PLEISTOCENE VERTEBRATES FROM THE UPPER BECERRA (BECERRA SUPERIOR) FORMATION, VALLEY OF TEQUIXQUIAC, MEXICO, WITH NOTES ON OTHER PLEISTOCENE FORMS

BY
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VOLUME XII

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INTRODUCTION AND ACKNOWLEDGMENTS

THE abundance of Pleistocene vertebrates in Mexico has long been well known. Antonio del Castillo (1869), Cuataparo y Ramirez (1875), Villada (1897), and many later workers have recorded their occurrence. For many years, too, Mexico has been recognized as the late Cenozoic pathway between northern North America and South America, for the exchange of terrestrial animals. During the Pleistocene Mexico afforded an area of refuge for plant and animal life, the extent of which shifted southward with the advance of glacial ice. Many of the forms that reached Mexico from the north remained; others returned north with the retreat of the glaciers.

This report is based chiefly upon specimens that were housed in the Instituto de Geologia of the Universidad Nacional Autonoma de Mexico and other specimens that were collected August 9 to 12, 1949, from the exposures of the Upper Becerra (Becerra Superior) formation (Bryan, 1948; Arellano, 1951) along the banks of Canal del Desagüe and Barranca de Acatlán and its tributaries, in the vicinity of Tequixquiac in the northern part of the state of Mexico. The field party consisted of Ing. A. R. V. Arellano, in charge; Professor Bernardo Villa R., Instituto de Biologia; Luis Aveleyra Arroyo de Anda and Arturo Romano Pacheco, Instituto de Antropologia; and Dick Vieth and Claude W. Hibbard.

The geology of the region will be described later by Ing. A. R. V. Arellano. Meanwhile, I am grateful to him for furnishing a map of the area (Fig. 1), which gives the localities near Tequixquiac where the vertebrate fossils were collected.

My investigation of the late Pleistocene vertebrates of Mexico was made possible by an invitation, from Ing. Ricardo Monges Lopez, Director de Instituto de Geofisica y Geodesia, and Ing. Teodoro Flores, Director de Instituto de Geologia of the Universidad Nacional Autonoma de Mexico, to join a co-operative study of the Cenozoic of Mexico. I am grateful to Professor L. B. Kellum, Director of the Museum of Paleontology, University of Michigan, for permission to participate in the project.

In addition to those collected, the study was aided by the loan of specimens that were under the care of Dr. Roberto Llamas, Instituto de Biologia, Universidad Nacional Autonoma de Mexico; Dr. H. E. Anthony, Dr. E. H. Colbert, and Dr. G. G. Simpson, American Museum of Natural History; Dr. W. H. Burt, University of Michigan; Dr. J. T. Gregory, Yale University; Dr. R. A. Stirton, University of California; the late Dr. J. W. Stovall, University of Oklahoma; Dr. W. M. McLeod, Kansas State College; Dr. H. R. Roberts, Academy of Natural Sciences of Philadelphia;
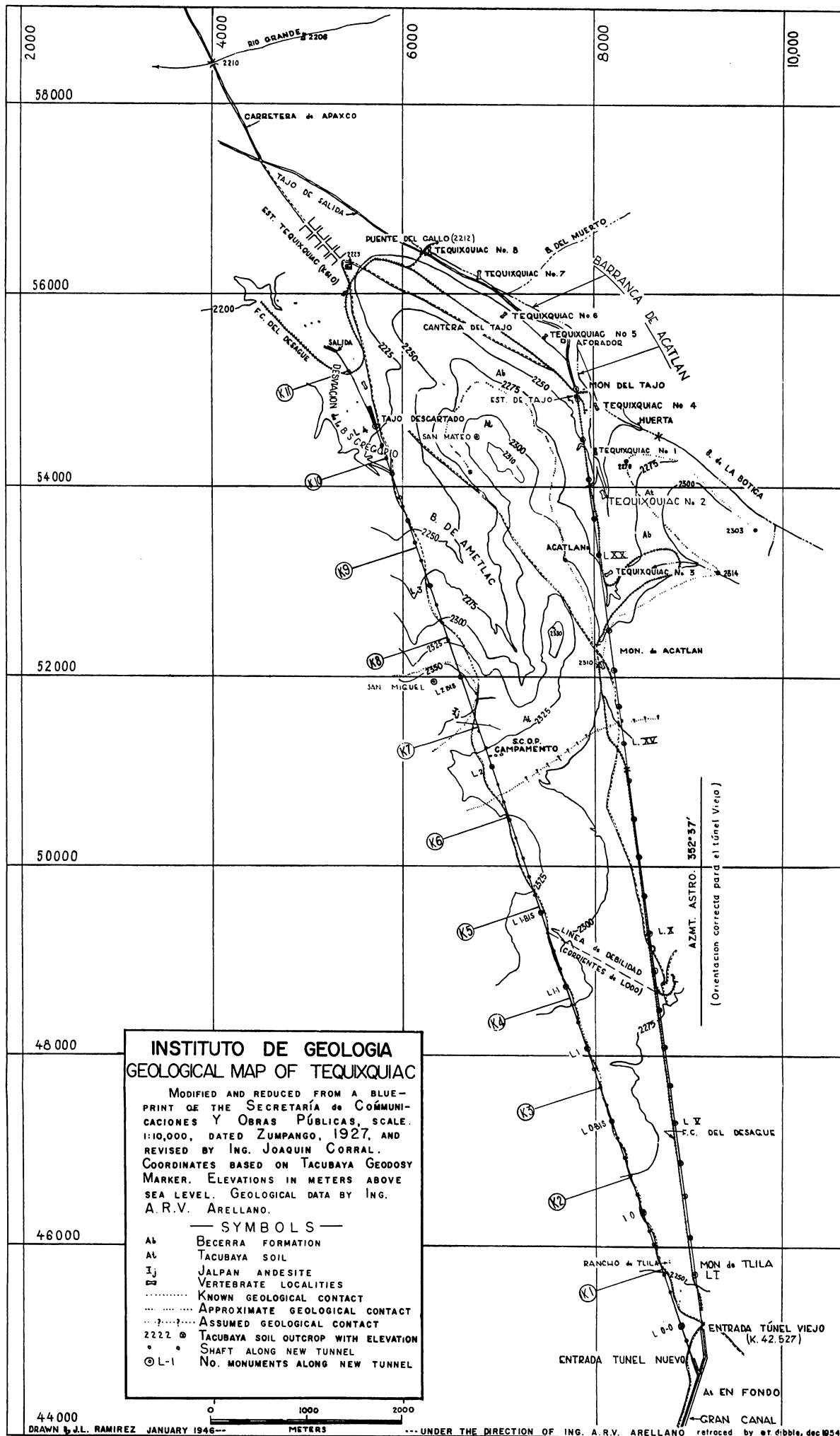
FIG. 1. Tequixquiac region, with numbered localities from which the vertebrate remains were recovered.

Names of institutions have, for the most part, been abbreviated as follows: A.M.N.H. (American Museum of Natural History); C.M.N.H. (Colorado Museum of Natural History); I.G.M. (Instituto de Geologia, Universidad Nacional Autonoma de Mexico); M.N.H.N. (Museo Nacional de Historia Natural, Universidad Autonoma de Mexico); P.M.N.H. (Peabody Museum of Natural History, Yale University); U.M.M.P. (University of Michigan Museum of Paleontology); and U.S.N.M. (United States National Museum). When catalogue numbers are given without identification, they are those of the Instituto de Geologia.

PLEISTOCENE VERTEBRATES
CLASS AMPHIBIA

Remains of frogs or toads, No. 49–26, were recovered August 9, 1949, at Locality 8, from the Upper Becerra formation.

CLASS REPTILIA

Fragmentary remains of pond and river turtles were taken in association with the amphibian remains above. At this same locality (8) but from the Lower Becerra (Becerra Inferior), which is exposed in the bed of Barranca de Acatlán, the remains of a large land turtle (*Testudo*) was recovered.

CLASS AVES

A tarsometatarsus, No. 49–26A, was taken with the amphibian remains at Locality 8, from the Upper Becerra. The bone was tentatively re-

ferred to *Toxostoma ocellatum* (Sclater) by Robert W. Storer (1954, pp. 144–45).

CLASS MAMMALIA
ORDER EDENTATA

Family Dasypodidae
Holmesina septentrionalis (Leidy)
(Pl. I, Fig. 3)

Glyptodon septentrionalis Leidy, 1889, Proc. Acad. Nat. Sci. Phila., p. 97.
Chlamytherium humboldtii Lund, Hay, 1902, Bull. U.S. Geol. Surv., No. 179, p. 581.
Holmesina septentrionalis (Leidy), Simpson, 1930, Amer. Mus. Novitates, No. 442, p. 3.

A single scute, No. 46–1, of this large armadillo was collected by Helmut De Terra in 1946, between Localities 1 and 2, at Tequixquiac along Barranca de Acatlán. It is the first record of *Holmesina septentrionalis* from Mexico, although the species is known from Florida, Oklahoma, and Texas in the United States.

Family Glyptodontidae
Brachyostracon mexicanus (Cuataparo and Ramirez)

Glyptodon mexicano Cuataparo and Ramirez, 1875, Bol. Soc. Geogr. Estad. Rep. Mex., Vol. 2, pp. 354–62.
Brachyostracon mexicanus (Cuataparo and Ramirez) Brown, 1912, Bull. Amer. Mus. Nat. Hist., Vol. 31, Art. 17, pp. 167–77.
Glyptodon Nathorsti Felix and Lenk, 1899, Beitrage zur Geologie und Palaeontologie der Republick Mexiko, Theil II, Heft 1, pp. 41–44, Tafle 1, Fig. 5..

Thirty-two scutes, No. 49–62, from the carapace of *Brachyostracon mexicanus* were found in the silty clay of the Upper Becerra formation along the west bank of Barranca de Acatlán, upstream from its junction with Barranca de la Botica. They occurred at the same horizon as the skull and tusks of an elephant taken August 11, 1949, from these deposits. The scutes agreed in all details with those of a specimen of *B. mexicanus* in the Museo Nacional de Historia Natural (figured by Villada, 1903, Pl. I).

A scute, No. 49–54, which was taken August 12, 1949, from the bank of Barranca de Acatlán approximately 600 meters upstream from Locality 8 (Fig. 1) appears to belong to this species.

Another scute, No. 49–65, (Pl. I, Fig. 2), of a large glyptodon, was recovered August 9, 1949, at Locality 8, from the Lower Becerra, which is exposed in the bed of Barranca de Acatlán. It was in place, associated with fragments of a large land turtle (*Testudo*) and the proximal end of a metapodial, No. 49–22, of a small horse. The scute has a maximum

width of 63.0 mm. The central figure is round and deeply excavated and is surrounded by a single row of eight figures. Each of the encircling figures is as deep as is the central one in the specimen of *Brachyostracon mexicanus,* but no pronounced groove separates them as in *B. mexicanus, B. nathorsti,* or *B. cylindricus* Brown. This may, in part, be due to a weathering of the surface and, if so, the excavations were originally much deeper. Owing to the depth of the excavation of the central figure the specimen is more nearly like that described as *B. nathorsti* by Felix and Lenk (1899) from Ejutla, Oaxaca, Mexico. When more material is available the scute may prove to represent a distinct species. I have followed Maldonado-Koerdell (1948, p. 19) in considering *Brachyostracon nathorsti* a synonym of *B. mexicanus.* Until the range and variation of *Brachyostracon mexicanus* is known, however, there is as much justification for recognizing *B. nathorsti* as for recognizing *B. cylindricus.*

Ing. A. R. V. Arellano collected on August 11, 1949, eleven scutes and a fragmentary caudal vertebra, No. 49–52 (Pl. I, Figs. 4–6), of a large glyptodon from a deposit below the Lower Becerra at Locality 7, just downstream from the junction of Barranca del Muerto with Barranca de Acatlán. One of the scutes (Pl. I, Fig. 4) is from a caudal sheath. The others differ from any of *Brachyostracon mexicanus* studied; they (Pl. I, Figs. 5–6) resemble, both in size and shape, the scutes of *Boreostracon floridanus* Simpson (Holmes and Simpson, 1931, p. 406, Fig. 15*c*).

The glyptodon remains from Tequixquiac were recovered from three separate formations and the material from each appears to be distinct.

ORDER RODENTIA

Family Geomyidae
Thomomys sp.

A left ramus, No. 49–25, without teeth, of this small gopher was recovered on August 9, 1949, at Locality 8, from the bank of Barranca de Acatlán in deposits of the Upper Becerra. The transverse width of the incisor is 2.0 mm. Length of the diastema from the incisor to alveolus of P_4 is 7.5 mm. Depth of the ramus below P_4, taken on the outside, is 9.7 mm. No gopher of this genus is known to occur in the immediate area at the present time.

The specimen, No. 46–51, in the Instituto de Geologia, which was reported by De Terra (1949, p. 44) as *Thomomys* sp., was examined by Villa and Hibbard and compared with other specimens from Mexico and found to belong to the genus *Cratogeomys.*

Cratogeomys cf. *tylorhinus* (Merriam)
(Fig. 2D–E)

A left lower jaw bearing P_4–M_3, No. 49–25a (Fig. 2E), of a gopher of the genus *Cratogeomys,* was obtained August 9, 1949, at Locality 8 in association with the jaw of *Thomomys* sp. (No. 49–25). The transverse width of the incisor is 2.9 mm. Length of the diastema from the incisor to P_4 is 10.3 mm. Occlusal length of the tooth row is 8.5 mm. A second left lower jaw bearing P_4–M_2, No. 49–75 (Fig. 2D), was taken, August 11, 1949, about 150 meters above the Puente del Gallo, along the bank of Tajo Desagüe Viejo from the top of the Upper Becerra. The two specimens correspond in size to *Cratogeomys (Platygeomys) tylorhinus arvalis* Hooper from the Valley of Mexico.

