POST-PLEISTOCENE HORSES (EQUUS) FROM MÉXICO

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Abstract.—For more than a century many paleontologists, biologists, paleoecologists, and archaeologists have contended that Equus species (American horse) became extinct on the North American continent by about 13,000 calibrated years BP - all part of the Late Pleistocene (Ice Age) extinction event. The paleontological project presented here that focuses on Equus from Rancho Carabanchel, San Luis Potosí, México became chronologically intriguing to us in having the horse consistently radiometrically dating into the Holocene, well beyond the presumed extinction event. Our approach to this observation was to conduct successive radiocarbon dates (n=19) tied as closely as possible to fossil remains and to stratigraphic units. The remains of the extant horse, Equus caballus, were recovered only in the upper-most Unit I while the extinct Equus cf. mexicanus, E. cf. conversidens, and E. cf. tau were recovered from the underlying Units II – VI of the late Holocene to approximately 45,000 calibrated years ago. We discuss how our data adds to the growing information which implies that horses may have persisted in this region of México well after the classical Late Pleistocene extinction event. Our conclusions may well illustrate that the extinction episode was actually a process lasting well into the Holocene and was not the event that many paleoecologists and archaeologist envision.

Keywords: Quaternary, Holocene, extinction, Carabanchel

As the late Pleistocene (Rancholabrean Land Mammal Age, LMA; Bell et al. 2004) came to an end in North America, some 38 genera of mammals had vanished, both herbivores and carnivorans (Martin 1967, 2005; Koch & Barnosky 2006; Meltzer 2015; and references within). The majority of these taxa are considered megafauna (\geq 44 kg mass),

yet five genera are smaller, ≤44 kg (e.g., Aztlanolagus [Aztlan rabbit; Leporidae], Capromervx [diminutive pronghorn; Antilocapridae]). Typically listed among the late Pleistocene extinction participants in North America are the various species within the genus Equus, an important aspect to our data presented here. How, why, and precisely when these genera disappeared is still of debate with proposed extinction drivers to include (1) environmental modifications due to climate change (a complex amalgamation of temperature, precipitation, and seasonality shifts), (2) human induced impacts (including 'overkill'), or (3) some combination of the two (details in Koch & During the early phases of describing and Barnosky 2006). understanding the late Pleistocene extinctions, the process was labeled as an 'event', all happening within a geologically short period of time and completed by ~ 13,000 cal YBP (calibrated years before present; Martin 1967). With the increase in assessment of fossil localities over the past number of decades and with the advent of direct AMS radiocarbon dating, the time of extinction appears to be more of a 'process' – over a longer period of time, possibly spanning much of the Wisconsinan late glacial (Martin & Klein 1984). Yet the question still remains – did the extinction process progress into the Holocene?

With the increase in fossil sites and their detailed analyses, select megafaunal taxa are now known to have also survived the terminal extinction date of $\sim 13,000$ cal YBP in select regions of the northern hemisphere. The youngest age for *Mammuthus primigenius* (woolly mammoth) survival in eastern Siberia is 10,700 YBP (Nikolskiy et al. 2011). Small insular populations of *M. primigenius* are known to have survived as relicts on St. Paul Island (Alaska) until $\sim 5,600$ cal YBP (Graham et al. 2016; see also Veltre et al. 2008) and Wrangel Island (northeastern Siberia) until perhaps $\sim 4,020$ cal YBP (Vartanyan et al. 2008). *Bison priscus* (steppe bison) persisted in the southern Yukon until $\sim 6,000$ cal YBP (Zazula et al. 2017) with purported genetic data suggesting its survival to as recently as a few hundred years ago (Heintzman et al. 2017). Using ancient DNA from sedimentary deposits (*seda*DNA), the record of both *M. primigenius* and *Equus*

survived until \sim 7,000 cal YBP from interior Alaska and the Yukon, living in the Mammoth Steppe environment (Haile et al. 2009; Murchie et al. 2020, 2021). More and more evidence seems to imply that select megafaunal species may have persisted through the presumed extinction event, suggesting that the process progressed well into the Holocene (reviewed in Murchie et al. 2021). Important to the data presented here is the existence of data indicating the Holocene persistence of *Equus*, albeit in more northern latitudes. A major question continues as to whether Holocene persistence of *Equus*, and other now-extinct taxa persisted in more southern latitudes, hence our presentation here creating a paradigm shift.

At least nine megafaunal mammalian genera are well known survivors of the late Pleistocene extinction process in North America, including the herbivores *Alces* (moose; Cervidae), *Antilocapra* (pronghorn; Antilocapridae), *Bison bison* (bison; Bovidae), *Cervus* (wapiti; Cervidae), *Odocoileus* (deer, Cervidae), *Oreamnos americanus* (mountain goat; Bovidae), *Ovis* (bighorn; Bovidae); *Ovibos* (muskox; Bovidae), and *Rangifer* (caribou; Cervidae). The point to be made is that select taxa did not only make it through the extinction 'event' but still persist today with many of these occurring in more southern latitudes of North America. Within a few of these genera there are species that became extinct, such as with *Oreamnos harringtoni* and possibly within *Bison* and *Ovis*.

Here we present the data about fossils from one locality, Rancho Carabanchel (RC; also known locally as Rancho Córdova), San Luis Potosí, México. Sediments at RC provide a record of late Pleistocene megafaunal fossils interfacing with human artifacts in select stratigraphic layers. Fossils at RC were first discovered in 2016 by Juan Rojas, an amateur collector from the nearby city of Matehuala, who found a *Mammuthus* rib along with three articulated vertebrae (Torres-Roldán 2017). Later this find came to the attention of archaeologists at the Universidad Autónoma de San Luis Potosí (UASLP) as well as to researchers at the Instituto Nacional de Antropología e Historía (INAH) and at the Universidad Nacional Autónoma de México (UNAM), both

in México City. Subsequent investigation at the locality revealed archaeological as well as additional fossil specimens. Only an abstract has been published concerning this locality (Pérez-Roldán et al. 2019). While the topic of a Holocene occurrence of a presumed late Pleistocene-age extinct taxon is controversial, we feel that the data recovered from this fossil locality in northeastern Mexico deserves presentation to further the attention to the possibility that select megafaunal species did persist beyond the conventional late Pleistocene extinction event of $\sim 13,000$ cal YBP.

MATERIALS & METHODS

Locations.—Rancho Carabanchel is located near the municipality of Cedral, San Luis Potosí, Mexico at 23.8131° N, 100.7023° W on the regional plateau Altiplano Potosino, which measures on average about 2000 m above sea level (Figs. 1, 2). The general vegetation today consists of a high desert habitat, and includes many low shrubs, cacti, grasses, and relatively small trees, mostly mesquite (*Prosopis*). The site is a roughly circular depression approximately 25.0 m across and about 4.5 m to 5.0 m in depth.

Geology.—The overall geology of the region was presented by Cortés & Flores-Díaz (2012) who indicated that carbonate layers extend to a depth of about 7 m. The exposed stratigraphic layers (Fig. 3) represent predominantly spring and paludal deposits along with some shallow lacustrine deposition. While the exposed strata from which fossil specimens were collected and presented here show some variation, the major components consist of various forms of tufa (precipitated calcium carbonate), thus of the roughly 5 m of exposed stratigraphic units, all have a high carbonate signature. In several instances the exposed strata show some abrupt contact with overlying and underlying beds. In other instances the contacts are barely discernable. Based on repeated AMS 14C ages obtained throughout the section (see below),

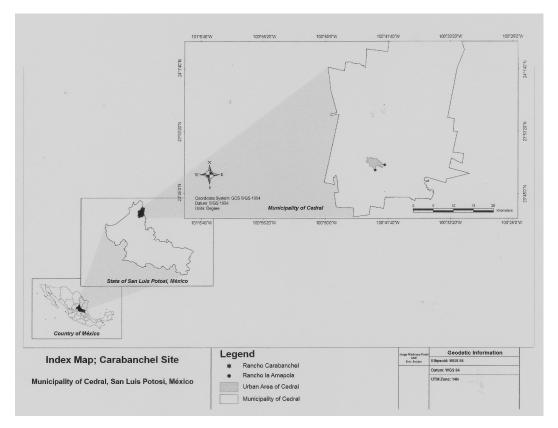


Figure 1. Index map showing location of both Rancho Carabanchel and Rancho la Amapola, San Luis Potosí, México.

there must be undetectable disconformities. Two paleosols were identified between the bottommost two strata.

