México, D.F.

LATE TERTIARY EQUIDS FROM THE STATE OF HIDALGO, MEXICO

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ABSTRACT

This paper is a taxonomic revision of the late Tertiary equid species, known so far from the Zacualtipán basin in the State of Hidalgo. The studied material includes the equids from the Tehuichila fauna housed in the Museo de Geología, UNAM, as well as the species Calippus (Grammohippus) castilli and Dinohippus interpolatus, collected (in situ) in the Zietla locality. Based on the presence of these two species, the age of this fossil site is assigned to the early Hemphillian. The mastofauna of Zietla is the only known reference in which a fossil assemblage is reliably tied into the stratigraphical sequence of the Zacualtipán area (from which the Tehuichila fauna is derived).

To elucidate the taxonomic position of the species present in Zietla, the equids from the Tehuichila fauna and elsewhere in Mexico were examined. Surprisingly, when the localities of Zacualtipán—Zietla and Tehuichila—were compared with the Hemphillian and Blancan material from other localities in Mexico, it was found that the horses from Tehuichila correspond to two different ages, despite the fact that they were described as a single faunal association.

Finally, this study was extended to the equids of Tehuichila and from this analysis it was found that *Neohipparion rectidens* is equivalent to *Neohipparion eurystyle*—a species widely represented in the late Hemphillian faunas of Mexico—and that *Nannippus montezuma* and *Nannippus peninsulatus* are two Blancan species that are in need of taxonomic revision due to noticeable similarities.

Key words: Hidalgo, Mexico, Tehuichila fauna, Hemphillian, Blancan, equids, Calippus (Grammohippus) castilli, Dinohippus interpolatus, Neohipparion rectidens, Neohipparion eurystyle, Nannippus montezuma, Nannippus peninsulatus.

RESUMEN

En este estudio, se hace la revisión taxonómica de las especies de équidos del Terciario tardío, conocidas hasta ahora en la Cuenca de Zacualtipán, Estado de Hidalgo. Este artículo incluye el material de équidos correspondiente a la fauna Tehuichila, alojado en el Museo de Geología del Instituto de Geología, UNAM, así como a las especies Calippus (Grammohippus) castilli y Dinohippus interpolatus, recolectadas (in situ) en la localidad de Zietla. La presencia de estas dos especies permite asignar una edad correspondiente al Henfiliano temprano para esta localidad. La mastofauna de Zietla es la única asociación fósil del Terciario tardío que ha sido refererida confiablemente dentro de la secuencia estratigráfica del área de Zacualtipán (de donde proviene la fauna de Tehuichila).

Para dilucidar la posición taxonómica de las especies descritas de Zietla, se revisó el material fósil de équidos proveniente de la fauna de Tehuichila y de otras localidadess conocidas del Terciario tardío de México. Sorprendentemente, se encontró que cuando las dos localidades de Zacualtipán—Zietla y Tehuichila—fueron comparadas con el material del Henfiliano y Blancano de México, los caballos de Tehuichila correspondieron a dos edades diferentes, no obstante que fueron descritas como una sola asociación faunística contemporánea.

Finalmente, en relación con la revisión taxonómica de los équidos de Tehuichila, se tiene que *Neohipparion rectidens*, es equivalente a *Neohipparion eurystyle*—especie ampliamente representada en las faunas del Henfiliano tardío de México—y *Nannippus montezuma y Nannippus peninsulatus* son dos especies del Blancano que necesitan ser revisadas, debido a sus marcadas semejanzas.

Palabras clave: Hidalgo, México, fauna Tehuichila, Henfiliano, Blancano, équidos, Calipus (Grammohippus) castilli. Dinohippus interpolatus, Neohipparion rectidens, Neohipparion eurystyle, Nannippus montezuma, Nannippus peninsulatus.

INTRODUCTION

Fossil horses represent an important group in the Hemphillian—late Miocene— and Blancan—Pliocene—faunas of Mexico. These mammals are well-represented in fossil assemblages of these ages in northern and central Mexico and, from them, in past years numerous species have been described.

Some of these taxa are surely still valid, nevertheless, particularly in the central area, a few have been synonymized, whereas others are in need of taxonomic revision.

One possible explanation for this problem is the subjective and unclear systematic criteria of some past authors, mostly due to fragmentary or insufficient material. Such practice resulted in inadequate comparisons of the fossil material leading to the description of new species of dubious taxonomic value. The presence of so many different species has hampered the biostratigraphic correlations of Mexican late Tertiary faunas.

More recently, Miller and Carranza-Castañeda (1984) and later Carranza-Castañeda (1991) restudied the most impor-

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tant of these equid faunas. Due to the need of correlation among them, the authors mentioned above reexamined all of the horse species known so far. The revision was undertaken in the two following localities of central Mexico: Rancho El Ocote in the State of Guanajuato, and Rancho La Goleta in the State of Michoacán. In these sites—mainly in Rancho El Ocote—new fossil material was collected, the stratigraphic markers of each rock unit were defined, and the biostratigraphic sequence was adequately established. The results of these studies produced an amended and useful list of horse species that occur in the Hemphillian and Blancan faunas of Mexico.

The only known early Hemphillian locality is La Presa from the San Miguel de Allende area in the State of Guanajuato, where *Dinohippus interpolatus* and *Calippus* have been reported (Carranza-Castañeda, 1989). In contrast, there are numerous late Hemphillian localities, including: Yepómera in the State of Chihuahua; and Rinconada, Coecillos, Rancho El Ocote and Arroyo Tepalcates in the State of Guanajuato. The following equid species occur at these localities: *Dinohippus mexicanus*, *Astrohippus stocki*, *Neohipparion eurystyle* and *Nannippus minor* (Miller and Carranza-Castañeda, 1984; Carranza-Castañeda, 1991; Carranza-Castañeda, 1992; Carranza-Castañeda and Walton, 1992).

