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LATE PLEISTOCENE VERTEBRATE FAUNA AND BAT GUANO DEPOSIT OF LA TETERA CAVE, ARIZONA, USA

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ABSTRACT

La Tetera is a cave formed in the mid-late Paleozoic limestones of the Rincon Mountains of southern Arizona, USA. The cave was sealed since the late Pleistocene and preserves a small vertebrate fauna reflecting the Rancholabrean NALMA including two extinct large mammals, horse (*Equus conversidens*) and camel (*Camelops hesternus*), as well as an extinct vampire bat (*Desmodus stocki*). Additional recovered biotic remains include hackberry endocarps (*Celtis*), charcoal, and a harmonious assemblage of vertebrates including toad (*Anaxyrus*), tortoise (*Gopherus*), squamates (*Heloderma*, *Dipsosaurus*, *Phrynosoma, Uta* or *Urosaurus, Aspidoscelis, Sonora, Rhinocheilus, Masticophis* or *Coluber,* and *Crotalus*), roadrunner (*Geococcyx*), wren (*Salpinctes*), owl (cf. *Athene*), heteromyid and cricetid rodents, rabbits, *Myotis* sp., and shrew. Further investigation will likely reveal additional biotic remains. Preservation of bone is relatively poor, probably due to as-yet-undetermined, corrosive geochemical processes. Fossils occur as isolated skeletal elements scattered sparsely in several areas of the small cave or those recovered by screening of unconsolidated cave floor sediments (in which *Desmodus* is the second most commonly recovered taxon, after toads). A large, stratified paleoguano deposit in one room provides the potential to recover ancient environmental DNA from the bats, their dietary sources, and autochthonous and allochthonous microorganisms. A sample of the guano deposit gave a calibrated radiocarbon age of 23.7 ka, confirming a late Pleistocene age for the deposit and placing it within late Wisconsinan full glacial time and within Marine Isotope Stage 2. The radioisotopic age(s) of the vertebrate fossils are unknown. Several of the fossil vertebrates reflect a desertscrub fauna similar to that of the region today, and may reflect a southwestern lowland refugium for arid-adapted biota during the late Pleistocene.

INTRODUCTION

Herein we describe the vertebrate fauna from La Tetera Cave (LTC), a recently discovered cave in the Rincon Mountains, a metamorphic core complex in southern Arizona within the southern Basin and Range morphotectonic region of southwestern North America. The Rincon Mountains cover about 520 square kilometers and range in elevation from about 900 m to 2643 m. The eastern slopes face the San Pedro River Valley while the western slopes drain into the Santa Cruz River. LTC occurs in Colossal Cave Mountain Park (CCMP), in the southwestern part of the Rincon Mountains, where the sedimentary rocks are largely Permian limestones of the Horquilla and Earp Formations (Drewes, 1977). LTC and other caves in the vicinity may have developed from an early Neogene event (beginning ca. 25 Ma) that gave rise to the Tortolita-Catalina-Rincon metamorphic core complex (Drewes, 1977; Davis, 1980; Davis et al., 2023; Muchmore and Pape, 1999). Ecologically, the area in and near Colossal Cave Mountain Park is covered with vegetation of the Arizona Upland/Eastern Sonoran Basins of the Sonoran Basin and Range and of the Apachean Valleys and Low Hills of the Madrean Archipelago (Griffith et al., 2014).

Peachey (1993) described nearby Arkenstone Cave, also in Colossal Cave County Park and within 1 km of LTC, as a hypogenic type cave (showing deep origins that are due to processes largely separate from meteoric waters). Arkenstone Cave appears to have undergone speleogenesis as a direct result of physical and geochemical conditions associated with the Catalina-Rincon metamorphic core complex. Speleogenesis appears to have been initiated during the Oligocene-Miocene as a result of the translation of Paleozoic carbonates over Laramide orogeny intrusives by a low-angle detachment fault. During an estimated movement of 20-40 km, the carbonate rocks of the upper plate were buried at a depth of 8-10 km, and were dilated while undergoing elevated temperatures and infusions of brines. Along high angle tear faults, iron-rich silica melts produced distinctive red matrix breccias (seen also in LTC). Minor replacements of carbonates near the detachment faults by barite are notable features in the immediate vicinity of Arkenstone Cave. Following further isolation from meteoric waters through burial by thousands of meters of syntectonic sediments, the terrain was uplifted to its present elevation during block faulting of the Basin and Range orogeny (12-9 Ma ago; Davis, 1980; Davis et al., 2023). Drainage and the possibility of surface openings to Arkenstone Cave may have occurred as early as 3.5 Ma as local base level dropped when regional stream integration is thought to have been achieved. Much of the same is probably true also for LTC, which has not been studied in regard to its speleogenesis. Today, Arkenstone Cave exhibits a ramiform passage plan with extreme variations in both cross sections and profiles. It has no connections

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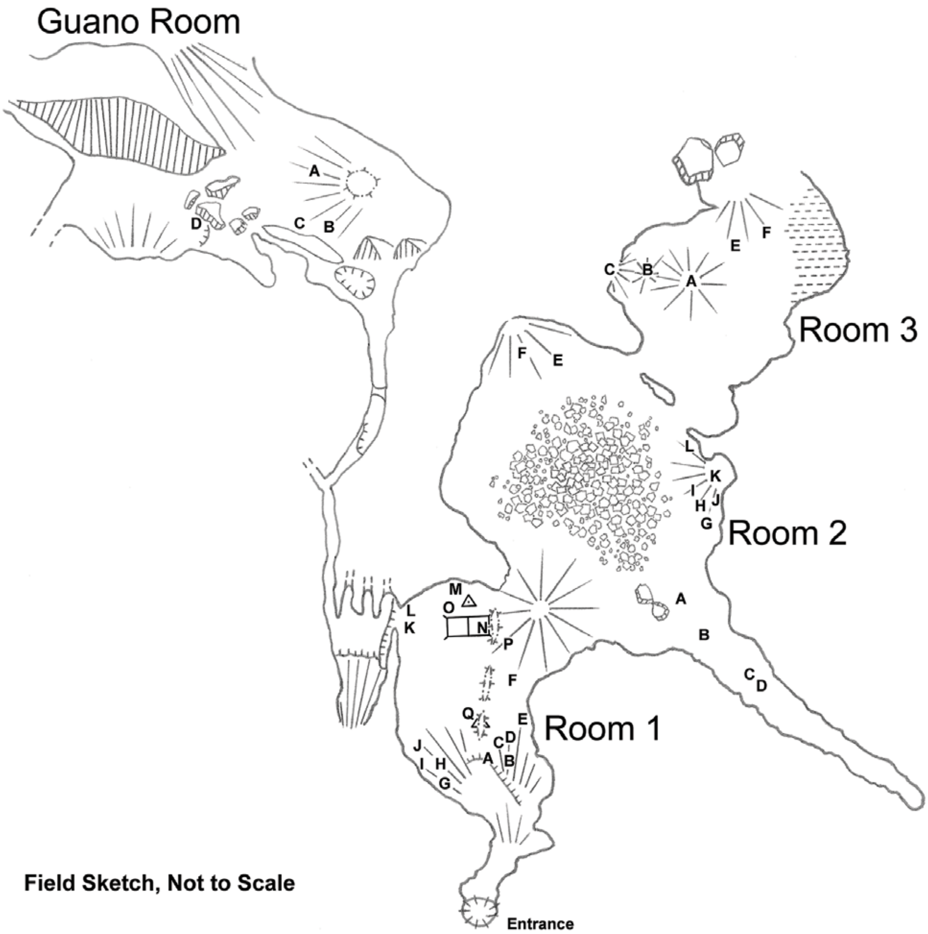

Figure 1. Preliminary plan map of La Tetera Cave, Colossal Cave Mountain Park, Pima County, Arizona, with locations of vertebrate fossils indicated by letters (keyed to museum catalog numbers in taxonomic accounts and Table 1). In Room 1 where the Camelops pelvis occurred at the surface (Room 1 bone N), the two adjoined test pits excavated (1m x 1m x 30cm) also produced a camel metapodial, partial phalanx, two lumbar vertebrae, and a patella of Camelops, and a scapula of Gopherus. Not to scale. Top of map is approximately North, but magnetic interference in area needs to be addressed.

to either a local recharge or discharge system. Except for minor entrance debris, speleothems, and internally derived clays, Arkenstone Cave contains no sedimentary deposits. In partial contrast, LTC has numerous unconsolidated debris cones (Fig. 1).

METHODS

We visited LTC several times between 2002 and 2004. LTC is Oklahoma Museum of Natural History (OMNH) locality V1182, Colossal Cave Mountain Park (east of Tucson), Pima County, Arizona. The initial discovery of LTC had been made by Dave Arrand, then a staff member of CCMP, a few years previously when the entrance consisted only of a small <10 cm diameter opening on the surface. The entrance is at about 1100 m elevation. The entrance slowly enlarged naturally until a camera probe lowered on a rope indicated a pristine cave. The entrance hole was manually enlarged and gated for safety and protection before human entry. The cave opens to a 12 m vertical drop that levels out into passages with five rooms. Upon an initial survey numerous loose debris cones were noted in each room visited; all but one of them showed one to several bones on the surface, while one debris cone had many bones on its surface. We drew a preliminary sketch plan map of the cave and mapped the surface bones onto it (Fig. 1; Table 1). Two contiguous 1 m^2 test pits were excavated by 10-cm increments to a depth of 40 cm in the first room where a large animal pelvis occurred in the floor sediments beneath a row of solutional pendants in the ceiling. The first of these was called Pit 1 and the second called East Pit. No stratification was observed in the test pits, probably because the floor sediments consisted of the sudden input of debris cones from ceiling chutes. In the process of excavating the test pits, several additional large animal bones were recovered. Sediments removed from the test pits were dry- and wet-screened with window mesh and 0.6 mm mesh screens to recover microvertebrates. In addition to the vertebrate bones, the surface held a few half-endocarps of hackberry, *Celtis* sp., that were encrusted with calcite crystals and presumed to be approximately the same age as the bones that were similarly encrusted. In a large room with flowstone decorations (draperies and a large stalagmite), a floor deposit interpreted as ancient bat guano was discovered and was sampled for radiocarbon dating.

All specimens recovered from LTC were cataloged into the Vertebrate Paleontology collection of the Oklahoma Museum of Natural History (OMNH), University of Oklahoma, Norman; all catalog numbers cited herein are OMNH catalog numbers. A sample of the sediment from the guano deposit was submitted to Rafter Radiocarbon Laboratory in New Zealand for a ^{14}C AMS radiocarbon date.

Table 1. Key to fossils indicated in La Tetera Cave sketch map (Fig. 1) and museum catalog numbers. Taxonomic identifications are of cleaned and prepared specimens but only the genera are provided here; for specific identifications see the taxonomic accounts and Table 6.

Room	Map Letter	Taxon	Skeletal Element	OMNH catalog number
1	A	*Camelops*	Radius-ulna? badly splintered	Not collected
1	B	Unidentified	Long bone fragment	
1	C	*Gopherus*	Peripheral	80558
1	D	Unidentified	Long bone fragment	Not collected
1	E	Mammalia	Rib fragment beneath rock	Not collected
1	F	Mammalia	Scattered splinters of large animal bone (3 pcs.)	Not cataloged
1	G	*Gopherus*	Bone fragments	80564
1	H	*Gopherus*	Scapula, shell fragments	80563
1	I	*Gopherus*	Peripheral	80556
1	J	*Gopherus*	Shell fragment	
1	K	*Gopherus*	Plastron fragments	80557
1	L	*Gopherus*	Humerus or femur shaft	80554
1	M	*Salpinctes*; *Gopherus*; Anura; Rodentia	Partial skeleton; Ulna; Radioulna or tibiofibula frag.; Tibia prox. frag.	80618; 80555; 81091; 81092
1	N	*Camelops*; *Gopherus*	Pelvis; Scapula	72383; 80562
1	O	*Gopherus*	Head of humerus or femur	80560
1	P	*Desmodus*; Anura	Radius shaft fragments; Long bone fragment	80512; 81090
1	Q	*Gopherus*	Peripheral fragment	80559
2	A	*Desmodus*	Radius shaft (2 pcs.)	81095
2	B	Aves?	Long bone shaft fragments	Not cataloged
2	C	Rodentia	Right i1	81093
2	D	*Celtis*; Unidentified	Endocarp halves (several); ?rib	Not cataloged; Not cataloged
2	E	*Gopherus*	Plastron fragment	80567
2	F	*Gopherus*	Shell fragment	80568
2	G	*Equus*	Digit III phalanx 1	72091
2	H	*Equus*?	Thoracic vertebrae (2)	72087, 72088
2	I	*Equus*	Digit III phalanx 3 (ungual)	72089
2	J	*Equus*	Distal metapodial III + phalanx 3	72093 + 72090
2	K	*Equus*	Metacarpal III	72092
2	L	*Chaetodipus*	Partial skeleton	Holocene intrusive; not cataloged
3	A	*Gopherus*	Shell fragments (numerous)	80571
3	B	*Lepus*; Cf. *Mephitis*	Assoc. m2, radius shaft, humerus shaft, metatarsal; Axis fragment + fibula?	80542; 80545 + 80544
3	C	*Gopherus*; *Lepus*	Costal, 2 peripherals + Ischium, centrum, peripheral, frags.; Thoracic vertebra	80569 + 80570; 80543
3	E	*Lepus*	Rib	80540
3	F	*Lepus*	Ulna	80541
Guano	A	Mammalia	Rib fragment?	Not collected
Guano	B	*Gopherus*	Scapula, shell fragments	80656
Guano	C	Rodentia	I1s (2)	Not cataloged
Guano	D	*Onychomys*; *Lepus*	Dentary with i1 & m1; Metatarsal	80513; Not collected

Terminology for the identification of anurans follows Sanchiz (1998), Holman (2003), Bever (2005), and Gómez and Turazzini (2016). Terminology for the squamate osteology predominantly follows Evans (2008) and Gauthier et al. (2012) for lizards and Auffenberg (1963) and LaDuke (1991) for snakes. Terms used for bird anatomical remains follow Howard (1929), Baumel et al. (1979), and Proctor and Lynch (1993); those used for mammal remains follow Martin et al. (2001) and Ryan (2010). Modern comparative specimens used in this study are at The Mammoth Site, Hot Springs, South Dakota, and the OMNH.

