JOURNAL OF CAVE AND KARST STUDIES

December 2025
Volume 87, Number 4
ISSN 1090-6924
A Publication of the National Speleological Society

DEDICATED TO THE ADVANCEMENT OF SCIENCE, EDUCATION, EXPLORATION, AND CONSERVATION

Published By
The National Speleological Society

http://caves.org/pub/journal

Office
6001 Pulaski Pike NW
Huntsville, AL 35810 USA
Tel:256-852-1300
nss@caves.org

Editor-in-Chief
Malcolm S. Field
Washington, DC
703-347-8601
field.malcolm1@gmail.com

Production Editor
Scott A. Engel
Knoxville, TN
225-281-3914
saecaver@gmail.com

Copyeditor
Bert Ashbrook
caving.ashbrook@comcast.net

Meredith Hall Weberg
merecaver@yahoo.com

Sarah Marquart
srmarquart@gmail.com

The *Journal of Cave and Karst Studies* , ISSN 1090-6924, CPM Number #40065056, is a multi-disciplinary, refereed journal published four times a year by the National Speleological Society. The *Journal* is available by open access on its website, or check the website for current print subscription rates. Back issues are available from the NSS office.

POSTMASTER: send address changes to the National Speleological Society Office listed above.

The Journal of Cave and Karst Studies is covered by the following ISI Thomson Services Science Citation Index Expanded, ISI Alerting Services, and Current Contents/Physical, Chemical, and Earth Sciences.

Front Cover: Excavation test pit in Parker's Pit, Black Hills, SD. Photo by Christopher Jass. See Mead et al. and Graham et al. in this issue.

PREFACE

It was at the June 2022 annual National Speleological Society Convention held in Rapid City, Black Hills, South Dakota, that a number of us convened a Paleontology Session about the importance of caves and other karst features to the understanding of the fossil record and the documentation of the environmental changes that have occurred in the Northern Hemisphere throughout the Quaternary. At that conference we decided to pull together and publish a number of articles highlighting the significance about caves being not only a warehouse of fossil information but also a non-renewable resource that is often hidden in plain sight. This special issue of the Journal of Cave and Karst Studies presents some of these cave paleontological discoveries.

At that NSS convention it was pointed out that paleontologists who focus on the Quaternary, especially the Late Pleistocene, rely heavily on the data preserved in talus cones deep within caves, filled-in sinkholes, flooded cenotes, breccia pipes, lava tubes, and in often well-lit entrance chambers. But there are not that many paleontologists working with caves and the fossils found within them. They need help in finding these fossil deposits, and that of course could come from the number of cavers out there actively exploring the voluminous caves of the world. Cavers are acutely aware of their surroundings and assess and often map every nook and cranny in caves, but not all have the background to fully comprehend that the occasional bone observed may actually be an incredibly scientifically important find. The active caver becomes the "eyes" for the paleontologist with the two skill sets complementing each other.

The book *Ice Age Cave Faunas of North America* edited by Blaine Schubert, Jim Mead, and Russ Graham sprung out of the 1997 NSS convention in Sullivan, Missouri. That volume, published in 2003 (Indiana University Press), proved to be a catalyst to encouraging the avid caver to be aware of, and to assess, the paleontological resources they may encounter deep within caves. Incredible information was recovered and described such as ground sloths, voles, tapirs, and entire faunas from caves in the Yucatán to Alaska. We also wish to dedicate this issue to Fred Grady in recognition of his tireless efforts working with the caving community to document and preserve fossil remains in caves. He will be missed, as his recent passing leaves a large void in the study of fossils preserved in caves in both the scientific and avocational communities.

There are so many incredible places to hold a cave convention, but the Black Hills of South Dakota and Wyoming, with its countless limestone caves, is a critical region because these caves are now beginning to show a wealth of paleontological information of a mid-continent territory that is just now starting to be understood. This special issue highlights fossil discoveries such as bats in cave faunas, vampire bats and tortoises from southern Arizona, pronghorns from natural traps, sloths from Yucatán cenotes, nighttime carnivores in the Grand Canyon, large cats in Oregon, badgers in the Great Basin, and of course, complex vertebrate faunas in the Black Hills.

You never know what you might have just observed.

Jim I. Mead
H. Gregory McDonald

E. Ray Garton and H. Gregory McDonald. Frederick Von Hofe Grady (1948-2023) - An Appreciation-. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 106-107. DOI:10.4311/2024PA0121

FREDERICK VON HOFE GRADY (1948-2023)
– AN APPRECIATION-

E. Ray Garton and H. Gregory McDonald

The June 2022 National Speleological Society (NSS) Convention held in Rapid City, Black Hills, South Dakota, included a Paleontology Session focusing on the importance of caves and other karst features on the preservation of fossils critical to understanding the environmental change that has occurred in the Northern Hemisphere. Given the positive response and participation in the session it was decided to pull together and publish formal articles based on the talks highlighting the significance about caves being not only a warehouse of fossil information but also non-renewable resources, and often hidden in plain sight. This special issue of the Journal of Cave and Karst Studies presents some of these cave paleontological discoveries. During the review and editing of the manuscripts for this volume it quickly became clear that there was one individual whose many contributions over the years to the study of fossil vertebrates, their collection from caves, and the preservation of caves containing fossil vertebrates stood out, Fred Grady. Thus, it was decided that in recognition of his many contributions to the unique combination of caves and fossil vertebrates, the volume resulting from this session would be dedicated to Fred in recognition of his many contributions to the field. While Fred regularly attended the annual convention of the NSS and participated in previous sessions on paleontology and caves, due to his health he was not able to attend the one in Rapid City. While we had hoped to have the special volume completed in time to present to Fred, unfortunately this was not the case, with him succumbing to leukemia before the volume could be completed. The volume was never intended as a Festschrift, as is often the case in these situations, but rather a testament, recognition and appreciation of all the various ways Fred had contributed to both scientific caving and the science of vertebrate paleontology. Anyone who studies fossil vertebrates from caves, in one way or another, has benefited from Fred's efforts. We therefore present this volume as a recognition of those efforts.

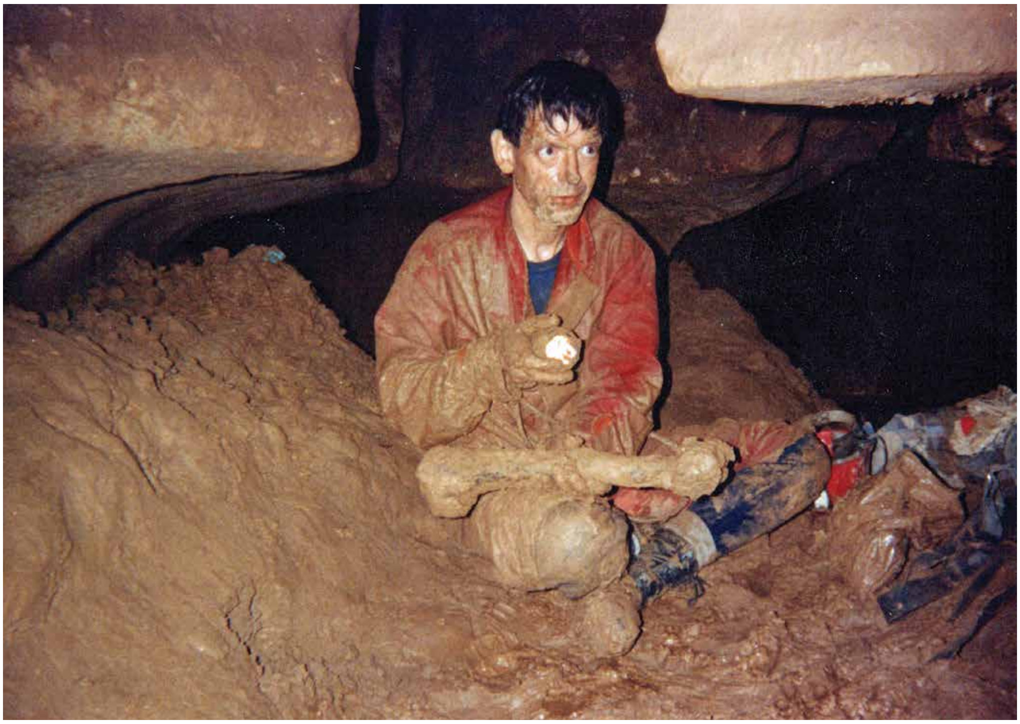


Fig. 1. Fred Grady in Island Ford Cave, Virginia recovering the skeleton of the giant short-faced bear, *Arctodus simus*. Photo by Mary Sue Socky NSS 24206.

Fred Grady began his life's work in Pleistocene vertebrate paleontology with excavations in Durham Cave, Pennsylvania in 1968. There he learned excavation techniques, specimen sorting, labeling, and identification, with much mentoring from John E. Guilday, a curator of vertebrate paleontology at Carnegie Museum of Natural History in Pittsburgh, Pennsylvania. Fred graduated in 1970, with a Bachelor of Science Degree in Biology, from Lafayette College, in Easton, Pennsylvania. He then completed two years of graduate work at the University of Michigan.

Fred joined the staff of the U.S. National Museum (Smithsonian) Section of Vertebrate Paleobiology in 1975 as a vertebrate fossil preparator, where he worked for 28 years. He was the lab supervisor for 14 of those years. Upon his retirement, Fred returned to the Smithsonian as a volunteer in the same department and lab for an additional 15 years. During his tenure at the Smithsonian, Fred worked on the preparation of Oligocene mammals and reptiles as well as dinosaurs and spent hours acid etching fossils from limestone deposits. In addition to his decades of preparation efforts on behalf of the National Museum of Natural History (NMNH) in both research and exhibits, he was a regular member of the team that set-up identification tables at fossil fairs, where he drew upon his encyclopedic knowledge of mammal anatomy. He was an enthusiastic and accomplished fossil collector with his efforts resulting in nearly 3,000 lots of specimens that are now part of the NMNH paleobiology collections. In recognition of this contribution, he was awarded the Morris F. Skinner award of the Society of Vertebrate Paleontology in 1999. Many of these collections were a byproduct of another passion of Fred's: caving. He mapped hundreds of miles of caves, many of which contained significant Pleistocene fossils in Virginia, West Virginia, and elsewhere. He was often the first human being in those spaces, where he would fearlessly squeeze himself through the smallest of cracks to document the unexplored passages and subsequently hauled hundreds of pounds of matrix out the cave for screenwashing for microvertebrates. Most of these collections were made when Fred was not working at the museum. He regularly spent his weekends discovering, digging, processing, cataloging, and identifying Pleistocene fossils from dozens of cave sites in West Virginia and Virginia, as well as several other states. He also spent many weekends as a volunteer working at the New Paris field station of Carnegie Museum of Natural History.

Fred's first big discovery and project was the Pleistocene bone deposit in New Trout Cave, found in February 1979. This led to dozens of trips into the cave and the subsequent removal of over seven tons of bone bearing matrix for processing and study. He identified nearly 100 taxa of vertebrates including mammals, fish, birds, reptiles, and amphibians. In addition to discoveries in New Trout Cave, Fred discovered and identified three large Pleistocene (Irvingtonian) cats from Hamilton Cave. The cats included the saber-tooth cat *Smilodon gracilis*, the cheetah-like cat *Miracinonyx inexpectatus* and the jaguar *Panthera onca augusta*.

Fig. 2. Fred on saltpetre works in Haynes Cave, West Virginia where the first specimens of *Megalonyx jeffersonii* was found, and where he found a *Megalonyx* scapula. The cave was purchased by Fred and donated to the West Virginia Cave Conservancy. Photo by Cliff Lindsay NSS 11224.

Fred began caving with the Monongahela Grotto and moved to the Washington DC area around 1978. He joined the Potomac Speleological Club in 1978 and was assigned PSC #402 in 1980. He joined the DC Grotto in 1978 or 1979 and the NSS in 1978 (NSS # 19586) and was a Life Member. Fred became a Fellow of the NSS and received a Certificate of Merit for his efforts in acquiring the Trout Rock property, now the John Guilday Caves Nature Preserve. He received the American Spelean Association's Peter Hauer Spelean History Award for his contributions to research and publication of spelean history. Most prominent of this research was determining the location of the cave that yielded the specimen of the ground sloth *Megalonyx*, described by Thomas Jefferson. He purchased the property with Haynes Cave and in 2012 donated it to the West Virginia Cave Conservancy. In recognition of his many contributions, in 2016 Fred was presented the Science Award of the National Speleological Society, which is presented to a NSS member who, over time, has demonstrated outstanding dedication to the scientific study of caves.

A new species of extinct owl, *Aegolius gradyi*, the Bermuda Saw-whet Owl was named in honor of Fred in 2012 by Dr. Storrs Olson, a biologist and ornithologist at the Smithsonian and one of the world's foremost avian paleontologists. Olson had this to say about Fred in his dedication "To Frederick V. Grady, my companion in the field on many trips to Bermuda, Hawaii, and the West Indies. A diligent and indefatigable collector of vertebrate fossils, Grady's extraordinary ability and perseverance in identifying and sorting small fossils from vast amounts of washed and screened matrix have added immeasurably to the knowledge of paleoenvironments everywhere he has worked."

Vincent L. Santucci, John-Paul Hodnett, Patricia Seiser, Justin S. Tweet, John "Jack" Wood. National Park Service cave paleontology: 2002-2023. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 108-116. DOI:10.4311/2024PA0119

NATIONAL PARK SERVICE CAVE PALEONTOLOGY: 2002–2023

Vincent L. Santucci[1], John-Paul Hodnett[2], Patricia Seiser[1], Justin S. Tweet[1C], John "Jack" Wood[1]

ABSTRACT

The first published inventory of paleontological resources associated with National Park Service (NPS) caves was issued in 2001 (Santucci et al. 2001). This report documented occurrences of fossil resources within caves in 35 NPS units and the challenges of managing and protecting these paleontological resources. Many significant NPS cave paleontology discoveries have been made in the following two decades. Highlights include: the first paleontological inventory of Carlsbad Caverns National Park, which documented both Permian fossils in cavern bedrock, and bones of Quaternary megafauna; reassessments of Quaternary fossils, particularly avifauna, from rock shelters and caves of Channel Islands NP; the discovery of thousands of Pleistocene–Holocene mummified bats from a cave in Grand Canyon NP, and the identification of an American cheetah skull from Rampart Cave; documentation of extinct or locally extirpated taxa from Great Basin NP; discoveries of abundant Mississippian fossils, particularly sharks, in cave bedrock of Mammoth Cave NP and Natchez Trace Parkway; the relocation of the Port Kennedy Bone Cave site in Valley Forge National Historical Park; and an inventory of *Neotoma* middens from across the NPS. The rise of photogrammetry as an investigative technique has been key to facilitating study of in situ specimens in these challenging settings. The possibility of paleontological resources in caves is now addressed during any paleontological inventory work in NPS units. We can expect that many more cave paleontology discoveries from NPS caves will be made in the decades to come.

INTRODUCTION

Paleontological resources found in cave settings include some of the most remarkable fossils of the National Park Service (NPS). The NPS's cave fossils were first inventoried in Santucci et al. (2001), which listed 35 parks with known paleontological resources in cave settings. These records include fossils of organisms, especially vertebrates, that entered the cave context after the cave began to form, and fossils of organisms in the cave bedrock now exposed by the same processes forming the cave. Many new discoveries have been made in the two decades since then, as well as discoveries of overlooked data. The original list of 35 NPS units now includes 60 units (Fig. 1; Table 1). Of these, 40 have paleontological resources in more "traditional" cave settings, and the other 20 have records restricted to pre-modern packrat middens found in protected rock shelters, talus voids, and other small and/or shallow features. Below are notable park reports and updates for the period 2002-2023.

NEW INFORMATION

Carlsbad Caverns National Park (New Mexico)

A paleontological resource inventory was conducted at Carlsbad Caverns National Park (NP) in 2019 by Geoscientists-in-the-Parks intern Scott Kottkamp (Kottkamp et al., 2020). This was the first time that a comprehensive inventory of fossil resources had been attempted for the park, bringing together various publications, a wealth of internal park reports and other gray literature, and other paleontological information for dozens of park caves. Many of the caves of Carlsbad Caverns NP contain Quaternary paleontological resources, primarily bones, with at least 18 extinct and 13 extralimital taxa represented (Table 2); further information on the Quaternary assemblage can be found in Kottkamp et al. (2022). The Permian bedrock of the caves, pertaining to the Capitan Reef Complex, is also extensively fossiliferous. Weathering has exposed beautifully preserved examples of Permian invertebrates, such as brachiopods with internal anatomy and articulated crinoids.

Channel Islands National Park (California)

Paleontologically notable caves of Channel Islands NP have been discussed in several publications since 2001. A San Miguel Island cave used as a barn owl roost contains a record of small vertebrates from the latest Pleistocene through the Holocene. This site has been studied for decades but continues to reveal new information. The bird record from this site was most recently summarized in Collins et al. (2018a), which documented 88 species. Mead et al. (2018) published the first report of the chorus frog *Pseudacris* from the cave, and Mychajliw et al. (2020) documented the occurrence of a metacarpal from a short-faced bear (*Arctodus simus*). This unexpected find is thought to be the result of a scavenging bird bringing a portion of a mainland bear carcass to the cave (Mychajliw et al., 2020). A similar barn owl cave roost on Santa Barbara Island, to date confined to the Holocene, has been recently documented for the NPS

---

[1] National Park Service
[2] Maryland-National Capital Park and Planning Commission
[C] Corresponding author: justin_tweet@nps.gov

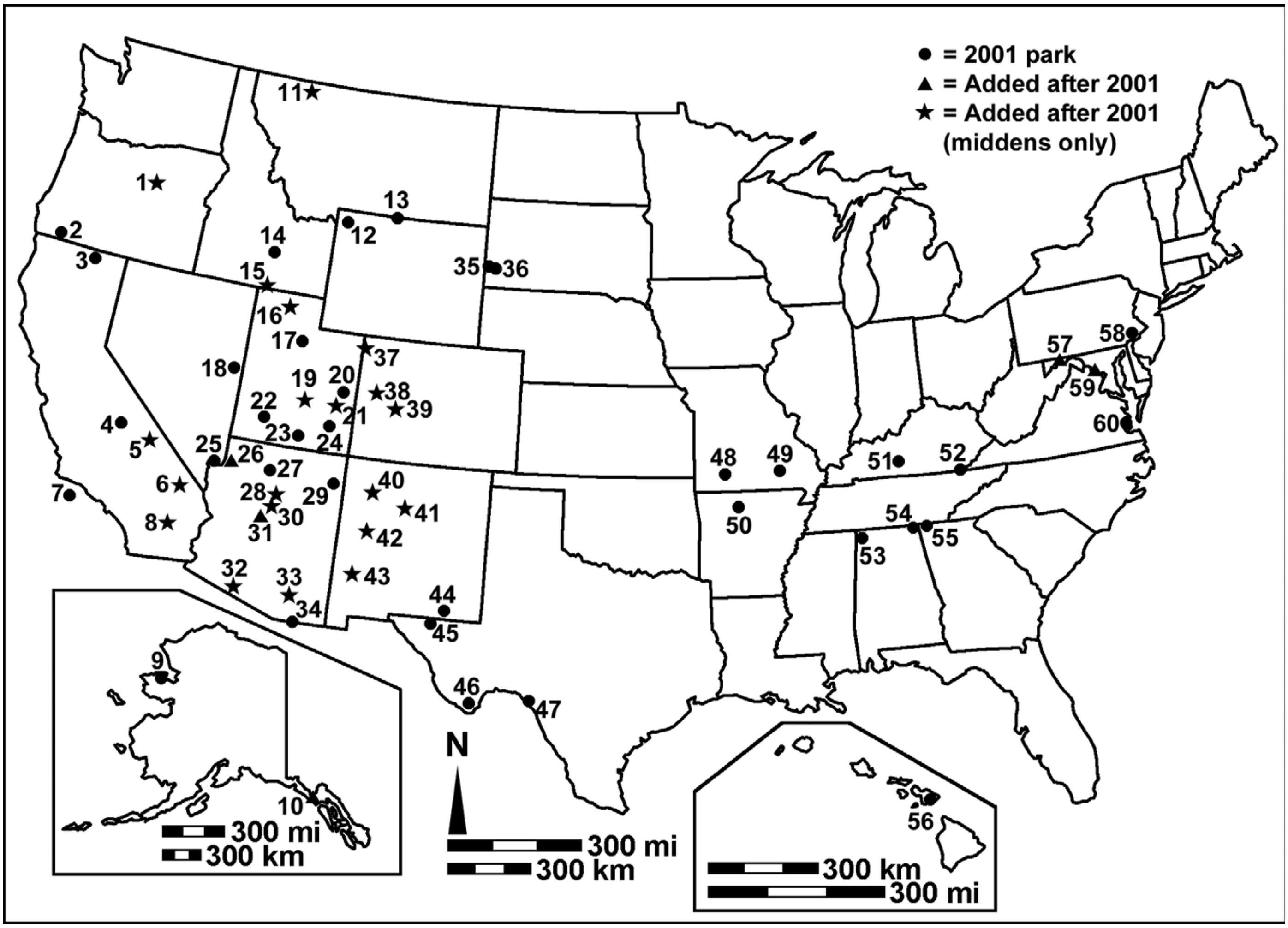


Figure 1. Map of NPS units with fossils from cave settings. The parks documented in Santucci et al. (2001) are marked with circles. Parks recognized as having pre-modern packrat middens but no other cave fossils to date are marked with stars. Other park occurrences recognized since 2001 are marked with triangles. 1. John Day Fossil Beds National Monument (NM); 2. Oregon Caves NM; 3. Lava Beds NM; 4. Sequoia and Kings Canyon National Parks (NPs); 5. Death Valley NP; 6. Mojave National Preserve (NPres); 7. Channel Islands NP; 8. Joshua Tree NP; 9. Bering Land Bridge NPres; 10. Glacier Bay NP&Pres; 11. Glacier NP; 12. Yellowstone NP; 13. Bighorn Canyon NRA; 14. Craters of the Moon NM; 15. City of Rocks NPres; 16. Golden Spike NHS; 17. Timpanogos Cave NM; 18. Great Basin NP; 19. Capitol Reef NP; 20. Arches NP; 21. Canyonlands NP; 22. Cedar Breaks NM; 23. Glen Canyon NRA; 24. Natural Bridges NM; 25. Lake Mead National Recreation Area (NRA); 26. Parashant NM; 27. Grand Canyon NP; 28. Wupatki NM; 29. Canyon de Chelly NM; 30. Walnut Canyon NM; 31. Montezuma Castle NM; 32. Organ Pipe Cactus NM; 33. Saguaro NP; 34. Coronado National Memorial; 35. Jewel Cave NM; 36. Wind Cave NP; 37. Dinosaur NM; 38. Colorado NM; 39. Curecanti NRA; 40. Chaco Culture National Historical Park (NHP); 41. Bandelier NM; 42. El Malpais NM; 43. Gila Cliff Dwellings NM; 44. Carlsbad Caverns NP; 45. Guadalupe Mountains NP; 46. Big Bend NP; 47. Amistad NRA; 48. Wilson’s Creek NB; 49. Ozark National Scenic River; 50. Buffalo NR; 51. Mammoth Cave NP; 52. Cumberland Gap NHP; 53. Natchez Trace Parkway; 54. Russell Cave NM; 55. Chickamauga and Chattanooga National Military Park; 56. Haleakalā NP; 57. Potomac Heritage National Scenic Trail; 58. Valley Forge NHP; 59. Chesapeake and Ohio Canal NHP; 60. Colonial NHP.

(Collins et al., 2018b); they reported 43 bird taxa identifiable to genus or species in the pre-historic deposits. The San Miguel and Santa Barbara cave sites contribute to perhaps the richest record of Quaternary birds in the entire NPS. A summary of the paleontological resources of Channel Islands NP can be found in Tweet et al. (2020), the recent paleontological resource inventory report.

Chesapeake and Ohio Canal National Historical Park (District of Columbia–Maryland–West Virginia)

Trilobites have been informally reported in the Conococheague Limestone bedrock of a cave in the vicinity of Dam 4 within Chesapeake and Ohio Canal National Historical Park but were not observed during a 2009 visit (Clites and Santucci, 2010).

Glacier Bay National Park and Preserve (Alaska)

Reconnaissance by Kevin Allred and Wayne Howell in 2001 located several caves in Glacier Bay NP and Preserve. Among them was a vertical pit, dubbed “Ai Chi Pit”, containing an undated skull of a mink or marten (Heaton, 2002). Caves in the park so far pertain to the Silurian Willoughby Limestone (P. Burger, pers. comm., August 2023).

Table 1. A concise summary of NPS units with fossils found in cave settings. *=new since 2001; **=*Neotoma* midden record only (not included in 2001); †=units with fossils found in deep cave settings as well as small-scale features with *Neotoma* middens

Amistad NRA
Arches NP†
Bandelier NM**
Bering Land Bridge NPres
Big Bend NP†
Bighorn Canyon NRA†
Buffalo NR
Canyon de Chelly NM†
Canyonlands NP**
Capitol Reef NP**
Carlsbad Caverns NP†
Cedar Breaks NM
Chaco Culture NHP**
Channel Islands NP
Chesapeake & Ohio Canal NHP*
Chickamauga/Chattanooga NMP
City of Rocks NPres**
Colonial NHP
Colorado NM**
Coronado NMem
Craters of the Moon NM†
Cumberland Gap NHP
Curecanti NRA**?
Death Valley NP**
Dinosaur NM**
El Malpais NM**
Gila Cliff Dwellings NM**
Glacier NP**
Glacier Bay NP&Pres*
Glen Canyon NRA†
Golden Spike NHS**
Grand Canyon NP†
Great Basin NP†
Guadalupe Mountains NP†
Haleakalā NP
Jewel Cave NM†
John Day Fossil Beds NM**
Joshua Tree NP**
Lake Mead NRA†
Lava Beds NM†
Mammoth Cave NP
Mojave NPres**
Montezuma Castle NM*
Natchez Trace Parkway
Natural Bridges NM†
Oregon Caves NM
Organ Pipe Cactus NM**
Ozark NSR
Parashant NM*†
Potomac Heritage NST*
Russell Cave NM
Saguaro NP**
Sequoia / Kings Canyon NP†
Timpanogos Cave NM†
Valley Forge NHP
Walnut Canyon NM**
Wilson’s Creek NB
Wind Cave NP
Wupatki NM**
Yellowstone NP†


Figure 2. A mummified myotid bat preserved in a Grand Canyon NP cave (NPS/Shawn Thomas).

Grand Canyon National Park (Arizona)

Caves are one of the outstanding sources of paleontological resources in Grand Canyon NP (Santucci and Tweet, 2021). The abundance and quality of the cave fossils has led to them being documented in inventories at various scales: a single cave (Rampart Cave; Carpenter, 2003); a region of the park (eastern Grand Canyon; Mead et al., 2003); and the entire park (Kenworthy et al., 2004; Mead et al., 2021a). Still, the information that can be gained from the park’s cave fossils is nowhere near being exhausted. Numerous publications have incorporated fossils from Grand Canyon NP caves over the past two decades; a full list is omitted here for brevity, but Mead et al. (2021a) provides a lengthy bibliography. Two significant events have occurred in the past few years. First, a remote cave has been found to include hundreds to thousands of mummified bats representing at least eight species (Fig. 2) (Mead et al., 2021a). This discovery documents a record of bats ranging in age from more than 43,500 YBP (C. Chambers, pers. comm., 2022) to 3,500 YBP (Mead et al., 2021a). The exquisite preservation, abundance, and taxonomic diversity of these bats will permit an unprecedented glimpse of the life and ecology of these animals from the latest Pleistocene through much of the Holocene. Second, felid remains from three caves previously identified as *Puma concolor* (mountain lion) have been reidentified as elements of the extinct North American cheetah *Miracinonyx trumani*, which has implications for the ecology of this species as being adaptable to near vertical rocky terrain and canyons like some modern large felids (Hodnett et al., 2022a).

Table 2. Extinct and extralimital Quaternary vertebrate taxa found in the caves of Carlsbad Caverns NP, as determined in Kottkamp et al. (2022).

Extinct	Extralimital
Cathartidae: undetermined extinct genus	Testudinidae: *Gopherus* cf. *G. morafkai*
Cathartidae: *Coragyps occidentalis*	Sciuridae: *Marmota flaviventris*
Nothrotheriidae: *Nothrotheriops shastensis*	Sciuridae: *Tamiasciurus hudsonicus*
Soricidae: *Notiosorex dalquesti*	Cricetidae: *Microtus ochrogaster*
Molossidae: *Tadarida constantinei*	Cricetidae: *Microtus pennsylvanicus*
Felidae: *Miracinonyx trumani*	Cricetidae: *Neotoma cinerea*
Felidae: *Panthera atrox*	Leporidae: *Sylvilagus nuttalli*
Canidae: *Canis armbrusteri*	Soricidae: *Cryptotis parva*
Canidae: *Aenocyon dirus*	Soricidae: *Sorex cinereus*
Equidae: *Equus conversidens*	Soricidae: *Sorex merriami*
Equidae: *Equus occidentalis*	Soricidae: *Sorex monticolus*
Tayassuidae: *Platygonus* sp.	Soricidae: *Sorex palustris*
Camelidae: *Camelops hesternus*	Bovidae: *Ovis canadensis*
Cervidae: *Navahoceros fricki*	
Antilocapridae: *Capromeryx furcifer*	
Antilocapridae: *Stockoceros conklingi*	
Bovidae: *Euceratherium collinum*	
Bovidae: *Oreamnos harringtoni*	

Great Basin National Park (Nevada)

Great Basin NP in eastern Nevada has long been known for caves; in fact, the park was originally established as Lehman Caves National Monument in 1922. Vertebrate remains were known from the caves for decades and were among the components of the park paleontological resource inventory undertaken by Gorden Bell from 2010 to 2015. The park’s caves include a variety of Quaternary remains of amphibians, reptiles, birds, and mammals. Among them are extinct taxa (rabbits *Aztlanolagus agilis* and *Brachylagus coloradoensis*), locally extirpated taxa (pika *Ochotona princeps*, pocket gopher *Thomomys talpides*, and an unidentified marten), and taxa that are much less abundant in the Snake Range at present than in the cave deposits (marmot *Marmota flaviventris*) (Bell et al., 2016).