ORDER CARNIVORA
Family Canidae
Canis sp.
(Fig. 4E)

A right ramus, bearing P_2 and M_1, No. 49-48, of a small wolf, was taken August 9, 1949, at Locality 8 from the base of the Upper Becerra along the bank of Barranca de Acatlán, just northwest of Puente del Gallo. The jaw is well preserved. The anterior tip, which is missing, was broken off at the anterior edge of the alveolus of the canine. The distance from the posterior border of the canine alveolus to the posterior border of the alveolus of M_3 is 88.15 mm. Crown length of M_1 is 22.8 mm. Depth of jaw below the anterior part of M_1, inside measurement, is 23.4 mm. and below P_1 is 20.5 mm. The M_1 is larger than any observed of *Canis latrans* Say and the depth of the jaw is greater. Alveolar length from the canine to M_3 is approximately equal to that in *Canis latrans*. The specimen is smaller than *Canis lupus* Linnaeus and appears closely related to *Canis niger* (Bartram). But the true relationship will not be known until the upper dentition is found.

Family Ursidae
Tremarctotherium simus (Cope)
(Pl. I, Fig. 1)

Arctotherium simus Cope, 1879, Amer. Nat., Vol. 13, p. 791.
Arctotherium simus Cope, Fruedenberg, 1910, Geol. Palaeon. Abh., Vol. 9, Heft 3, p. 199.
Tremarctotherium Kraglievich, 1926, An. Mus. Nac. Buenos Aires, Vol. 34, pp. 1–16.

A toe bone, No. 49–43, of *Tremarctotherium simus* was associated with *Bison chaneyi* Cook at Locality 5. In the collection at the Instituto de
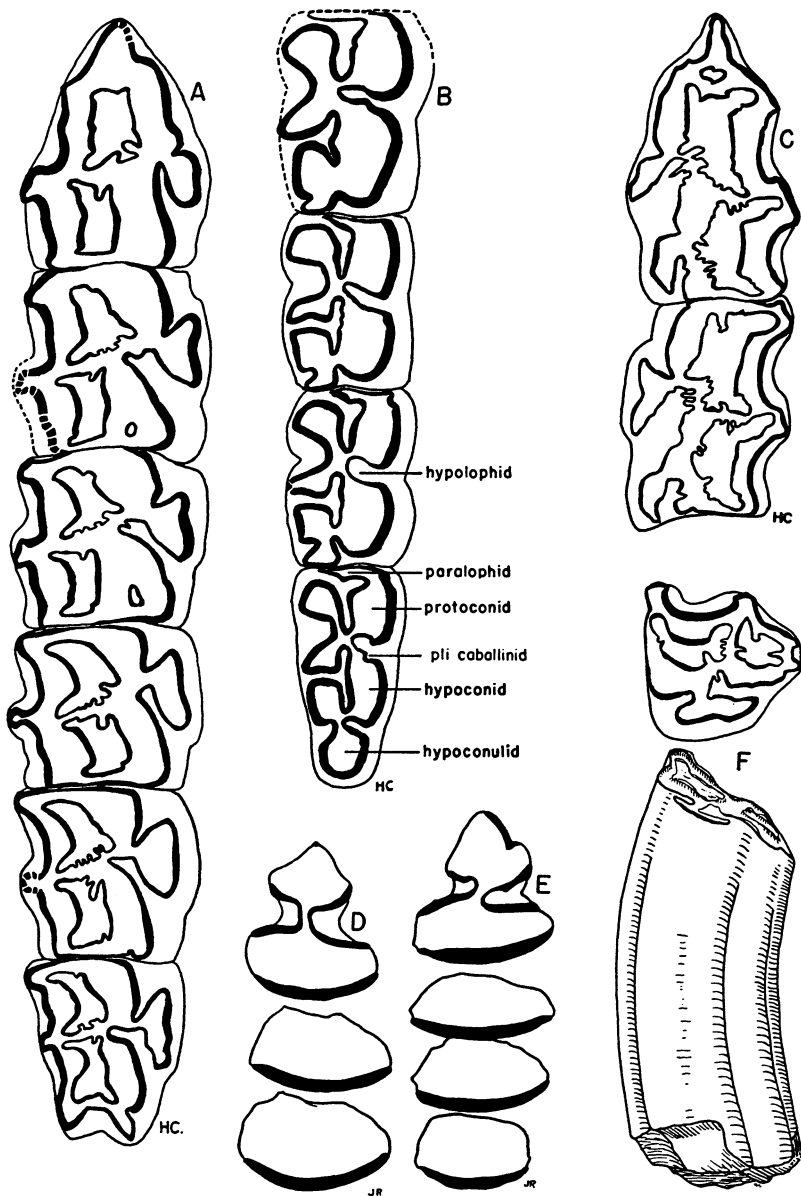
FIGURE 2

(A, B, C) *Equus* cf. *conversidens* Owen. (A) Right P²–M³, No. 400; (B) Right P₄–M₁, No. 49–36; (C) Left DP² and DP³, No. 49–34, occlusal views. Natural size.

(D, E) *Cratogeomys* cf. *tylorhinus* (Merriam). (D) Left P₄–M₂, No. 49–75; (E) Left P₄–M₃, No. 49–25a, occlusal views. ×6.

(F) *Equus* cf. *conversidens* Owen. Left M³, No. 49–58, occlusal and lingual views. Natural size.

Geologia is a fragment of a left maxillary, No. 85 (Pl. I, Fig. 1), of this large bear, which contains M¹–M². It was taken some years ago at Tequixquiac and the type of preservation indicates that it came from the Upper Becerra.

ORDER PROBOSCIDEA

Mammuthus cf. *imperator* (Leidy)

Elephas imperator Leidy, 1858, Proc. Acad. Nat. Sci. Phila., Vol. 10, p. 10.

The remains of elephants are common in the silt, clay, and bog deposits of the Upper Becerra formation near Tequixquiac, as well as in later deposits of the Valley of Mexico (Arellano, 1946). The study of the elephants and mastodons of Mexico presents a major problem in taxonomy and stratigraphy and much has been written about them (Freudenberg, 1922; Reyes, 1923; Hay, 1925; Osborn, 1936 and 1942).

Material taken near Tepexpan, and identified by Hibbard for De Terra (1949, p. 43), is assigned to *Mammuthus* cf. *imperator* (Leidy) on the basis of the tooth plates. The entire problem of identification refers back to the type specimens *Elephas columbi* Falconer and *Elephas imperator* Leidy. The two names may turn out to be synonymous, regardless of whether or not one accepts the concept of an Imperial elephant group and a Columbian elephant group. Mexican elephants possess broad enamel ridges. In any study of fossil elephants sex and age variations must be considered. This kind of variation very likely accounts for the subspecies recognized by Freudenberg. All stratigraphic evidence points to a late arrival of the elephants in North America; that is, near the middle of the Pleistocene.

In the Instituto de Geologia is a tooth, No. 44–1 (Pl. II, Fig. 2) of an American mastodon, *Mammut americanus* (Kerr) recorded as having been taken in Mexico. The locality at which the specimen was recovered is unknown. The tooth appears to be that of a late Pleistocene form and resembles the post-Cary mastodon teeth from the bog deposits of Michigan (cf. Pl. II, Figs. 1 and 3).

ORDER PERISSODACTYLA

Family Equidae

Genus *Equus* Linnaeus, 1758

The genus *Equus,* in an all inclusive sense, includes the recent horses, zebras, and Asiatic and African asses and the closely related Pleistocene

forms. Since Linnaeus established *Equus* with *E. caballus,* the domesticated horse, as genotype, many workers have subdivided the genus and placed the living forms in a number of genera. Some of the "genera" are recognized as subgenera chiefly for their convenience as group names. The subgenus, *Equus, sensu stricto,* comprises the true horses: *Equus (Equus) caballus* Linnaeus, the many variants of the domesticated horse, *E. przewalskii* Poliakov, and a few closely related Pleistocene forms. Grevy's zebra (*E. grevyi grevyi* Oustalet) and related subspecies have been assigned to the subgenus *Dolichohippus* Heller (1912). The other zebras, *E. burchellii* (Gray), *E. quagga* Gmelin, and *E. zebra* Linnaeus, are generally placed in the subgenus *Hippotigris* Hamilton Smith (1841). The African asses and the domestic asses (*E. asinus*) have been restricted to the subgenus *Asinus* Gray (1824) and the Asiatic asses (*E. hemionus* Pallas) to the subgenus *Hemionus* by Stehlin and Graziosi (1935).

The North American Upper Pliocene and Pleistocene "zebrine" horses have been assigned either to the genus or subgenus *Plesippus* Matthew (1924). At present, it seems best to retain *Plesippus* as a subgenus, at least until the North American, Asiatic, and European fossil zebrine-like horses are better known and their relationship to each other and to the Recent forms is better understood. The use of the term "zebrine" is after Hopwood (1936).[1] McGrew (1944) pointed out that the relationship of *Plesippus* to *Hippotigris* was so close that he considered the terms synonymous.

When the North American Pleistocene Equidae are further investigated, it is probable that they, like the living forms, can be divided into a number of distinct groups, such as zebras, asses, and true horses. It may be found as well that many, if not all, of the subgenera of *Equus* originated in North America and spread from thence into Asia, Europe and Africa. The history of the Pleistocene horse of North America will never be even relatively complete until more information concerning the equids of the Upper Pliocene and Pleistocene of Mexico is at hand. The recognition of separate groups of equids during the Pleistocene in North America would contribute to a better understanding of the horizontal and vertical range of the forms and the conditions under which these lived. It is doubtful that any hybridization will be found between the several groups of Pleistocene horses, for most subgeneric differentiation occurred prior to the Pleistocene.

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[1] For a discussion of the fossil zebrine forms of North America and Europe, see Boule (1900), Gidley (1930), Gazin (1936), Hopwood (1936), Schultz (1936), Stirton (1942), McGrew (1944), and Dietrich (1949).

Equus conversidens Owen

(Pl. III; Figs. 2A–C, F and 3)

Equus conversidens Owen, 1869, Philos. Trans. Royal Soc. London, Vol. 159, p. 563, Pl. 61, Fig. 1.

Equus tau Owen, Cope, 1884, Proc. Amer. Philos. Soc. Phila., Vol. 22, p. 12.

Equus barcenaei Cope, 1884, Proc. Amer. Philos. Soc. Phila., Vol. 22, p. 15.

Equus cfr. *tau* Owen, Freudenberg, 1910, Geol. Palaeont. abh. n.f. Vol. 9, Heft 3, Taf. 1, Fig. 6.

Equus littoralis Hay, 1913, Proc. U.S. Nat. Mus., Vol. 44, pp. 575–76, Figs. 17–18.

Type locality.—Valley of Mexico.

Holotype.—No. 403, Instituto de Geologia, Universidad Nacional Autonoma de Mexico, the maxillaries and part of the palate, with right and left P²–M³, of a small young adult horse. The specimen was figured by Owen (1869, Pl. 61, Fig. 1).

Description of holotype.—Owen's figure of the type was poor and much discussion has resulted over it. The type specimen is here refigured (Pl. III and Figure 3). It consists of the right and left maxillaries with both series of premolar-molar teeth, and part of the palate (Pl. III). The specimen is from a horse that had reached early maturity, for the M³ had just come into nearly full use and the crowns of all the teeth are in an early stage of wear. Measurements that were taken in December, 1949, by Morris F. Skinner and Hibbard, are given in Table I.

TABLE I

MEASUREMENTS OF UPPER MOLAR SERIES OF THE HOLOTYPE, No. 403, OF *Equus conversidens* OWEN, 1869

Measurements taken by M. F. Skinner and C. W. Hibbard in 1949; Owen's (1869) figures for length and width given for comparison. Measurements in parenthesis are approximate.

	Crown Height (in mm.)	Anteroposterior Length* (in mm.)			Transverse Width† (in mm.)			Protocone Length (in mm.)	
		Right	Left	Owen, 1869	Right	Left	Owen, 1869	Right	Left
P²	51.7	...	33.3	30	(22.9)	(20.7)	25	8.6	8.3
P³	62.5	24.6	24.3	25	23.7	23.8	25	11.2	11.2
P⁴	70.0	24.6	25.2	..	22.9	22.3	..	11.3	12.3
M¹	(62.3)	21.7	22.0	22	(22.0)	21.7	21	10.5	11.1
M²	66.0	21.7	21.9	..	20.8	(19.8)	..	11.3	(11.0)
M³	58.5	20.4	20.6	19	17.0	17.2	18	10.7	10.7

Occlusal length of left P²–M³ = 147.7 mm.

Occlusal length of left P²–P⁴ = 82.2 mm.

Occlusal length of left M¹–M³ = 65.8 mm.

* Anteroposterior length is measured on the center line.

† Transverse width is measured from enamel of protocone to enamel of mesostyle, inclusive.

The type and Owen's figure agree in having the anterior face of the right P² missing, the right maxillary broken at M¹, the angularity of the broken portion of the right palate showing the same breaks and fossilization cracks, the posterior outer part of the left P² and the anterior outer face of the left P³ missing, and the left maxillary broken opposite the inner half of the left M².

To continue the description: The protocone of P² is medium sized. In P³–M³ the protocones are fairly large, flattened, and anteriorly projecting, with a deep preprotoconal groove and a tendency for the development of an indentation along the lingual mid-line of the protocones of P³–M² and in P³–M² they are internally convex on the labial side.[2]

The pli caballin fold is present in the premolars and absent in the molars. The postprotoconal valley is narrower in the premolars than in the molars.

The fossettes of the premolars are much more complex than those of the molars. The plications of the metaloph into the prefossettes and post-fossettes of P³ and P⁴ are highly folded, while those of M¹ and M² are less folded. The metaloph of M³ is very narrow and the fossettes are nearly united. The premolars all possess a moderately developed pli protoloph. The molars have the pli protoloph poorly developed or absent. The pli hypostyle is moderately developed on the premolars to poorly developed or absent on the molars. The parastyles, mesostyles, and metastyles are well developed and the external valleys between the parastyles and mesostyles and between the mesostyles and metastyles are rather deep. The enamel borders between the styles are strongly concave on the outside (see Fig. 3).

