lingual or labial side; it is convex labially with faint groove in the middle. The lingual side in the most anterior part is reduced with slight groove in the end; the rest of the lingual side is convex without lakes. The p4 has two roots and a triangular outline 20 mm in length; its posterior part wider; its fossettid is worn away without evidence to be open in lingual or labial side; in the left p4 is present a small residue of enamel that is evidence of the fossettid; the anterolingual part has a shallow groove and ends in a sharp lingual apex oriented lingually.

The protoconid and hypoconid of the molars are U shaped; parastylids are present in m2-3 but very weak in m1; protostylids are absent in molars. The metastylid is evident only in the m3, the trigonid and talonid fossa are narrow and large, and the ectolix is deep. The hypoconulid of m3 is lobular, U shaped, and deflected slightly to the labial side.

**DISCUSSION.** The jaw from the Juchipila deposits is here referred to *Alforjas* by its most robust size in comparison with other species of *Hemianchena* and by the presence of the p1, double-rooted p3, and no lakes or open fossettid in the lingual or labial side of the premolars. In addition, the horizontal rami of the jaw is deep, with strong angular process, and the coronoid process is long and oriented posteriorly, the condyle being concave and slightly convex in the dorsal part, features that differentiate it from other Lamiini.

When comparing the measurements of the teeth of *A. taylori* from those in the Edson Local fauna, Kansas (Harrison, 1979), the proportions of the specimen from Zacatecas are similar and fall within the range of the individual variation determined by age or abrasion of the teeth (Table 11).

In comparison with Camelops, it differs in the absence of p1-p3, the reduced p4, high degree of hypsodonty in molars, and the shape of the dorsal surface of the condyle. In comparison with *Pleolama mckennai*, the Juchipila jaw shares the presence of p1-3 and similar shape of p4; however, the larger dimensions of *Alforjas* from Juchipila (Fig. 18) contrast with the measurements of *P. mckennai* (Webb and Meachen, 2004) and *Hemianchena vera* from Mexico or the Coffee Ranch as well as *Hemianchena blancoensis* from the Blancon faunas of Mexico (Dalquest, 1980; Jimenez-Hidalgo and Carranza-Castañeda, 2010).

**DISTRIBUTION IN MEXICO.** *Alforjas* has been collected only in the Hemphillian localities of San Miguel de Allende graben, state of Guanajuato.

Subfamily Tayassuinae Palmer, 1897

Gen. and sp. indet.

**REFERRED SPECIMEN AND LOCALITY.** Locality ZJ 30-8, MPGJ 1700, C1 in the alveolus.

**DESCRIPTION.** The specimen is a fragment of the right symphysis with only part of the root of the canine. Its triangular

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### Table 10 Comparative measurements (in mm) of the skulls of *Cosoryx* and *Plioceros* from the Juchipila Basin, Zacatecas, Mexico. ~ indicates estimates.

|          | Cosoryx | Plioceros |
|----------|---------|-----------|
| Width    | 34      | 32        |
| Length   | 47      | 43        |
| Height   | 37      | 39        |
| Width    | 68.7    | 75        |
| Height   | 28      | 23        |
| Width    | 33      | 63        |

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Figure 17  MPGj 2042, Sphenophalos sp., left horn with small anterior flange. Locality ZJ 47 El Resbalón, Juchipila, Zacatecas.
shape in cross section is comparable with tusks of maxillae collected in different Hemphillian localities in central Mexico faunas.

**DISTRIBUTION IN MEXICO.** The only previous report of peccaries in the study area is *P. rex*, mentioned by López (1991). Fossil remains of peccaries have been collected in all late Hemphillian localities of the San Miguel de Allende Basin and the Tecolotlán Basin (Fig. 1).

**BIOCHRONOLOGIC CORRELATION OF THE HEMPHILLIAN FAUNAS FROM CENTRAL MEXICO**

The results of our investigations in the northern part of the Mexican Volcanic Belt have proven the existence of at least 12 fossil sites containing material referred to the late Hemphillian age. From these, eight localities have been widely discussed in the
specialized literature related to Neogene continental biostratigraphy of Mexico, and six new sites, discovered in the central western states of Jalisco, Nayarit, and Zacatecas, are presented for the first time in this article.

The eight localities previously known, particularly those in the San Miguel de Allende area, state of Guanajuato, and in the Tecolotlán area, state of Jalisco, and their late Hemphillian faunas have been widely investigated. The information derived from multiple taphonomical and geochronological studies carried out in these areas within the last 25 years (Carranza-Castañeda, 1989, 1992, 1994; Carranza-Castañeda and Ferrusquia Villafranca, 1978, 1979; Carranza-Castañeda and Espinosa Arrubarrena, 1994; Carranza-Castañeda and Miller, 2004; Flynn et al., 2005; Jimenez Hidalgo and Carranza-Castañeda, 2010; Miller and Carranza-Castañeda, 1984, 1998b, 2001; Wang and Carranza-Castañeda, 2008) has demonstrated the validity of certain taxa as biostratigraphic indicators of the Hemphillian ages (Hh2 and Hh3). For instance, the presence of the equid *Calippus*, collected in the Juchipila, Zietla, La Presa, Santo Domingo, and Jalostotitlan localities, has been critical to characterize what we consider as the Hh2 age. Furthermore, it is important to indicate that *Naunipus aztecus* in the areas investigated has been found only in Hh3 (never in Hh2). On the other hand, the six new areas investigated (Fig. 1) encompass the following sites: 1) Santo Domingo and Los Velis localities (in the limits of the states of Jalisco and Zacatecas), 2) the Jalostotitlan locality (in the same general area as Teocalitlán) in the state of Jalisco, 3) El Gigante and El Trapiche localities (in the state of Nayarit), and 4) the Juchipila fauna (in the state of Zacatecas). Although this last locality is characterized by its abundant and diverse fauna (in terms of macromammals), it is important to mention the total absence of rodents and lagomorphs. Interestingly, that seems to be the case in almost all the known Hemphillian faunas in the central part of Mexico, with the only exception of the basal layer of the Rancho El Ocote fauna, rich in cricetid materials.