RESULTS

The radioisotopically-dated sample consisted of a small bulk sample of iron-rust-colored dry sediment of presumably degraded bat guano, as well as cave silt, clay, and a few rock fragments. The sample was treated with acid/alkali/acid washes until the liquid was clear. In the chemical pretreatment process the original sample weight decreased by 73 %. The sample (NZA 38096) was 8.4 +/- 0.09 % modern and gave a date of 19,839 +/- 85 rcybp. This is equivalent to a calibrated radiocarbon age ranging from 23,857 cal ybp to 23,543 cal ybp (68 % confidence interval; 95 % confidence interval is 23,984 cal ybp to 23,351 cal ybp). The result confirms a late Pleistocene age for the deposit and places it within the late Wisconsinan full glacial climatic regime and within Marine Isotope Stage 2 (Elias, 2023).

The vertebrate fossils found in other areas within the cave likely also date to the late Pleistocene, as indicated in part by the extinct taxa noted below, but are not necessarily contemporaneous with the dated guano-sediment sample. Vertebrate taxa identified in LTC are as follows. Discussion of justification for the taxonomic identifications is minimized especially for small mammals that are routinely found as late Pleistocene fossils in southwestern North America. Lengthier discussion is provided for taxa less well known as late Pleistocene fossils, or whose identification might be more readily confused with other morphologically similar taxa.

Systematic Paleontology

Class Amphibia

Order Anura

Family Bufonidae

Anaxyrus sp. (toad)

Material and Provenience: OMHH 72135, right ilium Pit 1 0-10 cm; OMNH 72139, right ilium Pit 1 0-10 cm; OMNH 72176, right ilium Pit 1 10-20 cm; OMNH 72175, left ilium Pit 1 10-20 cm; OMNH 72222, left ilium Pit 1 20-30 cm.

Discussion: All ilia are in various states of completeness except for OMNH 72135, which is complete. The pars ascendens and pars descendens (dorsal and ventral acetabular expansions) are present. The acetabular fossa is preserved on each specimen. The tuber superior (dorsal tubercle and the dorsal prominence) are distinct on all specimens but not overly large and are not positioned greatly anterior to the acetabular fossa. The dorsal prominence varies in robustness but all have a distinct knob appearance; some are roughened with grooves (character state #4 in Bever 2005). This prominence varies from gradual to steep on the anterior and posterior slopes (Tihen 1962, Bever 2005). There is no evidence of a dorsal ilial crest on any specimen.

Based on modern comparative specimens and Holman (2003), the lack of a dorsal ilial crest indicates that the fossils do not belong to any member of Ranidae (frogs). The ilial shafts are distinctly more robust than occurs in either *Spea* or *Scaphiopus*; therefore, the fossils are not Scaphiopodidae (spadefoot toads). The size and robustness of the fossil ilia negates their belonging to any members of the North American Hylidae (tree frogs), Craugastoridae (barking frogs), or Microhylidae (narrow-mouthed frogs). Thus, by process of elimination, the fossil ilia from LTC are identified as belonging to a bufonid. Bever's (2005) analysis of *Bufo* indicated that there is much interspecific variation within ilial characters making species level identifications suspect. The analysis of "*Bufo*" species by Bever (2005) included species that are now included in *Anaxyrus*, *Incilius*, and *Rhinella* (Frost et al., 2006), although we are not certain as to how much this might change the overriding results. In using character #4 (surface of dorsal prominence smooth or rough) of Bever (2005) and our analysis of our modern comparative collection, it appears that the fossil ilia do not belong to any species of *Incilius* or *Rhinella*. Accordingly, we identify the most complete fossil ilium as a member of *Anaxyrus*. We agree with Bever (2005) that we cannot use his character #4 to identify the ilium to a particular species within *Anaxyrus*.

Five species of *Anaxyrus* are extant in southern Arizona, with three of them, *A. cognatus*, *A. punctatus*, and *A. woodhousii,* occurring in the Tucson Basin region (Murphy, 2018). Fossils of true toads (and spadefoot toads, tree frogs, and narrow-mouth frogs) are reported from the late Pleistocene of Arizona (Mead, 2005).

Anura indet.

Material and Provenience: OMNH 72136, scapula; 72137, urostyle; 72138, associated partial skeleton; 72140, right ilium; 72141, humerus; 72142, humerus; 72143, radioulna; 72144, long bone; 72145-72147, vertebrae from Pit 1, 0-10 cm. OMNH 72177, urococcyx; 72178, tibiofibula; 72179-72181, vertebrae; 72183, ?urococcyx fragment from Pit 1, 10-20 cm. OMNH 72223, ilium; 72224-72227, vertebrae; 72228, urococcyx from Pit 1, 20-30 cm. OMNH 80576, distal humerus; 80577, sacral vertebra; 81113, scapula?; 81114, vertebra from E pit, 0-10 cm. OMNH 80599, tibiofibula; 80600, vertebra, humerus and tibiofibula; 81115, vertebrae, urococcyx, long bones from E pit, 10-20 cm. OMNH 80602, urococcyx; 80603, humerus; 80604-80605, left ilia; 81117, vertebrae & long bones; 81118, long bone & 2 scapulae from E pit, 20-30 cm. OMNH 81090, long bone fragment from Room 1 bone P. OMNH 81091, radioulna or tibiofibula fragment from Room 1 bone M.

Discussion: Due to incompleteness and/or damage, these skeletal remains cannot be identified beyond the level of Anura.

Class Reptilia

Order Testudines

Family Testudinidae

Gopherus **sp. indet. (tortoise)**

Material and Provenience: OMNH 80552, plastron fragment from Pit 1, 20-30 cm. OMNH 80553, shell fragments, 3 pcs. from Pit 1, 0-10 cm. OMNH 80554, humerus or femur shaft from Room 1 bone L. OMNH 80555, left ulna from Room 1 bone M. OMNH 80556, peripheral from Room 1 bone I. OMNH 80557, shell fragments 4 pcs. From Room 1 bone K. OMNH 80558, peripheral, potentially left 2nd , from Room 1 bone 1C. OMNH 80559, shell fragments (30 pcs.) from Room 1 bone Q. OMNH 80560, proximal fragment of left femur and long bone shaft from Room 1 bone O. OMNH 80561, costal, potentially left 2nd or 4th , associated with Room 1 bone 7A. OMNH 80562, right scapula nearly complete from Room 1 bone N. OMNH 80563, shell fragment from Room 1 bone H. OMNH 80564, long bone fragment from Room 1 bone 1G. OMNH 80565, right scapula from Guano Room. OMNH 80566, shell fragment near survey marker B-23. OMNH 80567, plastron fragment from Room 2 bone E. OMNH 80568, shell fragment from Room 2 bone F. OMNH 80569, right partial ischium, vertebral centrum, peripheral, numerous shell fragments from Room 3 debris cone C. OMNH 80570, costal and two peripherals, probably right 9th and 10th , from Room 3 bone C. OMNH 80571, numerous shell fragments from Room 3 debris cone A. OMNH 80573, two ungual phalanges and vertebra fragments (posterior centrum with condyle, anterior centrum with cotyle, zygapophyses, and small centrum fragment); 80574, distal right humerus showing entepicondylar foramen from E pit, 0-10 cm. OMNH 80601, carpal/tarsal or osteoderm from E pit, 10-20 cm.

Discussion: Many specimens of a tortoise were recovered in LTC, all in poor condition of preservation. Although nearly all skeletal elements appear morphologically to be from tortoises, only two scapulae (OMNH 80562, 80565; Fig. 2), two peripheral carapace bones (OMNH 80570), and two ungual bones (OMNH 80573) permit a robust identification as *Gopherus*.

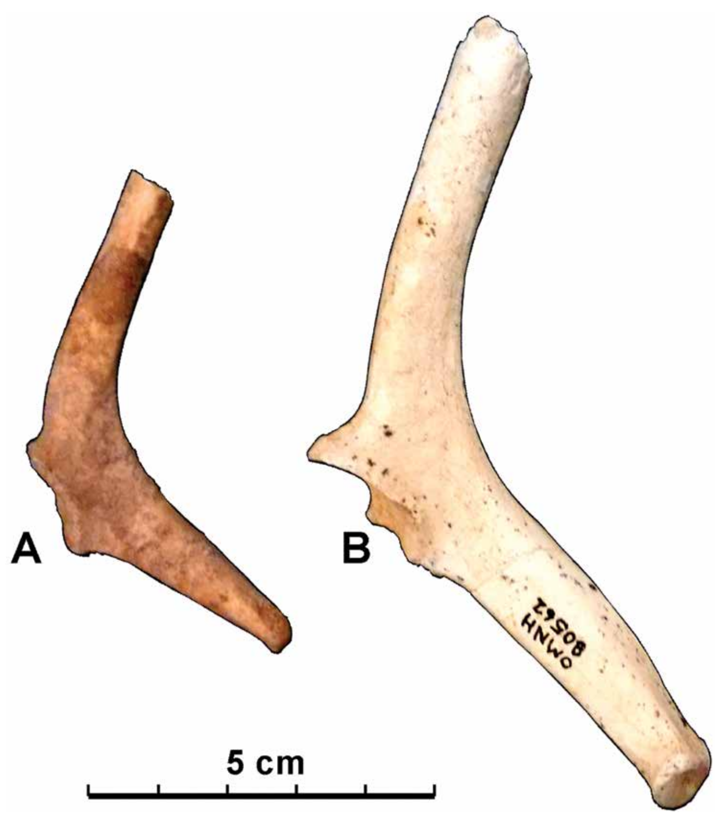

Figure 2. Pleistocene scapulae of *Gopherus* sp. from La Tetera Cave, Arizona in anteromedial view. A, OMNH 80565, B, OMNH 80562.

One of the scapulae (OMNH 80562) has the long arm (dorsal scapular process) broken, the short arm (acromion process) length from middle of humeral socket (glenoid fossa) to end of arm 59 mm, angle between arms ~120°, and the bone has fine scale possible chemical etching or insect/detritivore feeding marks on its surface penetrating down into the cortical bone. The other scapula (OMNH 80565) has the long arm broken, short arm length from middle of humeral socket 38 mm, angle between arms 110°. Based on size alone, these represent two different individuals. The bases of the arms of both scapulae appear relatively robust compared with those illustrated in Auffenberg (1976:figs. 10-13). The partial femur OMNH 80560 has the proximal epiphysis broken but its diameter can be estimated at approximately 25 mm. These bones thus pertain to a medium to large species of *Gopherus*. On some of the shell fragments (e.g., OMNH 80567), the scale-bordering sulci have raised edges characteristic of the genus *Gopherus*. However, the multiple species of *Gopherus* known in the late Pleistocene of southwestern North America are distinguished from one another on the basis of cranial morphology, complete shells, or selected elements of the shell such as nuchals (Van Devender et al., 1976; McCord, 2002; Joyce and Bell, 2004; Reynoso and Montellano-Ballesteros, 2004; Cruz et al., 2009; Jass and Bell, 2010; Carbot-Chanona et al., 2020), none of which are available among the specimens from LTC. As a result, a specific identification cannot be attempted at this time.

As currently defined, today *Gopherus agassizii* occurs in southwestern Utah, southern Nevada, and southeastern California to the Colorado River at Arizona. *Gopherus morafkai* occurs throughout much of southern Arizona and southward to Sonora and further into Mexico (Murphy et al., 2011; Edwards et al., 2015). The extant population in the area around LTC would be *G. morafkai* based on the current taxonomy. No characters are known to distinguish fragments of skeletal remains between these two species, hence our identification is only to the generic level.

Order Squamata

Family Helodermatidae

Heloderma sp. (Gila monster/beaded lizard)

Material and Provenience: OMNH 80515, osteoderm from E Pit, 20-30 cm.

Discussion: Only a single osteoderm was recovered (Fig. 3A). The specimen has the typical circular, domed shape, although it lacks a ring-extension (bony flange) found on many cranial osteoderms of this genus (Mead et al., 2012). The size is relatively small and lacks the polygonal shape found on the cranium of most individuals of *Heloderma suspectum* and *H. horridum*. OMNH 80515 is 2.1 mm in diameter. Based on a study of an extant specimen with a snout-vent length of 320 mm (near maximum size; Mead et al., 2012), individual osteoderms range from 1.5 to 6.5 mm in diameter. OMNH 80515 has a high dome with a surface covered with ridge-and-pit sculpturing that is accentuated with a spicule pattern similar to osteoderms recovered as Neogene-age fossils in eastern Arizona (Mead et al., 2015), southwestern Oklahoma (but without the ring-extension; Mead et al., 2021), and eastern Tennessee (Mead et al., 2012). The size and shape of the high-domed, spicule-patterned osteoderms do not seem to be species-specific based on a study of the living taxa in Arizona-Nevada-Utah south to southern Guatemala (see map distribution in Beck, 2005; Mead et al., 2021). Today, *Heloderma suspectum* is found within the Tucson Basin and is expected to occur in the vicinity of LTC during the late Pleistocene (Brennan and Holycross, 2009; Murphy, 2018).

