

Research Article

Paleobiology of a large mammal community from the late Pleistocene of Sonora, Mexico

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Abstract

A paleontological deposit near San Clemente de Térapa represents one of the very few Rancholabrean North American Land Mammal Age sites within Sonora, Mexico. During that time, grasslands were common, and the climate included cooler and drier summers and wetter winters than currently experienced in northern Mexico. Here, we demonstrate restructuring in the mammalian community associated with environmental change over the past 40,000 years at Térapa. The fossil community has a similar number of carnivores and herbivores whereas the modern community consists mostly of carnivores. There was also a 97% decrease in mean body size (from 289 kg to 9 kg) because of the loss of megafauna. We further provide an updated review of ungulates and carnivores, recognizing two distinct morphotypes of *Equus*, including *E. scotti* and a slighter species; as well as *Platygonus compressus*; *Camelops hesternus*; *Canis dirus*; and *Lynx rufus*; and the first regional records of *Palaeolama mirifica*, *Procyon lotor*, and *Smilodon* cf. *S. fatalis*. The Térapa mammals presented here provide a more comprehensive understanding of the faunal community restructuring that occurred in northern Mexico from the late Pleistocene to present day, indicating further potential biodiversity loss with continued warming and drying of the region.

Keywords: Community ecology, Mammals, Ungulates, Carnivores, Rancholabrean, Sonora, Conservation paleobiology

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INTRODUCTION

Conservation paleobiology aims to use knowledge of the past to make informed predictions about the future of Earth's threatened biodiversity (Dietl and Flessa, 2011, Dietl et al., 2015, Barnosky et al., 2017). These studies provide a baseline of what community structures looked like in the past, how extant communities might respond to impending changes, and how we should approach conservation. For example, in the Greater Everglades Ecosystem, paleoecological data from pollen and invertebrates have been used to establish pre-anthropogenic trends and cycles, predict future changes, and identify restoration targets for anticipatory resource management efforts (Wingard et al., 2017). Other similar work has documented the presence of *Bison* in the Grand Canyon region (Martin et al., 2017), inspired interagency conservation and management plans for *Bison* today (Plumb and McMullen, 2018), and encouraged restoration of threatened plant species in Hawaii (Burney and Burney, 2007).

Increasingly xeric landscapes, such as those in the southwest US and northwest Mexico, are challenging for natural resource management (Sayre et al., 2013). Integration of fossil sites with climate patterns may reveal potential future areas for faunal refugia and migratory corridors as fauna must shift their geographic ranges or risk extinction (Blois and Hadly, 2009). Additionally, studying past faunal change may reveal trends in restructuring of faunal communities, which may enhance anticipatory natural resource management decisions and strategies. In particular, large animals and plants are disproportionately important for ecosystem function (Enquist et al., 2020), and changes in these communities can indicate environmental change (Blois and Hadly, 2009).

Paleobiology of mammal communities has commonly focused on body size and diet because they can be inferred from fossil remains. Smith et al. (2018) demonstrated a widespread 95% decline in mean body mass of North American mammal communities (e.g., from 100 kg to 5 kg) associated with the loss of the Pleistocene megafauna. Stegner and Holmes (2013) investigated mammalian community structure over 16 million years and demonstrated static diversity of dietary functional groups except in times of major environmental pressures. In the Pleistocene of Mexico, mammal communities were more taxonomically diverse, with more large-bodied taxa and a more similar ratio between

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herbivores and carnivores as compared to modern communities (Ferrusquía-Villafranca et al., 2010).

Overall, our knowledge of the fossil mammals of Mexico is biased toward taxa of larger sizes and younger geological ages, possibly because of collection methods (Montellano-Ballesteros and Jiménez-Hidalgo, 2006; Ferrusquía-Villafranca et al., 2010). Of 64 Neogene sites in Sonora, Mexico, only three sites have detailed faunal records: El Golfo, San Clemente de Térapa (hereon, Térapa), and Rancho la Brisca (White et al., 2010). El Golfo is the only known Irvingtonian LMA site in northern Mexico (Lindsay, 1984; Croxen et al., 2007; Sussman et al., 2016). Rancho La Brisca is from the Rancholabrean LMA but has a slightly different fauna than is preserved at Térapa and other sites in the region because its record is biased toward small and medium fish, amphibians, and reptiles (Van Devender et al., 1985). Additional small and isolated records in the region, including La Botana, Llano Prieto, and Chinobampo, consist of mostly large mammals, such as *Bison*, *Equus*, *Mammuthus*, *Glyptotherium*, and *Camelops* (White et al., 2010; Cruz-y-Cruz et al., 2018). West of Térapa, La Playa has fossils of *Bison*, *Platygonus*, *Mammuthus*, *Equus*, camelids, and other large mammals, but also has the first record of *Cynomys* in Sonora, which suggests more small mammals may be found at other sites (Mead et al., 2010).

Located in Sonora, Mexico, Térapa (29°41'N, 109°39'W; 605 m elevation; Fig. 1) provides an excellent case study of faunal response to environmental and climatic changes in an area vulnerable to continued alteration because of its geographic location in an ecotone between the northern Nearctic climate and the southern Neotropical climate. Modern (i.e., interglacial) Sonoran and Chihuahuan deserts are typified by scrubland ecosystems with warm tropical-subtropical climates, and at present, this area is situated on the margin of the Madrean Archipelago and the Sinaloa-Sonora Hills and Canyons (Morrone et al., 2017). However, when the fossil-bearing sediments were deposited in the Térapa basin, western Sonora was more temperate, with cooler, drier summers and wetter winters than are seen today (Nunez et al., 2010), and was typified by pinyon-juniper-oak woodlands (Van Devender, 2007). Stable isotope analyses of carbon and oxygen from ungulate teeth (Nunez et al., 2010) and ostracodes (Bright et al., 2016) recovered at Térapa suggest that, at least in the valley, marsh and grasslands were likely present at the time of deposition. Previous studies of Térapa avifauna (Steadman and Mead, 2010; Oswald and Steadman, 2011), crocodylians (Mead et al., 2006), bats and shrews (Czaplewski et al., 2014), and ostracodes (Bright et al., 2016) indicate that the environment was an elevational mosaic of temperate to tropical-subtropical marsh and savanna/grassland with a slow-moving freshwater stream flowing from north of Térapa down to the Río Moctezuma and Río Yaqui to the Gulf of California.

Discovered in 2000, late Pleistocene (MIS/OIS 3) faunal deposits at Térapa include fossils of more than 60 taxa (Mead et al., 2006). A preliminary faunal list is provided in Mead et al. (2006), and an updated faunal list is provided in Supplemental Table S1. Recent publications have described *Mammuthus* and *Cuvieronius* (Mead et al., 2019), *Glyptotherium cylindricum* and *Pampatherium* cf. *P. mexicanum* (Mead et al., 2007), two shrews and six bats (Czaplewski et al., 2014), and 39 species of birds (Steadman and Mead, 2010; Oswald and Steadman, 2011). With *Bison* present throughout the stratigraphic profile, Térapa represents one of the few Rancholabrean North American Land

Mammal Age (LMA) sites studied in detail in Sonora (Bell et al., 2004; Mead et al., 2006). However, the Holarctic genus *Bison* did not arrive in Mexico until much later than in the northern part of the continent. This biochronological delay complicates assigning LMA ages to Mexican sites, and also illustrates the need to further explore Mexico for fossil sites that can provide insight into North American fauna during the Pleistocene.