Regarding the Blancan faunas, there are the following: La Concha locality, in the State of Chihuahua; Rancho La Goleta, in the State of Michoacán; and Rancho Viejo and Los Galvanes localities, in the State of Guanajuato. The following equid species occur at these localities: *Nannippus peninsulatus* and *Equus (Dolichohippus) simplicidens* (Carranza-Castañeda and Miller, 1988; Carranza-Castañeda, 1991).

Regardless of these previous studies, the Tehuichila fauna, located in the State of Hidalgo—southeast of the Central Mesa, in the eastern side of the Sierra Madre Oriental—remained in need of revision. The Tehuichila fossils—mainly the equids—in spite of their location—less than 200 km southeast from the well-known localities of the Guanajuato area—and that historically were some of the first species described for the late Miocene of Mexico (Leidy, 1882; Cope, 1885, 1886), were completely left out of the context of the faunal associations reported for this age. Even in more recent works, the Tehuichila fauna was just superficially described and inadequately compared, as is the case in the reviews that were discussed above.

Three important reasons urged the present authors to undertake this work: (a) the taxonomic problems involved with these interesting fossil equids; (b) the lack of stratigraphic and geographical information associated with the collections from Tehuichila (Ferrusquía-Villafranca, 1978; Carranza-Castañeda, 1991); and (c) the need for biostratigraphic correlations between the Hemphillian and Blancan faunas of the Mesa Central—e. g., states of Guanajuato and Michoacán—and adjacent areas—e. g., the northeastern portion of the State of Hidalgo.

Taking in consideration the problems mentioned above and to contribute to the better understanding of the Tertiary continental biostratigraphy in Mexico, a joint project was developed between the Instituto de Geología, UNAM and the Instituto de Investigaciones en Ciencias de la Tierra, UAEH. One major objective of this project was to study the carboniferous basin of Zacualtipán in the State of Hidalgo, the general area in which the Tehuichila fauna has been located (Leidy, 1882; Cope, 1885; Ferrusquía-Villafranca, 1978; MacFadden, 1984). As a significant result, from the first field season of this project, in 1992 a new locality—within the area of study—known as Zietla, was discovered by the senior author of this paper.

The information related to the equids recently found in the Zietla locality has already been discussed by Carranza-Castañeda (1994); nevertheless, in this paper all of the equid species of the State of Hidalgo—known so far—are reviewed, and their biostratigraphic and taxonomic problems are discussed. To support and complement the analysis on the equid taxa mentioned in this paper, the species from other faunas of the same age in Mexico were compared when discussing age and correlation. Therefore, this study deals with the most representative faunas of the late Tertiary in Mexico and the species of equids present in them.

PREVIOUS WORKS IN THE TEHUICHILA AREA

The first fossil site in the Tehuichila area, State of Hidalgo, central Mexico, located six kilometers east of the city of Zacualtipán (Figure 1), was mentioned by Leidy (1882). That report corresponds to the first description of *Hippotherium montezuma*. Later, Cope (1885, 1886) described *Protohippus castilli*, *Hippotherium peninsulatum*, and *Hippotherium rectidens*.

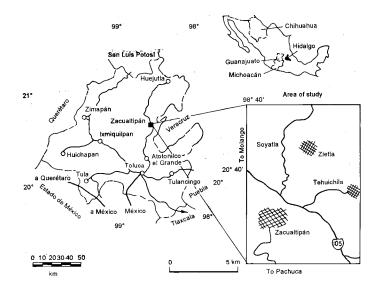


Figure 1.- Index map of the State of Hidalgo, showing the Tehuichila and Zietla localities. Other states mentioned in the text are indicated in the general map of Mexico that appears at the upper right corner of the figure.

Freudenberg (1922) made a faunal list of all of the taxa present in Tehuichila; Ferrusquía-Villafranca (1978) reexamined the fossil assemblage and assigned the whole fauna to the early? or middle Pliocene, and more recently MacFadden (1984) reexamined the type specimen of "Hippotherium" peninsulatum and concluded that Nannippus peninsulatus was the senior synonym for this taxon.

One of the major contributions of this study—reported herein—is the description of Hemphillian vertebrates—collected *in situ*—from the Zietla locality, indicating that in the Zacualtipán area, the late Miocene is represented, in addition to the Pliocene that has been mentioned previously (Freudenberg, 1922; Ferrusquía-Villafranca, 1978; MacFadden, 1984). Also, this means that the previous interpretation of the Tehuichila fauna as one coeval assemblage is inaccurate. The presence of several stages, as evidenced by the equid species, requires that future work pay much closer attention to details of the stratigraphic sequence in the Zacualtipán basin.

MATERIALS AND METHODS

For the equid material described in this study, isolated molars and premolars of horses collected in the locality of Zietla were examined. This material is well preserved and shows a minimal degree of deformation.

The original material from the Tehuichila fauna—with no stratigraphic control—was provided by M.Sc. René Hernández, the manager of the old fossil collections housed in the Museo de Geología of the Instituto de Geología, UNAM.

To do the taxonomic analysis of the equid species described in this paper, the holotype of *Hippotherium montezuma* and the duplicates of all the holotypes of the other species from Tehuichila were studied at the vertebrate fossil collections of the Smithsonian Institution.

The comparisons of the Zietla and Tehuichila equids with material from central Mexico were done at the Museum of Paleontology of the Instituto de Geología, UNAM, using the San Miguel de Allende collections. To complement the study, several descriptions and illustrations from published materials were employed, including the information on *Calippus (Grammohippus) castilli* and *Dinohippus interpolatus* from Zietla, recently described and illustrated in Carranza-Castañeda (1994). Additionally, two specimens from these collections were sectioned transversely to observe the variation in the structure of the occlusal surfaces.