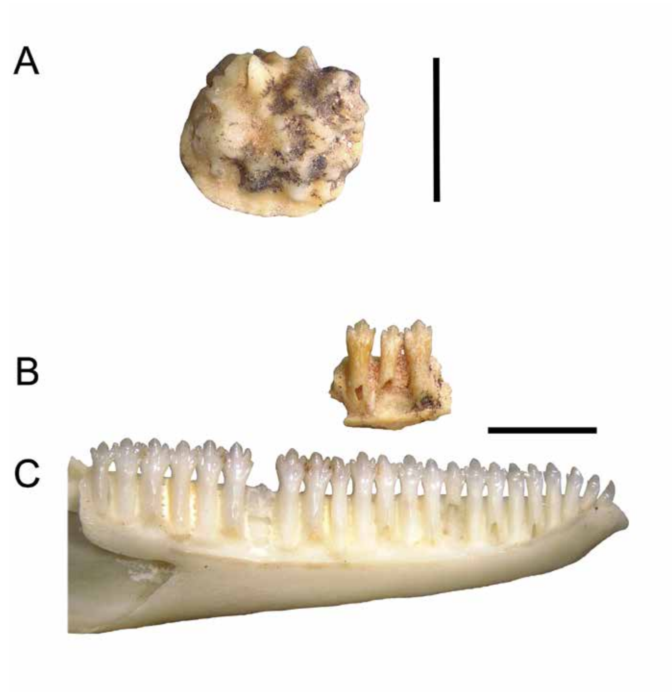

Figure 3. Pleistocene squamates from La Tetera Cave, southern Arizona. A, OMNH 80515, fossil osteoderm of *Heloderma*, dorsal view. B, OMNH 80593, fragment of fossil dentary of *Dipsosaurus*, lingual view. C, modern complete dentary of *Dipsosaurus* for comparison, lingual view. Scale bars 2 mm.

Family Iguanidae

Dipsosaurus sp. (Desert iguana)

Material and Provenience: OMNH 80593 dentary fragment East Pit 10-20 cm.

Discussion: This specimen is a small, fragmented dentary 2.2 mm long with three tricuspate teeth originating from mid-length along the tooth row. Each tooth is well-formed with three distinctly pointed cusps. Each tooth is straight, i.e., not showing the posterior orientation as is found on the more anterior dentition of many lizards. The central cusp is bordered by two somewhat smaller cusps. The central cusp on one tooth shows a minute secondary 'cusplet'. Each tooth flares antero-posteriorly from the main shaft of the tooth column. In addition, there is a distinct bulging lingually just below the apical flare. The cusps appear to show some usage wear (Fig.3B). No part of the Meckelian fossa is preserved, thus there is no indication for the presence of a Meckelian groove or the inframeckelian and suprameckelian lips.

The distinctively tricuspate and flared tooth pattern is indicative of members of Iguanidae of the North American Quaternary. Related iguanians that have a tricuspate pattern, such as members of *Sceloporus* (e.g., *S. magister, S. clarki, S. poinsettia, and S. orcutti,* to name a few of the larger species similar in size to OMNH 80593) do not have the extreme apical cone pattern but instead have lateral cusps that are minute, often mere nubbins in size, and unlike those observed in *Dipsosaurus*. *Sauromalus ater* juveniles (svl=111 mm; and with teeth the size of those in *Dipsosaurus*) have a highly flared apical display of five to seven cusps above the tooth column. Anterior teeth near the symphysis may have three cusps but each tooth column lacks the bulge below the apical flare. *Ctenosaura conspicuosa* juveniles (svl=146 mm; with tooth size comparable to those in *Dipsosaurus*) also have a tricuspate apical pattern but the lateral cusps are distinctly smaller than the central cusp. The central cusp has a central longitudinal ridge on the lingual face, which is distinct from the tooth morphology observed on *Dipsosaurus* and OMNH 80593. In addition, the area occupied by the apical cusps is less wide, as observed on *Dipsosaurus* and OMNH 80593. Additional morphological traits of iguanids (sensu stricto) can be found in de Queiroz (1987) and Evans (2008).

Both *Dipsosaurus dorsalis* and *Sauromalus ater* are extant in southwestern and western Arizona but do not occur in the Tucson Basin today (Brennan and Holycross, 2009; Jones and Lovich, 2009). Additional species of *Dipsosaurus*, *Sauromalus*, and various species of *Ctenosaura* are known from northern Mexico (Lemm, 2009, Rorabaugh and Lemos-Espinal, 2016). Thus, given the above characters, OMNH 80593 is identified as belonging to *Dipsosaurus* sp. until the morphological characters are fully understood for all reported species/forms.

The fossil record of *Dipsosaurus* is poorly understood; thus, the report here from LTC and the Tucson Basin is of interest (Mead, 2005). *Dipsosaurus dorsalis* today occurs in expansive sandy flats in desert hummock terrain often containing *Larrea* (creosote bush) (Lemm, 2009).

Family Phrynosomatidae

*Phrynosoma solare (*Regal horned lizard)

Material and Provenience: OMNH 72182 left dentary fragment Pit 1 10-20 cm.

Discussion: OMNH 72182 is a fragment of dentary illustrating the lateral flanging of the base. Basal portions of eight peg teeth are preserved in the dental gutter. Tooth row is 4.7 mm long. Although slightly damaged, the Meckelian fossa is open. It is not fused or as closed as in *P. douglasii/hernandesi* or *P. modestum* and some other species. The ventrolateral surface is curved, as is typical of *Phrynosoma,* and it has tubercles and a flange such as are present on *P. cornutum*, *P. holmani*, *P. mcalli* (and related spp.), *P. modestum*, *P. platyrhinos*, and *P. solare*. This surface on the dentary from LTC is not smooth and rounded, as are those belonging to *P. adinognathus*, *P. asio*, *P. braconnieri*, *P. coronatum*, *P. ditmarsi*, *P. douglasii*, *P. orbiculare*, and *P. taurus*. Its retention of the lateral flange permits the bone to be positioned with the dental arcade oriented occlusally without rolling to the side. Based on modern comparative specimens many species of *Phrynosoma* have some sort of rugose, lateral flange to the dentary, while others do not. Only *P. solare* has the flange at such a great, stationary extent (see also Reeve, 1952; Mead et al., 1984; Mead et al., 1999).

Phrynosoma solare occurs today in the region of LTC and elsewhere in the hot-arid Sonoran Desert, while *P. hernandesi* is extant in a variety of habitats locally and adjacent (Jones and Lovich, 2009). Additional species of horned lizards are extant in regions bordering Arizona (Jones and Lovich, 2009). The late Pleistocene occurrence of the regal horned lizard is only known elsewhere from Deadman Cave, north of LTC on the north side of the Santa Catalina Mountains (Mead et al., 1984; Mead, 2005).

Uta or *Urosaurus* sp. (Side-blotched lizard or brush lizard)

Material and Provenience: OMNH 80607 left dentary from E Pit 20-30 cm.

Discussion: This is a fragment of the anterior end of a left dentary with 10 teeth present (some broken) and spaces for 5 additional tooth replacements within 2.6 mm length. Basal part of the bone is not preserved, therefore, it lacks the inframeckelian lip area; however, it shows that the suprameckelian lip progressed and curled ventrally enough to illustrate that the Meckelian fossa opened ventrally. Teeth are narrow, giving them a minute appearance with vertical, parallel-sided columns culminating in a single minute cusp with diminutive lateral cusps.

Teeth of *Holbrookia* and *Cophosaurus* are wider than those of *Uta*, *Urosaurus,* and OMNH 80607, as well as more robust, with the more anterior teeth not minutely tricuspate. Those of *Callisaurus* are similar but typically more pointed, having less of a tricuspate pattern on a slightly wider tooth column. Teeth of *Petrosaurus* are comparatively short and distinctly broad, with a widely divergent tricuspate apical cone pattern in which the lateral cusps are short and pointed. Tooth pattern and size are unlike those of the smaller species of *Sceloporus*. Tooth structure and implantation on the dentary on OMNH 80607 are distinctly different from those in the gecko, *Coleonyx,* and in the night lizard, *Xantusia*. Thus, with the above characters, OMNH 80607 is identified as belonging either to *Uta* or *Urosaurus*. Multiple species of these two genera occur today in the arid Southwest with *Urosaurus ornatus* and *Uta stansburiana* in the Tucson area today (Jones and Lovich, 2009). Quaternary-age fossils of *Urosaurus* are not common, known only from Deadman Cave and Picacho Peak localities, whereas remains of *Uta* are common in Arizona (Mead, 2005).

Family Teiidae

Aspidoscelis sp. (Whiptail lizard)

Material and Provenience: OMNH 72155 left maxilla Pit 1 0-10 cm; OMNH 72245 right maxilla Pit 1 20-30 cm.

Discussion: OMNH 72245 is a 3 mm long, eroded maxillary fragment containing two intact teeth (0.3 mm wide at base) showing the bicuspidate dentition distinct to the teiid *Aspidoscelis* (*Cnemidophorus*). OMNH 72155 is missing much of the dorsal aspect of the frontal process but preserving its 5.0 mm length. Although the specimen does not preserve the anteriormost or posteriormost portions of the maxilla, it is 6.5 mm long. There are 15 teeth or bases of teeth (0.3 mm wide at base), all somewhat damaged. No tips of cusps are preserved. The dominating length of the frontal process (which is all in one plane) compared to the overall length of the maxilla implies that the fossil belongs to *Aspidoscelis*. Iguanine members typically have a relatively short frontal process (compared to the maxilla length) that is characteristically curved at the anterior end. Some of the geckos (e.g., *Coleonyx reticulatus*) and night lizards (*Xantusia*) can have a length-dominating frontal process but the teeth are classically thin pillars with single pointed cusps, often recurved. *Xantusia* also has a lower number of teeth on a wide dental gutter.

Both fossil specimens are identified as *Aspidoscelis* sp. based on the above observed characters. At least 12 species of large and small whiptail lizards are extant in various parts of Arizona today, with additional species occurring nearby (Jones and Lovich, 2009). For this reason and the lack of complete specimens, we have not taken the fossils to species level. Various species of *Aspidoscelis* are recorded from the Late Pleistocene of Arizona (Mead, 2005).

Lizard indeterminate

Material and Provenience: OMNH 72154 left dentary Pit 1 0-10 cm; OMNH 72242 scapula fragment Pit 1 20-30 cm; OMNH 72243 humerus Pit 1 20-30 cm; OMNH 72241 scapula fragment Pit 1 20-30 cm; OMNH 81118 pelvic and humerus fragments E Pit 20-30 cm; OMNH 81119 highly fragmented cranial and post-cranial bones from E Pit 20-30 cm.

Discussion: OMNH 72154 is a fragmented left dentary 4.5 mm long from near the symphysis curvature to just posterior to the splenial facet. Two fragmented teeth are preserved just above this facet. Although missing the tip of the single cusp, the column of the tooth is parallel and 0.2 mm wide. The length of the Meckelian fossa is predominantly closed by the junction of the suprameckelian and inframeckelian lips; the anterior portion is slightly open ventrally. This junction is not a fusion as found on the geckos (*Coleonyx*) or night lizards (*Xantusia*). A predominantly closed but not fused Meckelian fossa can be found on a number of lizard taxa including *Callisaurus*, *Cophosaurus* among others (see discussion in Scarpetta, 2021). Because of the incompleteness of this specimen, the identification could not be made to family or genus. Other skeletal specimens were not identified due to the degree of fragmentation.

Family Colubridae

Sonora sp. (Ground snake)

Material and Provenience: a single mid-trunk vertebra OMNH 72163 from Pit 1, 10-20 cm.

Discussion: This vertebra is short and wide with a centrum length of 1.8 mm and a width of 1.4 mm. The postzygapophysis-postzygaphophysis distance is 2.8 mm. The neural arch appears somewhat flattened as viewed anteriorly. The cotyle is circular but slightly flattened dorsally and ventrally. The zygosphene is bowed slightly convexly in anterior view and has a convex shape in dorsal view. There are two pinhole paracotylar foramina. The parapophyses are minute and do not project ventrally or anteriorly to the cotyle. The neural spine is low, 0.5 mm tall, and has a slight thickening at the apical ridge; anterior and posterior ends are undercut. Accessory processes are blunt, rounded, and short, protruding only 0.2 mm beyond the prezygapophyses, and are directed more anteriorly than laterally. The prezygapophyseal facets are oval in shape and are oriented horizontally (i.e., not bowed dorsally). The neural arch laminae are slightly convex as viewed from the posterior. There is no epizygapophyseal spine on the postzygapophyseal area. The hemal keel is slightly eroded but an indication is that it is flattened, spatulate in shape, and is wider posteriorly than anteriorly. There are slight subcentral ridges but no subcentral troughs (subcentral lymphatic fossae of LaDuke, 1991). The subcentral foramina are minute pinholes.

The angle of the prezygapophyses and the flattened shape of the hemal keel preclude the fossil from belonging to *Heterodon* (Auffenberg, 1963, Jurstovsky, 2021). Trunk vertebrae of *Diadophis*, *Tantilla*, *Carphophis*, *Rhadinaea*, and *Opheodrys* may have a depressed neural arch but also have an elongate centrum, which omits this from being the identity of OMNH 72163. The lack of a sigmoid-shaped hypapophysis indicates that the fossil is not a natricine snake such as *Thamnophis*, *Nerodia*, *Neonatrix* or the smaller *Storeria* and *Tropidoclonion*, nor the venomous elapid, *Micrurus* (see Auffenberg, 1963, Mead and Steadman, 2017).

The characters 1) short-wide vertebra, 2) depressed neural arch, and 3) neural spine that is lower than long and has overhangs at both ends of the ridge imply that the vertebra could be that of either *Heterodon* or *Farancia* (Auffenberg, 1963, Holman, 2000, Jurstovsky, 2021). These authors also indicate that the hemal keel is characteristically flattened and distinctly wide throughout its length anterioposteriorly, which OMNH 72163 lacks. Modern comparative specimens examined show variation in the shape and width of the hemal keel within the length of individual snakes and show similarities with OMNH 72163; however, the upturned angle of the prezygapophyses of modern specimens and the fossil are not similar to those of *Heterodon* and *Farancia*.

Rhinocheilus and *Arizona* have medium-length and wide mid-trunk vertebrae but also have a tall neural arch and spine resembling *Lampropeltis* and *Elaphe* (see Van Devender and Mead, 1978). Due to these traits, these genera are excluded from providing the identification of OMNH 72163. The vertebrae of *Trimorphodon* are distinctly larger and have different vertebral features as described in Van Devender and Mead (1978), and therefore, do not identify OMNH 72163. Vertebrae of *Chionactis* and *Chilomeniscus* are small, short, and wide, but have neural arches that are fairly tall and have pointed accessory processes that protrude well beyond the prezygapophyses, hence not the identification of OMNH 72163.