Two charcoal (carbon) layers, about 2 cm each in thickness, are deposited within the thick tufa unit; these likely represent burned vegetation zones (Fig. 3). On the south wall of the excavation there is exposed a 2.5 cm thick carbonaceous mudstone seam which separates the main tufa unit from the overlying tan, calcareous silty mudstone. Charcoal fragments are present in all layers, many which are used to create a radiocarbon chronology throughout the section (see below, Table 1).

Chronology.—The entire thesis of this report about Holocene survival of *Equus* is tied to the chronology at the locality, thus the



Figure 2. Aerial photo of Altiplano Potosino, looking east, and graben containing Rancho Carabanchel.

greatest concern is how this chronology was constructed. The entire chronology was based on radiocarbon dating. Two radiocarbon laboratories were used for these analyses: Beta Analytic (Miami, Florida; Beta) and University of Arizona AMS Laboratory (Tucson, Arizona; AA). Their procedures for processing samples can be found at their web sites.

Fossil specimens.—All the Equus specimens mentioned and described in this paper are curated and cataloged at the Laboratorio de Arqueología de la Universidad Autónoma de San Luis Potosí. All bones and teeth collected at the RC quarry were measured with Vernier calipers using standard parameters and were photographed. Comparisons were made with similar specimens housed at the Natural History Museum of Los Angeles County and with those at the Laboratorio de Arqueozoología, Subdirección de Laboratorios y Apoyo Académico, Instituto Nacional de Antropología e Historía in México City. The material at the latter institution contains many Equus specimens from another site, Rancho la Amapola, located near RC (Fig.

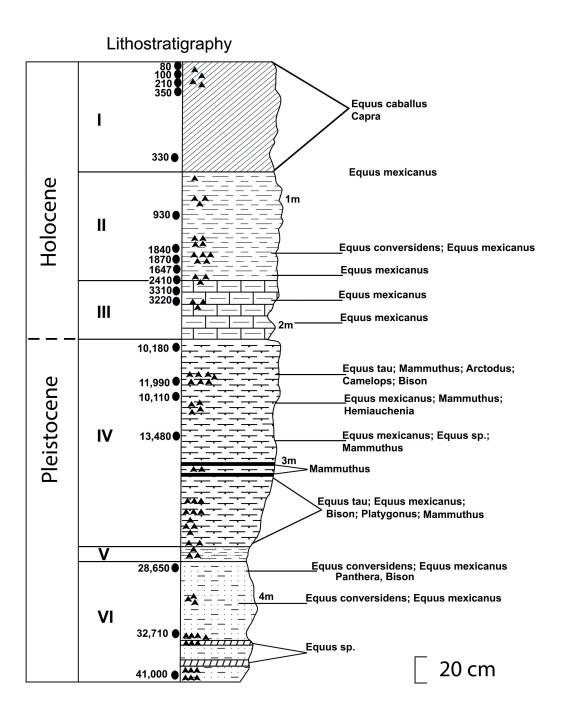


Figure 3. Schematic section of sedimentary units at Rancho Carabanchel, México. Solid black circles are radiocarbon samples (see Table 1 and text). Black triangles refer to location of *Equus* remains and radiocarbon dates as discussed in text. For simplicity of reading, *Equus* species designations leave out the notation 'cf.'.

Table 1. Radiocarbon chronology based on AMS analysis for stratigraphy and *Equus* remains from Rancho Carabanchel, México. Material assessed for the radiocarbon analysis is provided. Samples of *Equus* that did not provide sufficient collagen to produce an analysis are not reported, therefore, directly associated charcoal (or other material, see text) was used to develop a chronology. The taxon of *Equus* either used for the ¹⁴C analysis or recovered adjacent to the alternate radiocarbon sample is shown. Not all species of *Equus* (e.g., *E.* cf. *tau*) reported here are recovered directly with associated charcoal or other organic remains used for dating; thus their age is indicated indirectly by stratigraphy (Fig. 3). Identification details of *Equus* are provide in the text. Both conventional radiocarbon ages and the calibrated age ranges are given for each specimen, along with d13C analyses when provided. Samples are reported by depth of recovery. Abbreviations: A, Accelerator Mass Spectrometry Lab, University of Arizona, Tucson, Arizona; B, Beta Analytic, Miami, Florida. Cal YBP, calibrated years before present as ranges at 95% probability.

Material Analyzed	Taxon Associated with ¹⁴ C Sample	Lab & Number	¹⁴ C Age yr BP	d ¹³ C °/ ₀₀	Cal yr BP	Sample Depth (m)
Equus bone	E. cf. caballus	B 591840	80±30	-	Historic	Surface
Capra bone	Capra	B 512134	210±30	-9.6	216-144 Historic	Surface
Equus bone	E. cf. caballus	B 516199	100±20	-11.9	145-15 Historic	Surface
Equus bone	E. cf. caballus	В 543767	350±30	-	412-315 Historic	Surface
Equus bone	E. cf. caballus	B 591839	330±30	-	310-295 Historic	0.7
Charcoal	E.cf. mexicanus	B 520208	930±30	-23.1	925-785	0.9
Charcoal	Equus sp.	В 532075	1840±30	-23.4	1864-1708	1.4
Charcoal	E. cf. mexicanus & Equus sp.	B 515177	1870±30	-23.0	1877-1724	1.5
Charcoal	E. cf. mexicanus	A 111334	1647±57	-23.5	1697-1408	1.5
Wood	E. cf. mexicanus	B 543764	2410±30	-21.2	2498-2350	1.6

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Table 1. Cont.							
Material Analyzed	Taxon Associated with ¹⁴ C Sample	Lab & Number	Age yr BP	d ¹³ C °/ ₀₀	Cal yr BP	Sample Depth (m)	
Charcoal	E. cf. mexicanus	В 532076	3310±30	-23.9	3610-3458	1.7	
Charcoal	E. cf. mexicanus & E. cf. conversidens	B 512136	3220±30	-22.6	3494-3374	1.8	
Charcoal	E. cf. conversidens & Equus sp.	B 512137	10,180±40	-	12,055-11,706	2.1	
Aquatic Mollusk shell	E. cf. mexicanus	B 520762	11,990±40	-6.3	13,988-13,740	2.3	
Organic sediment	Equus sp.	B 543763	10,110±30	-17.1	11,842-11,602	2.5	
Charcoal	E. cf. mexicanus & Equus sp.	В 520207	13,480±50	-23.5	16,442-16,026	2.7	
Wood	E. cf. conversidens	B 515178	28,650±160	-23.2	33,328-32,047	3.8	
Organic sediment	E. cf. conversidens & E. cf. mexicanus	B 512138	32,710±190	-18.7	37,410-36,170	4.3	
Wood	Equus sp.	A 111486	41,000±1,300	-23.0	47,954-42,610	4.9	

1). Some Recent horse skeletal remains in the collections of Brigham Young University (Monte L. Bean Life Science Museum and the Geology Museum of Paleontology) were also used for comparative purposes.

Institutional abbreviations.-BYU, Brigham Young University, Provo, Utah, U.S.A.; INAH, Instituto Nacional de Antropología e Historía in México City, México; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.; UASLP Universidad Autónoma de San Luis Potosí, San Luis Potosí, México; USLPA Universidad Autónoma de San Luis Potosí, San Luis Potosí, México, Archaeological and Paleontological Collections. Additional abbreviations: L, length measurement; M, maxillary (upper) molar; m, mandibular (lower) molar; P, maxillary (upper) premolar; p, mandibular (lower) premolar; W, width measurement.

RESULTS & DISCUSSION

Chronology.—A total of 26 samples were analyzed to create the chronological sequence at RC (Table 1; Fig. 3). Of primary importance was to date *Equus* skeletal elements. Note that the ages presented in Table 1 include both the conventional radiocarbon ages and their calibrated ages. Those ages shown in Figure 3, for simplicity of reading, are only the conventional radiocarbon ages. Calibrated ages typically are not a specific age but are a range of possible ages.