In Figure 19, we summarize the biochronologic ranges of all the taxa contained within the 11 mammalian faunal assemblages discussed in this work (Table 12). The importance of the information displayed in Figures 19 and 20 rests in two major aspects. One is the stratigraphic control of the fauna contained in the collected sequences, and the second is related to the volcanoclastic nature of the sediments bearing the paleontological materials that yielded confirmable radiometric dates for the assemblages. Through the integration of these two aspects, the correlation of Hh2 ages, present in five localities (Zietla, La Presa, Santo Domingo, Jalostotitlan, and Juchipila), was established. The results of the Hemphillian Mexican faunas are enlisted following the scheme used by Tedford et al.'s (2004) mammalian biochronology of the Neogene, and rather than proposing a Mexican definition of the subdivisions of the Hemphillian, our intention is to point out some significant differences, such as *Naunipus-Calippus* in separated strata and the new finds of *Plometanastes, A. ansae*, Cosoryx, Piloceros, and *Sphenophalos* in central Mexico and Zacatecas. Although the biostratigraphic correlation of faunas from central Mexico and elsewhere are still in progress, the importance of these results is supported by the radiometric dates obtained from the main localities discussed.

**SOME NOTES CONCERNING THE IMPORTANCE OF THE MEXICAN HEMPHILLIAN FAUNAS**

To support the data used in assembling Figure 20, a brief discussion of the most important localities is included in this work. To avoid needless extension of this article, it is recommended to consult the following references, where the stratigraphic sections of all the Mexican Hemphillian faunas are broadly discussed: Carranza-Castañeda (1989, 2006), Miller and Carranza-Castañeda (1984), and Carranza-Castañeda and Miller (2004). Nevertheless, in order to give an overview of the basic aspects of the materials discussed in Table 12, we present a brief discussion of the major stratigraphic, lithologic, and faunistic aspects of the 12 localities (Fig. 1) that appear in Figure 20, with some important comments regarding their biochronologic correlations.

**THE TEHUICHLA AND LA PLEGARIA AREAS IN THE STATE OF HIDALGO**

Tehuichila represents the oldest locality in Mexico, where a Hemphillian fauna has been described. The first reports of horses and other mammals come from Leidy (1882) and Cope (1885, 1886, 1893). The problem is that all the fossils were collected by the coal mine workers, without any stratigraphic control. Therefore, the assemblage was assigned only to the upper Miocene, “Loup Fork Formation” (Cope, 1885).

In the 20th century, Almanza (1956), besides establishing the stratigraphy of the Zacualtipan basin, reported the discovery of a horse tooth “Hipparion (?)” embedded in a coal layer and placed in the lower part of the section. This is the first report where any fossil from Tehuichila is situated in specific layer in the sequence. More recently, Ferrusquia Villafranca (1978) assigned all the Tehuichila fauna (a single unit) to the “Early or Middle Pliocene age.” During the 1990s in the Zietla Village, Carranza and collaborators studied the lower section of the Tehuichila beds (in the context of Almanza’s op cit. Zietla stratigraphic sequence). In their results, they reported the taxa Agrostotherium, Teleoceras, Danohippus, Calippus, and Hexobolomeryx and two teeth of small megalonychids. The fauna was assigned to the early-late Hemphillian age (Hh2) by the presence of Calippus and Danohippus.

The outcome of this investigation clearly indicates that the Zietla fauna (Carranza-Castañeda, 1994) corresponds to the lower part of the Tehuichila stratigraphic sequence (“Tehuichila Fauna”) that have been extensively mentioned in the literature.

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**Table 11 Measurements (in mm) of the teeth of MPG 1998, *Altorius taylori* from Juchipila, Zacatecas and Edson local fauna, Kansas.**

| Measurement | Juchipila | Edson local fauna |
|-------------|-----------|-------------------|
| c1-m3 Length | 2.34 | 19.25-19.99 |
| p1-m3 Diastema | 2.04 | |
| p3-m3 Length | 1.39 | 12.46-13.29 |
| c1-p1 Diastema | -1.9 | 1.19-2.05 |
| p1-p3 Diastema | -5.3 | 2.86-4.24 |
| c1 Length | -1.3 | 0.97-1.42 |
| p1 Width | -0.78 | 0.46-0.85 |
| p3 Width | -0.58 | 0.39-0.42 |
| p4 Length | 1.93 | 1.91-2.12 |
| m1 Length | 2.87 | 2.24-3.31 |
| m2 Length | 3.48 | 2.81-3.92 |
| m3 Length | 4.30 | 3.85-4.65 |
| Width of condyle | 2.76-3.32 | 1.31-1.89 |
Furthermore, present biostratigraphic evidence suggests that Cope's (1885) *Hippotherium peninsulatum* (= *Nannippus peninsulatus* sensu MacFadden, 1984) comes from the upper beds that belong to the Blancon age of the Tlatoxca Layers, reported by Almanza (1956), and not from the lower part of the section, where the rest of the fauna has been collected. Within the area represented in Figure 20 for the Tehuichiha area, the dotted lines symbolize surfaces that during our fieldwork were covered by dense vegetation or altered by human activities.

