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CRANIUM OF *DINOHIPPUS MEXICANUS* (MAMMALIA: EQUIDAE) FROM THE EARLY PLIOCENE (LATEST HEMPHILLIAN) OF CENTRAL MEXICO, AND THE ORIGIN OF *EQUUS*

Bruce J. MacFadden[1] and Oscar Carranza-Castañeda[2]

ABSTRACT

A newly discovered skull of *Dinohippus* is described from the latest Hemphillian (early Pliocene) Rancho El Ocote locality of Guanajuato, Mexico, which is dated at 4.8 Ma. This cranium is referred to *D. mexicanus*, the senior synonym for the latest Hemphillian species otherwise known from several localities in northern Mexico and the southern United States. Although crushed, this is the most complete skull known for this extinct species. With the diagnostic configuration of the dorsal preorbital fossa, distinctive dental pattern, and moderate tooth curvature, this cranium demonstrates a morphology similar to, although slightly more primitive than, that of closely related and slightly more derived Blancan *Equus*, such as *E. simplicidens*. As represented by occurrences in central Mexico and southern California, *D. mexicanus* coexisted with *Equus* during the middle Blancan from about 4.5 to 3 million years ago. Despite traditional interpretations of anagenetic speciation, the current study demonstrates that primitive species of *Equus* originated from *D. mexicanus* by cladogenesis.

RESUMEN

En este trabajo, se describe el reciente descubrimiento de uno cráneo de *Dinohippus* de la localidad de Rancho El Ocote, Henfiliano tardío (Plioceno temprano) del estado de Guanajuato, que ha sido fechado en 4.8 Ma. Este cráneo es referido a *Dinohippus mexicanus*, senior sinónimo de las especie del Henfiliano tardío, que se conoce en diferentes localidades del norte de México y sur de los Estados Unidos. El cráneo es mas completo que se conoce de esta especie *D. mexicanus*. Con la configuración diagnóstica de la fosa preorbital dorsal, los diferencias en el patrón oclusal y la moderada curvatura de los molariformes, este cráneo demuestra una morfología similar a *Dinohippus*, ligeramente mas primitive que aquellos que mas relacionados con *Equus* del Blancano, como *E. simplicidens*. Los registros en el centro de México y el sur de California, indican que *D. mexicanus* coexistió con *Equus* durante el Blanceano medio desde 4.5 hasta 3 Ma. A pesar de los interpretaciones de especiación anagénica, el presente estudio demuestra que los especies primitivas de *Equus*, se originaron de *D. mexicanus* por cladogénesis.

Key words: *Dinohippus, mexicanus*, *Equus*, Hemphillian, Blancan, Mexico

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B. J. MacFADDEN and O. CARRANZA-CASTAÑEDA. 2002. Cranium of *Dinohippus mexicanus* (Mammalia: Equidae) from the early Pliocene (latest Hemphillian) of central Mexico, and the origin of *Equus*. Bull. Florida Mus. Nat. Hist. 43(5):163-185. [End of Vol 43.]

INTRODUCTION

The latest Hemphillian (early Pliocene) about 5 million years ago was a very interesting time in equid evolution when four to six sympatric species coexisted at many localities in North America. Several studies have asserted that the latest Hemphillian species *Dinohippus mexicanus* (Lance) 1950 is of prime importance in understanding the origin of the modern genus *Equus*. In fact, *D. mexicanus* is hypothesized to be the closest sister-species of primitive species of *Equus,* such as *E. simplicidens* (Cope) 1893 (e.g., Bennett 1980; MacFadden 1984; Prado and Alberdi 1996; Kelly 1998).

The species *Dinohippus mexicanus* originally was described as *Pliohippus mexicanus* based on a large collection of latest Hemphillian horses from the Yepómera Local Fauna of Chihuahua, Mexico (Lance 1950). This horse has since been found at other localities in Mexico and the United States, and although these occurrences have sometimes been given new species names, they all seem close to, or conspecific with, *D. mexicanus* (MacFadden 1984; Carranza-Castañeda 1992). Over the past several decades, intensive geological and paleontological excavations have yielded an excellent assemblage of latest Hemphillian fossil mammals from the state of Guanajuato, Mexico. One of the specific localities in this region, Rancho El Ocote, has a rich and diagnostic fauna, including abundantly represented horses, particularly *D. mexicanus* and another monodactyl species *Astrohippus stockii* (Lance) 1950, but also including the rarer tridactyl *Neohipparion eurystyle* (Cope) 1893 and *Nannippus aztecus* Mooser 1968 [= *N. minor* (Sellards) 1916; Carranza-Castañeda and Ferrusquia-Villafranca 1978; also see Hulbert 1990, 1992]. Despite many years of field work at Rancho El Ocote, the large collection of horses from this locality has until now consisted of isolated teeth, dentitions, and postcranial remains. The facial morphology of *Dinohippus mexicanus*, which is of fundamental importance to understanding Neogene equid systematics, was previously unknown from Rancho El Ocote, poorly represented from Yepómera, and unknown from other latest Hemphillian localities (Lance 1950; MacFadden 1984, 1986; Azzaroli 1988).

During a field trip in 1997, the authors visited Rancho El Ocote and collected a nearly complete, although crushed, skull of *Dinohippus mexicanus,* one of only two known from this species as it is broadly defined (e.g., MacFadden, 1984). This new skull is significant because *D. mexicanus* is hypothesized to be the closest relative of primitive species of *Equus* (Bennett 1980; MacFadden 1984; Prado and Alberdi 1996; Kelly 1998), and the evolution of craniofacial morphology is critical to understanding the systematics of Neogene equids (see review in MacFadden 1992). The new skull from Rancho El Ocote therefore elucidates previous phylogenetic hypotheses concerning the origin of *Equus*. In addition to the skull of *D. mexicanus* described here from Rancho El Ocote, new teeth of equine horses collected from an early Blancan locality in Jalisco, Mexico, elucidate the mode of speciation that gave rise to primitive *Equus*.

ACKNOWLEDGMENTS

This project was supported by NSF EAR 99-02898. We thank Gerardo Álvarez for specimen preparation, Antonio Altamira-Gallardo and Erika Simons for photography, Merald Clark for preparing the line drawings, Dr. Sam McLeod, Dra. María del Carmen Perrilliat, and Dr. Richard Tedford for access to, respectively, the LACM, IGM, and AMNH collections, and Richard C. Hulbert Jr., Everett H. Lindsay, Charlotte M. Porter, and Fred G. Thompson for helpful comments that improved the manuscript. This is University of Florida Contribution to Paleobiology number 520.

MATERIALS, METHODS, TERMINOLOGY, AND ABBREVIATIONS

The following vertebrate paleontology collections were examined during this study and are abbreviated in the text as follows:

AMNH, American Museum of Natural History, New York.
F:AM, Frick:American Mammals, part of the AMNH.
IGM, Instituto de Geología Museum, Ciudad Universitaria, Universidad Nacional Autónoma de México.
LACM, Natural History Museum of Los Angeles County.
UF, University of Florida.
UMNH, Utah Museum of Natural History, University of Utah.

All measurements are in millimeters, and are reported to the nearest tenth mm (teeth) or mm (cranial measurements). Statistical calculations were done using Microsoft Excel™.

The following abbreviations and/or codes are used in the text:

A; adult wear stage, occlusal pattern moderately worn.
APL; greatest anteroposterior tooth length, excluding cement.

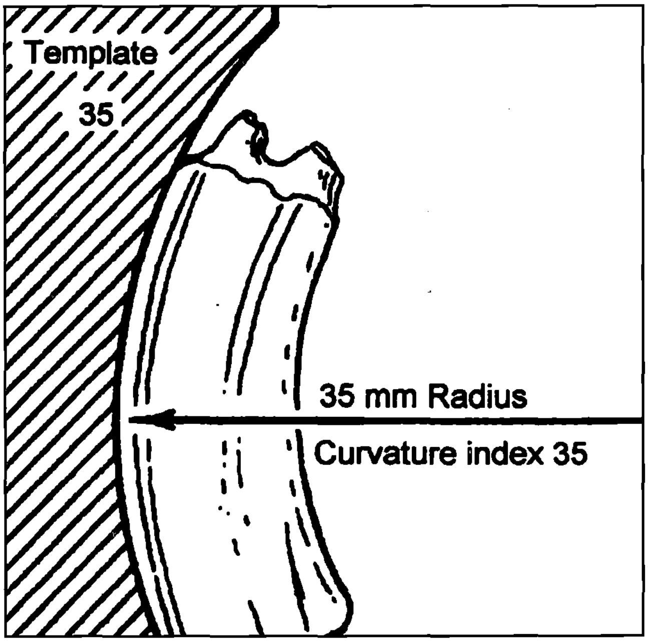

Figure 1. Method for determining the radius of curvature, CURV, of upper cheek teeth of fossil horses (modified from Skinner and Taylor [1967]; also see Appendix). Reproduced courtesy of the American Museum of Natural History.

C; upper canine.
CURV, curvature of mesostyle, as measured in the radius of circle inscribed (Fig. 1, taken from Skinner and Taylor 1967; also see Appendix).
DPOF; dorsal preorbital fossa.
I; upper incisor.
J; juvenile wear stage; tooth unworn or little worn; this is used to measure individuals that demonstrate maximum potential crown height (see MSTHT, below).
L; left side.
L.F.; local fauna; a geographically and temporally restricted fossil assemblage.
M; m; molar (upper, lower).
Ma; megannum, millions of years ago, in reference to a point in time.
MSTHT; mesostyle crown height.
O; old age, tooth heavily worn; these individuals were removed from pooled analyses representing characteristic dental measurements (Table 1).
P, p; premolar (upper, lower).
R; right side.
TRN; greatest transverse width, excluding cement.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus †*Dinohippus* Quinn, 1955
†*Dinohippus mexicanus* (Lance) 1950
(Figs. 2-11; Tables 1-2)

Synonomy of Rancho El Ocote referred sample:
large *Pliohippus* sp. Arellano 1951, p. 613
Hippotigris ocotensis Mooser 1958, p. 360
Protohippus muelleri Mooser 1965, p. 157
Dinohippus muelleri Mooser 1973, p. 258
Equus (Dolichohippus) mesamericanus Mooser 1973, p. 261
Pliohippus mexicanus Carranza-Castañeda and Ferrusquia-Villafranca 1978, p. 165
Dinohippus ocotensis Dalquest and Mooser 1980, p. 8
Dinohippus mexicanus Carranza-Casteñeda 1992, p. 186

Holotype.—"*Pliohippus*" *mexicanus*, LACM-CIT (California Institute of Technology) 3697, partial L maxilla with P2-M3 and part of zygomatic arch, from CIT locality 286, Yepómera L. F., Chihuahua, Mexico (Lance 1950).

Referred specimen.—IGM 7596, cranium with R I3, P2-M3, L I2-I3, P2-M3; also cast UF 206861.