All of the material described in this paper is housed in the Museo de Paleontología of the Instituto de Geología, UNAM.

ACRONYMS AND MEASUREMENTS AND ABBREVIATIONS

The measurements are in millimeters (mm) and the acronyms are as follows:

— Universidad Nacional Autónoma de México = UNAM

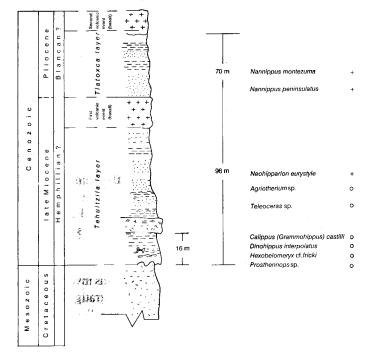
- Universidad Autónoma del Estado de Hidalgo = UAEH
- Museo de Paleontología del Instituto de Geología, UNAM = IGM
- United States National Museum (Smithsonian Institution) = USNM
- American Museum of Natural History = AMNH

Abbreviations as they appear in the text: M = upper molar; m = lower molar; P = upper premolar; P = lower premolar; P = upper deciduous premolar; P = lower deciduous premolar.

ZIETLA

This fossil site, known as Potrero de Zietla (IGM-loc. 2873), lies within the carboniferous basin of Zacualtipán, 4 km north of the Tehuichila ranch in the State of Hidalgo (Figure 1). This site is located in the Sierra Madre Oriental and locally is known as the Sierra Alta de Zacualtipán. The main access to this area is through the road 105 that connects the cities of Pachuca and Huejutla.

The specific fossil locality is situated in the northern portion of the Zietla ranch and was first reported in Carranza-Castañeda (1994). This area belongs to a bigger extension of land denominated "Rancho El Suspiro". The fossil material was found in the bottom part of the "Tehuitzila Layer" (Almanza, 1956), only 16 m above from a unit of Cretaceous rocks. The lithology that contains the vertebrate remains consists mainly of siltstone and claystone (Figure 2).



- Collected in situ
- Material housed in the Museo of Geología of Instituto de Geología, UNAM
 The stratigraphic position is assumed

Figure 2.- Biostratigraphic section of the Zacualtipán basin (modified from Almanza [1956], and Carranza-Castañeda [1994]).

SYSTEMATIC PALEONTOLOGY

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Subfamily Equinae Steinman and Doderlein, 1890
Genus *Calippus* Matthew and Stirton, 1930

Calippus (Grammohippus) castilli (Cope, 1885) new combination

Protohippus castilli Cope ,1885, was the last equid species to be described from the Tehuichila fauna. The holotype (AMNH-8344) consists of an upper molar, possibly an M1.

In the spring of 1992, several isolated cheek teeth were collected in the Zietla locality. The main characteristic observed in the occlusal surface of these elements was that the protocone is connected with the protoselene; whereas, in all the other species of equids from the Zacualtipán (Tehuichila) area, the protocone and the protoselene are completely isolated. Apparently, this condition has only been observed in *Protohippus castilli*. Hence, the material will be described and the possible relationships with the species named by Cope in 1885 will be discussed. The description of this species and that of *Dinohippus interpolatus*, as they appear here, were taken from Carranza-Castañeda (1994), a preliminary paper that deals with the overall mastofauna of the Zietla locality.

Material—IGM 6563, P4; IGM 6564, M1; IGM 6585, dp2; IGM 6576, dp1 or dp2.

DESCRIPTION OF THE MATERIAL

Upper molariforms

The stage of wear exhibited by IGM 6563, P4, represents an adult individual (Figure 3, A). The occlusal surface is simple. The protocone is small and oval-shaped, with a straight lingual border and a small lingual furrow. The protocone is connected with the protoselene by a narrow isthmus. The plicaballin is small and simple, and there is no hypoconal furrow. The prefossette shows a small loop in its posterior border. There are no other folds in the premolar. The post-fossette is simple and has no folds. The mesostyle is wide, the parastyle is well-developed and the metastyle is reduced. The height of the premolar measured on the metastyle is 36 mm.

The specimen IGM 6564, M1, represents a young individual, with an almost unworn occlusal surface (Figure 3, B). In this specimen the protocone is elongated and it narrows markedly at the preprotoconal furrow level. Its posterior end broadens gradually, describing a triangular shape. As in the previous specimen, the protocone is connected to the protoselene by a narrow isthmus. The plicaballin is simple and small. The furrow of the hypocone is deep and the hypocone is narrow. It ends in an elongate structure and the tip is acute. The

prefossette also shows a small loop, with a very small fold above it, and the postfossette has no folds at all. The mesostyle is narrow, and the parastyle is wide and straight (Figure 3, B).

The specimen was sectioned at its medial part to observe the variation of the structures in an advanced stage of wear (Figure 3, C). At this level of segmentation, the protocone diminishes in size, acquiring a lobate shape, and the isthmus gets slightly wider. The plicaballin and the hypocone disappear and the prefossette loses some of its features, becoming a simpler structure.

Lower premolars

The two specimens are deciduous. In one of them, IGM 6576, there is almost no wear and therefore no structures on the occlusal surface were observed. On specimen IGM 6585 (Figure 3, D), the metaconid and the metastylid are clearly distinguishable and have a lobate shape. The metaconid is more elongate and the linguaflexid is deeper and has the shape of an open "V". The ectoflexid is very deep and almost meets the enamel layer of the linguaflexid. The paralophid is elongate and ends in the same plane as the entoconid, the protostylid is well-developed.

DISCUSSION OF THE SPECIES

The Zietla specimens described above were compared with their equivalent species from the Tehuichila fauna and it was found that the Zietla specimens closely resemble *Protohippus castilli* described by Cope (1885). Also, the Zietla specimen—molar—IGM 6564, compared favorably with a molar, IGM 6554, from the early Hemphillian La Presa locality, in the San Miguel de Allende area, of the State of Guanajuato.