Six samples of *Equus* bone/tooth did not contain enough collagen to produce an analysis for the entire sequence and therefore are not shown in Table 1. Four *Equus* samples did produce radiocarbon dates, however, these were all historic age *Equus caballus* elements found in the upper-most stratigraphic layer (Unit I; Fig. 3). An element of *Capra* (goat) from the surface also produced a historic radiocarbon age. These dates illustrate that Unit I (top 80 cm) shown in Figure 3 is all historic in age and possibly bioturbated to some extent but only within this uppermost unit. Only extant taxa are recovered in this stratigraphic layer, i.e., no *Mammuthus* or other megafaunal species from lower units, thus no major bioturbation.

Units II and III (down to just below 2.0 m depth; Fig. 3) contain no directly dated *Equus* elements (all specimens lacked sufficient collagen to produce radiocarbon analyses). To augment this chronological gap, charcoal, wood, organic sediment, and one freshwater clam shell were used. We completely agree with statements that an assessed charcoal

sample recovered adjacent to a skeletal element does not necessarily create a precise age for that vertebrate specimen. However, some radiocarbon dated charcoal samples were recovered from within millimeters of Equus bones. Return field trips to RC were conducted to obtain additional charcoal samples adjacent to Equus skeletal elements as shown in Table 1. Charcoal samples were recovered adjacent to Equus sp., E. cf. mexicanus, and E. cf. conversidens skeletal remains (see identification descriptions below). The seven samples from Units II and III imply a fairly consistent series of dates in stratigraphic order except for the sample AA-111334 (Table 1; Fig. 3; 1647 YBP) that appears to be out of stratigraphic order by two to three hundred years. The lowest two samples in this series indicate slight overlap in ages. As with Unit I, no extinct faunal remains such as Mammuthus or Camelops were recovered in Units II and III, thus, these upper Holocene-age units were not affected by bioturbation from the Pleistocene units IV, V, and VI below.

Below a depth of approximately 2 m the radiocarbon chronology and the faunal remains drastically change. At this depth the lithology changes to a tufa deposit (Fig. 3). Megafaunal remains include Equus sp., E. cf. tau, E. cf. mexicanus, E. cf. conversidens, Mammuthus, Camelops (extinct camel), Hemiauchenia (extinct llama), Bison (B. cf. latifrons, extinct large-horned bison), Platygonus (extinct peccary), and Arctodus (extinct short-faced bear). The radiocarbon ages (Table 1; Fig. 3) indicate that there is an unconformity at about 2 m depth with a lack of ages representing the middle and early Holocene, which implies either a lack of deposition or an erosional hiatus during this time interval. Radiocarbon ages indicate that the top of this unit, below the unconformity, represents the latest Pleistocene. Again, the ages are in fair stratigraphic order with the freshwater shell (Beta 520762) possibly causing some issues and maybe indicating slight bioturbation at about 2.5 m depth, but only within this stratigraphic layer (Unit IV). No charcoal, wood, or organic remains recovered from this unit produced radiocarbon ages representing the Holocene, thus implying no major bioturbation with the above Units I, II, or III.

At a depth of approximately 3.75 cm, the lithology again changes to a calcareous mudstone in Units V and VI. Radiocarbon analyses imply another possible unconformity (Fig. 3). The few radiocarbon analyses suggest that the time represented by the late and full Wisconsinan glacial are missing (Table 1; Fig. 3). Skeletal specimens of *Panthera* (extinct large cat) and *Bison* sp. were recovered along with *Equus* sp., E. cf. *conversidens* and *E*. cf. *mexicanus*.

Fossil specimens.—The following fossil material was recovered from the Rancho Carabanchel site:

Equus mexicanus Hibbard 1955 Equus cf. mexicanus

Referred Specimens.—Occiput (USLPA 018), upper left and right dentition, P3 – M3 (USLPA 012), mandible minus incisors (USLPA 039), P3 or P4 (USLPA 013), anterior 1/2 of a tibia (USLPA 025), upper cheek tooth (USLPA 041), upper molar (USLPA 043), M3 (USLPA 045), P2 – P4 (milk dentition, USLPA 005), p3 – 4 (milk dentition, USLPA 011), m3 (USLPA 014), m1 or m2 (USLPA 006, 007,015, 020), incisors (USLPA 016-017, 044), complete metacarpal (USLPA 038), fragmented metatarsal (USLPA 047), distal end of metapodial (USLPA 034), phalanx II (USLPA 022), and partial phalanx III (USLPA 024).

Hibbard (1955) reported three species of *Equus* found in the late Pleistocene Upper Becerra Formation in the Tequixquiac Valley of central México. With his analysis of the various *Equus* remains, he concluded with the naming of the new taxon *E. mexicanus* (holotype; 48 [HV-3], IGM 4009; Carranza-Castañeda & Miller 1987). The other forms at the locality were *E. conversidens* and *E. crenidens* (the latter from Azzaroli (1998), regarded as a doubtful species). Four upper cheek teeth (P3 – M2) of a young individual and a mandible containing p2 – m3 were questionably assigned by Hibbard (1955) to the new species. Apparently, all were not in close association. *Equus mexicanus* has been recognized as valid by most subsequent researchers (e.g.,

Winans 1985; Azzaroli 1998; Pichardo 2008; Alberdi et al. 2014). It represents the most common large Pleistocene equid in México, with a distribution that covers most of western North America.

Large equids from Pleistocene deposits in North America, as with smaller species of the same age, present problems regarding taxonomic validity. Azzaroli (1998) considered E. scotti (Gidley 1900) to be a synonym of E. excelsus (Leidy 1858). Leidy (1860, 1869) considered E. occidentalis to be in synonymy with his earlier named E. excelsus. Hibbard (1955) synonymized E. occidentalis (Leidy 1865) with E. mexicanus. Savage (1951), Miller (1971), and others considered E. occidentalis to be a nomen vanum. However, Eric Scott (pers. comm. 2018) regarded both E. scotti and E. occidentalis as valid species. Since Hibbard named E. mexicanus in 1955, most workers have considered this the dominant (if not the only) large Pleistocene equid in México. It is beyond the intent of this paper to go into detail on all large North American Pleistocene horses that have been named. We prefer to use E. cf. mexicanus for the large horse found at RC. It has been identified at many fossil sites throughout México as shown in the literature. With further research, though, this too may change.

Both dental and postcranial elements of E. cf. mexicanus were recovered from RC. This species clearly exceeds the other two known species from this site in size. A cheek- tooth series is shown in Figure 4 (USLPA 012, P3 – M3) and a nearly complete right dentary (USLPA 039, p2 - m3) is shown in Figure 5. Unlike other bones from the site, this latter specimen shows evidence of weathering and compaction. It also can be seen that some crushing took place. The dentary with dentition, along with several isolated lower cheek teeth, were compared to a referred E. mexicanus jaw that Hibbard (1955) briefly described in the discussion of his new species. The Hibbard specimen (Specimen No 401 (1)) shows tiny plicaballinids on the p3 through m3 and a longer isthmus than in USLP 039. Some of the isolated lower cheek teeth from RC show identical features with Specimen 401 (1). Tooth sizes are comparable in both cases along with dental wear patterns. The nearly complete upper left and right cheek tooth series (P3 – M3) from RC (USLPA 012) can reasonably be assigned to E. cf. mexicanus based on

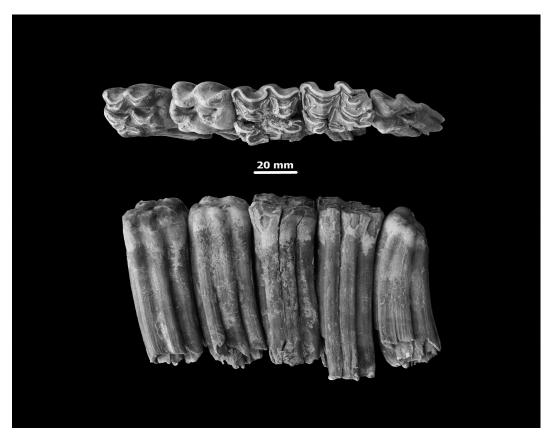


Figure 4. Left P3-M3 cheek tooth series of *Equus* cf. *mexicanus* (USLPA 012). A: occlusal view, B: lingual view.

similar size and occlusal wear patterns between the holotype and USLPA 012 (Table 2).