Locality, Age, and Collector.—Rancho El Ocote, Ravine de La Caretta, IGM locality GTO 2b, Guanajuato, Mexico, latest Hemphillian (early Pliocene), ca. 4.8 Ma. Collected by the authors on 29 May 1997.

Specific Diagnosis.—Medium-sized monodactyl equine horse, basilar skull length ca. 430 mm; mean moderately worn (ontogeny = A) M1-M2 APL = 24.5 mm and TRN = 24.0 mm (Table 1). Nasal notch retracted to a position lying dorsal to the P2. Moderately hypsodont with mean unworn (ontogeny = J) M12 MSTHT = 69.0 mm (Table 1). Cheek teeth moderately curved transversely, with mean CURV = 73 mm. DPOF moderately well developed dorsally, ventrally, and posteriorly, although characteristically lacking a distinct rim. Long preorbital bar between DPOF and orbit. Malar fossa very poorly developed, or absent. Cheek tooth enamel pattern generally simple. Upper cheek tooth protocones oval and moderately elongated, especially posterior to the connection with the protoloph, and pre- and postfossettes crescentic in occlusal cross section with few plications. Hypoconal groove well developed and persists until late wear. Lower cheek tooth metaconids and metastylids have rounded borders and are well-separated, ectoflexid moderately deep in the premolars and deep in

Table 1. Comparison of dental measurements from *Dinohippus interpolatus* (from Miami = Coffee Ranch Quarry, Texas, in AMNH collection), *Dinohippus mexicanus* (pooled sample from Florida, Texas, and Mexico in F:AM, IGM, LACM and UF collections), and primitive *Equus* (pooled sample from Florida, Idaho, Nebraska, Texas, and Mexico in AMNH, F:AM, IGM, LACM, UF, and UMNH collections). Tooth measurements are taken on M1 or M2. Measurements are reported in the following sequence for each entry: N, number of specimens measured; x, mean; s, standard deviation; range, i.e., observed minimum to maximum. See text for abbreviations.

Character	*Dinohippus interpolatus*	*Dinohippus mexicanus*	primitive *Equus*	ANOVA Prob[1]	Different?[1]
APL[2]	12, 25.8, 0.8, 24.6-27.3	21, 24.5, 1.1, 22.5-26.7	12, 27.2, 1.4, 24.8-29.0	<0.001	Yes
TRN[2]	12, 25.1, 1.1, 22.8-26.4	20, 24.0, 1.6, 20.7-27.8	12, 28.2, 1.9, 25.1-31.3	<0.001	Yes
MSTHT[3]	9, 69.0, 4.9, 62.1-78.1	9, 69.0, 6.0, 60.1-77.4	5, 90.3, 5.5, 86.3-99.8	<0.001	Yes
CURV	5, 60, 0, 60-60	6, 73, 6.1, 65-80	11, 115.5, 25.4, 90-185	<0.001	Yes
TRL	3, 159.6, 1.1, 158.4-160.6	3, 157.0, 6.2, 151.0-163.3	34, 188.5, 7.9, 168.8-204.3[4]	—	—

[1] ANOVA probability level for the three species and whether or not these samples are statistically different.

[2] Adult wear stage (A), i.e., juveniles (J) and old age (O) individuals removed from pooled sample.

[3] Juvenile wear stage (J) in which tooth crowns are unworn or little worn, to indicate maximum MSTHT.

[4] Data for *Equus* taken from MacFadden (1989) for sample of *Equus simplicidens* from Idaho.

the molars, and pli caballinids poorly developed or absent (also see Lance 1950; MacFadden 1984).

Dinohippus mexicanus differs from contemporaneous *Astrohippus stockii* because of its larger size, lack of a ventral (malar) fossa, and details of the enamel pattern (e.g., shape of the protocone and less flared metaconids and metastylids). *D. mexicanus* differs from more primitive species within this genus (such as *D. interpolatus*) in less transversely curved cheek teeth and possibly slightly less defined DPOF. *D. mexicanus* differs from primitive species of *Equus*, such as *E. simplicidens*, in smaller size, shorter crown heights, more transversely curved upper cheek teeth, less elongated protocones with rounded enamel, and less expanded metaconids and metastylids with rounded enamel borders.

Specimen Description.—With a mean cheek tooth row length of 157.9 mm and a mean M12 APL of 23.3 mm (Table 2), IGM 7596 represents a moderately large equine horse. As evidenced by tooth measurements, IGM 7596 falls at the lower end of the observed range for the current, geographically broader concept of the species *Dinohippus mexicanus* (Table 1). The occipital condyles are not preserved, but the basioccipital region just anterior to the condyles indicates an approximate basilar skull length (i.e., tip of foramen magnum to anterior-most portion of symphysis; Osborn 1912) slightly greater than 430 mm (Fig. 2). The skull is badly crushed but preserves many important characters of this species, in particular the morphology of the facial region and dorsal preorbital fossa (DPOF). The nasal notch is retracted to a position that lies dorsal to the posterior half of P2. The infraorbital foramen appears to lie dorsal to P3. An apparent depression directly anterior to the DPOF seems to have resulted from crushing during fossilization. The DPOF is best preserved on the left side (Fig. 3). It is positioned high on the cheek ~75 mm above the dorsal part of the

Table 2. Dental measurements (excluding cement) of *Dinohippus mexicanus*, IGM 7596 (UF 206861) from Rancho El Ocote (GTO 2b), Guanajuato, Mexico.

Measurement	I3	P2	P3	P4	M1	M2	M3	P2-M3
R anteroposterior length (APL)	18.3	34.3	26.3	25.8	22.5	22.6	23.8	152.4*
R transverse width (TRN)	10.6	24.9	26.0	25.0	24.2	23.8	21.6	
L anteroposterior length (APL)	18.5	35.0	26.0	—	—	24.8	25.0	163.3
L transverse width (TRN)	9.9	27.0	26.8	—	—	25.5	21.0	

*Postmortem gap between M2 and M3 (3.4 mm) subtracted from 155.8 mm to yield 152.4 mm, the latter of which is taken as the actual P2-M3 APL.

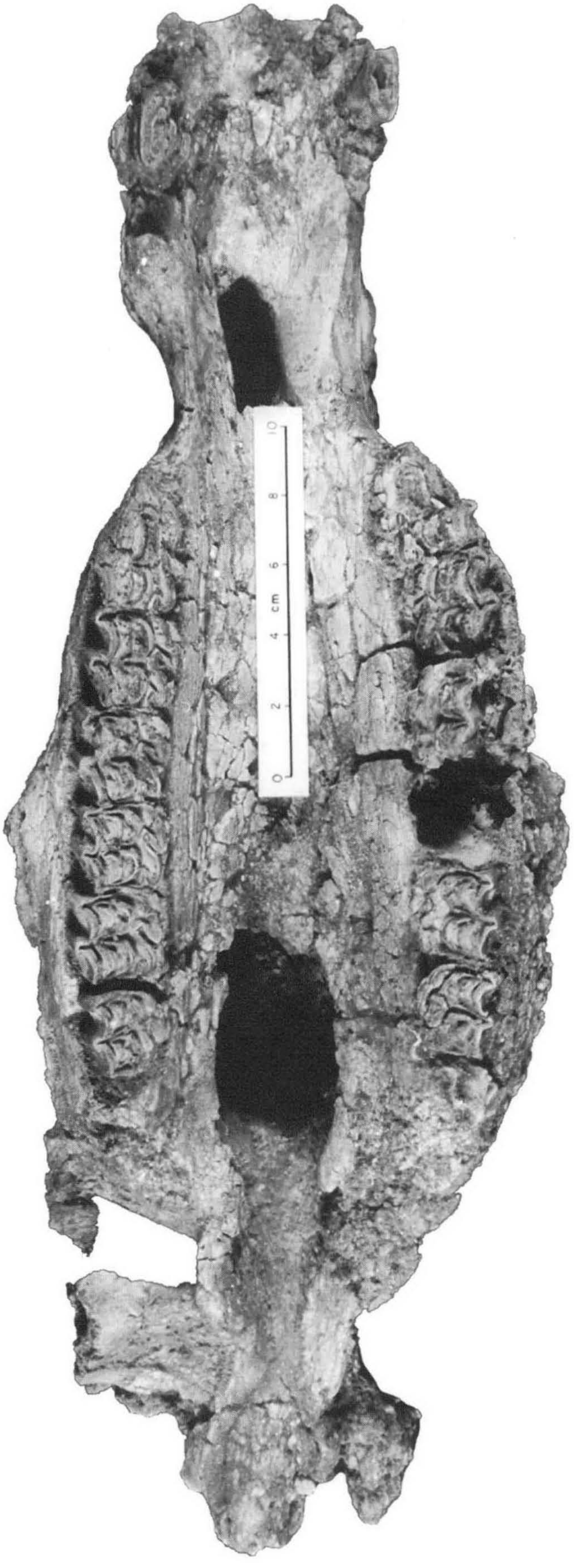

Figure 2. Ventral view of cranium of *Dinohippus mexicanus*, IGM 7596 (= UF 206861, cast), from Rancho El Ocote, latest Hemphillian of Guanajuato, Mexico.

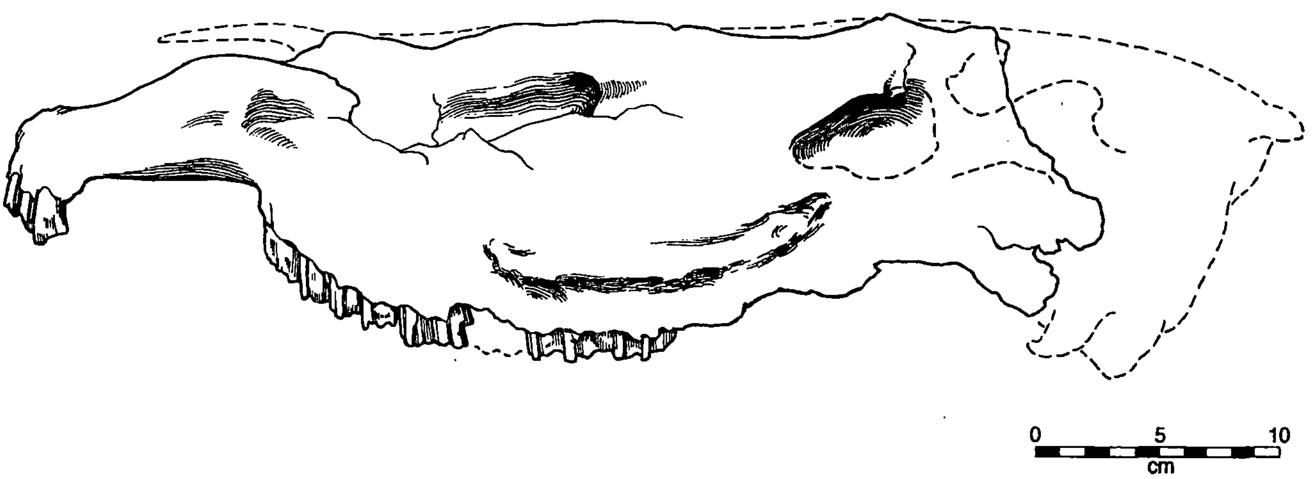

Figure 3. Left lateral, reconstructed view of cranium of *Dinohippus mexicanus*, IGM 7596 (= UF 206861, cast) from Rancho El Ocote, latest Hemphillian of Guanajuato, Mexico.

tooth row (above M1). The DPOF has well-developed edges, including the dorsal margin (also see Kelly 1998 for the significance of this morphology). Posterior to the crushed region that lies anterior to the DPOF, the anteroposterior length of the DPOF is greater than ~65 mm, the dorsoventral height is ~25 mm, and this fossa is ~10 mm deep in the center (also see Eisenmann et al. 1988 for measurement conventions), although this depth may be accentuated by crushing. The posterior margin of the DPOF is situated far forward of the orbit, i.e., there is a long preorbital bar of ~80 mm. The sutures of individual bones are not well preserved, but it appears that the DPOF lies on the nasal and maxillary bones anterior to the lacrimal bone. The region of the malar facial fossa, located ventrally, is not preserved on the left side, but there is an indication of a faint depression on the right side (not illustrated). As represented on the right side, a strong transverse malar crest is located on the ventral region of the face. The muzzle region is very broad (74 mm) and robust. There is a slight postcanine constriction (so that the corresponding transverse width just posterior to the canine is 56 mm).