The Zietla and the La Presa materials share the following diagnostic characters: shape and size of the protocone; fossettes with no enamel folds and with a simple appearance; hypoconal furrow absent; and a strong distinctive curvature along the lateral sides of both molars. It is interesting to note that specimens from both sites exhibit a similar pattern of wear.

This Tehuichila material compares closely with *Pliohippus hondurensis*, from the Gracias Fauna in Honduras. Previously, these similarities have been discussed by Olson and McGrew (1941) and by Hulbert (1988) in his reexamination of the protohippines. More recently, Carranza-Castañeda (1994) considered this species as *Calippus* (*Grammohippus*) sp. cf. *C.* (*G.*) *hondurensis*, and for the purpose of this paper, we find that *Protohippus castilli* is undistinguishable from the topotypes of *Calippus* (*G.*) *hondurensis*.

Based on Hulbert's (*op. cit.*) diagnosis of *C.* (*Grammohippus*) hondurensis, the Zietla specimens closely resemble this taxon. The shape and size of the protocone are the same; so are the furrow of the hypocone and the presence of the plicaballin. Likewise, Hulbert (*op. cit.*) established some ratios

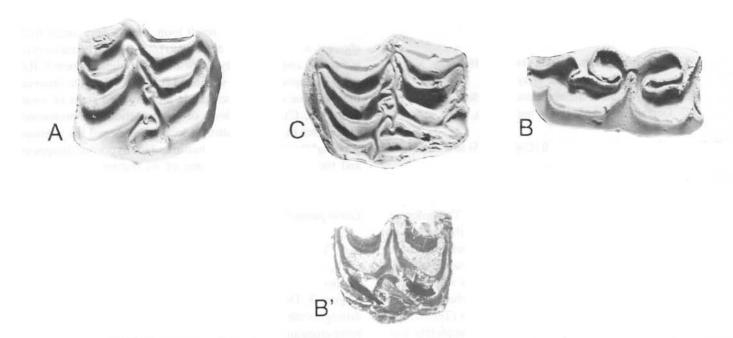


Figure 3.- Several views of Calippus (Grammohippus) castilli, from the Zietla locality (all illustrations x 2). A, IGM 6563, P4; occlusal surface of an adult individual; B, IGM 6564, M1; occlusal surface of a young individual; C, IGM 6564, same M1; transverse section, equivalent to the structures (occlusal surface) that shows an adult specimen; D, IGM 6585, dp2; occlusal surface.

between the maximum length of the protocone and the maximum length of the anteroposterior axis of the occlusal surface. Also, in these measurements, the similarities are noticeable between the Zietla material and what is reported in the literature. Hulbert (op. cit.) gave a ratio for P3-4 of 26% and for M1 of 31%.

Regarding the Zietla specimens, in IGM 6563—that corresponds to a P4—the maximum length of the protocone was 5 mm and the same measurement for the anteroposterior axis of the occlusal surface was 18 mm; this relationship expressed in percentage is 27.7%, very similar to Hulbert's 26% for P3-4. In IGM 6564—that belongs to an M1—the length of the protocone was 7 mm and the same measurement for the anteroposterior axis of the occlusal surface was 21 mm, the ratio in percentage is 33%, also close to Hulbert's 31% for an M1. At the level where the Zietla molar-specimen IGM 6564-was sectioned to observe the changes in the structures of the occlusal surface, the maximum length of the protocone was of 6 mm, whereas the length of the anteroposterior axis of the occlusal surface was of 17 mm, leaving a ratio of 31%, also very similar-if not the same-to what Hulbert reported for the M1s of the Gracias Fauna, e. g., Calippus (Grammohippus) hondurensis. Thus, all of Hulbert's and Zietla ratios appear to fall within the same range, although the sample size for Mexico does not allow statistical discrimination.

After comparing the Gracias Fauna from Honduras and the Zietla material from Hidalgo, it is concluded here, as it has been previously suggested by Carranza-Castañeda (1994), that both taxa represent the same species. However, there is a nomenclatorial problem to be solved when referring the material from the two localities. *Calippus (Grammohippus) hondurensis* (Olson and McGrew, 1941) must be considered a

junior synonym of *Calippus* (*Grammohippus*) castilli (Cope, 1885), because the species from Hidalgo was described previously. Nevertheless, this conclusion remains tentative. In order to know more adequately the range of variation of the various structures of the occlusal surface, and to determine the similarity index between the material from both localities—Zietla and Gracias—a proper analysis must ponder a much larger sample.

Considering the few specimens that have been studied so far, for the present time the material from Zietla is referred to Calippus (Grammohipphus) castilli, which is the same species that occurs at La Presa locality in the area of San Miguel de Allende, State of Guanajuato. The presence of this particular species in the Hidalgo—Zietla—and Guanajuato—La Presa—localities indicates that the age determination for them must correspond to the early Hemphillian.

Dinohippus interpolatus (Cope, 1893)

Previously, this species had been reported in Mexico from La Presa in the area of San Miguel de Allende, Guanajuato, and more recently in Zietla, Hidalgo (Carranza-Castañeda, 1989; Carranza-Castañeda, 1994).

Material—IGM 6584, right P2.