Fossils found at Térapa were deposited where the Tonibabi basalt flow dammed and diverted the Río Moctezuma and created a shallow lake at the northern extent of the Sierra Madre Occidental (Mead et al., 2006). Río Moctezuma sediments beneath the basalt dam date to 42.9 ± 3.3 ka using infrared stimulated luminescence, providing a maximum age estimate for the fossils (Bright et al., 2010). Also using infrared stimulated luminescence, sediments 1 m above the basalt date to 40.2 ± 3.2 ka (Bright et al., 2010). Using radiocarbon dating, charcoal near the top of the 11-m-thick sequence of medium- to fine-grained sediments dates to 41.7 ± 1.0 cal ka BP (Bright et al., 2010). Additional dates throughout the sequence using amino-acid racemization on ostracodes and radiocarbon analysis on a bivalve confirm deposition between 40 ka and 43 ka (Bright et al., 2010). Because of Térapa's geographic location and diverse fossil record at a time of extensive environmental change, ongoing research on this fauna will contribute to a better understanding of the late Pleistocene in northwestern Mexico.

Here, we use the fossil record at Térapa to investigate changes in large mammal community structure in response to environmental change. To do this, we explore community structure, as represented by feeding strategy and body size, by describing Térapa specimens and their traits, and discussing their geographic distributions in the North American desert region. We hypothesize that changes in this site's large mammal community structure at the end of the Pleistocene are because of a loss of herbivores and large-bodied taxa. We expect that the fauna described in this paper will help to further refine paleoecological interpretations as well as provide a long-term record of faunal change in a region that is vulnerable to ongoing climate change.

METHODS

Taxa described here were presented by Mead et al. (2006) as: *Equus*, *Tapirus*, cf. *Platygonus*, *Camelops*-sized camelid, *Hemiauchenia*-sized camelid, *Canis dirus*, *Lynx rufus*, and *Procyon*. Mead et al. (2006) also included cf. *Odocoileus*, *Capromeryx*, *Stockoceras*, and *Bison* on the preliminary list of fauna, but these additional artiodactyl specimens have been excluded from this analysis because they either require additional detailed revision or are part of another review.

Systematic paleontology

To determine taxonomic assignments, we primarily used comparative reference specimens from the Florida Museum of Natural History (FLMNH) and the East Tennessee Museum of Natural History (ETMNH). When possible, linear measurements and the related citations are provided within the taxonomic descriptions. Geographic occurrences were determined using The Paleobiology Database (<https://paleobiodb.org>) and literature. Records were downloaded from The Paleobiology Database on 27 July 2017 for: Taxonomy = "*Equus*, *Palaeolama*, *Camelops*, *Platygonus*, *Canis*, *Lynx*, *Procyon*, *Smilodon*," Time = "Rancholabrean," and Location = "North America."

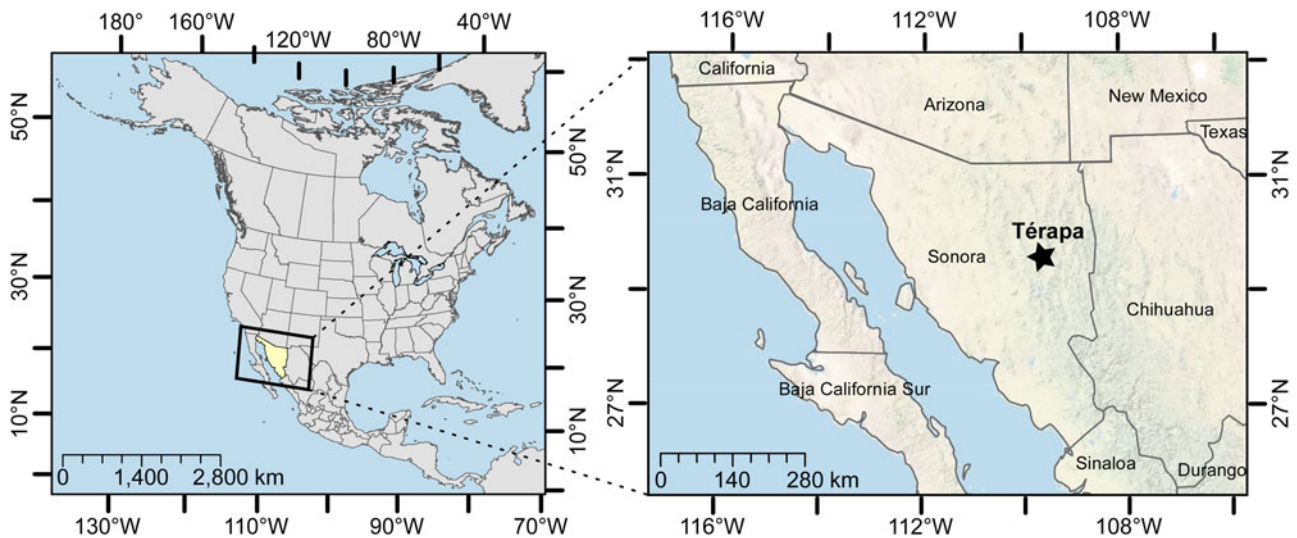


Figure 1. (For interpretation of the reference to color in this figure legend, the reader is referred to the web version of this article) Geographic location of study area (Left), inset figured in (Right) with Sonora, Mexico highlighted in yellow; (Right) location of Térapa (black star) within Sonora, Mexico.

Species identifications for equid post-crania were determined using a quadratic discriminant analysis implemented in the R statistical computing environment using the package MASS (R Core Team, 2016). Training data used in the analyses are from Sertich et al. (2014) and McHorse et al. (2016). For analysis of the phalanx, training data included *Equus occidentalis*, *E. conversidens*, *E. lambei*, *E. scotti*, and a northwestern stilt-legged taxon. For analysis of the metacarpal, training data included *Equus complicatus*, *E. conversidens*, *E. occidentalis*, and *E. scotti*. R code for this analysis is given in Supplementary Materials.

Community structure

To investigate how community structure has changed at Térapa through time, the fossil community of Perissodactyla, select Artiodactyla, and Carnivora presented here was compared to the same three orders from the modern community. Modern mammal range maps were downloaded from the IUCN (2018). Range maps were sampled at the geographic point of Térapa to assemble a faunal list. Taxa were limited to those that are extant and either native or reintroduced. Antilocapridae, Bovidae, and Cervidae were excluded from both communities because, although they are known from Térapa (Mead et al., 2006), they are not within the scope of the discussion within this manuscript.

Feeding strategies were obtained from Paleobiology Database (<https://paleobiodb.org>) on 10 August 2020 by searching for taxonomic names. Strategies were grouped into herbivore, herbivorous omnivore, carnivorous omnivore, and carnivore. Body mass (BM; kg) averages were extracted from the MOM database (Smith et al., 2003) for each species. Mass estimates include males and females across distribution ranges and are not precise values for the southern geographic location of Térapa. However, they provide a measure to estimate temporal changes in the fauna.

RESULTS

From the mammalian fauna found at Térapa, we provide descriptions for eight species in seven genera, including *Equus*, *Platygonus*, *Camelops*, *Palaeolama*, *Canis*, *Procyon*, *Lynx*, and

Smilodon. Six of these genera appeared on the preliminary faunal list of Mead et al. (2006), and two of these genera (*Palaeolama* and *Smilodon*) are new additions to the known faunal community. Specimens from Térapa are housed temporarily at The Mammoth Site, Hot Springs, South Dakota, USA, and are curated with numbers prefixed with TERA. Specimens will be permanently housed at the Instituto Nacional de Antropología e Historia in Sonora, Mexico.