Although the R & L I1 and I2 are not preserved, as inferred from the alvoeli and R & L I3, the shape of the incisor series is moderately curved (Fig. 2), i.e., it is neither very rounded, as in some browsing mammals, nor is it very linear, as in such extinct grazing horses as *Calippus*. Neither of the canines is preserved. The post-canine diastema (R = 54.0 mm, L is not preserved) is much larger than the precanine diastema (R = 15.8 mm, L is not preserved). The dP1 is absent. The cheek teeth represent a mature adult in late middle wear. The perimeter of the tooth crowns is covered with thick cement. Although direct measurements of CURV cannot be taken, as represented by the alveolus for the left M1 and adjoining P4 and M2, the cheek teeth are moderately curved in IGM 7596 (see Table 1 for CURV for other specimens of *Dinohippus mexicanus, D. interpolatus*, and primitive *Equus*). The enamel forming the exterior of the tooth and internal fossettes is relatively thick (Fig. 4). There are prominent parastyles and mesostyles on the ectoloph. The fossette borders are relatively simple (in contrast to *Equus* or some advanced hipparionines) with no, or one, plication on the anterior border of the prefossette and posterior border of the postfossette. In contrast, the posterior half of the prefossette and anterior half of the postfossette contain one or two plications. The hypoconal groove is moderately developed. Because the protocone is at a relatively advanced stage of wear, the pattern exposed on the occlusal surface is only moderately distinct. The characteristic advanced protocone seen in equines, which consists of a wooden-shoe shape with angular posterior border, is particularly evidenced in M2 and M3.

DISCUSSION

Nomenclature, geographic distribution, and age of *Dinohippus mexicanus*.—The genus *Dinohippus* was proposed by Quinn (1955) to encompass those species previously referred to *Pliohippus* that lack a well-developed ventral preorbital fossa. *Pliohippus sensu*

Figure 4. Occlusal view of right (reversed) P2-M3 of *Dinohippus mexicanus*, IGM 7596 (= UF 206861, cast) from Rancho El Ocote, latest Hemphillian of Guanajuato, Mexico.

stricto is retained for horses with very complex facial pits, including those with well-developed dorsal and ventral fossae. As currently envisioned, *Dinohippus* is first known from middle Miocene (?Barstovian, but certainly Clarendonian) localities from California (*D. leardi* (Drescher) 1941 from Black Hawk Ranch; Kelly 1998) and specimens in the AMNH/F:AM collections from the mid-continent (e.g., Webb 1969; Skinner and Johnson 1984). Thereafter, *Dinohippus* is relatively widespread until the end of the Hemphillian (MacFadden 1992; also see discussion of Blancan localities below). Several species names have been applied to large monodactyl horses within the concept of advanced, i.e., late Hemphillian, *Dinohippus* Quinn 1955. During the early late Hemphillian, as exemplified by localities in the Texas panhandle (e.g., Coffee Ranch = Frick Miami Quarry), *Dinohippus* has traditionally been assigned to the species *D. interpolatus* (Cope) 1893 (Matthew and Stirton 1930, as *Pliohippus*) and *D. leidyanus* (Osborn) 1918 from the Snake Creek Formation and equivalent units in Nebraska (Osborn 1918; Matthew 1924a; Stirton 1940, as *Pliohippus*). Kelly (1998) describes *Dinohippus interpolatus* from Oakdale, California. In addition to these localities, large, essentially undescribed, early-late Hemphillian collections of *Dinohippus*, either referable to *D. interpolatus* or *D. leidyanus,* are represented in the AMNH/F:AM collections from elsewhere in North America, including large quarry samples from Edson, Kansas, Optima (= Frick Guymon), Oklahoma, and Redington, Arizona, as well as smaller collections from South Dakota, New Mexico, and Nevada (MacFadden pers. observ. 2001). All these samples are early-late Hemphillian, ca. 6 Ma (Tedford et al. 1987). Early-late (ca. 6 Ma) and latest (ca. 5 Ma) Hemphillian mammalian faunas in North America contain different equid species assemblages. The typical early late Hemphillian equid fauna consists of *Dinohippus interpolatus* or *D. leidyanus*, *Astrohippus ansae* (Matthew and Stirton) 1930, *Neohipparion eurystyle* (or *N. gidleyi*), and *Nannippus lenticularis* (Cope) 1892 (*sensu* Hulbert 1988, 1993, = *Hipparion lenticulare* of Matthew and Stirton, 1930). In contrast, typical latest Hemphillian faunas contain *Dinohippus mexicanus*, *Astrohippus stockii*, *Neohipparion eurystyle*, and *Nannippus aztecus* (= *N. minor*, see Hulbert 1990).

Lance (1950) originally described the species *Pliohippus mexicanus* from the Yepómera L.F. of Chihuahua, Mexico. Quinn (1955) erected the genus *Dinohippus* for larger "pliohippine" horses from the late Miocene and early Pliocene of North America that lack the complex facial fossae seen in *Pliohippus sensu stricto*. As his study was mostly confined to earlier Miocene faunas from the Texas Gulf Coastal Plain, he did not address the generic allocation of "*Pliohippus*" *mexicanus* within the genus *Dinohippus*. Mooser (1973) followed Quinn's (1955) generic designation, although not accepting Lance's (1950) species for the large latest Hemphillian horse from Rancho El Ocote. Mooser first allocated the Rancho El Ocote *Dinohippus* to *Hippotigris ocotensis* (Mooser 1958), then *Protohippus muelleri*

(Mooser 1964), and finally, following Quinn (1955), to the genus *Dinohippus* as *D. muelleri*. Dalquest and Mooser (1980) assert that *D. ocotensis* from Rancho El Ocote differs from *D. mexicanus* from Yepómera in having more elongated, angular, and deeply grooved protocones, and "in having an anterior extension or spur extending in advance of the isthmus" (p. 10). The exact significance of this latter character is ambiguous; it seems to imply the difference in development of the pli caballinid in the lower cheek teeth. Carranza-Castañeda and Ferrusquia-Villafranca (1978) and Carranza-Castañeda (1992) did not accept the validity of *Dinohippus muelleri* or *D. ocotensis* from Rancho El Ocote and other equivalent-aged localities in Guanajuato and referred these latest Hemphillian horses to the species *mexicanus* (first as *Pliohippus,* and more recently to *Dinohippus*). Other workers (e.g., Bennett 1980; MacFadden 1984; Prado and Alberdi 1996; Kelly 1998) have mostly included *mexicanus* in *Dinohippus*. Statistical analyses of measured dental characters of early late and latest Hemphillian *Dinohippus* seem to represent continuous variation within two morphologically similar, closely related species, i.e., *D. interpolatus* and *D. mexicanus* (the latter *sensu lato*, i.e., encompassing a pooled sample from Ocote, Yepómera, and Florida; Fig. 5). We therefore assert that the differences used by Dalquest and Mooser (1980) to distinguish *D. ocotensis* and *D. mexicanus* represent individual variation that can be seen within different wear stages within a population. Thus, the latest Hemphillian species of large monodactyl horse is referable to *D. mexicanus* and it was widely distributed throughout southern North America.

With the revised, geographically more inclusive, concept presented here, *Dinohippus mexicanus* is known from several latest Hemphillian fossil localities in North America (Fig. 6). In central Mexico, *D. mexicanus* occurs at Rancho El Ocote (including Arroyo de Carretta, GTO 2b, location of IGM 7596), as well as several other localities in Guanajuato, including Rinconada (IGM locality GTO 43; Carranza-Castañeda 1992), Arroyo Tepalcates (GTO 52), and Rancho San Martín (GTO 42). In Chihuahua, *D. mexicanus* is known from the extensive LACM collection from Yepómera (Lance 1950). *D. mexicanus* also occurs from the Bone Valley deposits collected from open-pit phosphate mines in central Florida (MacFadden 1986). In the Texas panhandle, *D. mexicanus* occurs at the Christian Ranch L.F. and Rentfro Pit 1 locality (Schultz 1977; Tedford et al. 1987; MacFadden pers. observ. 2001). As far as is known, *D. mexicanus* does not occur in the western U.S. at any localities in California, Oregon, or Washington. It also does not occur in the northern Great Plains of the U.S. and Canada (north of the Texas panhandle). Whether this limited geographic distribution is a result of a paucity of latest Hemphillian sites (see Tedford et al. 1987), or represents the actual biogeographic distribution of *D. mexicanus*, cannot be determined at the present time.

Craniofacial morphology and transitional dental characters.—In the context of the present paper, many essential cranial characters pertain to the development of preorbital pits, or fossae, in the cheek region on either the maxillary or nasal bones. The function of these preorbital fossae, which do not occur in modern *Equus* and lack any direct functional analog, is not certain. They have been purported to be sexually dimorphic and some workers have argued that these structures are not of taxonomic utility. We do not intend to rehash this argument here as it has been amply addressed in the literature (see review in MacFadden 1992). Suffice it to say that, as also discussed in MacFadden (1984) for the Yepómera horses, the preorbital facial fossa (in this case the DPOF) is of fundamental importance in understanding the morphological differences between, and phylogenetic interrelationships of, late Cenozoic equids. As far as is known, *Pliohippus* and *Astrohippus* have very complex facial fossa that consist of multiple pits located both dorsally and ventrally on the cheek region (e.g., Bennett 1980; MacFadden 1984; Kelly 1998). With the exception of a weakly developed DPOF in *Equus grevyi* (Skinner and Hibbard 1972), extant *Equus* lacks any preorbital fossae. With the addition of the new specimen (IGM 7596) from Rancho El Ocote described here, the evolution of preorbital facial fossa in Hemphillian *Dinohippus* and primitive Blancan *Equus* can be further clarified.