DESCRIPTION OF THE MATERIAL

This tooth represents a young individual (Figure 4, A). On the labial side, the border of the occlusal surface still shows part of the cement and the fossettes are still connected with the internal borders of the enamel. Also, the general shape of the

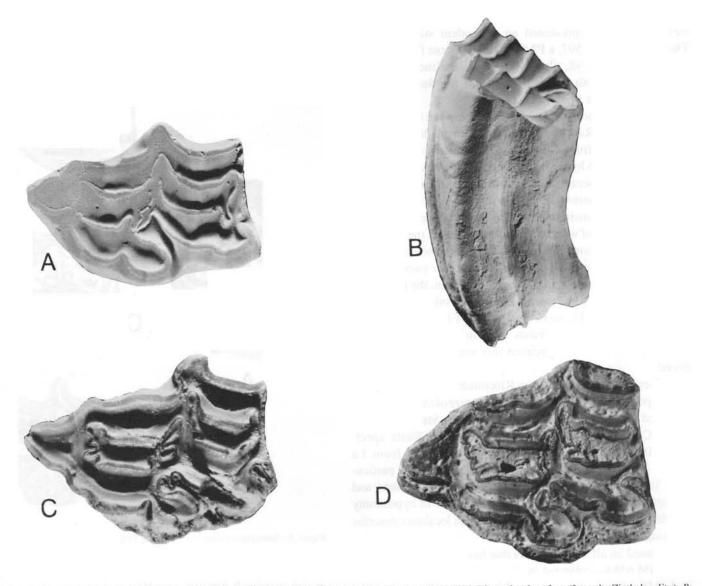


Figure 4.- Several views of *Dinohippus interpolatus* from various localities (all illustrations x 2). A, IGM 6584, P2; occlusal surface (from the Zietla locality); B, IGM 6584, P2; lateral view (from the Zietla locality); C, IGM 6597, P2; occlusal surface (from the Rancho El Ocote in the State of Guanajuato); D, IGM 6598, P2; occlusal surface (from the Rinconada locality in the State of Guanajuato).

specimen is curved (Figure 4, B), as was observed in the holotype illustrated by Osborn (1918). The structures of the occlusal surface are simple; nevertheless, there are three protuberances along its transverse axis. The lowest elevation is located in the anterior portion of the anterostyle and the other two higher elevations lie parallel to the transverse axis and cross the medial part of the pre- and postfossettes. This arrangement creates a deep depression that runs from the protocone to the mesostyle (Figure 4, A).

The protocone is slightly elongated and its posterior end has a lobate shape. It is connected to the protoselene by a wide isthmus. The preprotoconal furrow is moderately deep and the hypoconal furrow is very small. The prefossette is simple, although a small fold can be seen on its posterior border. The postfossette shows an extension of the enamel in the lower end of the posterior border. The mesostyle is wide and represents the only well-developed column that can be observed on its

labial side. The anterostyle is prominent, wide and has a lobular shape.

Measurements of the specimen

Maximum length of the anteroposterior axis, 30 mm; maximum transverse length across the mesostyle and the posterior border of the protocone, 22 mm; maximum length of the protocone from the protoconal furrow to the posterior border, 6 mm; maximum height throughout the mesostyle, 45 mm; maximum height from the base of the mesostyle to the medial portion of the postfossette, 48 mm.

DISCUSSION OF THE SPECIES

The specimen IGM 6584—right P2— from Zietla (Figure 4, A) was compared with several specimens of *Dinohippus*

mexicanus—that represented an equivalent stage of wear. These were: IGM 6597, a P2 from the El Ocote fauna (Figure 4, C) and IGM 6598, also a P2 from the Rinconada fauna (Figure 4, D). Both faunas come from the San Miguel de Allende area in the State of Guanajuato.

There were noticeable differences between the Zietla and the Guanajuato-Rancho El Ocote and Rinconada-materials. In D. mexicanus from Guanajuato, the molariforms are less recurved and more hypsodont. The occlusal surface is flat and transverse protuberances were not observed in either the fossettes or the anterostyle. The fossettes show a large number of foldings that remain in advanced stages of wear. In molars with equal degree of wear to the Zietla specimen, the protocone was found to be more elongated, with a more acute posterior end, and with the enamel of the lingual border parallel to the lingual border; whereas, in the Zietla specimen, the major axis of this structure is tilted toward the lingual side and its size is much smaller. In D. mexicanus-from El Ocote and Rinconada—the hypocone persists even in advanced stages of wear and in the Zietla specimen this structure is clearly reduced.

Besides the material from Rinconada and El Ocote, several upper molars of *Dinohippus* cf. *interpolatus* have been collected in La Presa locality, also from the State of Guanajuato (Carranza-Castañeda, 1989). When the Zietla specimen—IGM 6584—was compared with an M2 from La Presa—IGM 6582—the similarities were remarkable, particularly in the simplicity of the fossettes and the shape and arrangement of the protocone. Also, the degree of hypsodonty and the curvature that the molars from both localities describe are similar.

Based on all the characters that have been discussed, the P2—IGM 6584—collected in the locality of Zietla, is identified as *Dinohippus interpolatus*; this new record represents the second—after the occurrence in La Presa locality—from Mexico (Carranza-Castañeda, 1989; Carranza-Castañeda, 1994).

SOME CONSIDERATIONS ON THE TEHUICHILA EQUID SPECIES

After the description of the material of *Calippus* and *Dinohippus* found in Zietla, the following comments on the other Tehuichila equids are added.

Nannippus montezuma (Leidy, 1882)

Material—The holotype—USNM-3304—consists of a right P3 or P4 (Figure 5, A).

The first species of equid that was known from this area—the Tehuichila fauna—is *Hippotherium montezuma*, described by Leidy (1882). This species has been mentioned in numerous publications with different names; some of these references will be discussed next.

