Late Pleistocene (Rancholabrean) Glyptodont and Pampathere (Xenarthra, Cingulata) from Sonora, Mexico

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ABSTRACT

The fossil-rich deposits of Térapa (east-central Sonora) contain more than 60 zoological taxa, many with tropical affinities such as Crocodylus (crocodylian), Hydrochaeris (capybara), and many birds. The deposits also contain the dermal ossicles (osteoderms) of two extinct xenarthrans, a glyptodont (Glyptotherium cylindricum) and a pampathere (giant armadillo; Pampatherium cf. mexicanum). Glyptodont remains are also known from other less-well studied localities in Sonora. The faunas from these localities also contain the genus Bison, which indicates that the deposits are of the Rancholabrean Land Mammal Age, late Pleistocene. The presence of Pampatherium at Térapa and the presence of Glyptotherium at Térapa and the Río Mayo/Río Yaqui sites represent the first published accounts of these species from Sonora, and greatly extends their known geographical distribution during the Rancholabrean by about 1,100 km into northwestern Mexico.

Key words: Xenarthra, pampathere, glyptodont, Rancholabrean, Pleistocene, Sonora, Mexico.

RESUMEN

Los yacimientos ricos en fósiles de Térapa (área centro-oriental de Sonora) contienen más de 60 taxon zoológicas, muchos con afinidades tropicales como Crocodylus (crocodrilo), Hydrochaeris (capibara), y muchas aves. Los depósitos contienen además la dermis ósea de oído (osteodermis) de dos xenartros extintos, un gliptodonte (Glyptotherium cylindricum) y un armadillo gigante (Pampatherium cf. mexicanum) (Mammalia, Xenarthra). También se han hallado restos de gliptodonte en otras localidades de Sonora menos estudiadas. Las faunas de estas localidades contienen además el género Bison, lo cual indica que los depósitos son del Rancholabreano (Rancholabrean Land Mammal Age), Pleistoceno tardío. La presencia de Pampatherium en Térapa y de Glyptotherium en Térapa y los sitios del Río Mayo/Río Yaqui representa el primer recuento publicado de estas especies en Sonora y extiende grandemente su distribución conocida durante el Rancholabreano, o pleistoceno tardío, en unos 1,100 kms hacia el noroeste de México.

Palabras clave: Xenartra, pampaterio, gliptodonte, Rancholabreano, Pleistoceno, Sonora, México.

INTRODUCTION

Members of the mammalian order Xenarthra comprise a prominent part of the South American fauna. Most of the evolutionary history of the group occurred on that continent, yet by the late Miocene some members dispersed over the emerging Panamanian land bridge of Central America to populate Mexico, the United States, and portions of Canada (Webb and Rancy, 1996). This dispersal was part of the Great American Biotic Interchange (GABI) of Neotropical and Nearctic taxa. As recorded in the North American fossil record, it occurred primarily during the latest Miocene (early Hemphillian Land Mammal Age (LMA); 9-7 Ma) and continued intermittently through the late Pliocene to early Pleistocene (late Blancan LMA and early Irvingtonian LMA; 2.7-1.0 Ma) (Morgan, 2005).

Living and extinct members of each of the two suborders of xenarthrans, the pilosans (sloths and anteaters) and cingulates (armadillos, pampatheres, and glyptodonts) (McDonald, 2002) are known from Mexico. Representatives of these suborders dispersed during the GABI. Knowledge about the evolutionary history and distribution of these taxa has been based primarily on fossils from the United States. The records of fossil xenarthrans in Mexico are less extensive and inadequately understood as compared to those in the United States, and the review of xenarthran fossils by McDonald (2002) clearly illustrated a latitudinal bias to the known distribution. This is unfortunate as the geographic position of Mexico represents today the northern extension of the Neotropics and the southern extension of the temperate climates and biotic communities of the Nearctic. The northern state of Sonora represents this critical boundary between the two biomes, a zone that shifted north and south with the pulsating changes of glacial and interglacial climate changes during the Pleistocene.

Although many xenarthrans were present in North America during the Neogene, some apparently were restricted to the environments of Mexico and did not venture into the temperate United States. The record of xenarthrans from Mexico is intriguing yet clearly insufficiently studied to permit adequate statements about distribution patterns and dispersal routes relative to chronology and environmental change. Any evidence, especially from the northern portion of Mexico, is significant and of biogeographic and environmental importance. Of interest here are the cingulates, which include three subgroups: Dasypodidae (living and extinct armadillos), Pampatheriidae (extinct pampatheres or giant armadillos), and Glyptodontidae (extinct glyptodonts). The earliest record of cingulates in Mexico is from early Blancan deposits in the state of Guanajuato. Pampatheres are represented there by the genus *Plaina* in deposits dated between 4.7 and 4.8 Ma, and for the glyptodonts by *Glyptotherium* from layers dated between 3.9 and 3.1 Ma (Flynn *et al.*, 2005). Here we report remains of glyptodonts and pampatheres from the deposits at Térapa in east-central Sonora and other less studied localities within the state.

Today the only xenarthran to inhabit Sonora is the nine-banded armadillo (*Dasypus novemcinctus*, Dasypodidae), which lives in southern-most portion of the state at Alamos (Mendoza-Durán, 2005).

FOSSIL LOCALITIES IN SONORA

Térapa

The fossil-rich deposits of Térapa contain more than 60 zoological taxa, many with tropical affinities such as *Crocodylus* (crocodylian) and *Hydrochaeris* (capybara), along with many birds and *Bison* (bison) (Mead *et al.*, 2006). Carranza-Castañeda and Roldán-Quintana (2007) briefly mention their recovery of surface finds of *Bison* and *Equus* (horse) from Térapa. Térapa is located along the Río Moctezuma in interior east-central Sonora (Figure 1; 29° 41' N latitude; 109° 39' W longitude, 605 m elevation). The Río Moctezuma joins the Río Yaqui and enters the Gulf of California (28°N, 111°W), positioning Térapa 350 km inland. The geological context and stratigraphy of the deposits at Térapa are described in Mead *et al.* (2006). A lava flow within the Moctezuma volcanic field described by Paz-Moreno *et al.* (2003) created at least one catchment basin approximately 1 by 2 km adjacent to the Río Moctezuma. *Bison* teeth and post-cranial remains recovered by Mead *et al.* (2006) from throughout the 11 m of stratified sediments prescribe an assignment for the deposit and encased fauna to the Rancholabrean (RLB) LMA of the late Pleistocene (see Bell *et al.*, 2004).

All fossil specimens from Térapa are temporarily archived into the Laboratory of Quaternary Paleontology, Quaternary Sciences Program, Northern Arizona University (NAU QSP), Flagstaff, Arizona, USA. Within this system, all specimens are curated into a numbering classification specifically for Térapa (TERA) and eventually will be returned to Sonora.