The M³ is strongly curved and slightly reduced. The left M³ has a small hypoconal fossette which is lacking on the right M³. The hypoconal groove is present on P²–M².

The infraorbital foramen is high on the face; the distance from the center of the foramen to the alveolar border is 70.0 mm. The foramen is located above the anterior face of P⁴ and is directed downward approximately at a 45° angle to the maxillary tooth row. There is no evidence of a lacrimal (malar) fossa on the part of the face present. The masseter ridge ends above the posterior half of P⁴, a distance of 32.0 mm. above the alveolar border. The palatine foramina open internally opposite the center of M².

Referred material.—No. 406 is a series of ten upper premolars and

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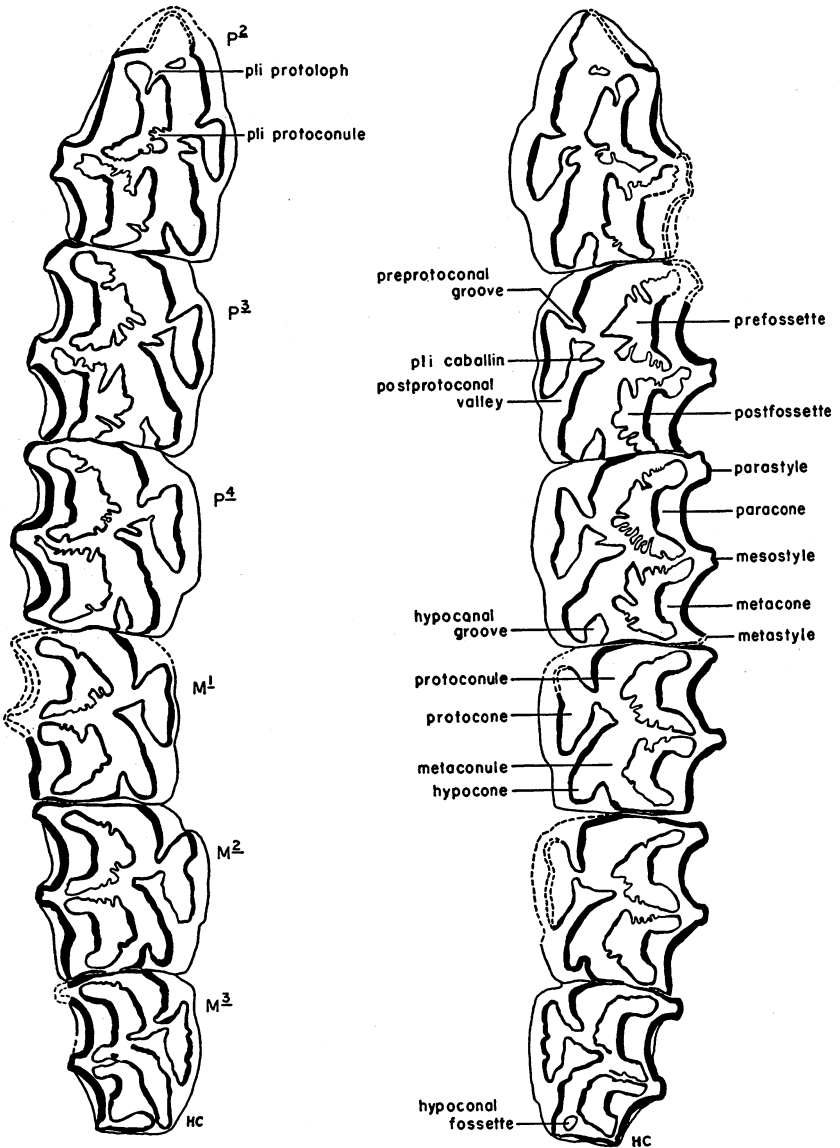[2] For a detailed discussion of the dental nomenclature in horse teeth, see Stirton, 1941.

FIG. 3.—*Equus conversidens* Owen, holotype, No. 403, occlusal view of premolar-molar series. Natural size.

molars of a young horse. The specimen is questionably referable to *Equus conversidens* and nothing is known of it other than that it came from the Valley of Mexico. Both right and left P² are missing. A part of the left maxillary is present with the infraorbital foramen. The teeth are like those of the type of *E. conversidens* with the exception that M¹–M³ possess well-developed pli caballin folds. The roots of P⁴ are just closed and the crown is fully worn. M¹ and M² have closed roots. The crown of M³ is unworn and the root not closed. Right M³, right M², and right P³ have been sectioned, but the pli caballin folds are still present on M³, 26.0 mm. below the crown surface and on M², 38.0 mm. below the crown surface. Dimensions of the teeth are given in Table II.

TABLE II

MEASUREMENTS OF UPPER MOLAR SERIES, SPECIMEN No. 406,
? Equus conversidens OWEN

	Crown Height	Anteroposterior Length	Transverse Width	Protocone Length
LP³	74.5 mm.	26.3 mm.	23.5 mm.	11.1 mm.
LP⁴	81.0	23.9	21.8	10.9
LM¹	78.1	23.0	21.2	10.7
LM²	80.4	23.6	19.6	11.2
LM³	75.0	21.0	17.2	11.0

Anteroposterior length of LP³–LM³ = 120.0 mm.

No. 400 (Fig. 2A), is part of the right maxillary of an old horse and bears P²–M³ (Nos. 35 and V32*a*) and left P², P⁴–M³ (No. V32*b*), and is questionably referred to *Equus conversidens*.[3] In size the dentition corresponds to that of the type of *E. conversidens,* except for the M³. The M³ is longer anteroposteriorly than that of the type and resembles the tooth described as *Equus tau* Owen except that it possesses a greater transverse width. Old age does not account for all of the increase in the anteroposterior length of the tooth. The M³ of No. 400 is not only slightly larger than the M³ of the type but is also larger than those of No. 406 and No. 49–58, specimens questionably assigned to *E. conversidens.* The M³ also differs from the above upper third molars assigned to *E. conversidens* in that a deep and broad valley separates the metastyle and the hypocone (Fig. 2A); this character is not due entirely to age. In the other upper third molar,

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[3] Many horse teeth in the collection have been sectioned. There is no record of this study, but it is thought that William Freudenberg made it at the time he planned to publish upon the vertebrate fossils of Mexico. All sectioned series have new numbers preceded by the letter V.

No. 49–58, (Fig. 2F) the metastyle and hypocone are closely joined and only a very shallow groove separates them to the base of M³; this may be an individual variation within *E. conversidens*. No. 400 has a small pli caballin fold on the left M¹ and on the M², but none on the right molars. Measurements of No. 400 are given in Table III.

TABLE III

MEASUREMENTS OF UPPER MOLAR SERIES, SPECIMEN No. 400,
? Equus conversidens OWEN

	Crown Height	Anteroposterior Length	Transverse Width	Protocone Length
LP²	31.8 mm.	33.0 mm.	23.6 mm.	7.9 mm.
RP³	....	24.2	24.5	9.6
LP⁴	47.3	23.55	24.3	9.8
LM¹	41.2	21.7	23.0	11.1
LM²	48.8	22.5	22.9	10.8
LM³	47.9	24.9	18.7	11.1

The following specimens from the Upper Becerra may belong to *E. conversidens*. No. 49–58 (Fig. 2F), a left M³, was taken August 11, 1949 at Tajo de Tequixquiac along the edge of Barranca de Acatlán, north of Locality 6. The tooth has a height of 53.5 mm., an anteroposterior length of 20.9 mm., and a transverse width of 19.0 mm. There is a well-developed pli caballin fold like that on No. 406. No. 49–55 (Fig. 4D–D¹), a small left M³, was taken at Locality 6. This tooth has a height of 56.0 mm. Figure 4D gives an occlusal view and Figure 4D¹ is a view of a cross section taken 25.0 mm. below the crown surface. No. 49–34 (Fig. 2C), a fragment of a left maxillary bearing DP² and DP³, was recovered at Locality 5 with the skull of *Bison chaneyi*, No. 49–33, and No. 49–36 (Fig. 2B), the posterior part of a right ramus with P_4–M_3, was taken there 3 meters above the skull.

Discussion.—It is evident that Owen's descriptions of *Equus conversidens* and *E. tau* were taken from the photographs sent to him, since the length of the molar series of P²–M³ of the left maxillary of *E. conversidens* as figured by Owen is the same as the length given by him. But in Owen's illustration the left maxillary is foreshortened and poorly portrayed. Neither the right nor the left tooth patterns, as he showed them, are completely correct. At the same time that he described *Equus conversidens*, Owen (p. 18) described *Equus tau*. He gave no measurements for the latter, but figured two series of teeth, left P³–M³ and left DP_2–DP_4, and stated that they were of natural size. Owen said, furthermore, that the upper teeth of *Equus tau* are smaller than the corresponding ones of *Equus conversidens;* that is, with the exception of M³. In *Equus tau* this molar has a greater relative size, especially in anteroposterior length. Since the figure of *Equus*

conversidens is distorted, that of *Equus tau* probably is also. Measurement of the illustration published by Owen of *Equus tau* establishes a greater anteroposterior length for the P³–M³ series than for the same series in the illustration of *Equus conversidens*. If, however, the illustration by Owen of *Equus tau* is correct, the length for the P³–M³ series is the same as that in the type specimen of *Equus conversidens* (measured from the type). According to the measurements *Equus tau* was not a smaller horse than *Equus conversidens*, for the anteroposterior length of the premolar-molar series appears to be the same in both horses. No molar teeth possessing characters assigned to *Equus tau* were found in the collections, nor was the type specimen or any part of it recognized. There is no real evidence, therefore, that *Equus tau* is the smaller horse that it has been considered by previous workers. The name *Equus tau* is probably a synonym of *Equus conversidens*.

Cope (1884) stated that he saw a palate in the collection, preserved in the manner figured by Owen, which he thought was probably the specimen of *Equus conversidens* that was photographed for Owen's study. Although he did not recognize any specimens from which the figures of *Equus tau* were taken, he believed they might have been from some that he examined. Since he did not surely identify the type of *Equus tau*, one does not know on what basis Cope decided to make *Equus conversidens* a synonym of *Equus tau*. He did, however, consider the two forms as belonging to the same species.

There is no record as to the date of restoration or by whom the maxillaries of *Equus conversidens*, figured by Owen, were restored to a relatively normal position. Osborn (1905, p. 931) saw the palate and teeth of a small horse, the size of a donkey, in the Instituto de Geologia which had been labeled by Castillo in 1866. Without doubt, the specimen seen by Osborn was the type of *Equus conversidens*.

Gidley (1901, p. 118) designated that portion of the upper jaw of the right side containing the full molar-premolar series of Owen's type the type of *Equus conversidens*. He was not convinced that the figure published by Owen was distorted as suggested by Cope (1884, p. 13), but believed that it was caused by a placing together of the upper jaws of opposite sides of two different individuals. It is now evident that Cope was correct in regarding the figure as having been distorted, in restoration and by photography.

Freudenberg (1910, Taf. 1, Fig. 6) figured the type of *Equus conversidens* Owen as later restored and labeled *Equus* cfr. *tau* Owen. Only after considerable study was this specimen recognized as Owen's type by Skinner and Hibbard in the fall of 1949. The removal of the thick plaster from the palatal region established definite proof.

Hay (1913, p. 575, Figs. 17–18) described the species *Equus littoralis,* which he based on small-sized molars from Peace Creek, Florida. All the characters he gave as typical of this small horse, such as length and width of grinding surface of the teeth, the rather strongly folded enamel surrounding the lakes, the slight curvature of the teeth, the narrowness of the post-protoconal valley, and the way the valley falls far short of reaching halfway to the median style (mesostyle) of the outer face of the tooth, are characteristic of the type of *Equus conversidens* Owen, except one, the presence of the pli caballin fold on the tooth considered by Hay as an upper left molar. *Equus littoralis* is considered to be a synonym of *E. conversidens.*

The only characters that appear to separate the Texas Pleistocene horse *Equus francisci* Hay (1915, p. 535) from *E. conversidens* are its smaller size, the lack of the highly folded plications in the fossettes of P^3 and P^4 and only a moderate folding in the other fossettes. Whether or not these are individual or sexual differences is unknown. Hay remarked that in all the upper premolars and molars the styles descending on the outer face were strongly developed, with those of the premolars distinctly broader than those of the molars. This is typical of *Equus conversidens.* The two forms appear, therefore, to be closely related if not identical.

Equus (Plesippus) crenidens Cope
(Fig. 4A–B)

Equus crenidens Cope, 1884, Proc. Amer. Philos. Soc., Vol. 22, p. 12.

Type.—Cope (1884, p. 12) stated that, "the typical specimen (of *Equus crenidens*) includes the three premolars of the upper jaw of an adult in perfect preservation." I did not find Cope's type in the Instituto de Geologia collection and I was unable to examine the collection in the Escuela des Minas.