Mid-trunk vertebrae of *Sonora* (based on examinations of *S. aemula, S. espiscopa*, and *S. semiannulata*; see below about species designations) are 1) short and wide (condyle length = 1.35 – 1.80 mm; neural arch width = 0.9 – 1.4 mm; n=4 individuals), have a 2) relatively low, but sometimes mid-tall, neural arch, 3) low neural spine that overhangs both anteriorly and posteriorly, 4) short, rounded/blunt accessory processes, 5) zygosphene that is convex or crenuate and a hemal keel that is low, somewhat flattened, and typically spatulate (see descriptive details in Van Devender and Mead, 1978). Vertebrae of *Hypsiglena* are similar to those of *Sonora,* but are larger (length and width), have a more pronounced hemal keel (not flattened or spatulate shape), and have more pronounced accessory processes that are rounded, almost globular or blunt (in a way that is also characteristic of *Lampropeltis getulus*, see LaDuke, 1991: fig 13). Considering all the features mentioned above, OMNH 72163 is identified as belonging to *Sonora* sp. We find no morphological feature that permits the separation of the various species of *Sonora* based on vertebrae.

Cox et al. (2018) contended that the snakes *Chionactis* and *Chilomeniscus* are nested within the genus *Sonora,* and therefore, are in synonymy with it, giving the genus some 15 species from central Mexico to northwestern USA. Despite the potential osteological implications of this conclusion, we believe we can differentiate the species originally within *Chionactis* and *Chilomeniscus* from those of *Sonora* sensu stricto skeletally. The number of species of *Sonora* to be recognized are uncertain (Cox et al., 2020). *Sonora semiannulata* is found in and around the region of LTC today (Cox et al., 2020), as well as from Late Pleistocene cave and woodrat midden deposits from the Grand Canyon south to southern Arizona (Mead, 2005).

Rhinocheilus sp. (Long-nosed snake)

Material and Provenience: OMNH 72234–72235, vertebrae from Pit 1, 10-20 cm.

Discussion: Two vertebrae are assigned to this genus. Specimen OMNH 72234 is fragmented with only the ventral portion preserved. OMNH 72235 is complete and will be used for identification purposes. The ventral portions of both specimens are identical.

The vertebra is short and wide with a centrum length of 2.2 mm and a width of 1.7 mm. The postzygapophysis-postzygaphophysis distance is 3.1 mm (slightly broken edge). The neural arch is moderately vaulted, not flattened, as viewed anteriorly. The cotyle is circular but slightly flattened dorsally and ventrally. The zygosphene is bowed slightly convexly in anterior view and has a crenate shape in dorsal view. There are two pinhole paracotylar foramina. The parapophyses are small, but distinct, and project slightly ventrally or anteriorly relative to the cotyle. The paracotylar notches are distinct. The neural spine is relatively low, 0.9 mm, and it has a thickening at the apical ridge; anterior and posterior ends are undercut. Accessory processes are blunt-rounded (globular), protrude only 0.5 mm beyond the prezygapophyses, and are directed laterally. The prezygapophyseal facets are oval in shape and are oriented horizontally (i.e., not bowed dorsally). The neural arch laminae are slightly convex as viewed from the posterior. There is no epizygapophyseal spine on the postzygapophyseal area. The hemal keel is a thin, distinct ridge (gladiate condition of Auffenberg, 1963). The subcentral ridges are distinct, but not overly developed, and there are no subcentral troughs (subcentral lymphatic fossae of LaDuke, 1991). The subcentral foramina are minute pinholes.

Many of the vertebral characters of small colubrid snakes are discussed under the account of *Sonora*. In addition to those, vertebrae of *Rhinocheilus* are larger than those of *Sonora*. The neural spine is typically thickened (or flat topped) dorsally. The accessory processes are blunt and laterally oriented (or sometimes dorsally; Auffenberg, 1963; Van Devender and Mead, 1978). Subcentral lymphatic fossae are distinct but not as strong as those found in the smaller species of *Lampropeltis* (LaDuke, 1991). Vertebrae of *Hypsiglena* are smaller with a more depressed neural arch (Van Devender and Mead, 1978; LaDuke, 1991).

Given the vertebral morphological features listed above, and those for the more complete fossil specimen, OMNH 72235 and 72234 are identified as belonging to *Rhinocheilus* sp. Brennan et al. (2020) discussed aspects of the number of living species assignable to the genus *Rhinocheilus*, but most authors seem to conclude that there is only a single extant species, *R. lecontei*. No extinct species are listed by Holman (2000). Because of the uncertainty in the number of extant species and the fact that we were unable to examine the other discussed forms, we list the fossils only to genus.

Rhinocheilus lecontei is common today in the southern regions of Arizona having desertscrub, grassland, and shrubland, including the area of LTC (Brennan et al., 2020). This snake has been found in a number of late Pleistocene cave and woodrat midden deposits in Arizona (Mead, 2005).

Masticophis or *Coluber* (Whipsnake or racer)

Material and Provenience: OMNH 72189, vertebra from Pit 1, 10-20 cm.

Discussion: The mostly well-preserved single vertebra is long and slender with a centrum length of 3.8 mm and a width of 2.4 mm. The postzygapophysis-postzygaphophysis distance is 4.2 mm. The neural arch is well vaulted as viewed anteriorly. The zygosphene is bowed slightly convexly in anterior view and shows a crenate shape in dorsal view. The cotyle is slightly oval with a distinctly flattened ventral base; its diameter is equal to that of the neural canal (1.5 mm). The pinhole paracotylar foramina are doubled on each side. The parapophyses are small, but distinct, and project slightly ventrally. The paracotylar notches are distinct. The somewhat low neural spine is thin, 1.0 mm high and 2.9 mm long, with a distinct overhang posteriorly. Accessory processes are largely not preserved but one fragmented area implies that they were long and likely pointed. A single base preserved on one shows that they were laterally oriented. The prezygapophyseal facets are obovate (Auffenberg, 1963) in outline and are oriented horizontally. The neural arch laminae are slightly convex as viewed from the posterior. There is an epizygapophyseal spine on the postzygapophyseal area. The hemal keel is distinct, low, and spatulate in shape. The subcentral ridges are distinct and there are no subcentral troughs (subcentral lymphatic fossae of LaDuke, 1991). The subcentral foramina are minute pinholes.

Based on the overall large size and length/width proportions of OMNH 72189, the fossil does not belong to any of the smaller species discussed above or to *Phyllorhynchus*. Vertebrae of *Pituophis* are as large or typically larger and heavier than the fossil (Van Devender and Mead, 1978; LaDuke, 1991). Vertebrae of *Trimorphodon* are similar in size but have a more compressed neural arch, relatively small neural canal, a small zygosphene, and short accessory processes (Van Devender and Mead, 1978). The ratio of the centrum length to the neural arch width (cl/naw of Auffenberg, 1963) has been used to help differentiate various species of snakes with varying success. This ratio in the fossil, OMNH 72189 is 1.58. In *Masticophis* this ratio is 1.48-1.75 (Van Devender and Mead, 1978). Auffenberg (1963) listed this ratio for the following taxa as: *Farancia* (0.91-1.14), *Masticophis* (1.34-1.64), *Coluber* (1.23-1.53), *Elaphe* spp. (0.86-1.11) *Pituophis* (1.05-1.18), and *Lampropeltis* spp. (0.85-1.18). We also determined this ratio for *Salvadora* (1.40-1.47) and *Oxybelis* (1.88-2.16). Vertebrae of *Salvadora* are typically smaller (shorter and wider) than those of *Masticophis* and *Coluber* of the same snout-vent length, giving a different cl/naw ratio (Holman, 2000). *Coluber* and *Masticophis* have epizygapophyseal spines posterior to the postzygapophyses. Holman (2000) indicated that *Salvadora* does not have this spine, although *S. grahamiae* clearly can have this trait (Holman, 2000: fig. 118). The neural spine is typically shorter in height in *Salvadora* versus those found in *Masticophis* and *Coluber*, although this clearly is a variable feature (Van Devender and Mead, 1978; LaDuke, 1991). The cotyle, condyle, and neural canal are smaller in *Salvadora* than those found in *Masticophis* and *Coluber* of similar size (Van Devender and Mead, 1978).

Given that OMNH 72189 is relatively long and narrow (cl/naw) and has a cotyle, condyle, and neural canal all about the same magnitude in size (relatively large), we identify the fossil as either *Masticophis* or *Coluber* and not *Salvadora*. Some researchers have stated there is a distinction between vertebrae of *Coluber* and *Masticophis* (Mead et al., 1984; Van Devender et al., 1985; LaDuke, 1991), but it is clear that the vertebrae are very similar to each other and overlap in many characters. Several studies on extant members of the two genera have suggested that western hemisphere *Masticophis* be synonymized with *Coluber* (see discussion in Persons and Drost, 2020). Given that OMNH 72189 is slightly fragmented, we do not feel that we can determine which of the two genera the fossil may belong to. Only *Masticophis* spp. are found living in southern Arizona today, with *Coluber* occurring in the higher elevations and biotic communities of the Colorado Plateau (Holycross and Mitchell, 2020).

Squamata (snake) indet.

Material and Provenience: OMNH 72156, vertebra; 72157, vertebra; 72158, ribs from Pit 1, 0-10 cm. OMNH 72164, quadrate; 72165, vertebra; 72166, ribs; 72185, vertebra; 72186, vertebra; 72233 vertebra; 72187, jaw fragment; 72188, rib from Pit 1, 10-20 cm. OMNH 72236-72237, vertebrae; 72238, rib; 72239-72240, vertebrae from Pit 1, 20-30 cm. OMNH 80579, right quadrate; 81111, vertebra; 81112, three vertebrae from E pit, 0-10 cm. OMNH 80595-80598, vertebrae; 81116, vertebrae & ribs from E pit, 10-20 cm. OMNH 80608-80609, vertebrae; 81120, parietal in 2 pcs. from E pit, 20-30 cm.

Discussion: These skeletal elements probably represent more than one kind of nonvenomous snake; for example, at least one (OMNH 80595) has a sigmoid-shaped hypapophysis, while others have a narrow, straight-sided hemal keel (OMNH 80596, 80597) or a broad, flat hemal keel (OMNH 80598). However, these vertebrae are too fragmented and lack critical morphological features to permit reliable generic assignments.

Family Viperidae

Crotalus sp. (rattlesnake)

Material and Provenience: OMNH 72149, vertebra; OMNH 72150, vertebra; OMNH 72151, vertebra; OMNH 72152, vertebra fragment; OMNH 80580, vertebra from Pit 1, 0-10 cm. OMNH 72190, vertebra; OMNH 72191, vertebra; OMNH 72192, fang from Pit 1, 10-20 cm. OMNH 72232, four vertebrae from Pit 1, 20-30 cm. OMNH 80592, fang; OMNH 80594, two vertebrae from E pit, 10-20 cm. OMNH 80610-80611, vertebrae, and OMNH 80612, two fangs from E pit, 20-30 cm.

Discussion: Mid-trunk vertebrae of crotalines are distinct from all other North American snakes in having a well-developed hypapophysis that is long, straight, projecting posteriorly well beyond the condyle, distally oriented, and distinctly pointed. The parapophyses project ventro-anteriorly well beyond the edge of the cotyle. The paracotylar foramina are distinct but small (resembling a pinhole). The overall shape is that of an antero-posteriorly short and broad vertebra. Other characters can be found in Auffenberg (1963), Brattstrom (1964), Holman (1965), LaDuke (1991), Szyndlar (1991), and Parmley and Holman (2007).

Although the related *Agkistrodon* (copperhead and cottonmouth) and *Sistrurus* (massasauga and pygmy rattlesnake) are less well constrained than *Crotalus* in terms of their vertebral distinctiveness (and are in need of detailed skeletal comparison), their morphological characters are described in Holman (1965, 2000), none of which are apparent on any LTC vertebra. The paracotylar foramen on *Agkistrodon* is large and is a singular opening whereas on *Crotalus* it is smaller and can have multiple openings (Holman, 2000); this feature is not completely described for *Sistrurus*. *Sistrurus* is distinct from *Agkistrodon* and *Crotalus*, with a more elongate centrum and greater vaulted neural arches (Auffenberg, 1963; Holman, 1965; Parmley and Holman, 2007). These traits are incipiently constrained, qualitatively or quantitively, in Auffenberg (1963). *Sistrurus* may have a minute spine on the zygosphene anterior to the neural spine, and a keel may or may not be present on the dorsal surface of the zygosphene (Auffenberg, 1963; Holman, 1965; Parmley and Holman, 2007: fig. 1). We observed the minute spine on an adult modern member of *S. catenatus* (snout-vent length 653 mm), a trait that varies through the length of the specimen. The spine is absent on juvenile specimens but all had the dorsal keel. The minute spine appears to us to be an ontogenetic outgrowth of the dorsal keel. Snake vertebrae from LTC all have the characters of *Crotalus* listed above and lack the traits of *Agkistrodon* and *Sistrurus*. Although some researchers distinguish the various species of *Crotalus* based on selected vertebral characters (e.g., Holman, 2000), we feel that we cannot make species distinctions based on the sample from LTC. Moreover, it is unclear to what extent Holman's (2000) identifications were based on geographic assumptions rather than morphological distinctions.