Lake Mead National Recreation Area (Arizona–Nevada)

During the production of a paleontological resource inventory for Lake Mead National Recreation Area (Bonde et al., 2018), it was found that a cave previously reported in the literature, Catclaw Cave, is within the recreation area. This large shelter is the source of the holotype of the bighorn sheep *Ovis catclawensis* Hibbard and Wright (1956). This species is now generally considered to be a synonym of *O. canadensis* but may potentially represent a distinct subspecies within that species.

Mammoth Cave National Park (Kentucky)

The cave paleontological resources of Mammoth Cave NP have been a subject of documentation and research since Santucci et al. (2001). As of 2023, a paleontological resource inventory report was being prepared to summarize the park’s paleontology. Until recently, the vast majority of fossils reported from the cave system were remains of Quaternary vertebrates. Colburn (2005) provided a detailed inventory of these finds, with a further summary in 2017. Among the notable discoveries was the recognition of a *Smilodon* fibula, the first record of this genus in the state. Although there was hope that the proboscidean noted in Santucci et al. (2001) would prove to be a Mammoth Cave mammoth, it has been identified as an American mastodon (Colburn 2005). A pair of publications in 2015 focused on bat paleontology in the park’s caves. Colburn et al. (2015) determined that the bat bonebed of Bat Cave represents deposition during at least 11 flooding events between 10,800 and 2,200 years ago. Widga and Colburn (2015) focused on guano deposits in several areas, which together present a record greater than 54,000 years in duration, from the present to in excess of the limit of radiocarbon dating. Bones in the guano beds almost entirely represent bats, including locally extirpated taxa such as *Tadarida brasiliensis* (Mexican free-tailed bat) present during an interstadial.

Although fossils have long been recognized in the Mississippian-age bedrock cave surfaces in Mammoth Cave NP, it was not until recent years that a concerted effort has been made to formally document and describe them. An unprecedented diversity of Mississippian chondrichthyans and bony fish has been found since 2019, along with well-preserved echinoderms, other invertebrate fossils, enormous invertebrate burrows, and conodonts. To date more than 110 chondrichthyan species have been found in four Middle to Late Mississippian formations, including several that are new to science. These chondrichthyan fossils include teeth, dermal spines and denticles, and complete to nearly complete cartilaginous skeletal material, some of which are articulated (Fig. 3) (Hodnett et al., 2022b). One new taxon, the petalodont chondrichthyan *Strigilodus tollesonae*, was named in 2023 (Hodnett et al., 2023a), with others in prep.

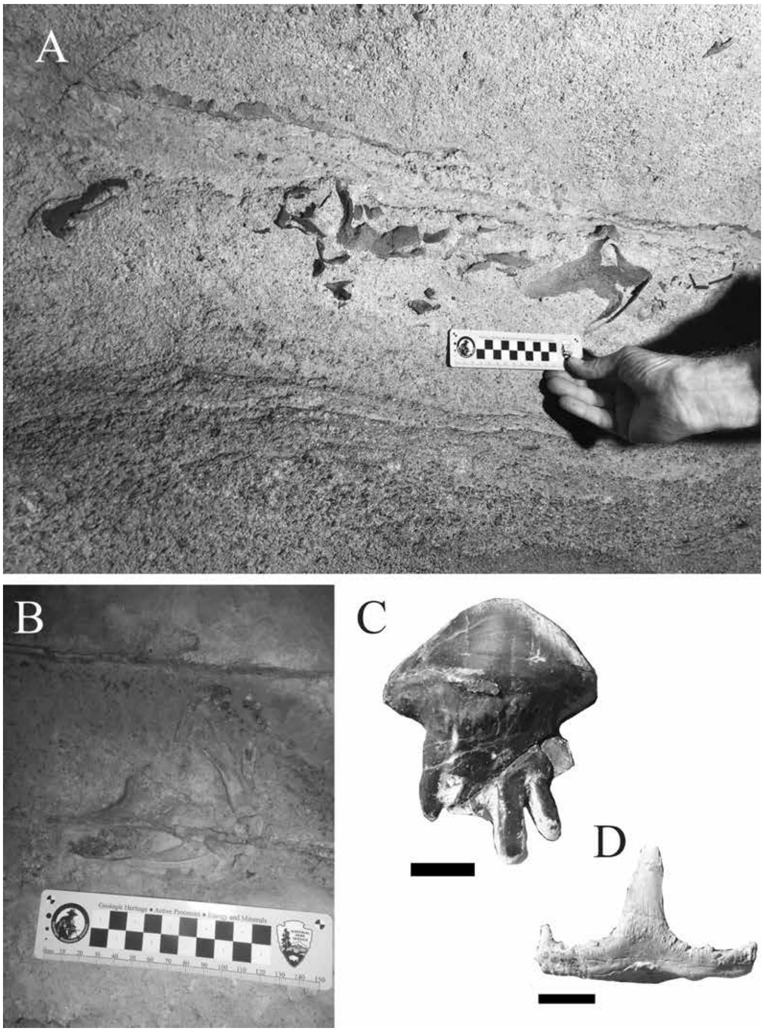


Figure 3. Samples of chondrichthyan fossils from Mammoth Cave NP. (a) The lower jaw, cranial cartilage, and teeth of the ctenacanthiform shark *Saivodus striatus* in situ of the cave wall in the Middle Mississippian Ste. Genevieve Formation (NPS/JP Hodnett); (b) The articulated upper and lower jaws, gill arches, and teeth of the ctenacanthiform *Glikmanius* sp. in situ of the cave wall in the Middle Mississippian Ste. Genevieve Formation (NP/ Rickard Toomey); (c) An isolated tooth of *Polyrhizodus concavus* from the Middle Mississippian St. Louis Formation, scale 1 cm (NPS/JP Hodnett); (d) An isolated tooth of *Saivodus striatus* from the Late Mississippian Girkin Formation, scale 1 cm (NPS/JP Hodnett).

Montezuma Castle National Monument (Arizona)

The cave paleontological resource record of Montezuma Castle National Monument was overlooked in Santucci et al. (2001), so is included here. The sinkhole known as Montezuma Well includes a cave in the Pliocene Verde Formation, which was investigated in the 1950s by Arthur Lange. Lange (1957) reported that the cave had few speleothems except for calcite that had recrystallized in molds left by decomposed twigs and other organic remains. The cave’s fissure fill also includes remains of birds and small rodents (Lange, 1957).

Natchez Trace Parkway (Alabama–Mississippi–Tennessee)

During a reconnaissance survey in advance of construction, NPS associate J. P. Hodnett visited a cave within Natchez Trace Parkway and observed both bedrock fossils and Quaternary faunal remains that potentially include Pleistocene fossils. Fossils in the cave bedrock include specimens of productid and spiriferid brachiopods, crinoids, and multiple chondrichthyan taxa. These cave bedrock fossils represent a shallow Middle Mississippian marine facies, with some of the chondrichthyan taxa similar to those found at Mammoth Cave NP (Hodnett et al., 2022b). Quaternary remains include bones, teeth, and scales of fish, reptiles, birds, and small mammals. Use as a roost and/or carnivoran den is suspected. Documentation of the fossils has been published in a paleontological resource inventory (Hodnett et al., 2023b).

Parashant National Monument (Arizona)

Parashant National Monument, also known as Grand Canyon-Parashant National Monument, is geologically similar to adjacent Grand Canyon NP but much more poorly known in terms of paleontology. Resource management is complicated by joint administration; only about 20 percent of the monument is administered by the NPS, most of the rest being administered by the Bureau of Land Management. Like Grand Canyon NP, Parashant National Monument has numerous caves and rock shelters, some of which contain paleontological resources. A preliminary inventory of Quaternary fossils was produced by Jim Mead (Mead, 2003). Several years of cave inventorying and fossil collection followed, but the results have not yet been published (Tweet et al., 2021).

During the fall of 2020, Geoscientists-in-the-Parks interns Holley Flora and Summer Rose Weeks conducted a paleontological inventory at the monument; the published report (Tweet et al., 2021) is the first formally published document to refer to these cave fossils.

Figure 4. The entrance to Cumberland Bone Cave along the Great Allegheny Passage trail (J.-P. Hodnett).

Potomac Heritage National Scenic Trail (District of Columbia–Maryland–Pennsylvania–Virginia)

Although the Potomac Heritage National Scenic Trail was established in 1983, it has undergone a number of expansions. One such expansion that occurred after 2001 put the notable Cumberland Bone Cave on the Great Allegheny Passage portion of the trail, northwest of Cumberland (Fig. 4). Cumberland Bone Cave, uncovered during work on the Western Maryland Railroad in the early 1910s, is a former sinkhole that accumulated a large quantity of bones at close to the early–middle Pleistocene boundary; Withnell et al. (2020) dated peccary teeth from the site to 790 ± 53 and 722 ± 64 ka. It is comparable in many ways to Port Kennedy Bone Cave in Valley Forge National Historical Park (see below), except the site has not been buried and is still producing fossils. See Gidley and Gazin (1933) and Norden (2006) for summaries. With both Cumberland Bone Cave and Port Kennedy Bone Cave, the NPS is serendipitously associated with two of the most significant mid-Pleistocene (Irvingtonian) vertebrate localities in the eastern United States. A monograph reviewing the Cumberland Bone Cave was in preparation in 2023 (R. Eshelman, pers. comm., 2022), and a complementary NPS report has been produced (Hodnett et al., 2023c).

Valley Forge National Historical Park (Pennsylvania)

At the time Santucci et al. (2001) was written, Port Kennedy Bone Cave was assumed to be within the boundaries of Valley Forge National Historical Park, but its location was unknown. The bone-filled fissure had been buried along with the surrounding quarry during the early 20th century and then forgotten. In the 1990s, Valley Forge NHP natural resources manager Brian Lambert initiated an effort to relocate the site. Historical research narrowed the search field (Daeschler et al., 2005), and geophysical investigation using gravity and electrical resistivity surveying in 2004 and 2006 established the location of the buried site (Hojdila et al., 2005; Baughman et al., 2006; Bechtel and Baughman, 2006). Further direct investigation of the site is not anticipated, due to asbestos-bearing quarry fill.

Wind Cave National Park (South Dakota)

Abundant Quaternary fossils have been found in the recently discovered Persistence Cave located within Wind Cave NP. Most of the fossils have not yet been formally published, except for voles (Jass et al., 2020) and a pine marten (Mead et al., 2021b, which also includes an occurrence from Wind Cave itself), but informal reports and abstracts state that the site includes both invertebrates (gastropods and insects) and vertebrates (frogs, salamanders, snakes, lizards, bats, shrews, pikas, rabbits, rodents, mustelids, bears, canids, *Bison*, and extinct horses and camels). A paleontological resource inventory was conducted at the park in 2022 by Scientists in Parks intern Theodore Herring (Herring et al., 2023).

Packrat Middens

Middens constructed by packrats/wood rats (*Neotoma* spp.) are among the most abundant paleontological resources found in caves and rock shelters and are extremely useful as “paleoecological time capsules”. An inventory of NPS packrat middens (Tweet et al., 2012) found records of 35 NPS units with ancient or modern middens, and six more have been identified since then (Carlsbad Caverns NP, Glacier NP, John Day Fossil Beds NM, Petrified Forest NP, Sequoia and Kings Canyon NPs, and Walnut Canyon NM). In many cases the sources are rock shelters rather than deep caves, but they are still of interest. Sites with modern middens only and no other cave paleontological records (Mesa Verde NP,

Figure 5. Taking photogrammetric images of a prepared specimen (the *Euceratherium* skull from Musk Ox Cave, now *Speleotherium logani*) (NPS/Vincent Santucci).

Petrified Forest NP, Pipe Spring NM) are omitted from Table 1 and Fig. 1.

Photogrammetry

Photogrammetry, a photo-documentation technique that can be used on both in situ and excavated fossils (Matthews et al., 2006; Matthews and Breithaupt, 2011; Mallison and Wings, 2014), has become a powerful tool for documenting cave fossils since 2001. This technique produces three-dimensional images of objects from multiple photos taken at various angles. The three-dimensional image can then be studied or viewed in a digital environment or printed using rapid prototyping technology to produce a physical representation of the object similar to a cast. This technique is especially useful for studying fossils that cannot be collected. One of the earliest uses of photogrammetry to document an NPS cave fossil was the modeling of a Carlsbad Caverns NP *Euceratherium* skull in October 2016 at the Smithsonian (USNM PAL 598576) (Fig. 5). More recently, photogrammetry has been used to document two in situ shark skeletons at Mammoth Cave NP. The benefits of this kind of non-destructive documentation of fossils in a cave setting are readily apparent: caves are not ideal settings for extracting fossils, and the potential for damaging other resources is greatly reduced. Examples of online digital photogrammetric models of NPS cave fossils can be seen at:

- https://3d.si.edu/object/3d/euceratherium-cf-sinclairi:7a5211b8-2d58-4681-ac31-3f7cb4b8302a (Carlsbad Caverns NP *Euceratherium*)
- https://www.nps.gov/articles/000/shark-fossil-glikmanius.htm (Mammoth Cave NP *Glikmanius*)
- https://www.nps.gov/articles/000/shark-fossil-saivodus-striatus.htm (Mammoth Cave *Saivodus*)

CONCLUSIONS

Inventory and monitoring for paleontological resources, including within caves, is an important activity undertaken by the National Park Service Paleontology Program. Through these inventories the scope, significance, distribution, and management issues associated with fossils have been identified, providing important baseline paleontological resource data to inform park management in planning and decision-making. Frequently, paleontological resource inventories in parks have resulted in important new fossil discoveries, as outlined in this publication. Preservation of these cave fossils through documentation, photography, photogrammetry, and collection will enhance opportunities for scientific research, public education, and resource stewardship of this important non-renewable record of life from NPS caves.

ACKNOWLEDGMENTS

We have had the good fortune to work with many wonderful NPS personnel, affiliates, and interns over the years. Significant contributors to the cave paleontology work discussed above include: Mary Carpenter (Badlands NP); Rod Horrocks and Scott Kottkamp (Carlsbad Caverns NP); Ken Convery and Laura Kirn (Channel Islands NP); Gordon Bell (Great Basin NP); Kim Besom, Colleen Hyde, Anne Miller, and Mark Nebel (Grand Canyon NP); Aubrey Bonde and Erin Eichenberg (Lake Mead NRA); Rick Olson, Kelly Tolleson, and Rick Toomey (Mammoth Cave NP); Deanna Boensch and Christina Smith (Natchez Trace Parkway); Holley Flora, Eathan McIntyre, and Summer Rose Weeks (Parashant NM); and Theodore Herring and Marc Ohms (Wind Cave NP). We would also like to thank our many cave paleontology collaborators outside the NPS, including Carol Chambers (Northern Arizona University), Ralph Eshelman (Calvert Marine Museum), Nick Gardner (West Virginia University Potomac State College), Jim Mead (Mammoth Site of Hot Springs), Gary Morgan (New Mexico Museum of Natural History and Science), Shawn Thomas (Bat Conservation International), Ben Tobin (Kentucky Geological Survey), and George Veni (National Cave and Karst Research Institute). Finally, we thank two anonymous reviewers and Greg McDonald (associate editor, Journal of Cave and Karst Studies) for their helpful reviews.

REFERENCES

Baughman, S.H., Bechtel, T.D., DeMayo, T., and Hojdila, J.L., 2006, Port Kennedy Bone Cave; rediscovered with geophysics: Abstracts with Programs - Geological Society of America, v. 38, no. 2, p. 82.

Bechtel, T.D., and Baughman, S.H., II, 2006, Geophysical detection and imaging of a lost mid-Pleistocene bone cave beneath Valley Forge National Historical Park, PA: Abstracts with Programs - Geological Society of America, v. 38, no. 7, p. 319.

Bell, G.L., Jr., Tweet, J.S., and Santucci, V.L., 2016, Great Basin National Park: Paleontological resource inventory: Fort Collins, National Park Service, Natural Resource Report NPS/GRBA/NRR—2016/1285, 117 p.

Bonde, A., Santucci, V.L., Tweet, J.S., Eichenberg, E., and Moore, B., 2018, Lake Mead National Recreation Area: Paleontological resources inventory. Fort Collins, National Park Service, Natural Resource Report NPS/LAKE/NRR—2018/1618, 227 p.

Carpenter, M.C., 2003, Late Pleistocene Aves, Chiroptera, Perissodactyla, and Artiodactyla from Rampart Cave, Grand Canyon, Arizona: [M.S. thesis], Flagstaff, Northern Arizona University, 333 p.

Clites, E.C., and Santucci, V.L., 2010, Preliminary paleontological resource field survey: Chesapeake and Ohio Canal National Historical Park: Fort Collins, National Park Service, Natural Resource Report NPS/NRPC/NRR—2010/197, 82 p.

Colburn, M.L., 2005, Paleontological inventory project: vertebrate remains found in select passages and caves at Mammoth Cave National Park, Kentucky: Springfield, Illinois State Museum, 316 p.

Colburn, M.L., 2017, Under foot: the paleontology of Mammoth Cave: *in* Hobbs, H.H., III, Olson, R.A., Winkler, E.G., and Culver, D.C., eds., Mammoth Cave: A Human and Natural History, Cham, Switzerland, Springer International Publishing AG, p. 175-189

Colburn, M., Toomey, R., Widga, C., and Olson, R., 2015, Holocene paleontology of Bat Cave, Edmonson County, Kentucky: Journal of Cave and Karst Studies, v. 77, no. 2, p. 91–98. https://doi.org/10.4311/2014PA0107.

Collins, P.W., Guthrie, D.A., Whistler, E.L., Vellanoweth, R.L., and Erlandson, J.M., 2018a, Terminal Pleistocene–Holocene avifauna of San Miguel and Santa Rosa islands: identifications of previously unidentified avian remains recovered from fossil sites and prehistoric cave deposits: Western North American Naturalist, v. 78, no. 3, p. 370–404. https://doi.org/10.3398/064.078.0311.

Collins, P.W., Ainis, A.F., Rodriguez, J., Ceniceros, S., Sperati, J.L., Guttenberg, R.B., Thomsen, S.K., and Vellanoweth, R.L., 2018b, Faunal and floral deposits from Barn Owl Cave: a proxy for natural and anthropogenic change on Santa Barbara Island during the past ~1,500 years: unpublished report prepared by the Santa Barbara Museum of Natural History, Santa Barbara for the National Park Service and Montrose Settlements Restoration Program, 94 p.

Daeschler, E.B., Lamanna, M.C., and Carfioli, M., 2005, On the trail of an important Ice Age fossil deposit: Park Science, v. 23, no. 2, p. 31–34.

Gidley, J.W., and Gazin, C.L., 1938, The Pleistocene vertebrate fauna from Cumberland Cave, Maryland: United States National Museum Bulletin 171, p. 1–99.

Heaton, T.H., 2002, Ai Chi Pit: https://web.archive.org/web/20200117043657/http://apps.usd.edu/esci/alaska/aichi.html (accessed October 25, 2023). Part of "Ice Age Paleontology of Southeast Alaska" (https://web.archive.org/web/20201130230904/http://apps.usd.edu/esci/alaska/index.html), University of South Dakota.

Herring, T., Tweet, J.S., and Santucci, V.L., 2023, Wind Cave National Park: Paleontological resource inventory (public version): Fort Collins, National Park Service, Natural Resource Report NPS/WICA/NRR—2023/2536, 135 p. https://doi.org/10.36967/2299620.

Hibbard, C.W., and Wright, B.A., 1956, A new Pleistocene bighorn sheep from Arizona. Journal of Mammalogy, v. 37, no. 1, p. 105–107. https://doi.org/10.2307/1375535.

Hodnett, J.-P.M., White, R., Carpenter, M., Mead, J., and Santucci, V.L., 2022a, *Miracinonyx trumani* (Carnivora; Felidae) from the Rancholabrean of the Grand Canyon, Arizona and its implications on the ecology of the "American cheetah": New Mexico Museum of Natural History and Science Bulletin, v. 88, p. 157–186.

Hodnett, J.-P.M, Tweet, J.S., and Santucci, V.L., 2022b, The occurrence of fossil cartilaginous fishes (Chondrichthyes) within the parks and monuments of the National Park Service: New Mexico Museum of Natural History and Science Bulletin, v. 90, p. 183-208.

Hodnett, J.-P.M., Toomey, R., Olson, R., Tweet, J.S., and Santucci, V.L., 2023a, Janassid petalodonts (Chondrichthyes, Petalodontiformes, Janassidae) from the Middle Mississippian (Viséan) Ste. Genevieve Formation, Mammoth Cave National Park, Kentucky, USA: Historical Biology. https://doi.org/10.1080/08912963.2023.2231955.

Hodnett, J.-P.M., Boensch, D.M., Smith, C.E., Tweet, J.S., and Santucci, V.L., 2023b, Natchez Trace Parkway and Natchez Trace National Scenic Trail: Paleontological resource inventory (sensitive version). Fort Collins, National Park Service, Natural Resource Report NPS/NATR/NRR—2023/2521, 167 p. https://doi.org/10.36967/2299391.

Hodnett, J.-P.M., Eshelman, R.E., Gardner, N., and Santucci, V.L., 2023c, Geology, Pleistocene paleontology, and research history of the Cumberland Bone Cave: Potomac Heritage National Scenic Trail: Fort Collins, National Park Service, Natural Resource Report NPS/POHE/NRR—2023/2493, 99 p. https://doi.org/10.36967/2296839.

Hojdila, J., DeMayo, T., Baughman, S., Bechtel, T., and Carfioli, M., 2005, The long-lost cave has been found!: Park Science, v. 23, no. 2, p. 35.

Jass, C.N., Mead, J.I., and Swift, S.L., 2020, Late Quaternary voles from Persistence Cave, Black Hills, South Dakota: Western North American Naturalist, v. 80, no. 4, p. 521–530. https://doi.org/10.3398/064.080.0409.

Kenworthy, J., Santucci, V.L., and Cole, K.L., 2004, An inventory of paleontological resources associated with caves in Grand Canyon National Park: in van Riper, C., III, and Cole, K.L., eds., The Colorado Plateau: Cultural, Biological and Physical Research, Tucson, University of Arizona Press, Tucson, p. 211–228.

Kottkamp, S., Santucci, V.L., Tweet, J.S., Horrocks, R.D., Lynch, E., and Morgan, G.S., 2020, Carlsbad Caverns National Park: Paleontological resource inventory (public version): Fort Collins, National Park Service, Natural Resource Report NPS/CAVE/NRR—2020/2148, 171 p.

Kottkamp, S., Santucci, V.L., Tweet, J.S., Horrocks, R.D., and Morgan, G.S., 2022, Pleistocene vertebrates from Carlsbad Caverns National Park, New Mexico: New Mexico Museum of Natural History and Science Bulletin, v. 88, p. 267–290.

Lange, A.L., 1957, Studies on the origin of Montezuma Well and Cave, Arizona: Cave Studies, v. 9, p. 39–53.

Mallison, H., and Wings, O., 2014, Photogrammetry in paleontology: a practical guide: Journal of Paleontological Techniques, v. 12, p. 1–31.

Matthews, N.A., and Breithaupt, B.H., 2011, 3D image capture and close-range photogrammetry: an overview of field capture methods: *in* Bonde, J.W., and Milner, R.C., eds., Field Trip Guide Book, 71st Annual Meeting of the Society of Vertebrate Paleontology, Las Vegas, Nevada State Museum, Paleontological Papers 1, p. 32–39.

Matthews, N.A., Noble, T.A., and Breithaupt, B.H., 2006, The application of photogrammetry, remote sensing, and geographic information systems (GIS) to fossil resource management: New Mexico Museum of Natural History and Science Bulletin, v. 34, p. 119–131.

Mead, J.I., 2003, Pleistocene and Holocene animal and plant communities of Grand Canyon-Parashant National Monument: an evaluation of caves and other fossil resources. Interim report: internal report, available in Lake Mead National Recreation Area archives.

Mead, J. I., Coats, L.L., and Schubert, B.W., 2003, Late Pleistocene faunas from caves in the eastern Grand Canyon, Arizona: *in* Schubert, B.W., Mead, J.I., and Graham, R.W., eds., Ice Age Cave Faunas of North America, Bloomington and Indianapolis, Indiana University Press, p. 64–86.

Mead, J.I., Wilkins, J., and Collins, P.W., 2018, Late Quaternary Chorus Frog (*Pseudacris*) from the Channel Islands, California: Bulletin of the Southern California Academy of Sciences, v. 117, no. 1, p. 52–63. https://doi.org/10.3160/soca-117-01-52-63.1.

Mead, J.I., Tweet, J.S., Santucci, V.L., Tobin, B., Chambers, C.L., Thomas, S.C., and Carpenter, M.C., 2021a, Pleistocene/Holocene cave fossils from Grand Canyon National Park—Ice Age (Pleistocene) flora, fauna, environments, and climate of the Grand Canyon, Arizona: *in* Santucci, V.L., and Tweet, J.S., eds., Grand Canyon National Park Centennial Paleontological Resource Inventory—A Century of Fossil Discovery and Research, Salt Lake City, Utah Geological Association, Special Publication 1, p. 221–240.

Mead, J.I., Swift, S.L., Jass, C.N., Meyers, J.I., and Weaver, S.E., 2021b, Late Pleistocene pine marten (*Martes*; Mustelidae) from the Black Hills, South Dakota: Northwestern Naturalist, v. 102, no. 2, p. 109–119. https://doi.org/10.1898/NWN20-20.

Mychajliw, A.M., Rick, T.C., Dagtas, N.D., Erlandson, J.M., Culleton, B.J., Kennett, D.J., Buckley, M., and Hofman, C.A., 2020, Biogeographic problem-solving reveals the Late Pleistocene translocation of a short-faced bear to the California Channel Islands: Scientific Reports, v. 10, article 15172. https://doi.org/10.1038/s41598-020-71572-z.

Norden, A., 2006, The Cumberland Bone Cave: a window into Maryland’s past: The Maryland Natural Resource, v. Fall 2006, p. 4–7.

Santucci, V.L., and Tweet, J.S., eds., 2021, Grand Canyon National Park Centennial Paleontological Resource Inventory—A Century of Fossil Discovery and Research: Salt Lake City, Utah Geological Association, Special Publication 1, 343 p.

Santucci, V.L., Kenworthy, J., and Kerbo, R., 2001, An inventory of paleontological resources associated with National Park Service caves: Denver, National Park Service Geological Resources Division, Technical Report NPS/NRGRD/GRDTR-01/02, 50 p.

Tweet, J.S., Santucci, V.L., and Hunt, A.P., 2012, An inventory of packrat (*Neotoma* spp.) middens in National Park Service areas: New Mexico Museum of Natural History and Science Bulletin, v. 57, p. 355–368.

Tweet, J.S., Santucci, V.L., Convery, K., Hoffman, J., and Kirn, L., 2020, Channel Islands National Park: Paleontological resource inventory (public version): Fort Collins, National Park Service, Natural Resource Report NPS/CHIS/NRR—2020/2171, 309 p.

Tweet, J.S., Flora, H., Weeks, S.R., McIntyre, E., and Santucci, V.L., 2021, Grand Canyon-Parashant National Monument: Paleontological resource inventory (public version): Fort Collins, National Park Service, Natural Resource Report NPS/PARA/NRR—2021/2338, 259 p.

Widga, C., and Colburn, M., 2015, Paleontology and paleoecology of guano deposits in Mammoth Cave, Kentucky, USA: Quaternary Research, v. 83, no. 3, p. 427–436. https://doi.org/10.1016/j.yqres.2015.01.008.

Withnell, C.B., Joannes-Boyau, R., and Bell, C.J., 2020, A reassessment of the age of the fauna from Cumberland Bone Cave, Maryland, (middle Pleistocene) using coupled U-series and electron spin resonance dating (ESR): Quaternary Research, v. 97, p. 187–198. https://doi.org/10.1017/qua.2020.30.

Richard S. White and Gary S. Morgan. Natural traps, shelters, or predator dens: why are Pleistocene Fossil Pronghorn (Mammalia: Antilocapridar) found in caves. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 117-136. DOI:10.4311/2023PA0110

NATURAL TRAPS, SHELTERS, OR PREDATOR DENS: WHY ARE PLEISTOCENE FOSSIL PRONGHORN (MAMMALIA: ANTILOCAPRIDAE) FOUND IN CAVES?

Richard S. White[1C] and Gary S. Morgan[2]

ABSTRACT

We examine the Pleistocene record of fossil pronghorn (Mammalia: Antilocapridae) bones found primarily in caves throughout the Intermountain West of the United States and Mexico, but also in Florida, noting the different species present and their distribution in time and space. We briefly review the development of a framework for investigating the taphonomy of vertebrate fossils in caves. We review previously published explanations for pronghorn fossils found in caves and karst features. We then examine population structures, taphonomic factors, preservation biases, and abundance to identify patterns in the record that can resolve those different explanations. We focus on Pleistocene (Ice Age) sites known from Arizona, Colorado, Florida, Nevada, New Mexico, Texas, Wyoming, and in Mexico for the broader perspective, and on 4 species of pronghorn from late Pleistocene (Rancholabrean) cave sites for a narrower perspective. The taxa include: the extinct Stock's pronghorn *Stockoceros conklingi* from Papago Springs Cave in southern Arizona, Shelter Cave and Muskox Caves in New Mexico and San Josecito Cave in Nuevo Leon, Mexico; the dwarf pronghorn, *Capromeryx furcifer* from multiple sites; an older species of dwarf pronghorn, *Capromeryx arizonensis*, from the early Pleistocene Inglis 1A site in Florida; and the extant pronghorn *Antilocapra americana* from Natural Trap Cave in Wyoming. We conclude that pitfall deaths account for those caves with large numbers of pronghorn fossils, while caves with smaller numbers of specimens are likely the result of carnivore activity, scavenging activity by rodents, or sporadic habitation by pronghorn.