In overall morphology of the preorbital fossae, *Dinohippus interpolatus* and *D. leidyanus* are generally similar (also see Kelly 1998). Although the type of *"Pliohippus" interpolatus* Cope 1893 is based on a single M2 from near Goodnight, Texas (Osborn 1918), large samples referred to this species are described from Coffee Ranch, Texas (Matthew and Stirton 1930), and there is a similarly large, essentially undescribed, collection from the equivalent Frick Miami Quarry at the AMNH. As exemplified by F:AM 116171 and 116172 (the latter being the type of *Pliohippus bakeri* Azzaroli 1988 (Azzaroli 1988, plate 1), a concept not followed here), the preorbital facial morphology of *D. interpolatus* can

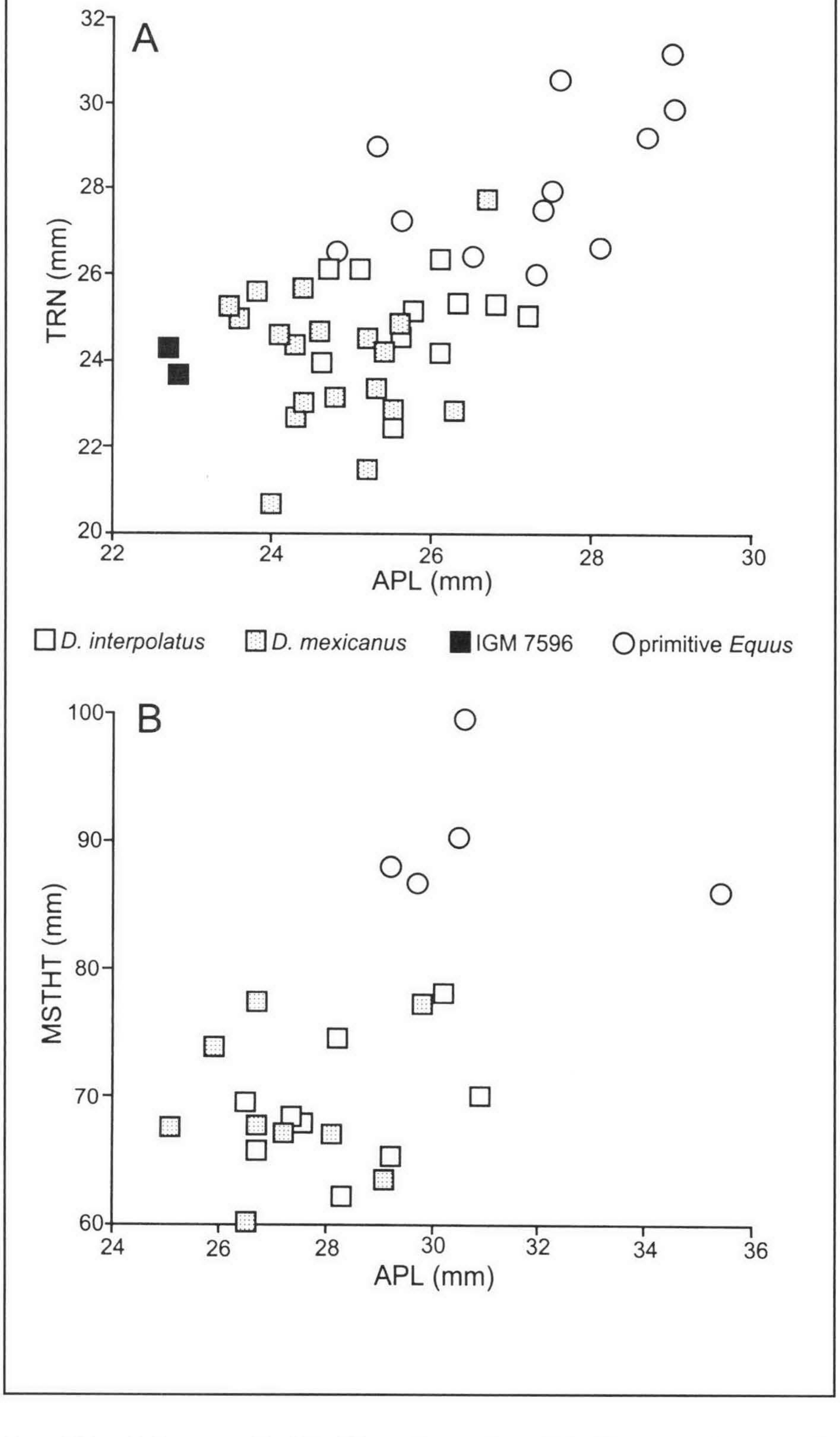

Figure 5. Bivariate plots of dental characters for *Dinohippus interpolatus*, *Dinohippus mexicanus*, and primitive *Equus*. (A) Anteroposterior M1 or M2 length versus transverse M1 or M2 width, middle wear (juveniles and old age individuals removed). One outlier of *Equus* from Sand Draw, Nebraska (APL = 33.1 mm, TRN =28.7 mm) is removed from the plot. (B) Anteroposterior M1 or M2 length versus unworn to little worn (juvenile) M1 or M2 crown height.

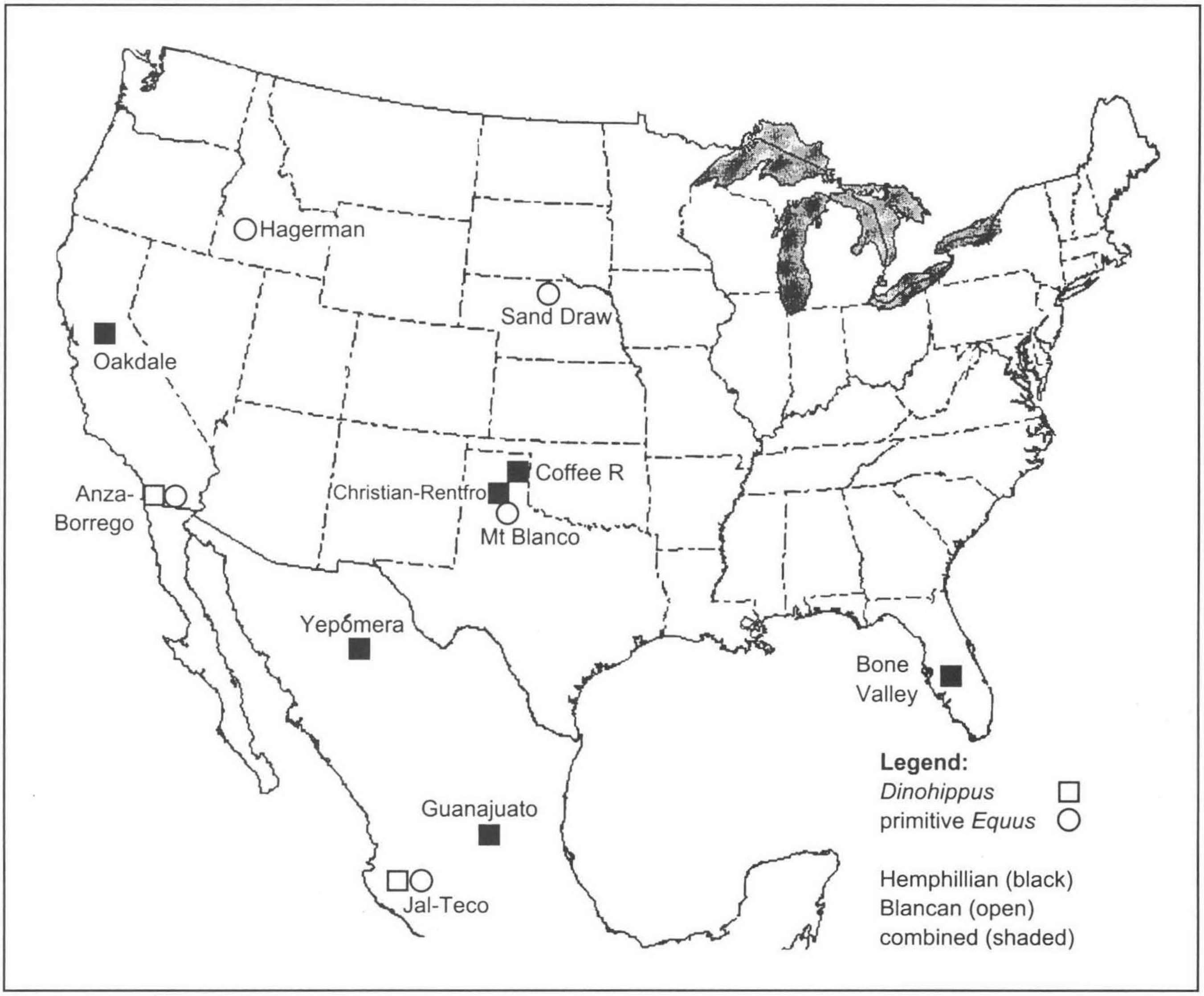

Figure 6. Selected late Hemphillian and early Blancan localities from North America with occurrences of *Dinohippus* and *Equus*, as discussed in this paper. Christian-Rentfro refers to the Christian Ranch L. F. and Rentfro Pit I locality in the Texas panhandle (Schultz 1977; Tedford et al. 1987).

be characterized as having a poorly developed ventral (malar) fossa and a moderately well developed DPOF. The ventral fossa is essentially a faint, exceedingly shallow depression lying principally on the maxillary bone, but with its posterior-most extent developed on the maxillary-malar suture. The DPOF is a well defined oval-shaped depression that lies on the nasal and maxillary bones. Although the general configuration of the DPOF is consistently developed in different individuals, there is some variation in the development of the margins of the DPOF. For example, in F:AM 116171 and 128143 of *D. interpolatus* from Miami Quarry, the DPOF margins are well defined dorsally, ventrally, and posteriorly, and these margins are delinated by a curving of the bone into the pit. In the other well preserved specimen (F:AM 116172; see Azzaroli 1988, plate 1) from Miami Quarry, the general configurations of the fossae are similar, although the dorsal and posterior margins of this structure are delineated by a distinct rim. In both specimens, as also seen in other species of *Dinohippus*, the anterior part of the DPOF is weakly defined.