In the first decade of the 21st century, the southwestern part of the state of Hidalgo, the area of Tepeji Del Rio, was investigated by Padilla-Gutierrez (2004); here he described an interesting late Hemphillian assemblage in an locality known as La Plegaria. The results of Padilla-Gutierrez (op cit.) correlate with at least three Hh3 sites in Guanajuato.

**THE SAN MIGUEL ALLENDE BASIN FAUNAS IN THE STATE OF GUANAJUATO**

In Rancho El Ocote area, the age assignments given to the mammalian species discussed in this article were based on the biostratigraphic implications of the Rancho El Ocote fauna (Carranza-Castañeda, 1989; Carranza-Castañeda and Ferrusquia-Villafranca, 1978, 1979). The reason to consider the Rancho El
Table 12: Faunal list of the Hemphillian faunas from central Mexico.

| Taxa                        | Gunajuato                        | Hidalgo                        |
|-----------------------------|----------------------------------|--------------------------------|
|                             | Rancho El Ocote                  | San Miguel de Allende Basin    | Tepeji del Rio Basin | Zacualtipán Basin |
|                             | Rino layer                      | White layer                   | Rinconada           | Arroyo Tepalcates | Coecilos | La Presa | Plegaria | Tehuitzila | Zictla |
| Xenarthra                   |                                  |                                |                     |                    |          |          |          |            |        |
| Megalonyx sp.               |                                  | X                              | X                   | X                   | X        |          |          |            |        |
| Paranylodon sp.             |                                  |                                |                     |                     |          |          |          |            |        |
| Phororctonastes sp.         |                                  |                                |                     |                     |          |          |          |            |        |
| Carnivora                   |                                  |                                |                     |                     |          |          |          |            |        |
| Conepattus sanniguelensis   |                                  |                                |                     |                     |          |          |          |            |        |
| Canis ferox                 |                                  |                                |                     |                     |          |          |          |            |        |
| Borophagus secundus         |                                  | X                              | X                   | X                   | X        |          |          |            |        |
| Agriotherium schneideri     |                                  |                                |                     |                     |          |          |          |            |        |
| Taxidea mexicana            |                                  |                                |                     |                     |          |          |          |            |        |
| Taxidea sp.                 |                                  |                                |                     |                     |          |          |          |            |        |
| Pseudaelurus? Intrepidus     |                                  |                                |                     |                     |          |          |          |            |        |
| Proboscidea                 |                                  |                                |                     |                     |          |          |          |            |        |
| Gomphotheriidae             |                                  |                                |                     |                     |          |          |          |            |        |
| Rhynchotherium              |                                  | X                              | ?                   | X                   | ?        |          |          |            |        |
| Perissodactyla              |                                  |                                |                     |                     |          |          |          |            |        |
| Neohipparchon eurystyle     |                                  | X                              | X                   | X                   | X        |          |          |            |        |
| Nannipippus aztecus         |                                  |                                |                     |                     |          |          |          |            |        |
| Astrohippus stocki          |                                  | X                              | ?                   | X                   | X        |          |          |            |        |
| Astrohippus ansae           |                                  |                                |                     |                     |          |          |          |            |        |
| Dinohippus mexicanus        |                                  | X                              | X                   | X                   | X        |          |          |            |        |
| Dinohippus interpolatus     |                                  |                                |                     |                     |          |          |          |            |        |
| Calippus (Grammohippus)     |                                  |                                |                     |                     |          |          |          |            |        |
| bicornutus                  |                                  |                                |                     |                     |          |          |          |            |        |
| Tylocoerus fossiger         |                                  | X                              | ?                   | X                   | X        |          |          |            |        |
| Artiodactyla                |                                  |                                |                     |                     |          |          |          |            |        |
| Kyploceras sp.              |                                  |                                |                     |                     |          |          |          |            |        |
| Heliocharta gracilis        |                                  | X                              | ?                   | ?                   |          |          |          |            |        |
| Heliocharta indet.          |                                  |                                |                     |                     |          |          |          |            |        |
| Heliocharta vera            |                                  | X                              | X                   | X                   | X        |          |          |            |        |
| Allocas sp.                 |                                  | X                              | X                   | X                   | X        |          |          |            |        |
| Allocas taylori             |                                  |                                |                     |                     |          |          |          |            |        |
| Megalopolops matthewi       |                                  | X                              | X                   | X                   | X        |          |          |            |        |
| Placocheros sp.             |                                  |                                |                     |                     |          |          |          |            |        |
| Splenopolaos sp.            |                                  |                                |                     |                     |          |          |          |            |        |
| Cosorix sp.                 |                                  |                                |                     |                     |          |          |          |            |        |
| Tezoceros sp.               |                                  |                                |                     |                     |          |          |          |            |        |
| Ct. Subantilocapra          |                                  |                                |                     |                     |          |          |          |            |        |
| Hexoberoceryx fricki        |                                  | X                              | X                   | X                   | X        |          |          |            |        |
| Prosthenius sp.             |                                  |                                |                     |                     |          |          |          |            |        |
| Catalogus brachydontus      |                                  | X                              | X                   | X                   | X        |          |          |            |        |

Ocote as the type or reference locality for the late and latest Hemphillian in central Mexico is 1) the abundance and diversity of mammalian fossil indexes that have been recovered in the last 25 years (Table 12) and 2) the reliable stratigraphical and taphonomical information derived from multiples studies that have been applied in the characterization of three stratigraphic levels, bracketed with radiometric dates (Carranza-Castañeda, 1989; Kowallis et al., 1999).