Systematic paleontology

Class Mammalia
Order Perissodactyla
Family Equidae
Genus *Equus* Linnaeus, 1758
Equus scotti Gidley, 1900

Material: Left distal metacarpal (TERA 313), left partial phalanx 1 (TERA 320), phalanx 2 and sesamoid (TERA 319).

Description: The left metacarpal (TERA 313) is broken transversely across the diaphysis, but the distal end is complete (Fig. 2A). The left partial first phalanx (TERA 320) is missing the lateral, distal portion (Fig. 2B). The metacarpal and phalanx articulate. The second phalanx is complete (TERA 319; Fig. 2C) and articulates with a sesamoid. The first and second phalanges do not articulate.

Identification: In quadratic discriminant analyses, the second phalanx (TERA 319) was identified to species level with 87.5% confidence, and the distal metacarpal (TERA 313) was identified with 100% confidence.

Remarks: *Equus* is widespread across the US and Mexico during the Rancholabrean (Ferrusquía-Villafraña et al., 2010, 2017), including in Sonora (Cruz-y-Cruz et al., 2018). Taxonomy of *Equus* introduces complex questions surrounding species identifications. *Equus scotti* is a stout-legged horse that has been documented across the North American desert region during the Rancholabrean (Harris, 2014), including in the Tule Springs local fauna (Scott et al., 2017). Recent efforts to revise equid taxonomy have considered *E. scotti* to be synonymous with

E. mexicanus (see Alberdi et al., 2014) and *E. excelsus* (see Priego-Vargas et al., 2017), but by convention we use *E. scotti* to be consistent with the data sources used in the analyses. Previous work identified *E. excelsus* at Térapa (Carranza-Castañeda and Roldán-Quintana, 2007), and it is likely the same as our *E. scotti*. However, equid taxonomy needs to be thoroughly and formally evaluated before these issues can be confidently resolved.

Equus cf. *E. scotti* Gidley, 1900

Material: Right P4 (TERA 284), right M2 (TERA 287), right M3 (TERA 285), right P4 and M1 (TERA 291), right P3 and P4 (TERA 168), left P2 (TERA 282, 289), left P4 (TERA 290), left M2 (TERA 286, 288), left M3 (TERA 283), right p4 (TERA 310), lower left tooth (TERA 308), upper left tooth and lower right tooth (TERA 266).

Description: Most of the teeth are complete with moderate wear. These teeth (Fig. 3A–D) are larger and have more complex enamel patterns than the teeth assigned to *Equus* sp. (Fig. 3E–H).

Identification: We hypothesize that the teeth are from the same species as the postcranial elements previously identified as *Equus scotti* because of their large size. More specific identification is difficult with isolated teeth because they lack a majority of diagnostic characters (Famoso and Davis, 2014).

Equus sp.

Material: Right P3 (TERA 166), right M1 (TERA 263), right M2 (TERA 157, 169, 296, 300), right M3 (TERA 298), left M2 (TERA 303), left P4 and M1 (TERA 293), left P3–M1 and right M1 (TERA 297), upper right tooth (TERA 299, 307), upper tooth (TERA 267), right m2 (TERA 295), right m3 (TERA 262, 305, 306), left m2 with fragment (TERA 312), left m3 (TERA 322), lower left molar (TERA 301, 302), lower right tooth (TERA 309), lower left tooth (TERA 311), lower tooth fragment (TERA 264, 265, 304), mandibular symphysis (TERA 294), left partial distal humerus (TERA 314), left magnum (TERA 318), right distal tibia (TERA 317), left partial calcaneum (TERA 315, 316), right cuneiform and lunar (TERA 321).

Description: The postcranial elements are slight compared to extant *Equus caballus* and the Térapa specimens conferred to *Equus scotti*, and these teeth (Fig. 3E–H) are noticeably smaller and have less complex enamel patterns than those assigned to *E. cf. E. scotti* (Fig. 3A–D).

Identification: It is unknown if the post-cranial elements are of the same species as the dentition. At this time, there are no morphological features to confirm species designations.

Remarks: Previous work on different specimens also identified *E. conversidens* at Térapa (Carranza-Castañeda and Roldán-Quintana, 2007), and, because of the smaller size, it is possible that our *Equus* sp. refers to the same taxon. Occurrence of both *E. scotti* and a smaller-sized horse is common at RanchoLabrean sites, and the smaller horse is often identified as *E. conversidens* (Harris, 2014). Again, most isolated teeth can only be identified to genus because of the lack of diagnostic characters (Famoso and Davis, 2014).

Mead et al. (2006) listed *Tapirus* sp. among the taxa found at Térapa based on a mandibular symphysis (TERA 294; Fig. 4A). However, this specimen is now identified as *Equus* sp. Depth of the mandible suggests hypsodont teeth as in *Equus*. The narrow intermandibular space extends anterior to the second premolar as in *Equus*. In *Tapirus*, this space is closed at the anterior end of the second premolar. The mandibular foramen is located

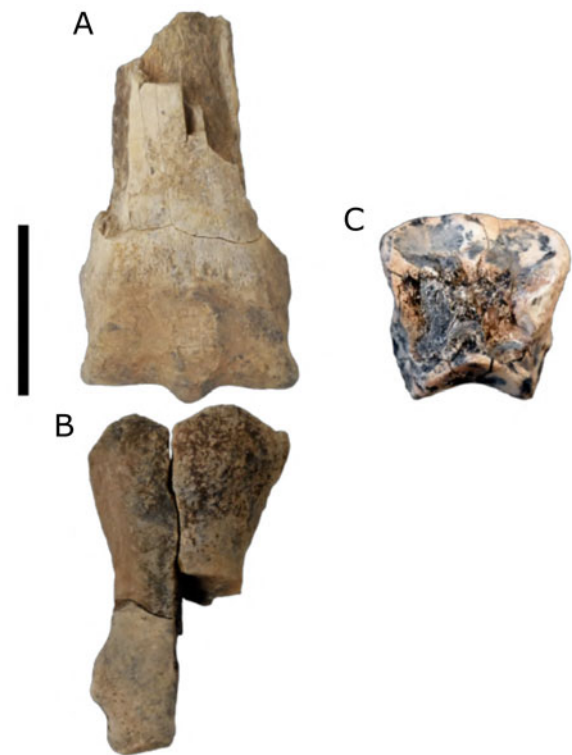


Figure 2. (color online) *Equus scotti* specimens. (A) left distal metacarpal (TERA 313); (B) left partial phalanx (TERA 320); (C) second phalanx (TERA 319). (A) and (B) articulate. Scale bar = 5 cm.

well anterior to the tooth row as in *Equus*. In *Tapirus*, the mandibular foramen is inferior to the anterior second premolar.

Order Artiodactyla

Family Tayassuidae

Platygonus LeConte, 1848

Platygonus compressus LeConte, 1848

Material: Molar fragments (TERA 167), deciduous upper premolar (TERA 280), right upper canine (TERA 281).

Description: The molar fragments (TERA 167) are hypsodont and zygodont (Fig. 5A). The deciduous tooth (TERA 280) is complete and more bunodont than the molar fragments (Fig. 5B). The canine is complete (TERA 281) and has an anterior occlusal surface (Fig. 5C).

Identification: This specimen was initially identified as cf. *Platygonus* by Mead et al. (2006). Comparisons with fossil material at FLMNH suggest that these teeth are *Platygonus* because the cusps are more zygodont, as in *Platygonus*, rather than bunodont as in *Mylohyus*. Because *Platygonus* is monotypic in the middle and late RanchoLabrean (Kurtén and Anderson, 1980; Wright, 1998), these specimens are assigned to *P. compressus*.