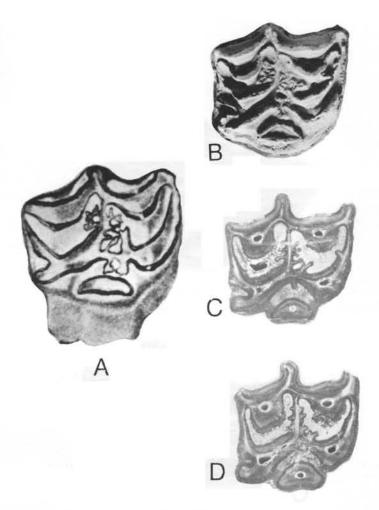


Figure 5.- Nannippus montezuma from the Tehuichila fauna (all illustrations x 2). A, USNM-3304, as illustrated in Osborn (1918, p. 198. fig. 162); B, IGM 6590, M1; occlusal surface of a young individual; C, IGM 6590, same M1; transverse section (1) equivalent to the structures (occlusal surface) that shows an adult specimen; D, IGM 6590, same M1; transverse section (2), in a deeper level, equivalent to the structures (occlusal surface) that shows an individual when is old.

Osborn (1905), in his work on the evolution of the horse in America, considered *Hippotherium montezuma* as *Equus montezumae*, but in 1918 he assigned it to the species *Hipparion montezuma*. In his faunal list, Gidley (1907) mentioned *H. montezuma* as *Neohipparion montezuma* stressing the similarities between this species and *Hippotherium peninsulatum*, based on the magnitudes of the anteroposterior and transverse axes and on the height of the molars. On the other hand, without any taxonomic arguments, Freudenberg (1910) reassigned *Neohipparion montezuma* to *Hippotherium montezuma*.

Matthew and Stirton (1930) included *Neohipparion montezuma* within the subgenus *Nannippus*, and later Stirton (1940) included it in his genus *Nannippus*. Finally, Ferrusquía-Villafranca and Carranza-Castañeda (1979), in their revision of the genus *Neohipparion* of Mexico, assigned *N. montezuma* to *Neohipparion floresi*.

DISCUSSION OF THE SPECIES

When the holotype of *Nannippus montezuma* was studied at the USNM collections, it was found that the shape of the protocone, the height of the crown and the anteroposterior and transverse diameters of this taxon are diagnostic characters of the genus *Nannippus* (Matthew, 1926; Stirton, 1940; MacFadden, 1984). Therefore, the specimen described by Leidy (1882) is a valid species within that genus and must be referred to *Nannippus montezuma*. Also, the species *Neohipparion floresi*, proposed by Ferrusquía-Villafranca and Carranza-Castañeda (1979), must be regarded as a junior synonym.

When the holotype of *Nannippus montezuma* was compared with several specimens of *Nannippus peninsulatus*—collected in the Blancan localities of the San Miguel de Allende, Guanajuato area—it was found that there are no significant differences between the size of the anteroposterior and transverse axes. Also, the height of the crown in both taxa is very similar.

The main criterion that holds N. montezuma as a separate species, is based on the peculiar morphology of the enamel at the level of the occlusal surface (Figure 5, A), but this stems from the stage of development of the holotype which corresponds to a young individual. In horses in general, the enamel in juveniles shows a wide range of variation in pattern and number of foldings. This particular process was discussed extensively by Carranza-Castañeda and Ferrusquía-Villafranca (1979). These features make young individuals appear much different from adults and older specimens, within the same population. When the juveniles mature and with the natural wear of the teeth, the accessory foldings of the enamel disappear and the structures of the occlusal surface acquire the normal diagnostic characters of the species. Hence, when working with isolated horse teeth, the characterization of a particular species should be based on the structures of the occlusal surface of individuals at different stages of wear. Also, the anatomical position of the teeth-premolars and molars—should be considered within the variation range.

When the old collections from the Tehuichila fauna, housed in the Museum of Paleontology of the Instituto de Geología, UNAM, were examined, several of the original fossils—collected at the turn of the century—were found. There is no indication in any of the museum's catalogues, neither of locality data, nor of the stratigraphical position of the fossils. However, the documentation that was found with the specimens and the type of preservation, leave no doubt that they were collected from the Zacualtipán basin. The equid material includes: *Nannippus montezuma*, *Nannippus peninsulatus* and *Neohipparion*, as follows:

Specimen IGM 6590 is a juvenile M1 from the right side (Figure 5, B). The tooth shows on its occlusal surface many foldings in the postfossette and in the prefossette. Besides the foldings, it shows a subquadrate-shaped loop. These characters make this specimen similar to the holotype of *N. montezuma*

(USNM-3304), not only in the occlusal surface structures, but also in the—approximate—similar wear stage.

The measurements of specimen IGM 6590 were: length of the anteroposterior axis, 19 mm; length of the transverse axis, 18 mm; and from the base of the mesostyle to the crown, 47 mm. Gidley (1907) reported the following measurements for the holotype (USNM-3304): length of the anteroposterior axis, 19.5 mm; length of the transverse axis, 17 mm; and height of crown, external, 47 mm—measured from the base of the mesostyle to the crown. Comparing the measurements of the holotype with the specimen from Hidalgo, it can be seen that the similarities are remarkable.

In order to study the variation of size and shape of the foldings at the posterior border of the prefossette, which are very characteristic in *N. montezuma*, specimen IGM 6590 was sectioned at two different levels. This resulted in a remarkable change in shape and size in the structures of the occlusal surfaces at different levels of the tooth.

The occlusal surface in its natural wear shows numerous foldings in the prefossette (Figure 5, B). The largest one describes a simple loop of subquadrate shape that is directed toward the lingual border of the tooth. The plicaballin is bifurcated and the hypocone is elongated and has a deep hypoconal groove. All of these structures coincide with the diagnostic characters of *N. montezuma*.

When the first—or higher—section was observed (Figure 5, C), the size and shape of all the structures changed significantly. The loop of the prefossette is shaped like an elongate folding; the same occurs with the other structures in the pre- and postfossettes. The size of the plicaballin is also reduced at this level and only its distal portion maintains a slightly crannied appearance.