The cingulate remains from Térapa come from the lowest As1/As2 sediments that represent the initial filling of the basin and from the lower (Bp1) and upper (Bp2) marsh units (Mead *et al.*, 2006). Although it is not yet understood how much time it took to fill the basin with 11 meters of sediments and fossils, it is apparent that cingulates utilized the local environments throughout the depositional history of the catchment.

Río Mayo / Río Yaqui Localities

Howard Scott Gentry traveled extensively throughout northwestern Mexico in the 1930s where he recorded fossil deposits, as well as the modern vegetation. Although his contributions about the vegetation are well published (see references in Martin *et al.*, 1998), his fossil discoveries are less well known, mostly unpublished, and documented by
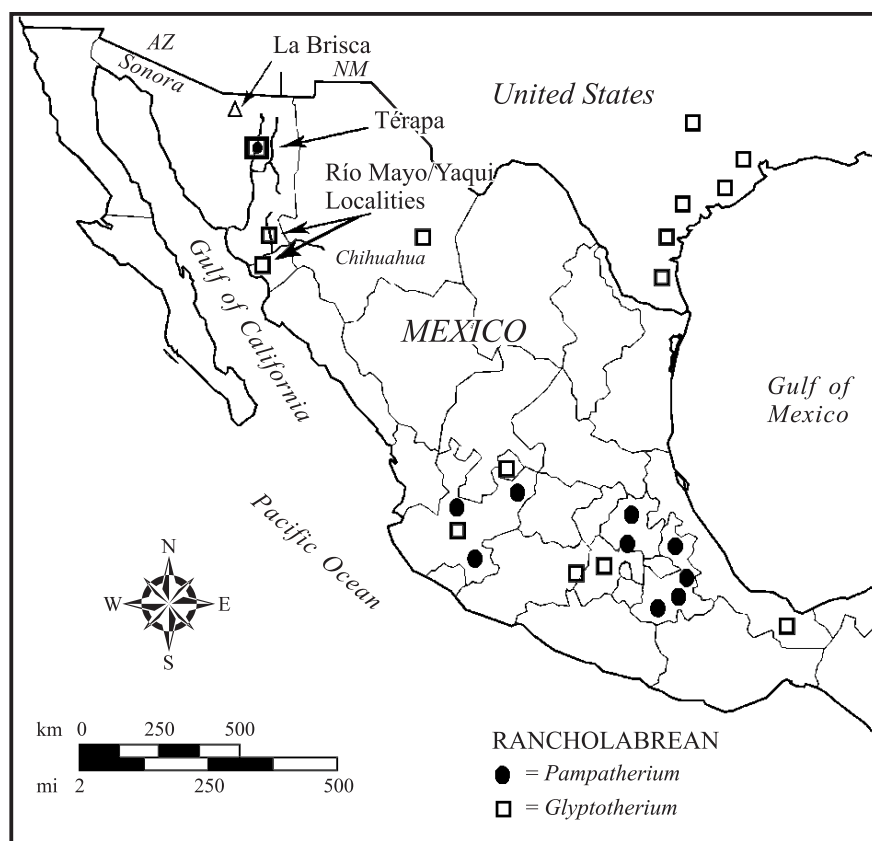
Figure 1. Map of Mexico and adjacent USA showing distribution of *Glyptotherium* (open square) from Gillette and Ray (1981) and McDonald (2002) and *Pampatherium* (dot) from McDonald (2002) in relationship to the locations of Térapa, the Río Mayo/ Río Yaqui deposits, and La Brisca (open triangle) from Van Devender *et al*., (1985). More detailed discussion about locations can be found in the text and in Mead *et al*. (2006).

field notes and letters to Childs Frick (Gentry and Hadley, 1995:237-243). These letters and notes are archived in the Department of Paleontology, American Museum of Natural History (AMNH), New York. The materials collected by Gentry in Sonora are preserved in the vertebrate paleontology collections at the AMNH. We have examined these briefly, but have not produced a detailed analysis. Only those localities with remains of cingulates are presented here. Clearly, additional studies of these fossil localities are greatly desired; we plan further study of Gentry's Rancholabrean material from Sonora.

La Botana

Gentry described three localities from the vicinity of Tesopaco: 1) 8 km southeast, 2) 16 km west and north, and 3) 25 km west and north. Gentry's field notes for his first few weeks in this area are confusing. It appears likely that his Tesopaco Locality 1 is what he later called Los Coyotes, that Tesopaco Locality 2 is probably La Botana, and that Tesopaco Locality 3 is Llano Prieto (the latter two are described below).

Gentry first visited La Botana between May 5th and May 10th, 1936, based on his plant collecting notes in the Herbarium at the University of Arizona. La Botana is located at approximately 490 m altitude and is about 10 km. west of the town of Tesopaco. (Figure 1). The site is located close to the divide between the Río Yaqui and Río Mayo drainages, which are not clearly delineated on available maps. Gentry, in a letter to the Frick Lab, also indicates that it is in the Río Yaqui drainage. Martin *et al*. (1998) also thought that the site was likely in the Río Yaqui drainage

Fossils were abundant and included *Glyptotherium* in association with *Bison*, which indicates a RLB age for the deposits. Gentry also recovered *Equus*, *Camelops*, *Mammuthus*, and *Odocoileus*. Fossils were removed from an 'argillaceous lime' unit. Brief site descriptions and a map of collecting localities are recorded in Gentry's field notes submitted to C. Frick, June 1, 1937. The locality was visited on March 23, 1975 by Paul S. Martin and one of his students, Geoff Spaulding (both then at the University of Arizona, Desert Laboratory, Tumamoc Hill, Tucson, Arizona). They made a small collection of vertebrate fossils (Martin, pers. com.). Fossil recovered by the UA party include the *Glyptotherium* osteoderms documented below, and *Equus*, *Bison*, and cf. *Capromeryx*. Specimens from La Botana are curated at NAU QSP (via the University of

Arizona, Laboratory of Paleontology, Tucson) and in the collections at the AMNH.

Llano Prieto

The Llano Prieto fossil locality is located north of La Botana, up the headwaters of the Río Cedros, a tributary of the Río Mayo. As noted below, Llano Prieto was originally referred to as Tesopaco 3 by Gentry. An 'argillaceous lime and gravel' unit with fossils is located about 6 m below surface. *Bison* and an unverified record of *Glyptotherium* were recovered together from the locality, and indicate a RLB age for the remains. Data is recorded in H. S. Gentry's field notes submitted to C. Frick, June 1, 1937. We have not been able to locate a specimen of *Glyptotherium* from this locality in the AMNH collections.