The other early late Hemphillian species of *Dinohippus* was originally described as *Pliohippus* *leidyanus* Osborn 1918 from the Snake Creek Fauna of Nebraska. The holotype, AMNH 17224, consists of a beautifully preserved cranium and mandible of a subadult female (with the M3 almost fully erupted but not in wear, Fig. 7A). Another specimen from the Snake Creek Fauna, AMNH 18972 (not illustrated here), represents an adult male in which the malar fossa is essentially absent. Because the ventral region of the holotype is distorted by post-mortem crushing, it is not possible to see any original morphology of the malar preorbital fossa. In these specimens the DPOF is well developed and its general morphology is similar to that for *D. interpolatus*, with well developed dorsal, posterior, and ventral margins.

Given the description above, the two species of early late Hemphillian *Dinohippus*, i.e., *D. leidyanus* and *D. interpolatus*, are very similar in facial morphology, as they also are in such other characters as size and dental pattern. In addition to those described above from Coffee Ranch/Miami and Snake Creek, excellent quarry samples exist in the AMNH for early late Hemphillian *Dinohippus*, e.g., from Optima = Guymon, Oklahoma, and Edson, Kansas. These large quarry samples could be used in the future to further assess the intrapopulational variation in the DPOF (as Skinner and MacFadden 1977 did for *Cormohipparion*), as well as those characters that could be used to differentiate the closely related *D. interpolatus* from *D. leidyanus*.

MacFadden (1984) described a partial skull of *Dinohippus mexicanus* (LACM 275/3732; Fig. 7B) from the latest Hemphillian of Yepómera (sublocality 275) that preserves the preorbital region. The Yepómera fossil horizons occur within a normally magnetized zone correlated to the early Gilbert magnetic chron. Lindsay et al. (1984) present an extrapolated age of ca. 4.6 Ma for the locality, placing it in the latest Hemphillian, an age that is roughly the same as for the Guanajuato sites that contain the same mammal faunas, including the other skull of *D. mexicanus* (IGM 7596). Both skulls have well-preserved preorbital regions in which the DPOF is well defined dorsally, ventrally, and posteriorly, whereas the anterior region is confluent with the cheek region. The malar region is not preserved in IGM 7596, but in LACM 275/3733 this region is essentially smooth and the malar fossa is absent. The overall morphology of the preorbital region in *D. mexicanus* is therefore similar to that demonstrated in *D. interpolatus* and *D. leidyanus*.

The late Pliocene (Blancan) species of primitive *Equus* have been given many names, and there currently is not universal agreement as to their nomenclature and distribution. The resolution of the nomenclature of "primitive *Equus*" species is outside the intended scope of this paper. We therefore refer to it here as primitive *Equus*, but note that it embodies the concept of, or is close to, *Equus simplicidens*, as it was first known from the Texas panhandle. Primitive *Equus*, which has been referred variously to *E. simplicidens, E. shoshonensis* Gidley 1930, and *Plesippus idahoensis* (Merriam) 1918 (Gazin 1936; Skinner and Hibbard 1972; Repenning et al. 1995), is also known from the extensive collection of skeletons from the Horse Quarries at Hagerman, Idaho. One skull of *E. simplicidens*, AMNH 22077, from Crawfish Draw, Mt. Blanco, is the type locality for this species. This nearly complete skull preserves the preorbital region, including the DPOF and malar fossa. In this specimen the malar fossa is weakly developed as a shallow depression on the maxillary and malar bones. The DPOF has well-developed dorsal and posterior margins, whereas the ventral and anterior parts of this structure are confluent with the adjacent cheek region. By far the most comprehensive sample known for primitive *Equus* is from Hagerman, as exemplified by four adult specimens in the AMNH/F:AM (32555 [female], 32553 [male], 32551 [female], and 32556 [male]). In all these specimens the configuration of the facial fossae is similar. The malar fossa is usually poorly developed and represented by a small pit on the maxillary bone just anterior to the maxillary/zygomatic suture. The DPOF is present, although it seems slightly less well defined than in *Dinohippus*. In particular, the ventral and anterior margins are not distinct, thus these parts of the fossa are confluent with the adjoining part of the cheek region. In the Hagerman sample, the mean length of the DPOF is 95 mm and the mean height is 36 mm (see Eisenmann et al. 1988, p. 11, for exact location of measurements, i.e., B33 and B35). The relative size of the DPOF in primitive *Equus* is therefore similar to that of *Dinohippus mexicanus*. Hence the morphological changes in the development of the DPOF from *Dinohippus* to *Equus* involve the weakening of the anterior and ventral margins, and not a relative reduction in size.

Several important characters related to size and dental morphology distinguish *Dinohippus mexicanus* from primitive *Equus*, such as *E. simplicidens*. Primitive *Equus* is a larger horse, with a mean basilar skull length of 540 mm (N = 4; specimens AMNH 20077, 32551, and F:AM 32553, 32555), whereas *D. mexicanus* (IGM 7596) has a basilar length of 430 mm. Although there is

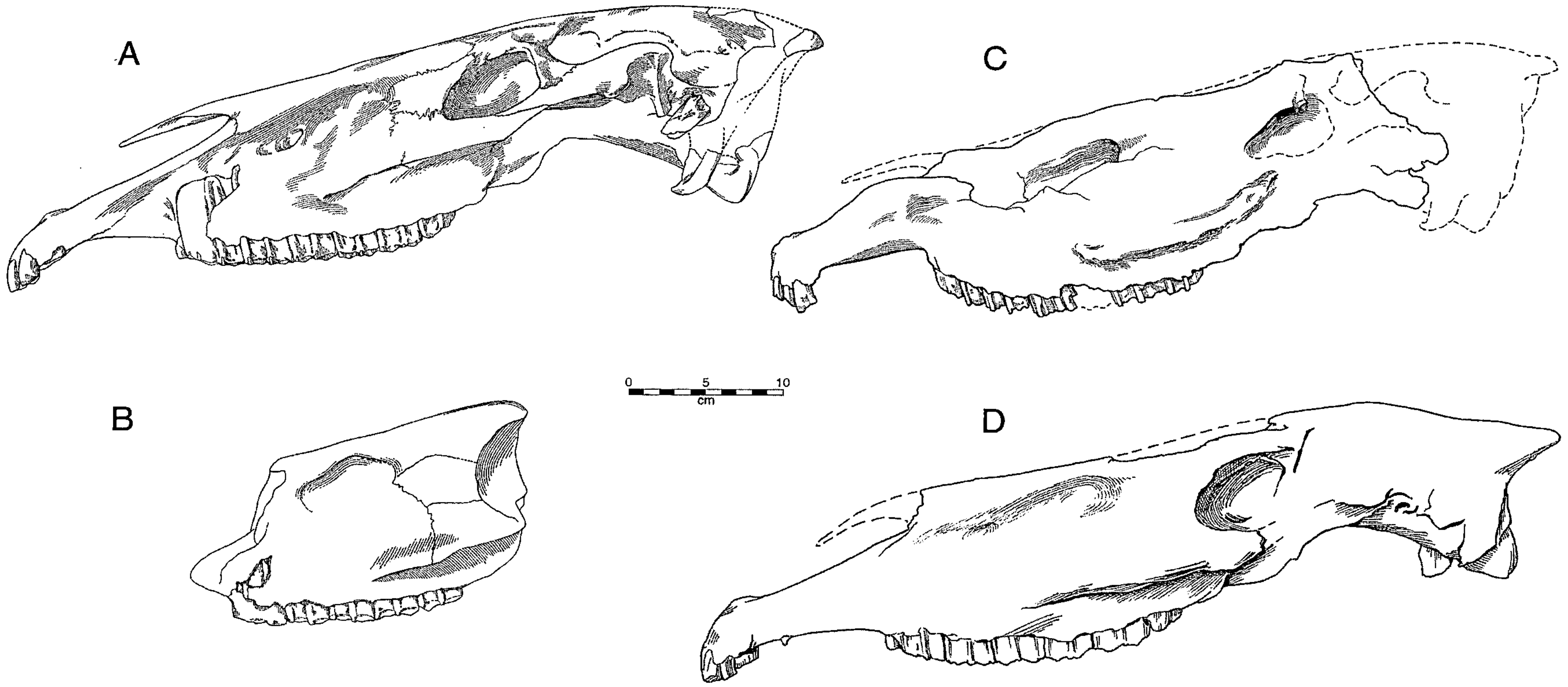

Figure 7. Comparison of lateral views of crania of (A) *Dinohippus leidyanus*, AMNH 17224, holotype, modified from Osborn (1918), (B) *Dinohippus mexicanus*, LACM-CIT 275/3723, from Yepómera (from MacFadden 1984), (C) *Dinohippus mexicanus*, IGM 7596 (= UF 206861, cast), from Rancho El Ocote, and (D) *Equus simplicidens*, F:AM 32555, from Hagerman, Idaho.

some overlap of individual specimens (Fig. 5A), the M1 and M2 APL and TRN of primitive *Equus* are statistically larger than in *D. mexicanus* (Table 1). Primitive *Equus* also has significantly higher crowns, with juvenile, little worn M1 or M2s having a mean MSTHT of 90.3 mm, whereas *D. mexicanus* has the corresponding mean MSTHT of 69.0 mm (and *D. interpolatus* also has a mean M1 or M2 MSTHT of 69.0 mm; Table 1, Fig. 5B). The upper cheek tooth crowns are most highly curved in *D. interpolatus* (mean CURV = 60 mm), moderately curved in *D. mexicanus* (mean CURV = 75 mm), and less curved in primitive *Equus* (mean CURV = 115.5 mm; Table 1). This represents a morphocline from the more primitive, highly curved crowns found in *Dinohippus* during the early late Hemphillian on the one hand to the relatively straight crowns found in primitive *Equus* during the Blancan on the other hand.

The protocone also shows a morphocline from *Dinohippus* to *Equus* (also see Kelly 1998). In relatively primitive monodactyl horses (pliohippines and dinohippines, i.e., excluding *Equus*), the protocone is small and connected to the protoloph (Fig. 8A). In "typical" or middle wear of *D. mexicanus*, the protocone is characteristically elongated posterior to the connection to the protoloph and has the advanced "wooden-shoe" shape in which the lingual margin of the protocone is concave (Figs. 4, 8B; also see Dalquest 1988). In more advanced wear this wooden-shoe shape is weakened and the lingual margin of the protocone is anteroposteriorly straight. In both primitive and advanced *Equus*, the anterior margin of the protocone is greatly expanded towards the anterior of the tooth (Fig. 8C). In the lower cheek teeth the metaconids and metastylids of *D. mexicanus* are typically rounded, whereas in primitive *Equus* they typically have angular borders (also see discussion below).