In the Instituto de Geologia collection are four upper premolars, No. 407, that agree with the measurements and the description given by Cope for *E. crenidens.* These teeth consist of RP^2 and P^3 associated in a piece of the maxillary. Glued to the RP^3 is the right premolar or molar that had been sectioned. It is evident that the RP^4? (Fig. 4A) was not a part of the original premolar series. The maxillary along the outer posterior edge of P^3 shows signs of a fresh break as though P^4 had been removed. The original P^4 was probably removed at the time sections were being made of the horse teeth and a different tooth was substituted by error. There is no record that the LP^2, No. 407, was found associated with the RP^2 and P^3.
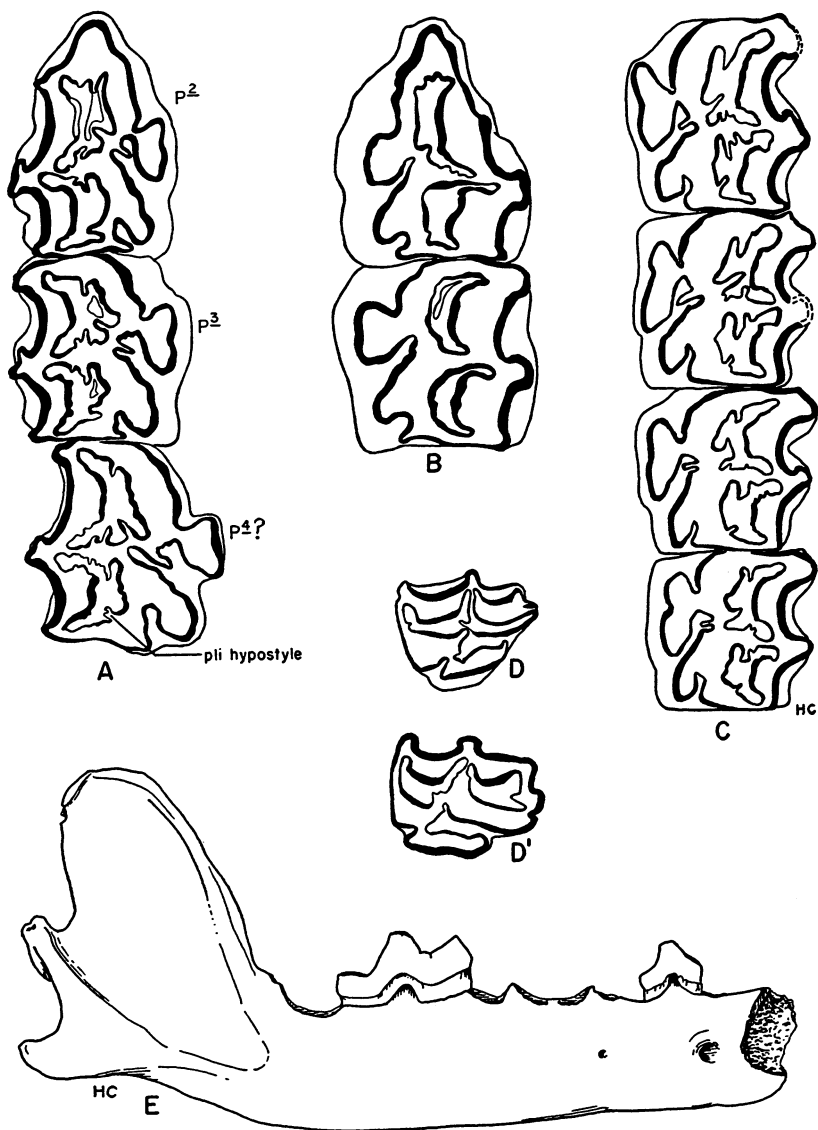
FIGURE 4

(A)   *Neotype* of *Equus (Plesippus) crenidens* Cope. Right P²–P³, No. 407, occlusal view. The P⁴? illustrated was restored with the above teeth, but does not belong with them. ×¾.

(B)   *Equus (Plesippus) crenidens* Cope. Left P² and P³, No. 80, occlusal view. ×¾.

(C)   *Equus* cf. *(H.) mexicanus*. Left P³–M², No. 49–51, occlusal view. ×¾.

(D) and (D¹).   *Equus* sp. Left M³, No. 49–55; D, occlusal view; D¹, view of crown 25.0 mm. below occlusal surface. Natural size.

(E)   *Canis* sp. Right ramus bearing P₂–M₁, No. 49–48, lateral view. ×¾.

Neotype.—The right P² and P³, No. 407 (V16), associated in a fragment of the maxillary is here designated as the neotype of *Equus (Plesippus) crenidens* Cope.

The following characters were listed by Cope (1884, pp. 10–12) as distinguishing this horse from other species known at that time: "a large species with the crowns of the third and fourth premolars long and slightly curved; the long diameter of the anterior internal lobe [protocone] of superior molars not greater than one-third the long diameter of the crown; borders of lakes crenate; internal lobe notched on the inner side so as to be bilobate."

Cope also considered the close and strong wrinkling of the enamel border of the lakes of the superior molar teeth an important feature. This character, although present, is not so marked as in *Equus pectinatus* Cope.

Description of neotype.—The teeth are those of a young adult animal. The pli caballin fold is well developed in the two premolars. P² has short roots which are nearly closed. The greatest height of the tooth is 71.8 mm. Wear on the anterior inner face of the tooth indicates that a small P¹ was present. The small protocone has a slight indentation (lingual groove) on the inner enamel face.

P³ has short roots that are nearly closed. The greatest height is 79.5 mm. The protocone is oval with a lingual groove extending to the base. The anterior part of the protocone does not reach far forward.

The P⁴? illustrated (Fig. 4A), which has been sectioned, was added at some unknown time and is clearly not the original tooth. As much as 16.0 mm. of the upper part of the crown of P⁴ is missing. The base of the tooth is still open with the roots just beginning to form. The protocone is oval but lacks the lingual groove present on P³. Allowing 16.0 mm. for the missing upper section of the crown, the tooth would have a height of 83.0 mm. For measurements of the three teeth see Table IV.

The whole specimen with the added P⁴? has been treated with hot wax which gives it a light reddish color. There is no matrix present to show from what horizon it was taken.

Referred material.—In the collection is part of a left maxillary, No. 80, bearing P² and P³, an old adult of this species. The catalogue states that the maxillary was taken at Tequixquiac. No date of recovery or horizon is given for the specimen. The height of the crown of the P², above the roots, is 25.5 mm. (Fig. 3B).The P³ has an anteroposterior crown length of 30.8 mm.; a transverse width of 31.4 mm. (see Table IV). Another tooth, No. 82 (A/10 and V10), is a right P³ or P⁴, which is slightly curved. It has a crown height of 66.7 mm., an anteroposterior crown length of 33.8 mm. and a crown width of 34.1 mm. The anteroposterior length of the protocone is

10.5 mm. All measurements are taken on the occlusal surface of the enamel. The tooth is typical *Equus (P.) crenidens.*

Discussion.—No. 407, Valley of Mexico, Tequixquiac, had been given two other numbers, No. 77 and No. V16. No records pertain to them, but the number V16 apparently was placed on the specimen at the time it was

TABLE IV

MEASUREMENTS OF UPPER MOLAR TEETH OF NEOTYPE, No. 407,
OF *Equus (Plesippus) crenidens* COPE

Cope's (1884) measurements of the type are listed and, for comparison, those of an old adult, No. 80.

Dimension	Cope, 1884	No. 407 (Over-all)	No. 407 (Enamel)	No. 80 (Enamel)
P², anteroposterior diameter	43.0 mm.	42.3 mm.	41.4 mm.	41.2 mm.
transverse diameter	30.5	30.5	28.6	29.0
anteroposterior diameter of protocone .	...	10.4	10.4	8.5
P³, anteroposterior diameter	33.5	33.0	33.0	30.3
transverse diameter	34.0	32.7	30.0	31.4
anteroposterior diameter of protocone .	...	12.2	12.2	10.4
P⁴?, anteroposterior diameter	31.0	36.1	36.1	...
transverse diameter	35.0	35.1	35.1	...
anteroposterior diameter of protocone .	...	11.5	11.5	...

sectioned. Most of the Pleistocene and Pliocene specimens assigned to the Valley of Mexico were probably recovered at the time of the construction of the great drainage canal and tunnel. This canal passes through at least four recognizable Cenozoic formations. No specimen referable to *Equus (Plesippus) crenidens* Cope was recovered in August, 1949, from the Becerra formation.

Equus crenidens exhibits closer relationship to the subgenus *Plesippus* than to the subgenus *Equus* in the development of the upper molars. This is revealed by the small oval protocone, the slightly concave enamel borders between the parastyle and the mesostyle and between the mesostyle and the metastyle, and the slight curvature of the molars. Gidley (1901, p. 99) came to the conclusion that the anteroposterior diameter of the protocone in all teeth of a series remains the same for the whole length of the crown. He considered that the ratio of the anteroposterior diameter of the protocone was a rather poor diagnostic character, because the anteroposterior diameter of the crown is ever changing through wear; hence, the relation of the protocone to the crown in an old and much worn tooth is necessarily different from that in a tooth which has just come into use. Merriam (1913, p. 405) recorded considerable variation in the form and size of the protocone, among the individual specimens of horses assigned to *Equus occidentalis* Leidy from Rancho La Brea, California. He judged this to be both an individual variation and an age difference. The type of protocone in

Equus (Plesippus) crenidens is not like that in many of the more advanced forms of *Equus* and appears to be especially distinctive of *Plesippus*.

The true relationship of this horse will probably not be established until associated lower and upper teeth are found. All that can be said, meanwhile, is that *E. (Plesippus) crenidens* appears to be rather closely related to *Equus (Plesippus) idahoensis* Merriam, a conclusion based upon the description of the latter by Schultz, 1936. *Equus (P.) crenidens* does not appear to be as advanced as *E. (P.) idahoensis* in that the protocone does not extend as far forward in P^3 and P^4.

Hesperohippus subgen. nov.

Subgenotype.—*Equus (Hesperohippus) mexicanus,* sp. nov., No. 48 (HV-3), Museo Nacional de Historia Natural, Universidad Nacional Autonoma de Mexico; a nearly perfect skull, of an old individual, lacking the LM^3, tips of the nasal bones, paraoccipital processes, and the crowns of the incisors.

Diagnosis.—A horse in which the lower borders of the occipital condyles flex forward so that the posterior faces of the condyles are at an angle of approximately 90° to the frontal plane. The foramen magnum leaves the skull at a 90° angle to the palatal axis and not, as in Recent or other known Pleistocene forms, at a 45° to 58° angle. The paraoccipital processes are directed forward and the posterior edges form 130° angles with the frontal plane. In the skulls of other equids the processes are nearly vertical or directed slightly backward. There is no shelf or pit on the ventral surface of the processes as in all forms examined, and the ventral surface is directed sharply upward and forward at approximately a 45° angle to the palatal axis of the skull. The premaxillaries are flattened anteriorly and do not curve sharply downward anteriorly as in other species of *Equus* that were observed.

Equus (Hesperohippus) mexicanus, sp. nov.
(Pl. IV, Figs. 1–3; Fig. 5A–B)

Equus excelsus Leidy, Cope, 1884, Proc. Amer. Philos. Soc., Vol. 22, pp. 13–15.
Equus occidentalis Leidy, Villada, 1903, Anal. Mus. Nacl. la epoca, Vol. 7, p. 445, Pl. 2.

Holotype.—No. 48 (HV-3), Museo Nacional de Historia Natural; a nearly perfect skull lacking the LM^3; taken from a Pleistocene deposit at Tajo de Tequixquiac, Estado de Mexico. For dimensions see Table V.

Description of holotype.—The skull of a large old adult asslike form which, because of the well-developed canines, appears to be that of a male (Fig. 5A). The orbital region is flat, but just back of the posterior border
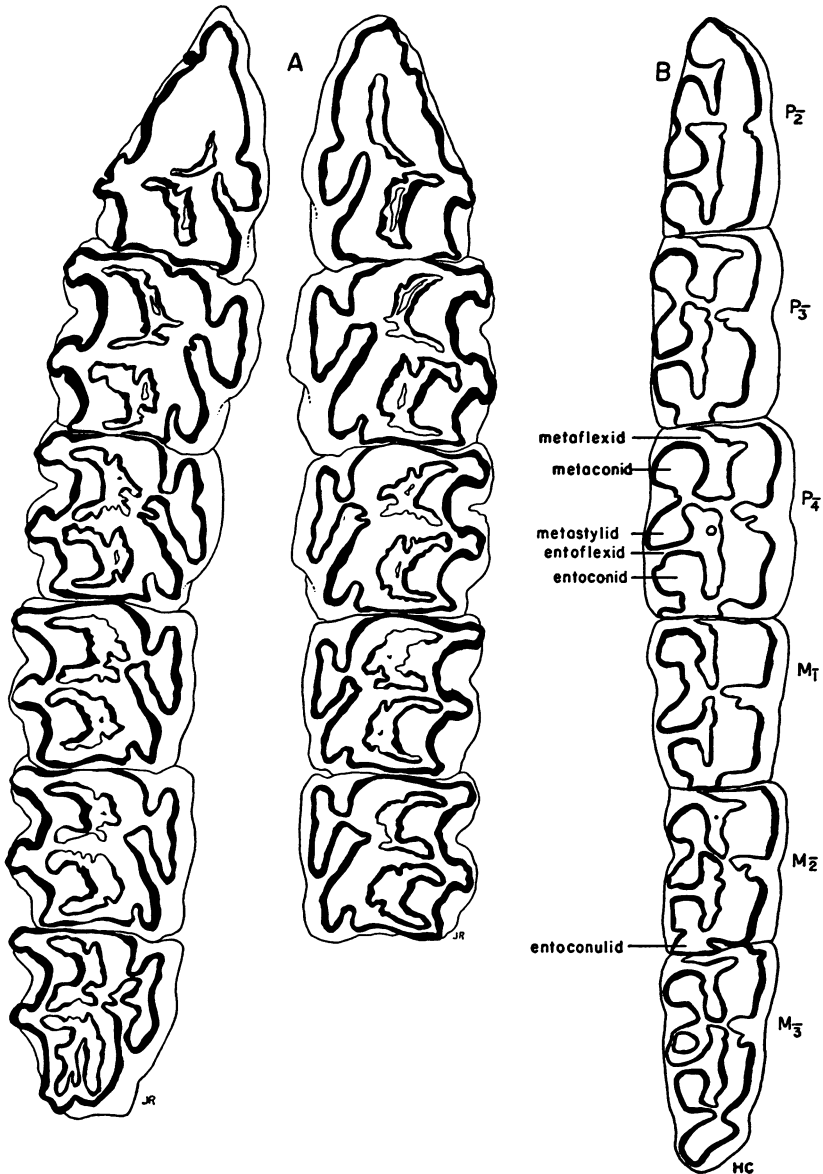
FIGURE 5

(A) Holotype of *Equus (Hesperohippus) mexicanus,* sp. nov., No. 48 (HV-3), M.N.H.
     N., LP²–M³ and RP²–M². Occlusal view. ×¾.
(B) *Equus* cf. *(Hesperohippus) mexicanus,* No. 401(1), ramus with P₂–M₃, occlusal
     view. ×¾.

of the orbits is a slight depression between the temporal ridges. The occipital crest is broad (85.0 mm. in greatest width) and extends 63.5 mm. posterior to the occipital condyles. The brain case is large and slopes from the frontal plane to the posterior edge of the occipital crest at a 30° angle.