Crotalus are relatively well-known as late Pleistocene fossils in the Southwest, especially in Arizona (Mead, 2005). The multitude of extant species of *Crotalus* in Arizona occupy almost all of the region's biotic communities. In Arizona, Holycross and Mitchell (2020) recognized 12 extant species of *Crotalus*, while Schuett et al. (2016) recognized 14 species. These estimates are within the approximately 30 species of rattlesnakes known in North America north of Mexico (Rubio, 2010). In the greater Tucson Basin and immediate mountain ranges, five species of *Crotalus* are known to occur today, including *C. atrox* (western diamond-backed rattlesnake), *C. scutulatus* (Mohave rattlesnake), *C. cerberus* (Arizona Black rattlesnake), *C. molossus* (black-tailed rattlesnake), and *C. tigris* (tiger rattlesnake), with additional species nearby (Brennan and Holycross, 2009; Holycross and Mitchell, 2020); all of these potentially could have occurred near, and could be in, LTC. Extant or extinct species of *Agkistrodon* are not known from western North America (Stebbins, 2003). *Sistrurus* can be found today in the desert grasslands, meadows, tall grass prairies, and other diverse habitats of southeasternmost Arizona and further east into New Mexico and Texas (Rubio, 2010; Feldner et al., 2016).

Class Aves

Order Cuculiformes

Family Neomorphidae

Geococcyx californianus californianus

Material and Provenience: OMNH 80539, left proximal tibiotarsus from 5 m South of survey marker B-20.

Discussion: The tibiotarsus is broken at its distal end and the shaft is curved possibly due to postdepositional distortion, because in life the shaft is normally straight (Larson, 1930). The tibiotarsus is not yet known in the extinct Pleistocene form *G. c. conklingi* and no comparative measurements of this element are available for that subspecies. Measurements of the tibiotarsus (Table 2) from LTC are slightly smaller or within the ranges of tibiotarsal measurements of modern *G. californianus californianus*. Thus, the size of the bone from LTC suggests that it represents the recent subspecies *G. c. californianus* and not the larger late Pleistocene subspecies *G. c. conklingi* of Southwestern late Pleistocene faunas in New Mexico, Texas, and Chihuahua, (Harris and Crews, 1983) and from Kartchner Caverns east of Tucson and LTC (Carpenter and Mead, 2003).

Order Strigiformes

Family Strigidae

Cf. *Athene cunicularia*

Material and Provenience: OMNH 72148, os premaxillare-maxillare from Pit 1, 0-10 cm.

Discussion: The specimen is poorly preserved and includes mostly the os premaxillare and anterior portions of the palate with left and right crista tomialis, broken off at about the zona elastica palatina; the tip is damaged and most of the dorsal surface (culmen) is broken away. A few of the neurovascular foramina are preserved above the right tomial border near the tip. Enough remains of the tomial borders to indicate the contour of the lower edge of the upper mandible, which is strongly hooked in lateral view. Size is that of a small owl, larger than *Micrathene whitneyi* and smaller than *Asio otus*. The size and qualitative characteristics compare most closely with *Athene cunicularia*. The os premaxillare in basal (palatal) view differs from a specimen of *Glaucidium gnoma* in having a constant taper from the lateral edges to the tip instead of a mild constriction of the tip relative to the lateral borders (tip is not slightly laterally compressed), in having an evenly rounded posterior edge to the bony palate instead of a small posterior projection, and in having the medial edges of the tomial branches slightly concave rather than approximately parallel-sided. Skeletons of *Otus* *kennicottii, O. trichopsis*, and *O. flammeolus* were unavailable, but the LTC fossil differs from the os premaxillare of the eastern species *Otus asio* in smaller size, in having a slightly narrower tip, narrower tomial branches, and narrower palatal opening.

The burrowing owl *Athene cunicularia* has a broad modern distribution in the western hemisphere, as well as widespread late Pleistocene records in South America (Campbell, 1979), the Bahamas Islands (Olson and Hilgartner, 1982), and North America including parts of the Southwest (southern California, New Mexico, and Chihuahua; Miller and DeMay, 1942; Harris, 2014).

Order Passeriformes

Family Troglodytidae

Salpinctes obsoletus

Material and Provenience: OMNH 80618, associated partial skeleton (including the upper mandible, proximal coracoid, ulna, humerus shaft, proximal femur, distal tibiotarsus, tarsometatarsus shaft, proximal tarsometatarsus, and fragments) from Room 1 bone M.

Discussion: The bones are encrusted with calcite. The identification is based mainly on shape of the upper mandible. This species is known as a Pleistocene fossil also from Stanton's Cave and Papago Springs Cave, Arizona, and from Shelter, Pendejo, and U-Bar caves, New Mexico (Harris, 2014).

Class Mammalia

Order Carnivora

Family Mephitidae

Table 2. Measurements (in mm, as defined by Bickart, 1990) of the *Geococcyx* tibiotarsus OMNH 80539 from La Tetera Cave, Arizona, and recent comparative specimens of *Geococcyx californianus californianus* from Oklahoma and Texas in the Ornithology Range osteology collection of the OMNH. F = female, M = male

Specimen	Length	Shaft Width	Shaft Depth	Width of Proximal End	Depth of Proximal End
La Tetera, OMNH 80539	---	3.9	3.7	9.4	11.8
OMNH 12052 M, OK	93.7	4.5	4.3	10.9	12.8
OMNH 6918 M, OK	96.0	5.0	4.3	11.0	13.0
OMNH 10706 F, TX	86.4	4.7	4.2	8.9	11.8
OMNH 18233 F, OK	86.0	4.2	3.8	9.7	11.0

Cf. *Mephitis*

Material and Provenience: OMNH 80544, proximal fibula? from Room 3 bone B. OMNH 80545 centrum of axis vertebra from Room 3 debris cone B.

Discussion: The specimens are too fragmentary and lacking in diagnostic characters for a more precise identification.

Order Perissodactyla

Family Equidae

Equus conversidens

Material and Provenience: OMNH 72085, distal fragment of tibia diaphysis from Room 2 bone GHI. OMNH 72086, five rib fragments; 72087, thoracic vertebra; 72088, thoracic vertebra. OMNH 72089, ungual phalanx from Room 2 bone I. OMNH 72090, ungual phalanx and sesamoid from Room 2 bone J. OMNH 72091, first phalanx, digit III from Room 2 bone G. OMNH 72092, left metacarpal from Room 2 bone K. OMNH 72093, distal metapodial with incompletely fused epiphysis from Room 2 bone J. OMNH 80572 paired associated sesamoids (accompanying the joint between the distal end of metapodial III and proximal phalanx of the same digit) from Room 2.

Discussion: These elements (OMNH 72085-72093 and 80572) probably represent two individuals given the distal metapodial with incompletely fused epiphysis (OMNH 72093), presumably from a subadult, and the metacarpal with completely fused distal epiphysis (OMNH 72092, Fig. 4A), representing an adult. Only postcranial remains of this horse were recovered; all seem to pertain to a relatively small species with stout-legged metacarpal and first phalanges but relatively small ungual phalanges (Fig. 4; Table 3). The measurements agree with those of *E. conversidens* from caves in southern New Mexico identified as *E. conversidens* (Harris and Porter, 1980; Heintzman et al., 2017). The phalanges are slightly smaller than phalanges of this species from Papago Springs Cave, Arizona (Czaplewski et al., 1999), 50 km south of LTC.

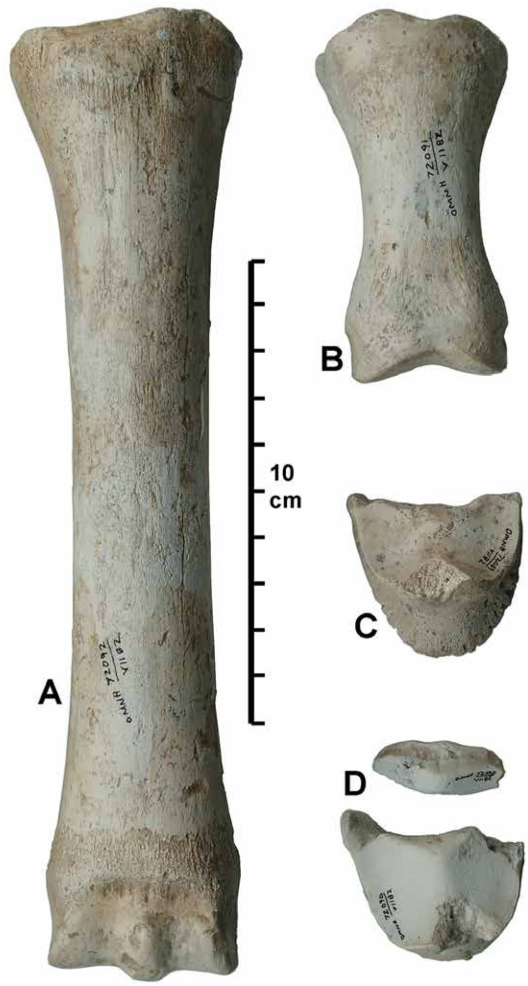

Figure 4. Pleistocene remains of *Equus conversidens* from La Tetera Cave, Arizona. A, OMNH 72092, left metacarpal III in anterior view; B, OMNH 72091, digit III phalanx 1 in anterior view; C, OMNH 72089, digit III ungual phalanx in anterodorsal view; D, OMNH 72090, digit III ungual phalanx and sesamoid in proximal view.

Equus conversidens is widespread in North America and relatively common as a late Pleistocene fossil in the North American southwest (Harris 2014; NEOTOMA online database, neotomadb.org/explorer/; Williams et al., 2018). At U-Bar Cave and Sierra Diablo Cave, New Mexico, *E. conversidens* was also associated with *D. stocki* (Harris, 1987, 2016) as at LTC. Mesowear studies of the teeth of this horse species in east-central and southern Mexico indicated the species was a grazer (Bravo-Cuevas et al., 2011; Jiménez-Hidalgo et al., 2019) and isotopic studies of specimens from central Mexico indicated it fed mostly upon C_4 plants (Marín-Leyva et al., 2016).

Order Soricomorpha

Family Soricidae

Genus and species indet.

Material and Provenience: OMNH 80520, nearly complete humerus and distal fragment of humerus from E pit, 0-10 cm.

Discussion: The commonest shrew in this region today is a member of the *Notiosorex crawfordi* species complex (Baker et al., 2003). Unfortunately, the humeri are insufficiently diagnostic to identify the LTC fossils.

Order Chiroptera

Family Phyllostomidae

Desmodus stocki

Material and Provenience: OMNH 80511, left proximal radius (2 pieces) from Room 1, surface near Bone B. OMNH 80512, shaft fragments of radius (2 pieces) from Room 1 bone P. OMNH 80514, right c1 near survey marker B-21. OMNH 80516, distal humerus fragment; 80518, right I1; 80519, ungual phalanx from E pit, 0-10 cm. OMNH 80517, complete left clavicle; 80522, left dentary condyle from E pit, 10-20 cm. OMNH 80521, left unciform from E pit, 20-30 cm. OMNH 72112, radius shaft fragment; 72116, radius shaft fragment; 72121, left distal clavicle fragment from Pit 1, 0-10 cm. OMNH 72159, left distal clavicle fragment; 72160, right I1 tip of crown; 72173, radius shaft fragment; 72208, right I1 from Pit 1, 10-20 cm. OMNH 72204, two ungual phalanges; 72206, right i1 or i2; 72209, edentulous left dentary; 72210, left p3; 72211, lumbar vertebra; 72212, radius shaft fragment from Pit 1, 20-30 cm. OMNH 72111, right distal humerus; 72113, right I1; 72117, right petrosal; 72118, proximal femur; 72119, right proximal metacarpal V; 72122, two ungual phalanges; 72123, left proximal metacarpal III; 72124, radius shaft fragments (3 pcs.) from Pit 1, 0-10 cm. OMNH 72174, left proximal radius fragment from Pit 1, 10-20 cm. OMNH 72207, right dentary with p3-m1 from Pit 1, 20-30 cm. OMNH 81095, radius shaft frags. (2 pcs.) from Room 2 bone A. OMNH 72114, radius shaft fragment; 72115, right proximal radius fragment from LTC, no provenience.

Discussion: Morphology and measurements of La Tetera Cave specimens confirm that they represent *Desmodus stocki* (Figs. 5A-D, 6; Table 4; Morgan et al., 1988: tables 1, 2). Several different elements of the skeleton of *D. stocki* were recovered mostly by screenwashing LTC deposits. The clavicle and fragments of the radius are among the commonly recovered elements of *D. stocki* in LTC deposits. These same bones in the extant species *Desmodus rotundus* are stout, reflecting their role in the agile aerial and terrestrial locomotion required of these bats (Altenbach, 1979, 1988). The enamelless upper incisors and other teeth closely resemble those characteristic also of *D. rotundus*, which similarly maintained sharpness by thegosis (Phillips and Steinberg, 1976). The distinctive dentaries exhibit the relatively straight ventral edge with strong ventrolateral longitudinal ridge and shelf, and sharp-edged, narrow cheek teeth.

This bat is relatively abundant in LTC with a NISP (number of identified specimens) of 35 compared to a single *Myotis* cf. *velifer* jaw, unlike nearby Arkenstone Cave, in which *D. stocki* was rare but another bat, *Myotis thysanodes*, was extremely abundant, numbering in the thousands of NISP (Czaplewski and Peachey, 2003).

Field observations, stable isotopes, and molecular analysis of fecal samples from modern vampire bats showed that they have a strong preference for domesticated animals (chickens, turkeys, pigeons, guinea pigs, rabbits, cattle, pigs, llamas, water buffalos, goats, horses, burros, dogs, and humans; Greenhall, 1972a, b, 1988; Turner, 1973;

Table 3. Measurements (mm) of *Equus conversidens* remains from La Tetera Cave, Pima County, Arizona. Measurement numbers correspond to those defined by Harris and Porter (1980).