Origin of *Equus*.—The fossil evidence documenting the origin of primitive *Equus* during the Pliocene has both fascinated and perplexed paleontologists since the second half of the nineteenth century. Marsh (1879) not only produced his orthogenetically arranged chart of equid morphological and presumed evolutionary stages, but also recognized that *Pliohippus* was a "near ally of the modern horse" (p. 504). Gidley (1907) revised the Miocene and Pliocene Equidae from North America and allocated Cope's *Equus simplicidens* to *Pliohippus* because he believed that this species had more of an overall resemblance to that genus than to *Equus*. Based on some then-recently excavated equid skeletal material from Mt. Blanco, Texas, Matthew (1924b) proposed the generic name *Plesippus*, and also assigned Cope's material of *Pliohippus simplicidens* from the same locality to this new genus. This Pliocene equid genus was purported to be morphologically similar to (e.g., in tooth curvature), although more advanced than, *Pliohippus*, but also shared similarities (e.g., the great reduction in the facial fossa) with *Equus sensu stricto*. Matthew (1926) arranged all North American fossil Equidae into nine morphological levels, or grades, starting with *Hyracotherium* ("*Eohippus*") and ending with *Equus*. As evidenced from the resulting phylogenetic chart (Matthew 1926, p. 167), *Plesippus* is depicted as having been descended anagenetically (i.e., with no temporal overlap) from *Pliohippus* in the early Pliocene, and *Equus* from *Plesippus* at the beginning of the Pleistocene.

Stirton (1940, 1942) did not follow Matthew's designation of *Plesippus* as a valid genus. Rather, he considered it a subgenus within *Equus*. Interestingly, in these same papers, Stirton mentions the possibility that primitive *Equus* was descended polyphyletically from two or more species of *Pliohippus*. Stirton (1940, p. 194) noted: "More careful work, however, needs to be done to trace the descent of the different species from the Lower to Middle Pliocene forms." Based on several characters of the upper and lower cheek tooth morphology, Dalquest (1978, 1988) and Bennett (1980; reproduced as Fig. 9) also supported the notion of a polyphyletic origin for the genus *Equus* from *Astrohippus* on the one hand (giving rise to *Asinus*) and *Dinohippus* ("*Pliohippus*") on the other hand (giving rise to zebras and caballines).

In a significant departure from the accepted dogma of the time, Quinn (1955) hypothesized that living equids are represented by three extant genera, *Hippotigris* (zebras), *Asinus* (asses), and *Equus sensu stricto* (horses), and that these were descended from a common ancestor, *Eoequus wilsoni* Quinn 1955, from the middle Miocene Hemingfordian Cold Spring Fauna of the Texas Gulf Coastal Plain. This radial vertical taxonomy has not met with subsequent acceptance. A legacy of Quinn's (1955) work, however, was his creation of the new genus *Dinohippus* for pliohippine horses lacking the complex facial fossa seen in *Pliohippus*. Interestingly, and also at odds with subsequent studies, Quinn (1955, Fig. 3) indicated that *Dinohippus* became extinct in the early Hemphillian and is not involved in the ancestry of *Equus*.

Skinner (in Skinner and Hibbard 1972) allocated the Pliocene species *simplicidens* to *Equus*, and included it in the subgenus *Dolichohippus*, which has otherwise been used to denote Grevy's zebra *Equus* (*Dolichohippus*)

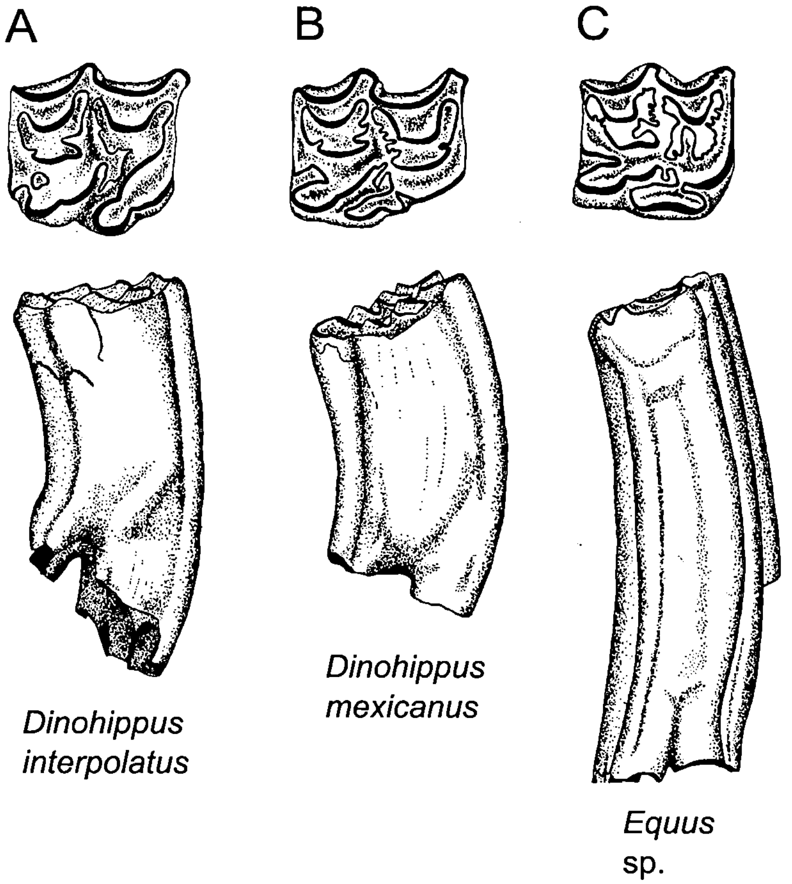

Figure 8. Comparison of protocone shapes and hypsodonty (taken from Dalquest 1988, Fig. 4; scale not indicated, but presumed to be at, or close to, original scale). Occlusal (top) and lateral (bottom) views of (A) *Dinohippus interpolatus* from the Coffee Ranch (= Frick Miami) L. F., late Hemphillian of Texas, (B) *Dinohippus mexicanus* from the Rancho El Ocote L. F., latest Hemphillian of Guanajuato, Mexico, and (C) *Equus* sp. from the Cedazo L. F., Pleistocene of Aguascalientes, Mexico.

grevyi. Skinner's belief was that the Blancan *Equus* species *E. simplicidens* was widespread throughout North America, including Mt. Blanco (the type locality), Hagerman, Idaho (previously referred to as *E. shoshoensis* by Gazin 1936), Kansas, and numerous localities in Nebraska.

Bennett (1980) was the first worker to produce a cladogram of the interrelationships of *Equus* and its closest sister taxon *Dinohippus*. In the pre-computer days, this cladogram was "hand drawn," and therefore did not benefit from the rigorous phylogenetic character analysis that has developed since her study. In this scheme, the species *D. mexicanus* was the closest sister-species of *Equus "shoshoensis."* MacFadden (1984) discussed the interrelationships among *Dinohippus*, *Astrohippus*, and *Equus*. In contrast to what previous workers had said about the polyphyletic origins of *Equus*, MacFadden (1984) indicated that, based on the very complex facial fossa morphology, *Astrohippus* is not closely related to *Equus*. If this were the case, as has been previously asserted based on dental characters, then *Astrohippus* with its complex DPOF and malar fossa, would have to undergo a considerable morphological transformation in order to be closely related to the origin of *Equus*. MacFadden (1984; also 1986) states that *Dinohippus* is close to *Equus simplicidens*, in particular the advanced species *D. mexicanus*. Azzaroli (1988) analyzed the morphology of late Hemphillian monodactyl horses from Coffee Ranch. Although we do not agree with the designation of a new species, *Pliohippus bakeri*, from this important locality (also see Kelly 1998), several conclusions of Azzaroli (1988) are relevant here, including: (1) the taxonomic importance of the facial pits in understanding the interrelationships of late Cenozoic equine horses, and (2) the close relationship between *Dinohippus* (including *D. leidyanus* [= *interpolatus*] and *D. mexicanus*) and *Equus*. Although the possible polyphyletic origin of *Equus* is still arguable, the current consensus is that *Dinohippus*, in particular *D. mexicanus*, is the closest outgroup to some segment of primitive *Equus* that existed in North America during the Blancan.

Within the past decade, several phylogenetic studies that include the interrelationships of *Dinohippus* and *Equus* have been presented for Neogene equids from North America (Evander 1989; Hulbert 1989; Prado and Alberdi 1996; Hulbert 1996; Kelley 1998). Of these, the study by Kelly (1998) presents the most comprehensive cladistic analysis using 40 cranial, dental, and post-cranial characters for the Tribe Equini, including the species of *Dinohippus*, i.e., *D. leardi, D. interpolatus, D. leidyanus, D. mexicanus*, and *Equus simplicidens*. The synapomorphies that Kelly (1998) uses to justify his cladogram (Fig. 10) are mostly confirmed, or further demonstrated, by the cranium of *D. mexicanus* IGM 7596 described here. In particular, the depth of the nasal notch (character/state 1.2), configuration of the DPOF (10.2, 5.0, 9.0, 6.0), deep hypoconal groove (26.0), oval protocone (18.2), and protocone never connected to hypocone (21.0) are all characters that are seen in the *Dinohippus* species morphocline, including *D. mexicanus* from Rancho El Ocote.

While we are in general agreement with the observations presented by Kelly (1998), the development of the malar fossa deserves some comment here. Kelly (1998) indicates that the malar fossa is present and well separated from the DPOF (8.1) in *D. leardi* and *D. leidyanus*, but this feature is absent in *D. leidyanus* and *D. mexicanus* (8.0). Studies of the populations referred to *D. interpolatus* and *D. leidyanus* at the AMNH indicate that there may be more variation in the development of the malar fossa and its separation from the DPOF than is coded in Kelly's (1998) cladistic analysis. Other than this, Kelly's (1998) study presents a solid basis for understanding the morphological and inferred phylogetic transformations seen in the species of *Dinohippus*.

Kelly (1998) also discusses the synapomorphies that

Table 3. Synapomorphies used to support nodes in cladogram presented by Kelly (1998, Fig. 10 here) for Neogene equine horses from North America and the character states demonstrated in *D. mexicanus* from Rancho El Ocote.

Node	Ocote *D. mexicanus*
Dinohippus-Equus clade (Node 8)	
Nasal notch dorsal to posterior half of P2 (character 1, state 2)	1.2
Preorbital bar long (character 10, state 2)	10.2
TRL > 160 mm (character 37, state 4)	*
Dinohippus interpolatus (Node 9)	
Shallow DPOF (character 5, state 0)	5.0
DPOF posterior margin without rim, no pocket (character 9, state 0)	9.0
Hypoconal groove open to base of crown (character 26, state 0)	26.0
Presence of intertubercular crest (INT) on humerus (character 40, state 1)	?
Dinohippus leidyanus (Node 10)	
Dorsal margin DPOF rounded (character 6, state 0)	6.0
Malar fossa absent (character 8, state 0)	8.0
Protocone never connects to hypocone (character 21, state 0)	21.0
Dinohippus mexicanus-Equus simplicidens (Node 11)	
Protocone oval (character 18, state 2)	18.2

*With a mean P2-M3 TRL of 157.9 mm for IGM 7596, this is transitional between character/state 37.3 (TRL between 126-160 mm) and 37.4 (TRL > 160 mm).