TABLE V

MEASUREMENTS OF THE HOLOTYPE, No. 48(HV-3), M.N.H.N., OF
Equus (Hesperohippus) mexicanus, SUBGEN. ET SP. NOV.

Vertical length, median incisive border to middle of occipital crest .... 614.0 mm.
Basilar length, median incisive border to anterior edge of foramen magnum . 527.0 mm.
Frontal width, at posterior border of orbits .... 236.0 mm.
Cephalic index, frontal width × 100 ÷ basilar length 44.78%
Facial length, median incisive border to middle of line connecting posterior
    border of orbits .... 415.0 mm.
Faciocephalic index, facial length × 100 ÷ basilar length 78.74%
Cranial length, middle of line connecting posterior border of orbits to
    middle of occipital crest .... 218.0 mm.
Craniocephalic index, cranial length × 100 ÷ basilar length 41.36%
Palatal length .... 292.0 mm.
Palatal width, at M^2 .... 73.0 mm.
Occiput-vertex angle, between vertex and line connecting most posterior
    point of occipital crest and condyles .... 52°
Anteroposterior length of orbit .... 72.0 mm.
Vertical height of orbit .... 63.5 mm.
Orbital index, vertical height of orbit × 100 ÷ anteroposterior length .... 88.2 %
Distance from posterior border of palate to middle of posterior edge of
    vomer .... 125.0 mm.
Distance from middle of posterior edge of vomer to anterior edge of for-
    amen magnum .... 115.0 mm.
Vomer index, distance from posterior border of palate to middle of pos-
    terior edge of vomer × 100 ÷ distance from same point on vomer to
    anterior edge of foramen magnum .... 107.0 %
Convexity of nasofrontal suture, distance from posterior end of internasal
    suture to middle of line connecting two most posterior points of
    frontonasal suture .... 31.0 mm.
Diastema length I^3–P^2 .... 89.7 mm.
Muzzle width, at posterior alveolar border of I^3 .... 90.0 mm.
Molar-premolar series, occlusal length, P^2–M^3 .... 191.0 mm.
Molar-premolar series, alveolar length, P^2–M^3 .... 198.0 mm.
Length of premolar series, occlusal surface, P^2–P^4 .... 103.0 mm.
Length of molar series, occlusal surface, M^1–M^3 .... 88.0 mm.

The exoccipital region between the condyles slopes downward and forward. In the subgenera *Equus* and *Hippotigris* this region slopes slightly backward or descends vertically to the frontal plane; in *Hemionus* and *Asinus* as a rule it descends vertically to the frontal plane, though in *E.*

(Hemionus) hemippus there is a very slight forward slope. A deep narrow groove separates the posterodorsal face of the occipital condyles from the exoccipital region.

The paraoccipital process is directed forward at a 40° angle to the posterior face of the occipital condyles. The ventral surface of the paraoccipital slopes upward at approximately a 45° angle and does not form a shelf. The paraoccipital is separated from the postglenoid process by 20.7 mm., a distance equal to that in the small skull of a male Syrian wild ass (*Equus (Hemionus) hemippus*), No. 1637, Peabody Museum of Natural History, Yale University.

The basioccipital joins the basisphenoid at a slightly steeper angle than in the Peabody Museum specimen of *E. (H.) hemippus* or in a male specimen of *E. (H.) hemionus hemionus* from Mongolia, No. 57207, American Museum of Natural History. The basioccipital-basisphenoid region is flattened to form a broad concave arch as in *Hemionus*. Posterior to the basilar process on the posteroventral surface of the basisphenoid are two broad shallow pits.

The postglenoid processes are massive. The squamosal condyles have a transverse width of 66.0 mm. The hamular process of the pterygoid is well developed. The pterygoid process of the sphenoid and the posterior part of the palatine are separated from the maxillary by a distinct narrow groove. The dorsoanterior edge of the pterygosphenoid process is like that in *Hemionus* and does not possess the shelf observed in *Hippotigris* or *Asinus*. The anterior part of the posterior narial notch is small; it ends on a line with the anterior edge of the protocone of M^3. The greatest width anterior to the hamular process is 47.7 mm. The distance from the hamular process to the anterior edge of the narial notch (posterior nares) is 51.0 mm. The opening posterior to the hamular processes is larger than the anterior one between the processes and the posterior edge of the palatines.

The anterior palatine foramina end posterior to the protocone of M^3. They are situated as in the domestic horse.

The supraorbital foramina are 165.0 mm. apart and located 10.2 mm. from the border of the temporal fossa and 25.5 mm. from the border of the orbit. There are two notches on the anterior part of the left superciliary border (as mentioned by Cope) and a long deep notch on the right border. There is a short prominent exostosis on each side in front of the preorbital border and in line with the supraorbital border, which is larger than any observed in the domestic horse. The supraorbital process of the frontal, the zygomatic arch, and the maxillary process are strongly developed. The dorsal border of the orbits is 26.0 mm. below the flat dorsal surface of the skull. The greatest transverse width of the skull is across the posterior

border of the orbits as in the subgenera *Equus, Asinus,* and *Hemionus.* The transverse width, where the jugal joins the squamosal, is slightly less than the greatest transverse width and compares with that of the skull of *E. (Hemionus) hemippus.* In the domesticated horse the zygomatic arch at the posterior border of the orbits slopes abruptly posteriorly toward the cranium. The zygomatic arch in *Asinus* and *E. (H.) hemionus hemionus* is intermediate in regard to the backward slope of the arch posterior to the orbits. In the zebras examined the greatest width of the skull is posterior to the orbits where the jugal joins the squamosal.

The diastema between I^3–P^2 is short, 89.7 mm. in length, which is approximately equal to the occlusal length of M^1–M^3, but it is slightly shorter than the occlusal length of P^2–P^4. The shortness of this diastema distinguishes the skull from that of the subgenus *Equus* and the zebrine group. A diastema of 55.0 mm. separates the canine and P^2. The anterior part of the premaxillaries is broad, flattened on the ventral surface in comparison to Recent forms, and does not curve abruptly downward as in the domestic horse and the zebra. This broad and flat development of the premaxillaries, which is not due entirely to age, seems to be a compensation for the strong flexure of the occipital region. *Hesperohippus* carried its muzzle more nearly at a right angle to the neck vertebrae than other Recent or Pleistocene forms. The upper surface of the anterior end of the premaxillaries does not bend abruptly downward but continues on nearly the same slope from the nasopremaxillary notch to the alveolus of I^2.

In *Hemionus* (Asiatic asses) there is a deep fossa, just anterior to P^2 and posterior to the canine, in the anterior part of the maxillary between the diastema and the maxillary suture with the premaxillary. No name has been given to this fossa and in this paper it will be called the "diastemal fossa." The great depth of the diastemal fossa seems to be distinctive for *Hemionus.* On the skull of *Equus (Hesperohippus) mexicanus* the diastemal fossa is anterior to P^2 but near the suture between the premaxillary and the maxillary. It is not as deep as that in the Asiatic asses. The dorsal location of the fossa in *Hesperohippus* may be owing to the greater width of the maxillary in this region.

The suture between the premaxillary and the nasal appears to be at the nasal notch, which is situated above the anterior edge of P^3. Cope's description and measurements of this skull are, in general, accurate, except that he asserts that both third upper true molars are lacking and then gives measurements for the RM^3.

The tips of the nasal bones on the holotype of *E. (H.) mexicanus* are now broken, but Cope (1884, p. 13), stated that "the apex of the nasal bones is above the superior canine." The dorsal surface of the nasals above

the nasal notch is convex. Posteriorly the nasals are slightly concave to the orbital region.

The infraorbital foramen is above the posterior edge of the second column of P⁴. The distance from the posterior edge of the infraorbital foramen to the posterior border of the orbit is 196.0 mm. and the distance from the posterior border of the foramen to the posterior edge of the alveolus of I³ is 202.0 mm. In Table VI the skull indices and occiput-vertex angles of representatives of the subgenera of *Equus* are compared.

TABLE VI

COMPARATIVE OCCIPUT-VERTEX ANGLES AND INDICES IN SKULLS OF *Equus*

Species	Occiput-vertex Angle*	Franck's Vomer Index†	Dental Index‡	Diastemal Index§	Diastemal Skull Index‖
Equus (Hesperohippus) mexicanus, No. 48 (HV-3), M.N.H.N. .	52°	107.0%	37.1%	47.2%	14.9%
Equus (Hemionus) hemippus, No. 1637, P,M.N.H.	60	. . . .	39.8	40.0	13.8
Equus (Hemionus) hemionus hemionus, No. 57207, A.M.N.H	58	117.4	37.5	45.3	14.8
Equus (Asinus) asinus, U.S.N.M., No. 252293, burro	59	118.1	35.5	51.7	16.0
Equus (Asinus) asinus, Kansas State College, jack	60	108.8	31.0	71.0	19.3
Equus (Hippotigris) burchellii antiquorium, No. 83452, A.M.N.H.	68	82.4	32.7	62.6	18.1
Equus (Hippotigris) zebra, No. J54-318, U.M.M.P.	62	105.4	32.3	70.7	19.8
Equus (Equus) caballus, No. J55-413, U.M.M.P.	73	87.0	32.3	69.0	20.3

* Occiput-vertex angle,. angle between vertex and line connecting most posterior points of occipital crest and condyles, measurements by John A. Dorr, Jr. All of the indices are taken from Osborn, 1912, p. 84.
† Franck's vomer index, distance from posterior border of palate to middle of posterior edge of vomer × 100 ÷ distance from same point on vomer to anterior edge of foramen magnum.
‡ Dental index, molar-premolar series, P²–M³, alveolar length × 100 ÷ basilar length of skull.
§ Diastemal index, diastemal length, I³–P², × 100 ÷ molar–premolar series, P²–M³, alveolar length.
‖ Diastemal–skull index, diastemal length × 100 ÷ length from median incisive border to middle of occipital crest.

The teeth are well worn. The incisors are broken at, or below, the alveolar border. They were large and appear to have been strongly curved. The canine has an anteroposterior length of 15.5 mm. and a transverse width of 13.3 mm.

An elongated and flattened protocone is characteristic of P³–M³. The preprotoconal groove is deep and the protocone extends well forward along the lingual side of the tooth. This character of the protocone separates *Equus (Hesperohippus) mexicanus* from *Equus (Plesippus) crenidens*, an-

other large horse from this region. In *E. (P.) crenidens* the protocone is short and rounded posteriorly and the preprotoconal groove is shallow (Fig. 4A and B). The hypoconal groove in *E. (H.) mexicanus* is well developed, considering that the teeth are old and worn, and narrower than in teeth of *E. (P.) crenidens* of comparable age wear. The pli caballin fold is still evident on P³, P⁴, and M³. It was probably present on P², M¹, and M², but has disappeared with old age. Many of the details of the tooth characters are lacking for the same reason. The fossettes of P⁴ are more complex than in the other teeth, but even so they do not appear to have ever had as many

TABLE VII

COMPARATIVE MEASUREMENTS OF UPPER TEETH OF PLEISTOCENE EQUIDS

Dimension	Holotype, Equus (Hespero-hippus) mexicanus, No. 48	Holotype, Equus laurentius (After Hay, 1913)	Holotype, Equus niobrarensis (After Hay, 1913)	Equus scotti, No. 10628 (After Hay, 1914)
P², occlusal length	42.5 mm.	35.0 mm.	38.0 mm.	42.0 mm.
occlusal width	28.1	24.5	27.0	31.0
length of protocone .	10.5	8.0	10.0	...
P³, occlusal length	31.9	26.0	30.0	35.0
occlusal width	34.0	24.5	28.0	33.0
length of protocone .	16.2	9.0	13.5	14.0
P⁴, occlusal length	30.0	25.0	29.0	33.0
occlusal width	32.0	25.0	27.0	33.0
length of protocone .	18.0	10.0	14.0	15.0
M¹, occlusal length	26.9	22.0	27.0	30.0
occlusal width	29.5	23.5	28.0	30.0
length of protocone .	14.8	10.5	13.0	14.5
M², occlusal length	28.8	23.0	27.0	31.0
occlusal width	30.5	23.5	25.0	29.0
length of protocone .	16.0	13.0	14.0	15.0
M³, occlusal length	32.8	30.0	26.0	30.0
occlusal width	26.2	22.0	23.0	25.0
length of protocone .	17.5	14.0	14.0	16.0

plications as were observed in *Equus conversidens*. In *E. (H.) mexicanus* the external valleys between the parastyles and mesostyles and between the mesostyles and metastyles are very deep, even deeper than in *Equus (P.) crenidens*. The enamel borders of the external valleys are concave. Dimensions of the teeth of the holotype, No. 48, are compared with those of other forms in Table VII.

Referred material.—Four associated upper molars, LP³–M², No. 49–51 (Fig. 4C), were taken in August, 1949, at the base of the Upper Becerra in the bed of Barranca de Acatlán about midway between Localities 2 and 3 (Fig. 1). The teeth are those of a young adult horse and, although smaller than those of the holotype of *Equus (Hesperohippus) mexicanus,* are questionably referred to it (see Table VIII for tooth dimensions).

Two other specimens in the collection are tentatively assigned to this species. One, a right M_1, No. 49-57, was taken north of Locality 6 on the bank of Barranca de Acatlán. The tooth has a height of 93.0 mm. and an occlusal crown length of 31.0 mm. The other, No. 401 (1), is the right ramus, with P_2–M_3, of as large a horse from the Pleistocene of Mexico (Fig. 5B) as *Hesperohippus*. The crown height of P_2 is 44.0 mm. (for other dimensions, see Table IX). The metaconid is distinctly round in outline. The pli caballinid, though only faint on P_2 and M_1, is present on all the teeth.