Chinobampo

The site of Chinobampo is located along the Arroyo Chinobampo, which appears to drain northwards into the Río Mayo, and is about midway between Navajoa and Alamos. The settlement of Chinobampo is shown on the Mexican Topographic Map (1:50,000) Masiaca G12B56. Some older maps show a ranch named 'Agua China' in the same area. According to Gentry, 'Chinobampo' means 'Chinaman Well'. Since the word "chino" locally also means the tree palo chino (*Havardia mexicana*), Martin *et al*. (1998) translate the place name as "Chino in the water". The site was mentioned briefly in Aveleyra Arroyo de Anda (1964) and is notable for having produced a human skull and some fragmentary postcranial remains, possibly from the same layers that produced the Rancholabrean fossil mammals. Gentry discovered the site January 10, 1937 (based on both a geological report written by John C. Blick (another one of Frick's collectors) and submitted to Frick December 13, 1937, and Gentry's plant collecting notes in the Herbarium at the University of Arizona. Blick and Gentry returned to Chinobampo in March of 1937 at Frick's request to make an intensive examination of the geology. The geologic situation at Chinobampo appears to be very similar to that described for Tèrapa, Sonora, by Mead *et al*. (2006). A basalt flow dammed the arroyo, causing an impoundment in which sediments consisting of 'argillaceous lime, lime, and black lime' were deposited. Blick lists the following fossils in his notes: a palate of a large species of *Camelops*, a horse skull (*Equus*), and the partial skeleton of a *Canis* sp. (wolf). The 'wolf' skeleton is listed in the Frick Laboratory receiving notes as 'cat.' The same receiving notes list a *Bison* sp. mandible fragment and four glyptodont osteoderms. A RLB age is assigned based on the recovery of *Bison* with extinct species. Specimens from Chinobampo are curated in the Department of Paleontology, AMNH.

SYSTEMATIC PALEONTOLOGY

Order Xenarthra Cope, 1889
Suborder Cingulata Illiger, 1811
Superfamily Glyptodontoidea Gray, 1869
Family Glyptodontidae Gray, 1869
Genus *Glyptotherium* Osborn, 1903

Glyptotherium cylindricum (Brown) Gillette and Ray, 1981

Fossil material. Osteoderms (dermal ossicles) assigned to *Glyptotherium cylindricum* include:

Térapa— TERA-25, 27-30, 50: interior carapace osteoderms; TERA-24, 49: lateral osteoderms near border; TERA-26, 31: caudal border carapace osteoderm; TERA-32-36, 45-48: conical osteoderms; TERA-37-44: anterior osteoderm of caudal ring: TERA-51: large section of carapace from single individual.

La Botana— NAU QSP-17887: one mid-carapace osteoderm; NAU QSP-17886: one lateral border osteoderm; AMNH 59592 and 59693: 163 isolated and 6 articulated osteoderms; AMNH 59594: two mid-carapace osteoderms; AMNH 96369: one mid-carapace osteoderm.

Llano Prieto— Mentioned in field notes; no osteoderms were observed in the AMNH collections.

Chinobampo— Four mid-carapace osteoderms: AMNH 59595. Only the ventral side of these osteoderms is preserved. The dorsal side is obscured with a thick coating of caliche-like carbonate.

Remarks and identification. North American glyptodonts are distinct from the South American forms and placed in their own genus *Glyptotherium*, which is closely related to the South American genus *Glyptodon* (Gillette and Ray, 1981). The earliest glyptodont in Mexico, *Glyptotherium* sp., is recorded from early Blancan deposits in central Mexico (Carranza-Castañeda and Miller, 2004). There are three recognized species of *Glyptotherium* from Mexico: *G. cylindricum* [Rancholabrean LMA; one locality], *G. floridanum* [Rancholabrean LMA; two localities], and *G. mexicanum* [Rancholabrean LMA; one locality] (Gillette and Ray, 1981; McDonald, 2002). Additional species are described and are restricted to the United States and older deposits (*G. arizonae* [Irvingtonian LMA] and *G. texanum* [Blancan LMA]).

The distribution of the genus was more extensive during the Blancan and Irvingtonian with remains occurring in Arizona and New Mexico respectively (Morgan and Lucas, 2005; Morgan and White, 2005; White and Morgan, 2005), and even north into Oklahoma (Czaplewski, 2004). Records of late Pleistocene, RLB, *Glyptotherium* in the United States are concentrated along the Gulf States region (Gillette and Ray, 1981). Consequently from the Blancan to the Rancholabrean there was a reduction in the range of the genus to the east and south in the United States. Extensive

field studies have shown that no Rancholabrean records of *Glyptotherium* exist in the Southwest United States (Mead *et al.*, 2005; Morgan and Lucas, 2005). Until now its distribution in Mexico during the Rancholabrean was thought to be restricted to central and southern portions of the country (McDonald, 2002; Figure 1).

The dermal armor of glyptodonts is their single most outstanding characteristic. Consequently the morphology of the osteoderms has long been recognized as taxonomically important. Each osteoderm that covers the body region (carapace) is polygonal (six- or four-sided) and is tightly sutured to its neighbors, inhibiting trunk mobility. For a discussion of the development of the osteoderms, see Holmes and Simpson (1931) and Hill (2006). The typical hexagonal osteoderm has a central figure and several peripheral figures symmetrically arranged around the center, producing a characteristic and diagnostic rosette pattern (terminology of Hill, 2006). Identification characters used here follow Gillette and Ray (1981). In *G. texanum,* the central figure is larger than the peripherals, and is convex and slightly raised above the level of the flattened peripheral figures. In *G. arizonae* and *G. cylindricum*, the central figures are relatively smaller than the peripherals, not greater than 50 percent of the entire osteoderm diameter, and are generally flat to weakly convex. In *G. floridanum* the central figure is approximately equal in size to those of the peripherals, and is typically raised and weakly concave. The central figure on the osteoderms of *G. mexicanum* is generally large, never smaller than half (50 percent) of the osteoderm diameter.

Although seemingly distinct for all the species, we recognize that there is variation of the rosette size and pattern within and among species. Isolate osteoderms may be difficult to accurately identify in all cases. Complicating this is the fact that *G. cylindricum* and *G. mexicanum* are less than adequately understood, being known only from the type localities (Carranza-Castañeda and Miller, 1987; McDonald, 2002). Better material may show that these two taxa are synonomous. Until more complete carapaces of *Glyptotherium* from Mexico are studied in detail and apomorphies established for the osteoderms, we identify our specimens from Sonora using the characters outlined above from Gillette and Ray (1981). In addition, we omit *G. arizonae* and *G. texanum* from consideration of the Rancholabrean glyptodonts based on their earlier age assignment. Clearly much remains to be understood about Mexican glyptodonts.