INTRODUCTION

Pleistocene fossil remains of pronghorn (Antilocapridae) have been found in caves and karst fissures primarily in the Intermountain West of North America, but also in karst deposits in Florida. The factors responsible for their presence in caves and fissures are seldom considered, except in those instances where large numbers of pronghorn fossils are recovered. Accumulation by packrats, porcupines or raptors, human activity, habitation by pronghorn, pitfalls or natural traps, carnivore den accumulations and transport by water flowing into the caves have all been invoked as potential explanations.

We collected data from the literature and from examination of museum collections documenting the recovery of pronghorn remains from Ice Age (Pleistocene; 2.6 Ma–10 Ka) sites in North America. Seventy-six such sites were identified, with by far the greatest number (66 sites, or 86.8%) dating to the Rancholabrean (250 Ka – 11 Ka) North American Land Mammal Age (NALMA). Earlier Pleistocene records from the Irvingtonian (1.6 Ma – 250 Ka) and Blancan (2.6 Ma – 1.6 Ma) NALMAs are much rarer, reflecting the general rarity of cave and karst deposits containing fossils of those ages. Four of the 6 Blancan localities are fissure fills in Florida. Due to subsequent weathering and erosion, these fissures are not preserved in their entirety, so that the mechanism of accumulation of the deposits is less easily determined.

MATERIALS AND METHODS

Sites with significant numbers of antilocaprid specimens were selected for detailed analysis (Fig. 1). The sites, the institutions housing the collections, and the number of specimens and individuals are detailed in Table 1. The following acronyms and abbreviations are used: AMNH, American Museum of Natural History, New York; FLMNH, Florida Museum of Natural History, Gainesville; KU, Biodiversity Institute and Natural History Museum, University of Kansas, Lawrence; LACM, Natural History Museum of Los Angeles County; UF, University of Florida, Gainesville; USNM, United States National Museum, Washington, D.C.; LF, Local Fauna; MNI, Minimum Number of Individuals; NALMA, North American Land Mammal Age; NISP, Number of Identified Specimens.

Potential Explanations for the Presence of Animal Bones in Cave Deposits

The earliest discussion of the possible origin of bone accumulations in caves appears to be that of Buckland (1822), who attributed the bone accumulation in Kirkdale Cave, North Yorkshire, England, to animals brought into the cave by denning hyenas. Other English bone caves, such as Kent's Cavern in Dorset and Brixham Cave in Devon (McFarlane and Lundberg, 2005; Pengelly, 1873)) also occasioned speculation as to the origin of the bones, some believing the bones to

---

[1]The Mammoth Site, Hot Springs, South Dakota USA
[2]New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA
[C]Corresponding Author: rswhite@mammothsite.org

Figure 1. Map of North America showing Pleistocene pronghorn (Antilocapridae) sites discussed in the text. Sites are numbered in the order in which they are discussed in the text. 1. Papago Springs Cave, Arizona. 2. San Josecito Cave, Nuevo Leon, Mexico. 3. Shelter Cave, New Mexico. 4. Natural Trap Cave, Wyoming. 5. Muskox Cave, New Mexico. 6. Inglis 1A, Florida.

have been carried into the caves by the action of surface water, others thought that the remains were brought in by carnivores. This question became the impetus to determine ways to distinguish natural (that is, non-human) bone accumulations from those caused by the activities of early humans. Thus, much of the work on cave taphonomy, especially in Europe and Africa, still focuses on that problem.

Several different systems to describe the taphonomic origins of bone accumulations have been proposed (Dart, 1958; Brain, 1981; Andrews, 1990; Rogers and Kidwell, 2007). Table 2 provides a comparison and rough correlation of these various classificatory schemes. Dart (1958) divided caves into two main types, those suitable for habitation, with six subtypes, and those unsuitable for habitation, with two subtypes. Brain (1981) divided the animals found in caves into two groups, the autopods (literally, those who walked into the caves on their own feet) and allopods, those animals whose bones were brought into the caves by other species. Andrews (1990) simplified the classification to just 4 categories: (1) animals living in caves; (2) animals falling in by accident; (3) animal taken in by predators; and (4) animal remains transported in after death, such as by water.

Rogers and Kidwell (2007) built a genetic framework for skeletal concentration in their study of bone beds, intended for much wider application than just cave deposits. They divide bone accumulations into two major types, biogenic concentrations and physical concentrations. Biogenic concentrations are further divided into intrinsic and extrinsic. Intrinsic concentrations are from the behavior and activity of the animals included in the assemblage, while extrinsic concentrations result from the feeding behavior and collecting activities of other animals. Physical concentrations include hydraulic concentration, where bones accumulate due to the action of water, wind, or sediment, and sedimentologic concentration, where bones accumulate due to processes such as erosion.

Table 1. Collections utilized in this study.

Site	Species	Collection	MNI and/or NISP	
Papago Springs Cave	*Stockoceros conklingi*	AMNH, OU	3236 (NISP)	76 (MNI)
San Josecito Cave	*Stockoceros conklingi*	LACM	? (NISP)	174 (MNI)
Shelter Cave	*Stockoceros conklingi*	LACM	136 (NISP)	4 (MNI)
	Capromeryx furcifer		9 (NISP)	1 (MNI)
Muskox Cave	*Stockoceros conklingi*	USNM	143 (NISP)	4 (MNI)
	Capromeryx furcifer		3 (NISP)	1 (MNI)
Natural Trap Cave	*Antilocapra americana*	KU	152 (NISP)	13 (MNI)
Inglis 1A	*Capromeryx arizonensis*	FLMNH	1169 (NISP)	38 (MNI)

Our classification of bone accumulating processes and agents is listed in Table 2, and criteria for their recognition compiled in Table 3. As used in this paper, the processes are as follows:

1. Human Activity: The actions of humans inhabiting caves can be responsible for the accumulation of animal bones in cave-fill deposits. This has been the focus of archaeologists and zooarchaeologists as mentioned earlier, who desire to differentiate bone accumulations that result from ‘natural’ (that is, non-human) causes from those due to human occupation of the caves. Humans bring bone into caves after hunting and trapping them in the surrounding countryside. They may bring either an entire or partial carcass back to the cave for butchering, cooking, and

Table 2. Comparison of bone accumulation classification schemes proposed in the literature and those used in this paper.

Dart 1958	Brain 1981	Andrews 1990	Rogers and Kidwell 2007	This paper
Caves unsuitable for shelter or habitation				
Natural death traps		Animals falling in by accident.		Natural traps and pitfalls
			Hydraulic concentrations	
Bones transported into caves by water		Animal bones transported in after death	Sedimentological concentration	Bones transported by water
Caves suitable for shelter or habitation				Shelter or habitation
				Human activity
Primitive men				
				Carnivore den/lairs
Hyaenas	Allopods	Animals taken into caves by predators	Extrinsic biogenic concentrations	
Leopards				Raptors
Owls				Scavengers
Porcupines				
Natural deaths	Autopods	Animals living in caves	Intrinsic biogenic concentrations	Natural deaths and roosting or hibernation

consumption, or they may field-dress the kills and carry back only the meaty portions, resulting in differential bone element representation in the cave bones, termed the ‘Schlepp Effect’ (Perkins and Daly, 1968; Daly, 1969). Binford (1981: 184) completely rejected the Schlepp Effect, calling it “bizarre...accommodative fantasy”. Partial skeletal representation has also been attributed to carnivore activity and to excavation methods (Turner, 1989). Brain (1981) listed criteria for recognizing bones accumulated by human activity. Scarcity of carnivore remains, association with artifacts, association with traces of fire, depressed fractures on skulls, and consistent size of bone flakes were emphasized, while the presence of spiral fractures and the presence of wear and polish were rejected as diagnostic because other agents can produce the same results (Brain 1981). Human activity can result in the uncovering and burning of bones previously deposited in the caves, including fossils that date to long before human habitation.

2. Scavenging: Scavengers bring animal bones into caves. Carnivores can do this on occasion, but by far, the most active scavengers are rodents. Packrats (*Neotoma* spp.) and porcupines (*Erethizon dorsatum* in the New World, and *Hystrix* spp. in the Old World) are well-documented bone collectors. Mead (2005:2) identified “…10 different factors that may account for the existence of animal remains recovered in packrats middens: commensals, porcupine, owl, eagle-hawk, vulture, human, large carnivore, small carnivore, local community, and ancient community”. In other words, any process or agent that brings bone into or near the cave in which packrats are living can furnish bones to incorporate into their middens. Porcupines as agents of bone accumulation have been well studied in Africa, because of their potential role in the accumulation of animal bones in caves that have produced early hominid remains, summarized and combined with his own observations by Brain (1981). The presence of the characteristic wide, trough-like, gnaw marks on defatted and weathered bones is diagnostic for African porcupines and when such bones are present in significant numbers, porcupine denning is indicated (Brain 1981). We have been unable to find any actualistic studies of modern *Erethizon dorsatum* dens in North America in the literature. Rodents often use bones to sharpen and hone their incisors, rather than to supplement calcium or phosphorus in their diet.
3. Natural traps and pitfalls: These are cave or karst features with a surface opening having a vertical or near-vertical drop into the cave chamber, such that animals which fall in are unable to escape. Animals may die upon impact or shortly thereafter, or they might survive and move beyond the area of the debris cone deeper into the cave before starving or perishing from infections or other injuries sustained when they fell into the cave. Hearty et al. (2004) provide a thorough discussion of fissure and cave deposit formations in Bermuda; their study concerned mostly the record of land snails preserved in those caves, although abundant vertebrates were recovered in some of them. Likewise, the work of Czaplewski et al. (1999a) determined the geologic history of Papago Springs Cave, described the mechanisms by which bones entered the cave, and the nature of the resulting sediments. Lava blisters, while not a true karst feature, form caves that can attract and trap carnivores to the injured or dead animals that have fallen into them (White et al., 1984). Although a pattern of bone fractures expected when medium or large mammals fall to their deaths in a pitfall trap has

been suggested, the specific characteristics of the fractures has not been discussed, and we could find no actualistic studies that have documented a specific pattern. Pitfall sites are usually not dominated by a single species of large mammal. A notable exception to this is sinkhole accumulations where a single species dominates, such as mammoths at The Mammoth Site in South Dakota (Agenbroad and Mead, 1997) and bison at the Vore Site, an evaporite karst sinkhole feature in Wyoming, into which bison were driven by Native Americans (Epstein and Doctor, 2013).

4. Raptors: Birds, especially owls, roost in caves and their regurgitated pellets accumulate in the cave beneath their roosts. Andrews (1990) describes in detail the taphonomy of bone accumulations formed by owls. Owls, and presumably other raptors, often roost in caves or near the cave opening, and their pellets contain numerous small bones. Owls roosting outside, but near the entrance to the cave can result in an accumulation of pellets that potentially can be washed into the cave by rainwater; packrats can collect the bones and perhaps the pellets themselves and bring them into the caves where they are incorporated into their nests and middens. Terry (2007) demonstrated that damage on bones of small mammal species can be used to separate damage by owls from that done by diurnal raptors and mammals, but that the specific identity of those predators cannot be reliably distinguished.
5. Habitation: Many animals use caves for shelter. Bats spend their days roosting in caves leaving extensive deposits of their guano beneath them, which contain bones of bats that have died in the cave, sometimes in the tens of thousands of bones. Morgan and Czaplewski (this volume) provide a review of fossil bats from cave and karst features. Larger mammals, such as bears and sloths, may use caves as temporary shelters on a daily or seasonal basis to escape temperature extremes (Kurten, 1995; McDonald, 2003), while others, including elephants, deer, and likely bison, visit caves sporadically to exploit resources such as water or salt (Bowell et al., 1996; Lundquist and Varnadoe, 2006). Animals living in the arid Intermountain West of North America sometimes used caves as a secure latrine, in some cases accumulating dung blankets several meters in thickness. Dung deposits formed by ground sloths (Rampart Cave, Wilson, 1942; Martin et al., 1961; Hansen 1978), mammoth (Bechan Cave, Agenbroad et al., 1989; Karpinski et al., 2017), shrub ox (Mead et al., 2022; Kropf et al., 2007), bighorn sheep (Mead et al., 2021) and mountain goat (Mead et al., 1986) have been documented.
6. Carnivore dens: A special case of habitation, the dens of living mammalian carnivores have been intensively studied, particularly in Africa. Carnivores bring whole or partial prey carcasses back to their dens to consume, to provide food for their young, or to cache in the cave for later consumption. The resulting bone accumulations and criteria developed for identifying the specific predator that produced them have been developed for hyaenas (Kuhn et al., 2010), leopards (Sauque et al., 2014), lions (Arriaza et al., 2015), dholes (Mallye et al., 2012), wolves (Sattler, 1997; Fosse et al., 2012), and brown bears (Arilla et al., 2014). Differences exist in bone element representation, degree of fragmentation and the nature of chewing and gnawing marks. For example, the spotted hyaena *Crocuta crocuta* produces bone accumulations characterized by (1) remains of adult and young *Crocuta*, (2) remains of hunted or scavenged known prey of *Crocuta* with characteristic taphonomic signatures of gnawing and bone breakage and (3) hyaena coprolites (Palomares, et al., 2022). Numerous studies have described species-specific bone damage by large carnivores, almost exclusively on large-bodied ungulate prey species. Frisenhahn Cave in Texas was initially a pitfall trap, but as the debris cone built up, entrance into the cave by large carnivores became possible (Graham et al., 2013) with *Homotherium serum*, a scimitar cat, then using it as a denning site, where adult and young fed upon their preferred prey, juvenile mammoths. The presence of abundant remains of *Homotherium*, as compared to other carnivores, the occurrence of articulated skeletons and both juvenile and adult cats, and characteristic bone damage all support this interpretation. Binford (1981), in a study too little appreciated by paleontologists, characterized the damage done to bones by wolves and dogs, such as the longitudinal guttering of long bones with chipped edges, which had previously been attributed to human modification.
7. Natural deaths, hibernation, and roosting: Sporadic inclusion of animal bones, including complete skeletons can happen as animals living or hibernating in caves succumb to natural deaths from malnutrition, thermal extremes, disease, or from injuries suffered both outside the caves, as well as during entrapment. The classic example of this sort of accumulation is the cave bear (*Ursus spelaeus*), where attritional deaths over millennia accumulated huge numbers of bones (see Kurten, 1958, 1995 for a general description of cave bear hibernacula). Roosting bats and birds can also themselves become accumulated as individual die while roosting and fall to the cave floor, to be covered with guano, sediments or carbonate, sometimes in considerable numbers (see Morgan and Czaplewski, this volume). Kos (2002) describes a pitfall fauna from a cave that carnivores could not have used for denning, nor birds for roosting, highlighting the difficulty of separating carnivore bone accumulations from pitfall accumulations.
8. Bones transported into caves or fissures by water: Water entering the caves or fissures can transport bones from the surrounding land surface into caves, where they become entombed in the debris cone beneath a pitfall opening, or in water-laid sediments flowing through the cave.

Table 3: Bone accumulating agencies and criteria for their recognition..

AGENCY	CRITERIA	REFERENCES
1. Human activity	Direct association with cultural material. Evidence of butchering (cuts, spiral fractures). Dates to within accepted time range. High Fragmentation Index (FI) of large animal bones. Evidence of “Schelpp Effect”. Evidence of exposure to fire. Traces of chewing by humans (differs from carnivore and rodent)	Sadek-Koros, 1972) Brain, 1981 Perkins and Daly, 1968 Daly, 1969 Turner, 1989 Kirillova et al., 2021 Martinez, 2009
2. Rodent scavenging	Presence of bone in middens, accumulated along walls on cave floor, on elevated shelves, or beneath roof fall. Isolated bones or bone fragments. Porcupine lairs have larger bone fragments, including complete ungulate skulls; bones collected dry and extensively gnawed. Relatively fewer specimens, as contrasted with raptor pellet deposits. Diverse fauna of small / tiny bones with occasional somewhat large fragments. Gnawed by rodent incisors.	Andrews, 1999 O’Regan et al., 2011 Betancourt et al., 1990 Mead, 2005 Diedrich, 2009 Bountalis, and Kuhn, 2014 Brain, 1981
3. Raptors (Pellet deposits)	Diverse fauna of small/tiny bones with occasional larger fragments. Characteristic molar, incisor, and postcranial digestion. Characteristic breakage of skulls.	Andrews, 1999 Marin-Arroyo and Margalida, 2012 Lopez, 2020 Lauder and Selva, 2005 Terry, 2007
4. Pitfall / Natural trap	Vertical drop from surface opening or from horizontal cave entrance. Accumulation of a debris cone beneath opening. Large numbers of individuals. Fauna not dominated by single species. Presence of articulated / associated whole or partial skeletons. Absence of carnivore traces on the bones. Presence of males and females Presence of asphalt permeated matrix	Wolverton, 2001 Stock and Harris, 1992 Saunders, 1977
5. Habitation	Large cave opening with accessible surface entrance?). Presence of dung deposits. Large number of individuals of a dominant species within a single layer. Presence of articulated / associated whole or partial skeletons. Absence of carnivore traces on the bones. Presence of both males and females. Presence of all age groups Bones trampled and broken	Morgan and Czaplewski, this volume Bowell et al., 1996 Lundquist and Varnadoe , 2006 Wilson, 1942
6. Carnivore dens	Accessible surface entrance. Dens tend to be small. Entrance may be concealed by topography or elevation above surrounding countryside. Fauna not dominated by single species. Large numbers of individual prey species. Carnivores represented by more complete material than prey species – associated or articulated whole or partial skeletons. Presence of juvenile carnivores. Bones of prey broken and chewed by carnivores.	Haynes, 1980 Arilla et al., 2014 Bountalis and Kuhn, 2014 Palomares et al., 2022
7. Natural Deaths / Hibernation	Large numbers of individuals, particularly those whose modern analogs are known to inhabit or hibernate in caves. The presence of large numbers of bones in asphalt permeated sand matrix.	Kurten, 1958 Harris, 2015 Stock and Harris, 1992;
8. Transport by water	Evidence of exposure to the elements outside the cave prior to transport Geologic context in sediments washed into the cave.	Hanson, 1980 Behrensmeyer, 1978 Czaplewski et al., 1999a

Table 3 summarizes the explanations that have been suggested for the accumulation of bones in cave sediments. For each, we generated potential ‘test implications’ describing what one might expect to see in a bone accumulation caused by that agency. These criteria are based partly on the literature (as cited in Table 2 and others), and partly on our own ideas. We have not examined characteristics of individual carnivore species but rather have lumped them all into a single category. This provides a guide as we consider the specific sites, their previous interpretations, and our conclusions about each site.

It should be noted that none of these criteria alone are diagnostic in determining how bones accumulate in caves, with one exception. The presence of dung in dry caves in the Intermountain West of North America is a reliable indication that the animals whose dung we find there used the cave at least for shelter. All the other criteria have exceptions. Some are poorly defined, others apply to more than one agency of accumulation, and others are directly contradicted by one or more cave sites. For example, as noted earlier, while most pitfall or natural trap bone accumulations are not dominated by any single species (Gilbert and Martin, 1984; Skinner, 1942; Arroyo-Cabrales et al., 2021), some natural traps are dominated by a single species, such as by mammoths in the sinkhole at Hot Springs, South Dakota (Agenbroad and Mead, 1994), or mastodons at Boney Springs, Missouri (Saunders, 1977). The agency of bone accumulation in caves can also change drastically through time, as documented for Friesenhahn Cave, Texas, which changed sequentially over time from a pitfall trap to a carnivore den, then to a turtle hibernaculum, with characteristic taxa and taphonomy for each (Graham et al., 2013). Determining the most likely reason for the presence of pronghorn bones in each cave deposit requires consideration of multiple factors.

Pronghorn in Caves and Karst Features: Distribution and Site Descriptions

White and Morgan (2024) review the distribution of Pleistocene pronghorn in North America. Out of a total of 395 Pleistocene sites with antilocaprid fossils, 77 cave or karst sites containing pronghorn remains were identified, with by far the greatest number (66 sites, or 86.8%) dating to the Rancholabrean North American Land Mammal Age (NALMA). Earlier records from the Irvingtonian and Blancan NALMAs are much rarer, reflecting the general rarity of cave and karst deposits containing fossils of those ages. Four of the six Blancan localities are fissure fills or sinkholes in Florida. These fissures are not preserved in their entirety, making the form of the original feature and the mechanism of accumulation of the deposits difficult to determine. Table 4 lists the sites, their chronological and geographical distribution, and their taxonomic composition.

Four genera of pronghorn are known from the Pleistocene in North America. They are, in order of increasing size, *Capromeryx*, *Stockoceros*, *Antilocapra,* and *Tetrameryx*. *Capromeryx* is the most common, known from 42 cave localities. *Stockoceros* is recorded from 31 cave and karst sites, *Antilocapra* from 7, and *Tetrameryx* is unknown from cave and karst features. While *Capromeryx* is the most commonly found pronghorn in terms of the number of sites, it is not found in significant numbers in any Rancholabrean cave or karst site, although large numbers have been recovered from two of the Blancan karst localities in Florida. This difference in occurrence of Rancholabrean *Capromeryx* from its earlier, larger late-Blancan relative may be the result of a change in habitat or behavior that accompanied the dwarfing of the species through time, as suggested by White and Morgan (2010). *Stockoceros* is the most common large mammal in two sites, Papago Springs Cave, Arizona and San Josecito Cave, Nuevo Leon, and is also known from a significant sample from Shelter Cave, New Mexico. *Antilocapra* is only found in abundance in a single Rancholabrean site, Natural Trap Cave, Wyoming.

Table 4: North American cave and karst sites producing pronghorn remains.

Total Number of Sites	**77**	
Blancan	6	6.6%
Irvingtonian	3	3.9%
Rancholabrean	66	86.8%
Holocene	2	2.6%
Number of Sites with Each Taxon		
Capromeryx	32	42%
Stockoceros	21	27%
Antilocapra	7	9%
Unspecified antilocaprid	7	9%
Capromeryx and *Stockoceros*	10	13%
Geographic Distribution of Sites		
Mexico	**8**	**10.5%**
Arizona	**4**	**5.3%**
California	**4**	**5.3%**
Colorado	**3**	**3.9%**
Florida	**6**	**5.3%**
Idaho	**4**	**5.3%**
Missouri	**2**	**2.6%**
Montana	**1**	**1.3%**
Nevada	**5**	**6.6%**
New Mexico	**14**	**18.4%**
South Dakota	**1**	**1.3%**
Texas	**15**	**19.7%**
Utah	**2**	**2.6%**
Wyoming	**8**	**10.5%**

Most of the cave sites produced fewer than 5 pronghorn specimens so usually constitute only a small part of the total fauna recovered from the site. Such finds are likely to represent incidental events, particularly scavenging by rodents, especially packrats and porcupines, or having been transported into the cave by carnivores. Determining the taphonomic origin of those pronghorn would require a detailed study of the fauna and the cave sediments; few are published in sufficient detail to do so without examining the entire collection.

There are, however, a few sites which have produced large numbers of prong-

Figure 2. Papago Springs Cave, Santa Cruz County, Arizona. Photograph taken by Albert Potter, winter of 1937-1938. Arrow indicates approximate location of Skinner's Entrance A. Entrance B is located behind trees lower down on the slope below Entrance A. Photograph courtesy of Lee Potter.

horn specimens: Papago Springs Cave in Arizona, San Josecito Cave in Nuevo Leon, Mexico, Muskox Cave and Shelter Cave in New Mexico, Natural Trap Cave in Wyoming, and Inglis 1A, a fissure fill deposit in Florida. Here we will describe those sites in detail, based on both the literature and upon our own examination of the collections. For each site, we summarize the published data and note explanations that have been proposed to account for the large numbers of pronghorn specimens. We then synthesize that information with our own observations to evaluate each potential explanation for the presence of pronghorn in each cave.

Papago Springs Cave: Located in Santa Cruz County, southeast Arizona at an elevation of 1,536 m, Papago Springs Cave was discovered by Joseph W. Burden and Quentin Roosevelt in 1934 (White, 2008). With the assistance of Childs Frick, they published a brief notice on the pronghorn antelope they discovered, naming it *Tetrameryx onusrosagris* (Roosevelt and Burden, 1934). Additional fossils were recovered by Burden and Roosevelt in 1936, leading to a more thorough publication of the combined collections by Colbert and Chaffee (1939). In the winter of 1937-38, Morris Skinner, Howard Scott Gentry, and Albert Potter conducted further excavations recovering a substantial collection; this was further augmented by Skinner and Gentry in 1940. The resulting large collection was described in a monograph by Skinner (1942). Little additional information was published on the cave or its fauna until after Nicholas J. Czaplewski and his colleagues returned to the cave to conduct detailed studies of the geology and chronology of the cave deposits (Czaplewski et. al., 1999a) and the fauna (Czaplewski et al., 1999b). As a result of their intensive work, Papago Springs Cave is now one of the best documented Late Pleistocene cave deposits in North America (Fig. 2).

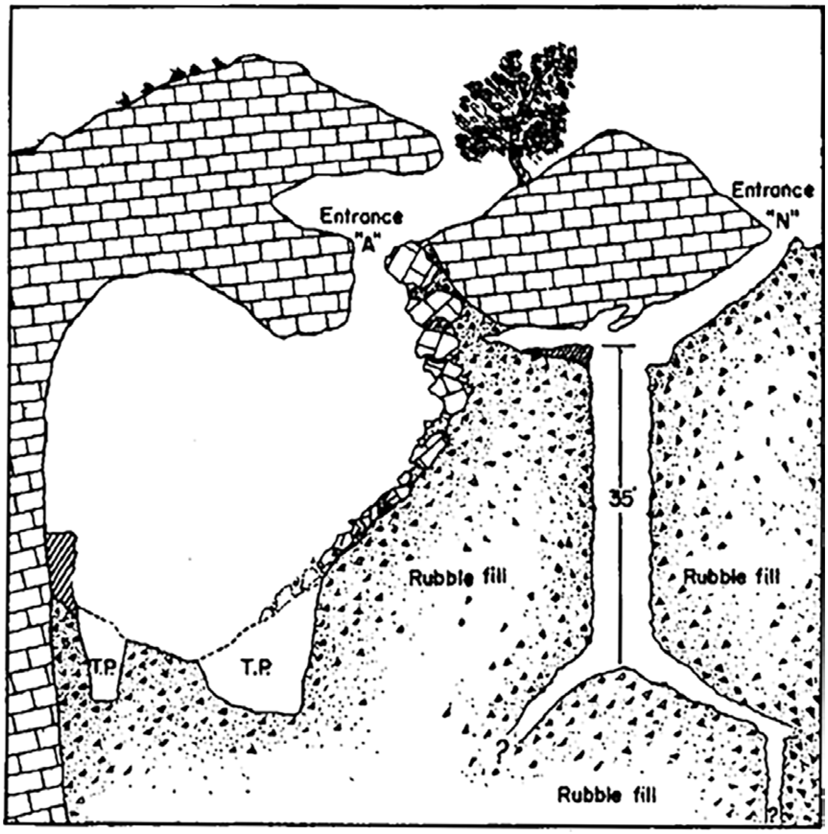


Figure 3. Cross section of Papago Springs Cave taken from Skinner, 1942: Fig. 1. The details of the cave fill sediments are oversimplified in this drawing. Czaplewski et al. (1999a) greatly clarified and amplified our understanding of those deposits. Entrance B of Skinner is not shown in this section.

Papago Springs Cave has produced a large fauna, with the most common large mammal taxon being Conkling's Pronghorn (*Stockoceros conklingi*). While Frick (1937) originally used *Stockoceros* as a subgenus of *Tetrameryx*, Skinner (1942) elevated it to full generic status. Various authors have suggested that *Stockoceros onusrosagris* is a junior subjective synonym of *S. conklingi*, with which we agree and have followed in previous work (White et al., 2022), as well as in this paper.