TABLE VIII

MEASUREMENTS OF UPPER TEETH OF SPECIMEN No. 49-51,
? Equus (Hesperohippus) mexicanus, SP. NOV.

Dimension	LP³	LP⁴	M¹	M²
Height of crown	66.5 mm.	76.2 mm.	68.2 mm.	74.5 mm.
Occlusal length	34.5	32.5	27.8	28.8
Occlusal width	31.9	29.9	28.5	26.3
Length of protocone ...	16.2	15.3	14.5	14.5

TABLE IX

MEASUREMENTS OF LOWER TEETH OF SPECIMEN No. 401(1),
? Equus (Hesperohippus) mexicanus, SP. NOV.

Dimension	P₂	P₃	P₄	M₁	M₂	M₃
Length of crown ...	37.5 mm.	33.2 mm.	33.5 mm.	30.0 mm.	27.7 mm.	38.0 mm.
Width of crown ...	17.5	19.8	22.5	19.7	17.7	17.0

Occlusal length of P_2–M_3 = 199.0 .mm
Occlusal length of P_2–P_4 = 104.7 mm.
Occlusal length of M_1–M_3 = 94.5 mm.

Discussion.—*Equus (Hesperohippus) mexicanus* is as large as, or slightly larger than, either *Equus (Plesippus) crenidens, Equus occidentalis,* or *Equus scotti* (cf. Table VII). The majority of the skull characters resemble those of the asses and are, in some respects, nearer to the Asiatic *(Hemionus)* than to the African *(Asinus)*. The skull does not show any close relationship to the true horses or to the zebrine forms, a fact noted by Cope. The lower jaws, when known, will add much to our knowledge.

In regard to the presence of a pli caballin fold more study is needed on both fossil and Recent forms. It has been generally held that the fold is absent in the asses. Colbert (1940, p. 3) cites Mr. C. H. Chubb, who studied the modern Equidae for many years. Chubb had observed that the pli caballin fold was absent in the asses, except in the Kiang in which it is very small, but present in the horses and zebras.

Stehlin and Graziosi (1935, p. 6) figure *Equus (Asinus) asinus somaliensis* Noack (= *Equus (Asinus) asinus somalicus* Scalter), the Somali wild

ass, as having a well-developed pli caballin fold in both the premolars and molars. It has not been possible for me to study a skull of this form. These authors also figure the Nubian wild ass with a pli caballin fold on P^2 and P^3.

The pli caballin fold is faintly developed on the P^2, P^3, P^4, and M^2 of a specimen, No. 57207, A.M.N.H., of *Equus (Hemionus) hemionus hemionus*. On P^2–M^2 of *Equus (Hemionus) hemippus*, No. 1637, P.M.N.H., the Syrian wild ass, it is present, deeply developed on M^2 and faintly on M^1. There is no pli caballin fold on the premolar-molar series of any of the burros that I examined, but there is a very shallow fold on the left and right M^3 of a large jack skull from the Department of Anatomy, Kansas State College, Manhattan, Kansas.

ORDER ARTIODACTYLA
Family Camelidae
Camelops cf. *hesternus* (Leidy)

Auchenia hesterna Leidy, 1873. Proc. Acad. Nat. Sci. Phil., pp. 259–60.

A left M_2, No. 49-35, of a camel was recovered August 10, 1949, at Locality 5. It was associated with the skull of the large bison, *Bison chaneyi*, No. 49-33. The tooth has a crown height of 69.5 mm. and an anteroposterior occlusal length of 48.3 mm.

A large toe bone, No. 49-59, was taken August 9, 1949, at Locality 8, on the bank of Barranca de Acatlán just opposite Puente de Gallo, from the upper part of the Upper Becerra. The bone has a length of 122.5 mm. and the greatest transverse width of the proximal end is 50.7 mm.

The two specimens are referred to *Camelops* cf. *hesternus* (Leidy), because the majority of specimens of *Camelops* taken from this area are assigned to that species. None of their characters, however, would distinguish them from *Camelops kansanus* Leidy, which is known as far south as Texas.

Family Bovidae
Subfamily Bovinae
Tribe Bovini
Bison (Platycerobison) chaneyi Cook
(Pls. V, Figs. 1–2; VI, Fig. 4)

Bison chaneyi Cook, 1928, Proc. Colorado Mus. Nat. Hist., Vol. 8, No. 3, pp. 34–37,
    2 figs.
Bison (Platycerobison) chaneyi Cook, Skinner and Kaisen, 1947, Bull. Amer. Mus. Nat.
    Hist., Vol. 89, Art. 3, pp. 197–99, Pl. 24, 1 fig.
Bison (Platycerobison) chaneyi Cook, Hibbard and Villa R., 1950, An. Inst. Biol. Mex.,
    Vol. 21, No. 1, pp. 243–54, lams. 3, Table 1.

The posterior part of a cranium with horn cores, No. 49-33, was taken just above the contact of the Upper Becerra with the underlying formation,

on the southwest side of Tajo del Desagüe Viejo, Locality 5, on August 10, 1949. The cranium is that of a large male and is referred to this species.

The horn cores are large and extend from the skull in a slightly posterior direction. They curve upward and slightly inward and are posteriorly bent at the tips. The frontal region of the skull is flat. The fact that the horn-core base is smaller and dorsoventrally flattened definitely separates this bison from *Bison latifrons,* in which the basal part of the horn core is larger and subcircular. For a comparison of this specimen with the holotype, No. 1147, C.M.N.H., see Table X.

TABLE X

COMPARATIVE MEASUREMENTS AND INDICES IN *Bison (Platycerobison) chaneyi* COOK

Measurements of No. 49-33, from Tequixquiac, were taken as suggested by Skinner and Kaisen (1947); the ones of the holotype No. 1147, C.M.N.H., from Texas, are those given by them (1947, p. 198). Measurements in parenthesis are approximate.

Dimension (in mm.)	No. 49-33	Holotype, No. 1147
Spread of horn cores, tip to tip	(1310)	1071
Greatest spread of cores on outside curve	1370	1068
Core length on upper curve, tip to burr	(795)	545
Core length on lower curve, tip to burr	(875)	630
Length, tip of core to upper base at burr	667	440
Vertical diameter of horn core at right angle to longitudinal axis	123	114
Circumference of horn core at right angle to longitudinal axis	440	412
Greatest width (of skull) at auditory openings	292	305
Width of condyles	145	149
Depth, occipital crest to top of foramen magnum	130	140
Depth, occipital crest to lower border of foramen magnum	...	185
Transverse diameter of core at a right angle to the longitudinal axis	152	147
Width between bases of horn cores	...	...
Width of cranium between horn cores and orbits	327	325
Index (in per cent)		
Core curvature	131	143
Core compression	80	78
Core proportion	180	132
Core length	243	167

The specimen came from the gravel and cobble zone that occurs at Locality 5 at the base of the Upper Becerra (see Pl. V, Fig. 1). It was associated with the remains of the large camel, No. 49-35; with part of the lower jaw, No. 49-36, of a medium-sized horse approximately the size of *Equus conversidens;* and with the toe bone of the large short-faced bear *(Tremarctotherium simus),* No. 49-43. An atlas and several cervical verte-brae of *Mammuthus* cf. *imperator* (Leidy) were taken from gray sandy silt approximately 10 feet above the cranium of *Bison chaneyi.*

Bison (Bison) cf. occidentalis Lucas
(Pl. VI, Figs. 1–3)

Bison occidentalis Lucas, 1898, Science, Ser. 2, Vol. 8, p. 678.
Bison (Bison) occidentalis Lucas, Skinner and Kaisen, 1947, Bull. Amer. Mus. Nat. Hist., Vol. 89, p. 169

The base of a cranium with both horn cores, No. 49-76, was found August 12, 1949, 340 meters upstream from Locality 7, on the left-hand side of Barranca de Acatlán. The skull was found embedded in a silty clay near the top of the Upper Becerra formation. Before removal could be completed, it was necessary to leave the specimen and the left horn core was broken loose and stolen. It has never been recovered. The skull is that of a large male and is referred to *Bison occidentalis*. Dimensions are given in Table XI. The horn cores are short, round, curve upward, and are posteriorly directed, with the distal tips posteriorly twisted. The horns extended above the frontal plane and posterior to the occipital.

TABLE XI

MEASUREMENTS OF SPECIMEN, No. 49-76, FROM TEQUIXQUIAC, REFERRED TO
Bison (Bison) cf. *occidentalis* LUCAS

Measurements taken as suggested by Skinner and Kaisen (1947, pp. 144–45); those in parenthesis are approximate.

Spread of horn cores, tip to tip	(750) mm.
Greatest spread of cores on outside curve	(760)
Core length on upper curve, tip to burr	198
Core length on lower curve, tip to burr	253
Length, tip of core to upper base at burr	187
Vertical diameter of horn core at right angle to longitudinal axis	90
Circumference of horn core at right angle to longitudinal axis	295
Greatest width (of skull) at auditory openings	315
Width of condyles	152
Depth, occipital crest to top of foramen magnum	118
Depth, occipital crest to lower border of foramen magnum	161
Transverse diameter of core at right angles to longitudinal axis	97
Estimated width between bases of horn cores	426

Subfamily Caprinae
Tribe Euceratherini

Genus *Euceratherium* Furlong and Sinclair

Euceratherium Furlong and Sinclair 1904, Publ. Univ. Calif. Amer. Archaeol. and Ethnol., Vol. 2, p. 18.

Generic characters.—Horn cores transversely flattened at base becoming rounded near tip, situated close together on the posterior extremity of the frontals, behind and above the orbits; solid except for the base which

possesses large pneumatic cavities continuous with the pneumatic cavities of the frontals. The frontals reach to the supraoccipital. The parietals do not form part of the cranial roof but are confined to the lateral sides of the skull between the squamosals and frontals. The basioccipital is developed as in the goats. The lachrymal pit is broad and shallow. The teeth are high crowned, large, and without cement or accessory cusplets.

Euceratherium collinum Furlong and Sinclair
(Pls. VII, Fig. 2; VIII, Fig. 2; IX)

Euceratherium collinum Furlong and Sinclair, 1904, Univ. Calif. Publ. Amer. Archaeol. and Ethnol., Vol. 2, p. 18.
Euceratherium collinum Sinclair and Furlong, 1904, Univ. Calif. Publ. Bull. Dept. Geol., Vol. 3, No. 20, p. 412, Fig. 1, Pls. 50-51.
Preptoceras cf. *sinclairi* Furlong, Freudenberg, 1922, Geol. u. Palaeont. abh. N.F., Band 14, Heft 3, p. 5.
Euceratherium collinum morrisi Schultz and Howard, 1935, Proc. Acad. Nat. Sci. Phila., Vol. 87, p. 290, Pl. 13.
Euceratherium bizzelli Stovall, 1937, Journ. Paleontol., Vol. 11, No. 5, p. 451, 3 figs.

Two fragments of a single specimen originally had different catalogue numbers in the collection of the Instituto de Geologia: No. 26 was given to the base of the skull and part of the left horn core and No. 212 to part of the right horn core. The two pieces fit together perfectly and are now catalogued as one, No. 26 (Pl. VII, Fig. 2). The record of the two numbers states that it was collected at Tequixquiac, Mexico.

No. 47-1 (Pl. VIII, Fig. 2) a specimen from Sonora, agrees closely with No. 26. It consists of a right horn core (base and tip missing), the basioccipital, and the occipital condyles. No. 47-1 was collected on September 15, 1946, by Francisco Cuhemaya in the immediate vicinity of La Guitarra, Sonora, about half-way between Tonichi and Sahuaripa. The specimen was recovered in a gravel pit, about 30 feet below the surface, from a deposit of fine sand and gravel. It was acquired by H. D. Langille of Salem, Oregon, who donated it to the Instituto de Geologia and furnished the data recorded here.

Since it is impossible to distinguish the holotype of *Euceratherium bizzelli* Stovall, 1937, from Hydro, Caddo County, Oklahoma, No. 701, University of Oklahoma (Pl. VIII, Fig. 1), either from *E. collinum morrisi* Schultz and Howard, 1935, from Burnet Cave, Eddy County, New Mexico, or from these two specimens from Mexico, all of them are considered to belong to *E. collinum* Furlong and Sinclair.

Description of Specimen No. 26, from the Pleistocene of Tequixquiac.—
The cranium must have been nearly complete at the time of discovery, for

it shows no signs of abrasion and all fractured surfaces are fresh. The actual specimen, however, consists of the base of the skull, including the brain case and approximately one-third of the right horn core (Pl. VII, Fig. 2) and the base of the left horn core. The brain case is broken just posterior to the orbits and at the suture between the basisphenoid and the presphenoid.

The cranium is judged to be that of an adult male. The frontals reach the supraoccipital, which extends 42.0 mm. along the mid-line anterior to the lambdoidal crest (nuchal crest) and meets the frontals at an acute angle. A distinct suture separates the supraoccipital and mastoid processes from the frontals, parietals, and squamosals. The parietals are separate and each is situated laterally on the side of the skull between the frontal and squamosal. They are bounded posteriorly by the suture between the frontals and the supraoccipital and extend forward between the squamosal and frontal to within 13.6 mm. of the superior orbital groove. The superior orbital groove is well developed. In *Ovibos* (musk ox) the parietals end approximately at the mid-line of the base of the horn cores.