The lower unit (named the Rhinol layer because of the presence of Teleoceras) is composed by clay and sandy gravel channels and contains the most representative mammals of the Hemphillian Hb3 age. The horses N. aztecs, N. eurystyle and A. stockii, and D. mexicanus, along with the carnivores Borophagus, Machair-
characterizes the Hemphillian Hh4 age. Here, the associated fauna is represented by the horses *D. mexicanus* and a few remains of *A. stockii*; the proboscidean *Rhynebotherium* sp.; the artiodactyls *Alforjas, Megatylopus*, and *Hexobelomeryx*; and the oldest record in North America of *Paramylodon garbanti*. Considering the horse distribution and absence of the main index fossils for the late Hemphillian, including the remains of any Blancan indicators, the fauna of this layer represents the latest late Hemphillian age (Hh4) in central Mexico.

The El Ocote locality is so important in the biostratigraphy of central Mexico that, above the latest Hemphillian, represented by the White layer, there are at least 2 m of early Blancan sediments. These deposits, rich in volcanic detritus, were analyzed by the 40Ar/39Ar method, and the age obtained from this analysis was $4.7 \pm 0.02$ Ma (Carranza-Castañeda, 1989; Kowallis et al., 1999). This result places the Hemphillian-Blancan boundary in Mexico between $4.74 \pm 0.14$ and $4.89 \pm 0.16$ (Bell et al., 2004; Flynn et al., 2005).

**THE RANCHO VIEJO AREA**

In the biostratigraphic sequence of this area, the basal layer contains the oldest fauna represented by La Presa locality, which contains the horse *C. (Grammohippus) bondarensis* and a few isolated molars of *D. interpolatus* (?) along with the artiodactyls *Megatylopus* and *Hexobelomeryx* that belong to the late-early Hemphillian (Hh2) age (Carranza-Castañeda, 2006; Carranza-Castañeda and Espinosa Arrubarena, 1994).
Overlying La Presa deposits, in unconsolidated lake sediments, the fauna from Arroyo Tepalcates has been recovered. This locality contains abundant materials of carnivores and horses (Table 12) that correlate with what has been reported from the Rio layer of Rancho El Ocote (Hh3).

Within the general Rancho Viejo area, another Hemphillian fauna is included in this work the Rancho San Martin locality. In this site, an almost complete skull of Notolagus velox has been recovered, and the type specimen of Canis ferox comes from this place (Miller and Carranza-Castañeda, 1998a).

**THE COECILLOS AREA**

In the Coecillos area, several sites with late Hemphillian fossils are collectively known as the Coecillos. Here, D. mexicanus, N. euthystyle, A. stockii, and N. azteca are common in the lower layers of the local section and correlate with the (Hh3) Rhino layer of Rancho El Ocote (Table 12). Recent research carried out toward the top of the section at the Arroyo de Emilio locality (within the same area) resulted in the recovery of the oldest skunk in central Mexico, Conepatus sanmiguelensis, involving the GABI (Wang and Carranza-Castañeda, 2008). It is important to mention that the discontinuity of the lines that form the column that correspond to the Coecillos locality does not represent an stratigraphic hiatus; it simply means that there is a discontinuity between the lower and the upper parts of the section, with a separation of less than 4 km.

**THE LOS GALVANES AREA**

At the base of the sequence lies the Rinconada locality, which contains the most abundant and diverse representation of carnivores and horses except for N. azteca (Table 12). Volcanic ash that is interbedded with the fossil-bearing strata was analyzed by the fission track method, which resulted in an age of 4.4 ± 0.3 Ma (Kowallis et al., 1999). The stratigraphic position of the fossils of Rinconada correlates with the lacustrine sediments of Arroyo Tepalcates, containing similar fauna to that of Rinconada and therefore correlating with the lower layer of Rancho El Ocote, and is referred to Hh3, late Hemphillian (Carranza-Castañeda, 1992).

**HEMPHILLIAN FAUNA OF THE STATE OF JALISCO**

**The Tecolotlán Graben**

Around 100 km west of Guadalajara lies an almost unknown basin where several Hemphillian sites have been recorded in the last 10 years (Miller and Carranza-Castañeda, 2001; Carranza-Castañeda and Miller, 2004). The two more important, therefore mentioned here, are the Santa Maria and La Hacienda localities. The early-late Hemphillian age (Hh3) is represented in the Santa Maria locality, mainly because of the abundance of the equids N. azteca, N. euthystyle, and D. mexicanus and a few remains of A. stockii besides several carnivores and other index fossils of this age (Table 12). However, the sequence in the Tecolotlán area is interrupted by sandy lacustrine sediments that crop out with a thickness of 6–8 m in the southern part of the graben, dividing the late Hemphillian sequence. Above the lacustrine sediments, the upper late Hemphillian strata that belong to the La Hacienda locality include the carnivores and artiodactyl index fossils of the same Hemphillian (Hh3) age. In addition, abundant material of rodents and lagomorphs have been recovered and are under investigation; in the near future, the Hacienda locality will be the second site in central Mexico, where microvertebrate remains have been reported. Although the equids Astrohippus and Nannippus have not been recovered in the site so far, D. mexicanus and N. euthystyle are fairly abundant. Samples of the volcanic ash interbedded with the fossil-bearing strata were collected in the locality La Hacienda. The result of the radiometric dating (³⁹Ar/³⁹Ar method) yielded an age of 4.89 ± 0.16 Ma (Kowallis et al., 1999). This age assignment coincides
with the Hemphillian (Hh3). The results of the Tecomltitlan basin, compared with other fauna in central Mexico, clearly show that the Santa Maria area correlates with the (Hh3) Rhino layer of Rancho El Ocate and the lower layer of Cocillos locality by the presence of *N. aztecs.* On the other hand, the La Hacienda locality (Table 12) correlates with the (Hh3) localities of Arroyo Tepalcates, Rinconada, and Rancho San Martin of the San Miguel Allende basin.