Element	Measurement number	Measurement	Measurement
		OMNH 72092	
Metacarpal	1	205	
	2	59.9	
	3	31.4	
	4	30.1	
	5	23.3	
	6	42.0	
	7	41.7	
	8	31.4	
	10 on prox. artic.	29.2	
	10 on dist. artic.	24.9	
	11	38.9	
Digit III Phalanx 1		OMNH 72091	
	1	76.2	
	2	69.1	
	6	31.0	
	11	36.4	
	12	26.1	
	13	42.9	
Digit III Phalanx 3		OMNH 72089	OMNH 72090
	1	39.2	40.1
	2	39.3	40.2
	3	36.2	37.6
	6	23.2	22.7
	10	34.2	35.3
	12	39.2	43.0
Distal tibia		OMNH 72085	
	8	53.5	

Voigt and Kelm, 2006; Bobrowiec et al., 2015). However, observations are relatively rare of them feeding upon wild mammals and birds, as they must have done prior to the global availability of domestic livestock in the last four centuries: in the wild they have been recorded feeding upon a rat snake (Villa-R and Lopez-Forment, 1966), Humboldt penguins (Luna-Jorquera and Culik, 1995), pelicans and cormorants (Mann, 1951), a spiny rat (*Proechimys*) and a squirrel (Allen, 1939; Greenhall,1972a, b), capybaras (Azcarate, 1980; Ibañez, 1981; Carranza and Campo, 1982; Greenhall, 1988), the lowland tapir (Castellanos and Banegas, 2015; Gnocchi and Srbek-Araujo, 2017), a yellow-shouldered bat (Lord et al., 1973), sea lions (Mann, 1951; Barquez et al., 1999; Catenazzi and Donelly, 2008), red brocket deer (Galetti et al., 2016), white-tailed deer (Sanchés-Cordeiro et al., 2011) and a giant armadillo (de Oliveira et al., 2022). Stock's vampire bat (*D. stocki*) and another extinct late Pleistocene vampire (*D. draculae*) were somewhat larger in body size than extant *D. rotundus* and probably preyed upon contemporaneous large mammals such as ground sloths, camels, horses, mastodons, mammoths (McDonald and Jefferson, 2008), and possibly birds and even large reptiles such as tortoises. Before the introduction of livestock, *D. rotundus* were certainly rare and lived physiologically at risk of starvation because of the mobility and unpredictability of free-ranging wild food sources (Wilkinson, 1988; Freitas et al., 2003, 2005). Accordingly, they are opportunistic foragers feeding on mammals, but lack specializations for preying upon specific host species (Voigt and Kelm, 2006). Common vampire bats usually form small colonies and have been found occupying caves (and human-made shelters; Mantovan et al., 2022) together with many other species of bats (Villa-R.,1966; Greenhall et al., 1983). They utilize a good roost site for long periods and often switch between several alternative roosts (Wilkinson, 1985; Kunz and Lumsden, 2003), as *D. stocki* might have done between LTC and Arkenstone Cave or other available caves in the Pleistocene.

The relative abundance of *D. stocki* fossils and the near absence of the fossil remains of other kinds of bats in LTC leads us to infer that the LTC guano deposit was produced by *D. stocki*, although confirmation of this possibility should be sought within the cave deposits (see Discussion). Depending on its preservation and diagenetic alteration, the guano might also yield ancient environmental DNA that potentially could reveal the extinct vampire's mammalian, avian, or reptilian prey species as well as the prey's food organisms and symbionts, whether animal, plant, fungal, or microbial, which made up the late Pleistocene biota of the area. Several widespread localities for Quaternary fossils of *D. stocki* are known in North America, including Mexico and the southern United States from the east to the west coast (Simmons et al., 2020). Other records of *D. stocki* in southwestern North America include Arkenstone Cave, Arizona (near to LTC and within Colossal Cave Mountain Park; Czaplewski and Peachey, 2003); Rampart Cave, Grand Canyon, Arizona (Carpenter, 2003; Ray et al., 1988); U-Bar Cave, New Mexico (Harris, 1987); Terlingua, Texas (Cockerell, 1930); Sierra Diablo Cave, Texas (Harris, 2016); Potter Creek Cave, California (Hutchison, 1967); San Miguel Island, California

Table 4. Measurements (mm) of La Tetera Cave, Arizona, Pleistocene bats for measurable specimens by element and by OMNH catalog number. Brackets [ ] indicate estimated measurement of broken specimen. Abbreviations: alv = alveolar; AP = anteroposterior; artic surf = articular surface; C = upper canine; c = lower canine; D = depth; diam = diameter; dist = distal; gr = greatest; I = upper incisor; L =anteroposterior length; lab = labial side; ling = lingual side; P = upper premolar; p = lower premolar; prox = proximal; M = upper molar; m = lower molar; TalW = talonid width of lower molar; TrigW = trigonid width of lower molar; W = transverse width

Desmodus stocki:
I1:
72113 L, 3.1; W, 0.9
72160 W, 1.1
72208 W, 1.05
80518 W, 1.0
Dentary:
72207 alv L mandibular toothrow (c1-m1), 5.3; dentary D at m1 dist root, lab 2.6, ling 3.1; p3 L, 1.5; p3 W, 0.7; p4 L, 1.1; p4 W, 0.5; m1 L, 1.7; m1 W, 0.3
72209 alv L mandibular toothrow (c1-m1), 5.2; dentary D at m1 dist root, lab 2.8, ling 3.2; c1 alv L, 1.4; c1 alv W, 0.9; p3 alv L 1.2; p3 alv W, 0.5; p4 alv L, 1.0; p4 alv W, 0.4; m1 alv L, 1.5; m1 alv W, 0.3
i1 or i2:
72206 L, 1.0; W, 0.6
c1:
80514 L, 1.4; W, 0.8
p3:
72210 L, 1.75; W, 0.6
Petrosal:
72117 gr diam of cochlea, 3.2
Lumbar vertebra:
72211 centrum W, 2.6
Clavicle:
80517 total L, 19.1
Humerus distal fragments:
72111 humerus midshaft diam, 2.7; dist gr W, 6.9; W of medial epicondyle, 2.6; W of dist artic surf, 4.2
Radius shaft fragments:
72115 gr W prox artic, 4.1
72174 gr W prox artic, 4.6
80511 gr W prox artic, [4.5]; gr W of shaft, 2.8
72112 gr W of shaft, 3.1
72114 gr W of shaft, 2.6
72116 gr W of shaft, 2.2
72124 gr W of shaft, 2.4
72173 gr W of shaft, 2.9
72212 gr W of shaft, 3.1
80512 gr W of shaft, 3.1

Femur:

72118 gr prox W, 4.6; head diam, 1.7

Ungual phalanges:

72122A gr prox D, 2.1; W of ungual process, 0.4

72122B gr prox D, 2.0; gr prox W (across base of ungual crest), 1.0; W of ungual process, 0.4

72204A gr prox D, 2.1; gr prox W (across base of ungual crest), 0.8; W of ungual process, 0.3

72204B gr prox D, 2.2; W of ungual process, 0.4

80519 gr prox D, 2.1; gr prox W (across base of ungual crest), 1.0; W of ungual process, 0.3

Myotis cf. *velifer*

80510, left dentary fragment with m2: dentary D at posterior alveolus of m1, lab 1.3, ling 1.7; m2 APL 1.6; m2 TrigW 1.05; m2 TalW 1.15.

(Guthrie, 1998); Cueva de San Josecito (type locality) and Cueva de la Boca, Nuevo León (Arroyo-Cabrales, 1992; Arroyo-Cabrales and Polaco, 2003, 2008); Cueva La Presita, San Luis Potosí (Arroyo-Cabrales, 1992); and Tlapacoya, estado de México (Álvarez, 1972).

Family Vespertilionidae

Myotis cf. *velifer*

Material and Provenience: OMNH 80510, left dentary with m2 from Guano Room in drapery cleft (Fig. 5E-G).

Discussion: Among Southwestern North American species of *Myotis*, measurements of the sole LTC specimen (Table 4) most closely correspond with those of modern *M. velifer* from the Southwest (California and Arizona), which are smaller than those from Kansas, Oklahoma, and Texas including the form *M. v. magnamolaris* that once was considered to be a larger Pleistocene species (Vaughan, 1954; Choate and Hall, 1967; Dorsey, 1977; Dalquest and Stangl, 1984). This species is one of the commonest recent bats at Colossal Cave Mountain Park (Sidner, 1988) and is a generalized insect feeder (Hayward, 1970; Kunz, 1974). It is known as a late Pleistocene fossil from several caves and open sites in Texas and southeastern New Mexico (NEOTOMA online database, neotomadb.org/data/category/explorer), as well as Papago Springs Cave and Kartchner Caverns, Arizona (Buecher and Sidner, 1999; Czaplewski et al., 1999).

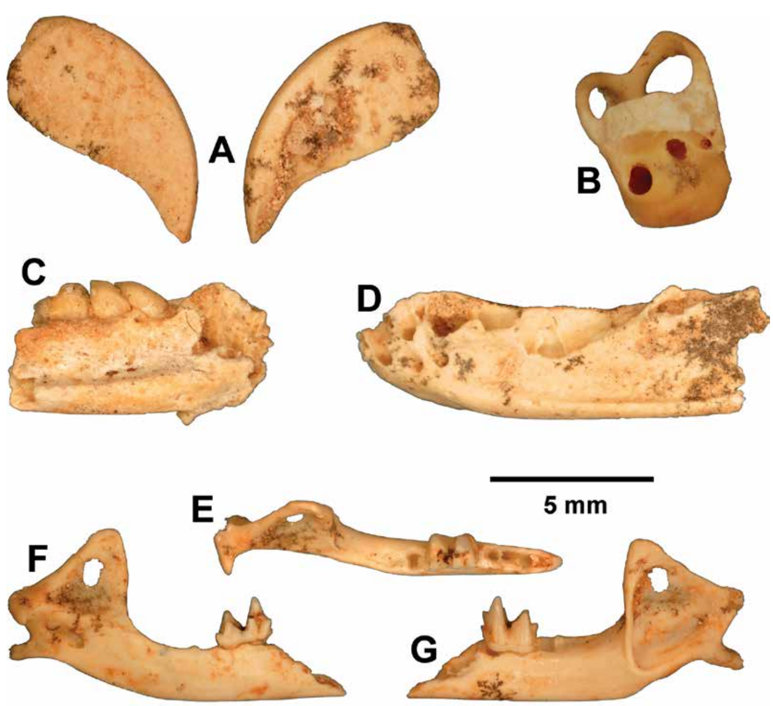

Figure 5. Craniodental remains of fossil bats from La Tetera Cave, Arizona. *Desmodus stocki* teeth, jaws, and petrosal: A, OMNH 72113, right I1 in labial and lingual views; B, OMNH 72117, right petrosal in lateral view; C, OMNH 72207, right dentary with p4-m2 in labial view; D, OMNH 72209, left edentulous dentary in labial view. *Myotis* cf. *velifer* left dentary fragment with m2 (OMNH 80510) in occlusal (E), lingual (F), and labial (G) views.

Order Artiodactyla

Family Camelidae

Camelops hesternus

Material and Provenience: OMNH 72383, pelvis and fragments from Room 1 bone N. OMNH 80546, left proximal metatarsus and fragments; 80547, diaphysis of proximal phalanx; 80548, rib head in 2 pieces from Pit 1, 10-20 cm. OMNH 80550, lumbar centrum unfused epiphysis and fragments; 80551, patella (2 pcs.) from E Pit, 10-20 cm. OMNH 80549, two lumbar vertebrae (probably about second and sixth) and ?palatine/vomer fragment from E Pit, 20-30 cm.

Discussion: All of the *Camelops* skeletal elements are rather poorly preserved. They were found in close proximity in Room 1 and probably represent parts of a single individual (Fig. 7). The lumbar vertebrae are larger and much longer than those in a modern specimen of

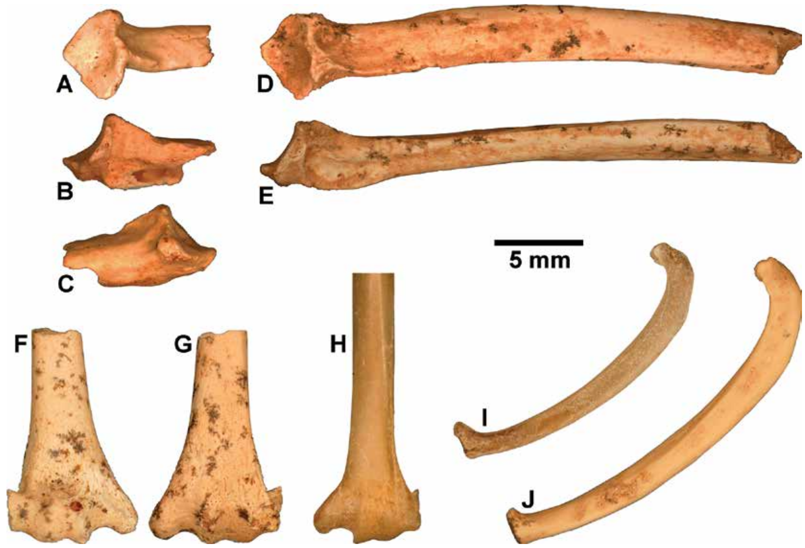

Figure 6. Postcranial fossils of *Desmodus stocki* from La Tetera Cave, Arizona, and modern comparative specimen of *Desmodus rotundus* from Sonora, Mexico. A-C, *Desmodus stocki* proximal left radius fragment (OMNH 72174) in anterior (A), medial (B), and lateral (C) views. D-E, *Desmodus stocki* proximal left radius (OMNH 80511) in anterior (D) and medial (E) views. F-G, *Desmodus stocki* distal right humerus (OMNH 72111) in anterior (F) and posterior (G) views, and *D. rotundus* distal right humerus in posterior view (H). *Desmodus rotundus* left clavicle (I) and *Desmodus stocki* left clavicle (J; OMNH 80517) in anterior views.

Camelus dromedarius and the transverse processes are thick and rounded at the bases, as described by Webb (1965). One of them (the probable second lumbar) preserves the postzygapophyses, one of which is damaged dorsally but the other retains an episphenial process that is better developed than the analogs in *C. dromedarius*. The metatarsus is crushed and incomplete distally, consisting of a little more than the proximal half of the element, and is of little use for identification.