The back of the skull is flat and a prominent median tubercle extends downward from the lambdoidal crest. On each side of the tubercle is a shallow pit, but this is not a large deep fossa as reported by Furlong (1905, p. 166) for *Preptoceras sinclairi*. Along the outer edge of the occipital condyles are well-developed buttresses, so that a groove exists between the condyles and the paraoccipital processes. The basioccipital, unlike that of *Ovibos* and *Ovis* (sheep), tapers anteriorly to the end of the basisphenoid. In *Euceratherium* the posterior pair of tubercles on the basioccipital are larger and farther apart (width across posterior tubercles is 63.1 mm.) than the smaller anterior tubercles (width across anterior tubercles is 54.4 mm.). The condyloid fossa is neither large nor deep. It is not separated from the ventral anterior face of the condyle, as in *Ovibos,* by a ridge extending from the posterior tubercles of the basioccipital to the paraoccipital. The paraoccipital is short but strongly developed. The squamosal swings downward at the posterior edge of the glenoid fossa and rests against the auditory bulla. The distance between the posterior edge of this downward-swinging process and the paraoccipital is approximately one-half that in *Ovibos* and *Bos* (cattle). It is approximately the same as in the Rocky Mountain sheep, even though the skull in *Euceratherium* is considerably larger. The opening of the auditory meatus is large. The basisphenoid is flexed dorsally and the fractured area of the presphenoid suggests a still greater flexure in a dorsal direction of that bone. The posterior border of the orbit is posterior to the opening of the anterior lacerate foramen,

whereas in *Ovibos* it is well in advance of this foramen. The flexure of the anterior part of the skull is nearly as great as in *Ovis*.

The horn cores rise near the posterior edge of the frontals. They swing upward and slightly backward, then bend outward and forward, and curve upward near the tips. The posterior swing of the horn cores extends back on a line with the most anterior part of the suture between the supraoccipital and the frontals. The horns are developed on a well-arched transverse

TABLE XII

COMPARATIVE MEASUREMENTS OF *Euceratherium collinum* FURLONG AND SINCLAIR, NO. 26, FROM TEQUIXQUIAC AND THE HOLOTYPE OF *Euceratherium bizzelli* STOVALL, NO. 701, UNIVERSITY OF OKLAHOMA

Measurement in parenthesis is approximate.

	No. 26	E. bizzelli
Greatest width across base of horn cores	(142.0) mm.	142.0 mm.
Greatest anteroposterior diameter of horn core	107.0	98.2
Greatest transverse diameter of horn core	63.0	57.0
Circumference of horn core at base	265.0	243.0
Greatest width at auditory openings	168.0	164.0
Distance between occipital protuberance and upper border of foramen magnum	51.8	47.1
Greatest width of occipital condyles	119.6	103.5
Distance from postglenoid process to paraoccipital (paramastoid) process	20.2	16.0
Greatest width across basioccipital at posterior processes ..	63.2	63.1
Distance from edge of foramen magnum to anterior edge of basisphenoid	88.2	90.2
Distance from ventral edge of foramen magnum to posterior edge of anterior lacerate foramen	85.5	88.1
Greatest transverse diameter of foramen magnum, measured between inner borders of occipital condyles	36.3	35.2
Greatest dorsoventral diameter of foramen magnum	30.5	29.4
Height of occiput measured from ventral surface of occipital condyles to superior border	108.3	108.3
Width of cranium measured between outer surface of lateral walls of parietals	95.2	101.5

frontal ridge as in *Ovis*. No burr is present on the horn cores. The horn sheath seems to have been similar to that in the sheep and the goats. The base of the horn core has no tendency to extend across the mid-frontal region as in *Ovibos*.

The skull from Tequixquiac is almost identical in all details with that of *E. bizzelli* from Oklahoma (see Table XII). Both specimens possess the same peculiar condition of the occipital condyles; that is, on the anterior ventral edge and the upper anterior edge of the condyles, the anterior faces

look as though they had been injured, because the outer edges of these surfaces are flattened and extend forward. The edges have grown slightly downward on the ventral rims and upward on the upper rims. From this it appears that these animals were tremendous "butters" and that the condyles, consequently, reflect the results of impacts.

Discussion.—Sinclair and Furlong (1904, p. 416) considered *Euceratherium* to be distinct from any group of the subfamily Ovinae (Caprinae) that occurred in North America. They were of the opinion that the animal was an inhabitant of lower hills rather than high mountain ranges as are the sheep and goats. In separate publications, Sinclair (1905, p. 151) stated that *Euceratherium* was not closely allied to the goat-antelopes, sheep, cattle or musk oxen, but possibly represents an Asiatic type which reached North America in the Pleistocene and that its ancestors are to be sought among the extinct forms of the Asiatic Pliocene. And Furlong (1905, p. 168) when he described *Preptoceras,* said that the new genus was nearer to *Euceratherium* than to any form known. He added that the two genera would probably have to be placed in a group by themselves when studied further.

Osborn (1910, p. 554) believed *Euceratherium* was closely related to the musk oxen and belonged to the Ovibovinae. Although Osborn has been followed by some later workers, he was not by Allen (1913, p. 169) who stated, "neither [*Euceratherium* and *Preptoceras*] . . . is nearly related to either *Symbos* or *Ovibos.*" Stovall (1937, p. 453) discussed the relationship of *Euceratherium* to both the Ovinae and the Ovibovinae. He decided that it was inadvisable to attempt to arrive at a definite conclusion concerning the subfamily to which the genus belonged, until more evidence was available, but suggested that *Euceratherium* and *Preptoceras* might constitute a new group.

Frick (1937, p. 548) included *Euceratherium, Preptoceras,* and (questionably) *Aftonius* Hay and *Taurotragus* ref. Gidley under a new subfamily, Euceratherinae, which he placed between the Antilopinae and the Ovinae. In the present study this subfamily is reduced to a tribe, Euceratherini, in keeping with the classification proposed by Simpson (1945, p. 157) for the family Bovidae. It is apparent that this tribe, Euceratherini, as Frick (1937) brought out, is not close to the tribe Ovibovini (= Ovibovinae, the musk oxen and related forms). The true status of the *Euceratherini* will probably not be determined until we have better material and know more about the Pliocene bovids. The group, as we visualize it, was composed of large specialized grazing forms that paralleled the sheep and goats in range in inhabiting the lower hills, as Sinclair and Furlong suggested, and not the high mountain ranges.

I was unable to study the type skulls of *Euceratherium* and *Preptoceras* recovered from California. Only casts of the horn cores of the types were available. These were distinctly different in shape. Stovall (1937, p. 454) thought that the difference was a generic rather than a sex distinction and commented that such marked divergence in horn development between members of the sexes of a species is rare among the bovids. It is known that owing to age the horns of individuals show change both in curvature and relationship to the skull in some groups of bovids. This is well illustrated in *Ovibos* (Allen, 1913). Whether such differences occur in *Euceratherium* and *Preptoceras* is still not certain. From a study of the description of *Preptoceras sinclairi* (Furlong, 1905; Stock and Furlong, 1927) the parietals seem not to be fused with the frontals in the roof of the skull but to occur as in *Preptoceras? mayfieldi* Troxell (1915), from Rock Creek, Texas. In *Preptoceras? mayfieldi* the frontal suture is distinct and extends posteriorly to the supraoccipital, which is approximately a centimeter above the lambdoidal crest (Pl. VII, Fig. 1). When he described *P.? mayfieldi,* Troxell misidentified the parietals as a fused bone which was really the supraoccipital. He then excludes them from the lateral sides of the skull and has the deep groove below the base of the horn cores formed by the squamosals and frontals. The parietals are present on the lateral sides of the skull as in *Euceratherium* and extend almost as far forward. They are separated from the supraoccipital by a distinct suture.

On the basis of the parietal, *Preptoceras? mayfieldi* belongs to the tribe Euceratherini. It possesses, however, an entirely different type of horn core from *Euceratherium collinum* and there are well-developed burrs. The horn cores in *P.? mayfieldi* are set wide apart on the skull in contrast to the closely set, nonburred horn cores in *E. collinum.* The horns lack the distinct oval cross section observed in *E. collinum.* The basioccipital and basisphenoid are developed in *P.? mayfieldi* as in *E. collinum.* One character distinctive of *Preptoceras? mayfieldi* is that it does not have the supraoccipital extending so far beyond the lambdoidal crest as in *Euceratherium.* In this character it is similar to the condition reported in *Preptoceras sinclairi.* The development of the supraoccipital in *E. collinum,* is like that in *Oreamnos* (Rocky Mountain goat), except that the frontals join the supraoccipitals and isolate the parietals to the lateral sides of the skull.

DISCUSSION

Age of Upper Becerra fauna.—The geology of this region will be discussed in detail later by Arellano. Furlong (1925, pp. 138–41) recognized two distinct Pleistocene horizons and faunas. He correlated the faunal horizon from the brecciated fissure deposit at the lime quarry, between

Tequixquiac and the former narrow gauge railroad station of El Tajo, with the faunal horizon at Rancha Le Brea, California.

Before a definite age can be assigned to the Upper Becerra, the vertical and horizontal distribution of the forms must be determined. The vertical (stratigraphic) distribution of some forms may vary greatly between the intermontane valleys of Mexico and the United States.

The younger formation and its fauna was assigned to the Upper Becerra by Bryan, Arrelano, and De Terra (in Bryan, 1948, Lám. I,). Bryan considered it to be equivalent to the Cochran stage of the Wisconsin (10,000 years). If these workers are correct in their interpretation of the age of the Upper Becerra the closing phase of the Wisconsin fauna was entirely different from what it has previously been assumed. A point that must be established is, at what time in a Pleistocene cycle did the downcutting and the deposition of cobbles, gravels, and sands occur? Their occurrence is cyclic. Can each cycle be explained as having the same cause as the preceding one, or does regional uplift account for some downcuttings and climatic changes for others? In general there appears to be evidence for both types of development.

The study of Pleistocene stratigraphy and faunas in North America has so far progressed that not only is the recognition of glacial and interglacial deposits and faunas regarded as necessary, but also that of the postglacial-preinterglacial and postinterglacial-preglacial faunas, for an understanding and interpretation of the faunal and floral shifts that follow climatic changes. Evaluation of faunas and floras can only be done through the complete co-operation of all specialists who contribute to the study of Pleistocene and Recent earth history.

I consider the fauna of the Upper Becerra in the Tequixquiac area to represent the closing phase of the Sangamon and Wisconsin subages; that is, I believe the valley in which the Upper Becerra was deposited developed in Sangamon time and became filled during the closing phase of the Sangamon and Wisconsin time. The present dissection is Recent.

Climatic change.—There is evidence that the climatic conditions of the present arid and semiarid regions of the southwestern United States and northern Mexico, as well as those of the east slope of the Sierra Madre Oriental and the high central plateau region of Mexico, were modified during Wisconsin glaciation. Smith (1936) demonstrated the presence of Pleistocene glaciation in New Mexico at elevations of approximately 9,500 to 10,000 feet. Both Skinner (1942) and Stearns (1942) showed that climatic conditions during Wisconsin glaciation were favorable for some forms of mammalian life in more southern latitudes and at lower elevations than their present range. Skinner reported *Marmota flaviventris* (Audubon and

Bachman) from the Papago Springs Cave fauna in Arizona, and noted that the most southern occurrence of *Marmota flaviventris* today is 350 to 400 miles north of this cave in the high mountains of New Mexico. Stearns found fossil remains of *Marmota flaviventris obscura* Howell at an altitude of 5900 feet on New La Bajada Hill, New Mexico; the same species is now living near and above timberline in the Sangre de Cristo Mountains.

Remains of elephants and giant bison are abundant in the Valley of Mexico and the Valley of Tequixquiac. Cushing (1945) reported those of *Synaptomys cooperi* and *Marmonta* and Findley (1953) of *Sorex cinereus* in a late Pleistocene fauna from the San Josecito Cave, near the town of Aramberri, southern Nuevo León. The locality is approximately 7400 feet above sea level, in mountainous country that supports a forest cover of pine and oak. Relict species of *Cynomys, Pitymys,* and *Glaucomys* are found in the present fauna of Mexico (Burt, 1949). The elephants, bison, *Cynomys* (prairie-dog), *Pitymys* (pine vole), and *Synaptomys* (bog lemming), must have grazed their way into Mexico at a time when strips or areas of grassland existed where semiarid conditions prevail today. The animals advanced with changing climatic conditions that supported the development of tall grasses or tall grasses and sedges.

The distribution of *Synaptomys* could only occur with the development of a tall-grass area. Cushing (1945, p. 184) states that "Apparently *(Synaptomys) cooperi* does not require a particularly cold climate." Howell (1927) reports that *Synaptomys cooperi* definitely belongs to a boreal fauna, but that at the southern limits of its range, even though trapped in moist and dry grass lands, it lives mostly in cold sphagnum bogs. These lemmings occur in northeastern Kansas in grassland, chiefly in heavy growths of Kentucky bluegrass or sedges along moist hillsides or in valleys. During July and August they are not too active. They were taken in southwestern Kansas in the summer of 1941 (Hibbard and Rinker, 1942) in a bog area around an artesian spring where both the water and soil are cool. Whether or not *Synaptomys* inhabited the tall-grass areas in the lowland valleys of that region prior to the "Dust Bowl" is not known. But in the period between 1937 and 1947 they were found confined to the small bogs, even though areas of tall grass lead from them into tall-grass meadow land along the valley.

Extension of the range of *Synaptomys* southwestward and into Mexico reflects a climatic condition which permitted the development and southward movement of a belt of tall grasses and sedges. Rainfall and temperature would vary throughout this region. If the mean annual temperature was lower than that of northeastern Kansas and if periods of summer drought did not exist during the time of glaciation, a smaller amount of

rainfall than occurs in northeastern Kansas would have allowed the development of grassland. Provided the elevation was essentially the same as it is today, a grassland route may well have existed during each successive period of glaciation. Retreat of the continental glacier would leave many of the migrating forms stranded in whatever natural refuge was available throughout the intermontane valleys of Mexico and along the sides of the mountains.

The statement by Flint (1949, p. 1306) that, "In no other division of earth history is research intercommunication among many sciences as necessary as in research on the Pleistocene," sums up the complexity of the problems facing future workers in the study of Pleistocene history. The problems are too great to be solved by any one person or through any one division of scientific study.