The level of the second—and deeper—section of the right M1 of the specimen IGM 6590 (Figure 5, D) corresponds to an old individual. In this view, all of the structures reduce their size even more than in the first section—performed in a higher level. The plicaballin is lost and the hypocone is still present with a different lobular shape and with a less-deeper furrow.

Another tooth studied from the Tehuichila horses was IGM 6596 (Figure 6, A and B). In this adult specimen, the structures of the occlusal surface coincide with no question to what MacFadden (1984) assigned to *Nannippus peninsulatus* (Figure 6, A). The tooth corresponds to a P4 and its measurements were: length of the anteroposterior axis, 19 mm; length of the transverse axis, 18 mm; and height from the base of the mesostyle to the crown, 34 mm. As in the case of IGM 6590, the tooth was sectioned at a level that could match the wearing of an old organism (Figure 6, B). When the surface was compared with the same level of specimen IGM 6590 (second section, Figure 5, D), the structures of the occlusal surfaces were similar. The folds in the fossettes reduce their size and number, the protocone shows the same shape and size in both forms, the plicaballin reduces its size to a point where it almost

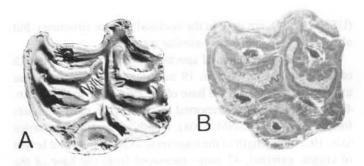


Figure 6.- Nannippus peninsulatus from the Tehuichila fauna (all illustrations x 2). A, IGM 6596, P4; occlusal surface of an adult individual; B, IGM 6596, same P4; transverse section, equivalent to the structures (occlusal surface) that shows an old specimen.

disappears and the hypocone and the hypoconal furrow maintain the same size and shape.

The only differences detected between specimen IGM 6596 and IGM 6590—at equivalent levels of section—can be interpreted as the natural variation in the enamel features between molars (IGM 6590) and premolars (IGM 6596) within individuals of the same population. Therefore, if specimen IGM 6590 was to be found showing a natural wear similar to the first or second sections (Figure 5, C and D), undoubtedly it would be identified as *Nannippus peninsulatus*.

Hypothetically, the same results could be obtained when sectioning the holotype of *N. montezuma*. The sections could be performed at different levels, representing several stages of development—age—and therefore different stages of wear. The cross-sections produced by this procedure would show a variation pattern similar—if not the same—to the one known from the specimens of *Nannippus peninsulatus* that have been studied in the Blancan localities of Mexico.

Gidley (1907) made some interesting observations concerning the relationships between *H. montezuma* and *H. peninsulatus*. He pointed out that the measurements of both holotypes were so similar that the slight differences between them could be interpreted as the expected variation between molars and premolars found in the same dental series. Adding to these (*op. cit.*) ideas regarding the Tehuichila materials, he stated "the localities from which both materials came from are so close, that this suggests that the species are identical". This comment is somewhat strange, due to the apparent lack of any record that indicates with precision where the Tehuichila material was collected. However, Gidley's comments are still valid and the specimens could have been collected in the same stratigraphic unit.

In summary, for the purposes of this paper, both taxa (N. montezuma and N. peninsulatus) have been considered as valid. Nevertheless, the evidence points out a strong possibility that they may be the same species. If this is the case, then N. montezuma described by Leidy in 1882 should be the valid senior synonym of these nomina. It is necessary to conduct more field work in the Zacualtipán area in order to obtain more information on the variation of the dentition in one—or both—species.

Nannippus peninsulatus (Cope, 1885)

Another equid species described from the Tehuichila fauna is *Hippotherium peninsulatum* Cope, 1885. The holotype (AMNH-8345) consists of an ?M2. Recently, MacFadden (1984) made an extensive revision of all the species of *Nannippus* from the North American faunas. In his paper, he discussed in detail the taxonomic position of the specimen from Tehuichila, and assigned it to the genus *Nannippus*, thus regarding Cope's species as valid. Therefore, the present taxonomic status of this species is *Nannippus peninsulatus*.

According to Lindsay (1984) and MacFadden (1984) Nannippus peninsulatus is considered as a stratigraphical index for the Blancan age in North America, and is also well-represented in the Blancan localities of Rancho Viejo and Los Galvanes, from the San Miguel de Allende area in the State of Guanajuato (Carranza-Castañeda, 1991). To complement this study herein, we have illustrated and dicussed specimen IGM 6596, a P4 housed in the collections of the Instituto de Geología, UNAM (Figure 6, A and B).

Neohipparion eurystyle (Cope, 1893)

From the Tehuichila fauna, Cope (1886) described *Hip*potherium rectidens. The holotype (AMNH-8346) consists of a right ?P (Figure 7). This species has undergone a much more stable nomenclatorial history than those described above.



Figure 7.- "Hippotherium" rectidens (AMNH-8343), as illustrated in Cope (1886, p.199, fig. 164).

Gidley (1907) assigned *H. rectidens* to the genus *Neohipparion*, based on the shape of the protocone, the foldings in the prefossettes, and crown height. The same author also considered that the material in which the species was based is so fragmentary that it was not possible to establish any adequate relationships with other species.

Osborn (1918) referred the species to *Hipparion rectidens*, whereas Stirton (1940) found in this specimen (holotype AMNH-8346) diagnostic characters of the genus *Neohipparion* and called it *Neohipparion rectidens*. Later, Ferrusquía-Villafranca and Carranza-Castañeda (1979), when they revised the species of the genus *Neohipparion* from the Mexican faunas, considered that the species from Tehuichila belonged to *Neohipparion floresi*.