Remarks: *Platygonus compressus* is known from the RanchoLabrean of Arizona (Murray et al., 2005), New Mexico, and eastern Texas, as well as the Central Plateau and Trans-Mexican Volcanic Belt (Ferrusquía-Villafraña et al., 2010, 2017). In Sonora, *Platygonus* sp. is known from La Playa and Bajimari (White et al., 2010) and *P. cf. P. vetus* is known from El Golfo (Croxen et al., 2007). Térapa provides the first record of *P. compressus* in Sonora, but it is not unexpected.

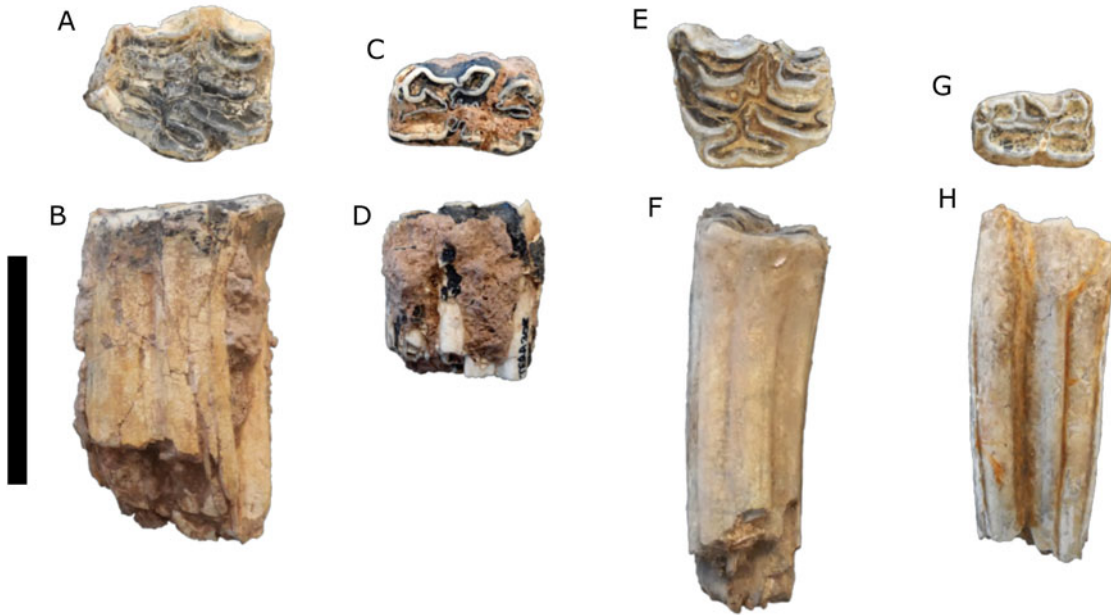


Figure 3. (color online) *Equus* spp. teeth. (A, B) *Equus* cf. *E. scotti*, upper left molar (TERA 286); (C, D) *Equus* cf. *E. scotti*, lower left molar (TERA 308); (E, F) *Equus* sp., upper left molar (TERA 303); (G, H), *Equus* sp., lower right molar (TERA 295). (A, C, E, G) in occlusal view; (B, D, F, H) in lingual view. Scale bar = 5 cm.

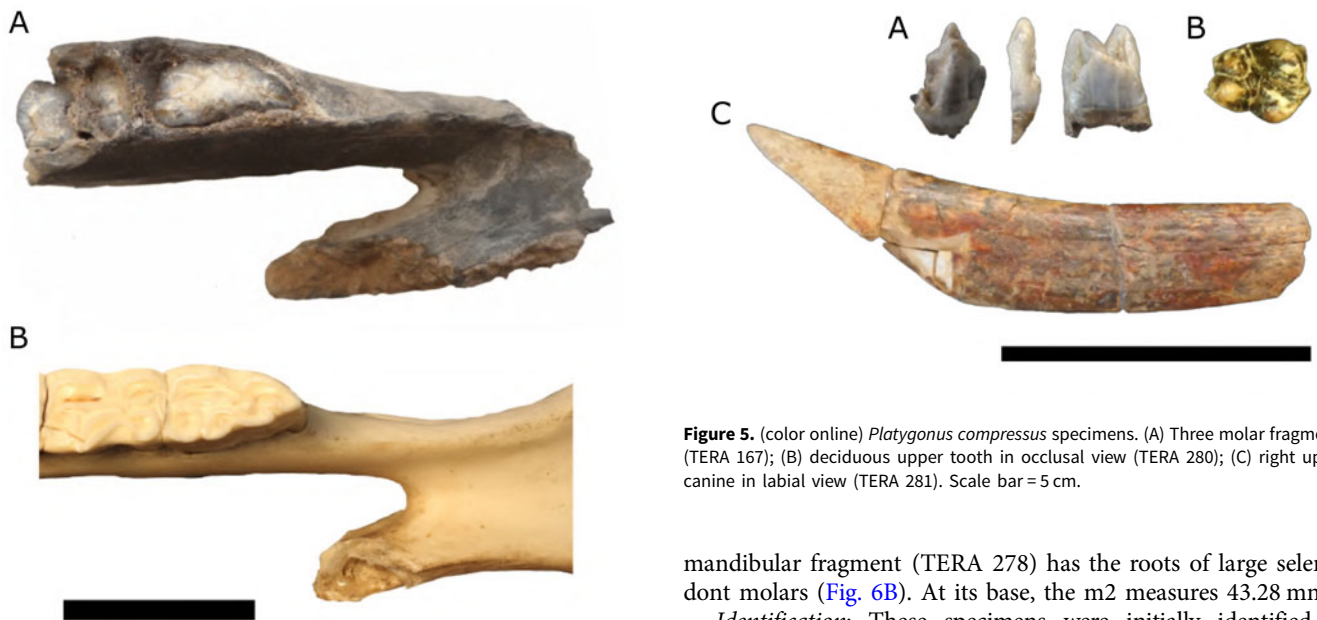


Figure 4. (color online) *Equus* spp. mandible fragments. (A) *Equus* sp. (TERA 294); previously identified as *Tapirus* by Mead et al. (2006); (B) *Equus caballus* (ETMNH-Z 15462); reference specimen. Scale bar = 5 cm.

Figure 5. (color online) *Platygonus compressus* specimens. (A) Three molar fragments (TERA 167); (B) deciduous upper tooth in occlusal view (TERA 280); (C) right upper canine in labial view (TERA 281). Scale bar = 5 cm.

mandibular fragment (TERA 278) has the roots of large selenodont molars (Fig. 6B). At its base, the m2 measures 43.28 mm.

Identification: These specimens were initially identified as “*Camelops*-sized” by Mead et al. (2006). The m2 measurement is within the range of *Camelops* provided by Honey et al. (1998) and Baskin and Thomas (2016). The mandible is also substantially larger than comparative material of *Palaeolama* and *Hemiauchenia*. The phalanx was also compared to phalanges of *Palaeolama* and *Hemiauchenia*, but it is considerably larger than specimens within both genera. *Camelops* is the only other Rancholabrean camelid, and it was large enough to have mandibles and phalanges of the size found at Térapa (Baskin and Thomas, 2016). The most recent review of *Camelops* described two species: *C. hesternus* in the Rancholabrean and *C. minidokae* in the Irvingtonian (Baskin and Thomas, 2016). Because *Camelops* is considered monotypic in the Rancholabrean and the specimens are consistent with the morphology, these specimens are assigned to *C. hesternus*.