Camelops is more closely related genomically and proteomically to eastern hemisphere camelids than to South American camelids (Heintzman et al., 2015; Buckley et al., 2019). The genus was widespread in North America in Beringia and south of the continental glaciers to northern Central America (Heintzman et al., 2015:fig.1i). The genus *Camelops* is relatively common in the American Southwest, with numerous localities across Arizona in the Blancan, Irvingtonian, and especially Rancholabrean NALMAs (Pasenko and Agenbroad, 2012; Harris, 2014). A recent review of the numerous species that had been assigned to this genus indicates that Rancholabrean occurrences all are attributable to *C. hesternus* (Baskin and Thomas, 2016).

Order Rodentia

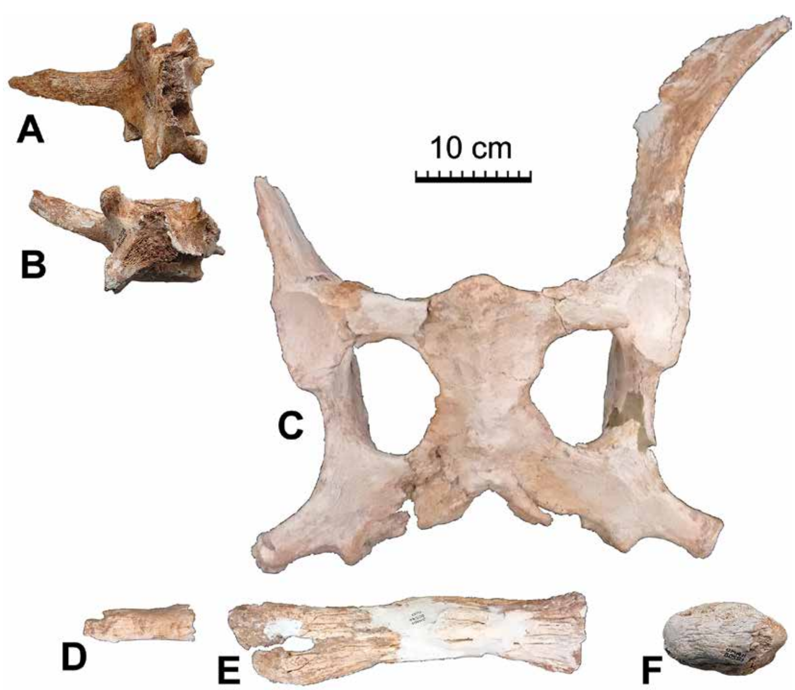

Figure 7. Pleistocene remains of *Camelops hesternus* recovered from La Tetera Cave, Arizona. A, B, OMNH 80549, two partial lumbar vertebrae in dorsal view; C, OMNH 72383, partial pelvis in dorsal view; D, OMNH 80547, proximal phalanx shaft in anterior view; E, OMNH 80546, left metatarsal in anterior view, with plaster restoration; F, OMNH 80551, patella in anterior view.

Family Heteromyidae

Perognathus or *Chaetodipus* sp. indet.

Material and Provenience: OMNH 72195, P4 from Pit 1, 10-20 cm. OMNH 80581, left m1 or m2; 80582, right m1 from E pit, 0-10 cm. OMNH 80616, P4 from E pit, 20-30cm.

Discussion: These few isolated teeth may all pertain to the same species of pocket mouse based on their sizes, but they do not allow the species to be identified. The small sample may represent more than one species.

Dipodomys sp. indet.

Material and Provenience: OMNH 72161, P4 from Pit 1, 10-20 cm.

Discussion: The single P4 is very high-crowned and from an immature individual as indicated by the occlusal surface, which shows little wear on the metaloph and none on the protoloph. It is not possible to identify the species.

Genus indet.

Material and Provenience: OMNH 72216, right I1; 72217, right I1 from Pit 1, 20-30 cm.

Discussion: In addition to the heteromyid cheek teeth noted above, these grooved upper incisors may pertain to the pocket mouse or kangaroo rat listed above.

Family Cricetidae

Neotoma albigula

Material and Provenience: OMNH 72125, left m1; 72126, right m2 from Pit 1, 0-10 cm. OMNH 72199, distal humerus from Pit 1, 10-20 cm. OMNH 80583, left m1; 80584, left M2 from E pit, 0-10 cm. OMNH 80588-80590, probably associated right M1-M3 and palatal fragment from E pit, 10-20 cm. OMNH 80613, possibly associated right maxilla with M1; 80614, left M1; 80615, right M2 from E pit, 20-30 cm.

Discussion: The m1s have no or only very low lingual dentine tracts at the base of the first loph; the antero-internal reentrant folds are also weakly developed. There are no accessory cusps in the posterolabial reentrants. By comparison with the species studied by Harris (1984a, b), these features and the m1 measurements (Table 5) most closely resemble those of *N. albigula*, and are somewhat larger than *N. micropus*. They differ from *N. cinerea, N. findleyi, N. floridana, N. goldmani, N. lepida, N. mexicana, N. pygmaea,* and *N. stephensi,* especially in the poor development of dentine tracts. For these reasons, we assign the LTC specimens to *N. albigula*.

Onychomys sp.

Material and Provenience: OMNH 80513, left dentary originally with i1 and m1 near survey marker B-21. OMNH 72218, left M1 from Pit 1, 20-30 cm. OMNH 80587, left m1 from E pit, 10-20 cm.

Discussion: The dentary measures 12.2 mm from condyle to anterior edge of incisive alveolus. The first upper and lower molars belong to a small *Onychomys* species, smaller than *O. leucogaster,* and possibly representing *O. torridus* or *O. arenicola*. The long coronoid process and m1 diagnostic of the genus (Kelly et al., 2022) that were originally present when OMNH 80513 was found (Fig. 8) agree with the generic identification based on the two isolated molar specimens; the coronoid process and m1 of this jaw were lost in preparation. Slight ridges indicating the attachment scars of masseteric and pterygoid aponeuroses on the dentary bone (as mapped by Satoh and Iwaku, 2006; Kelly et al., 2022) also are consistent with the generic identification. The LTC region is occupied in the present day by *O. torridus*, but the available specimens lack distinguishing characters and are not specifically diagnostic. Although *Onychomys* species typically occupy low and middle elevations and relatively arid habitats, they have also been noted in higher mountain areas (Jones et al. 1960), thus reflecting a broad habitat tolerance, obfuscating the taxon's use in paleoecological interpretation.

Peromyscus sp. indet.

Material and Provenience: OMNH 72127, left m1; OMNH 72128, edentulous right maxillary; OMNH 72129, right M2 from Pit 1, 0-10 cm. OMNH 72167, edentulous maxillary; OMNH 72196, right maxillary with M1-M2; OMNH 72197, left m2 from Pit 1, 10-20 cm. OMNH 72229, edentulous left dentary fragment from Pit 1, 20-30 cm. OMNH 80585, right m1 and OMNH 80586, M3 from E pit, 0-10 cm.

Discussion: These specimens show the accessory lophs and styles of *Peromyscus*, but the nine specimens including seven identifiable teeth are an insufficient sample by which to identify species, given the modern diversity of *Peromyscus* species in the region.

Table 5. Measurements (mm) of *Neotoma albigula* molars from La Tetera Cave, Arizona. Some measurements and a code for the m1s follow the methods of Harris (1984a): WD-m1 = greatest width of loph 2 of m1; TRACT = height of anterolateral dentine tract of m1; F1-F2 = distance from base of lingual fold 1 to base of fold 2 of m1; ANT-F2 = distance from base of lingual fold 2 to anterior face of m1; FOLD = code for the degree of development of the antero-internal reentrant fold of loph 1 on the m1.

Tooth locus / OMNH specimen no.	Length	Width	WD-m1	TRACT	F1-F2	ANT-F2	FOLD
M1 / 80589	3.50	2.35					
M1 / 80613	3.45	2.25					
M1 / 80614	---	2.20					
M2 / 80588	2.80	2.15					
M2 / 80615	2.75	2.10					
M2 / 80584	2.45	1.75					
M3 / 80590	2.15	1.70					
m1 / 72125	3.20	1.80	1.60	0.20	0.80	2.30	0.2
m1 / 80583	3.10	1.75	1.60	0.10	0.80	2.10	0.1
m2 / 72126	2.70	2.00					

Order Lagomorpha

Family Leporidae

Lepus sp.

Material and Provenience: OMNH 72194, lower cheek tooth fragment from Pit 1, 10-20 cm. OMNH 80540, right rib from Room 3 bone E. OMNH 80541, right proximal ulna from Room 3 bone F. OMNH 80542, left m2, radius shaft, humerus shaft, tibia shaft, proximal metatarsal III, other fragments from Room 3 debris cone bones B. OMNH 80543, posterior thoracic vertebra from Room 3 bone C.

Table 6. List of the Pleistocene vertebrates identified from La Tetera Cave, Pima County, Arizona.

Pleistocene Vertebrates
Amphibia:
• Anura:
• Bufonidae: *Anaxyrus* sp.
Reptilia:
• Testudines:
• Testudinidae: *Gopherus* sp.
• Squamata:
• Helodermatidae: *Heloderma* sp.
• Iguanidae: *Dipsosaurus* sp.
• Phrynosomatidae: *Phrynosoma solare*
• *Uta* or *Urosaurus* sp.
• Teiidae: *Aspidoscelis* sp.
• Colubridae: *Sonora* sp.
• *Rhinocheilus* sp.
• *Masticophis* or *Coluber* sp.
• Viperidae: *Crotalus* sp.
Aves:
• Cuculiformes:
• Neomorphidae: *Geococcyx californianus californianus*
• Passeriformes:
• Troglodytidae: *Salpinctes obsoletus*
• Strigiformes:
• Strigidae: cf. *Athene cunicularia*
Mammalia:
• Carnivora:
• Mephitidae: cf. *Mephitis*
• Perissodactyla:
• Equidae: *Equus conversidens*
• Soricomorpha:
• Soricidae
• Chiroptera
• Phyllostomidae: *Desmodus stocki*
• Vespertilionidae: *Myotis* cf. *velifer*
• Artiodactyla:
• Camelidae: *Camelops hesternus*
• Lagomorpha
• Leporidae: *Lepus* sp., *Sylvilagus audubonii*
• Rodentia:
• Heteromyidae: *Perognathus* or *Chaetodipus*, *Dipodomys* sp.
• Cricetidae: *Onychomys* sp., *Neotoma albigula, Peromyscus* sp.

Discussion: Three extant species of *Lepus* currently occupy the southwestern region of North America, *Lepus alleni* (antelope jackrabbit), *L. californicus* (black-tailed jackrabbit), and *L. callotis* (white-sided jackrabbit) (Kays and Wilson, 2002; Ceballos, 2014). Current knowledge of their dental-osteological differences, if any, is inadequate to distinguish the available LTC fossils.

Sylvilagus audubonii

Material and Provenience: OMNH 72110, distal humerus; 72213, distal tibia epiphysis; 80575, right tibia from E pit, 0-10 cm. OMNH 80617, p3 near survey marker B-21.

Discussion: Species identification is based on the p3, in which the occlusal morphology is typical for *S. audubonii* and distinguishable from the same tooth in *S. floridanus* (Hibbard, 1963).

DISCUSSION

The calibrated radiocarbon age of about 23,745 ybp puts the LTC guano deposit in the last full glacial (late Wisconsinan). The Wisconsinan glacial is sometimes divided into early, middle, and late phases. The late phase ran from about 29ka to 11.7 ka, and the full glacial from about 26 ka to 15 ka (Andrews 2009). Thus, the La Tetera Cave guano date falls within the late Wisconsinan and the early part of the last full glacial. As noted above, this single date does not necessarily apply to the bony remains found in other parts of LTC. The radioisotopic age of each of the specimens and fossil taxa in the LTC assemblage is yet to be determined. Although no biochronological 'marker' taxa are present in the LTC assemblage (Table 6), the presence of three extinct mammal species, *Equus conversidens, Camelops hesternus*, and *Desmodus stocki*, together with many extant taxa, establishes a Rancholabrean North American land mammal age (NALMA) for the vertebrate fauna of LTC. Other than the three extinct taxa, the LTC vertebrate list is representative of the vertebrate fauna of the Arizona Upland subdivision of the Sonoran Desert in the surrounding area today; no extralimital taxa were recovered as fossils. The fossil assemblage is likely a mix of allochthonous taxa (the larger vertebrates) and "autochthonous" troglophilic taxa (toads, lizards, snakes, rock wren, bats, rodents) that might have used the cave for shelter. However, many of the vertebrate remains were recovered from debris cones that appeared to have dropped into the cave from ceiling chutes. They imply some kind of overhead source area and a complex history of cave development and sedimentary deposition that we were unable to investigate. The fossiliferous deposits in LTC also have yet to be studied taphonomically. While we worked in the cave, we occasionally encountered small vertebrates (toad and black-tailed rattlesnake) that fell in and became trapped by the modern pitfall entrance and were released outside on the surface. Our preliminary casual observations and the occurrence of loose debris cones with Pleistocene fossils suggest the tiny modern pitfall entrance configuration is almost certainly different from the Pleistocene entrance(s) to LTC and it does not give clues to cave configuration. Careful mapping and future studies of geology, speleogenesis, deposit stratigraphy, radioisotopic chronology, environmental DNA, stable isotope patterns, paleofauna, and taphonomy in LTC could provide further insights into the Pleistocene paleoenvironment and history of the foothills of the Rincon Mountains and LTC area.

Figure 8. *Onychomys* sp. OMNH 80513, left dentary with i1 and m1 as originally found in La Tetera Cave, Arizona. The high coronoid process and m1 were lost in preparation. Condyle to incisive alveolus distance is 12.2 mm.