Skull fragments were discovered adjacent to the upper tooth series (USLPA 012) but were too small to identify as belonging to this individual. Overall, the dentitions of Hibbard's (1955) holotype and specimen USLPA 012 above show reasonably close similarity considering the former represents an old individual and the latter a young one. Sizes and dental wear patterns exist within close limits. The holotype of *E. mexicanus* exhibits a plicaballin distinctly only on P4. None are present on any of USLPA 012 cheek teeth. Both have elongate protocones. A noted difference lies in the pattern of fossettes. The holotype has distinct fossette plications while they are minimal in the

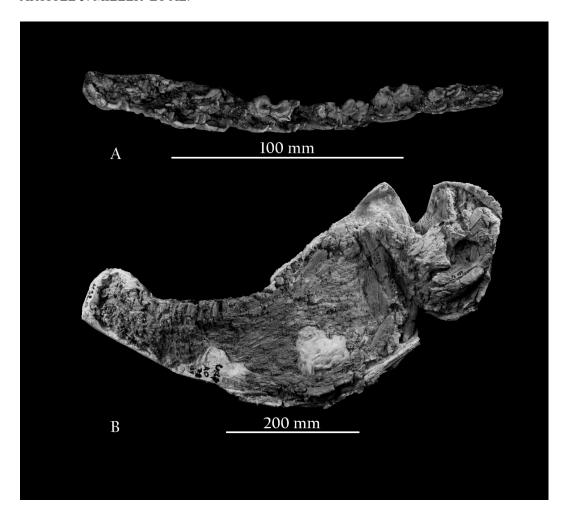


Figure 5. Right dentary with p2 – m3 of *Equus* cf. *mexicanus* (USLPA 039). A: occlusal view, B: lingual view.

horse from RC. Some differences are to be expected because of the difference in ontogenetic ages as well as those due to individual variation. However, they do not seem to exceed those within a given species of *Equus*.

Equus conversidens Owen, 1869 Equus cf. conversidens

Referred Specimens.—Upper left and right dentition, P2 – M3 (USLPA 036), P2 (USLPA 002), P3 – P4 (USLPA 051), M1 or M2 (USLPA 003), M2 – M3 (USLPA 004), nearly complete right dentary

Table 2. Measurements (mm) of the maxillary cheek teeth of Rancho Carabanchel specimen (USLPA 012) in comparison with the holotype of *Equus mexicanus* (Hibbard, 1955). L, length; W, width.

Occlusal	Holotype Equus mexicanus	Rancho Carabanchel
Measurement	48 (HV-3); GIM 4009	USLPA 012
P3-M3 L	148.0	147.0
M1-M3 L	88.0	86.0
P3 L	31.9	33.9
P3W	34.0	27.2
P4 L	30.0	32.7
P4 width	32.0	31.7
M1 L	26.9	32.4
M1 W	29.5	32.5
M2 L	28.8	31.8
M2 W	30.5	29.0

without dentition (USLPA 040), m3 (USLPA 008), proximal half of a scapula (USLPA 046), astragalus (USLPA 027), and proximal 1/3 of a metatarsal (USLPA 030).

Since it was first named by Owen in 1869, *Equus conversidens* has proven to be a much-discussed equid from the Pleistocene of North America. It represents one of the most numerous species which occurred from Central America (Bravo-Cuevas et al. 2011) to Canada (Barrón-Ortiz et al. 2017). As with many other Pleistocene species, it has a complicated history. Cope (1884, 1893) regarded *E. conversidens* to be a synonym of *E. tau*. But Hibbard (1955) synonymized *E. tau* with *E. conversidens*; then Winans (1989) as well as MacFadden (1992) and others challenged the validity of the holotype of *E. conversidens*. However, most researchers of the past few decades have referred to *E. conversidens* as a valid species (e.g., Scott 1990; Azzaroli 1998; Bravo-Cuevas et al. 2011; McHorse et al. 2016; Marin-Leyva et al. 2018).

There is a wide range of physical characters that has been reported in the literature for this taxon. For example the cheek teeth have been given as possessing complex enamel folding (Owen 1869, holotype; Hibbard 1955; Azzaroli 1998). Yet other authors have reported that the cheek teeth have simple or no enamel folding or plications (Dalquest 1979; Miller et al. 2008; Bravo-Cuevas et al. 2011). For the present

study the extensive collection of E. conversidens from San Josecito Cave, Nuevo Léon, México, housed at the LACM, was examined. It consists of the largest assemblage of specimens anywhere representing this species. Based on left astragali a minimum of 145 individuals is represented. Enamel patterns of cheek teeth are mostly simple containing few to no plications. Tooth sizes vary significantly, often from one side of the jaw to the other. This was also seen in RC specimen USLPA 036. The antero-posterior occlusal length of the left P2 measures 23.0 mm and the transverse width 19.2 mm. The right moiety, though, has an antero-posterior length of 31.6 mm and a transverse width of 22.3 mm. It should be pointed out that the USLPA 036 tooth sizes in general fit well within the variation noted for E. conversidens viewed at the above museum. These measurements are also compatible with the holotype measurements given by Hibbard (1955) and with other E. conversidens specimens (Dalquest & Hughes 1965; Bravo-Cuevas et al. 2011).

Equus conversidens has been considered a small horse by some (Hibbard 1955; Scott 2004) and, yet, medium-sized by others. Mooser & Dalquest (1975) indicate that the small size of Equus conversidens is its best identifying character. However, other authors regard this species to be of medium size (Alberdi et al. 2003; Melgarejo-Damián & Montellano-Ballesteros 2008; Marin-Leyva et al. 2019). Confusion persists. A comparison of skeletal elements shows that *E. conversidens* was about the same size as the zebra, E. burchellii. Barrón-Ortiz et al. (2017) suggest that there is a south to north cline in the degree of metapodial slenderness for Equus conversidens, such that specimens from San Josecito Cave (Nuevo León, Mexico) have stout metapodials, specimens from Natural Trap (Wyoming) have slender metapodials, and specimens from Dry Cave (New Mexico) have intermediate morphologies. Baskin & Mosqueda, (2002) state that this species had normal length metapodials. Dalquest & Hughes (1965) reported that a partial skeleton of E. conversidens had short, stout limb bones. Lundelius & Stevens (1970) indicated that this equid had short and broad metacarpals. In our study of the extensive collection of E. conversidens specimens at the LACM we noted that all metapodials

were only of moderate length and stout (Table 4). They could not be considered representative of a stilt-legged horse.

Alberdi et al. (2014) erected a new species of *Equus*, *E. cedralensis*, on material collected at Rancho la Amapola in Cedral, San Luis Potosí, México (Fig. 1). The holotype of the new species (DP-2675) consists of a complete right dentary with an attached portion of the left symphysial region. Both contain essentially complete dentitions. Paratypes include upper and lower dentitions as well as some postcranial bones. These fossils, stored as part of the paleontological collections INAH in México City, were studied by three of the present authors. It was found that much overlap in size and tooth patterns do exist between the E. cedralensis holotype, paratypes, and topotypes and material identified as E. conversidens from RC. Resemblances of this material to that in México City suggests E. cedralensis could be synonymous with E. conversidens. Alberdi et al. (2014) in their naming of this species indicate that the upper and lower cheek teeth are morphologically similar to other *Equus* species (*E. conversidens* and *E.* mexicanus) observed at Rancho la Amapola in Cedral. Barrón-Ortiz et al. (2017:30) stated that, "... several of the specimens that Alberdi et al. (2014) identify as E. cedralensis we identify here as E. conversidens." Thus, it appears that the use of E. cedralensis should be considered provisional.

Equus tau Owen, 1869 Equus cf. tau

Referred Specimens.—Partial right dentary with complete cheek tooth series, p2-m3 (USLPA 001), left cheek tooth series of juxtaposed teeth, p2 — m3 (USLPA 035), phalanx II (USLPA 019a), phalanx III (USLPA 019b), distal 2/3 of a tibia (USLPA 028), proximal 2/3 of a metacarpal (USLPA 029), proximal 1/2 of a metacarpal (USLPA 031), distal 1/3 of a metacarpal (USLPA 032), distal 1/2 of a metacarpal (USLPA 033).

Table 3. Measurements (mm) of lower cheek teeth of *Equus tau* from Dalquest (1977) with those from Rancho Carabanchel (USLPA 001). L, length; W, width.