Family Camelidae

Camelops Leidy, 1854

Camelops hesternus (Leidy, 1873)

Material: Left mandibular fragment with roots of m1-2 (TERA 278); left partial distal phalanx (TERA 279).

Description: The partial distal phalanx (TERA 279) has splayed ventral trochlea (Fig. 6A). This specimen is not a metapodial because of the lack of a condylar keel (Zazula et al., 2016). The

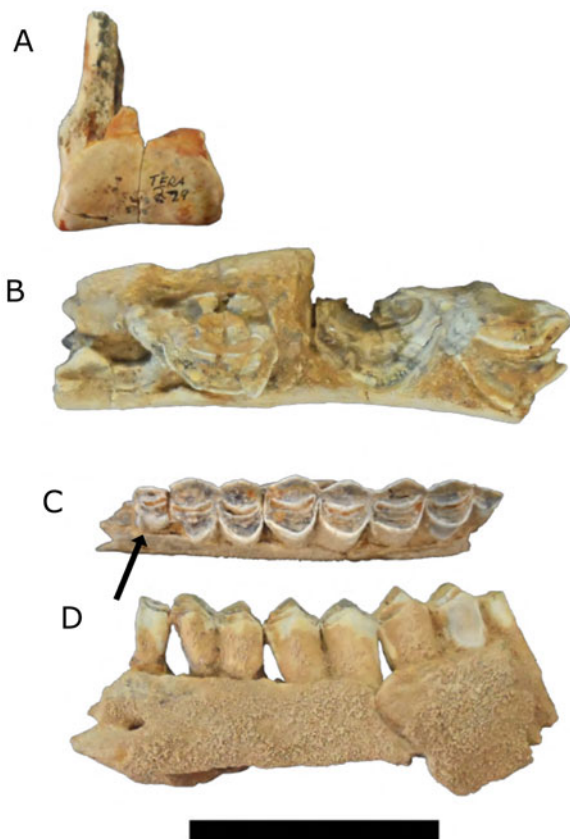


Figure 6. (color online) Camelidae specimens. (A) *Camelops hesternus*, partial left distal phalanx in anterior view (TERA 279); (B) *C. hesternus*, left mandibular fragment, including roots of first and second molars, in occlusal view (TERA 278); (C) *Palaeolama mirifica*, right dentary fragment with a partial fourth premolar and three molars in occlusal view and labial view (D) (TERA 156). Black arrow indicates the infolding on the p4 that is characteristic of *Palaeolama*. Scale bar = 5 cm.

Remarks: *Camelops hesternus* is widespread across the US and northern Mexico (Ferrusquía-Villafranca et al., 2010, 2017), including in Sonora (Cruz-y-Cruz et al., 2018). In the southern US, *C. hesternus* is known from Rancho La Brea (Jones and DeSantis, 2017), Diamond Valley Lake (Springer et al., 2009), Tule Springs (Scott et al., 2017), and throughout Arizona (Mead et al., 2005) and New Mexico (Harris, 2014).

Palaeolama Gervais, 1867

Palaeolama mirifica (Simpson, 1929)

Material: Left mandible fragment with partial p4–m3 (TERA 156).

Description: The mandibular fragment (TERA 156) has a partial p4 and m1–3 with brachyodont, selenodont dentition (Fig. 6C, D). The p4 has a vertical groove just posterior to the break. The m2 measures 19.18 mm at the base and 21.25 mm at the occlusal surface.

Identification: This specimen was initially identified as “*Hemiauchenia*-sized” by Mead et al. (2006). The groove on the p4 is indicative of the ‘complex infolding’ seen in *Palaeolama* (Fig. 6C; Kurtén and Anderson, 1980; Honey et al., 1998, p. 454). Both m2 measurements are within the range of *Palaeolama* provided by Honey et al. (1998). Because *Palaeolama* is monotypic in the Rancholabrean of North America (Honey et al., 1998) and the specimens fit the morphology, these specimens are assigned to *P. mirifica*.

Remarks: *Palaeolama mirifica* is found at Rancholabrean sites in Florida, California, and Texas (Kurtén and Anderson, 1980),

South Carolina (Sanders, 2002), Costa Rica (Pérez, 2011), and in the Mexican state of Puebla (Bravo-Cuevas and Jiménez-Hidalgo, 2015). However, it has not been documented in Arizona (Mead et al., 2005). *Palaeolama* sp. is documented at Irvingtonian sites at El Golfo in northwestern Sonora (Croxen et al., 2007) and Rio Tomayate in El Salvador (Cisneros, 2005), and from the Rancholabrean of Guatemala (Dávila et al., 2019). Térapa is the first Rancholabrean occurrence of *P. mirifica* in northwestern Mexico.

Order Carnivora

Family Canidae

Canis Linnaeus, 1758

Canis dirus Leidy, 1858

Material: Left mandible with c1–m2 (TERA 154), left maxilla and jugal with P3–M1, left mandible with partial c1–partial m2, right mandible with p4–m2, four incisors, two upper canines, two lower canines, one M1, one m3, and two unidentified fragments (TERA 450), distal left humerus (TERA 155).

Description: The left mandible with c1–m2 (TERA 154) and the distal humerus (TERA 155) were previously described in detail (Hodnett et al., 2009); the remaining specimens (TERA 450) are described here. All teeth in the maxilla and both mandibles are in an advanced stage of wear. The left maxilla is articulated with the left jugal, and the P3 is broken between the anterior and posterior roots (Fig. 7A, B). The left mandible is missing the coronoid process and angular process, but the condyle is complete (Fig. 7C). There is no evidence of an alveolus for a p1 on the mandible. The anterior mental foramen is inferior to the anterior p2, and the posterior mental foramen is inferior to the posterior p3. The right mandible is broken between the p4 and m1 and along the inferior masseter fossa (Fig. 7D). Only the anterior root of the m2 is present and the alveolus for a single-rooted m3 is broken. Cranial and dental measurements suggest a larger than average *C. dirus* (Fig. 8, Supplemental Table S2; Tedford et al., 2009).

Identification: Mead et al. (2006) initially identified *Canis dirus* at Térapa, and Hodnett et al. (2009) agreed for TERA 154 and TERA 155. Measurements on the left mandible indicate that this specimen is too large to be a different Rancholabrean-age canid, such as *C. latrans* or *C. lupus* (Fig. 8). *Canis armbrusteri* was also a large canid in the late Irvingtonian (Kurtén and Anderson, 1980; Harris, 2014) and is thought to have given rise to *C. dirus* (Tedford et al., 2009). The Térapa teeth are too worn to examine the cusp patterns, but the upper molars have reduced labial cingula as in *C. dirus* rather than *C. armbrusteri* (Tedford et al., 2009).

Remarks: *Canis dirus* is considered “one of the most common mammalian species in the Rancholabrean” and is found across the US and Mexico (Kurtén and Anderson, 1980, p. 171; Mead et al., 2005; Harris, 2014; Ferrusquía-Villafranca et al., 2017; Ruiz-Ramoni and Montellano-Ballesteros, 2019). In the southern US, *C. dirus* is common in the local faunas at Rancho La Brea (McHorse et al., 2012), Diamond Valley Lake (Springer et al., 2009), and Tule Springs (Scott et al., 2017). However, Térapa is the first occurrence of *C. dirus* in Sonora (Hodnett et al., 2009; Ruiz-Ramoni and Montellano-Ballesteros, 2019). There are at least three individuals of *C. dirus* found at Térapa based on lower left canines. The maxilla and mandibles of TERA 450 are likely from the same individual because of the similar degree of wear on the teeth. The extensive wear on the teeth and the large size suggests one older individual.