We censused only the collection held in the American Museum of Natural History from the earlier excavations by Roosevelt and Burden, and by Skinner. The University of Oklahoma Museum of Natural History collection includes a

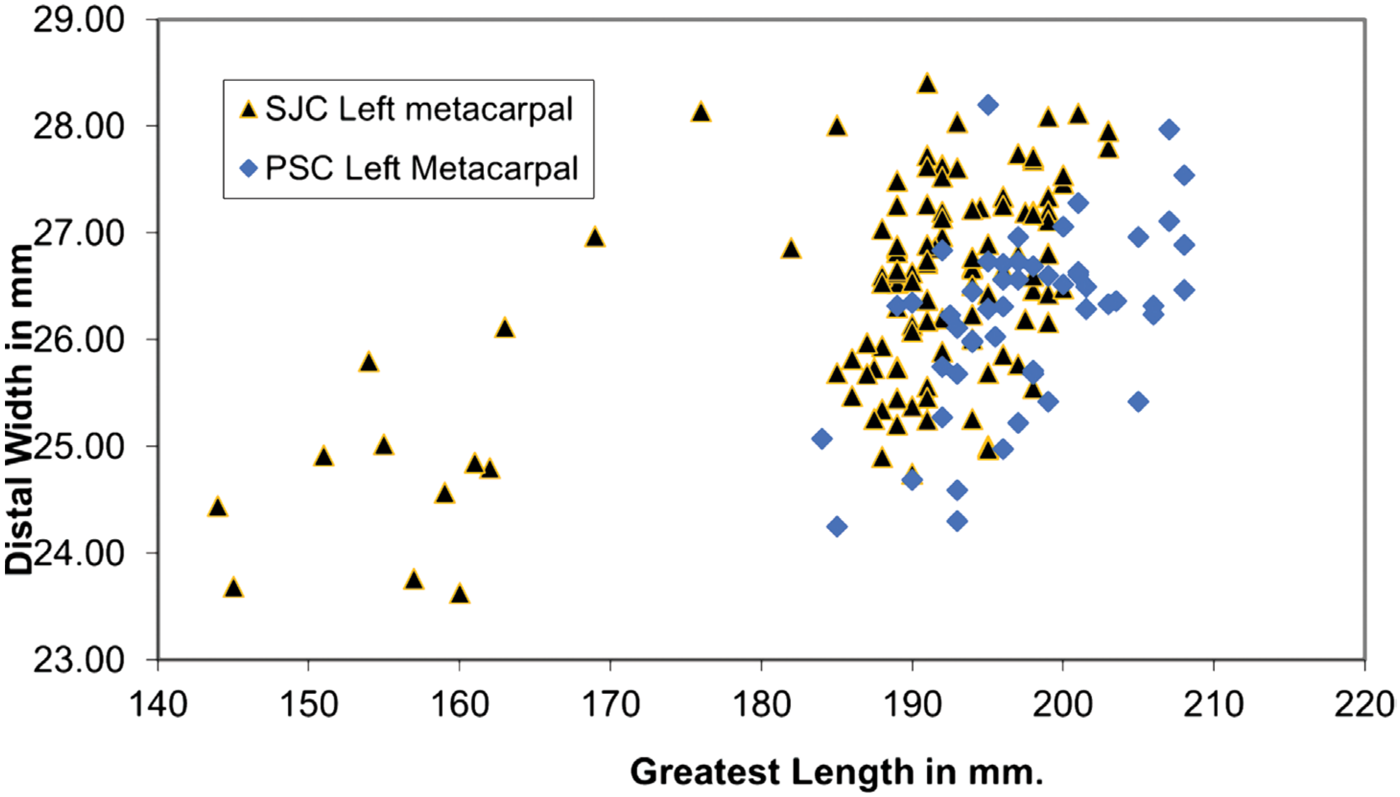


Figure 4. Bivariate plot of Greatest Length versus Distal Width of left metacarpals from San Josecito Cave (SJC) and Papago Springs Cave (PSC). The metacarpals from PSC are tightly clustered and the distribution is not bimodal. Those from SJC duplicate the tight PSC cluster, but show 13 individuals clearly outside that grouping, suggestive of either a bimodal distribution or the inclusion of younger individuals.

number of identified specimens (NISP) of 86 additional specimens with a minimum number of individuals (MNI) of 3 (based on the specimen list in Czaplewski et al., 1999b). The AMNH collection contains 58 whole or partial skulls, with a (NISP) of 3150 and a MNI of 107, based on left astragali. Skinner (1942) asserts a MNI of at least 125 individuals; the basis for that estimate is not given. Most are adult and all are horned, although a few juvenile individuals are represented in the collection. Seven articulated or partially articulated individuals were recovered. Skinner posited that either both males and females were horned, or that the cave collection represented a seasonal phenomenon in which only adult males were present (Skinner, 1942). The presence of small horns in female pronghorns is a characteristic of the derived antilocaprine pronghorns (Janis and Manning, 1998). Female *Antilocapra* have them, and they use them to protect their young, which follow them soon after birth. Skinner proposed that the cave had a large, nearly ground level entrance (his Entrance B, Figure 3), and was inhabited by the pronghorn for shelter and access to water and based on the near absence of juveniles, likely occupied in winter. Kurtén and Anderson (1980) accepted Skinner's interpretation, stating that the cave was open to the surface and used as a shelter by many species. Czaplewski et al. (1989) initially accepted Skinner's view that the cave had a large horizontal opening, but their later work, Czaplewski et al. (1999a), demonstrated that the main bone-bearing unit, their Type 2 breccia, was mostly formed as a debris cone beneath the pitfall opening of Entrance A. Additionally, Type 2 breccia was also formed by material washed into the cave and down the steeply sloping floor of Entrance B, which was repeatedly filled and eroded by water flowing into the cave from local drainages. Thus, the bone accumulation in general, and the pronghorn remains specifically, were formed by two processes (pitfall and water transport) acting over time to produce an attritional, episodic sampling of the pronghorn population inhabiting the area around the cave. Neither opening provided easy entrance into the cave, thus habitation/shelter and carnivore denning can be ruled out as causal agents for the bone accumulation. Additionally, we found no traces of carnivore feeding marks on the bones, and very few rodent gnawing marks.

The population structure of the pronghorn *Stockoceros conklingi* from Papago Springs Cave consisted of mostly adult animals, with juvenile individuals present but rare. Skinner (1942) constructed univariate plots of the articular length of the limb bones of *Stockoceros*. Those plots are unimodal, and do not appear to show any sexual dimorphism. To further evaluate potential dimorphism, we constructed bivariate plots of the greatest length versus the distal width of the metacarpals (Fig. 4). We plotted 51 left metacarpi from Papago Springs Cave, and 118 from San Josecito Cave. The metacarpals from San Josecito Cave revealed a broader distribution, with a tightly clustered group matching closely the distribution for Papago Springs Cave, but with 14 individuals outside that cluster, being shorter and somewhat narrower than the rest. Two possible explanations could account for the distribution seen in the San Josecito Cave specimens. The smaller ones could represent younger individuals that are not present in the Papago Springs Cave sample, or they could represent females, similarly not represented in the Papago Springs Cave sample. We eliminated 21 left metacarpals from the San Josecito Cave sample based on the absence of distal epiphyses, so we are certain that the earliest ages are not included in sample plotted. However, it could be that metacarpals where the epiphyses were present, but not completely fused, had been counted. A re-examination of the collection will be required to further evaluate this issue.

While examining the Papago Springs Cave collection we noted that, other than cranial fragments with horn cores attached, few fragments of skulls are present, although many isolated teeth were collected. This suggests that fragments of skulls lacking horncores or teeth were not saved. Female skulls, if hornless, would have broken into pieces that were not saved because they lacked horn cores. Given recovery of some 58 whole or partial skulls in the cave, it seems likely that, if females were present in the cave, such skulls would have been found.

When considering our data on *Stockoceros* from Papago Springs Cave and San Josecito Cave it is worthwhile to consider the sample of *Ovis canadensis* from Natural Trap Cave. As discussed below in the section on Natural Trap Cave, we have details only about the specimens obtained from the early excavations by Gilbert and Martin, but unlike the case with pronghorn from that cave, *Ovis canadensis* was recovered in much larger numbers from the small amount of the cave they excavated. Wang (1984, 1988) reports a NISP of 4,497 and a MNIs of 47 based on left astragali for *Ovis canadensis*. Skulls recovered numbered 11. None of the skulls was female; all showed massive horn cores as in the males of the living bighorn sheep. Analysis of a sample of 33 adult metatarsals showed 5 (15.2%) to be significantly smaller than the rest, and hence likely female. Dental cementum annulation analyzed for a sample of 28 first left incisors showed that 18 (64.3%) were less than 4 years old. Wang (1984) concluded that young males predominated in the population, likely for behavioral reasons, particularly the tendency for solitary, inexperienced males to wander into unfamiliar territory.

A similar explanation is possible for the Papago Springs Cave pronghorn. Papago Springs Cave certainly has few juveniles and may lack females. No evidence of carnivore feeding marks appears on the bones. Adult males seem to predominate in the collection. The pitfall and water transportation processes do not seem to have accurately sampled a natural population living around the cave, but to have selectively sampled adult males, perhaps because of the animal's behavior. Finally, we note that the large number of individuals of *Stockoceros* recovered from Papago Springs Cave does not necessitate that pronghorn fell into the pitfall trap with any appreciable frequency, so that the large number would represent a time-averaged sample. Based on the radiometric dates on bones reported by Czaplewski et al. (1999a) from 246 Ka to 23.1 Ka, one individual pronghorn falling into the cave every 2,083 years would account for the collection. This is not to say that the entrapment of pronghorn happened with great regularity; it is likely that more

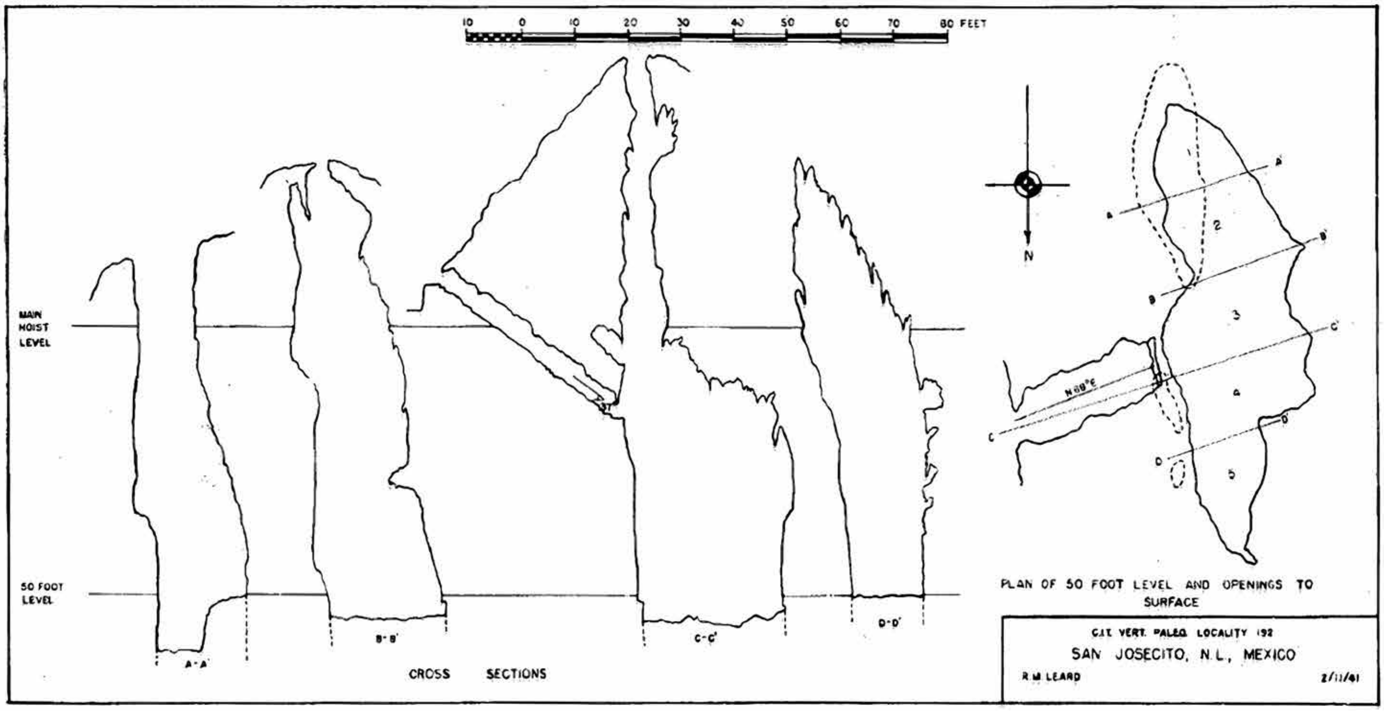


Figure 5. Sections and plan view of San Josecito Cave, Nuevo Leon, Mexico, taken from Stock, 1943.

fell during certain time periods and fewer in others, but it is not possible to determine if there is a pattern to indicate if most entrapments occurred in a specific season. The point is that the assemblage is an attritional one rather than a catastrophic accumulation.

San Josecito Cave: San Josecito cave, located in the Mexican state of Nuevo Leon, at an elevation of 2,300 m was discovered and excavated from 1935-1941 by Chester Stock of the California Institute of Technology (Stock, 1943). The cave consists of a large main chamber and a sloping narrower opening leading from lower on the mountain slope diagonally downward to open into the main chamber. At least 18 m of stratified deposits fill the lower portion of the main chamber, with a vertical drop of 12.2 m to the top of the debris cone (Fig. 5). A large collection of vertebrate fossils from the cave is housed in the Los Angeles County Museum of Natural History. Subsequent excavations in 1990 by Joaquin Arroyo-Cabrales clarified the geology of the cave (Arroyo- Cabrales 1994; Arroyo-Cabrales et al., 2021). The 1990 collections are catalogued in the collections of the Laboratorio de Paleozoologia, Instituto National de Antropologia e Historia (INAH), Mexico City.

Stock's excavations produced a NISP of at least several thousand specimens, with 50 whole or partial *Stockoceros* skulls, and an MNI of 174 individuals based on right astragali (Furlong, 1943). No adult skulls lacking horn cores or with greatly reduced horn cores were recovered. Both juvenile and adult individuals are present; partially articulated specimens are rare. In a sample of 195 metapodials, 27 (13.9 %) were juveniles lacking the distal epiphyses (RSW notes). Stock does not comment directly on the manner by which the fossils accumulated; but his cross sections (Stock, 1943: fig 1) and his comments indicate a pit-fall mechanism. When Furlong (1943) described the pronghorn remains he did not comment on the taphonomy or behavior of the animals. Kurtén and Anderson (1980) considered the cave as probably a carnivore lair, based largely on the presence of carnivores, including three canids, dire wolf (*Canis dirus*), coyote (*Canis latrans*), dhole (*Canis alpinus*), a felid, puma (*Puma concolor*) and two bears, black bear (*Ursus americanus*) and Florida cave bear (*Tremarctos floridanus*). Arroyo-Cabrales (1994) showed that deposits in different parts of the cave had different taphonomic histories. Most of the pronghorn remains came from debris-cone deposits beneath the opening above the main chamber. He also concluded that San Josecito Cave was not suitable as a carnivore den at any time.

Arroyo-Cabrales et al. (2021) date most of the large mammal material excavated by Stock as between 45 Ka and 28 Ka, an interval of about 17,000 years. While it is tempting to calculate how many pronghorn fell into the cave as was done for Papago Springs Cave earlier, this is not realistic, as only a tiny fraction of the cave deposits was excavated by Stock, while Skinner removed very nearly all of the fossiliferous deposit from the main room of Papago Springs Cave (Czaplewski et al., 1999a). Nevertheless, we are confident that the mechanism of accumulation operated over a significant period (about 17 Ka) and was attritional rather than catastrophic.

Shelter Cave: Located in the Organ Mountains of Doña Ana County, southwest New Mexico, at an elevation of 1517 m. The cave was excavated in 1929 and 1930 by a team from the Los Angeles County Museum (LACM) including W.M. Strong, H.A. Wylde, F.R. Fosberg and R.P. Conkling. The large collection of fossils in the LACM is mostly uncat-

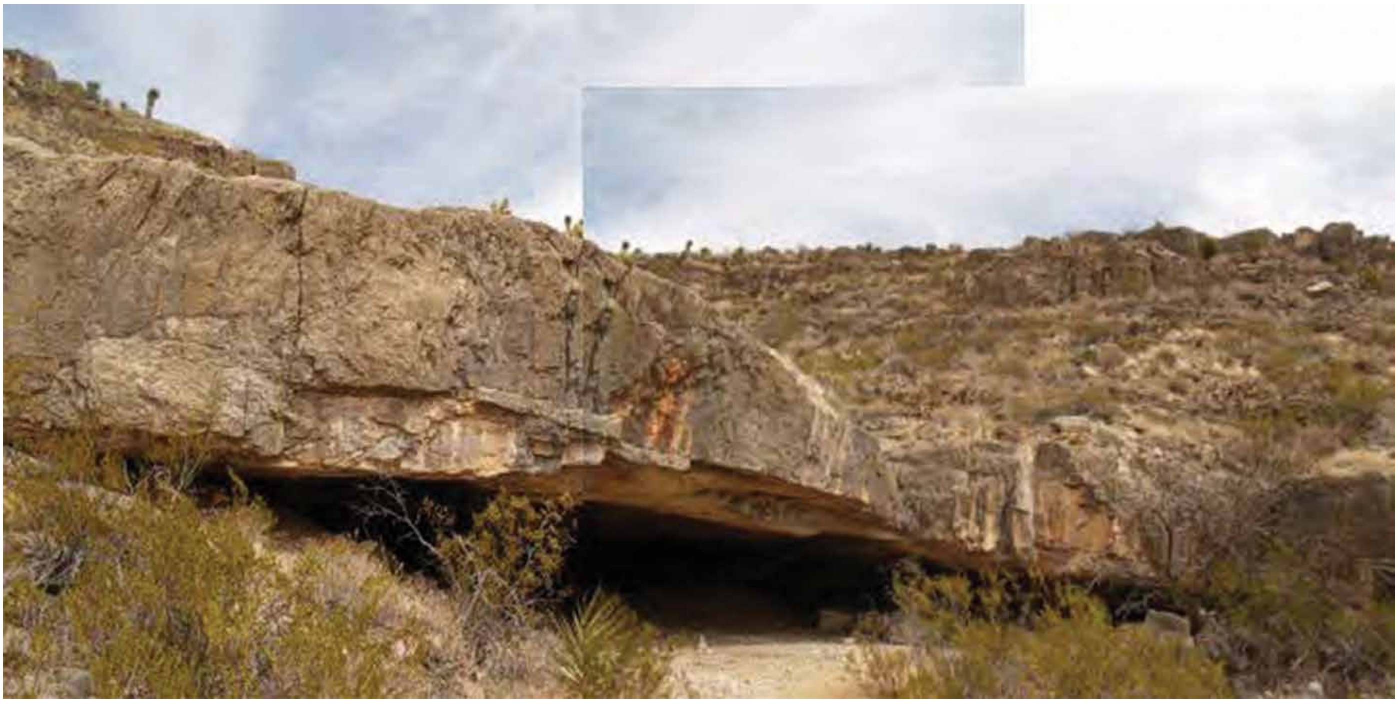


Figure 6. Shelter Cave, Doña Ana County, New Mexico. Photo courtesy of Arthur H. Harris.

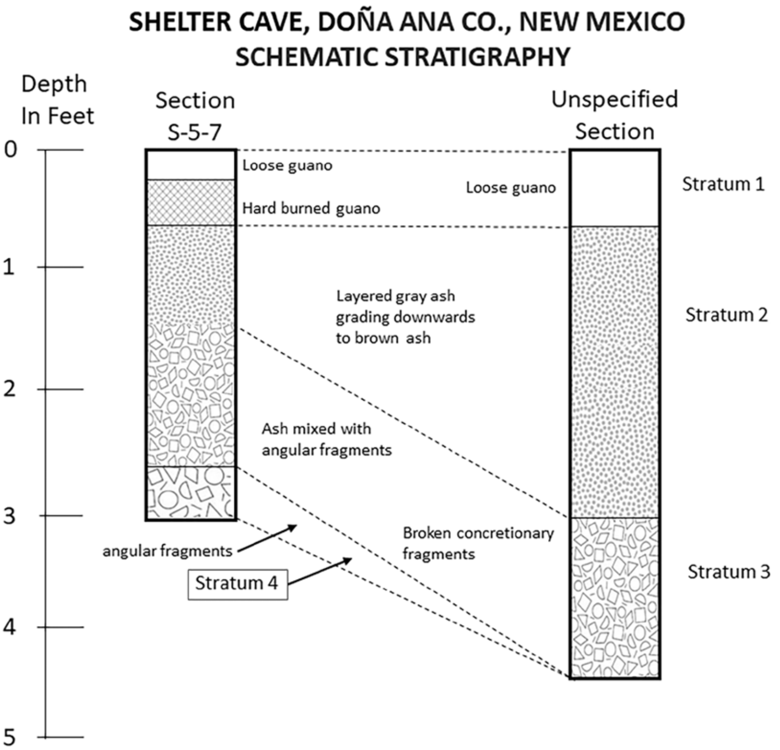


Figure 7. Schematic stratigraphic sections of Shelter Cave based on the excavator's field notes as quoted by Brattstrom (1964). The grouping of strata represents our interpretation of that data

alogued and much of it remains to be identified, apart from some of the plants (Fosberg, 1936), reptiles (Brattstrom, 1964; Van Devender et al., 1976), birds (Howard and Miller, 1933), and selected larger mammals, particularly the pronghorn *Stockoceros* and *Capromeryx* (Stock, 1930; Stock, 1932). The cave is a large, deep overhanging shelter on the side of Pyramid Peak (Bishop's Cap), accessible by walking up the southwest slope leading to Pyramid Peak (Fig. 6).

The cave also contained evidence of human occupation, with both lithic artifacts and artifacts of preserved plant materials, including cordage and woven sandals. Although Howard (1930, 1932, 1935) considered the extinct fauna as contemporaneous with the human occupation, the style of the artifacts is far too young to be late Pleistocene in age. Archival materials including field notes related to the excavation are housed in the LACM. Based on the field notes, Brattstrom (1964) described two measured sections of the cave deposits, one 37 inches deep and the other 53 inches. Figure 7 shows schematic stratigraphic sections based on those measurements. Fossil bones and later human artifacts were recovered from at least Strata 1-3. As the deposits are relatively shallow, the deposits were disturbed by the later human inhabitants, who likely dug storage pits and hearths resulting in a mixing of the sediments. Many of the fossil bones show evidence of exposure to fire, ranging from a slight brown or gray discoloration, to dark brown, black and in some cases completely calcined. Some of this burning may have been the result of the deposits being disturbed by the later human occupants and burnt in their cooking fires. The extensive ash deposits noted by the excavators may also indicate that there were previously thick dung deposits in the cave that burned when naturally occurring wildfires spread up the lower slopes of Pyramid Peak in Late Pleistocene or Holocene times. In any event, the deposits were mixed, and meaningful dates cannot be assigned to individual specimens based on their stratigraphic position in the deposits. Species of interest will have to be individually dated to determine when they were deposited in the cave. Stock did not study all the pronghorn material for his two reports (1930, 1932), concentrating on complete elements. Stock illustrated and provided measurements for complete skeletal elements, but the collection contains many additional specimens. The senior author made a preliminary survey of the collection in March 2023, yielding a NISP of 126 *Stockoceros* and 9 *Capromeryx*, with corresponding MNIs of 4 and 1. Approximately 100 addition specimens exist that were not included; they are mostly small fragments, but will certainly increase the NISP when completely studied.

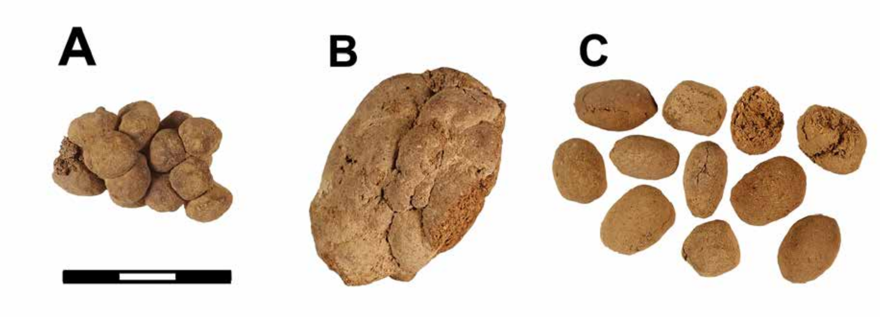


Figure 8. Antilocaprid dung from Shelter Cave and Dark Canyon Cave. A, Dark Canyon Cave, MSD-364; B and C, Shelter Cave. MSD-353, 354.

Stock (1932) reported and illustrated dung that he tentatively referred to *Stockoceros conklingi*. The two specimens each consist of individual ovoid pellets agglutinated into a mass. Art Harris provided The Mammoth Site with several additional masses of pellets that he had collected from Shelter Cave and Dark Canyon Cave in the 1970s (Figure 8). Samples of 4 pellets were submitted to UCIAMS for dating, along with a single sample from Dark Canyon Cave, with the results presented in Table 5. These dates, if accurate, are of recent age and indicate that the dung is from *Antilocapra americana*, rather than being attributable to either *Stockoceros* or *Capromeryx*, the two extinct antilocaprid taxa present

Table 5: Radiocarbon dates for Shelter Cave and Dark Canyon Cave pronghorn dung.

Site	Sample #	Material sampled	Lab Number	Calibrated Date	Notes
Shelter Cave, NM	SheltC 1	Single pellet half	UCIAMS 264179	215±20	Half of MSD 353; L=16.35; W = 8.31; W=8.01; Provided by A. Harris 70s;
Shelter Cave, NM	SheltC 2	Single pellet half	UCIAMS 264180	190±20	Half of MSD 354; L=14.38; W=10.53; W=10.42; Provided by A. Harris 70s;
Shelter Cave, NM	SheltC 3	Single pellet half	UCIAMS 264181	230±15	Half of MSD 354; L=11.10; W=9.86; W=9.52; Provided by A. Harris 70s;
Shelter Cave, NM	SheltC 4	Single pellet half	UCIAMS 264182	225±20	Half of MSD 354; L=15.16; W=10.90; W=10.03; Provided by A. Harris 70s;
Dark Canyon Cave, NM	DrkCC 1	1 dung pellet from cluster	UCIAMS 246178	Modern	MSD 664 Provided by A. Harris 70s;

in the fauna. The Dark Canyon Cave date supports the use of caves by modern pronghorn, as does a partial skeleton of *Antilocapra americana* recovered from nearby Conkling Cave, which appears to be recent based on preservation (LACM, RSW notes). If there was an appreciable dung deposit in Shelter Cave, which later burned to produce the ash layer, then it would likely have been from the Shasta ground sloth (*Nothrotheriops shastensis*) whose bones and dung were recovered in the cave (Thompson et al., 1980; McDonald and Morgan, 2011). In his first report on the pronghorn remains from Shelter Cave, Stock (1930) notes that Conkling, one of the excavators of the material, told him that the remains of the extinct mammals all came from the gray ashy layer, and within 48 inches of the cave's rock floor.

Fosberg (1936), another member of the team that excavated Shelter Cave, reported on the macrobotanical remains recovered. In his report he notes that "The depth was not satisfactorily determinable due to the looseness of the material and to possible and observed disturbance by Indians and animals. It is definite that none were taken from the partially consolidated lower layer. Indian material was found chiefly in the upper layers while the remains of extinct animals were found throughout the deposit, excepting possibly at the very top and the consolidated layer at the bottom" (Fosberg, 1936:154). Stock (1930) did not comment on the preservation of the pronghorn remains or the reason for their presence in the cave, but did so in his second, more detailed, report (Stock, 1932). He noted that he saw no evidence that the broken and burned pronghorn bones were the result of human activity, but rather due to natural taphonomic processes in caves. Specifically, he noted that "…where the mammalian remains have suffered from contact with heat or fire this has resulted from (1) the accumulation of hot ashes in the cave, (2) brush fires on the mountain slopes about the cave entrance, (3) spontaneous combustion of organic deposits which possibly formed part of cavern accumulation, or (4) campfires of the basketmakers, particularly in the fore parts of the cave" (Stock, 1932:8-9).

Brattstrom (1964) commented on the amphibians and reptiles from Shelter Cave and Conkling Cave that the deposits accumulated for several reasons: "…caves such as these offer, in such a harsh semi-arid environment, a shelter from intense solar radiation during the days...provide natural "homes" for the smaller carnivores and...harbor numerous bats….".

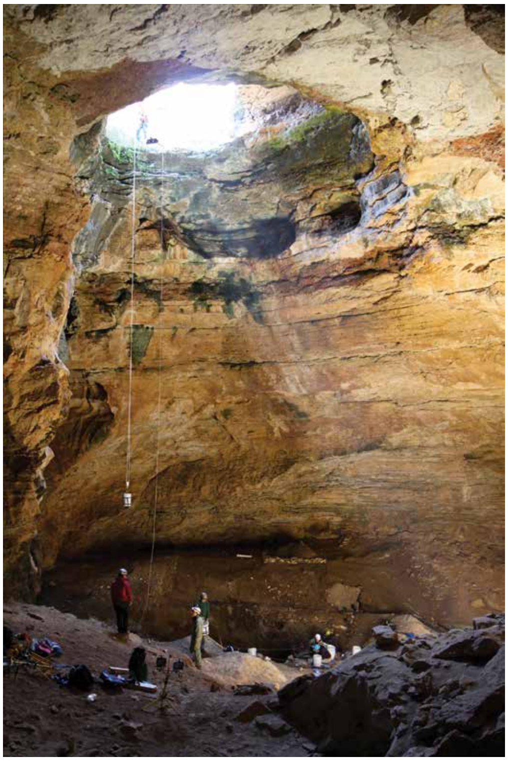


Figure 9. Natural Trap Cave, Wyoming. Photo courtesy of Justin S. Sipla, via Julie Meachen.

Shelter Cave, therefore, appears to have had a very different taphonomic history than either Papago Springs Cave or San Josecito Cave. Although complicated by the later occupation of the cave by Native Americans, the use of the cave as a temporary or seasonal shelter by pronghorn seems most likely. The large number of bones, presence of juveniles and adults, lack of carnivore feeding traces, and the presence of dung, if any, can be shown to be attributable to *Stockoceros* or *Capromeryx*, rather than to later visits by *Antiocapra*, would support this interpretation.

Natural Trap Cave: The only cave deposit with significant remains of the extant pronghorn, *Antilocapra americana*, is Natural Trap Cave, located in Big Horn County, north central Wyoming at an elevation of 1,512 m. The cave was discovered in 1970, with major excavations conducted by Larry D. Martin and B. Miles Gilbert (Martin and Gilbert, 1978; Gilbert and Martin, 1984) in the 1970s and early 1980s. Subsequent major excavations have been conducted from 2014 to the present by Julie Meachen and colleagues (Meachen and McGuire, 2023). The cave has a surface opening 8.5 m by 6 m, located in a depression along a major game trail leading to the Big Horn Mountains (Fig. 9). The floor of the main chamber is about 42.6 m x 44.2 m in diameter and is 24.6 m below the surface opening (Meachen and McGuire, 2023).