Occlusal Measurement	Aguascalientes Fauna Cedazo 62	Rancho Carabanchel USLPA 001		
p2-m3 L	118.8	113.0		
p2 L	24.7	18.9		
p2 W	11.4	15.6		
p3 L	20.2	18.8		
p3 W	12.6	13.0		
p4 L	19.8	20.0		
p4 W	12.6	12.1		
m1 L	19.4	16.0		
m1 W	11.2	13.9		
m2 L	17.2	16.5		
m2 W	11.2	12.9		

Equus tau (as with E. conversidens, both named by Owen in 1869) has a complex and confusing history. The complications started with Owen erecting these species based on casts and photographs, and having never seen the actual specimens. Owen's (1869) information given for E. tau lacks specimen numbers, a distinct holotype, and a scale for the photograph of the holotype consisting of P3 – M3 tooth series. What probably is a paratype or a topotype is composed of lower cheek teeth, p2 - p4. These appear to be deciduous premolars as shown in a photo. Owen commented that teeth of his newly named horse were much smaller than corresponding teeth of E. conversidens.

Dalquest (1977, 1979) indicated that a major character of E. tau is its small size and that it was the smallest of North American Pleistocene horses. He further stated that the length of upper and lower cheek tooth rows ranged from about 120 – 135 mm. Both cheek tooth rows of E. cf. tau from RC typically measure less than the lowest measurement given by Dalquest (1979) (Table 3). In specimen USLPA 001 the p2 – m3 series has a length of 113 mm, and that for USLPA 035 is 111 mm. Thus, based on size alone the RC specimens reasonably can be assigned to Equus tau. A competing Pleistocene species for small size is *Equus francisci*. Hay (1915) named this equid based on a partial skeleton recovered in Wharton County, Texas. The skeleton was fragmented

Table 4. Measurements (cm) of *Equus* spp. metapodials from Rancho Carabanchel, México. Taxon assignments are all 'cf.' (see text). Abbreviations; Adu, adult, A/p, greatest anterior-posterior; Ds, distal; Mc, metacarpal; Mt, metatarsal; Pr-ds, greatest proximal-distal; Pr, proximal; Tr, greatest transverse across epiphysis.

Element	Adu Mc	Adu Mc	Adu Mc	Adu Mc	Adu M?	Adu Mc	Adu Mt
Taxon	E. tau	E. tau	E. tau		E. mexicanus	E. mexicanus	E. conversidens
USLPA Specimen Number	029	031	032	033	034	038	030
A/p	2.46	2.68	2.62	2.70	4.00	Pr: 3.11 Ds: 3.28	3.83
Tr	3.57	3.20	3.20	3.69	5.30	Pr: 4.79 Ds: 5.18	4.11
Pr-ds Notes	13.5 Pr ^{2/3}	10.4 Pr ^{1/2}	10.2 Ds ^{1/3}	11.5 Ds ^{1/2}	7.6 Ds end	22.5 Complete	$7.7 ext{Pr}^{1/3}$

upon discovery. Apparently the broken metapodials when restored were made too short.

In a reevaluation of *E. francisci*, Lundelius & Stevens (1970) concluded that the metapodials were significantly longer than originally reported, making it a stilt-legged species of equid. We found in our study here that the upper and lower dentitions of the holotype were not well diagnosed by Hay (1915). However, the anterior-posterior length of the lower molar series was given as 66 mm. While those in the RC molar series USLPA 001 is 55.5 mm (Fig. 6), and that of USLPA 035 is 55.7 mm. We feel that it will take recovery of complete metapodials of the diminutive horse from RC for us to be certain of its identification. Unfortunately, the dentitions of both USLPA 001 (Fig. 6) and USLPA 035 are extremely worn. No meaningful characters can be discerned.

As discussed above several authors have stated that dental patterns in Pleistocene equid species are variable and not necessarily reliable in identifications (e.g., Harris & Porter 1980; MacFadden 1992; Alberdi et al. 2014). The few leg and foot bones referred here to E. *tau* are all distinctly small when compared to the other two horses at RC (Fig. 7).

ARTICLE 5: MILLER ET AL.

Pleistocene horses.-A multitude of articles have been published concerning fossil Equus. Differences of opinion regarding the ancestry of this genus have proliferated (Matthew 1924; Matthew & Stirton 1930; Stirton 1940; Lance 1950). With further writings the issue became somewhat more complex (Quinn 1955; Skinner and Hibbard 1972; Dalquest 1978). Most of the more recent authors regard Dinohippus mexicanus as the probable immediate ancestor to Equus (MacFadden 1984; Dalquest 1988; Carranza-Castañeda et al. 1998, 2003; Carranza-Castañeda 2019). There are specimens in the Tecolotlán Basin of central México that demonstrate intermediate characters between Dinohippus mexicanus and Equus simplicidens (Carranza-Castañeda & Miller pers. observ.). The transition between these two taxa occurred in very latest Hemphillian LMA to earliest Blancan LMA (~4.0 Ma). The apparent earliest recognized species of Equus is E. simplicidens from the Hagerman beds in Idaho (Savage 1951; Lindsay et al. 1980) and from Baja California (Miller 1980).

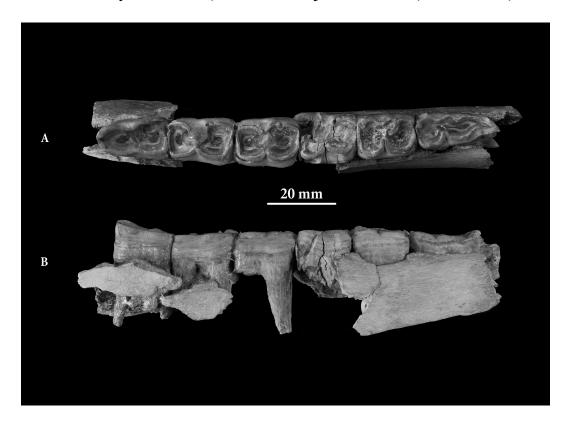


Figure 6. Right dentary of Equus cf. tau (USLPA 001). A: occlusal view, B: lingual view.

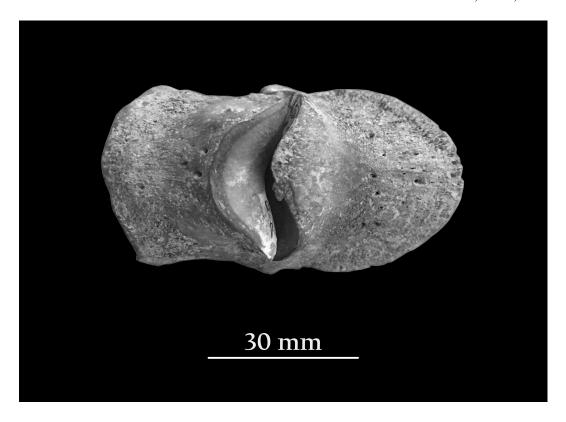


Figure 7. Anterior view of Phalanx II and III of *Equus* cf. *tau* (USLPA 012) showing minute size.

During the Pleistocene the genus *Equus* was probably the most common large land mammal in North America. Abundance of fossils of this taxon might be part of the problem in species' recognition as so many intermediate conditions exist. In North America most Pleistocene *Equus* fossils have been recovered in the central and western portions of the continent, from southern México to Alaska. Much of the history of *Equus* relates to fossils found in México where 26 species have been reported and holotypes of 12 species have been named (Mooser 1959; Alberdi et al. 2003, 2012, 2014; Melgarejo-Damián & Montellano-Ballesteros 2008; Priego-Vargas et al. 2016).

Most researchers agree that the status of valid Pleistocene *Equus* species exists in a great state of confusion (e.g., Savage 1951; Miller 1971; Miller et al. 2008; Barrón-Ortiz et al. 2017, among others). Harris & Porter (1980) as well as others have opined that at least 50 species

can be found in the literature. Current workers admit that this number is far too high but without agreement on how many have validity. Dental traits are some of the main characters used to determine the species of *Equus*. And, as expected, teeth are overwhelmingly the most common fossil of *Equus* found at RC.

Shape, size, and occlusal wear patterns constitute the basis for most species identifications. More and more studies find a significant overlapping of dental characters (e.g., Gidley 1901; Barrón-Ortiz et al. 2008, 2014, 2017; Melgarejo-Damián & Montellano-Ballesteros 2008). Barrón-Ortiz et al. (2008:335) stated that, "The occlusal pattern of the cheek teeth has traditionally been one of the most widely used features to determine equid species ... Nevertheless, its large ontogenetic variation and subjective assessment of characters has diminished its reliability." Geometric morphometrics were used in studies of *Equus* by Barrón-Ortiz et al. (2017) and Cucchi et al. (2017) which allows to avoid the subjectivity in assessment of dental traits.