TERA-24 measures 39.6 by 34.8 mm. The thickness varies from 11.2 to 12.6 mm which indicates that the osteoderm is from a lateral, near-border location (Figure 2a). Due to location on the carapace, the TERA-24 specimen does not have the typical rosette pattern.

TERA-25 is a typical rosette osteoderm of the mid-carapace (Figure 2b). Overall the osteoderm measures 37.4 by 45.1 mm, and is 16.3 mm in thickness. The central figure of the rosette measures 16.6 mm (36 percent of the greatest
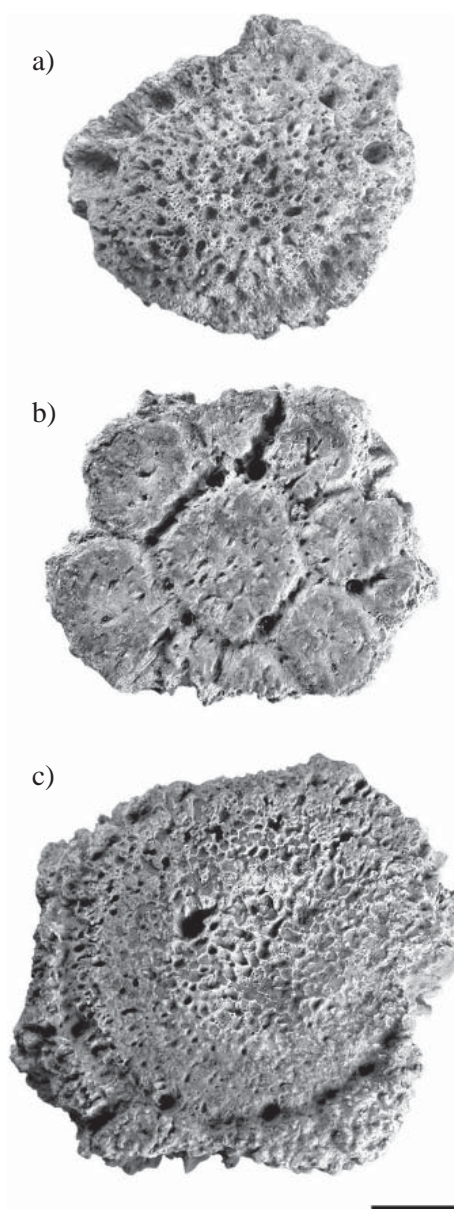

Figure 2. Osteoderms of *Glyptotherium* cf. *G. cylindricum* from Térapa. a: TERA-24; b: TERA-25; c: TERA-26. Scale is 10 mm.

diameter). The central figure is flat and only slightly larger than the peripheral figures, consistent with the pattern found on *G. arizonae* and G. *cylindricum* (Gillette and Ray, 1981). The above character would imply that the *Glyptotherium* from Térapa is more similar to *G. cylindricum* than to *G. mexicanum*. We use this solitary character to identify the fossil glyptodonts to species, omitting the posibility of *G. arizonae* based on age assignment. Additional interior carapace osteoderms have the typical rosette pattern with the central figure relatively small: TERA-27 (52.4 by 41.4 mm; 17.5 mm thick; central figure is 15.2 mm wide (29 percent of the diameter) and slightly depressed; TERA-29 (40.1 by 39.1 mm; 16.4 mm thick; central figure is 16.7

mm wide (42 percent of the diameter); TERA-30 (42.1 by 33.4 mm; 17.5 mm thick; central figure is 18.9 mm wide (45 percent of the diameter); and TERA-50 (38.5 by 37.3 mm; 16.3 mm thick; central figure is 16.6 mm wide (43 percent of the diameter).

TERA-26 is a large osteoderm (53.9 by 48.5 mm) that appears to be from the second row of osteoderms adjacent to the border osteoderms along the caudal edge of the carapace (Figure 2c).

TERA-51 is a 1.5m-long section of the carapace from a single individual *Glyptotherium* (Figure 3). Some of the osteoderms have the internal surface oriented up while others have the external surface oriented up indicating that sections of both the left and right side of the carapace are preserved or that some were flipped over during burial. Four osteoderms were measured: 35.0 by 41.8 mm (central figure is 16.1 mm, or 38 percent of the diameter), 35.8 by 39.9 mm (central figure is 15.9 mm, or 44 percent of the diameter), 40.9 by 37.3 mm, and 35.5 by 29.6 mm. The relative size of the central figures from this carapace section indicates that this specimen can also be referred to *G. cylindricum.*

The remains from La Botana include a small lateral border fragment (NAU QSP-17886) and a mid-carapacial osteoderm (NAU QSP-17887). The latter osteoderm is more complete and has a maximum diameter of 48.4 mm and a thickness of 20.1 mm. The central figure measures 19.8 mm. While the margin of the osteoderm is somewhat broken, enough remains that we are confident that our measurements are good approximations. In any case, a slightly larger maximum diameter would only serve to decrease the ratio of the diameter of the central figure to the maximum diameter of the osteoderm. As preserved, the central figure is 40.9 percent of the osteoderm diameter, placing it well within the range recorded for *Glyptotherium cylindricum* and well below the minimum for *G. mexicanus.*

The 12 best preserved osteoderms from La Botana (Tesopaco Locality 2) in the AMNH (59592, 59593 and 96369) gave an average maximum diameter of 51.6 mm (46.8 – 58.9), an average length of the central figure of 20.5 mm (18.1 – 21.9), with the central figure averaging 39.8 percent (33.6 – 45.2) of the osteoderm diameter. These osteoderms are also well within the range reported for *G. cylindricum* and well below the minimum for *G. mexicanus.*

We have examined the osteoderms in the AMNH from Chinobampo and confirm their identity as *Glyptotherium.* However, the dorsal surface is encrusted with a caliche-like carbonate which obscures the sulci and makes measuring the central figure inaccurate.

Superfamily Glyptodontoidea Gray, 1869
Family Pampatheriidae Paula Couto, 1954
Genus *Pampatherium* Gervais and Ameghino, 1880

Pampatherium cf. P. mexicanum Edmund, 1996

Fossil Material. Remains assigned to *Pampatherium* include isolated imbricating and buckler osteoderms (TERA-18-22).

Figure 3. A series of *in situ*, exposed osteoderms of *Glyptotherium* cf. *G. cylindricum* from a single section of carapace (TERA-51) from Térapa. Both internal and external faces of osteoderms are showed. Scale is 100 mm.