Table 6. Relative abundance of *Ovis*, *Antilocapra* and *Miracinonyx* at Natural Trap Cave

Taxon	NISP	MNI
Antilocapraa	152	12
Ovis	940	39
Miracinonyx	184	12

Table 7. Dietary proportions for large-bodied predators and prey from Natural Trap Cave, Wyoming.

Predator	Prey	Proportion
Cheetah	Pronghorn	40%
	Horse	26%
	Bison	19%
	Sheep	15%
Lion	Pronghorn	41%
	Bison	21%
	Horse	20%
	Sheep	19%
Wolf	Pronghorn	38%
	Horse	31%
	Bison	19%
	Sheep	13%

* Note: this is Figure 5 in Annear et al. (2023) rearranged to show prey preference of each predator from highest to lowest. Cheetah is Miracinonyx trumani; Lion is Panthera atrox, and Wolf is Canis lupus.

Only the pronghorn remains recovered during the earlier excavations by Martin and Gilbert have been published (Chorn et al., 1988); according to Redman et al. (2023) the sample includes a NISP of 152 and a MNI of 12. Gilbert and Martin sampled less than 5% of the deposits in the cave (Wang and Martin, 1993) including the excavations they conducted after 1979. The more recent work will certainly expand our understanding of *Antilocapra* from Natural Trap Cave.

Chorn et al. (1988) reported on the pronghorn remains. They state that adult skulls of both males and females are represented in the collection, but that juvenile elements are rare. None of the metapodials show incomplete fusion of the distal epiphysis. The number of metapodials is not given; 16 cataloged specimens are listed in their paper, but without indication of whether they were right or left; it is likely that these 16 represent only the complete specimens. Chorn et al. (1988) did not comment on the taphonomy of the pronghorn from Natural Trap Cave. A predator/prey relationship between the American cheetah-like cat (*Miracinonyx trumani*) that is well represented in the fauna (Adams, 1979) and the American pronghorn (*Antilocapra americana*) has been suggested, based largely on highly cursorial habits of both species; an evolutionary "arms-race" has been often discussed (Byers, 1997; 2003).

Redman et al. (2023) examined the rank abundance distribution of large-bodied mammals from the Gilbert and Martin excavations in the 1970s. Extracted from their fig. 5, Table 6 provides values for NISP and MNI, summed for all four stratigraphic levels. The analysis of Redman et al. (2023) was designed to evaluate whether changes in the Rank Abundance Distribution were due to taphonomic difference between the strata, or rather reflected the surrounding ecological conditions – that is, it accurately reflects those animals' abundance in the local ecosystem through time. We summed the values for *Ovis*, *Antilocapra*, and *Miracinonyx* over the 4 strata to examine relative abundance. If these values do reflect the animal's abundance locally, then *Antilocapra* was unlikely to be the primary prey of *Miracinonyx*; *Ovi*s is much more likely to have been its preferred prey. This would support the recent proposal of Hodnett et al. (2022) that the prey of *Miracinonyx* was similar to that of the living Asiatic cheetah (*Acinonyx jubatus venaticus*) and snow leopard (*Uncia uncia*), large felids adapted for pursuit of mountain and canyon ungulates over near vertical rocky and mountainous terrain. This suggestion

Figure 10. Scrubox skeleton covered in flowstone, partly under water in the Main Room of Muskox Cave. Visible is a skull, femur, scapula, and ribs. Photo courtesy of Carlsbad Caverns National Park, National Park Service.

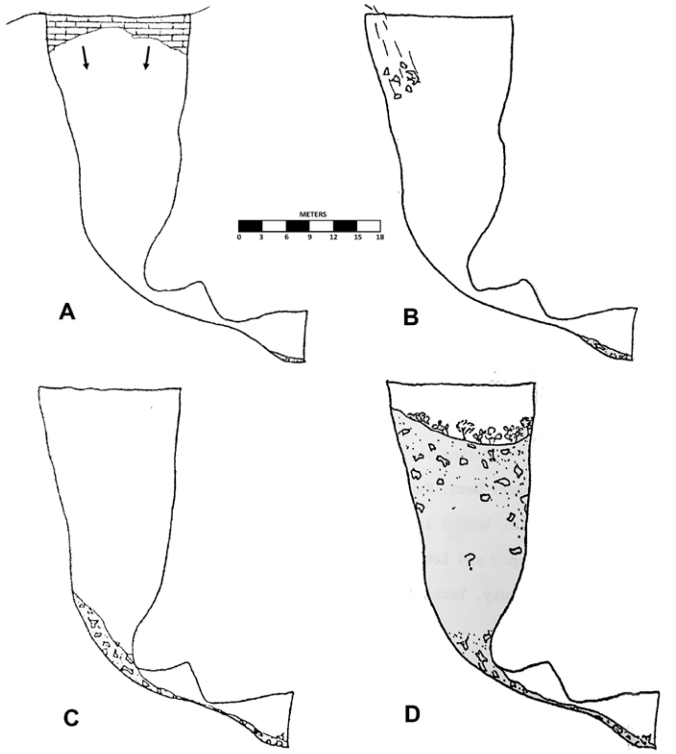


Figure 11. Schematic cross-sections showing the development of Muskox Cave. A, the collapse of the dome of the solution cavern to form a sinkhole; B, the pitfall entrapment of larger mammals; C, the filling of the cave with breakdown debris and sediments washing into the sinkhole; D, the filling of the original sinkhole opening with further breakdown and surface materials. Note that the scale is for the horizontal dimension only; Muskox Cave is considerably deeper than shown. Adapted from Logan (1979).

does not match the analysis using isotopic analysis of bone collagen reported by Higgins, et al. (2023) for Natural Trap Cave predators and prey. Table 7 presents their data for dietary proportions of cheetah (*Miracinonyx trumani*), lion (*Panthera atrox*), and Wolf (*Canis lupus*), rearranged. Their data show that pronghorn is the preferred prey of all three of the large carnivores, and sheep the least preferred. The percentages for cheetah seem odd, in view of the size of the prey – modern day cheetah seldom take prey as large as adult horses or bison. Recent study by Annear et al. (2023) suggests that the modern cheetah would focus on smaller prey species but expand their prey base by killing neonates and juveniles of the larger species as they became available seasonally.

Muskox Cave: Located in Carlsbad Caverns National Park, Eddy County, southeast New Mexico at an elevation of 1,600 m, Muskox Cave produced an important, but little studied, vertebrate fauna in excavations conducted by Lloyd Logan in 1976 and 1977 under the auspices of the Smithsonian Institution, the National Park Service, and Texas Tech University. The material recovered during that work has remained largely uncleaned, unsorted, and unstudied, apart from a study of the extinct mountain goat (*Oreamnos harringtoni*) (Jass et al., 2000). The extensive fauna contains 48 species of mammals, based on Logan (1979; 1981) and Harris (1993). The most unusual aspect of the fauna is that the most abundant large mammal is the scrubox (*scrubox (Speleotherium logani* (White et al. 2025)), which is otherwise rarely encountered in the Intermountain West. Also notable is that complete or nearly complete skulls of several of the large mammals have been recovered, which include besides the shrubox, dire wolf (*Canis dirus*), pronghorn (*Stockoceros conklingi*), and the extinct mountain goat (*Oreamnos harringtoni*). Many of the bones have been covered with flowstone, some completely encased (Figure 10). The fauna is currently under study by the authors and their colleagues.

Logan (1979; 1981) described the cave as a pitfall accumulation, with a drop below the cave opening of 75-80 m initially, but eventually reduced to about 35 m as the sinkhole filled with sediments (Figure 11). Logan (1979) mentions the absence of “bones broken in the manner of feeding carnivores” as suggesting that most of the (large) mammals in the fauna fell to their deaths, while the micro-mammals were introduced by roosting owls and moved around within the cave by packrats. Many of the bones we are currently examining appear to have had the ends of the bones chewed off by carnivores before being extensively gnawed by rodents, as well as the longitudinally guttered long bone shafts with chipped edges found by Binford (1981) to be characteristic of wolf gnawed bone, suggesting that a healthy population of both flourished in the cave. This in turn suggests that there was an entrance suitable at least for some mammals to enter and exit during the time the sediments were accumulating. Remains of pronghorn are abundant, with at least a NISP of 146 (143 *Stockoceros* and 3 *Capromeryx*) and a MNI of at least 5 (4 *Stockoceros* and 1 *Capromeryx*), which probably grossly underestimates the actual number of individuals when the as-yet undetermined length of time during which the sediments accumulated is considered. *Stockoceros conklingi* is the most abundant, with a smaller number of *Capromeryx furcifer*. Several probably associated partial skeletons of

Figure 12. Dragline being used to remove the bulk of the cave sediments from Inglas 1A, explaining why many of the bones were broken post fossilization. Photo courtesy of David Webb.

Stockoceros seem to be represented. Skeletal element representation suggests that the pronghorn entered the cave as entire animals, not as partial kills made outside the cave and dragged in by carnivores. It appears based on presently available evidence, that larger animals (*Speleotherium, Stockoceros* and *Oreamnos*) fell into the cave and were fed upon by carnivores, especially the dire wolf. However, it is possible that this interpretation may change as our study of the fauna progresses.

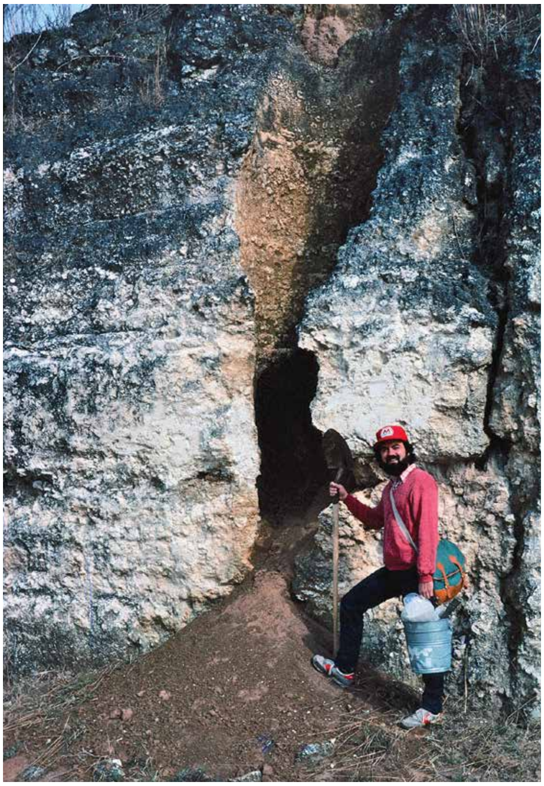


Figure 13. An example of the Florida cave and karst features. This shows a small, sediment-filled fissure in the Haile Quarry complex, near Newberry, Alachua County This site is much smaller than Inglis 1A but illustrates the geological context of the caves and fissures in the Eocene Ocala Limestone which became filled with surface sediments during the Pleistocene. Gary S. Morgan for scale. Photo courtesy of Richard Hulbert.

Inglis 1A: The Inglis 1A site is located on the north bank of the unfinished Cross Florida Barge Canal, near the town of Inglis in Citrus County, west-central peninsular Florida. Inglis 1A is about 10 km inland (east) from the Gulf of Mexico and only about 3–4 m above current sea level. In fact, the fossiliferous sediments comprising the lowest stratigraphic layers of the site are several meters below sea level**.** The site was discovered in 1967 by University of Florida paleontology graduate students Jean Klein and Robert Martin, shortly after the western portion of the barge canal had been dug. UF field crews excavated the site between 1967 and 1974. A major excavation was conducted at Inglis 1A from December 1973 to March 1974, under the direction of David Webb, involving the use of heavy equipment (dragline) to remove most of the remaining sediments from the site, consisting of about 300 m^3 of fossiliferous sands and clays (Figure 12). The sediments were either screen washed on site or taken to the FLMNH and screen washed through finer screens. The screening of all sediment from the Inglis 1A site resulted in the recovery of a remarkable sample of microvertebrates, including toads, lizards, snakes, birds, and small mammals (shrews, bats, rodents, and rabbits). However, the use of heavy equipment to remove the bulk of the sediments from the sinkhole resulted in damage to some of the larger vertebrate fossils.

Klein (1971) wrote a master's thesis on the carnivores and ungulates from Inglis 1A, including a review of the geology and stratigraphy. The geologic information on Inglis 1A presented here is based on Klein's (1971) thesis and a review of the site by Hulbert (2015). Inglis 1A is a karst deposit consisting of a large sinkhole with an opening of about 10 × 20 m, developed in marine Eocene limestone of the Inglis Formation. The sediment layers filling the Inglis 1A sinkhole varied from 3–4 m in thickness, with the stratigraphy consisting of a basal conglomerate unit, overlain by several layers of sand and clay, and capped by a cemented quartz sandstone. The sand units comprised the majority of the Inglis 1A deposit and also contained most of the fossils. On the basis of the taphonomy of the sinkhole deposit, in particular the abundance of cave-dwelling bats (Morgan, 1991), Inglis 1A was almost certainly a cave system when the site formed in the early Pleistocene (latest Blancan NALMA). However, the original cave has long since collapsed, and when discovered the site consisted of a sediment-filled sinkhole or large solution cavity (Fig. 13). Therefore, the taphonomy of the Inglis 1A site can only be interpreted based on the overall morphology of the sinkhole, the character of the sediments and stratigraphy, and the nature of the vertebrate fauna. This is unlike the five previously described late Pleistocene deposits that consist of caves in which features of the entrances and passageways were

Table 8. Skeletal element representation for *Capromeryx* at Inglis 1A.

Skeletal Element	NISP	MNI
Tibia	88	28
Radius	86	34
Humerus	79	38
Phalanx, distal	79	20
Femur	78	32
Metacarpal	62	27
Metatarsal	55	23
Astragalus	54	27
Scapula	53	26
Calcaneum	44	22
Ulna	38	19
Phalanx, proximal	34	5
Cubonavicular	31	16
Phalanx, medial	20	3
Cuneiform	17	9
Lunar	17	9
Scaphoid	16	8

Note: NISP is the Number of Identified Specimens. MNI is the Minimum Number of Individuals. This was calculated as MNI= NISP whole element unallocated to side, plus all elements identified to side minus the lesser number of distal or proximal ends) divided by 2 for all bones except for the phalanges, which were divided by 8.

important in interpreting the taphonomy of the fauna, and in particular, how pronghorn and other fossils entered the cave system.

The Ingis 1A LF is the oldest of the six Pleistocene antilocaprid fossil sites we describe in detail, and the only one of these sites in which *Capromeryx* is the most abundant pronghorn. Based on mammalian biochronology (Morgan, 2005), the Inglis 1A LF is early Pleistocene in age (latest Blancan NALMA; ~1.8–2.0 Ma). Klein (1971) first reported fossils of the small pronghorn *Capromeryx* from Inglis 1A, and Webb (1974) referred the Inglis pronghorn to *C. arizonensis*, originally described by Skinner (1942) from the Dry Mountain site (111 Ranch Fauna) in Arizona. Inglis 1A has the largest sample of *Capromeryx* known from any North American Pleistocene cave or karst deposit, with 1,169 NISP and a MNI 38 based on the humerus (Table 8).

The second largest cave or karst sample of *Capromeryx* is also from a late Blancan site in Florida, Santa Fe River 1, with 128 NISP and an MNI of 12 based on metacarpals (data from FLMNH vertebrate paleontology database). Santa Fe River 1 is an underwater site that was collected by scuba divers, and as a consequence very few smaller bones (carpals, tarsals, phalanges) of *Capromeryx* were recovered. Although the geology, stratigraphy, and taphonomy of Santa Fe River 1 are difficult to evaluate because the site is underwater, it appears to be of karst origin and represents a large solution feature, much like Inglis 1A.

Since the manner in which the specimens were collected undoubtedly contributed to the breakage/fragmentation of the bones, any measure of fragmentation index of frequency of breakage would be meaningless in terms of the taphonomy. One measure that can be applied is skeletal element representation. Table 8 presents preliminary data pending more intensive study of the collection by the authors. Given the similar numbers for all the major bones, it seems reasonable to conclude that the animals all entered the cave or fissure as whole animals, rather than as selected bones brought in by carnivores or by water transport. Juveniles are present but rare. We cannot determine the number of males or females, as it is unknown if the females had horns like the males or had reduced or no horns as in modern *Antilocapra*. No hornless or reduced horn *Capromeryx* skulls have been recovered in any site in North America, in spite of the large number of specimens at Inglis IA, 111 Ranch in Arizona, and from the tar pits at Rancho la Brea, California.

All the Florida sites containing *Capromeryx*, including Inglis 1A, Inglis 1B, Santa Fe River 1, Santa Fe River 8, Waccasassa River 9A, and Withlacoochee River 1A, are similar in age (early Pleistocene, late Blancan, ~1.8-2.5 Ma) and appear to represent karst solution features. The paleoecology of the Inglis 1A vertebrate fauna, in particular, the lizards and snakes, birds, and small mammals (Meylan, 1982; Emslie, 1998; Morgan and Emslie, 2010), indicates that the climate was considerably drier than present, with widespread savannas and grasslands and other types of xeric habitats.

Particularly notable is the occurrence of many vertebrates with western affinities in the Inglis 1A LF (Morgan and Emslie, 2010), including *Capromeryx,* which apparently dispersed to Florida in the early Pleistocene during a period when a more extensive development of grasslands was present. There are no younger records of *Capromeryx* from Florida, suggesting that *Capromeryx* went extinct there with the change in habitat, so that during the remainder of the Pleistocene antilocaprids were absent from Florida.

SUMMARY AND CONCLUSIONS

The information available for the six sites discussed in detail above is not as complete as we would wish. Field notes by some researchers have been lost or were never taken for some sites. The sites were excavated long before taphonomic analysis of cave faunas became as sophisticated as it is today. Unidentifiable fragments were often not saved, so breakage frequency and patterning cannot be adequately determined; nor can much refitting be attempted. We made detailed observations of the collections, except for the early collection from Natural Trap Cave, for which we relied on the published accounts. In some, perhaps all, cases several bone accumulation factors were responsible for the presence of animal bone in the cave sediments. Papago Springs Cave, San Josecito Cave, Natural Trap Cave, Muskox Cave, and probably Inglis 1A all functioned as natural pitfall traps for at least the large mammals, while Shelter Cave is the only cave where pronghorn could have inhabited the cave episodically or seasonally. Even in the pitfall trap caves, a portion of the fauna includes bones brought in by small carnivores, roosting birds, or moved around by packrats. Water transport into caves is not conclusively demonstrated in any of these caves; in the case of Papago Springs Cave, water transport may have disturbed bones already in the cave and moved them downslope into the deeper recesses of the cave, but the evidence is not convincing. Muskox Cave, based on our preliminary observations, appears to have been both a pitfall accumulation and a carnivore denning site, with evidence that large carnivores fed on the pronghorn carcasses. In Shelter Cave, where a dung deposit might have been present, we have no evidence that extinct pronghorn were responsible. Dung previously attributed to the extinct pronghorn from this cave appears to be recently deposited by the living pronghorn.

Finally, we emphasize the necessity of total recovery of faunal remains, including broken fragments which cannot be identified to the species or genus level. In those collections where such material was not saved, we are unable to meaningfully discuss fragmentation patterns that can provide important clues as to the process or agent responsible for the accumulation of bones in the cave.

ACKNOWLEDGEMENTS

We thank the organizers of the Symposium for which this paper was originally prepared, Sharon Holte Weaver and Jim I. Mead for inviting us to participate in the Symposium and this volume. Funds for the radiocarbon dates on pronghorn dung from Shelter and Dark Canyon Caves were provided by Jim I. Mead and The Mammoth Site. Staff at the AMNH (Richard Tedford, Judy Galkin, Susan Bell and Jin Meng), LACM (Sam McLeod), FLMNH (Richard Hulbert and Rachel Narducci) and the USNM (Amanda Millhouse, Jessica Nagano, and Kay Behrensmeyer) provided access to collections and helped arrange loans. Lee Potter provided Albert Potter's photographs from the 1937-1938 Papago Springs Cave excavations, Art Harris provided the photograph of Shelter Cave, Julie Meachen provided the photograph of Natural Trap Cave, and Richard Hulbert and David Webb provided the photos of Inglis 1A and the Haile Quarry. Sandy Swift did her usual photographic magic and gave advice on the preparation of the illustrations. We thank Jim Mead, Greg McDonald, and Earl Manning for helpful reviews that certainly improved the paper.

REFERENCES

Adams, D.B., 1979, The Cheetah: Native American: Science, v. 205, P. 1155-1158.

Agenbroad, L.D., Mead, J. I., Mead, E. M., and Elder, D., 1989, Archaeology, alluvium and cave stratigraphy: The record from Bechan Cave, Utah: The Kiva, v. 54, p. 335–351.

Agenbroad, L.D., and Mead, J.I., 1994, The Hot Springs Mammoth Site: A Decade of Field and Laboratory Research in Paleontology, Geology and Paleoecology: Hot Springs, The Mammoth Site, 457 p.

Andrews, P., 1990, Owls, Caves and Fossils: Chicago, University of Chicago Press, 231 p.

Annear, E., Minnie, L., Andrew, K., and Kerley, G.I.H., 2023, Can smaller predators expand their prey base through killing juveniles? The influence of prey demographics and season on prey selection for cheetah and lion: Oecologia, v. 201, p. 549-660.

Arilla, M., Rosell, J., Blasco, R., Dominguez-Rodrigo, M., and Pickering, T.T., 2014, The "bear" essentials: Actualistic research on *Ursus arctos* in the Spanish Pyrenees and its implications for paleontology and archaeology: PLOS ONE, v. 9 e102457. doi.org/10.1371/journal.pone.0102457.

Arriaza, M.C., Domínguez-Rodrigo, M., Yravedra, J. and Baquedano, E., 2016, Lions as bone accumulators? Paleontological and ecological implications of a modern bone assemblage from Olduvai Gorge: PLoS One, v. 11, p.e0153797.

Arroyo-Cabrales, J., 1994, Taphonomy and Paleontology of San Josecito Cave, Nuevo Leon, Mexico [Ph.D. dissertation]: Lubbock, Texas Tech University, 217 p.

Arroyo-Cabrales, Johnson, J.E., and Cruz, L.A., 2021, San Josecito Cave and its paleoecological contribution for Quaternary Studies in Mexico: Quaternary v. 20314, 34. doi.org/10.3390/ quat4040034.

Behrensmeyer, A.K., 1978, Taphonomic and ecologic information from bone weathering: Paleobiology, v. 4, p. 150-162.

Betancourt, J.L. Van Devender, T.R., and Martin, P.S., 1990, Packrat Middens: Tucson, University of Arizona Press, 478 p.

Binford, L.R., 1981, Bones: Ancient Man and Modern Myths: New York, Academic Press, 320 p.

Bowell, R., Warren, A., and Redmond, I., 1996, Formation of cave salts and utilization by elephants in the Mount Elgon region, Kenya: Geological Society of London Special Publications v. 113 p. 63-79.

Bountalis, A.C., and Kuhn, B.F., 2014, Cave usage by multiple taphonomic agents: Issues towards interpreting the fossil bearing cave deposits in South Africa: American Journal of Zoological Research v. 2, p. 55-61.

Brain, C.K., 1981, The Hunters or the Hunted? An Introduction to African Cave Taphonomy: Chicago, University of Chicago Press, 365 p.

Brattstrom, B.H., 1964, Amphibians and reptiles from cave deposits in south-central New Mexico: Bulletin Southern California Academy of Sciences v. 63, p. 93-103.

Bryan, W.A., 1929, The recent bone-cavern find at Bishop's Cap, New Mexico: Science N.S. v. 70, p. 39-41.

Buckland, W., 1822, Account of an assemblage of fossil teeth and bones of elephant, rhinoceros, hippopotamus, bear, tiger, and hyaena, and sixteen other animals; discovered in a cave at Kirkdale, Yorkshire, in the year 1821: with a comparative view of five similar caves in various parts of England, and others on the continent: Philosophical Transactions of the Royal Society of London v. 112, p. 171-236.

Buiter, D. I., and Berger, L.R., , 2000, Leopards as taphonomic agents in dolomitic caves—Implications for bone accumulations in the hominid-bearing deposits of South Africa**:** Journal of Archaeological Science v. 27, p. 665-684.

Byers, J.A., 1997, American pronghorn: social adaptations and the ghosts of predators past: Chicago, University of Chicago Press, 300 p.

Byers, J.A., 2003, Built for speed: Cambridge, Harvard University Press, 230 p.

Chorn, J., Frase, B.A., and Frailey, C.D., 1988, Late Pleistocene pronghorn, *Antilocapra americana*, from Natural Trap Cave, Wyoming: Transactions of the Nebraska Academy of Sciences v. 16, p. 127-139.

Colbert, E.H., and Chaffee, R.G., 1939, A Study of *Tetrameryx* and associated fossils from Papago Springs Cave, Sonoita, Arizona: American Museum Novitates 1034, 21 p.

Conkling, R. P., 1932, Conkling Cavern: The discoveries in the bone cave at Bishops Cap, New Mexico: West Texas Historical and Scientific Society Bulletin 44, p. 39-41.

Czaplewsi, N.J., Mead, J.I., Ku, T.-L., and Agenbroad, L.D., 1989, Radiometric age assessment for Papago Springs Cave deposits, southern Arizona: Southwest Naturalist, v. 34, p. 278-281.

Czaplewski, N.J., Peachey, W.D., Mead, J.I., Ku, T-L., and Bell, C.J., 1999a, Papago Springs Cave revisited, Part I: Geological setting, cave deposits, and radiometric dates: Occasional Papers of the Oklahoma Museum of Natural History Number 3, 25 p..

Czaplewski, N.J., Peachey, W.D., Mead, J.I., Ku, T-L., and Bell, C.J., 1999b, Papago Springs Cave revisited, Part II: Vertebrate paleofauna. Occasional Papers of the Oklahoma Museum of Natural History Number 5, 41 p.

Dart, R., 1958, The origin of bone accumulations in caves: Transvaal Museum Memoirs v. 11, p. 10-12.

Daly, P., 1969, Approaches to faunal analysis in archaeology: American Antiquity v. 34, p. 146-153.

Diedrich, C.G., 2009, Late Pleistocene *Hystrix* (*Acanthion*) *brachyura* Linnaeus 1758 from the Fuchshuken Cave near Saalfeld (Thuringia, Germany) – A porcupine and hyaena den and contribution to their paleobiogeography in Europe: The Open Paleontology Journal v. 2009, p. 1-9.

Epstein, J.B., and Doctor, D.H., 2013, Evaporite karst in the Black Hills, South Dakota and Wyoming, and the oil play in the Williston Basin, North Dakota and Montana NCKRI Symposium 2: Proceedings of the Thirteenth Multidisciplinary Conference on Sinkholes and the Engineering and Environmental Impacts of Karst, p. 161-175.

Emslie, S. D., 1998, Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida Peninsula: Ornithological Monographs, no. 50, 113 p.

Foshberg, F.R., 1936, Plant remains in Shelter Cave, New Mexico: Bulletin Southern California Academy of Science v. 35, p. 154-155.

Fosse, P., Selva, N., Wajrak, A., Fourvel, J-P., Madelaine, S., Nadal, M.S., Yravedra, J., Bryga, J-P., Prucca, I.A., and Haynes, G., 2012, Bone modification by modern wolf (*Canis lupus*): a taphonomic study from their natural feeding places: Journal of Taphonomy v. 10, p. 197-217.

Frick, C., 1937, Horned ruminants of North America: American Museum of Natural History Bulletin 69, 669 p.

Furling, E.L., 1943, The Pleistocene antelope, *Stockoceros conklingi*, from San Josecito Cave, Mexico: Carnegie Institution of Washington Publication, no. 551, p. 1-8.

Gilbert, B.M., and Martin, L.D., 1984, Late Pleistocene fossils of Natural Trap Cave, Wyoming, and the climatic model of extinction, *in* Martin, P.S. and Klein, R.G., eds., Quaternary Extinctions: A Prehistoric Revolution, Tucson, University of Arizona Press, p. 138-147.

Graham, R.W., Lundelius, E.L., Meissner, L., and Muhlestein, K., 2013, Friessenhahn Cave: Late Pleistocene paleoecology and predator-prey relationships of mammoths with an extinct scimitar cat: in Hunt, B.B and Catlos, E.J. (eds.), Late Cretaceous to Quaternary Strata and Fossils of Texas: Field Excursions Celebrating 125 Years of GSA and Texas Geology, GSA Field Guide 30, p. 15-31.

Hansen, R.M., 1978, Shasta ground sloth food habits, Rampart Cave, Arizona: Paleobiology, v. 4, p. 302-319.

Hanson, C.B., 1980, Fluvial taphonomic processes: Models and experiments, *in* Behrensmeyer, A.K. and Hill, A.P, eds., Fossils in the Making: Chicago, University of Chicago Press, p. 156-181.

Harris, A., 1993, Quaternary vertebrates of New Mexico. New Mexico Museum of Natural History and Science Bulletin 2: 179-197.

Harris, J.M. (Ed.), 2015, La Brea and Beyond: the paleontology of asphalt-preserved biotas: Los Angeles Museum of Natural History Science Series 42, p. 1-174.

Haynes, G., 1980. Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones: Paleobiology, v. 6, p. 341-351.

Hearty, P.J., Olson, S.L., Kauffman, D.S., Edwards, R.L., and Cheng, H., 2004, Stratigraphy and geochronology of pitfall accumulations in caves and fissures, Bermuda: Quaternary Research Reviews, v. 23, p. 1151-1171.