**The Tecomltitlan-Jalostotitan Basin**

This graben is located near 55 km northeast from the Juchipila basin. The preliminary research done in the Tecomltitlan area was carried out by Montellano-Ballesteros (1997), and her results are depicted a typical late Hemphillian (Hh3) age fauna that has been correlated with Rancho El Ocate and Rinconada from the San Miguel Allende Basin (Table 12, Fig. 20). The dotted lines depicted in the area of Tecomltitlan in Figure 20 represent the reasonable doubt that exists within such a large basin (3.5 km); we are not able yet to delimit either the base of the Tecomltitlan site or the top of the Jalostotitan section. More fieldwork will yield better areas in which the relationships of this unit are better expressed.

In the same basin, close to the Jalostotitan city (32 km to the southeast), in preliminary fieldwork, a complete jaw of *C. (Grammohippus) bonduresiensis* was collected. The single presence of this taxon allows the correlation with all other early-late Hemphillian (Hh2) sites in central Mexico (e.g., Juchipila, Santo Domingo, Zietia, and La Presa localities).

**THE HEMPHILLIAN FAUNAS FROM THE STATE OF MICHOACÁN**

**The Chincua Locality**

In this small area located 120 km south of the city of Morelia, an interesting mammal assemblage was collected. Until now, the following taxa have been reported: *D. interpolaris* (?), *Teleoceras* sp., *N. eurystyle*, *Megalotolopus* sp., *Catagonus* sp. (Garduno et al., 2009), unfortunately, after the 2006 field season, municipal urban development destroyed the fossiliferous outcrop.

**LATE HEMPHILLIAN FAUNAS OF THE STATE OF NAYARIT**

**El Gigante Locality**

During the early 1970s, the research in this area was performed by a crew of Los Angeles County Museum of Natural History, and therefore the collected materials are housed at this museum. Carranza-Castañeda (2006) reported additional material collected in the area that includes a jaw fragment of *Rhynchotherium*, isolated teeth of *D. mexicanus* and *N. eurystyle*, and some antilocaprid teeth fragments. So far the material has been assigned to the late Hemphillian (Hh3) age. In a more extensive area, 45 km south of the El Gigante locality (known as the El Trapiche Village), a small but representative Hemphillian fauna was collected. Here, remains of *Teleoceras*, isolated teeth of *Dinohippus* and *Neohipparion*, tooth fragments of a possible *Catagonus* sp., and fragments of mastodon limb bones are part of the collection. Samples of a volcanic ash layer located above the fossil strata were collected and dated by the U-Pb method. The outcome of this analysis gave an age of 5.12 ± 0.26 Ma. This radiometric result is in complete agreement with the late Hemphillian (Hh3) biochronologic age of this fauna and therefore correlates with the main Hemphillian faunas of the San Miguel Allende graben.

**TWO HEMPHILLIAN LOCALITIES FROM THE STATE OF ZACATECAS**

The sites are located in the Colotlán-Tlaltenango basin, only 50 km west of the Juchipila area. The basin is filled with lacustrine sediments about 100 m thick. Although fieldwork has been carried on for the last seven years, only a few fossils have been recovered. The most extensively collected is Santo Domingo locality, where *C. (Grammohippus) bonduresiensis*, *D. interpolaris* (?), and some antilocaprid remains have been found. The other site is close to the village Los Velas, 15 km north from Santo Domingo, where the leg of *N. eurystyle*, *Dinobippus* teeth, and a fragment of peccary have been collected.

**AGE AND CORRELATION IN THE JUCHIPILA BASIN**

The set of mammalian assemblages collected at different localities within the Juchipila Basin (Figs. 1 and 12) represent an example, among many others, of the importance of the continental sedimentary basins in central Mexico in relation to continental late Cenozoic biostratigraphy and the study of migration routes, dispersal processes, and extinction events that these mammalian faunas endured in Mexico and elsewhere in North America. The local faunas discussed in this article are referred to the late-late Hemphillian (Hh2) based on isotopic ages discussed above and on the presence of 1) megahyrnchids aff. *Plometanastes;* 2) the equids *C. (Grammohippus) bonduresiensis*, *A. ansae*, *N. eurystyle,* and *D. mexicanus;* 3) the merocodont *Cosoryx;* 4) the antilocaprids *Plioceros* and *Sphenophalos;* and 5) the camel *Altorjas taylorii,* which corresponds to the oldest record of this genus in Mexico.

To enhance the relevance of the biochronologic information related to the Juchipila assemblage Figure 19 shows the youngest and oldest occurrences of 11 taxa that have been documented in this region. These first and last occurrences in the Juchipila fauna are also compared with those reported from the main Hemphillian localities of North America in the same figure (Tedford et al., 1987, 2004; Janis and Manning, 1998).

Several important features recorded in Figure 19 must be stressed:

1. The *Plometanastes* fossil found in Juchipila is the youngest and southernmost record so far known in North America.
2. *Nannipptts aztecs,* which is not present in the Juchipila fauna, is restricted to Hh3 in Rancho El Ocate, Cocillos, and Santa Maria localities as opposed to other North American faunas in which this taxon ranges from the Clarendonian–Hemphillian boundary to the latest Hemphillian (Hh4).
3. The *D. mexicanus* specimen found in Juchipila is the oldest record so far known, and when the upper stratigraphic record of this taxon is compared with those in the North American faunas, it corresponds with that found in the central Mexico faunas.
4. *Calippus* (*Grammohippus*) *bonduresiensis* is found in Mexico in the Hh2 of Juchipila, La Presa, and Zietia localities. However, in Central America, the biostratigraphic range of this taxon spans from the early-early Hemphillian (Hh1) to its boundary with Hh2. In Florida, this taxon ranges from early Hh1 to late Hh2. In this context, it is important to mention the report of the genus *Calippus* in the El Granal Local Fauna reported by Ferrusquia Villafranca (1984),...
which by far represents the oldest record of *Calippus* in Mexico (early Barstovian).