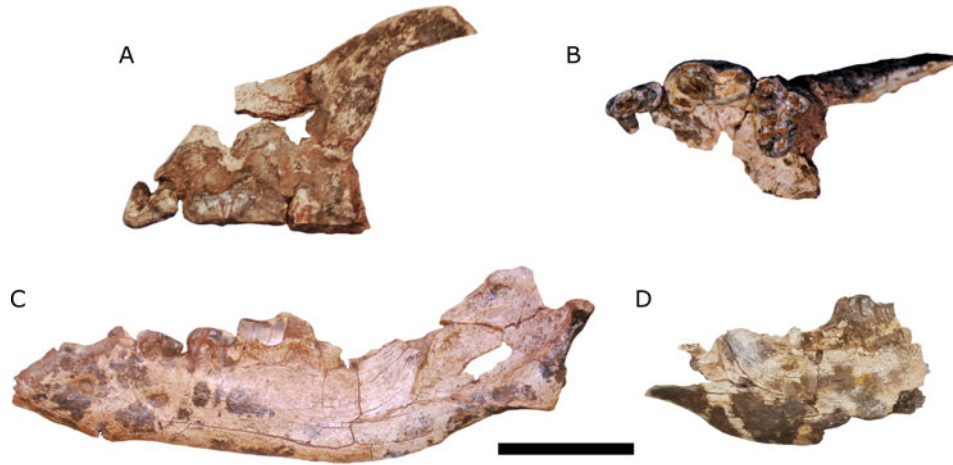


Figure 7. (color online) *Canis dirus* specimens (TERA 450). (A) Left maxilla and jugal with P3–M1 in lateral view; (B) left maxilla and jugal with P3–M1 in occlusal view; (C) left mandible with partial c1–partial m2 in buccal view; (D) right mandible with p4–m2 in buccal view. Scale bar = 5 cm.

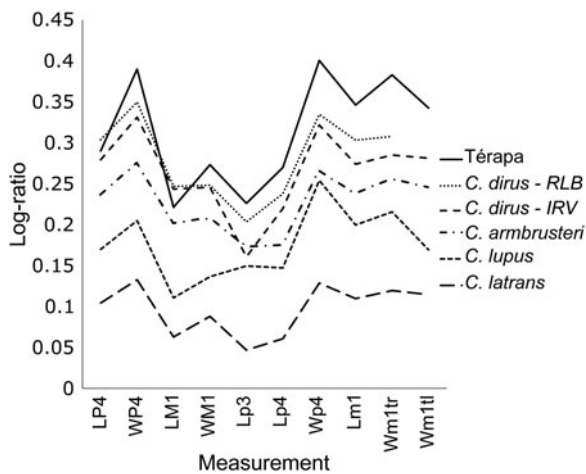


Figure 8. Log-ratios of measurements from Térapa *Canis dirus* (TERA 450) left maxilla and left mandible compared to *Canis dirus* from the Rancholabrean (RLB) and Irvingtonian (IRV), *C. armbrusteri*, *C. lupus*, and *C. latrans*. Measurements are relative to *Eucyon davisi*. Methods and reference data from Tedford et al. (2009), and data are available in Supplemental Table S2. Abbreviations: Left maxilla measurements: LP4 = length of P4; WP4 = width of P4; LM1 = length of M1; WM1 = width of M1. Left mandible measurements: Lp3 = length of p3; Lp4 = length of p4; Wp4 = width of p4; Lm1 = length of m1; Wm1tr = width of m1 trigonid; Wm1tl = width of m1 talonid.

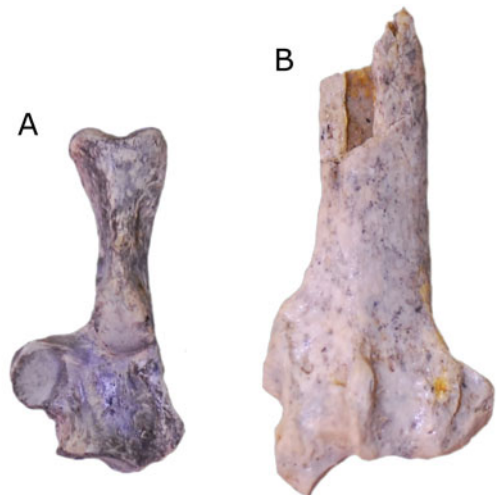


Figure 9. (color online) Carnivora specimens. (A) *Procyon lotor*, left calcaneum in anterior view (TERA 453); (B) *Lynx rufus*, distal left radius in anterior view (TERA 451). Scale bar = 1 cm.

Family Procyonidae
Procyon Storr, 1780

Procyon lotor (Linnaeus, 1758)

Material: Left calcaneum (TERA 453).

Description: The calcaneum (TERA 453) is complete (Fig. 9A). There is no tubercle present on the trochlear process, which has a minimal groove, and the calcaneum does not have an accessory surface between the anterior articular surface and the cuboid facet. The latter feature has a point on its dorsal edge. The greatest length of the calcaneum is 28.03 mm and the transverse breadth of the sustentaculum is 14.49 mm.

Identification: The calcaneum was previously identified as *Procyon* sp. (Mead et al., 2006). Following descriptions provided by Stains (1973; lack of a knob on the trochlear process), the calcaneum is now referred to *P. lotor*. Within *Procyon*, the calcaneum is assigned to *P. lotor* instead of *P. cancrivorus* because

of the minimal trochlear groove, the cuboid facet, and the lack of an accessory surface between the anterior articular surface and the cuboid facet (Stains, 1973). In addition, the length and breadth measurements are within the range of *P. lotor* provided by Stains (1973). Additional Pleistocene species of *Procyon* have been synonymized with *P. lotor* because the morphology was within the range of intraspecific variation (Kurtén and Anderson, 1980). Kurtén and Anderson (1980) recognized only one other fossil species, *P. rexroadensis*, which was limited to the Blancan LMA. Emmert and Short (2018) recommended synonymizing *P. rexroadensis* with *P. lotor* because of a lack of distinct morphological characters.

Remarks: Pleistocene-age *Procyon* has been found across North America and into northern South America (Kurtén and Anderson, 1980), but the fossil record is sparse (Harris, 2014). In Mexico, *Procyon* sp. is found at the Irvingtonian-age El Golfo (Croxen et al., 2007), and *Procyon lotor* is known from the Rancholabrean in California and New Mexico (Harris,

2014) as well as the Chihuahua-Coahuila Plateaus and Ranges, the Sierra Madre Oriental, the Trans-Mexican Volcanic Belt and the Yucatan Platform (Ferrusquía-Villafranca et al., 2010), so it is expected in the northwest of Mexico, although it is not reported from the Rancholabrean of Arizona (Mead et al., 2005).

Family Felidae

Lynx Kerr, 1792

Lynx rufus (Schreber, 1777)

Material: Distal left radius (TERA 451).

Description: The radius (TERA 451) is broken transversely across the diaphysis, which is compressed anteroposteriorly (Fig. 9B). The styloid process, dorsal tubercle, and lateral tuberosity are angular and pronounced. The greatest breadth of the distal end (Bd; von den Driesch, 1976) measures 19.41 mm.