Higgins, P., Meachen, J.A., and Lovelace, D.M., 2023, Were pronghorns (*Antilocapra*) primary prey for North American cheetahs (*Miracinonyx*)?: Quaternary International, v. 647-648. DOI: 10.1016/ j.quaint.2022.08.003.

Hodnett, J-P. M., White, R.S., Carpenter, M., Mead, J.I., and Santucci, V.L., 2022, *Miracinonyx trumani* (Carnivora: Felidae) from the Rancholabrean of the Grand Canyon, Arizona and its implications for the ecology of the "American Cheetah": New Mexico Museum of Natural History and Science Bulletin 88, p. 157-185.

Howard, E.B., 1930, Archaeological Research in the Guadalupe Mountains. University of Pennsylvania Museum Journal, 21, p.188-213.

Howard, E.B., 1932, Caves along the slopes of the Guadalupe Mountains: Bull. Texas Archeology and Paleontology. Society, v. 4, p.7-9.

Howard, E.B., 1935, Evidence of Early Man in North America: Based on Geological and Archaeological Work in New Mexico: University of Pennsylvania Museum Journal, v. 24, p. 61-62.

Howard, H., and Miller, A.H., 1933, Bird remains from cave deposits in New Mexico: The Condor, v. 35, p. 15-18.

Hughes, A.R., 1954, Hyaenas versus australopithecines as agents of bone accumulations: American Journal of Physical Anthropology, v. 2, p. 467-486.

Hulbert, R. C., Jr., 2015, Inglis 1A: Vertebrate Fossil Sites, Florida Vertebrate Fossils, Florida Museum of Natural History website. Accessed 5.18.2023.

Janis, C. M and Manning, E., 1998, Antilocapridae, p. 491-507, in Janis, C.M., Scott, K.M., and Jacobs, L.J., (eds.) Evolution of Tertiary Mammals of North America, v. 1, Cambridge, University of Cambridge Press.

Jass, C.N., Mead, J.I. and Logan, L., 2000, Harrington's extinct mountain goat (*Oreamnos harringtoni* Stock 1936) from Muskox Cave, New Mexico: Texas Journal of Science, v. 52, p. 121-132.

Karpinski, E.K., J.I. Mead and H.N. Poinar, 2017. Molecular identification of paleofeces from Bechan Cave, southeastern Utah, USA. Quaternary International, v. 443 DOI: 10.1016/j.quaint. 2017.03.068.

Kirillova, I.V., Borisova, O., Chernova, O.F., Haynes, G., Narina, N.V., Panin, A.V., Zanina, O,O,. Zazovskaya, E., Zhuraviev, A., and Zvyagin, V.N., 2021, Nonpyrogenic charring of Late Pleistocene large mammal remains in northeastern Russia: Boreas, v. 51: DOI: 10.1111/bor.12569.

Klein, J. G., 1971, The ferungulates of the Inglis 1A local fauna, early Pleistocene of Florida: M.Sc. Thesis, University of Florida, Gainesville, 115 p

Kos, A.M., 2002, Pre-burial taphonomic characterization of a vertebrate assemblage from a pitfall cave fossil deposit in southeastern Australia: Journal of Archaeological Science, v. 30, p. 760-779.

Kropf, M., Mead, J.I., and Anderson, R.S., 2007, Dung, diet and the paleoenvironment of the extinct shrub-ox (*Euceratherium collinum*) on the Colorado Plateau, USA: Quaternary Research, v. 67, p. 143-151.

Kuhn, B.F., Berger, L.R. and Skinner, J.D., 2010, Examining criteria for identifying and differentiating fossil faunal assemblages accumulated by hyenas and hominins using extant hyenid accumulations: International Journal of Osteoarchaeology, v. 20, p. 15-35.

Kurtén, B., 1958, Life and death of the Pleistocene cave bear: A study in paleoecology: Acta Zoologica Fennica 95, v. 59 p.

Kurtén, B., 1968. The Pleistocene Mammals of Europe: New York, Routledge, 317 pp.

Kurtén, B., 1995, The Cave Bear Story: Life and Death of a Vanished Animal: New York, Columbia University Press, 163 p.

Kurtén, B., and Anderson, E., 1980, Pleistocene Mammals of North America. New York, Columbia University Press, 442 p.

Lauder, F., and Selva, N., 2005, Ravens as small mammal bone accumulators: First taphonomic study on mammal remains in raven pellets: Paleogeography, Palaeontology, Palaeoecology, v. 226, p. 272-286.

Logan, L.E., 1979, The mammalian fossils from Muskox Cave and their paleoecologic implications: Unpublished report, National Park Service.

Logan, L.E., 1981, The mammalian fossils from Muskox Cave, Eddy County, New Mexico: Proceedings of the Eighth International Congress of Speleology 1, p. 159-160

Lopez, J.M., 2020 Actualistic taphonomy of barn owl pellet-derived small mammal bone accumulations in arid environments of South America: Journal of Quaternary Science, v. 2020, p. 1-13.

Lundquist, C.A., and Varnadoe, W.W., Jr., 2006, Salt ingestion caves: International Journal of Speleology, v. 35, p. 13-18.

Madeiros da Sila Trifilio, L.H., de Araijo, L.H., de Olivera, K., and de Souza Barbosa, F.H., 2022, Mammal taphonomy in a cave deposit from Quaternary of Brazil: Frontiers in Ecology and Evolution, v. 10: doi.org/10.3389/fevo.2022.830190

Maguire, J.M., Pemberton, D., and Collett, M.H., 1980, The Makapansgat limeworks grey breccia: Hominids, hyaenas, hystricids or hillwash?: Palaeontologica Africana, v. b23, p. 75-98.

Mallye, J-P., Costamagne, S., Boudadi-Maligne, M., Prucca, A., Lauroulande, V., Thiebaut, C., and Mourre, V., 2012, Dhole (*Cuon alpinus*) as a bone accumulator and new taphonomic agent? The case of the Noisetier Cave (French Pyrenees): Journal of Taphonomy, v. 10, p.305-336.

Marin-Arroyo, A.B., and Margalida, A., 2012, Distinguishing bearded vulture activities within archaeological contexts: Identification guidelines: International Journal of Osteoarchaeology, v. 22, p. 563-576.

Martin, LD., and Gilbert, B.M., 1978, Excavations at Natural Trap Cave: Transactions of the Nebraska Academy of Sciences, v. 6, p. 107-116.

Martin, P.S., Sabels, B.E. and Shutler, D., 1961, Rampart Cave coprolite and ecology of the Shasta ground sloth: American Journal of Science, v. 259, p. 102-107.

Martinez, G., 2009, Human chewing bone surface modification and processing of small and medium prey amongst the Nukak (Foragers of the Columbian Amazon): Journal of Taphonomy, v. 7, p. 1-20.

McDonald, H.G., 2003, Sloth remains from North American caves and associated karst features. pp. 1-16 in B.W. Schubert, B.W., Mead, J.I. and Graham, R.W. (eds.). Ice Age Cave Faunas of North America. Indiana University Press and Denver Museum of Nature and Science, Bloomington and Denver.

McDonald, H.G., and Morgan, G.S., 2011, Ground sloths of New Mexico: New Mexico Museum of Natural History and Science Bulletin 53, p. 652-663.

McFarlane, D.A., and Lundberg, J, 2005, The 19th Century excavation of Kent's Cavern, England: Journal of Cave and Karst Studies, v. 67, p. 39-47.

Meachen, J.A., and McGuire, J.L., 2023, Natural Trap Cave, Wyoming, U.S.A. records a detailed faunal, floral, aDNA, isotopic and geologic record of the late Quaternary. Quaternary International, v. 647-648:1-3.

Mead, J.I., 2005, Late Pleistocene (Rancholabrean) amphibians and reptiles of Arizona: New Mexico Museum of Natural History and Science Bulletin 29, p. 1-16.

Mead, J.I., Koenig, C., Black, S.L., and Jurgens, C.J., 2021, Late Pleistocene bighorn sheep dung from Eagle Cave, Lower Pecos River, Texas: The Southwestern Naturalist v. 65, p. 152-160.

Mead, J.I., Van Devender, T.R., Ferguson, G.M., and Hale, S., 2022, Late Pleistocene shrub-ox (*Euceratherium collinum*) Pontatoc Ridge Shelter, Santa Catalina Mountains, southeastern Arizona: Southwestern Naturalist, v. 66, DOI: 10.1894/0038-4909-66.2.102.

Mead, J.I., O'Rourke, M.K., and Foppe, T.M., 1986, Dung and diet of the extinct Harrington's Mountain Goat (*Oreamnos harringtoni*): Journal of Mammalogy, v. 67, p. 284-293.

Morgan, G. S., and Czaplewski, N. J., in press, The North American fossil record of bats (Mammalia: Chiroptera) from cave and karst deposits: Journal of Cave and Karst Studies.

Meylan, P. A., 1982, The squamate reptiles of the Inglis 1A fauna (Irvingtonian: Citrus County, Florida): Bulletin of the Florida State Museum, v. 27, p. 1–85.

Morgan, G. S., 1991, Neotropical Chiroptera from the Pliocene and Pleistocene of Florida: Bulletin of the American Museum of Natural History, v. 206, p. 176–213.

Morgan, G. S., 2005, The Great American Biotic Interchange in Florida: Bulletin of the Florida Museum of Natural History, v. 45, p. 271–311.

Morgan, G. S., and Emslie, S. D., 2010. Tropical and western influences in vertebrate faunas from the Pliocene and Pleistocene of Florida: Quaternary International, v. 217, p. 143–158.

O'Regan, H.J., Kuman, K., and Clarke, R.J., 2011, The likely accumulators of bones: five cape porcupine den assemblages and the role of porcupines in the post-member 6 infill at Sterkfontein, South Africa: Journal of Taphonomy, v. 9, p. 69-87.

Palomares, F., Ruiz-Villar, H., Morales-Gonzales, A., Calzada, J., Roman, J., Rivilla, J.C., Fernandez-Gil, A., and Delibes, M., 2022, Hyaenids, felids and canids as bone accumulators: Does the natural history of extant species support zooarchaeological inferences?: Quaternary Science Review, v. 284, 107459.

Pengelly, W. 1873, Report on the Exploration of Brixham Cave, conducted by a committee of the Geological Society, and under the superintendence of Wm. Pengelly, Esq., F.R.S., aided by a local committee; With descriptions of the animal remains by George Busk, Esq., F.R.S., and of the flint implements by John Evans, Esq., F.R.S., Joseph Prestwich, F.R.S., F.G.S., reporter: Philosophical Transactions of the Royal Society of London, v. 162, p. 471-572.

Perkins, D., and Daly, P., 1968, A hunter's village in Neolithic Turkey: Scientific American, v. 219, p. 96-106.

Redman, C.M., Moore, J.R., Lovelace, D.M., and Meachen, J.A., 2023, The rank abundance distribution of large-bodied vertebrates from Natural Trap Cave, Wyoming: Quaternary International, doi.org/10.1016/j.quaint.2021.11.004.

Rogers, R. R., and Kidwell, S. M, 2007. A conceptual framework for the genesis and analysis of vertebrate skeletal concentrations, *in* Rogers, R. R., Kidwell, S. M., Eberth, D. A., and Fiorillo, A. R., (eds.) Bonebeds: Genesis, Analysis, and Paleobiological Significance, Chicago, University of Chicago Press, p. 1-61,

Roosevelt, Q., and Burden, J.W., 1934, A new species of antilocaprine, *Tetrameryx onusrosagris*, from a Pleistocene cave deposit in southern Arizona: American Museum Novitates 754, 4 p.

Sadek-Koros, H., 1972, Primitive bone fracturing: A method of research. American Antiquity, v. 37, p. 369-382.

Sauque, V., Rabal-Garcés, R., Sola-Almagro, C., and Cuenca-Bescós, G., 2014, Bone accumulation by leopards in the Late Pleistocene in the Moncayo Massif (Zaragoza, NE Spain): Plos one, v. 9, p.e92144.

Sattler, R.A., 1997, Large mammals in Lower Rampart Cave, Alaska: interspecific utilization of an eastern Beringian cave: Geoarchaeology: An International Journal, v. 12, p. 657-688.

Saunders, J. J., 1977, Late Pleistocene vertebrates of the Western Ozark Highland, Missouri: Illinois State Museum Reports 33, 118 p.

Skinner, M.F., 1942, The Fauna of Papago Springs Cave, Arizona: Bulletin of the American Museum of Natural History, v. 80, p. 143-220.

Stock, C., 1930, Quaternary antelope remains from a second cave deposit in the Organ Mountains, New Mexico: Los Angeles Museum Publications 2, 18 p.

Stock, C., 1932, A further study of the Quaternary antelopes of Shelter Cave, New Mexico. Los Angeles Museum Publications, 44 p.

Stock, C., 1943. The cave of San Josecito, Mexico: Engineering and Science Monthly, September 1943, p. 11-14.

Stock, C., and Harris, J.M., 1992, Rancho La Brea: A record of Pleistocene Life in California: Los Angeles Museum of Natural History Science Series 37, 113 p.

Terry, R.C., 2007, Inferring predator identity from skeletal damage of small-mammal prey remains: Evolutionary Ecology Research, v. 9, p. 199-219.

Terry, R.C., Laney, J.A., and Hay-Roe, S.H., 2018, Quantifying the digestive fingerprint of predators on the bones of their prey using scanning electron microscopy: Palaios, v. 33, p. 487-497.

Thompson, R.S., Van Devender, T.R., Martin, P.S., Foppe, T., and Long, A., 1980, Shasta Ground Sloth (*Nothrotherium shastensis* Hoffstetter) at Shelter Cave, New Mexico: Environment, diet and extinction: Quaternary Research, v. 14, p. 360-376.

Turner, A., 1989, Sample selection, schlepp effects and scavenging: the implications of partial recovery for interpretations of the terrestrial mammal assemblage from Klasies River Mouth: Journal of Archaeological Science, v. 16, p. 1-11.

Van Devender, T.R., Moodie, K.B., and Harris, A.H., 1976, The desert tortoise (*Gopherus agassizi*) in the Pleistocene of the northern Chihuahuan Desert: Herpetologica, v. 32, p.298-304.

Voorhies, M.R., 1969, Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska: Contributions in Geology, Special Paper 1, Laramie, University of Wyoming Press, 69 p.

Wang, X., 1984, Late Pleistocene bighorn sheep (*Ovis canadensis*) of Natural Trap Cave, Wyoming [Master's thesis]: Lawrence, University of Kansas, 65 p.

Wang, X. 1988, Systematics and population ecology of late Pleistocene bighorn sheep (*Ovis canadensis*) of Natural Trap Cave, Wyoming: Transactions of the Nebraska Academy of Sciences, v. 16, p. 173-183.

Wang, X.M., and Martin, L.D., 1993, Paleoecology and Large Mammal Taphonomy, Natural Trap Cave, Wyoming: National Geographic Research and Exploration, v. 9, p. 422–435.

Webb, S.D., 1974, Chronology of Florida Pleistocene mammals; *in* Webb, S. D., ed., Pleistocene Mammals of Florida: Gainesville, Florida, University Presses of Florida, p. 5–31.

White, J.A., McDonald, H.G., Anderson, E., and Soiset, J.M., 1984. Lava blisters as carnivore traps: Carnegie Museum of Natural History Special Publication No. 8:241-256.

White, R.S., 2008, Papago Springs Cave, Pronghorns and Paleontology: Red Fields and the Burden of Proof: New Mexico Museum of Natural History and Science Bulletin 44, p. 65-74.

White, R.S, Morgan, G.S., Baskin, J.A., and Thomas, R.G., 2022, Late Pleistocene (Rancholabrean) and early Pliocene (Late Hemphillian) Antilocapridae from the Wright Gravel Pits, Nueces County, Texas: New Mexico Museum of Natural History and Science Bulletin 88, p. 197-211.

White, R.S., and Morgan, G.S., 2024, Ice age pronghorn of North America, p. 64-80 in Lindbloom, A.J., Wiechmann, L.M., and Norton, A.S., [eds], Proceedings of the Western States and Provinces 29th Biennial Pronghorn Workshop. South Dakota Game, Fish and Parks, Pierre, South Dakota, USA, 127 pp.

White, R.S., Mead, J.I., and Morgan, G.S., 2025, Logan's austral scrubox, a new ovibovine (Mammalia: Artiodactyla: Bovidae) from Muskox Cave, Eddy County, New Mexico: New Mexico Museum of Natural History and Science Bulletin 101, P. 472

Wilson, R. W., 1942, Preliminary study of the fauna of Rampart Cave, Arizona: Publication of the Carnegie Institution Washington, v. 530, 185 p.

Wolverton, S., 2001, Caves, ursids, and artifacts: A natural trap hypothesis: Journal of Ethnobiology, v. 21, p. 55-72.

Russell W. Graham, Joel A. Christine, Holmes A. Semken, Jr. Taphonomic implication of ontogenetic distributions for field mice (*Peromyscus* SPP.) populations from two debris cone deposits, Parker's Pit, Black Hills, South Dakota, USA. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 137-146. DOI:10.4311/2023PA0114

TAPHONOMIC IMPLICATION OF ONTOGENETIC DISTRIBUTIONS FOR FIELD MICE (*PEROMYSCUS* SPP.) POPULATIONS FROM TWO DEBRIS CONE DEPOSITS, PARKER'S PIT, BLACK HILLS, SOUTH DAKOTA, USA

Russell W. Graham[1,2,C], Joel A. Christine[1,3] and Holmes A. Semken, Jr.[3,4]

ABSTRACT

Fossils accumulate in caves in multiple ways. Each introduces biases that must be understood before interpreting the assemblage. The ontogenetic age distributions of individual specimens of field mice, Peromyscus spp., based on tooth wear, provides insight into taphonomic pathways for two different talus deposits in Parker's Pit, Black Hills, South Dakota. Main Cone accumulated under the modern 12 m vertical pit entrance throughout the Pleistocene and Holocene. The sink hole prohibits escape of randomly selected taxa. Red Cone formed as a talus slope in an old, now closed, entrance with a ramp-like slope that allowed animals to enter and exit the cave.

Differences in ontogenetic age distributions between these two populations are statistically significant. Main Cone individuals show a wider and generally older age distribution than those from Red Cone. The older age distribution results from individuals surviving the vertical fall and living into old age in an essentially predator-free environment. These individuals probably subsisted on organic debris washed into the cave and resident invertebrates as observed in a living population of Peromyscus pectorralis in Longhorn Cavern, central Texas. The Red Cone population is ontogenetically younger, as exhibited by less dental wear, than the Main Cone population but slightly older than living populations studied in Washington, USA, and British Columbia, Canada.

Bone damage indicative of predation by small carnivores, especially weasels (e.g., Mustela frenata) in the Red Cone sample is not apparent in the Main Cone population, reinforcing different taphonomic pathways of the two populations. The Red Cone sample is biased by predator selection. The Main Cone fossil assemblage likely represents a random, local sample of the biota around the cave that facilitates paleoecological analyses. The predator biased Red Cone sample is not amenable to reconstruction of communities but does provide insights into predator-prey interactions and selected species in the vicinity of the cave.

INTRODUCTION

Fossils provide information about the evolution of life, changes in diversity patterns, and insights into past environments and climates, to mention a few. However, the fossil record is not a snapshot of the past because it contains inherent biases that must be understood for correct interpretations. For example, fossils enter caves in a variety of ways that will introduce biases. For pit caves, animals that fall into the cave may not be able to escape. These types of cave deposits provide a relatively random sample of the biota immediately around the sink hole but not necessarily a regional perspective. However, the size of the entrance to a cave does serve as a filter. Small entrances (e.g., Don's Gooseberry Pit, South Dakota – Pardi and Graham, 2017) allows the accumulation of small animals (e.g., insectivores, rodents, lagomorphs, mustelids, etc.) but not large ones, except for fragmentary remains (e.g., isolated teeth, rib fragments, etc.). Larger entrances (e.g., Natural Trap Cave, Wyoming – Martin and Gilbert, 1978; Redman et al. 2023) permit larger animals to be sampled (e.g., mammoths, camels. Horses, etc.) more completely. The depth of a pit cave can also contribute to biases. Shallow pits will only trap animals that cannot climb out of the pit (e.g., turtles, small animals, etc.). As the pit becomes deeper, the trap becomes more effective for additional small as well as medium and larger sized animals (e.g., jack rabbits, coyotes, deer, mammoths, etc.).

Predators may contribute significant numbers of fossils to caves. Owls use caves as roosts and regurgitate pellets containing hair and bone (Andrews 1990). The size of the prey species and their proportions, as well as parts, will depend on the owl or owls that contribute to the deposits (Andrews, 1990). Owls, typically, only forage within a few square kilometers of their roost area. Thus, although prey is transported to the cave, they still represent a relatively local sample but not as localized as those animals falling into a pit.

Larger carnivores can sample larger prey over more extensive catchment areas. For example, the home ranges of foxes (e.g., *Vulpes* spp.), coyotes (*Canis latrans*), and wolves (*Canis lupus*) can vary significantly. However, there may be some overlap in diets for these carnivores. Foxes (e.g., *Vulpes* spp.) generally have smaller home ranges (ca. 0.95

---

[1] Department of Geosciences, The Pennsylvania State University, University Park, PA

[2] Current Affiliation: Department of Geology and Geological Engineering, Colorado School of Mines, Golden, CO and Adjunct Curator, Colorado University Museum, University of Colorado, Boulder, CO

[3] Deceased

[4] Department of Earth and Environmental Sciences, University of Iowa, Iowa City, IA

[C] Corresponding Author: rwg12@psu.edu

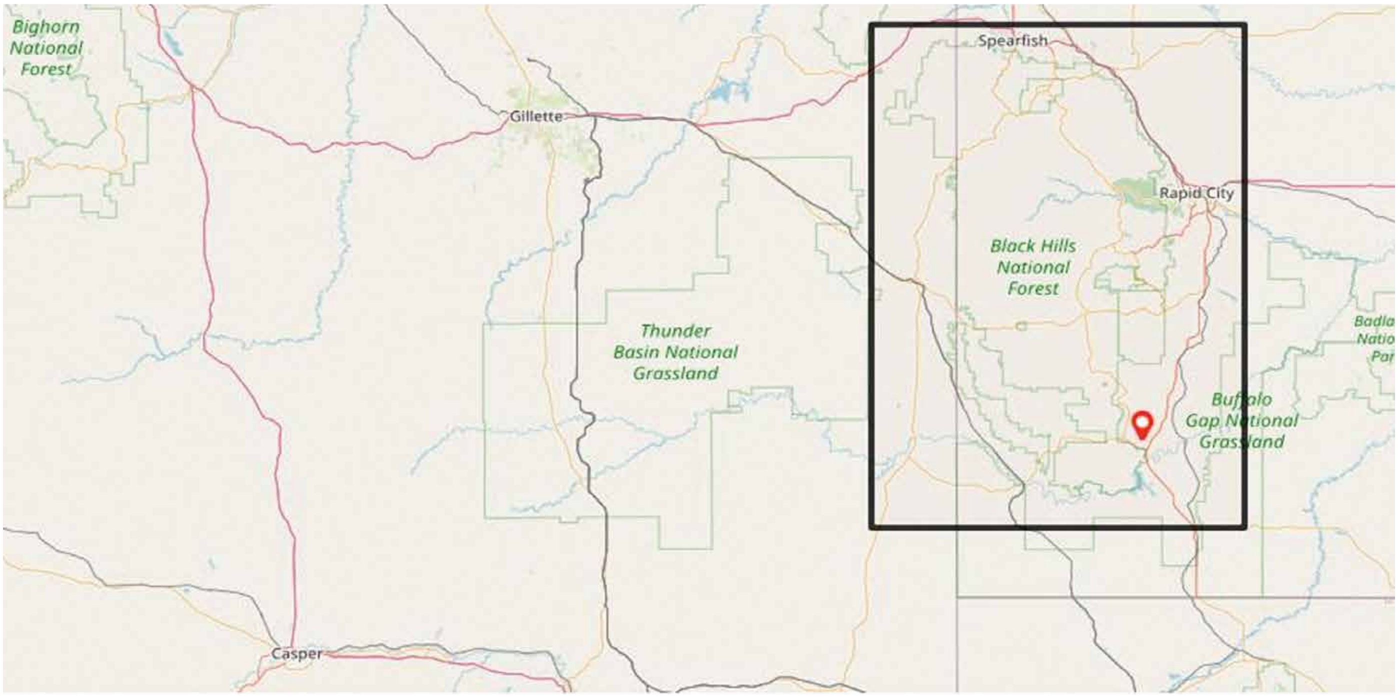


Figure 1. Location of Parker's Pit and Don's Gooseberry Pit (within 30 meters of each other) in the Black Hills (in rectangle, southwestern SD, USA. Longitudinal line in western portion of rectangle is the state line between SD on the right and WY on the left.

km^2 – 44 km$^{2)}$ (Walton et al., 2017), sampling more local environments, and eat smaller mammalian prey (e.g., insectivores, rodents, lagomorphs, small carnivores) (Casteñeda et al., 2022). Coyotes and wolves may range over hundreds to tens of thousands km^2 in their search for prey. Wolves have home ranges between 130 km^2 – 13,000 km^2 (Mech, 1974) and the home ranges of coyotes may range from 5.4 – 39.2 km^2 (Ward et al., 2018). Coyotes' mammalian prey may contain a similar size range as the fox but include some larger items like hares (*Lepus* spp.). Wolves may sample prey as large as deer, caribou, and bison.

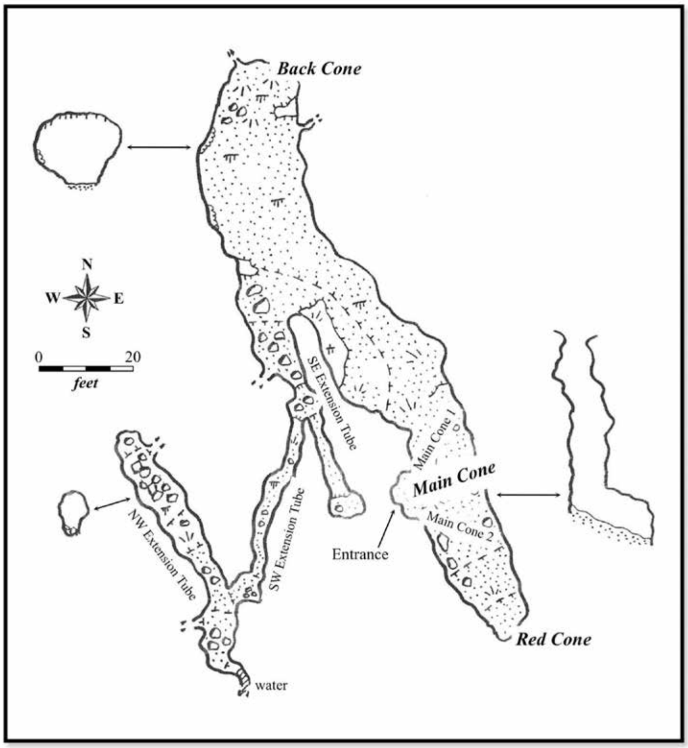


Figure 2. Plan view map of Parker's Pit.

Parker's Pit is a fossiliferous cave in the southeastern section of the Black Hills National Forest, South Dakota. It is located about 16 km north of the town of Hot Springs (Fig. 1). The cave is formed in the Mississippian-aged Pahasapa Limestone (Madison Group) (Petty, 2003). The cave opens just below the top of a northeast-southwest oriented ridge at ca. 1422 m elevation. There is a small intermittent stream below the ridge. The current sink hole entrance is 0.5 m x 1m with a 12 m vertical drop that ends at the top of a large debris cone (Figs. 2 and 3). This cone is referred to as the Main Cone. The cone is composed of stratified deposits of heterogeneous and unsorted angular to sub-rounded limestone rocks (generally smaller than 20 cm in diameter) intermixed with finer grained matrix. The current entrance was also open during the late Pleistocene as well as throughout the Holocene. It served as an effective trap for all animals, including many snakes, that fell into it. Most of the animals from Main Cone are smaller than black-tailed jack rabbits (*Lepus californicus*) that have an average weight of 11-15 kg (Jones et al., 1983) (Table 1).

The Red Cone is about 10 m to the southeast of the base of the Main Cone (Fig. 2). It is a filled former entrance without a surface exposure at present. Red Cone is a stratified talus slope with red to brown gravel to sand-size sediments. Unlike the vertical entrance of the

Table 1. Taxa identified from Parker's Pit.

Red Cone (N=7)	Red Cane	Main Cone
Cryptotis parva	X	
Vulpes velox	*X*	
Mustela spp.	X	
Mustela nigripes	*X*	
Speromphilus sp.	X	
Reithrodontomys sp.	X	
Odocoileus sp.	X	
Red and Main cones (N=15)		
Sorex sp.	X	X
Chiroptera	X	X
Mustela frenata	X	X
Sylvilagus audbonii	X	X
Sylvilagus spp.	X	X
Lepus californicus	*X*	*X*
Tamias minimus	X	X
Tamiasciurus hudsonicus	X	X
Marmota flaviventris	X	X
Thomomys sp.	X	X
Peromyscus spp.	X	X
Neotoma cinerea	X	X
Neotoma sp.	X	X
**Microtus* sp.	X	X
***Microtus* sp.	X	X
Main Cone (N=9)		
Sorex palustrus		X
Sorex arcticus		X
Canis latrans		X
Perognathus sp. (small)		X
Phenacomys intermedius		X
Myodes gapperi		X
Synaptomys cooperi		X
Zapus sp.		X
Bison sp.		X

*Microtus sp. (three closed triangle clade)
**Microtus sp. (5-7 closed triangle clade)

Main Cone, the Red Cone appears to have an acute slope that allowed easy entrance and egress from the cave (Fig. 3). This would have made Red Cone useful for small predators but not an effective trap (Fig. 2). Since the stratified deposits of the Red Cone only contain small animals (e.g., smaller than black-tailed jack rabbits) (Table 1), the entrance was probably quite small.