Remarks and identification. Pleistocene pampatheres are represented by seven species in two genera: *Holmesina* and *Pampatherium*. McKenna and Bell (1997) synonymized these genera without comment; we retain the two genera here. The osteoderms provide one mechanism for distinguishing these taxa (Edmund, 1996; Scillato-Yané *et al.*, 2005). Each osteoderm in the carapace bears a pattern reflecting the ornamentation of its covering keratinous osteoderm, which is distinctive for the genus and often for the species (Edmund, 1985, 1987, 1996). The carapace of all pampatheres has a mid-section consisting of three imbricating bands of osteoderms. Anterior to these bands are the pectoral buckler osteoderms and posterior to the bands are the pelvic buckler osteoderms. All of these are distinct in both ornamentation and size from the carapace osteoderms found in the dasypodid armadillos (Edmund, 1985).

Buckler osteoderms from *Pampatherium* are weakly ornamented (Figure 4b). The marginal band may be absent (typical of the Mexican population) or may consist of a narrow band of follicular pits on the posterior and lateral margins; the marginal band is not significantly depressed below the submarginal band (Edmund, 1996). The central portion of the buckler osteoderms in *Pampatherium* is broad and low with no boss or raised keel (Edmund, 1996). In contrast to those of *Pampatherium* and those recovered from Térapa, *Holmesina* buckler osteoderms have a distinct, almost continuous depressed margin, one with a submarginal band that is a clearly defined rectangle. The central region typically is raised, often with a keeled boss (Edmund 1985, 1987, 1996; Scillato-Yané *et al.*, 2005).

While three species of *Pampatherium* have been described, only *P. mexicanum* is present in North America (Edmund, 1996). Although the Térapa specimens appear to match the holotype for that species, we take a conservative approach here and only tentatively assign our fossils to species. The recovery of additional osteoderms or other skeletal elements is needed to permit a more definitive identification.

TERA-18 is the anterior half of either an imbricating osteoderm, or the anterior-most osteoderm of the pelvic buckler (Figure 4a). It preserves the inclined surface over which the osteoderm in front of it overlaps. The anterior-most edge of TERA-18 has been broken so that the edge is 5.3 mm in thickness. The osteoderm would match either the C or D osteoderm of Edmund (1985).

TERA-20 is a complete buckler osteoderm that measures 42.5 mm long by 25.4 mm wide at the anterior end and 29.1 mm wide at the posterior end, and 8.4 mm in maximum thickness (Figure 4b). TERA-20 is somewhat unusual in that the osteoderm is wider at the posterior end; most buckler osteoderms are either rectangular or slightly narrower at the anterior end. TERA-19 is the anterior half of a buckler osteoderm 24.6 mm wide and 7.2 mm in maximum thickness (Figure 4c). Both buckler osteoderms are rectangular in shape, lack the submarginal band and appear to have come from the pelvic buckler. Only a slight follicular pit band oc-
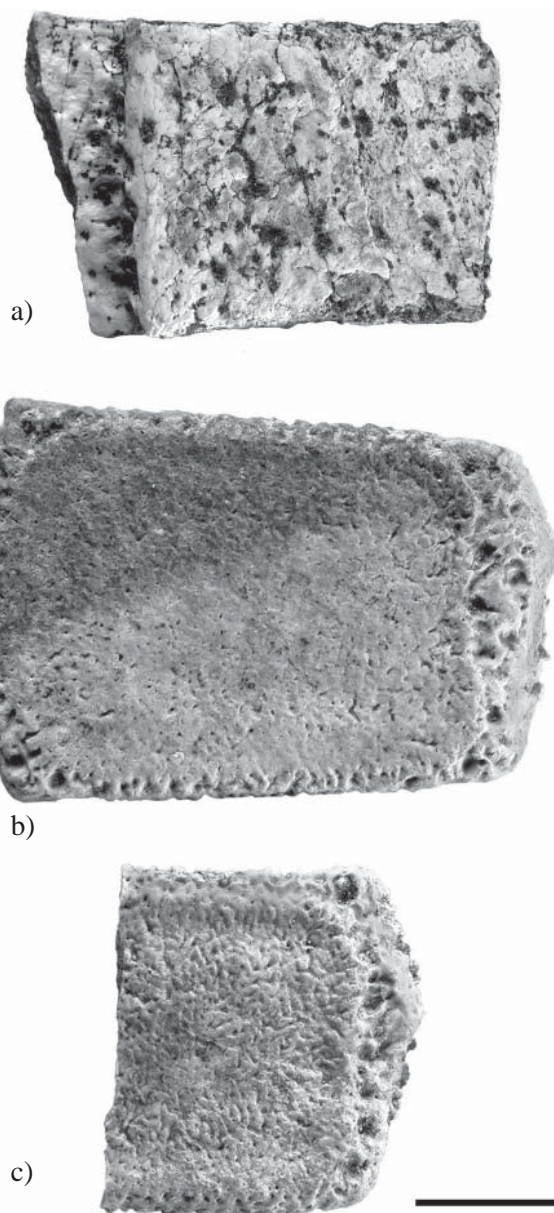

Figure 4. Osteoderms of *Pampatherium* cf. *P. mexicanum* from Térapa. a: TERA-18; b: TERA-20; c: TERA-19. Scale is 10 mm.

curs on TERA-20 and it is not depressed; the central figure is flattened and devoid of a keel or boss (Figure 4b). These combined characters indicate that TERA-19 and 20 belong to the genus *Pampatherium* and not *Holmesina*, although both taxa are known from Mexico.

TERA-22 is relatively small (21.6 by 19.3 mm) with a generally ovoid shape. It has only the slightest presence of follicular pits along the margin, and may represent a cephalic osteoderm. Although the specimens appear similar to those described as *P. mexicanum* (Edmund, 1996) we only tentatively ascribe the specimen to this species until a more complete carapace or collection of osteoderms is recovered from Térapa.

DISCUSSION AND CONCLUSIONS

Distributions

Late Pleistocene Rancholabrean-age deposits are common in Arizona and New Mexico, yet in adjacent northwestern Mexico (Sonora and Chihuahua) the published accounts of such faunas are extremely rare. The few analyzed Rancholabrean deposits and their faunas in Sonora either date to the late Wisconsinan Glaciation ($\sim \leq$ 80,000 years; Arroyo-Cabrales *et al.*, 2002) or possibly to the preceding Sangamon interglacial (Van Devender *et al.*, 1985). The deposits at Térapa represent the most extensively studied RLB deposits in Sonora, yet they may be of a different radiometric age than the few other described faunas (Mead *et al.*, 2006). Until now, *Glyptotherium* and *Pampatherium* dating to the RLB have not been reported from Sonora.

Miller and Carranza-Castañeda (2001) stated that the understanding of the fossil fauna of Mexico has been greatly enhanced through the investigations in central Mexico. As was clearly stated by Arroyo-Cabrales *et al.* (2002), the fossil history of northern Mexico is nearly void of information. Figure 1 shows the known distributions of *Glyptotherium* and *Pampatherium*. The presence of these taxa at Térapa represents the first published accounts of these species from Sonora and greatly extends their known distributions during the RLB into northwestern Mexico.