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CLAUDE W. HIBBARD

EXPLANATION OF PLATE I

FIG. 1.   *Tremarctotherium simus* (Cope). Left M^1–M^2, No. 85. Natural size.
FIG. 2.   *Brachyostracon* sp. Scute, No. 49–65, of a large glyptodon. Natural size.
FIG. 3.   *Holmesina septentrionalis* (Leidy). Scute No. 46–1. Natural size.
FIG. 4.   *Brachyostracon* or *Boreostracon* sp. Caudal scute, No. 49–52. Natural size.
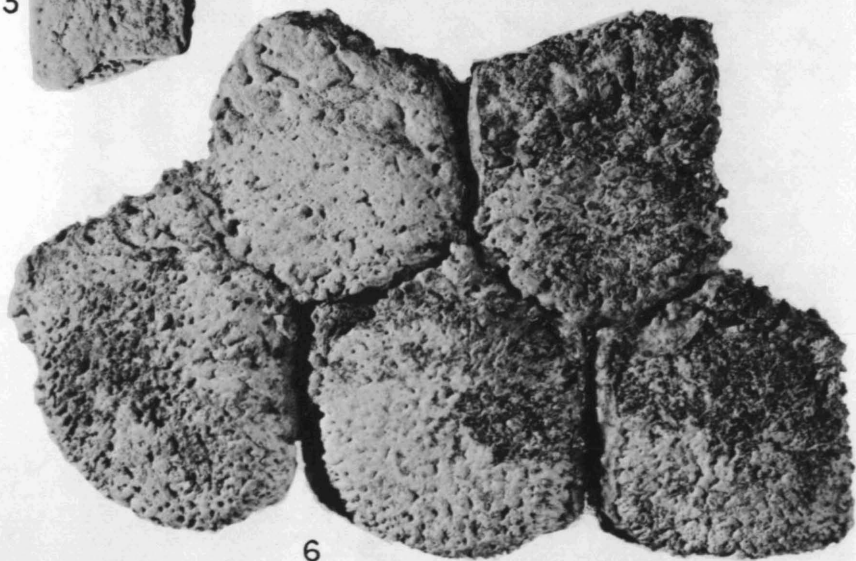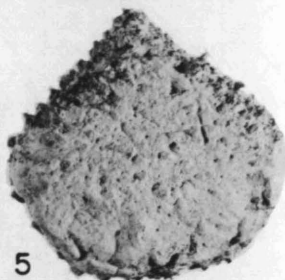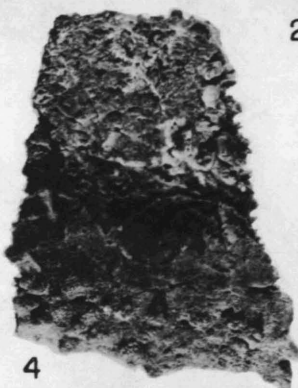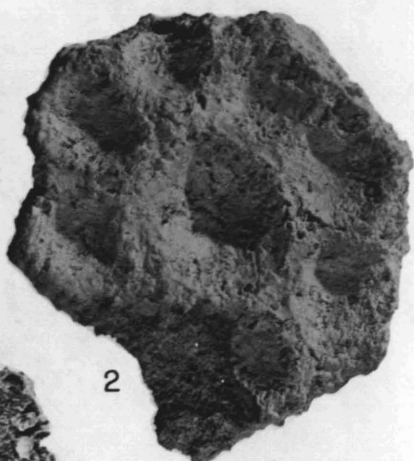FIGS. 5–6.   *Brachyostracon* or *Boreostracon* sp. Scutes, No. 49–52. Natural size.

PLATE I
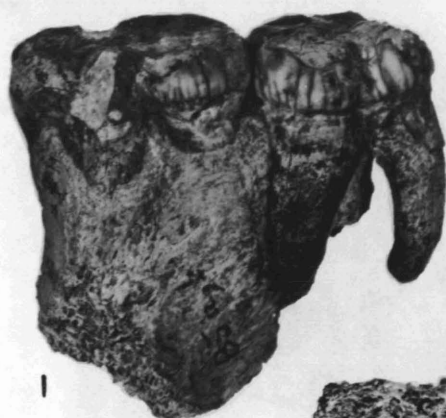
PLATE II
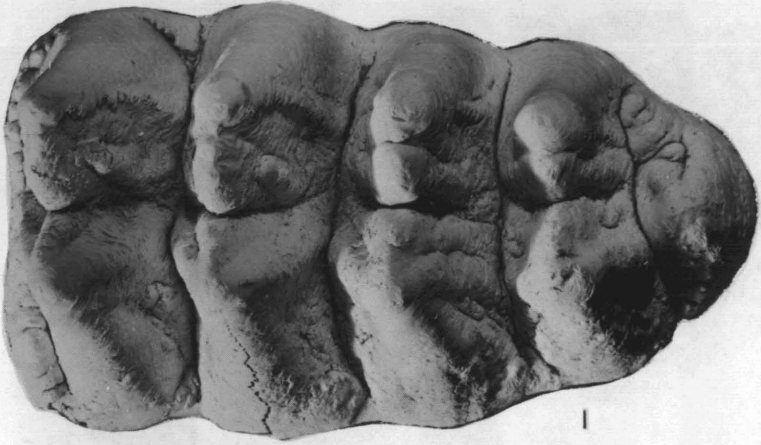
1

2
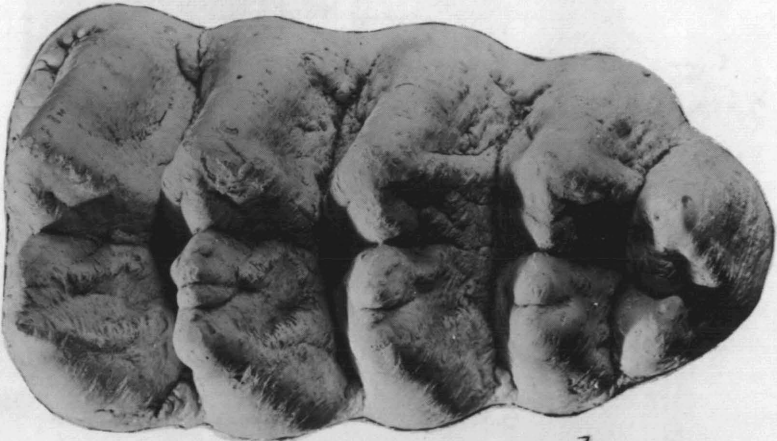
3

EXPLANATION OF PLATE II

Mammut americanus (Kerr)

FIG. 1. Left M³, No. 8394, U.M.M.P., from post-Wisconsin bog deposit, Michigan. ×⅚.
FIG. 2. Right M³, No. 44–1, from a Pleistocene deposit in Mexico. × ⅚.
FIG. 3. Right M³, No. 8394, U.M.M.P., from post-Wisconsin bog deposit, Michigan. × ⅚.

Photographs by George M. Ehlers and Erwin C. Stumm.

EXPLANATION OF PLATE III

Equus conversidens Owen

Holotype No. 403. Approximately ¾ natural size.

PLATE III

PLATE IV

EXPLANATION OF PLATE IV

Equus (Hesperohippus) mexicanus, sp. nov.

FIGS. 1–3. Ventral, dorsal, and lateral views, respectively, of the holotype, No. 48, M.N.H.N. Approximately × 1/5.

Photographs by Xavier Sivilla.

EXPLANATION OF PLATE V

Bison (Platycerobison) chaneyi Cook

Fig. 1. Specimen, No. 49–33, in place in basal gravels of the Upper Becerra, Locality 5.
Fig. 2. Same specimen after removal from formation.
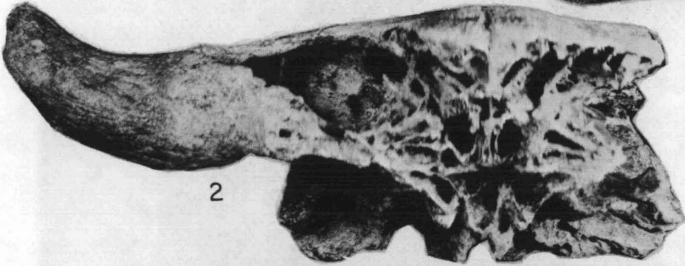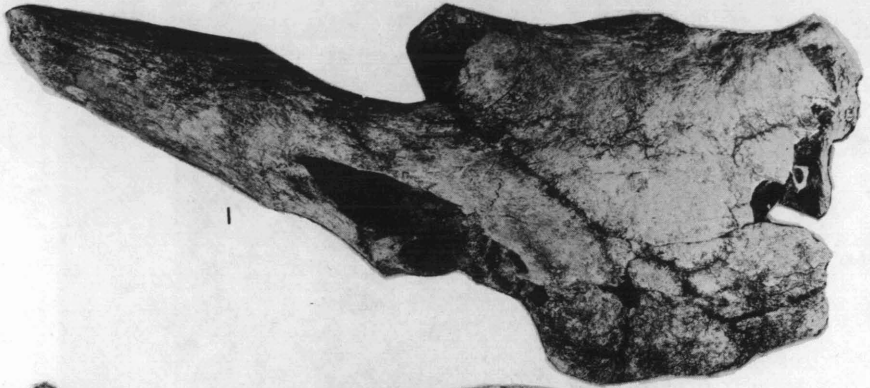
Photographs by Dick Vieth.

PLATE V

1

2

PLATE VI
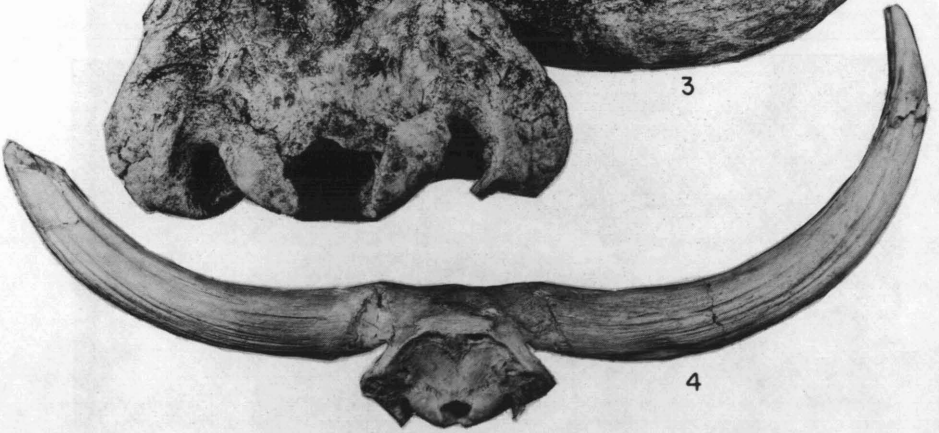
EXPLANATION OF PLATE VI

Bison (Bison) cf. *occidentalis* Lucas

FIG. 1. Dorsal view of posterior part of cranium, No. 49–76, with right horn core. Reduced.

FIG. 2. Anterior view of cranium. Reduced.

FIG. 3. Posterior view of cranium. Reduced.

Bison (Platycerobison) chaneyi Cook

FIG. 4. Posterior view of cranium, No. 49–33. Reduced.
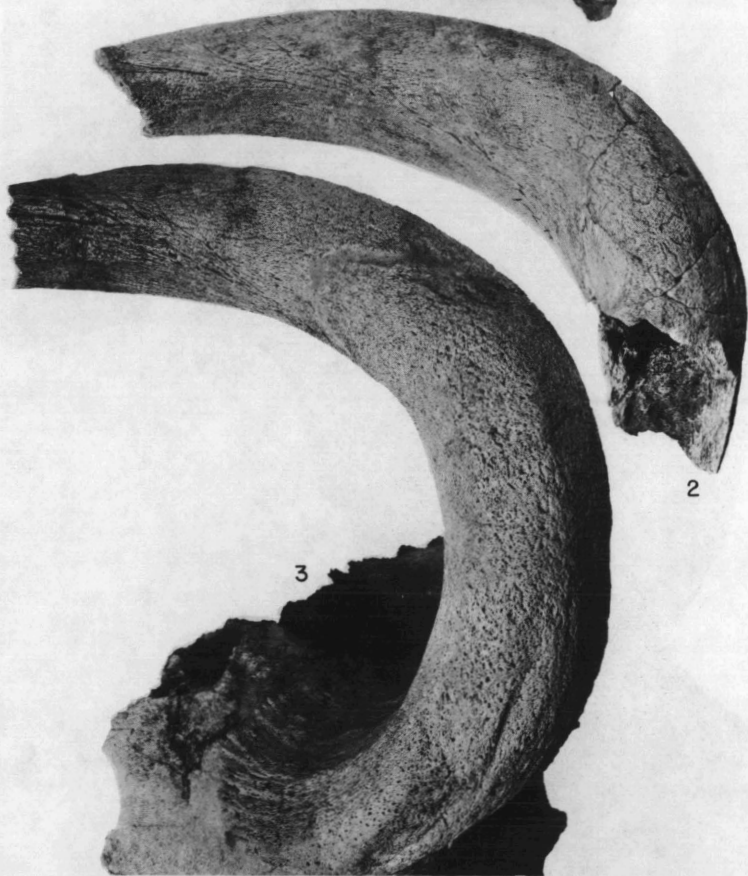
Photographs by Xavier Sivilla.

EXPLANATION OF PLATE VII

FIG. 1. *Preptoceras? mayfieldi* Troxell. Posterior view of holotype, No. 10920, Yale University, from Rock Creek, Texas. Reduced.

FIG. 2. *Euceratherium collinum* Furlong and Sinclair. Posterior view of No. 26, from Tequixquiac. Reduced.

PLATE VII

1

2

PLATE VIII

EXPLANATION OF PLATE VIII

FIG. 1. *Euceratherium bizzelli* Stovall, holotype No. 701, University of Oklahoma. Reduced.

FIG. 2. *Euceratherium collinum* Furlong and Sinclair. No. 47–1, part of a right horn core from Sonora Mexico. Reduced.

FIG. 3. *Euceratherium bizzelli* Stovall. Part of right horn core, No. 701, for comparison with that of *Euceratherium collinum,* No. 47–1. Reduced.

EXPLANATION OF PLATE IX

Euceratherium collinum Furlong and Sinclair

Restoration of the head, using the partial skull of the holotype of *Euceratherium bizzelli* Stovall as a guide.

Drawing by Carleton W. Angell.

PLATE IX