Identification: This radius was initially reported as *Lynx rufus* by Mead et al. (2006), and the identification is confirmed here. The distinct features are as in Felidae rather than Canidae, and the anteroposterior compression excludes *Felis* (Kelson, 1946). As in *L. rufus*, there is a distinct horizontal ridge superior to the distal articulation on the posterior surface, and a lack of mediolateral constriction between the diaphysis and epiphysis. *Lynx rufus* is known from the Rancholabrean of Mexico (Ferrusquía-Villafranca et al., 2010) and Arizona (Mead et al., 2005), whereas *Lynx canadensis* has not been found south of Utah (Lavoie et al., 2019).

Remarks: *Lynx rufus* is frequently found at North American Pleistocene sites (Kurtén and Anderson, 1980), including at Rancho La Brea (McHorse et al., 2012), Diamond Valley Lake (Springer et al., 2009), and Tule Springs (Scott et al., 2017). *L. rufus* is known across northern and central Mexico during the Rancholabrean (Ferrusquía-Villafranca et al., 2010, 2017). In Mexico, *L. rufus* is also known from the Irvingtonian of Cedazo in central Mexico (Mooser and Dalquest, 1975), and the latest Pleistocene or early Holocene of Jimenez Cave in Chihuahua (Messing, 1986).

Smilodon Lund, 1842

Smilodon cf. *S. fatalis* (Leidy, 1868)

Material: Fragment of right dP3 including ectoparastyle and parastyle (TERA 452).

Description: The tooth fragment (TERA 452) is mediolaterally compressed and has a distinct parastyle and ectoparastyle (Fig. 10B). The tooth fragment is lacking a distinct protocone and preserves no evidence of any lingual flaring that would indicate a protocone had been present. There is a minimal anterior cingulum on the tooth. Diagnostic measurements are not possible because of the fragmented nature of the specimen.

Identification: This specimen was initially identified as *Canis latrans* by Mead et al. (2006). However, the mediolateral compression and parastyle suggest this tooth is from Felidae and not Canidae. The size suggests a large cat, possibly *Panthera*, *Puma*, or *Smilodon*. The lack of a protocone excludes *Panthera* and *Puma* (Cherin et al., 2013; Babiarczyk et al., 2018), and the ectoparastyle and cingulum are as in *Smilodon* (Christiansen, 2013). Therefore, we confer the tooth fragment to *Smilodon*. Because *Smilodon fatalis* is common during the Rancholabrean, *S. populator* has not been found in North America, and *S. gracilis* is from the early Irvingtonian, we confer the specimen to *S. fatalis*.

Remarks: *Smilodon* is known throughout much of North America from the Irvingtonian and Rancholabrean LMAs (Kurtén and Anderson, 1980; Babiarczyk et al., 2018), but this is

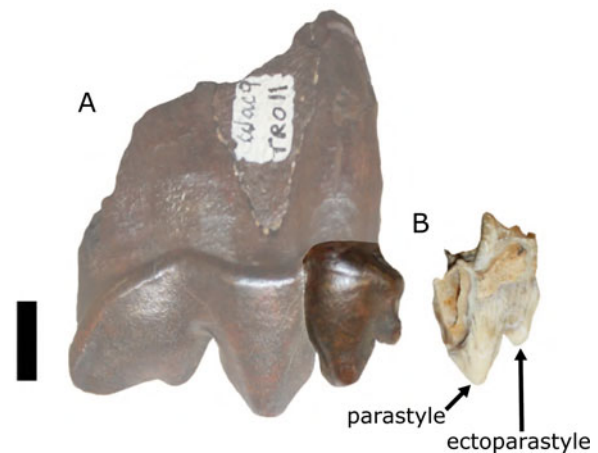


Figure 10. (color online) *Smilodon carnassials*. (A) *S. fatalis* adult upper right fourth premolar (UF/TRO 11) with parastyle and ectoparastyle shaded more opaquely; reference specimen; (B) *S. cf. S. fatalis* fragment of deciduous upper right third premolar in labial view with parastyle and ectoparastyle labeled (TERA 452). Scale bar = 1 cm.

the first record from the northwest of Mexico. In Mexico, *S. fatalis* has been found at Pleistocene sites across the Central Plateau, the Trans-Mexico Volcanic Belt, and the Sierra Madre Oriental (Ferrusquía-Villafranca et al., 2010, 2017). In the United States, *S. fatalis* is known from the Rancholabrean of eastern New Mexico and southern California (Kurtén and Anderson, 1980; Morgan and Lucas, 2001; Harris, 2014), including at Rancho La Brea (McHorse et al., 2012), Diamond Valley Lake (Springer et al., 2009), and Tule Springs (Scott et al., 2017). The presence in northwestern Mexico is novel but not wholly unexpected, although it has not been reported from the Rancholabrean of Arizona (Mead et al., 2005).

Community structure

The late Pleistocene and modern mammalian communities vary in their composition. The fossil community has two equids, two camelids, one tayassuid, one canid, two felids, and one procyonid, whereas in the present day, the Térapa region has one tayassuid, two canids, three felids, four mephitids, two mustelids, and three procyonids. The fossil community presented here consists of four herbivores from two orders of ungulates (Fig. 11). The four carnivores are equally divided into carnivores and carnivorous omnivores. Yet, the modern community is largely dominated by 11 carnivorous omnivores, with three carnivores, one herbivorous omnivore, and no herbivores (Fig. 11). *Lynx rufus* (carnivore) and *Procyon lotor* (carnivorous omnivore) are the only taxa to occur in both fossil and modern communities.

The faunal turnover of the taxa in this study corresponds with a 97% decrease in mean body mass (BM; kg) from 289 kg to 9 kg. *Odocoileus virginianus* is the largest ungulate at Térapa today (BM = 55 kg), but, in the past, the larger *Equus scotti* (BM = 555 kg), *Camelops hesternus* (BM = 1100 kg), *Palaeolama mirifica* (BM = 80 kg), and *Platygonus compressus* (BM = 110 kg) also occurred at the site. Similarly, with the loss of *Smilodon* cf. *S. fatalis* (BM = 400 kg), the largest carnivore today is *Puma concolor* (BM = 52 kg). *Canis dirus* (BM = 50 kg) was nearly the same mass as *P. concolor*. *Procyon lotor* (BM = 5.5 kg) is the smallest taxon in the fossil community presented here, but the modern community has eight species of Carnivora that are smaller than *P. lotor*.

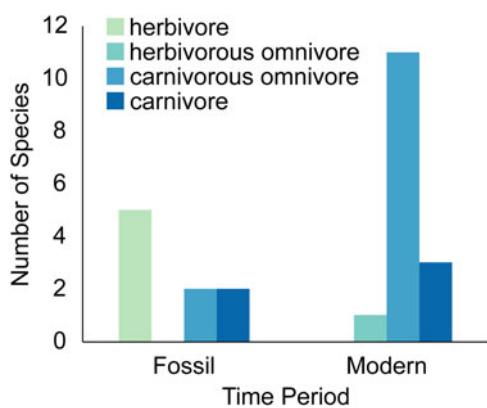


Figure 11. (color online) Feeding strategies of large-bodied mammals at Térapa in the fossil community ($n = 9$ species) and the modern community ($n = 15$ species).

DISCUSSION

Térapa provides the first Rancholabrean occurrences of *Palaeolama*, *Procyon*, and *Smilodon* in northwest Mexico and the first records of *Platygonus compressus* and *Canis dirus* in Sonora. *Equus*, *Camelops*, and *Canis* are well-represented at sites across the North American desert region and, although *Platygonus* and *Lynx* are sparsely represented in northern Mexico, they have extensive records in the southwestern US, making them expected at Térapa during the Rancholabrean.