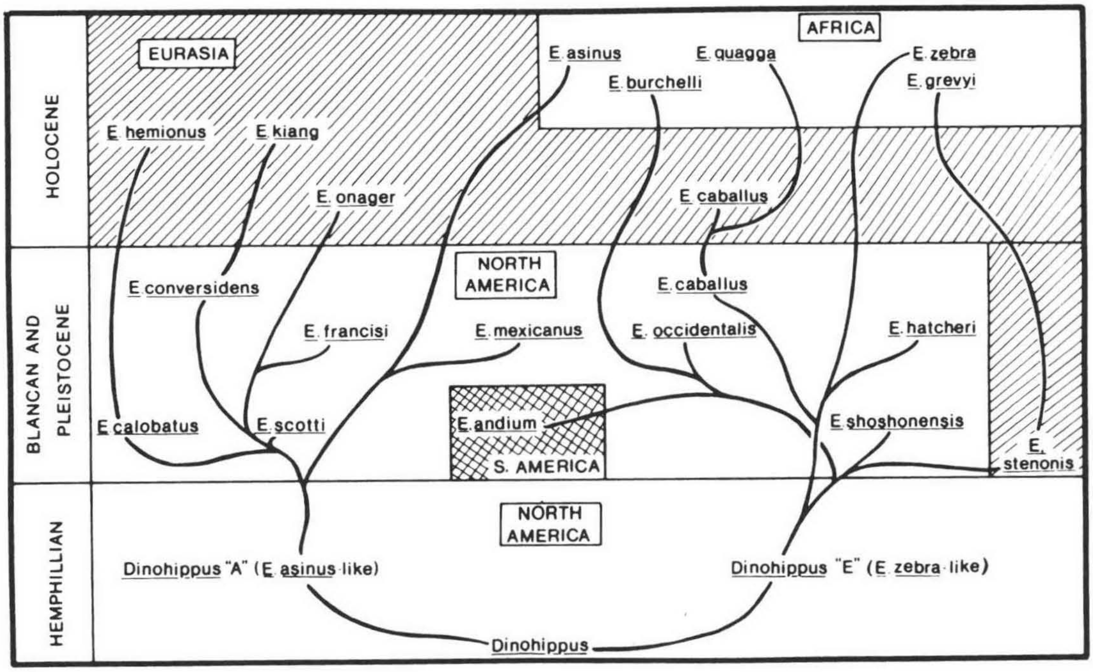

Figure 9. Origin of *Equus* from *Dinohippus*, from Bennett (1980) and reproduced with permission of the Society of Systematic Biologists.

justify the *Dinohippus mexicanus-Equus simplicidens* (= primitive *Equus* here) node (his 11) with 18.2, the shared presence of an oval protocone. In addition to this, our present study indicates that a decrease in CURV can also be used to justify this dichotomy. Kelly (1998) does not discuss the synapomorphies that separate *Equus* from more primitive *Dinohippus*, but numerous characters are presented in Bennett (1980), Hulbert (1989), and Prado and Alberdi (1996). The results of the present study indicate, or further confirm previous studies, that the following synapomorphies separate *Equus* from *Dinohippus*:

1. DPOF more poorly defined;
2. Increased overall size (e.g., as represented by basilar length, tooth row length, or upper molar dimensions;
3. Increased relative hypsodonty;
4. Reduced CURV; and
5. More flared protocone; metaconids and metastylids with angular enamel borders.

The question arises as to the mode of speciation that occurred between *Dinohippus mexicanus* and primitive *Equus*, such as *Equus simplicidens*. Early workers (e.g., Matthew 1926) indicated descent through grades, suggesting anagenesis. Dalquest (1988) believed that horse evolution in the Hemphillian and early Blancan was gradual and probably accelerated in the latest Blancan and Pleistocene. He further asserted that this increased rate of evolution provided an example of punctuated equilibria. Hulbert (1996) depicts *Equus* as originating from *Dinohippus* by anagenesis, i.e., phyletic speciation during the Pliocene. In fact, recognition and calibration of the exact evolutionary transition between *Dinohippus* and primitive *Equus* has been difficult to resolve because of the lack of superposed latest Hemphillian/early Blancan sites (Lindsay et al. 1984). Nevertheless, there are two localities that span this transition and potentially document evidence of the mode of speciation between *D. mexicanus* and *E. simplicidens*. One of these was previously reported (Downs and Miller 1994) and the other is a new locality from central Mexico that has transitional morphology represented by isolated teeth of advanced equine horses pertaining to *Dinohippus* and/or *Equus*.

Downs and Miller (1994) describe late Cenozoic horses from the well-calibrated sequence in the Anza-Borrego desert of southern California. Although the presence of *Dinohippus* is not surprizing from the late Hemphillian localities, they also describe a specimen that they tentatively refer to cf. *Dinohippus* sp. from overlying levels. If this assignment to *Dinohippus* is correct, then this occurrence extends the range of this species well into the Blancan, with a local range for this species from about 4 to 2.7 million years, indicating temporal overlap with the known range of *Equus simplicidens* (*sensu* Downs and Miller 1994) at Anza-Borrego.

Newly collected specimens further suggest an extension for the genus *Dinohippus* into the Blancan. These come from the previously unreported Jal-Teco 7 locality from Jalisco in central Mexico (Fig. 6), which is currently being worked by the IGM. This locality also has an occurrence of Pliocene equids that are of relevance to an understanding of the origin of *Equus*. One level, Las Gravas, within the continuous Jal-Teco 7 sequence, which spans late Hemphillian to Rancholabrean, overlies an ash dated at 4.8 Ma (unpublished data), contains glyptodonts, capybaras, and two types of equids, and is interpreted to be early Blancan age. There are several isolated equid teeth collected *in situ* from Las Gravas that represent two distinct morphologies. The more primitive morphology, which is referable to *Dinohippus mexicanus*, includes shorter crowned lower dentitions (Fig. 11, left) with relatively rounded metaconids and metastylids. The more advanced morphology, which is referable to primitive *Equus*, e.g., *E.* cf. *simplicidens*, includes relatively more hypsodont teeth with greatly expanded metaconids and metastylids with angular borders (Fig. 11, right). There are two possible explanations for this very interesting co-occurrence of ancestral and descendant species. These two morphologies could represent: (1) different individuals

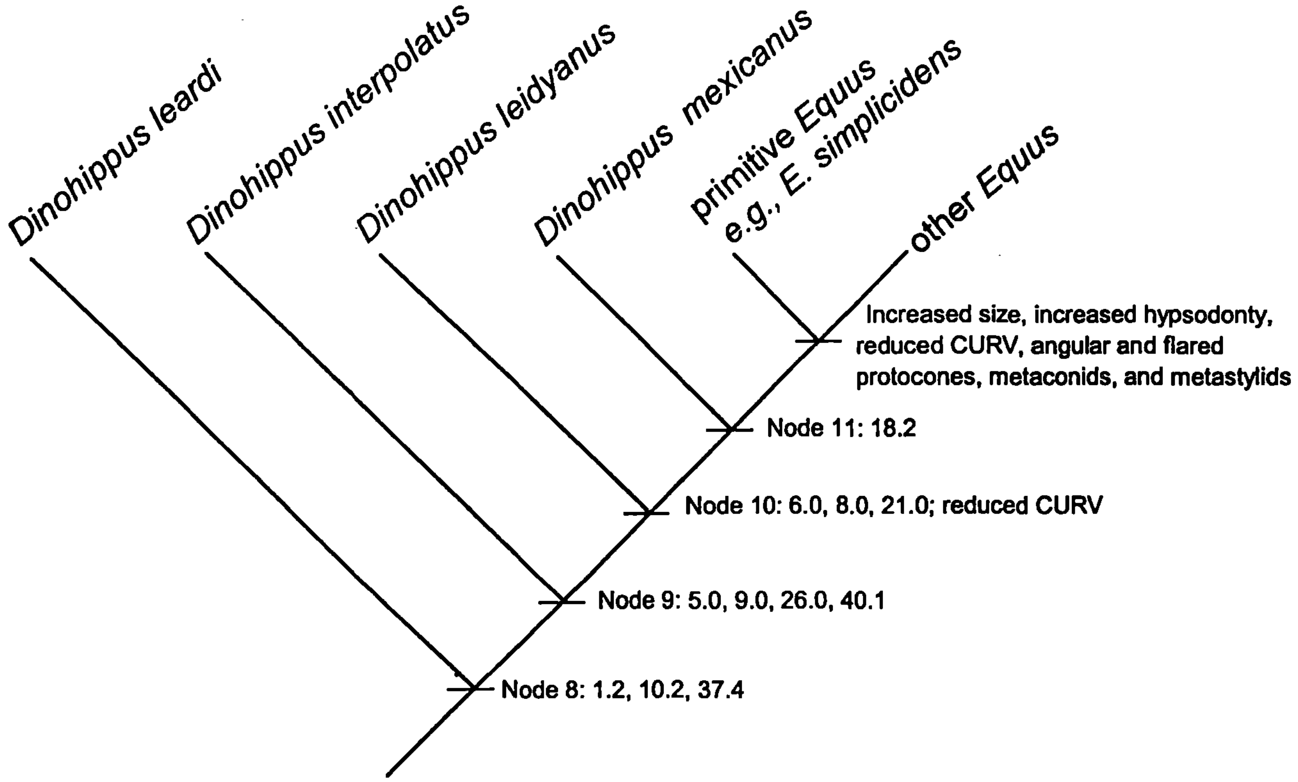

Figure 10. Portion of strict consensus cladogram presented by Kelly (1998; Fig. 10) representing *Dinohippus* and *Equus*, with coded synapomorphous character states justifying each node, as follows: (8) 1.2, nasal notch deep, i.e., dorsal to posterior half of P2 or deeper; 10.2, preorbital bar long; 37.4, mean TRL > 160mm; (9) 5.0, shallow DPOF, 9.0; posterior DPOF margin without pronounced rim and no pocket; 26.0, hypoconal groove open to near base of crown; 40.1, forearm intertubercular crest (INT) only moderately developed; (10) 6.0, DPOF with rounded dorsal margin; 8.0, malar fossa absent; 21.0, protocone never connects to hypocone; (11) 18.2, protocone elongate-oval. In addition to these characters, the present study indicates the following for *Equus* relative to *D. mexicanus*: reduction in CURV; and for *Equus* (node not analyzed in Kelly 1998): DPOF more poorly defined, increased size, increased hypsodonty, further reduced CURV, angular and flared protocones, metaconids, and metastylids.