5. Although *A. taylori* ranges from the late Hemphillian Hh3 in North America, in Juchipila (the only record in Mexico) this camelid is present in early-late Hemphillian (Hh2).

6. Even though the biostratigraphic ranges of *Plioceros* and *Cosoryx* in North America go from early Barstovian to late Clarendonian, their presence in the Hh2 of Juchipila (the only records in Mexico) must be noted. Future fieldwork in the northern basins of Mexico may fill this biostratigraphic gap. The Juchipila Hh2 record of *Sphenophalos* is the first in Mexico. Although its range falls within the much broader range in North America (early-late Hemphillian H1 to Hh3 late Hemphillian), its presence in Juchipila is important as it expands its southern geographic distribution in North America.

The radiometric U-Pb ages obtained from zircons recovered from ash-fall deposits interbedded with the fossil-bearing fluviolacustrine strata constitute a reliable age bracket that is consistent with the NALMA of the fossils found in the assemblage. It is important to mention that despite the presence of accidental zircons in all the ashes from Juchipila, there are 4 ashes that yielded reliable late Miocene ages (Fig. 5). Field data collected in this research, as well as those related to other localities shown in Table 13, clearly show the stratigraphic relation among the isotopically dated samples and the fossiliferous horizons.

The Juchipila megafauna age is pivotal in establishing the biochronologic correlation of the Hemphillian faunas of central Mexico (Fig. 20) and in a broader sense the chronologic correlation with the faunas of the Great Plains of North America. These correlations can be documented in isochronous sediments of the following localities in central Mexico: 1) San Miguel Allende Basin: Rancho El Ocote (Rhino layer), Rinconada, Arroyo Tepalcates, Rancho San Martin, and Cociellos; 2) Tecomoctan Basin: Santa Maria and La Hacienda localities; and 3) the poorly known El Gigante and El Trapiche localities in Nayari (Fig. 1), where *N. erystle*, *N. azteca*, *D. mexicanus*, *A. stockii*, *B. fossiger*, *B. secundus*, *Agriotherium schenideri*, and *Macrotherium cf. M. coloradensis* have been found. All these fossil horizons have been isotopically dated by fission track and \(^{18}Ar/\ ^{18}Ar\) (Kowallis et al., 1999) or U-Pb (zircon) methods (Fig. 20). This correlation is documented by the shared presence of *C. (Grammolhippus) bondurensis*, *A. ansae*, *N. erystle*, *D. mexicanus*, *Cosoryx sp.*, *Plioceros sp.*, *Sphenophalos sp.*, and *A. taylori*, similar to Mixson's Bone Bed and Leisey I C in Florida, Gracias in Honduras, Rak Camel Quarry and Chamita in New Mexico, Oskosh and Lomayne in Nebraska, and Dove Spring Fauna and the Siphon Canal locality in California (Fig. 19).

It is also worth noticing that so far there are no records of either rodents or lagomorphs within the Juchipila area. This unfortunate shortcoming represents an important limitation in establishing a more precise biostratigraphic correlation with other faunas of North America. Clearly, collecting microvertebrates from the Hemphillian sediments in the basins in central and northern Mexico is a goal that must be pursued in the future.

The associated fauna described in this work has provided new information about the last appearances within the stratigraphic range of different groups. The younger record of *Pliometanastes* is from Chamita Fauna (6.8 Ma) of New Mexico (Lindsay et al., 1984); *C. (Grammolhippus) bondurensis* is from Mixson’s Bone Bed, late-late Hemphillian of Florida; *A. ansae* is from Coffee Ranch, late Hemphillian of Texas (Dalquest, 1983; Lindsay et al., 1984); *Cosoryx* is from late Clarendonian of Nettle Spring Fauna (James, 1963) and Dove Spring Fauna (Whistler and Barb, 1992; Whistler et al., 2009), both faunas from California; the last appearance of *Plioceros* is recorded from the late Clarendonian of the Dove Spring Fauna (Whistler and Barb, 1992; Whistler et al., 2009); and *Sphenophalos* is reported for the first time in Mexican faunas, and it survived to the end of the Hemphillian, Wikkiew Fauna late Hemphillian of Arizona. All these records are depicted and summarized in Figure 19.

This suggests that some events that have been documented in localities in the United States do not necessarily occur in central Mexico. In addition, it is necessary to emphasize that in comparison with the United States, there is practically no information regarding the Cenozoic sedimentary basins of northern Mexico and that much work is still needed to fill this hiatus of paleontological information if we want to link the different processes observed in southern and central Mexico with the rest of North America.

Some of the most important remarks regarding the Juchipila megafauna can be discussed as follows:

1. Juchipila represents the youngest and southernmost record of the megalonychid aff. *Pliometanastes* in North America. However, this particular anatomical determination rests on a single element (MTIII), and therefore the generic assignment must be considered as tentative. This fossil means that the geographic range of this taxon must be extended from the lower part of the southern Chamita Fauna late-late Hemphillian, New Mexico (Lindsay et al., 1984; Tedford et al., 2004), and Withlacoochee River site, late-late Hemphillian of Florida (Webb, 1969), to the late-Hemphillian of Zacatecas in central Mexico.