Glyptotherium of RLB age is found in central, eastern, and Gulf Coastal Plain Texas and southeastern USA (predominantly Florida; Gillette and Ray, 1981). In Mexico, *Glyptotherium* of RLB age is recorded from southeastern Ciudad Delicias, Chihuahua (Silva-Bárcenas, 1969), Cedazo, Aguascalientes (Mooser and Dalquest, 1975), Ameca, Jalisco (Brown, 1912), and localities farther south (McDonald, 2002; Figure 1). The Térapa and other Sonoran localities firmly place *Glyptotherium* during the RLB at least 425 km farther west and 1,150 km farther north than previously recorded. Formerly, the farthest north occurrence of *Pampatherium* during the RLB was in Jalisco (McDonald, 2002; Figure 1).

Environmental Setting

Térapa is situated today at the northern extent of the subtropical thornscrub biotic community of the Neotropical Realm (classification of Brown *et al.*, 1998). More precisely, the local vegetation today is part of the Foothills Thornscrub – a transition between the Sonoran Desertscrub and the Tropical Deciduous Forest (which occurs in the foothills of the Sierra Madre Occidental within 250 km of the Arizona border). Summer rains and protection from deep winter frost are essential for tropical biota (Martin and Yetman, 2000). Today the northern limits of the Neotropics are in central Sonora, with a relatively abrupt transition between 28° and 32° N latitude (Van Devender *et al.*, 2000). Tropicality increases from sea level inland into the foothills of the Sierra Madre Occidental. The northern limit of the Neotropics is not along the coast but inland where it approaches 28° 30'N. The Foothills Thornscrub reaches farther north to within about 100 km of the Arizona border in the Moctezuma and Bavispe drainages (Van Devender *et al.*, 1994). Térapa is on a tributary of the Río Yaqui at 29° 41' N (Figure 1). Tropical species reach their northern limits by being effectively 'squeezed' between the cold temperatures of higher latitudes and the inadequate summer moisture found at lower elevations (Martin *et al.*, 1998; Martin and Yetman, 2000). It is this 'edge-effect' that shifted north and south or up and down in elevation as climate, particularly rainfall and temperatures, cycled through glacial and interglacial regimes.

The recovered sediments, ostracodes, mollusks, and vertebrates indicate that during the RLB local habitats at Térapa included a slow moving stream, ponded water, marsh, and submerged to emergent grasslands (Mead *et al.*, 2006). These authors inferred from the size of the present Río Moctezuma valley that, during the late Pleistocene, the setting permitted a well-developed riparian corridor with tropical habitats that extended 350 km from the coastal environments of the Gulf of California to the interior location at Térapa. While the current imprecise age assignment does not allow us to place the fauna from Térapa within a particular Marine Isotope Stage, the fauna which includes a crocodilian, capybaras, and most of the recovered birds clearly indicate the presence of a subtropical habitat farther north of its current boundary. A more precise chronological analysis of the deposit is being conducted.

A precise chronology and environmental setting for each of the three Río Mayo/Rio Yaqui localities of RLB age is not yet available. However, tropical environments currently extend up the drainage from the coast today, and likely would have also done so during some or most climate regimes during the Pleistocene. The Tropical Deciduous Forest reaches about 1,000 m altitude within the drainage (see Martin *et al.*, 1998). We speculate that at least low elevations along larger drainages, and the region of the coast farther north of the Río Mayo, would have harbored a robust tropical habitat during suitable Pleistocene climatic regimes. What is not understood at present is whether or not the required climate for the extension of tropical flora and fauna to more northerly and /or more interior regions occurred during a glacial or interglacial regime. Continued detailed analysis of the Térapa locality, and our studies of additional unpublished localities in Sonora, may hold the answer to this and other questions.

Habitat Requirements

The habitat requirements for the extinct *Glyptotherium* and *Pampatherium* are not fully known. As with the living armadillos, the naked carapace on glytodonts and pam-

patheres results in a high thermal conductance (McNab, 1978). The result is a smaller differential between body temperature and the environment. Consequently, armadillos, and presumably glyptodonts and pamapatheres, despite their larger size and improved body-mass to surface-area ratio, would show a greater demand to increase metabolism in order to maintain body temperature in response to small changes in the ambient temperature. While *Glyptotherium* fossils are known from farther north of Térapa into the USA during the RLB, they are restricted to areas along the Gulf of Mexico in the eastern portion of the continent. Associated faunal elements in these regions imply a tropical or at least subtropical habitat. It is also not yet determined whether *Glyptotherium* and *Pampatherium* were tropical obligates. This seems doubtful given the more northern range of *Glyptotherium*. However, given the restricted southern distribution of *Pampatherium* in North America in comparison to *Holmesina*, and given that the other known species of the genus are restricted to the tropics, it appears more likely that *Pampatherium* was an obligate inhabitant of tropical conditions.

We speculate that glyptodonts and pampatheres lived in a habitat with abundant grass, and were grazers. Webb (1978) included the *Glyptotherium* as one of nine genera of savanna grazers that participated in the GABI. In contrast, Gillette and Ray (1981) suggested that they were likely "aquatic grazers" along with the capybaras. Fariña (1995) questioned Gillette and Ray's interpretation of *Glyptotherium* as having a preference for marshy, lowland habitats based on a biomechanical analysis of different South American genera of glyptodonts. The jaw and dentition of *Glyptotherium*, as in other glyptodonts, is well adapted for the processing of grasses. The jaw is deep with extremely hypsodont, ever-growing teeth. The teeth are among the most complex of any xenarthran teeth, being trilobate with an arrangement of osteodentine in the center to compensate for the lack of enamel, and the elongated and massive zygomatic arch with a descending flange to orient the masseter muscles to better grind abrasive vegetation such as grasses (Ferigolo, 1985; Fariña, 1985, 1988).

In South America, all species of *Pampatherium* are thought to be better adapted to extreme arid and semi-arid environments than *Holmesina* (Scillato-Yané *et al*., 2005). Based on a functional analysis of mastication in *Pampatherium*, De Iuliis *et al*. (2000) concluded that among the pampatheres, this genus was the most adept grazer of resistant vegetation. Among the herbivorous cingulates, the main differences in skull morphology reflected the degrees of vegetation coarseness they were capable of processing. Such differences probably reflected competitive exclusion through niche partitioning within a shared biome or utilization of different habitats (see Vizcaino *et al*., 1998). While common in the Pampean region of Argentina, the range of *Pampatherium typum* extended through Uruguay into southern Brazil and west into Bolivia. Its widespread occurrence in this region is thought to reflect its adaptation to

a more arid environment (De Iuliis *et al*., 2000). The other species, *P. humboldtii*, is known from the more tropical portions of South America, particularly northern and eastern Brazil. Types of vegetation in these regions varied through time. Vegetation during interglacial intervals resembled that of the modern flora while, during glacial times there was increased aridity, with large portions of the Amazon Basin becoming savanna and cerrado habitat. The distribution of *P. humboldtii* overlapped that of *Holmesina paulacoutoi* in this region. This distribution reflects the dynamics of this changing habitat, and the two taxa may not have been contemporaneous. They may have lived in the region alternatively, with *Pampatherium* being present during the times when more arid savanna habitat predominated.