One of the most abundant animals represented in both cones is the "field mouse" (*Peromyscus* spp.). The respective accumulations of *Peromyscus* spp. remains at each entrance's debris cone provided an opportunity to test for different taphonomic pathways for specimens from a single source. Our hypothesis is that the *Peromyscus* spp. populations at Main and Red cones are different in their ontogenetic age distributions. Red Cone will have predominantly younger individuals because it reflects a predator accumulation, whereas Main Cone will have older mice that were trapped but survived the fall; and consequently, lived in a predator-free environment within the cave.

To this end, we compared the ontogenetic age distributions for individuals of *Peromyscus* spp. from the two different cone deposits. For small mammals like rodents, the durability and distinctiveness of teeth make them a useful, and sometimes preferred, choice for age determinations (Bryant, 1991; Macêdo, et al., 1987; Morris, 1972; de Oliveira, *et al*., 1998; Sheppe, 1963). The null hypothesis in this study was that the two sample populations, Main Cone and Red Cone, would show no significant differences in their age distributions and physical conditions. The alternative hypothesis was that Main Cone and Red Cone would have a statistically significant difference in their respective age distributions, which would reflect differing taphonomic processes. A similar set of null and alternative hypotheses were devised for comparisons between Main and Red cones and the Sheppe's (1963) wear stage data for wild populations of *Peromyscus areas and P. maniculatus*.

In addition, during excavations for fossils in 1957, Holmes A. Semken, Jr. collected data on *Peromyscus pectoralis* populations living inside and outside Longhorn Cavern in central Texas. Although these data (body length, tail length, weight, etc.) are not directly comparable to the other data sets in this study, they do provide insight into how mice can survive in a cave environment for an extended time and reflect an older population that has relevance to the Main Cone *Peromyscus* spp. population.

METHODS

Excavations of both cones were conducted with trowels in 10 cm and 5 cm intervals within natural stratigraphic units that were defined by sediment types and other stratigraphic data (Graham, 2008). A single relative elevation datum was arbitrarily set at 1000 m in the cave. The same datum was used to measure relative elevation of excavation units for both cones. Excavated sediments were placed in individually numbered bags, labeled with cone name, stratum, excavation level, and excavator. Large pieces of rock were removed and discarded in the cave. The bags were then transported to a location for wet screening. Each bag of sediment was weighed before it was processed. Sediments were placed in screens (3-mm mesh) and then sprayed with water to remove the clays, silts and fine sands. Conspicuous jaws and individual teeth were removed from the screen and placed in labeled vials to avoid further damage. The

Table 2: Criteria for identifying relative ages of individual *Peromyscus* using lower jaw molars (modified from Sheppe, 1963; m1 = 1st molar, m2 = 2nd molar, m3 = 3rd molar).

WEAR STAGE	DESCRIPTION OF LOWER MOLAR WEAR
Stage I	m3 not fully erupted and without wear, m1 and m2 without wear
Stage II	m3 fully erupted, m3 without wear or slightly worn, m1 and m2 with very little wear (wear forms narrow bands of dentine linking cuspids, cuspids distinct
Stage III	m3 basined but cuspids still apparent, m1 and m2 worn with dentine band forming lophids between cuspids
Stage IV	all molars basined, cuspids of m3 worn away but re-entrant angles still apparent
Stage V	cuspids and re-entrant angles of m1 and m2 worn away, roots usually protruding beyond the alveoli

residue was then placed on canvas tarps and allowed to dry. Smaller pieces of limestone and chert were examined for signs of human workmanship and then discarded. The dried matrix was collected and placed in resealable plastic bags with interior and exterior labels. These bags were also weighed.

These materials were transported to a field lab where additional specimens were removed from the matrix. These specimens were put in bags or vials that were labeled with all provenience data. All material was transported back to the vertebrate paleontology laboratory at the Pennsylvania State University. Students and other volunteers then picked the matrix for all bones and teeth and these materials were then reunited with specimens previously sorted in the field laboratory. Using synoptic collections and identification keys, Russell Graham and students supervised by him identified teeth, mandibles, maxilla and other identifiable bones to the lowest taxonomic unit possible. These data were then entered into an EXCEL database.

Peromyscus maniculatus and *P. leucopus* both occur in the Black Hills today with *P. maniculatus* being the most abundant and widespread (Turner, 1974). Because these two species are difficult, if not impossible, to identify based upon their dental structure (Semken and Falk, 2014), specific separation was not attempted. The referral of specimens only to genus should not affect our longevity analyses.

Lower jaws of *Peromyscus* spp. with complete molar dentitions were selected at random from both the Main and Red cones. A binocular microscope with adjustable magnification and lighting was used to examine the degree of molar wear of each specimen. To categorize wear, we employed five wear stages used by Sheppe, (1963) who had studied live populations of *P. areas* (N= 274) and *P. maniculatus* (N= 376) from both British Columbia, Canada and the northwestern US. Sheppe's (1963) system had five stages of wear ranging from Stage 1 (essentially no wear on cusps) for the youngest to Stage 5 (cusps on molars obliterated) for the oldest. His system, like other similar systems for rodent age determination, used upper molars. Since fewer upper jaws than mandibles of *Peromyscus* spp. are preserved in Parker's Pit, we applied comparable wear stages to the lower jaws (Table 2). This significantly increased the sample size of specimens analyzed. In cases where the tooth wear appeared to be between two stages, the youngest age stage was selected.

Twenty-three specimens were used from Main cone and another 22 for Red Cone. Specimens were selected from different stratigraphic and elevation levels to get a more representative sample from each cone. All provenience data for each specimen were recorded in an EXCEL file along with the assigned wear stage. Graphing functions from EXCEL were used to compare samples.

Since Sheppe's (1963) samples for his living populations were orders of magnitude larger than our samples from Parker's Pit, we averaged the data for Sheppe's wild populations. The averaged sample's total size was 320.5, much larger than the Parker's Pit samples of 23 (Main Cone) and 22 (Red Cone). To make comparisons easier, we adjusted or "normalized" the averaged Sheppe population by using percentages to create a total closer in size to the average number of individuals (21) from Main and Red cones. A Student's *t*-test was used to evaluate statistical significance. Histograms of age classes permitted easy comparison of age structures for each of the three populations.

For the study of *P. pectoralis* populations in Longhorn Cavern, 10 traps were evenly distributed throughout the cave between the entrance just beyond the twilight zone to the beginning of the Hall of Marble (Semken 1961: Fig. 2) well within the dark zone. All traps were baited with Baby Ruth candy chips. Five additional traps were placed on the surface above the cave. Captured specimens were subdued with ether, uniquely marked for individual identification by toe clipping, weighed, measured, and released. Traps in the cave were checked three times per night, those on the surface in the morning. A flash flood in the cave removed all underground traps and none were recovered. Thus, no study skins or skulls are available. Because only three mice were captured on the surface, additional proxy data were taken from museum specimens collected from Burnet and surrounding counties housed in the Department of Zoology Collection, University of Texas at Austin (now in the Texas Memorial Museum). Standard measurements (weight, body length, tail length, hind foot length and ear length) were taken of the 32 individuals trapped in the cave and compared to measurements of 27 University of Texas Repository specimens that served as proxies for the Longhorn surface sample.

Table 3. A summary of the molar wear stage data from Main Cone, Red Cone and Sheppe's 1963 paper on live Peromyscus populations. The Sheppe data in this table, derived from a study of two different populations, is an average that was "normalized" to a size comparable with Main and Red Cone samples (see text for methods).

SOURCE	STAGE I	STAGE II	STAGE III	STAGE IV	STAGE V	TOTAL
Main Cone	0	5	13	3	2	23
Red Cone	0	8	13	1	0	22
Sheppe Data	1	14	4	2	0	21

RESULTS

In inspecting the results for the Main and Red cone samples, there are both obvious similarities and differences (Figs. 4 and 5; Table 3). Both cones consist primarily of Stage 3 individuals (13 for each site), neither exhibited Stage 1 individuals, and both showed more Stage 2s than either Stage 4 or Stage 5. But Main Cone has only five Stage 2s with three Stage 4s and two Stage 5s. The Red Cone had eight Stage 2s and a single Stage 4 and no Stage 5 individuals. Clearly, the population at Red Cone is younger overall than that at Main Cone.

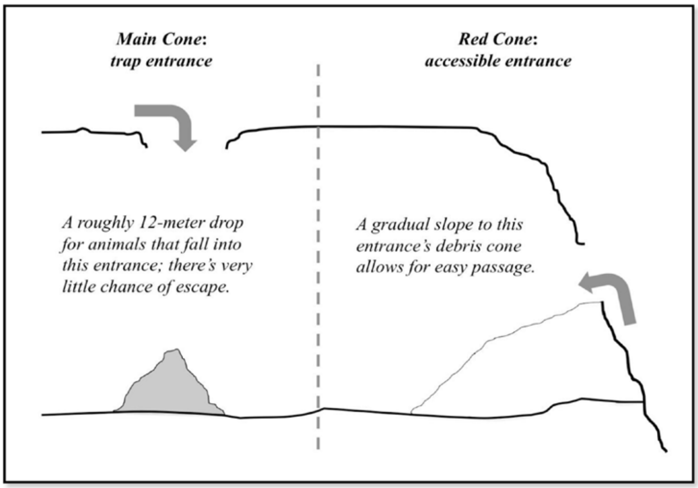


Figure 3. Comparison of cones and entrances to Parker's Pit. The Red Cone is depicted as open but it is currently a sealed entrance without a surface expression.

The averaged wild *Peromyscus* populations from Sheppe's (1963) study show yet another variation in age distribution (Table 3, Figure 6). Red and Main cones have no Stage 1 specimens, whereas, Sheppe's (1963) sample had one. Sheppe's (1963) deer mice populations are composed of younger individuals than Red or Main cone samples with Stage 2 being the most abundant (N=14). Stages 3 and 4 have four and two, respectively and no Stage 5s (this last result is due to a rounding issue in proportionally reducing the sample size). So Sheppe's (1963) deer mice populations were generally younger than those found in either of Parker's Pit cones (Fig. 6).

The Student's- *t* test results showed that all three populations were significantly (at $p < .05$) different than alike in their age distribution patterns (Table 3). The comparison of the Main Cone sample to that of the Red Cone demonstrated to a 95.5% confidence level that they were statistically dissimilar to each other (Table 4). This suggests that they represent either samples from different populations or the results document different processes of accumulation. Likewise, in comparing Main Cone to Sheppe (99.8% confidence level) and Red Cone to Sheppe (91.8% confidence level), the differences in age distribution outweighed the similarities. This result also suggests either difference source populations or different taphonomic processes.

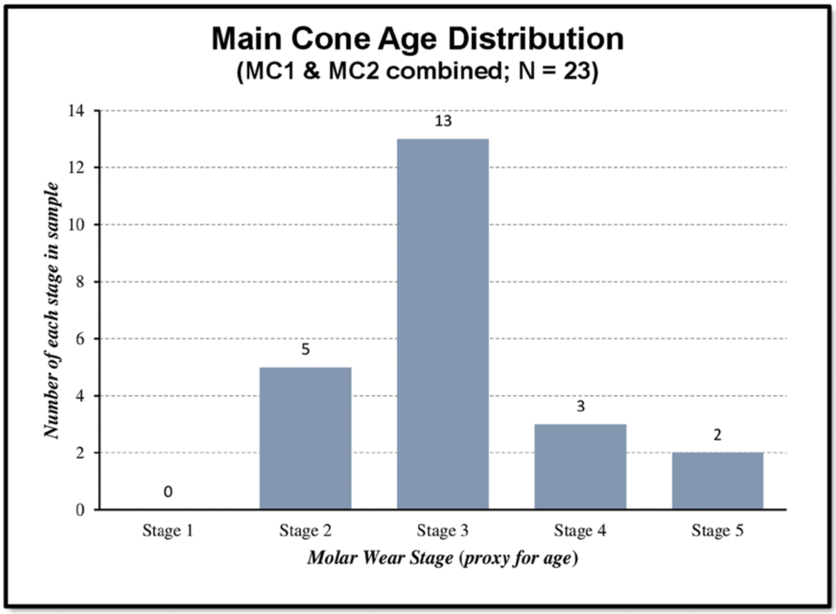


Figure 4. Histogram showing the distribution of the five age categories for *Peromyscus* spp. from Main Cone.

In Longhorn Cavern, only three individuals were captured on the surface over eight trap nights. Although the surface sample above the cave was small, no surface mice were captured inside the cave and no cave mice were documented on the surface. Hence, the cave mice and surface mice populations appear distinct with little, if any, interchange between populations. All traps throughout the cave attracted mice and illustrated that the mice occupied the entire cave system. Mice were usually captured in the same or juxtaposed traps. As a commercial cave, Longhorn Cavern had a food concession area. Although the presence of food in the concession area could have served as a resource for the cave mice, it was clear that the distribution of cave mice was independent of the concession area because the mice inhabited the entire cave. Furthermore, no concession food was left in the cave overnight. Mice living in the cave probably were feeding on cave crickets that are abundant in the cave.

Table 4: A summary of the Student's *t*-test results for the Main Cone (MC), Red Cone (RC) and the "normalized" Sheppe data, showing confidence levels.

PAIRS TESTED	NULL REJECTED	CONFIDENCE LEVEL
MC vs RC	YES	95.5%
MC vs Sheppe Data	YES	99.8%
RC vs Sheppe Data	YES	91.3%

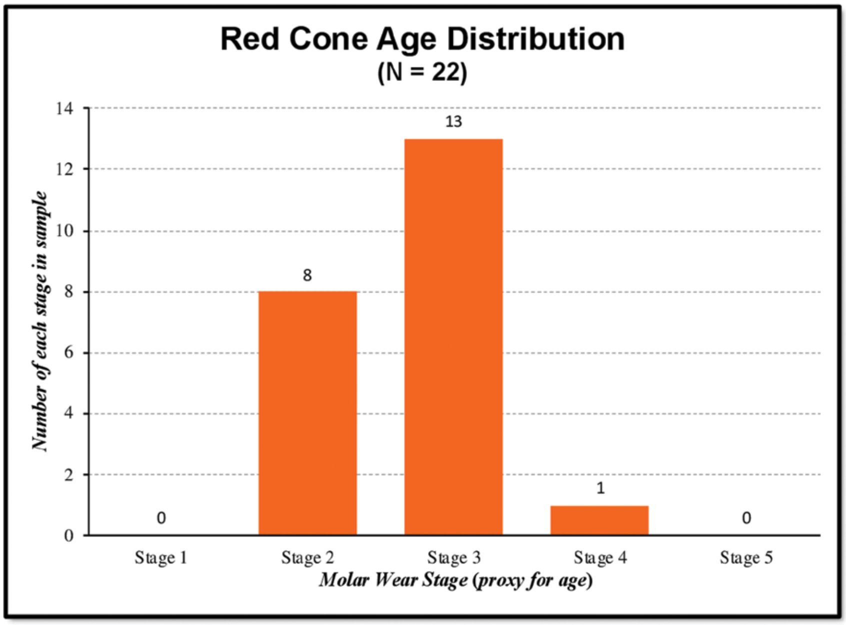


Figure 5. Histogram showing the distribution of the five age categories for *Peromyscus* spp. from Red Cone.

Data comparisons verified that the mice living in the cave were larger than those living on the surface (Fig. 7). Although there was broad overlap in all the measurements for the two populations, body weight was the most significant. All measurements showed a trend in larger size for the population that lived in the cave (Fig. 7). Because the specimens were lost when Longhorn Cavern flooded, skins and skulls were not collected and dental wear could not be documented.

DISCUSSION

At Parker's Pit there are no Stage 1 individuals recovered from either entrance's debris cone. In Sheppe's (1963) study populations, he found that Stage 1 mice were never very abundant. These observations are not surprising. They can be explained by the prolonged time for young deer mice to stay in their mother's nest as they develop physical skills before setting up in a territory of their own (Vestal, et al., 1980; Lyman et al., 2001). The presence of this "training period" in their early days would tend to exclude these mice from being caught by traps and most accumulation processes.

The Main Cone sample of *Peromyscus* spp. should represent individuals that randomly fall into the pit. Based on research into small animals recovered from natural pitfall traps, it has been shown that the older individuals tend not to fall in as often, perhaps due their greater experience (Andrews, 1990). Therefore, the presence of older deer mice in Main Cone seems somewhat enigmatic with regards to a standard pit trap sample. However, once the entire process of entrapment is understood (i.e., mice living in the cave), the older ages of individuals is explained.

Peromyscus is a relatively small rodent (in Colorado *P. leucopus* ranges from 20-36 grams and *P. maniculatus* is from 14-27 grams – Fitzgerald et al.,1994). Therefore, as noted in the quote by Haldane (1926) at the beginning of this paper, the terminal velocity of a mouse (i.e., *Peromyscus* spp.) is low, so it could survive a fall of 12 m. Voles, for instance, have been observed living on the floor of a 30 m shaft in Britain (Andrews, 1990). Blaine Schubert (personal communication) has also documented living *Peromyscus* individuals in Natural Trap Cave that has a vertical fall of about 30 m. Furthermore, abundant organic debris washes into Parker's Pit regularly. Since *Peromyscus* is omnivorous, able to eat a variety of plant and animal materials (Reid, 2006), the organic debris could provide adequate food for the trapped individuals after they had survived their fall. Finally, since the mice cannot escape and there are not any predators in the cave, the trapped individuals can live until they die naturally. Hence, the trapped population would tend to be composed of older individuals.

These data are consistent with a study of mice living inside and outside of Longhorn Cavern conducted by Holmes A. Semken, Jr. in 1957. His study documented that the mice could survive in the dark zone of the cave and that there was

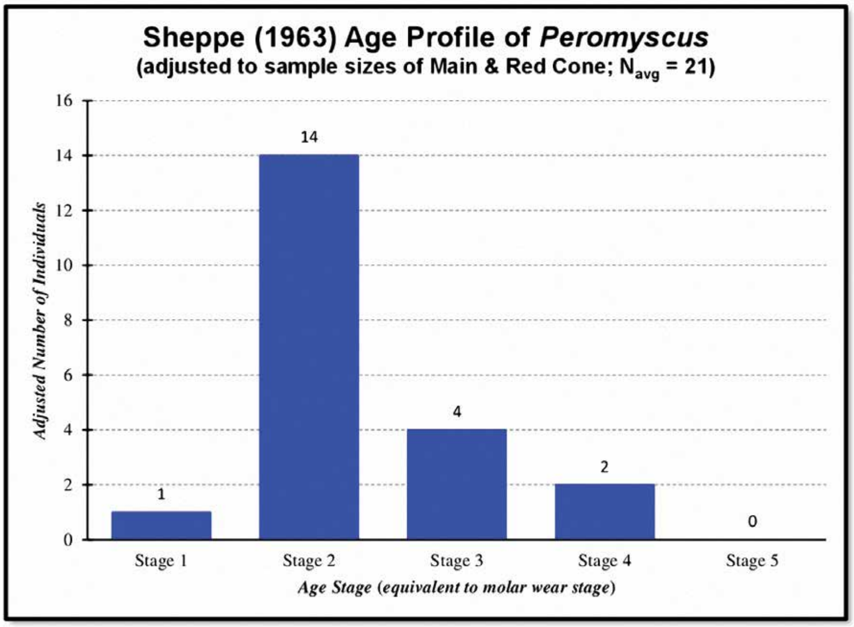


Figure 6. Histogram showing the distribution of the five "normalized" age categories for *Peromyscus* sp. from Sheppe's (1963) study.

little, if any, interchange with the surface population. Furthermore, the larger body size of the cave population in comparison to the surface population is attributed to lack of predation, as was older age for the Main Cone population in Parker's Pit. Unfortunately, as noted before, it was not possible to conduct age studies based on tooth wear on the Longhorn Cavern population.

Semken and Falk (2014:255) found a preponderance of aged *Peromyscus* ("completely worn dentitions") preserved in late Holocene earth lodges in North Dakota. They interpreted this older population as indicating "… that the village supported a resident population of *Peromyscus* that was enabled by a stable food supply and a reduced chance of predation." Main Cone represents a similar situation. Likewise, Romaniuk et al. (2016) found that the age distributions between voles (*Microtus arvalis*) and wood mice (*Apodemus sylvaticus*), the European vicar for *Peromyscus*, were significantly older in ontogenetic age distributions from excavations of Neolithic village sites on Orkney Islands, Scotland than in living populations. The Neolithic vole population was decidedly younger than that of the associated wood mice. Romanuik et al. (2016) felt that voles preferred open habitats to human habitations, whereas door mice are frequently commensal in human structures. Therefore, like the *Peromyscus* from North Dakota villages and Main Cone, the Orkney door mice are indicative of protected and predator-free environments.

The age distribution for the Red Cone population of *Peromyscus* is significantly different from either the Main Cone or surface populations studied by Sheppe (1963). Red Cone has but 1 mouse older than Stage 3 versus 5 in the Main Cone sample. The age distribution of *Peromyscus* from Red Cone is significantly younger than the population from Main Cone (Table 3). Furthermore, the Red Cone population is significantly older than the samples of *Peromyscus* studied by Sheppe (1963) that were derived from living populations from the surface.

One of the primary causes of mortality in small mammal populations is predation, which is also a major source for small mammal bone accumulations in caves (Andrews, 1990). Studies have revealed that predators can be selective for a particular prey type (e.g., Andrews, 1990; Brain, 1981; Lyman and Power, 2001; Mushtaq-ul-Hassan, *et al*., 2007) as well as age group. Different predators will exhibit different preferences or "tastes" in their prey choices. Thus, accumulations of bones by predators will reflect their preferences (Korth, 1979) more than the composite biological community living around the cave. A predator's success can depend upon the age, and thus, the experience level of

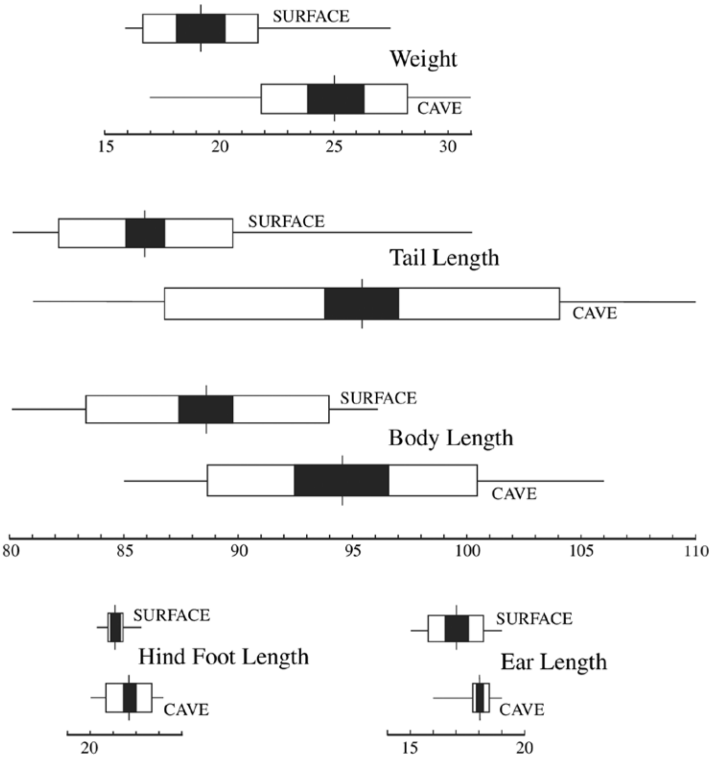


Figure 7. Summary statistics for measurements of *Peromyscus pectoralis* that lived inside Longhorn Cavern in comparison to P. pectoralis from the University of Texas Department of Zoology repository that served as a proxy for the surface population at Longhorn Cavern. Lengths are in millimeters and weight is in grams. The vertical line is the mean, the black box is one standard deviation, and the white box is two. The central horizontal line is the range.

its target prey. This age preference can show up in the remains left behind (Bryant, 1991; Lyman and Power., 2001), and can be detected by examination of the ontogenetic age of the animal remains (Lyman and Power, 2001; Morris, 1972). Because of predator selection, any small mammal accumulation found in the fossil record should be considered a possible predator accumulation until it has been demonstrated to be otherwise (Andrews, 1990).

Red Cone, which had a small ramp-like entrance into Parker's Pit, would have allowed a variety of differently sized animals to enter and leave at will. In other words, it was not a trap. It would have been easy for deer mice to come and go, but not likely that they would choose to live in the cave where resources were limited, unless they were trapped. Hence, it is unlikely that the *Peromyscus* in Red Cone represent a resident population in the cave. Thus, it is more probable that the *Peromyscus* found at Red Cone are the result of predators using the cave as a den. Predators actively prey on *Peromyscus*, catching almost exclusively the less experienced younger individuals. The result would be a selectively produced accumulation of *Peromyscus* remains in the debris pile at Red Cone, uniquely biased in the selection of prey and the ages of individuals based upon the preferences and abilities of the predator.

Many animals (small to medium mammal carnivores, owls and other raptors, as well as snakes) prey on *Peromyscus*. Snakes can be eliminated as the primary predator for the Red Cone accumulation since none of the *Peromyscus* bones exhibit extensive erosion and pitting characteristic of bones from a serpentine's digestive system (Doherty, 2009), if they even survive the digestive process (Secor, 2009). The restricted nature of the entrance for the Red Cone is not conducive to raptor access. Furthermore, raptors also leave diagnostic damage patterns on bones (Andrews, 1990; McGuire et al., 2023), none of which have been observed on specimens from Red Cone. To this end, small mammal carnivores are most likely the source of the Red Cone *Peromyscus*.

Weasels (*Mustela* spp.), especially the long-tailed weasel (*Mustela frenata*), are generalist predators on rodents and smaller lagomorphs (King, 1990). Weasels have been referred to as "hair-trigger mouse traps with teeth." (King,1990: 4). At least two species of weasels are relatively abundant in Red Cone (Table 1). Weasel remains are rare in Main Cone. The weasels from Red Cone can be divided into two groups based on size. There is a small weasel that could be *M. erminea* and/or *M. nivalis*. The other weasel is significantly larger and can be assigned to *M. frenata* unequivocally (Sheffield and Thomas, 1997) and it is the most common weasel in Red Cone. The tubular shape of weasels allows them to navigate small narrow passages like the entrance to Red Cone.

Several *Peromyscus* skulls from Red Cone exhibit small puncture marks, which is the strongest evidence for predation. The size of these punctures is consistent with the morphology of the canine of *M. frenata*. While trapping small mammals in Laguna Bélgica Educational Park, Chiapas, Mexico, Vaca-Leon et al. (2019) captured one male *M. frenata* along with a dead Mexican deer mouse (*Peromyscus mexicanus*) in the same trap. The *Peromyscus* had incision marks on the skull indicative of capture by the weasel. Therefore, it is most likely that a large part of the *Peromyscus* accumulation in Red Cone has been derived by predation of *M. frenata*.

Micromammal bones that pass through small mustelids and felids are generally fragmented and consist of largely unidentifiable bone flakes (Andrews and Evans, 1983; Mellet, 1974). There are lots of unidentifiable bone fragments of small mammals from both cones in Parker's Pit. Some of this damage may be due to mustelid predation but there is also fragmentation by trampling, sediment compaction, transport, etc. Many of the *Peromyscus* mandibles from Red Cone are complete. These mandibles and the numerous other complete bones could result from forgotten food caches that weasels are known to create (King, 1990: 83-84). As King (1990:83) states, "A typical [weasel] cache would contain 40-50 freshly killed mice with the typical puncture marks of the weasel's teeth in the neck."

According to Korth, (1979:249) any coprocoenosis from both avian and mammalian carnivores "… should give a relatively close approximation to the living population of mammals. From the descriptions of fecal and pellet material… it should be possible to determine if a single type of predator or a combination of predators has contributed to an assemblage" Finally, the difference in age distributions between Red Cone and Sheppe's (1963) modern samples strongly suggest that the predator also has a proclivity for mice of a particular age. Sheppe's (1963) samples were significantly younger than the Red Cone population (Table 3) and much younger than that of the Main Cone. One possibility for this difference is that dispersing individuals are more vulnerable to predation than resident individuals (Jamison, 1975). The difference between Sheppe's (1963) sample and Red Cone may, therefore, indicate that mice need to reach a certain age before they disperse and are captured by predators.

CONCLUSION

Parker's Pit has two different fossiliferous debris cone deposits. Main Cone is at the bottom of the 12 m modern vertical shaft with an entrance 0.5 m in circumference. Red Cone is a closed, small entrance with a ramp-like approach into the cave. That the taphonomy of these cones varied is documented by different ontogenetic age structures for their fossil samples of *Peromyscus* spp. Mice from the Main Cone are significantly ontogenetically older than those from the Red Cone. It appears that after falling, mice in Main Cone survived and were able to live in a predator-free environment feeding on organic material that washed into the cave. These mice died of natural causes as older individuals.

On the other hand, the ontogenetically younger *Peromyscus* sample from the Red Cone were victims of predation presumably by the long-tailed weasel (*M.* f*renata*). Evidence of predation is suggested by puncture marks the size of canines of *M.* f*renata* on some *Peromyscus* skulls. In addition, observations of predator induced modification on some other *Peromyscus* bones are consistent with the damage documented on bones that have been fed upon by predators: tooth marks, bone removal and exposure to stomach acid while passing through a predator's digestive tract (Andrews, 1990). Also, the Red Cone population is older than the populations of living *Peromyscus* monitored by Sheppe (1963) in the Pacific northwest. The very young mice are missing, presumably because they were nursing or still developing in their nest. Furthermore, the lack of very young mice may result from the fact that transient mice composed of slightly older individuals are more vulnerable to predation than are resident mice (Jamison, 1975). Mice may need to reach a certain age before they are able to disperse.