2. It has been accepted that some of the younger records of the meercodont *Cosoryx* in the Great Plains correspond to the Burge and Minniechaduza faunas of Nebraska, Nettle Spring Fauna of California (James, 1963; Tedford, 1981; Tedford et al., 1987, 2004), the South Tejon Hills Fauna from California, and the southernmost locality of Round Mountain Quarry in La Española Basin, New Mexico, all of them Clarendonian in age (Lindsay et al., 1984; Tedford, 1981; Tedford et al., 2004). Therefore, the Juchipila meercodont material represents the youngest evidence of this taxon in North America, extending its previous Clarendonian records to the late-late Hemphillian. In addition, its geographical range is also modified from the northern La Española Basin of the Great Plains, New Mexico, to the more southern Juchipila Basin, where it is described for the first time in Mexico.

3. The antilocaprids *Sphenophalos* and *Plioceros* are fossils of the late-late Hemphillian age in North American faunas, and their presence in Juchipila is reported for the first time in a locality south of the U.S.-Mexico border, a fact that extends their geographic distribution from localities situated within the Great Plains (Tedford et al., 2004) to central Mexico. It is interesting to mention that so far the oldest reported camelid *Allotherium* known in Mexico was documented by Jimenez-Hidalgo and Carranza-Castañeda (2010) from the late Hemphillian lower layer (Rhino) of Rancho El Ocote locality in Guanajuato. Therefore, the report of *A. taylori* in Juchipila represents the oldest record in Mexico, as compared with its presence in the Coffee Ranch local fauna (Dalquest, 1983).

4. The remains of *C. (Grammolhippus) bondurensis* recovered in the study area represent the most abundant materials so far collected in Mexico. Other sites in which *Calippus* has been abundantly found are the Mixson’s Bone Bed, Florida,
and the Rancho Lobo from Honduras (Olson and McGrew, 1941; Hulbert, 1988). As is the case in other faunas of central Mexico (Table 12), it is important to point out that this taxon has never been found associated with N. azteces in Mexico. Although it is known that several faunas in North America show that Nanimnippus and Calippus can be present in the same strata (Tiedford et al., 1987, 2004; Leite, 1990), in fact, in our investigations on the Neogene continental faunas in central and northern Mexico, we have not been able to document such significant equid association. After 25 years of fieldwork in the central and northern areas of the Mexican Volcanic Belt, we have documented at least five faunal assemblages in which Nanimnippus and Calippus do not occur in the same layer (Carranza-Castañeda and Espinosa Arrubarea, 1994; Carranza-Castañeda, 2006).

The association of C. (Grammohippus) bonaduresis and A. anseae is reported for the first time in faunas of Mexico and supports the late-early Hemphillian age assigned to the Juchipila fauna, in contrast with the known late Hemphillian equid associations in which N. azteces, N. eurystyle, A. stockii, and D. mexicanus are found together. According to Carranza-Castañeda (2006), N. azteces shows a restricted biostratigraphic distribution within the lower section of the late Hemphillian faunas, which throughout this article correspond to the late Hemphillian Age (Hb3).

5. A skull collected in the Mixtox locality has been identified as D. mexicanus, based primarily on the structure and characters of the molars. The variations observed in the facial region differentiate this skull from other specimens of late Hemphillian Mexican faunas, which are referred to D. mexicanus. If this preliminary designation is corroborated by future investigations, the occurrence of D. mexicanus in Juchipila would be regarded as the oldest record in the Hemphillian faunas of Mexico.

An important aspect that must be considered when establishing the biochronologic correlations between localities in central Mexico and other areas is that, so far, only the associations of several species of horses with other large mammals from the same stratigraphic level are employed. This limitation is due to the paucity of rodent and lagomorph records that until now have only been reported from the basal layer of Rancho El Ocote (Carranza-Castañeda and Walton, 1992) and, to a lesser extent, in other Hemphillian faunas in the central part of Mexico. This lack of biostratigraphic information precludes a more accurate correlation with the late-early Hemphillian faunas from the Great Plains of North America.

SUMMARY AND CONCLUSIONS

This article reveals the importance of the Juchipila assemblage and draws attention to continued paleontological investigations in northern Mexican basins to fill up the big gaps of biostratigraphic information related to Clarendonian–early Hemphillian ages as well as to elucidate the migration patterns and mammal interchange across the central and northern regions of Mexico and the southern Great Plains of North America. The late Hemphillian faunas from central Mexico (19°–23° N) have been intensely studied in the past decades. This long-term research has established the mammalian diversity in the faunas and has compiled information about faunal migrations across Mexico during the late Tertiary. The data have been used to refine several established models regarding the timing of important biological events. It has also shown that the diversification of important mammalian lineages, such as the radiation of camelids, took place in central Mexico. In addition, this work includes the description of older faunal assemblages in Juchipila, never before described in Mexico.

The Juchipila Basin contains the most abundant and diverse Hb2 (Table 12) faunal assemblage in the sedimentary basins of central Mexico. The inferred age of the fauna was based on the presence of the equids C. (Grammohippus) bonaduresis, N. eurystyle, A. anseae, and D. mexicanus. In addition to this, it is reported to be the youngest and southernmost record of Cosoryx in North America, and it is present for the first time in Mexican faunas. Furthermore, the discovery of Plioceros and Sphenophalos south of the U.S. border extends their geographic range from localities within the North American Great Plains to central Mexico. Moreover, the oldest record of A. taylori in Mexican faunas is discussed. The megalyonchid material found in Juchipila is referred to Plomontanastes, which, if confirmed with additional material, represents the only record in Mexico and the southernmost occurrence in North America that can be placed in a stratigraphic context.