Weinstock et al. (2005) suggested that possibly only two quite variable species existed, a caballine and a stilt-legged stenonine. To us, this seems unlikely, though, that there were only two valid Late Pleistocene species in North America. Significant size differences alone seem to argue against this. Several authors have indicated that at least three Pleistocene *Equus* species existed at single locality (Dalquest & Schultz 1992; Scott 2004; Alberdi et al. 2014). At RC specimens of a large, medium, and very small-sized equid have been collected at a geographically and chronologically restricted site. The species identifications, as described above, though, must be considered tentative in view of the still confused status concerning which ones are valid. Recent studies have indicated that Pleistocene *Equus* species determined by currently available DNA data are far fewer than those identified on morphological grounds (Barrón-Ortiz et al. 2017).

Pleistocene horse species have also been distinguished based on their size, as well as on skull and dental characters. The problem with this is that small, medium, and large size introduces more subjectivity into the analysis. Forsten (1987) did attempt to quantify these terms but only gave parameters based on metapodials and the first phalanx, albeit, she only defined "small-sized" equids in this way. Different interpretations of size and of dental characters abound in the literature. These differences of opinion help to explain the on-going confusion in identifying Pleistocene horse species. A further complicating factor in this dilemma is the naming of a new genus, a stilt-legged horse from the Pleistocene, *Haringtonhippus* (Heintzman et al. 2017). However, Barrón-Ortiz et al. (2019) based on their research suggested that this genus should be regarded as a synonym of *Equus*. Other researchers are hesitant to accept the new genus as valid pending additional analyses.

CONCLUSIONS

For more than a century most paleontologists, biologists, and archaeologists have contended that *Equus* became extinct on the North American continent by about 13,000 cal YBP (Broughton & Weitzel 2018), to about 10,000 YBP (MacFadden 1992), or even to roughly 8,000 YBP (Churcher & Stalker 1970). Many authors, however, do not attempt to list a Last Appearance Date in years for *Equus* in North America, but only indicate that they became extinct at the conclusion of the Pleistocene Epoch, end of the Rancholabrean LMA, ~12,000 years ago.

A small contingent of researchers has held the opinion that *Equus* survived well beyond the close of the Pleistocene (Rancholabrean) in North America. Our paleontological project that focused on horses from RC became chronologically interesting to us in having *Equus* radiometrically dating well into the Holocene so our approach was to conduct successive radiocarbon dates tied as closely as possible to fossil remains and to stratigraphic units (Table 1; Fig. 3). The lower jaw of *Equus* cf. *mexicanus* (USLPA 039) was recovered from the same stratigraphic layer with human artifacts. These lithic artifacts will be presented elsewhere. Other researchers in México have indicated the contemporaneity of extinct megafaunal species with humans (e.g., Heilprin 1891; Mercer 1896; Irwin-Williams 1967; Pichardo 2000, 2001, 2004, 2008). We feel that each locality and association of

Holocene-age *Equus* needs to be fully evaluated on its own merits, hence, our presentation here for one such locality in northern México.

The remains of *Equus* that we recovered from RC from multiple stratigraphic layers all with associated radiocarbon dates, all in a fair stratigraphic continuum (Fig. 3), and showing no mixing between geological units imply that horses may have persisted in this region of México well after the classical late Pleistocene extinction time. As seemingly an incongruous data set as compared to the accepted extinction hypothesis, our data here from RC appear to be adding to a growing set of data that the late Pleistocene extinction was more a process (over many thousands of years) rather than the typicallyaccepted and presumed extinction event. We suggest that researchers view our data set, as well as others, as a developing hypothesis, which is testable rather than just avoided. We also suggest that with the continued testing with different dating systems be utilized (e.g., Optically Stimulated Luminescence, Cosmogenic, among others, see Noller et al. 2000) in combination with the often-used radiocarbon dating to determine which chronology best fits the data analyses such as conducted at the fossil site of Térapa in Sonora, México (Bright et al. 2010) and elsewhere in northern México.

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LITERATURE CITED

- Alberdi, M. T., J. Arroyo-Cabrales & O. Polaco. 2003. Cuántas especies de caballo hubo en una sola localidad del Pleistoceno Mexicano? Rev. Esp. Paleontol. 18:205–212.
- Alberdi, M. T., J. Arroyo-Cabrales & O. Polaco. 2012. Cuantas especies de caballo hubo en una sola localidad del Pleistoceno Mexicano? Pp. 195–206 *in* Un sitio arqueológico-paleontológico pleistocénico-holocénico con restos de actividad humana (L.E. Mirambell, ed.), Inst. Nac. Antropol. Hist. México City, México. Ser. Memoría.
- Alberdi, M. T., J. Arroyo-Cabrales, A. H. Marin-Leyva & O. Polaco. 2014. Study of Cedral horses and their place in the Mexican Quaternary. Rev. Mex. Ciencia. Geol. 31:221–237.
- Azzaroli, A. 1998. The genus *Equus* in North America The Pleistocene species. Palaeontograph. Ital. 85:1–60.
- Barrón-Ortiz, C. I., G. Riva-Hernández & R. Barrón-Corvera. 2008. Morphometric analysis of equid teeth using a digital image processor: A case study of the Pleistocene Cedazo local fauna equids, México. Rev. Mex. Ciencia. Geol. 25:334–345.
- Barrón-Ortiz, C. I., J. M. Theodor & J. Arroyo-Cabrales. 2014. Dietary resource partitioning in the Late Pleistocene horses from Cedral, north-central México: Evidence from the study of dental wear. Rev. Mex. Ciencia. Geol. 31:260–269.
- Barrón-Ortiz, C. I., A. T. Rodrigues, J. M. Theodor, B. P. Kooyman, D. Y. Yang & C. F. Speller. 2017. Cheek tooth morphology and ancient mitochondrial DNA of late Pleistocene horses from the western interior of North America: Implications for the taxonomy of North American Late Pleistocene *Equus*. PLoS One: https://doi.org/10.1371/journal.pone.0183045, 1–39.

- Barrón-Ortiz, C. I., L. S. Avilla, C. N. Jass, V. M. Bravo-Cuevas, H. Machado & D. Mothé. 2019. What is *Equus*? Reconciling taxonomy and phylogenetic analyses. Front. Ecol. Evol. 7, 343:1–39; https://doi.org/10.1371/journal.pone.0183045.
- Baskin, J. A. & A. E. Mosqueda. 2002. Analysis of horse (*Equus*) metapodials from the Late Pleistocene of the Lower Nueces Valley, South Texas. Tex. J. Sci. 54:17–26.
- Bell, C. J., E. L. Lundelius, A. D. Barnosky, R. W. Graham, E. H. Lindsay, D. R. Ruez, H. A. Semken, S. D. Webb & R. J. Zakrzewski. 2004. The Blancan, Irvingtonian, and Rancholabrean Mammal Ages. Pp. 232–314, *in* Late Cretaceous and Cenozoic mammals of North America (M. O. Woodburne, ed.), Columbia Univ. Press, New York, 391 pp.
- Bravo-Cuevas, V. M., E. Jiménez-Hidalgo & J. Priego-Vargas. 2011. Taxonomía y habito alimentario de *Equus conversidens*(Perissodactyla, Mammalia) del Pleistoceno Tardío (Rancholabreano) de Hidalgo, Centro de México. Rev. Mex. Ciencia. Geol. 28:65–82.
- Bright, J., D. S. Kaufman, S. L. Forman, W. C. McIntosh, J. I. Mead & A. Baez. 2010. Comparative dating of a bison-bearing late-Pleistocene deposit, Térapa, Sonora, México. Quat. Geochron. 5:631–643.
- Broughton, J. M. & E. M. Weitzel. 2018. Population reconstructions for humans and megafauna suggest mixed causes for North American Pleistocene extinctions. Nat. Commun. 9, 5441:1–12.
- Carranza-Castañeda, O. 2019. *Dinohippus mexicanus* (Early-Late, Late and Latest Hemphillian) and the transition to genus *Equus* in Central México faunas. Front. Earth Sci 7, 89:1–16.
- Carranza-Castañeda, O. & W. E. Miller. 1987. Rediscovered type specimens and other important published Pleistocene mammalian fossils from central México. J. Vertebr. Paleontol. 7:335–341.
- Carranza-Castañeda, O, Miller, W. E. & B. J. Kowallis. 1998. New vertebrate faunas from the Transmexican Volcanic Belt, Central México, J. Vertbr. Paleontol. 18(3):31.
- Carranza-Castañeda, O., W. E. Miller & B. J. Kowallis. 2003. Relevance of the Late Tertiary mammalian faunas in central México, and the Great American Biotic Interchange. Geol. Soc. Am., Cordilleran Section, Abstr. Progr. 35:68.
- Churcher, C. S. & A. M. Stalker. 1970. A late, postglacial horse from Pashley, Alberta. Can. J. Earth Sci. 7:1020–1026.
- Cope, E. D. 1884. The extinct Mammalia of the Valley of México. Proceed. Am. Philoso. Soc. 22:1–23.
- Cope, E. D. 1893. A preliminary report on the vertebrate paleontology of the Llano Estacado. Geol. Soc. Tex., 4th Ann. Rep., 1892. 137 pp.
- Cortés, M. R. & A. Flores-Diaz. 2012. La geología del área de Cedral. Pp. 21–30 *in* Un sitio arqueológico-paleontológico pleistocénico-holocénico con restos de actividad humana. Mirambell, L.E., (coordinadora). Inst. Nac. Antropol. Hist. México City, México. Ser. Memoría.
- Cucchi, T. A. Mohaseb, S. Peigné, K. Debue, L. Orlando & M. Mashkour. 2017. Detecting taxonomic and phylogenetic signals in equid cheek teeth: towards new palaeontological and archaeological proxies. R. Soc. Open Sci. 4:160997
- Dalquest, W. W. 1977. *Equus tau* Owen from the Pleistocene of Mitchell County, Texas. Tex. J. Sci. 29:141.
- Dalquest, W. W. 1978. Phylogeny of American horses of Blancan and Pleistocene age. Ann. Zool. Fennici 15:191–199.