DISCUSSION OF THE SPECIES

Several teeth of Neohipparion eurystyle from Rancho El

Ocote, Guanajuato—specimens: IGM 6599; IGM 6600; IGM 6601; IGM 6602; and IGM 6603—were compared with a mold of the holotype of *Neohipparion rectidens*, housed in the US National Museum. The analysis showed that there are several structures that are very similar between them. These include the shape and size of the protocone and the folds and the loop of the prefossette. Particularly, when specimens IGM 6599 and IGM 6600 were studied, it was observed that the plicaballin is conspicuously bifurcated (Figure 8 A, B and C) as it is found in the holotype of *N. rectidens* (AMNH-8346). Also, according to Carranza-Castañeda and Ferrusquía-Villafranca (1979), the shape of the hypocone, the straightness of the molar and the crown height are characters that related the Tehuichila specimen to *N. floresi*. However, MacFadden (1984) determined that *N. floresi* was a junior synonym of *N. eurystyle*.

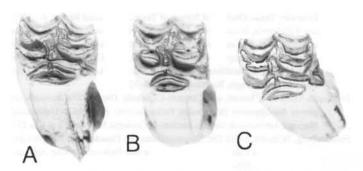


Figure 8.- Neohipparion eurystyle from Rancho El Ocote, Guanajuato. A, IGM 6599, M1; occlusal surface of an adult individual; B, IGM 6602, M1; occlusal surface of an adult individual; C, IGM 6600, M1; occlusal surface of an adult individual.

From the comparisons between the Tehuichila specimen and the Guanajuato material, it is evident that N. rectidens is equivalent to Neohipparion eurystyle. This creates a nomenclatorial problem, because "Hippotherium" rectidens was described in 1886, seven years before N. eurystyle, and thus should be the senior synonym for this species. Nevertheless, regarding the use of these two names, it must be noted that the name "H." rectidens was given to a single specimen with a questionable position in the maxilla (?P) and was described with neither geographical nor stratigraphical precise data. From Cope's (1886) original work; based on ambiguous characters and discussed-and compared-in terms of "Hippotherium peninsulatum", it is very difficult to separate "H." rectidens from other species of Neohipparion. On the other hand, Cope's (1893) description of N. eurystyle was based on a broken lower molar from the Palo Duro Canyon in Texas and complemented with four other isolated lower cheek teeth from the late Hemphillian Goodnight local fauna, also from Texas. Albeit the original description of N. eurystyle was based on lower cheek teeth, in the twentieth century new discoveries added important characters to this taxon, such as: cranial and postcranial elements, and a wide range of variability of upper and lower cheek teeth. This information has been summarized and discussed by MacFadden (1984), in his study of the New

World *Hipparions*. As a result of the more complete and better known characterization of *N. eurystyle*, this name has been extensively used in the descriptions of all the late Hemphillian equid faunas of Mexico and the United States (Lindsay, 1984; Miller and Carranza-Castañeda, 1984; MacFadden, 1984). Hence, although *N. rectidens* has precedence over *N. eurystyle*, the present authors suggest that the name *N. rectidens* be invalidated, favoring the usage of *N. eurystyle* as the senior synonym of this taxon.

AGE AND CORRELATION

When the equid species of the Tehuichila fauna were compared with the Hemphillian and Blancan species of Mexico, the authors found almost certainly that the Tehuichila fossils represent more than one age, even though they were described as a single faunal association. The exact levels or horizons where the fossil material was collected are still unknown. From the Zietla material, the oldest equid species—early Hemphillian—were identified as Calippus (Grammohippus) castilli and Dinohippus interpolatus. The material comes from mudstone, siltstone and coal beds located at the base of the "Tehuitzila Layer", described by Almanza (1956).

The presence of late Hemphillian equid species in the Tehuichila fauna, as is the case with *Neohipparion eurystyle*, means that the "Tehuitzila Layer" possibly corresponds—at least in part—to this particular age (Figure 2). On the other hand, the beds in which *Nannippus montezuma* and *N. peninsulatus* were collected are much younger and probably correspond to a sequence of siltstone and mudstone that lies between two volcanic events above the "Tehuitzila Layer". The age of this younger rocks, the "Tlatoxca Layer", also reported by Almanza (1956), should be assigned to the Blancan (Figure 2), and they correlate with the localities of Rancho Viejo and los Galvanes from the State of Guanajuato.

CONCLUSIONS

The information derived from the equid material described here represents an important contribution to the stratigraphy of the Zacualtipán carboniferous basin in the State of Hidalgo. As it has been discussed in Carranza-Castañeda (1994), the Zietla local fauna is the first fossil assemblage from this area that can be properly identified and adequately located within a geographical and stratigraphical framework. Nevertheless, this is valid only for the early Hemphillian level, in which the Zietla specimens—e. g., Calippus (Grammohippus) castilli, Dinohippus interpolatus, Teleoceras, Prosthennops and Agriotherium—were collected, because the material thought to represent younger beds in the Tehuichila fauna, still needs to be precisely relocated with proper stratigraphic control (Figure 2). This hopefully will be achieved with more prospecting in the area of study.

The revision of the equid species reported from the Tehuichila fauna shows that *Neohipparion rectidens* is equivalent to *Neohipparion eurystyle*. Regarding the use of this nomina, the concept that *N. rectidens* could be invalidated is favoured, leaving *N. eurystyle*—that has been widely used in the late Hemphillian localities of Mexico and the U.S.—as a senior synonym of this species.

Nannippus montezuma and N. peninsulatus, also present in the Tehuichila fauna (Leidy, 1882; Cope, 1885; Ferrusquía-Villafranca, 1978; Carranza-Castañeda,1991) are two Blancan species that are in strong need of taxonomic revision—due to the remarkable similarities between them. However, with the material known to date from the Zacualtipán area, there is not enough information to determine whether these species are two separate entities or just one.

Fortunately, N. peninsulatus is well-represented in several early Blancan localities (e. g., Miller's Place, Arrastracaballos and Arroyo El Tanque) from the San Miguel de Allende area, Guanajuato (Miller and Carranza-Castañeda, 1984) and should therefore shed new light on this current taxonomic problem.

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