According to the upper limit of the chronologic ranges of Cosoryx and Plioceros in North America, it has been agreed that their extinctions correspond to the end of the Clarendonian. However, the Juchipila findings suggest that they survived for a longer period of time in areas located south of the Great Plains. Calippus (Grammohippus) bonaduresis remains are common in Juchipila. A relatively large set of isolated teeth in all stages of wear and several jaws were used to study the structural variability of the occlusal surfaces. This information was compared with isolated materials described in previous works, and we were able to document the variability range of this equid taxon in Mexican faunas and correlate its presence in all the known localities where Calippus has been found.

Nanimnippus azteces is present in Hb3 layers near the base of the sequences at Coecillos, in the Rhizo layer of Rancho El Ocote, and in the Santa Maria locality in Tecolotlán. The absence of this equid in Juchipila supports the interpretation that the Juchipila fauna corresponds mostly to Hb2 (Table 12), whereas sections of the San Miguel de Allende and Tecolotlán basins are younger.

The partial skull of D. mexicanus from Juchipila is the oldest record in Mexican faunas; its facial morphology is a key to understanding the variability of this equid in the evolution of the genus Equus. It is concluded that this specimen does not correspond to D. leidyi ( = D. interoplatus). This conclusion is based on the faint DPOF pattern in the facial region and on the observed tooth structures, such as the well-developed protocone and a lingual border parallel to the lingual margin of the teeth (in some dental elements, the border is concave with a wooden-shoe shape), an unmistakable heel, and a hypocone groove deep and open and not connected with the protocone. All the mentioned characteristics are diagnostic of D. mexicanus. However, the Juchipila skull differs from other specimens of Dinohippus from the late Hemphillian faunas of San Miguel de Allende and Tecolotlán basins because in those the DPOF pattern is much more evident, deep, and limited posteriorly.

The presence of Cosoryx in the Juchipila fauna, besides being the only known record so far in Mexico, represents the youngest specimen reported in North America. The stratigraphic range of this genus in the Great Plains faunas encompasses the Clarendonian age in faunas of Colorado, Nebraska, Wyoming, Montana, Oklahoma, and New Mexico as well as California on the West Coast. However, there are no records of merycodontids in the late-early Hemphillian faunas of North America. This finding supports the hypothesis that some important lineages from the Great Plains faunas have more extended stratigraphic ranges at lower latitudes. This same condition has been shown in a
previous work by the younger record of the protocerid Pytyoceras (Jimenez-Hidalgo, 2005) in the late Hemphillian of Rancho El Oceo (Table 12). It is also clear that the record of Cosoryx in Juchipila extends its geographic range from the southern part of the Great Plains to central Mexico.

The partial skull of the antilocaprid Plioceros found in Juchipila is also the first record in any Mexican late Hemphillian faunas, although in the Great Plain faunas, this taxon has been recorded from the early-late Barstovian to the early Hemphillian faunas of New Mexico, from the Cretaceous to the late Hemphillian of California, as well as from the early Hemphillian of Kansas and Nebraska. It is interesting that in the Juchipila Basin, Plioceros coexisted with Cosoryx and Sphenopolas. On the other hand, while the remains of Cosoryx represent the youngest record of merocodontids in North America, the partial skull of Plioceros is the southernmost record and first antilocaprid ever reported in the Mexican Hemphillian faunas. The records of Cosoryx and Plioceros in the Juchipila Basin extend their geographic range from the southern Great Plains to central Mexico and imply that there is a great hiatus of information in the sedimentary basins of central and northern Mexico. Thus, in turn, implies important gaps in the paleontological information regarding the diversity and migration of the mammalian faunas during the late Cenozoic. The antilocaprids and horses from Juchipila suggest that the environment was similar to an open savanna or an area covered by shrub vegetation. Based on the presence of C. (Grammohippus) bondarense, N. enystyle, A. ansae, the oldest record of D. mexicanus, the bone-crushing dog B. secundus, the megachirodontine remains, and the first record of the antilocaprids Cosoryx, Plioceros, and Sphenopolas, as well as A. taylori, the Juchipala mammalian assemblage is referred to the HH2 age (late-early Hemphillian).

There are several volcanic ash layers interbedded with the fossil-bearing sediments in the Juchipala Basin. Zircons sampled from different ash layers were dated using the LA-ICPMS U-Pb technique. The results obtained were variable, as only four samples contained late Miocene zircons, consistent with the NALMA of the faunas. In contrast, all the ash samples studied contained middle-Cenozoic zircons, which are interpreted as accidental, probably incorporated in the ash from volcanic vent wall rocks. However, three samples yielded ages that are consistent with the HH2 NALMA of the fossils. The oldest sample has a U-Pb age of 6.95 ± 0.27 Ma (locality ZJ-38 “Tepezalá”) and a U-Pb age of 6.50 ± 0.11 Ma (locality ZJ 42 “Coltradía”). The youngest age is 5.59 ± 0.11 (locality ZJ-47 “El Resbalón”). These radiometric ages are equivalent to the stratigraphic range inferred for some well-known North American faunal associations (e.g., Lemoyne Fauna, Oshkosh Local Fauna, Coffee Ranch Local, and Chilcoita Local Fauna).

Other slightly younger late Hemphillian faunas known in central Mexico are referred to HH3 (Fig. 11) on the basis of the presence of D. mexicanus, N. enystyle, and A. stockii. The fact that in Juchipala N. azteca has not been found associated with C. (Grammohippus) bondarense suggests the older age of early-late Hemphillian. As discussed above, N. azteca has been recovered only from the lower layers of Rancho El Oceo and Cocellos localities in the San Miguel de Allende Basin, the state of Guanajuato, and the Santa Maria locality in the Tecolotlán Basin, Jalisco.

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