- Dalquest, W. W. 1979. The little horses (genus *Equus*) of the Pleistocene of North America. Am. Midl. Nat. 101:241–244.
- Dalquest, W. W. 1988. *Astrohippus* and the origin of Blancan and Pleistocene horses. Occas. Pap. Mus. Tex. Tech Univ. 116:1–23.
- Dalquest, W. W. & J. T. Hughes. 1965. The Pleistocene horse *Equus conversidens*. Am. Midl. Nat. 74:408–417.
- Dalquest, W. W. & G. E. Schultz. 1992. Ice Age mammals of northwestern Texas. Midwestern State Univ. Press, Wichita Falls, Tex., 309 pp.
- Forsten, A. 1987. The small caballoid horse of the upper Pleistocene and Holocene. Zool. Inst., Univ. Helsinki. 105:161–176.
- Gidley, J. W. 1900. A new species of Pleistocene horse from the Staked Plains of Texas. Bull. Am. Mus. Nat. Hist. 13:111–116.
- Gidley, J. W. 1901. Tooth characters and revision of North American species of the genus *Equus*. Bull. Am. Mus. Nat. Hist. 14:91–141.
- Graham, R. W., S. Belmecheri, K. Choy, B. J. Culleton, L. J. Davies, D. Froese, P. D. Heintzman, C. Hritz, J. D. Kapp, L. A. Newsom, R. Rawcliffe, E. Saulnier-Talbot, B. Shapiro, Y. Wand, J. W. Williams & M. J. Woolier. 2016. Timing and causes of mid-Holocene mammoth extinction on St. Paul Island, Alaska. Proc. Natl. Acad. Sci. 113:9310–9314.
- Haile, J., D. G. Froese, R. D. E. MacPhee, R. G. Roberts, L. J. Arnold, A. V. Reyes, M. Rasmussen, R. Nielsen, B. W. Brook, S. Robinson, M. Demuro, M. T. P. Gilbert, K. Munch, J. J. Austin, A. Cooper, I. Barnes, P. Möller & E. Willerslev. 2009. Ancient DNA reveals late survival of mammoth and horse in interior Alaska. Proc. Natl. Acad. Sci. 106(52):22352–22357.
- Harris, A. & L. Porter. 1980. Late Pleistocene horses of Dry Cave, Eddy County, New México. J. Mammal 61:46–65.
- Hay, O. P. 1915. Contributions to the knowledge of the mammals of the Pleistocene of North America. Proc. U.S. Natl. Mus. 48:515–574.
- Heilprin, A. 1891. Geological researches in Yucatan. Proc. Acad. Nat. Sci. Philadelphia 42:136–158.
- Heintzman, P. D., G. D. Zazula, R. D. E. MacPhee, E. Scott, J. A. Cahill, B. K. McHorse, J. D. Kapp, M. Stiller, J. J. Wooller, L. Orlaneintzmando, J. Southon, D. G. Froese & B. Shapiro. 2017. A new genus of horse from Pleistocene North America. eLife 6. doi:10.7554/eLife.29944.
- Hibbard, C. W. 1955. Pleistocene vertebrates from the Upper Becerra (Becerra Superior) Formation, Valley of Tequixquiac, México, with notes on other Pleistocene forms. Contrib, Mus. Paleont., Univ. Michigan 12:47–96.
- Irwin-Williams, C. 1967. Associations of early man with horse, camel and mastodon at Hueyatlaco, Valsequillo (Puebla, México). Pp 337–347, *in* Pleistocene Extinctions, the Search for a Cause (P.S. Martin and H.E. Wright, eds.), Yale Univ. Press, New Haven, Connecticut, 453 pp.
- Koch, P. L. & A. D. Barnosky. 2006. Late Quaternary extinctions: state of the debate. Annu. Rev. Ecol. Evol. Syst. 37:215–250
- Lance, J. F. 1950. Paleontología y estratigrafía del Plioceno de Yepómera, Estado de Chihuahua 1 parte: Equidos, except *Neohipparion*. Univ. Nac. Autónoma México, Inst. Geol. Boletín No. 54:1–81.

- Leidy, J. 1858. Notice of remains of extinct Vertebrata from the valley of the Niobrara River, collected during the exploring expedition of 1857, in Nebraska. Proc. Acad. Nat. Sci. Philadelphia 1858:20–29.
- Leidy, J. 1860. Description of vertebrate fossils. Holme's Post-Pliocene Fossils of South Carolina. 99–122.
- Leidy, J. 1865. Bones and teeth of horses from California and Oregon. Proc. Acad. Nat. Sci. Philadelphia 1865:94.
- Leidy, J. 1869. The extinct mammalian fauna of Dakota and Nebraska. J. Acad. Nat. Sci. Philadelphia 7:1–472.
- Lindsay, E. H., N. D. Opdyke & N. M. Johnson. 1980. Pliocene dispersal of the horse *Equus* and Late Cenozoic mammalian dispersal events. Nat. 287:135–138.
- Lundelius, E. L. & M. Stevens. 1970. *Equus francisci* Hay, a small stilt-legged horse, Middle Pleistocene of Texas. J. Paleont. 44:148–153.
- MacFadden, B. J. 1984. *Astrohippus* and *Dinohippus* from the Yepómera local fauna (Hemphillian, México) and implications for the phylogeny of one-toed horses. J. Vertebr. Paleont. 4:273–283.
- MacFadden, B. J. 1992. Fossil Horses: Systematics, Paleobiology, and Evolution of the Family Equidae. Cambridge Univ. Press, New York, 369 pp.
- Marin-Leyva, A. H., V. A. Pérez-Crespo & J. R. Torres-Hernández. 2018. Nuevo registro de los caballos del Pleistoceno *Equus conversidens* y *E. mexicanus* en San Luis Potosí. Paleontol. 7:81–92.
- Marin-Leyva, A. H., M. T. Alberdi, M. L. García-Zepeda, J. P. Ponce-Saavedra, P. Schaaf, J. Arroyo-Cabrales & M. Bastir. 2019. Morfometría geométrica en elementos óseos postcraneales de los caballos del Pleistoceno tardío en México. Implic. Taxon. Ecomor. 20:1–13.
- Martin, P. S. 1967. Prehistoric overkill. Pp. 75–120, *in* Pleistocene Extinctions, the Search for a Cause (P.S. Martin and H.E. Wright, eds.), Yale Univ. Press, New Haven, Connecticut, 453 pp.
- Martin, P. S. 2005. Twilight of the Mammoths. Univ. California Press, Berkeley, 250 pp.
- Martin, P. S. & R. G. Klein (eds.). 1984. Quaternary Extinctions. A prehistoric revolution. Univ. Arizona Press, Tucson, 892 pp.
- Matthew, W. D. 1924. Third contribution to the Snake Creek Fauna. Am. Mus. Nat. Hist., Bull. 50:59–210.
- Matthew, W. D. & R. A. Stirton. 1930. Equidae from the Pliocene of Texas. Univ. California Publ., Dept. Geol. Sci., Bull. 19:349–396.
- McHorse, B. K., E. B. Davis, E. Scott & D. L. Jenkins. 2016. What species of horse was coeval with North America's earliest humans in the Paisley Caves? J. Vertebr. Paleont. e1214595: 1–5.
- Melgarejo-Damian, M.P. & M. Montellano-Ballesteros. 2008. Quantitative differentiation of Mexican Pleistocene horses. Curr. Res. Pleistocene 25:184–186.
- Meltzer, D. J. 2015. Pleistocene overkill and North American mammalian extinctions. Annu. Rev. Anthropol. 44:33–53.
- Mercer, H. C. 1896. The Hill Caves of Yucatan: A search for evidence of man's antiquity in the caverns of Central America, being an account of the Corwith Expedition of the Department of Archaeology and Paleontology of the University of Pennsylvania. J.B. Lippincott, Philadelphia, 183 pp.
- Miller, W. E. 1971. Pleistocene vertebrates of the Los Angeles Basin and vicinity (exclusive of Rancho la Brea). Bull. Los Angeles Co. Mus. Nat. Hist. 10:1–124.