LTC occurs at a relatively low elevation (1100 m) and preserves a lowland desert vertebrate fauna including *Gopherus*, *Phrynosoma solare*, *Heloderma*, *Dipsosaurus*, *Geococcyx*, and *Dipodomys* (Table 6). Van Devender (2001) noted that some species associated with the modern Sonoran and Mohave Deserts, such as *Dipsosaurus dorsalis,* have a long evolutionary history in the region since at least the Pliocene or early Pleistocene (Norell 1989; Van Devender 2001). Relatively few nearby Pleistocene cave assemblages are available for comparison with LTC, and most of them are at higher elevations. Compared with Ventana Cave, on the Tohono O'odham Nation in the Sonoran Desert about 155 km W of LTC and ~350 m lower in elevation, the late Pleistocene assemblage of LTC shares only *Lepus* (*californicus*) and *Equus* ("*occidentalis*") (Colbert, 1950). Similarly, nearby Arkenstone Cave, with a depauperate Pleistocene vertebrate fauna (including *D. stocki, Myotis thysanodes, Myotis* sp., and *Peromyscus* sp.), shares only Stock's vampire bat and *Peromyscus* with LTC. Deadman Cave, on the northeastern slope of the Catalina Mountains about 50 km north of and 300 m higher than LTC (Mead et al. 1984), preserves an assemblage dating probably to either the late Rancholabrean mixed with early-middle Holocene or else to the transitional period between the latest Wisconsinan glacial and early post-glacial period (Mead et al 2005). Deadman Cave shares several herps (*Bufo/Anaxyrus, Heloderma, Phrynosoma solare, Uta/Urosaurus, Aspidoscelis, Masticophis/Coluber, Rhinocheilus*, and *Crotalus*) and mammals (*Perognathus/Chaetodipus, Dipodomys, Neotoma albigula, Peromyscus, Lepus, Sylvilagus, Myotis, Mephi-*

tis, and *Equus*) with LTC. Compared with Papago Springs Cave, which is only 50 km south of LTC but 475 m higher in elevation, Papago Springs Cave had a clearly middle elevation (1575 m) fauna including *Crotaphytus, Phrynosoma douglasi*, cf. *Cyrtonyx montezumae*, *Aphelocoma ultramarina*, *Sorex arizonae, Ursus* cf*. americanus, Stockoceros conklingi* (see Bravo-Cuevas et al. [2013] for use of this name), *Sciurus* cf*. aberti, Marmota flaviventris, Thomomys, Neotoma mexicana, Sigmodon, Microtus, and Aztlanolagus agilis,* as well as other widespread/eurytopic taxa. Papago Springs Cave and LTC share *Salpinctes obsoletus*, *Myotis velifer*, *Mephitis*, *Equus conversidens*, *Lepus*, *Sylvilagus* cf. *audubonii*, *Chaetodipus* or *Perognathus*, peromyscine, *Onychomys*, and *Neotoma albigula*. LTC lacks the grassland-inhabiting rodents *Sigmodon* and *Microtus* that PSC preserved. Pyeatt Cave is 60 km south and 555 m higher than LTC and contains a fairly diverse late Rancholabrean fauna associated with calibrated radiocarbon dates of 17,451 ± 257 calBP, 26,988 ± 736 calBP, and 41,290 ± 290 calBP (Lindsay and Tessman 1974; Czaplewski et al. 2022), Similar to Papago Springs Cave and consistent with its higher elevation, the Pleistocene vertebrate fauna from Pyeatt Cave is more of a montane assemblage than that of LTC, The two faunal lists share several widely-distributed reptiles (*Uta/Urosaurus, Masticophis/Coluber*, and *Crotalus*) and mammals (*Mephitis/Conepatus, Equus, Sylvilagus, Chaetodipus/Perognathus, Peromyscus*, and *Neotoma albigula*).

Ancient woodrat middens preserve an excellent record of Pleistocene and Holocene vegetation and climate in southwestern North America (Betancourt et al. 1990). Although not all are preserved in caves, most middens come from rock shelters and shallow grottos inhabited by woodrats where the middens accumulate and are protected from weathering. Many of them have been recovered and studied in the Sonoran and Chihuahuan Deserts (Van Devender 1990a, b). LTC occurs near the modern eastern limits of the Sonoran Desert and western limit of the Chihuahuan Desert west of the Continental Divide. Van Devender (2001, 2007) provided a recent synopsis of vegetational changes in southwestern North America leading to the development of the Sonoran Desert in the Miocene and its ongoing evolution to the Holocene. He described the historical Arizona Upland subdivision of the Sonoran Desert as a Holocene phenomenon that continues to change, but for which the pollen and plant macrofossil evidence from woodrat middens indicates a woodland of single-leaf piñon (*Pinus monophylla*), junipers (*Juniperus* spp.), shrub live oak (*Quercus turbinella*), and Joshua tree (*Yucca brevifolia*) through the Wisconsinan glacial period (45 ka-11 ka; Van Devender 2001). In the LTC region near the transition between the modern Sonoran and Chihuahuan Deserts, woodrat middens have been reported from Pontatoc Ridge, Catalina Mountains, the Tucson Mountains, Waterman Mountains, Wolcott Peak, and Picacho Peak in the eastern Sonoran Desert (Van Devender 1990a), and a series of middens has been analyzed from West Doubtful Canyon in the Peloncillo Mountains in the western Chihuahuan Desert (Holmgren et al. 2006). These middens provide most of the basis for inferring the piñon-juniper-shrub live oak woodland in this region during the Wisconsinan. However, vertebrate remains are far less common than those of plants and are less well-studied from woodrat middens. Van Devender and Mead (1978) reported amphibians and reptiles from nearby middens of late Pleistocene age in the Tucson Mountains and Wolcott Peak, 210 m and 240 m lower than LTC respectively; taxa shared with LTC include *Bufo (=Anaxyrus), Aspidoscelis, Rhinocheilus*, and *Masticophis/Coluber*.

Harris (2016) inferred that the extinct vampire bat *Desmodus stocki* occurred in the Southwest in mid-Wisconsinan and older Pleistocene strata and disappeared from the southwestern United States by the end of the mid-Wisconsinan, by 29ka. Harris (2016) noted in Sierra Diablo Cave and Fowlkes Cave, Texas, and U-Bar Cave, New Mexico, that *D. stocki* seemed to disappear in those faunas before the late Wisconsinan. Our late Wisconsinan age on the LTC guano deposit does not necessarily change this disappearance timing for southern Arizona, because the date on the guano does not necessarily apply to the body fossils of *D. stocki* in other rooms of the cave. Unfortunately, no faunal remains have yet been recovered from the guano deposit.

Bat guano deposits are rare and poorly documented in the fossil record of the Southwest. Hunt and Lucas (2018) described sloth coprolites from Rampart Cave, Grand Canyon, Arizona, and made mention of potential bat guano in the rear of the cave and in floor strata, citing Long and Martin (1974) as the source of that implication, but to our knowledge, the potential bat guano has not been investigated in Rampart Cave. Villa-Ramirez (1966:329) cited a personal communication from Aurelio Málaga about his observation of indurated ancient guano in a cave near Castolón, Texas, near Big Bend National Park that was characteristic of vampire bat guano. Villa-Ramirez (1966) was unable to locate or confirm this observation. Kottkamp et al. (2022) noted numerous occurrences of ancient guano in caves in Carlsbad Caverns National Park, New Mexico, which were either attributed to insect-eating bats or unidentified bats. None of these guano deposits are yet dated radioisotopically.

We point up the guano deposit in La Tetera (Fig. 9) because of its potential (as in other recent studies, e.g., Willerslev et al., 2003; Wurster et al., 2008; Walker et al., 2016, 2022; Zepeda Mendoza et al., 2018; Borry et al., 2020; Moore et al., 2020) to provide additional fossils or information regarding ancient environmental DNA and genetic/genomic information about (1) *D. stocki*, *Myotis*, or other bats, (2) the vertebrate taxa fed upon by *D. stocki* and the invertebrates fed upon by other bats, (3) invertebrate, fungal, or microbial communities associated with late Pleistocene ver-

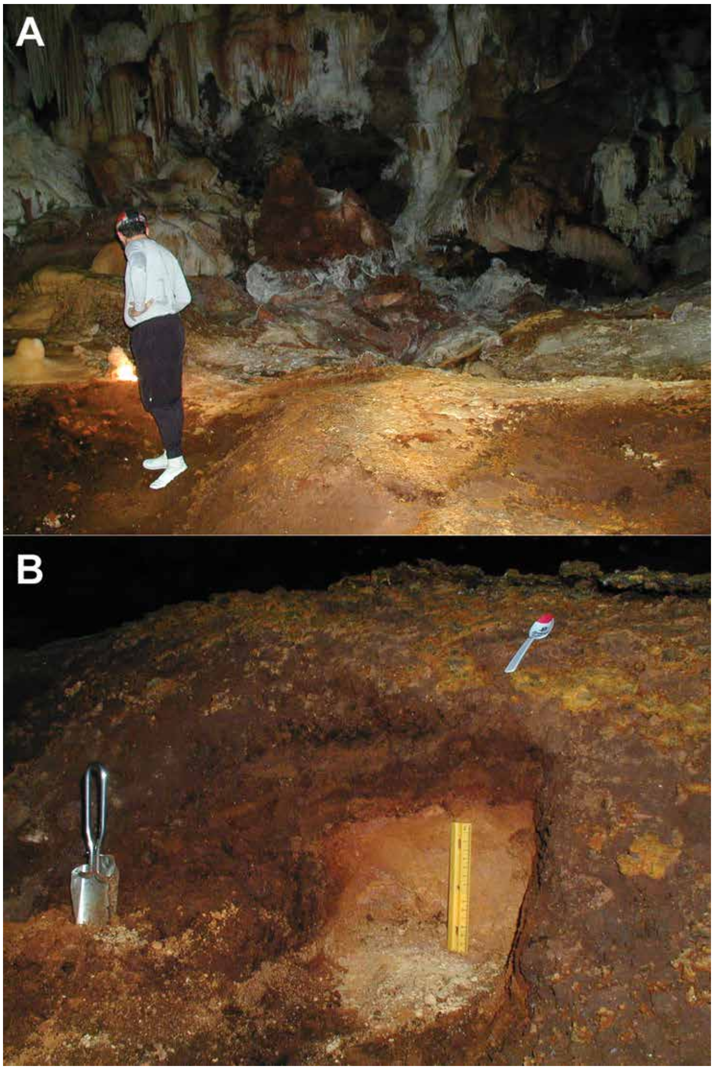

Figure 9. A, Caver and volunteer Steve Smith inspects the guano deposit in La Tetera Cave presumably attributable to *Desmodus stocki*. B, A small trench dug into an edge of the guano deposit from which a bulk sample provided the radioisotopic date for the deposit. Ruler in B is 15 cm long.

tebrates or their guano, (4) climatic phenomena for the late Pleistocene of the North American southwest, or other circumstances. Guano-supported cave systems tend to have higher biodiversity than similar systems without guano (Ferreira et al., 2007). Mineralogy could be used to confirm whether the LTC deposit actually represents ancient guano (Bertrand, 1950; Hutchinson, 1950; Shahack-Gross et al., 2004; Osborne and Jass, 2008), because the organic components will likely be degraded or absent. In addition to body fossils of bats, stable carbon isotopes within the deposit might be useful to determine whether the guano was produced by vampire bats. Hypothetically, these would probably be least depleted in the heavy isotopes, and most similar to the herbivorous megafauna upon which the vampires probably fed, as they are in modern *D. rotundus* [Voigt and Kelm, 2006]). They could be compared with guano of insect-eating bats (with medium depletion of heavy isotopes), or that of pollen-eating bats (probably most depleted in heavy isotopes). Oxygen isotopes could provide additional paleoenvironmental information, such as water availability and aridity (Fricke, 2007; Wurster et al., 2007; Giurgiu and Tamas, 2013). The results could be compared with those from herbivorous megafauna from the Southwest (e.g., Connin et al., 1998). The deposit might also yield phytoliths or pollen as in caves in the central USA (Maher, 2006) and elsewhere (Coles et al., 1989; Carrión et al., 2006; Geanta et al., 2012), although in our experience pollen is poorly preserved in southwestern cave deposits (personal observation). Of course, groundwater and/or corrosive geochemical processes that appear to have operated or to be operating in LTC and/or microbial activity could have altered the guano sediments, obscuring these kinds of data. In a discussion of a deposit of bat guano in Kartchner Caverns, Arizona, associated with the fossil remains of *Myotis velifer*, Buecher and Sidner (1999) provided four standard radiocarbon dates on the guano ranging from 40.2 ka to 49.3 ka, near the limit of resolution of radiocarbon dating and thus possibly even older. Kartchner Caverns is 35 km SE of, and 330 m higher than, LTC.

Oxygen isotope data from a stalagmite in Cave of the Bells, southern Arizona (about 40 km south of LTC and 600 m higher in elevation) showed abrupt intervals of more arid paleoclimate of the southwestern United States during the last glacial period in the late Pleistocene (Marine Isotope Stage 3) that co-varied with abrupt periods of warmth in the North Atlantic Ocean (Wagner et al., 2010). These abrupt changes are considered to have driven the late Pleistocene megafaunal extinctions (Cooper et al., 2015), whose disappearances could have contributed to the extinction of the bat *D. stocki*, which also might have been thermally sensitive to minimum winter temperatures, like its extant relative *D. rotundus* (Wimsatt, 1962; McNab, 1973; McDonald and Jefferson, 2008). Although the direct ages of the various fossil vertebrate taxa of LTC are as yet unknown, they probably are not all contemporaneous. The ~23.7 kybp date on the guano deposit may not pertain to the vertebrate fossils found in the other rooms of LTC. Considered as a contemporaneous assemblage, the LTC fauna collectively indicates a Rancholabrean age and an assemblage whose ecological requirements are generally consistent with an arid environment similar to that of the late 20th century. However, if Harris (2016) was correct in his consideration that *D. stocki* inhabited the Southwest in mid-Wisconsinan and earlier times, the LTC paleofauna could have encountered (or periodically avoided) a changing paleoclimate with wetter moisture and cooler temperature conditions during glacial stadials and drier/warmer conditions, with increased summer relative to winter precipitation, during glacial interstadials (Wagner, 2006; Wagner et al., 2010).

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