Térapa lies along the Pleistocene Sonora–Central America Pacific lowlands corridor and the Rocky Mountains–Sierra Madre Occidental corridor (Ceballos et al., 2010). The former allowed dispersal of tropical taxa north and the latter permitted the movement of temperate taxa south (Ceballos et al., 2010). Additional ‘holding pen’ areas would have been inhabited by taxa until more preferred environments allowed further migration (Ceballos et al., 2010; Woodburne, 2010). With the presence of water and diverse vegetation, Térapa likely acted as an area of faunal exchange. For instance, *Palaeolama* originated in South America (Webb, 1974), and researchers postulate that *P. mirifica* used tropical corridors along the Sonora–Central America Pacific lowlands and the Tamaulipas–Central America Gulf lowlands to move north across Mexico (Bravo-Cuevas and Jiménez-Hidalgo, 2015).

The fauna at Térapa documents a shift in feeding strategy from a community of primarily herbivores during the late Pleistocene to one of primarily carnivorous omnivores at present. Ranges of carnivorous species and the richness of carnivorous communities have been shown to be affected by climatically driven habitat changes during the transitions of the glacial and interglacial stages of the Pleistocene (Arias-Alzate et al., 2017, 2020). In this region of mosaic complexity and shifting ecosystems, these dynamic environmental changes may have driven faunal community change in this area, including the transition to a carnivorous-dominated community.

Previous studies have documented large declines in community average body mass at the transition between the late Pleistocene and Holocene (Stegner and Holmes, 2013; Smith et al., 2018). The mammalian fauna presented here indicates a similar change, with a 97% decline of community average body mass from 289 kg to 9 kg. The considerable change is due to the loss of megaherbivores and the reduction in body mass of the felids present. Average body mass decline has been linked to

rises in global temperature (Gardner et al., 2011; Martin et al., 2018; Martin and Barboza, 2020) as well as shortages in food availability (Huston and Wolverton, 2011; McNamara et al., 2016; Westover and Smith, 2020). Although Térapa provides a broad scope of temporal change at a single locality (with several sub-localities therein), it nevertheless captures broad environmental change as recorded by the reorganization of the terrestrial fauna.

If antilocaprids, bovids, and cervids had been included in the study of community structure, the fossil community would add four artiodactyl species (*Capromeryx* sp., *Stockoceros* sp., cf. *Odocoileus*, and *Bison* sp.; Mead et al., 2006) while the modern community would only add one species (*Odocoileus virginianus*). The inclusion of these taxa would only exacerbate the differences between the faunal communities during the two time periods. While it is likely additional species lived at Térapa and have not been recovered, it would require finding 59 additional species of Carnivora at Térapa to match the proportional community structure of carnivores and herbivores that is present currently. The dramatic shift from herbivores to carnivores at Térapa follows a similar pattern documented across Mexico (Arroyo-Cabrales et al., 2010; Ferrusquía-Villafranca et al., 2010).

The large mammalian fauna at Térapa aligns with previous faunal environmental analyses that described an elevational mosaic of a temperate to tropical/subtropical marsh, an adjacent semiarid savanna-grassland, a slow-moving freshwater stream, and a riparian forest area along the water (Mead et al., 2006; Nunez et al., 2010; Bright et al. 2016). The presence of both browsing and grazing herbivores implies a diverse assemblage of trees, forbs, and grasses at Térapa in the past. Currently, there are no grazing ungulates present at Térapa, and the region lacks expansive grasslands.

Additionally, the presence of *Lynx rufus* suggests a more restrictive paleoenvironmental interpretation and may be indicative of a mosaic-edge habitat associated with the nearby mountain foothills (~16 km). Extant *L. rufus* occupy strictly temperate habitats of savanna/grassland/chaparral but also occupy relatively large home ranges (3–96 km² for males and 1–38 km² for females; Larivière and Walton, 1997). The diet of *L. rufus* includes rodents, small ungulates, large ground birds, and reptiles (Larivière and Walton, 1997), which are all present in the fossil assemblage at Térapa (Mead et al., 2006).

During the glacial period when the fossils at Térapa were deposited, cooler global temperatures produced a more constricted Intertropical Convergence Zone (ITCZ) and increased precipitation in northwestern Mexico (Metcalfe, 2006). As temperatures warmed into the modern interglacial period, the ITCZ expanded poleward, and shifted the mid-latitude jet stream and associated precipitation poleward (Metcalfe, 2006). The poleward shift of the ITCZ and mid-latitude jet stream also shifted the biodiversity-rich savanna habitats northwards into the southwestern US and as a consequence, left behind the present-day scrubland habitats of northern Mexico (Metcalfe, 2006). As temperatures increased by ~6°C and precipitation decreased, Sonora became more arid, and species were forced to shift their ranges, often northward (Metcalfe, 2006).

With impending climate change and anticipated warming of an additional 4°C globally by the end of the 21st century, paleoecological studies of past faunas can have great implications for wildlife conservation because of the associated biodiversity shifts (Walther et al., 2002; Foley et al., 2005; Lipton et al., 2018). The Sonoran Desert is expected to continue expanding further

northwards in Arizona and New Mexico as climate projections suggest an increasingly arid climate (Magaña et al., 2012). With shifting environments, species may have to alter their geographic ranges, but only 41% of natural areas (i.e., areas with low effects of human modification) in the US are suitably connected to allow for species movement (McGuire et al., 2016). Conservation efforts on the margins of species ranges, especially those in or adjacent to the desert southwest of North America, may also help facilitate the preservation of unique genetic adaptations to harsh climatic pressures (Plumb and McMullen, 2018). Sustaining habitats and their connectivity for conservation may be difficult to facilitate, but we aim to provide a broad scope of anticipated biodiversity change in the presence of continued warming.

CONCLUSIONS

Relatively few fossil sites are well known from the RanchoLabrean LMA of northern Mexico (Ceballos et al., 2010; White et al., 2010), and Térapa provides an extensive faunal record in an area that was once a marsh savanna but is now xeric desert chaparral. At this site, we describe mammalian community restructuring due to the loss of the large-bodied, herbivorous ungulates in response to environmental change. Whereas the fossil community was nearly evenly split between carnivorans and herbivorous ungulates, the present community is dominated by carnivorans (Fig. 11). There is also an associated 97% decrease in mean body mass through time because of the loss of the largest taxa. We postulate that this change is largely due to rising temperature and shifting precipitation regimes and the resulting climatically driven changes in vegetation, such as the loss of grasslands. As the climate continues to warm and the deserts shift north, today's fauna in the southwestern US and northwestern Mexico will be similarly affected.

Long term records of faunal change, such as that at Térapa, provide valuable information for guiding modern conservation practices. The presence of eight taxa of Perissodactyla, Artiodactyla, and Carnivora in a community that existed approximately 40–43 ka (MIS/OIS 3) provides a critical spatial and temporal record, including the first RanchoLabrean occurrences of *Palaeolama*, *Procyon*, and *Smilodon* in northwest Mexico, and the first records of *Platygonus compressus* and *Canis dirus* in the state of Sonora. It is probable that more sites exist in this region and can contribute to a more complete understanding of the area but have yet to be found, fully analyzed, and reported upon. Future fossil recovery will provide much needed details about the fauna in and around Térapa and in Sonora, and will also enable further study of regional habitat and biodiversity shifts in the southwestern US.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/qua.2020.125>

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