- Miller, W. E. 1980. The Late Pliocene Las Tunas local fauna from southernmost Baja, California, México. J. Paleont. 54:762–805.
- Miller, W. E., C. R. Delgado de Jesús, R. Gómez-Núñez, J. I. Vallejo-Gonzales & J. López-Espinosa. 2008. Preliminary report of Pleistocene mammals from the state of Coahuila, México. Pp. 333–357, *in* Geology and vertebrate paleontology of Western and Southern North America. Contributions in honor of David P. Whistler (X. Wang & L.G. Barnes, eds.), Nat. Hist. Mus. Los Angeles Co., Sci. Ser. 41.
- Mooser, O. & W. W. Dalquest. 1975. Pleistocene mammals from Aguascalientes, central México. J. Mammal. 56:701–820.
- Mooser, O. 1959. La fauna "Cedazo" del Pleistoceno en Aguascalientes. Anal. Inst. Biol. 29:409–452.
- Murchie, T. J., M. Kuch, A. T. Duggan, J. L. Ledger, K. Roche, J. Klunk, E. Karpinski, D. Hackenberger, T. Sadoway, R. D. E. MacPhee, D. Froese & H. Poinar. 2020. Optimizing extraction and targeted capture of ancient environmental DNA for reconstructing past environments using PalaeoChip Arctice-1.0 bait-set. Quat. Res. 99:305–328.
- Murchie, T. J., A. J. Monteath, J. E. Mahony, G. S. Long, S. Cocker, T. Sadoway, E. Karpinski, G. Zazula, R. D. E. MacPhee, D. Froese & H. N. Poinar. 2021. Collapse of the mammoth-steppe in central Yukon as revealed by ancient environmental DNA. Nature Communications 2021:2:7120.
- Nikolskiy, P. A., L. D. Sulerzhitsky & V. V. Pitulko. 2011. Last straw versus Blitzkrieg overkill: climate-driven changes in the Arctic Siberian mammoth population and the Late Pleistocene extinction problem. Quat. Sci. Rev. 30:2309–2328.
- Noller, J. S., J. M. Sowers & W. R. Lettis (eds.). 2000. Quaternary geochronology methods and applications. Am. Geophys. Union, Washington, DC, 582 pp.
- Owen, R. 1869. On fossil remains of equines from Central and South America referable to *Equus conversidens*. Philosophical Trans. R. Soc. Lond. 159:559–573.
- Pérez-Roldán, G., W. E. Miller, R. Gómez-Núñez, V. Torrez-Roldán & J. Madrazo-Fanti. 2019. Mus. Nat. Hist., Univ. Oregon, Abstracts of Program, West. Assoc. Vertebr. Paleont. 28:9.
- Pichardo, M. 2000. Valsequillo biostratigraphy III: Equid ecospecies in Paleoindian sites. Anthropol. Anz. Jahrg. 58:275–298.
- Pichardo, M. 2001. Valsequillo biostratigraphy IV: Proboscidean ecospecies in Paleoindian sites. Anthropol. Anz. Jahrg. 59:41–60.
- Pichardo, M. 2004. Review of horses in Paleoindian sites of the Americas. Anthropol. Anz. Jahrg. 62:11–35.
- Pichardo, M. 2008. Identification guide for horses from North American Paleoindian time. Self-published, Minneapolis, Minnesota. 41 pp., plus appendices.
- Priego-Vargas, J., V. M. Bravo-Cuevas & E. Jiménez-Hidalgo. 2016. The record of Cenozoic horses in México: Current knowledge and palaeobiological implications. Palaeobio. Palaeoenv. 96:1–27.
- Quinn, J. H. 1955. Miocene Equidae of the Texas Gulf Coastal Plain. Univ. Tex. Bur. Econ. Geol., Publ. No. 5516:1–102.
- Savage, D. E. 1951. Late Cenozoic vertebrates of the San Francisco Bay region. Univ. Calif. Publ. Geol. Sci. Bull. 28:215–314.
- Scott, E. 1990. New record of *Equus conversidens* Owen, 1869 (Mammalia, Perissodactyla, Equidae) from Rancho La Brea. J. Vertebr. Paleont. 9(3):166.

- Scott, E. 2004. Pliocene and Pleistocene horses from Porcupine Cave. Pp. 264–279, *in* Biodiversity response to climate change in the Middle Pleistocene. The Porcupine Cave fauna from Colorado (A.D. Barnosky, ed.), Univ. California Press, Berkeley, 385 pp.
- Skinner, M. F. & C. W. Hibbard. 1972. Early Pleistocene pre-glacial and glacial rocks and faunas of north-central Nebraska. Am. Mus. Nat. History, Bull. 148:1–148.
- Stirton, R. A. 1940. Phylogeny of North American Equidae. Univ. California Publ. Geol. Sci. 25:165–198.
- Torres-Roldán, V. E. 2017. Proyecto de rescate Paleontológico Rancho Córdova, Cedral. Unpublished report (non-paginated).
- Vartanyan, S. L., K. A. Arslanov, G. P. Karhu & L. D. Sulerzhitsky. 2008. Collection of radiocarbon dates on the mammoths (*Mammuthus primigenius*) and other genera of Wrangle Island, northeast Siberia, Russia. Quat. Res. 70:51–59.
- Veltre, D. W., D. R. Yesner, K. J. Crossen, R. W. Graham & J. B. Coltrain. 2008. Patterns of faunal extinction and paleoclimatic change from mid-Holocene mammoth and polar bear, Pribilof Islands, Alaska. Quat. Res. 70:40–50.
- Weinstock, J., E. Willerslev, A. Sher, W. Tong, S.Y.W. Ho, D. Rubenstein, J. Storer, J. Burns, L. Martin, C. Bravi, A. Prieto, D. Froese, E. Scott, L. Xulong & A. Cooper. 2005. Evolution, Systematics, and Phylogeography of Pleistocene Horses in the New World: A Molecular Perspective. PLoS Biol. 3,8: e241.
- Winans, M.C. 1985. Revision of North American fossil species of the genus *Equus* (Mammalia, Perissodactyla, Equidae). Doctoral Diss. Univ. Tex., Austin, Texas.
- Winans, M.C. 1989. A quantitative study of North American fossil species of the genus *Equus*. In: The evolution of perissodactyls. Prothero. D. and R. Schoch (eds.). Oxf. Mono. Geol. Geophys. 15:262–297.
- Zazula, G. D., E. Hall, P. G. Hare, C. Thomas, R. Mathewes, C. La Farge, A. L. Martel, P.
 D. Heintzman & B. Shapiro. 2017. A middle Holocene steppe bison and paleoenvironments from the Versleuce Meadows, Whitehorse, Yukon, Canada. Can. J. Earth Sci. 54:1138–1152.