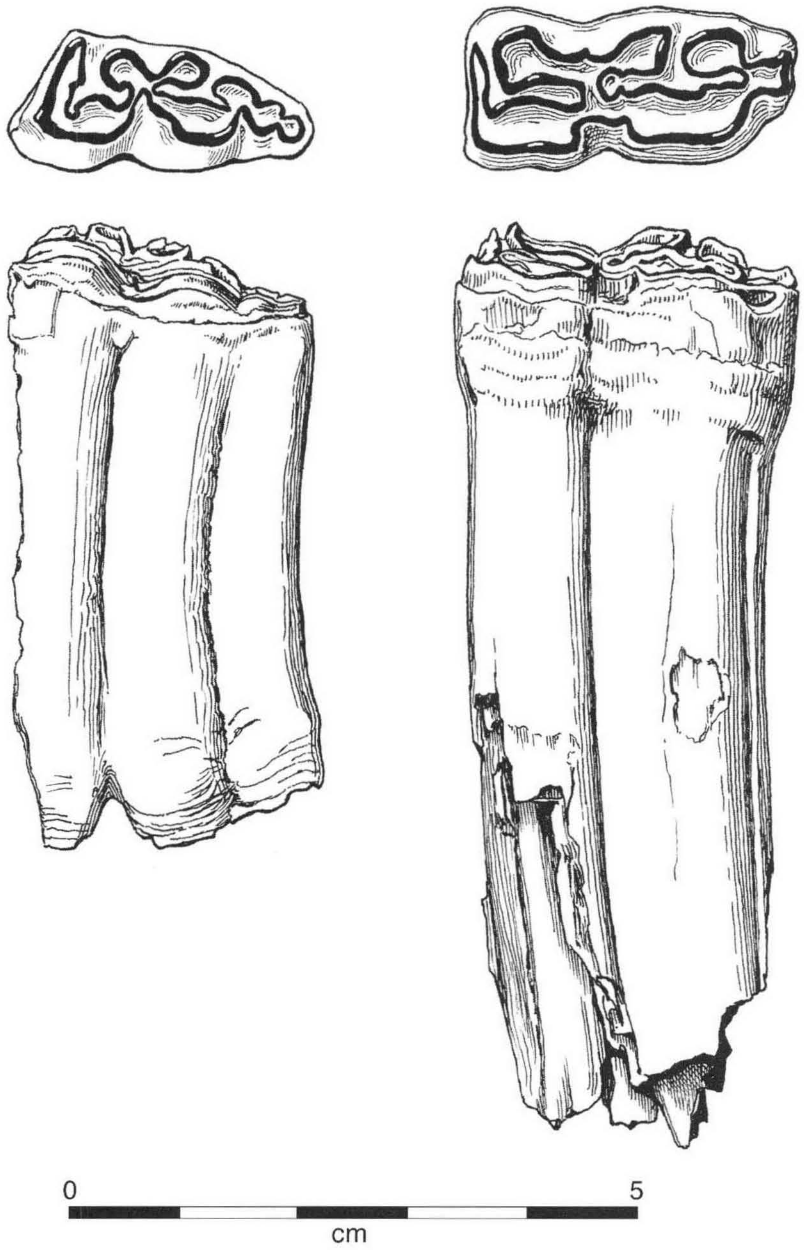

Figure 11. Comparison of occlusal (top) and external (bottom) views of lower molars of *Dinohippus mexicanus* (IGM 7597, left m3) with *Equus simplicidens* (IGM 7598, right m1 or m2) from the same locality, Jal-Teco7, Las Gravas, early Blancan, Jalisco, Mexico.

within the same population of one of the two species, or (2) two sympatric, sibling species soon after the cladogenesis resulting in primitive *Equus*. In either case, this example, along with that from the Anza-Borrego desert described above, indicate that primitive *Equus* originated from *Dinohippus mexicanus* via cladogenesis and that there was a time during the Blancan in which these two sister-species co-existed. This pattern has not been previously recognized because of the lack of suitable, well calibrated Blancan localities in North

America or the possible biogeographically restricted range of sympatry, or both.

In addition to the mode of speciation, it is interesting to attempt to reconstruct the diets of *Dinohippus* in order to better understand the origin of *Equus*. Although high-crowned, based on evidence from carbon isotopes and enamel microwear (MacFadden et al. 1999), *Dinohippus* had a variety of diets depending upon the local ecology. In western North America, *Dinohippus* (i.e., *D. interpolatus* and *D. leidyanus*) was principally a C4 grazer, whereas in Florida the slightly more advanced, but closely related, species *D. mexicanus* had a mixed diet with a considerable proportion of C3 plant foods, perhaps representing browse. Ongoing studies (MacFadden et al. in progress) of the carbon isotopes of *Dinohippus mexicanus* from relevant late Hemphillian localities in Mexico, including Yepómera and Rancho El Ocote, will further resolve geographical patterns of diets in the known southern range of this important species.

SUMMARY AND CONCLUSIONS

The discovery of the new skull of *Dinohippus mexicanus* described here adds to knowledge of the previously poorly represented facial morphology of this important late Cenozoic equid species. *D. mexicanus* is morphologically transitional in the distinctive facial morphology and dentition with respect to more primitive late Hemphillian *D. interpolatus* and *D. leidyanus* on the one hand and primitive Blancan *Equus* on the other hand. While classic interpretations of the evolution from advanced pliohippines (*Dinohippus* in the more recent literature) to primitive *Equus* mostly have advocated anagenesis, the co-occurrence of *Dinohippus* and *Equus* in the Blancan indicates cladogenesis. *Dinohippus mexicanus* was widespread in the southern U.S. and Mexico during the latest Hemphillian and it also ranged into the early Blancan during this time, although its latter distribution may have been more restricted. Ongoing studies from central Mexico will further resolve the calibration and paleoecology of the *Dinohippus*/*Equus* transition.

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APPENDIX

Practical method for determining the radius of tooth curvature

As is now well established, the evolution of transverse curvature of upper cheek teeth (CURV; Fig. 1) is of principal importance in distinguishing late Cenozoic horses and their phylogenetic interrelationships, in this case, the transition from *D. interpolatus* (and *D. leidyanus*), to *D. mexicanus*, to primitive *Equus*. As described by Skinner and Taylor (1967), a practical method for measuring this character was developed with a characteristically simple, decidedly "low-tech" method by M.F. and S.M. Skinner of the AMNH. Oftentimes, simpler is better and intuitively obvious to the practical-minded, and such is the case here. The Skinners produced both: (1) a series of stiff cards (made of oak-tag), each having one curve (or in some cases two or three curves for the smaller curvatures) cut out with radii of curvatures varying from 10 to 310 mm (Fig. A1, left), and (2) a glass plate with the equivalent (to those of the cards) curves defined by increasing radii of curvature (Fig. A1, right). In either of these cases, the researcher can take a particular tooth and slide it up or down along the glass plate, or determine the best fit from the cards, so that the curvature can be determined. Also, the oak-tag cards can be used for teeth still in maxilla and crania. The method works wonderfully, and produces measured data that can be quantified and statistically analyzed, as was done above (Table 2). Both the "prototypes" described here are available for use on the second "Horse" Floor in the Frick Collection at the AMNH.

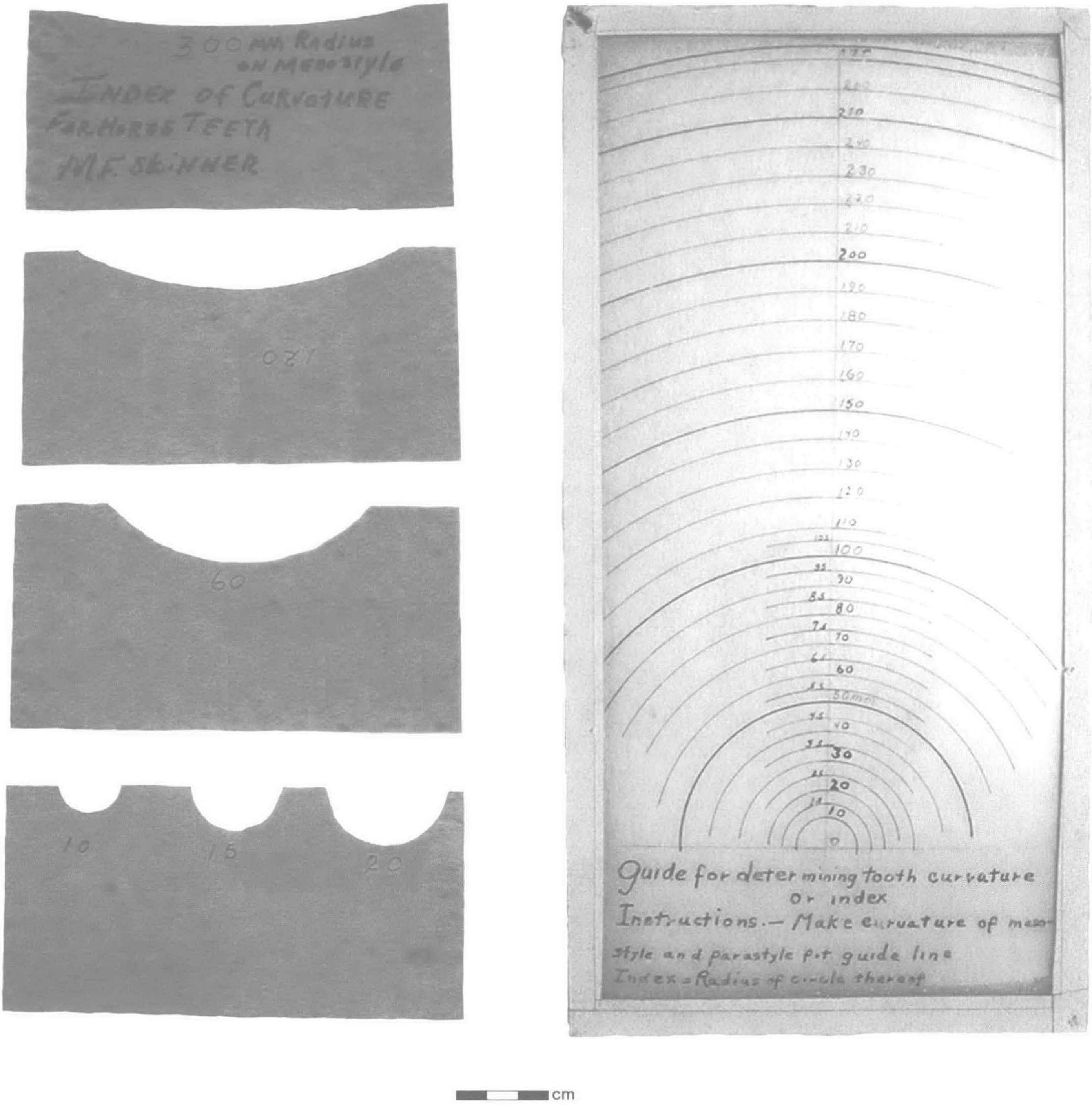

Figure A1. Card cutouts (left) and glass plate (right) used to measure radius of curvature (CURV) of the upper cheek teeth of fossil horses.

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