Although both *Glyptotherium* and *Pampatherium* were recovered at Térapa along with other tropical elements, there were also species in the fauna well adapted to a grassland/savanna habitat and more temperate climate, such as *Mammuthus*, *Equus*, *Camelops*, and *Bison*. The ranges of all these taxa also extend farther south of Térapa into central Mexico so their presence at Térapa is not unexpected. The distribution of *Glyptotherium* into the subtropical habitats of the southeastern USA and its absence in Arizona or New Mexico during the late Pleistocene RLB (Wisconsinan Glaciation) would imply that this grazer required some sort of tropical or subtropical element, including a permanent water source in its habitat. The pampathere, *Holmesina*, is known from eastern USA tropical habitats during the Pleistocene, but never ventured west of the Texas coastal region (Edmund, 1996). *Pampatherium* was not known to have dispersed farther north than south-central Mexico during the Pleistocene until it was found at Térapa. From this distribution pattern, we conclude that *Pampatherium* may have been a more tropical obligate than other South American species within the genus and *Glyptotherium*.

The report here of *Pampatherium* and *Glyptotherium* from RLB deposits in Sonora is unique and clearly illustrates that much about the Pleistocene of northwestern Mexico is only now beginning to be understood. More data is needed to fully characterize the habitat, and to determine whether the local plant community around Térapa during the RLB was a grassland, a savanna, or a more closed community with grass as an understory. Obviously the Neogene of Sonora is in need of additional detailed field and laboratory attention.

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REFERENCES

Arroyo-Cabrales, J., Polaco, O.J., Johnson, E., 2002, La mastofauna del cauternario tardío en México, *in* Montellano-Ballesteros, M., Arroyo-Cabrales, J. (eds.), Avances en los Estudios Paleomastozoológicos: México, D. F., Instituto Nacional de Antropología e Historia, Serie Arqueología, 103-123.

Aveleyra Arroyo de Anda, L., 1964, The primitive hunters, *in* Wauchope, R. (ed.), Natural Environment and Early Cultures, Handbook of Middle American Indians: Austin, Texas, University of Texas Press, 1, 384-412.

Bell, C.J., Lundelius, E.L., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez, D.R., Semken, H.A., Webb, S.D., Zakrewski, R J., 2004, The Blancan, Irvingtonian, and Rancholabrean mammal ages, *in* Woodburne, M.O. (ed.), Late Cretaceous and Cenozoic Mammals of North America: Columbia University Press, 232-314.

Brown, B., 1912, *Brachyostracon*, a new genus of glyptodonts from Mexico: American Museum of Natural History Bulletin, 31, 167-177.

Brown, D.E., Reichenbacher, F., Franson, S.E., 1998, A Classification of North American Biotic Communities: Salt Lake City, University of Utah Press, 141 p.

Carranza-Castañeda, O., Miller, W.E., 1987, Rediscovered type specimens and other important published Pleistocene mammalian fossils from central Mexico: Journal of Vertebrate Paleontology, 7, 335-341.

Carranza-Castañeda, O., Miller, W.E., 2004, Late Tertiary terrestrial mammals from central Mexico and their relationship to South American immigrants: Revista Brasileira de Paleontologia, 7(2), 249-261.

Carranza-Castañeda, O., Roldán-Quintana, J., 2007, Mastofaunula de la cuenca de Moctezuma, Cenozoico tardío de Sonora, México: Revista Mexicana de Ciencias Geológicas, 24, 81-88.

Cope, E.D., 1889, The Edentata of North America: American Naturalist, 23, 657-664.

Czaplewski, N.J., 2004, A glyptodont (Mammalia, Xenarthra) from northern Oklahoma: Oklahoma Geology Notes, 64, 4-9.

De Iuliis, G., Bargo, M.S., Vizcaíno, S.F., 2000, Variation in skull morphology and mastication in the fossil giant armadillos *Pampatherium* spp. and allied genera (Mammalia: Xenarthra: Pampatheriidae) with comments on their systematics and distribution: Journal of Vertebrate Paleontology, 20, 743-754.

Edmund, A.G., 1985, The armor of fossil giant armadillos (Pampatheriidae, Xenarthra, Mammalia): Texas Memorial Museum, University of Texas at Austin, Pearce-Sellards Series, 40, 1-20.

Edmund, A.G., 1987, Evolution of the genus *Holmesina* (Pampatheriidae, Mammalia) in Florida, with remarks on taxonomy and distribution: Texas Memorial Museum, University of Texas at Austin, Pearce-Sellards Series, 45, 1-20.

Edmund, A.G., 1996, A review of Pleistocene giant armadillos (Mammalia, Xenarthra, Pampatheriidae), *in* Stewart, K.M., Seymour, K.L. (eds.), Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals: Toronto, University of Toronto Press, 300-321.

Fariña, R.A., 1985, Some functional aspects of mastication in Glyptodontidae (Mammalia): Fortschritte der Zoologie, 30, 277-280.

Fariña, R.A., 1988, Observaciones adicionales sobre la biomecánica masticatoria en Glyptodontidae: Boletín de la Sociedad Zoológica del Uruguay, 4, 5-9.

Fariña, R.A., 1995, Limb bone strength and habits in large glyptodonts: Lethaia, 28, 189-196.

Ferigolo, J., 1985, Evolutionary trends of the histological pattern in the teeth of Edentata (Xenarthra): Archives Oral Biology, 30, 71-82.

Flynn, J.J., Kowallis, B.J., Nuñez, C., Carranza Castañeda, O., Miller, W.E., Swisher, III, C.C., Lindsay, E., 2005, Geochronology of Hemphillian-Blancan aged strata, Guanajuato, Mexico, and implications for timing of the Great American biotic interchange: Journal of Geology, 113, 287-307.

Gentry, H.S., Hadley, D., 1995, Listening to my mind: Journal of the Southwest, 37, 178-245.

Gervais, H., Ameghino, F., 1880, Les mammifères fossiles de l'Amérique du Sud: Paris, F. Savy, 225 p.

Gillette, D.D., Ray, C.E., 1981, Glyptodonts of North America: Smithsonian Contributions to Paleobiology, 40, 1-255.

Gray, J.E., 1869, Catalogue of carnivorous, pachydermatous, and dentate mammalia in the British Museum: London, British Museum (Natural History), 398 p.

Hill, R.V., 2006, Comparative anatomy and histology of xenarthrans osteoderms: Journal of Morphology, 267, 1441-1460.

Holmes, W.W., Simpson, G.G., 1931, Pleistocene exploration and fossil edentates in Florida: Bulletin of the American Museum of Natural History, 59, 383-418.

Illiger, C., 1811, Prodromus systematis mammalium et avium; additis terminis zoographicis utriusque classis, eorumque versione germanica: Berlin, C. Salfeld, 301 p.

Martin, P.S., Yetman, D.A., 2000, Introduction and Prospect. Secrets of a tropical deciduous forest, *in* Robichaux, R.H., Yetman, D.A. (eds.), The Tropical Deciduous Forest of Alamos. Biodiversity of a Threatened Ecosystem in Mexico: Tucson, The University of Arizona Press, 3-18.

Martin, P.S., Yetman, D., Fishbein, M., Jenkins, P., Van Devender, T.R., Wilson, R.K. (eds.), 1998, Gentry's Río Mayo Plants, The tropical deciduous forest and environs of northwest Mexico: Tucson, University of Arizona Press, 558 p.

McDonald, H.G., 2002, Fossil Xenarthra of México: a review, *in* Montellano-Ballesteros, M., Arroyo-Cabrales, J. (eds.), Avances en los Estudios Paleomastozoológicos: México, D. F., Instituto Nacional de Antropología e Historia, Serie Arqueología, 227-248.

McKenna, M.C., Bell, S.K., 1997, Classification of Mammals above the Species Level: New York, Columbia University Press, 631 p..

McNab, B.K., 1978, Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply, *in* Montgomery, G.G. (ed.), The Ecology of Arboreal Folivores: Washington, D.C., Smithsonian Institution Press, 153-162.

Mead, J.I., Czaplewski, N.J., Agenbroad, L.D., 2005, Rancholabrean (Late Pleistocene) mammals and localities of Arizona: Mesa Southwest Museum Bulletin, 11, 139-180.

Mead, J.I., Baez, A., Swift, S.L., Carpenter, M.C., Hollenshead, M., Czaplewski, N.J., Steadman, D.W., Bright, J., Arroyo-Cabrales, J., 2006, Tropical marsh and savanna environment during the

Late Pleistocene in northeastern Sonora, México: Southwestern Naturalist, 51(2), 226-239.

Mendoza-Durán, A., 2005, Armadillo, *in* Ceballos, G., Oliva, G. (eds.), Los Mamíferos Silvestres de México: México, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Fondo de Cultura Económica, 117-118.

Miller, W.E., Carranza Castañeda, O., 2001, Late Cenozoic mammals from the basin of Central Mexico: Bollettino della Società Paleontologica Italiana, 40(2), 235-242.

Mooser, O., Dalquest, W.W., 1975, Pleistocene mammals from Aguascalientes, central Mexico: Journal of Mammalogy, 56, 781-820

Morgan, G.S., 2005, The Great American Biotic Interchange in Florida, *in* Hulbert, R.C., Morgan, G.S., Baskin, J. A. (eds.), Cenozoic Vertebrates of the Americas, Papers to Honor S. David Webb: Florida Museum of Natural History Bulletin, 45(4), 271-311.

Morgan, G.S., Lucas, S.G., 2005, Pleistocene vertebrate faunas in New Mexico from alluvial, fluvial, and lacustrine deposits: New Mexico Museum of Natural History and Science Bulletin, 28, 185-248.

Morgan, G.S., White, R.S., 2005, Miocene and Pliocene vertebrates from Arizona: New Mexico Museum of Natural History and Science Bulletin, 29, 115-136.

Osborn, H.F., 1903, 'Glyptotherium texanum', a new glyptodont, from the Lower Pleistocene of Texas: Bulletin of the American Museum of Natural History, 19(17), 491-494.

Paula Couto, C. de, 1954, Sobre um gliptodonte do Uruguai e um tatu fossil do Brasil: Servicio Geologico y Mineralogico, Notas Preliminares e Estudios, Rio de Janeiro, 80, 1-10.

Paz-Moreno, F., Demant, A., Cochemé, J-J, Dostal, J., Montigny, R., 2003, The Quaternary Moctezuma volcanic field: a tholeiitic to alkali basaltic episode in the central Sonoran Basin and Range Province, México: Geological Society of America, Special Paper, 374,1-17.

Scillato-Yané, G.J., Carlini, A.A., Tonni, E.P., Noriega, J.I., 2005, Paleobiogeography of the late Pleistocene pampatheres of South America: Journal of South American Earth Sciences, 20, 131-138.

Silva-Bárcenas, A., 1969, Localidades de vertebrados fósiles en la República Mexicana: Universidad Nacional Autónoma de México, Instituto de Geología, Paleontología Mexicana, 28, 1-34.

Van Devender, T.R., Rea, A.M., Smith, M.L., 1985, The Sangamon interglacial vertebrate fauna from Rancho la Brisca, Sonora, Mexico: Transactions of the San Diego Society of Natural History, 21, 23-55.

Van Devender, T.R., Lowe, C.H., Lawler, H.E., 1994, Factors influencing the distribution of the Neotropical vine snake *Oxybelis aeneus* in Arizona and Sonora, Mexico: Herpetological Natural History, 2, 27-44.

Van Devender, T.R., Sanders, A.C., Wilson, R.K., Meyer, S.A., 2000, Vegetation, flora, and seasons of the Río Cuchujaqui, a tropical deciduous forest near Alamos, Sonora, *in* Robichaux, R.H., Yetman, D.A. (eds.), The Tropical Deciduous Forest of Alamos: Biodiversity of a Threatened Ecosystem in Mexico. The University of Arizona Press, Tucson, 36-101.

Vizcaino, S.F., De Iuliis, G., Bargo, M.S., 1998, Skull shape, masticatory apparatus, and diet of *Vassallia* and *Holmesina* (Mammalia: Xenarthra: Pampatheriidae): When anatomy constrains destiny: Journal of Mammalian Evolution, 5(4) 291-322.

Webb, S.D., 1978, A history of savanna vertebrates in the New World. Part II: South America and the Great Interchange: Annual Review of Ecology and Systematics, 9, 393-426.

Webb, S.D., Rancy, A., 1996, Late Cenozoic evolution of the Neotropical mammal fauna, *in* Jackson, J.B.C., Budd, A.F., Coates, A.G. (eds.), Evolution and Environment in Tropical America: Chicago, University of Chicago Press, 335-358.

White, R.S., Morgan, G.S., 2005, Arizona Blancan vertebrate faunas in regional perspective: Mesa Southwest Museum Bulletin, 11, 117-138.