The differing ontogenetic age structures and taphonomic pathways for the Main and Red cones has significant implications for interpretations of fossil remains from these deposits. The older age structure of the Main Cone population suggests that *Peromyscus,* as well as other faunal components, fell into the pit and could not get out. Also, animals are more randomly selected by pit traps than in other cave entrances. Therefore, the Main Cone fossil record is more representative of the community surrounding the cave and can be used for paleoecological analyses, assuming other taphonomic signals are not red flags for different biases. On the other hand, the Red Cone was not an effective trap because animals could enter and leave at will unless they were brought into the cave dead or severely injured. In addition, predators can be very selective with regards to their choice of prey and their age. Hence, Red Cone deposits have a strong bias and do not effectively represent the relative abundance of species in communities around the cave and are less useful for paleoecological interpretations, especially where the faunal list is limited. However, they do provide a good record for predator-prey interactions.

ACKNOWLEDGEMENTS

This paper is dedicated to Joel Christine who left us way too early! We thank the Hells Canyon branch of the U.S. Forest Service, U. S. Department of Agriculture, for permission to excavate Parker's Pit and their extensive support for the project. The Western Interior Paleontological Society (WIPS) provided monetary support, as well as loans of equipment and numerous volunteers who helped with the excavation and processing of the Parker's Pit local fauna. We also thank the numerous PSU undergraduate and graduate students who helped with the Parker's Pit Project. The Illinois State Museum provided funds, equipment, and volunteers, as well. We are especially indebted to Eric C. Grimm who was the co-director of the Parker's Pit project and the one who initiated the project. Peter Wilf at PSU assisted with photographing specimens. HAS thanks W. Frank Blair and Robert K. Selander (both now deceased), Department of Zoology, University of Texas, for inspiration regarding the Longhorn Cavern study. RWG thanks Jim Mead and Sharon Weaver for an invitation to participate in a National Speleological Society Symposium on cave paleontology at which an earlier version of this paper was presented. The research for this paper was started by Joel Christine as part of his Senior Thesis in the Department of Geosciences at the Pennsylvania State University. We alone are responsible for any errors.

REFERENCES

Andrews, P., 1990. Owls, Caves and Fossils: University of Chicago Press, Chicago. 231 p.

Andrews, P. and Evans, E. M. N. 1983. Small mammal bone accumulations produced by mammalian carnivores: Paleobiology, v. 9, no. 3, p. 289-307.

Brain, C. K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy: University of Chicago Press, Chicago. 365 p.

Bryant, J. D., 1991. Age-frequency profiles of micromammals and population dynamics of *Proheteromys floridanus* (Rodentia) from the early Miocene Thomas Farm site, Florida (USA): Palaeogeography, Palaeoclimate, Palaeoecology, v. 85, p. 1– 14.

Castañeda, I., Doherty T., Fleming, P., Stobo-Wilson, A., Woinarski, C. and Newsome, T.M., 2022. Variation in red fox *Vulpes vulpes* diet in five continents: Mammal Review: v. 52, p. 322-342.

Doherty, J. M., 2009. Comparison of digestion through examination of fecal contents over differing feeding regimens in *Elaphe guttata, Elaphe obsoleta*, and *Chelydra serpentina*. Unpublished Master's Thesis, University of Colorado, Boulder.

Fitzgerald, J. P., Meaney, C. A. and Armstrong, D. M., 1994. Mammals of Colorado: Denver Museum of Natural History and University Press of Colorado, Denver. 467 p.

Graham, R. W., 2008. Report on Excavations at Parker's Pit (Rainbow Cave) and Don's Gooseberry Pit in the Black Hills National Forest, Black Hills of South Dakota, August 2006 and August 2007: submitted in partial fulfillment of Permits CEM 292 and CEM 312: University Park, Pennsylvania State University, 18 p.

Haldane, J.S.B., 1926. On Being the Right Size: Harper's Magazine, 1926.

Jamison, V. C., 1975. Relative susceptibility of resident and transient *Peromyscus* subjected to weasel predation: Graduate Student Theses, Dissertations, & Professional Papers. 6759, 43 p. https://scholarworks.umt.edu/etd/6759

Jones, J. K., Jr., Armstrong, D. M., Hoffmann, R. S. and Jones, C., 1983. Mammals of the Northern Great Plains: University of Nebraska Press, Lincoln. 379 p.

King, C., 1990. The Natural History of Weasels and Stoats: Comstock Publishing Associates Cornell University Press, Ithaca. 253 p.

Korth, W. W., 1979. Taphonomy of microvertebrate fossil assemblages: Annals of Carnegie Museum, v. 48, no. 15, p.235-285.

Lyman, R. L. and Power, E., 2001. Ontogeny of deer mice (*Peromyscus maniculatus*) and montane voles (*Microtus montanus*) as owl prey: The American Midland Naturalist, 146:1, p. 72–79.

Macêdo, R. H. and Mares, M. R., 1987. Geographic variation in the South American cricetine rodent *Bolomys lasiurus*: Journal of Mammalogy. 68, no. 3, p. 578– 594.

Martin, L. D. and Gilbert, M. B., 1978. Excavations at Natural Trap Cave: Transactions of the Nebraska Academy of Sciences and Affiliated Societies, v. 336, p. 107-116.

McGuire, J. L., Woodruff, A., Iacano, J., Sethran, J. M., Schap, J. A., Redman, C. M., and Meachen, J. A., 2023. Evaluating the taphonomic consistency of microvertebrate assemblages at Natural Trap Cave, Wyoming, USA. Quaternary International, v. 647-648, p. 63-70.

Mech, D., 1974. *Canis lupus*: Mammalian Species: v. 37. p. 1-6.

Mellett, J. S., 1974. Scatological origins of microvertebrate fossil assemblages. Science 185 149-150.

Morris, P. A., 1972. A review of mammalian age determination methods: Mammal Review, v. 2, no. 3, p. 69–104.

Mushtaq-ul-Hassan, M., Ghazi, R. R. and Nisa, N. U., 2007. Food preference of the short-eared owl (*Asio flammeus*) and barn wl (*Tyto alba*) at Usta Muhammad, Baluchistan, Pakistan: Turkish Journal of Zoology, v. 31, p. 91–94.

de Oliveira, J. A., Strauss, R. E. and dos Reis, S. F., 1998. Assessing relative age and age structure in natural populations of *Bolomys lasiurus* (Rodentia: Sigmodontinae) in Northeastern Brazil: Journal of Mammalogy: v. 79, p. 1170–1183.

Pardi, M. and Graham, R. W., 2017. Time averaging and late Quaternary ecological replacement in Don's Gooseberry Pit, South Dakota, USA: Quaternary Research, v. 89, p. 307-317.

Petty, D. M. 2003. Sequence stratigraphy of the Pahasapa Formation (Madison Group) in the northeastern Black Hills: Insights from Regional Correlations: Mountain Geologist, v. 40, p. 19-34.

Redman, C. M., Moore, J. R., Lovelace, D.M., and Meachen, J. A., 2023. The rank abundance distribution of large-bodied vertebrates from Natural Trap Cave, Wyoming, Quaternary International, v. 647-648, p. 42-52.

Reid, F., 2006. Mammals of North America, 4th edition: New York, Houghton Mifflin Company, 579 p.

Romaniuk, A. A., Shepherd, A. N., Clarke, D. V., Sheridan, A. J., Fraser, S., Bartosiewicz, L., and Herman, J. S., 2016. Rodents: food or pests in Neolithic Orkney: Royal Society Open Science, 3: 160514. http://dx.doi.org/10.1098/rsos.160514

Secor, S. M., 2003. Gastric function and its contribution to the postprandial metabolic response of the Burmese python *Python molurus.* Journal of Experimental Biology: v. 206, p. 1621-1630.

Semken, H. A., 1961. Fossil vertebrates from Longhorn Cavern, Burnet County, Texas, Texas Journal of Science: v. 13, p. 290-310.

Semken, H. A., Jr. and Falk, C., 2014. Ecology and environmental degradation of two Little Ice Age villages in North Dakota: the micromammal evidence: Wisconsin Archaeologist: v. 95, p. 249-268.

Sheffield, S. R. and Thomas, H. H., 1997. *Mustela frenata*: Mammalian Species: No. 70. p. 1-9.

Sheppe, W. A., 1963. Population structure of the deer mouse, *Peromyscus*, in the Pacific Northwest: Journal of Mammalogy: v. 44, no. 2, p. 180–185.

Turner, R. L., 1974. Mammals of the Black Hills of South Dakota and Wyoming: University of Kansas, Lawrence. 178 p.

Vaca-Leon, O. I., Arellano, E. and Lopez-Medellín, X., 2019. Predation of the Mexican deer mouse (*Peromyscus mexicanus*) by long-tailed weasel (*Mustela frenata)* in Laguna Bélgica Educational Park, Ocozocoautla de Espinosa, Chiapas: Western North American Naturalist, v. 79, no. 4, p. 593-596.

Vestal, B. M., Coleman, W. C., Chu., P. R., 1980. Age of first leaving the nest in two species of deer mice (*Peromyscus*): Journal of Mammalogy: v. 61, no. 1, p. 143–146.

Walton, Z., Samelius, G., Odden, M. and Willebrand, T., 2017. Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration: PLOS One. https://doi.org/10.1371/journal.pone.0175291.

Ward, J., Hinton, J., Johannsen, K., Korlin, M., Miller, K. and Chamberlain, M., 2018. Home range size, vegetation density, and season influences prey use by coyotes (*Canis latrans*): PLOS One. https://doi.org/10.1371/journal.pone.0203703.

Nicholas J. Czaplewski, Jim I. Mead, and William D. Peachey. Late pleistocene vertebrate fauna and bat guano deposit of LA Tetera Cave, Arizona, USA. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 147-174. DOI:10.4311/2023PA0115

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

Nicholas J. Czaplewski[1C], Jim I. Mead[2], and William D. Peachey[3]

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

---

[1]Oklahoma Museum of Natural History, 2401 Chautauqua Avenue, University of Oklahoma, Norman, OK 73072, USA.
[2]The Mammoth Site, Hot Springs, SD 57747, USA.
[3]3331-B E. Flower St., Tucson, AZ USA.
[C]Corresponding author: nczaplewski2@gmail.com

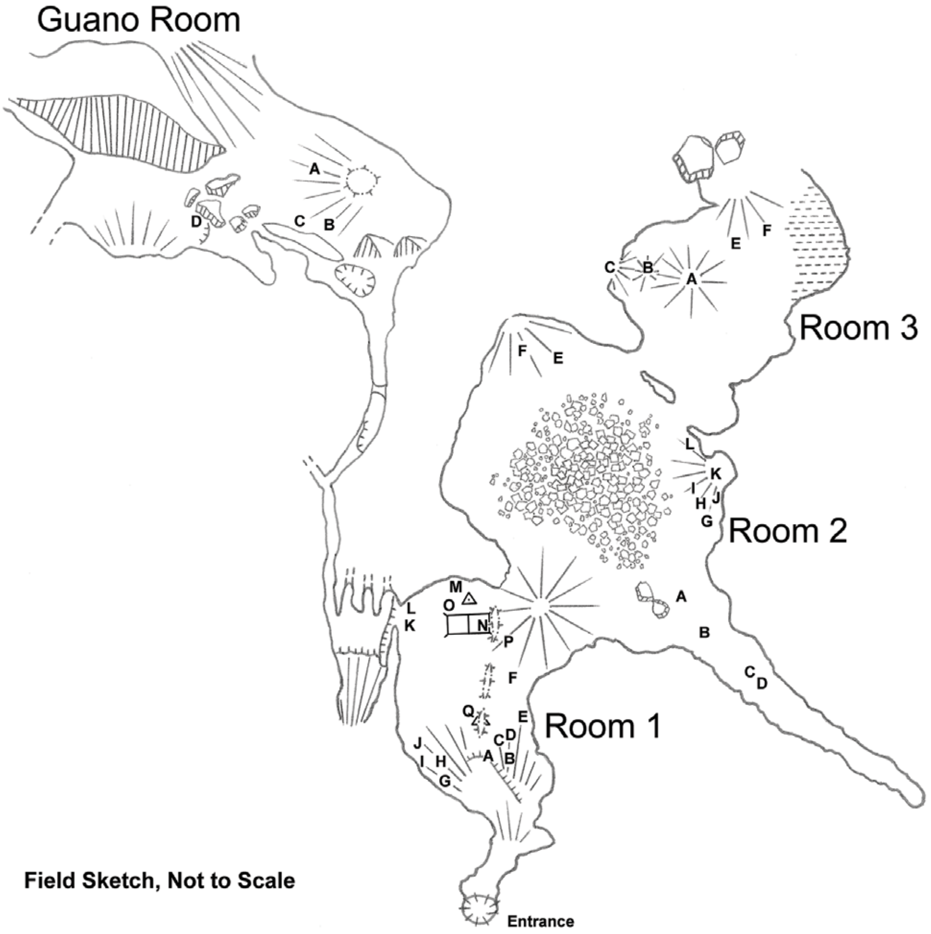


Figure 1. Preliminary plan map of La Tetera Cave, Colossal Cave Mountain Park, Pima County, Arizona, with locations of vertebrate fossils indicated by letters (keyed to museum catalog numbers in taxonomic accounts and Table 1). In Room 1 where the Camelops pelvis occurred at the surface (Room 1 bone 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*.

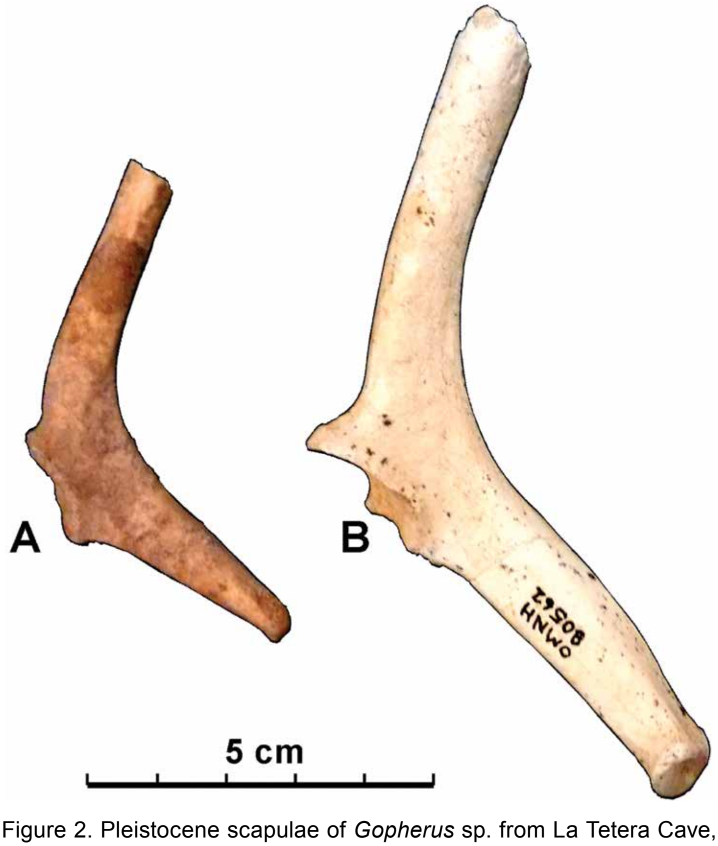


Figure 2. Pleistocene scapulae of *Gopherus* sp. from La Tetera Cave, Arizona in anteromedial view. A, OMNH 80565, B, OMNH 80562.

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.

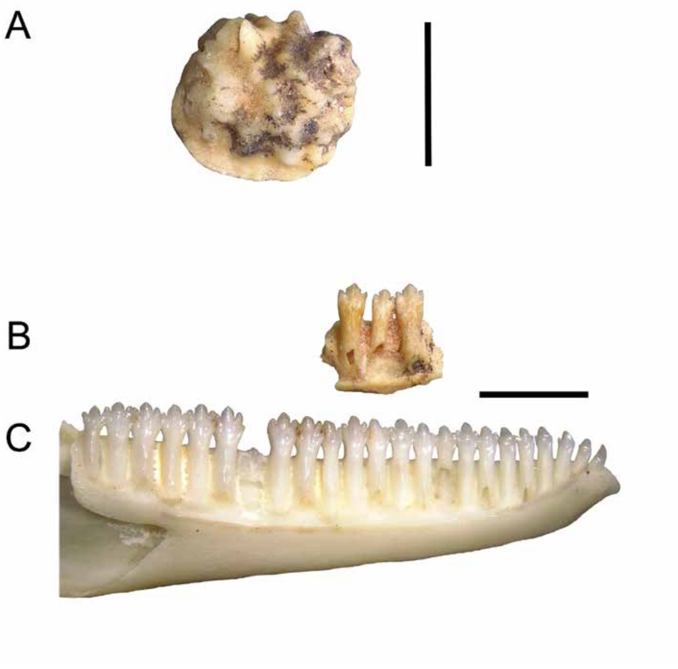


Figure 3. Pleistocene squamates from La Tetera Cave, southern Arizona. A, OMNH 80515, fossil osteoderm of *Heloderma*, dorsal view. B, OMNH 80593, fragment of fossil dentary of *Dipsosaurus*, lingual view. C, modern complete dentary of *Dipsosaurus* for comparison, lingual view. Scale bars 2 mm.

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).

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.

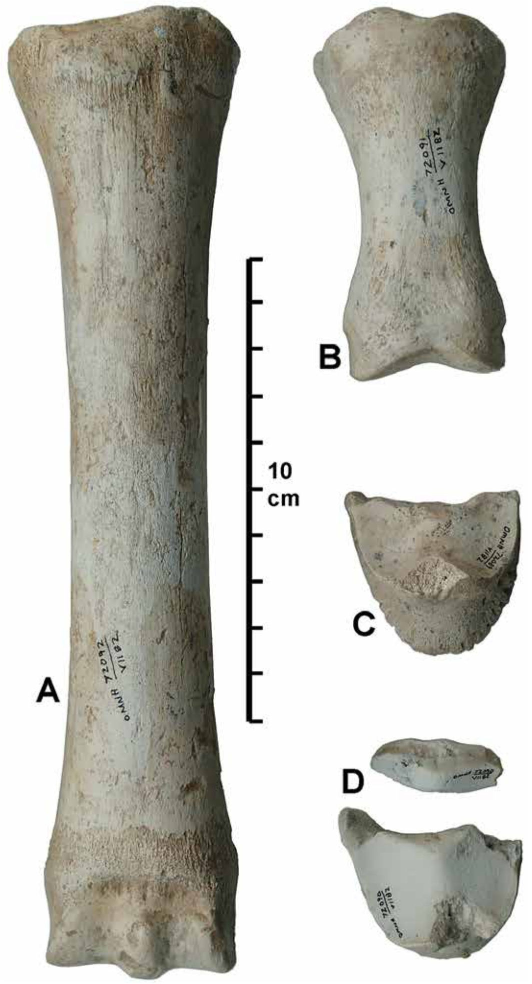


Figure 4. Pleistocene remains of *Equus conversidens* from La Tetera Cave, Arizona. A, OMNH 72092, left metacarpal III in anterior view; B, OMNH 72091, digit III phalanx 1 in anterior view; C, OMNH 72089, digit III ungual phalanx in anterodorsal view; D, OMNH 72090, digit III ungual phalanx and sesamoid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

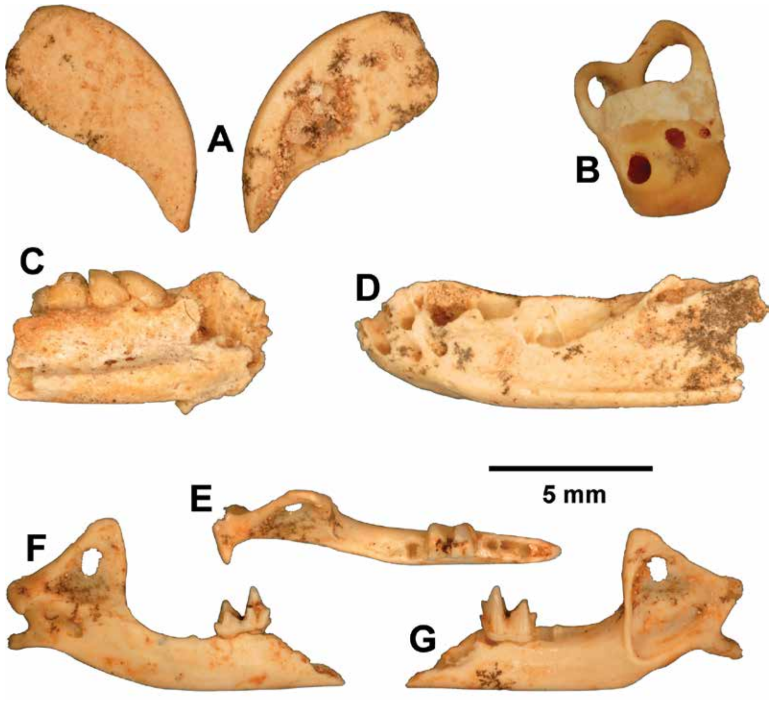


Figure 5. Craniodental remains of fossil bats from La Tetera Cave, Arizona. *Desmodus stocki* teeth, jaws, and petrosal: A, OMNH 72113, right I1 in labial and lingual views; B, OMNH 72117, right petrosal in lateral view; C, OMNH 72207, right dentary with p4-m2 in labial view; D, OMNH 72209, left edentulous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

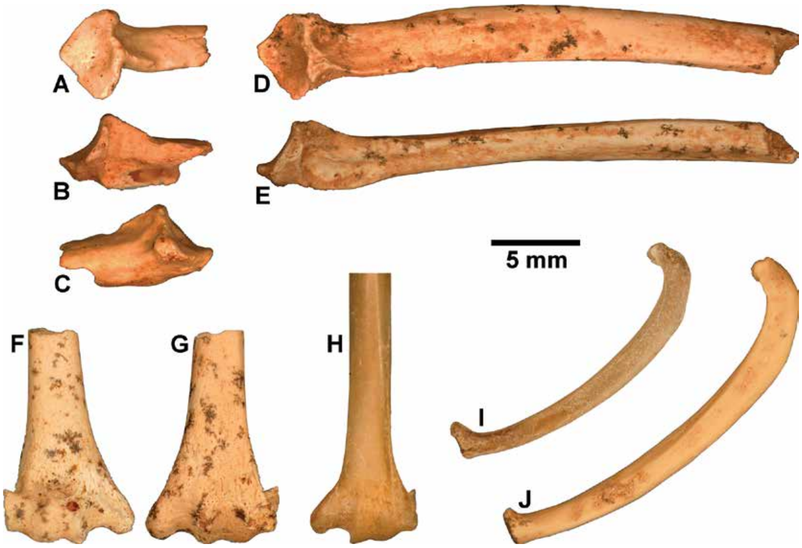


Figure 6. Postcranial fossils of *Desmodus stocki* from La Tetera Cave, Arizona, and modern comparative specimen of *Desmodus rotundus* from Sonora, Mexico. A-C, *Desmodus stocki* proximal left radius fragment (OMNH 72174) in anterior (A), medial (B), and lateral (C) views. D-E, *Desmodus stocki* proximal 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

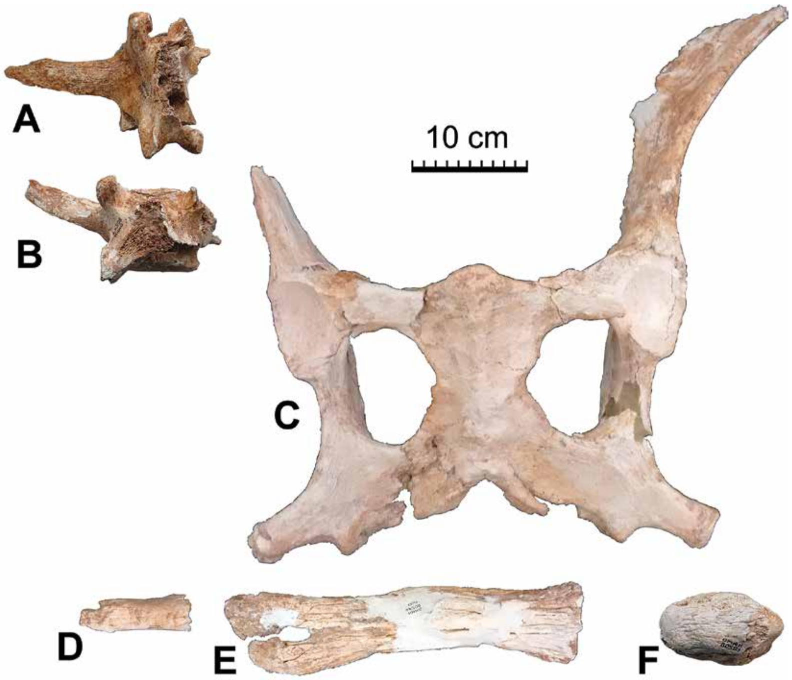


Figure 7. Pleistocene remains of *Camelops hesternus* recovered from La Tetera Cave, Arizona. A, B, OMNH 80549, two partial lumbar vertebrae in dorsal view; C, OMNH 72383, partial pelvis in dorsal view; D, OMNH 80547, proximal phalanx shaft in anterior view; E, OMNH 80546, left metatarsal in anterior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

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.

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.

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-

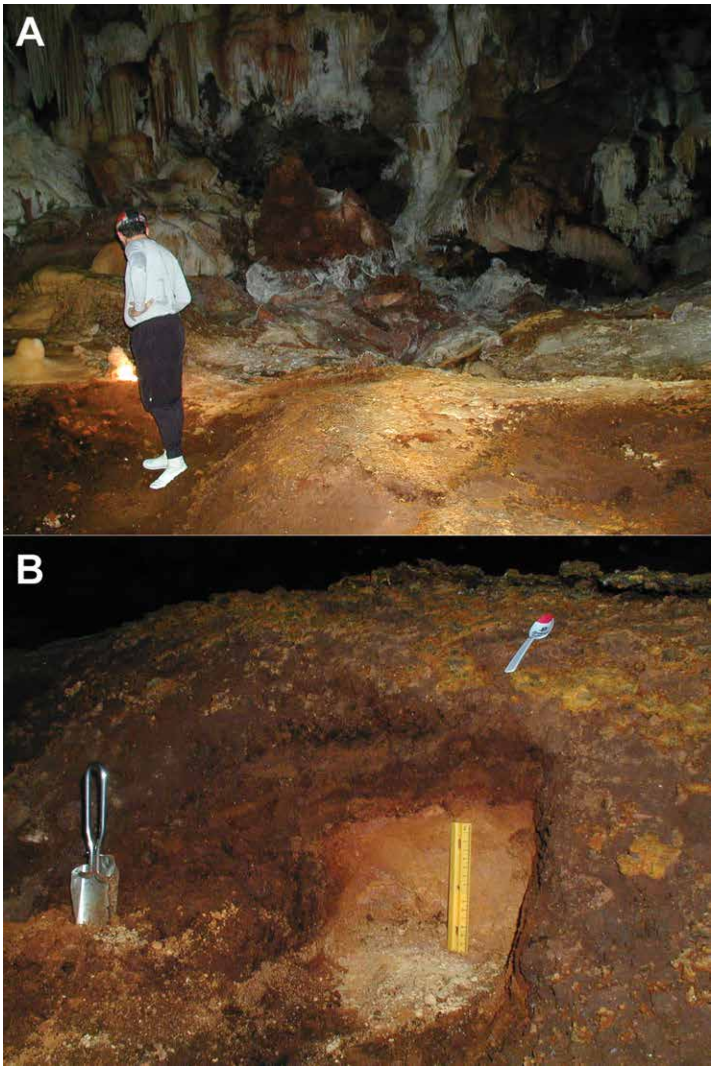


Figure 9. A, Caver and volunteer Steve Smith inspects the guano deposit in La Tetera Cave presumably attributable to *Desmodus stocki*. B, A small trench dug into an edge of the guano deposit from which a bulk sample provided the radioisotopic date for the deposit. Ruler in B is 15 cm long.

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).

ACKNOWLEDGMENTS

We thank Dave Arrand, Tom Bethard, Brett Cook, Jim Fink, Randy Gruss, Robert Pape, Esty Pape, Steve L. Smith, Tom Strong, Gene Wendt for help in field work, and Kyle Davies and Joe Baalke for preparing specimens. Bill May kindly picked and sorted specimens from screenwashed matrix. We deeply thank the O'odham people, traditional custodians of this land, for caretaking it for so many generations and for their ecological knowledge of the desert and mountains; may they once again interact with it as their own. We express our gratitude to John Madsen of the Arizona State Museum and Martie and the late Joe Maierhauser of CCMP regarding permission to work and collect in LTC. Richard Franz and Bob McCord gave helpful thoughts about gopher tortoise systematics and identification. Joseph Frederickson provided insightful discussion about stable isotopes and the potential of guano components, and George Davis provided insights about metamorphic core complexes. Tamaki Yuri and Janet K. Braun kindly allowed access to the OMNH bird osteology collection. Don G. Wyckoff helped in securing funding, and Arnold Coldiron provided the funding for the radioisotopic date. We appreciate Sandra Swift for photographing the lizard fossils.

REFERENCES

Allen, G. M., 1939, Bats: New York, Dover Publications.

Altenbach, J. S., 1979, Locomotor Morphology of the Vampire Bat, *Desmodus rotundus*: Special Publication no. 6, American Society of Mammalogists, p. 1-137.

Altenbach, J. S., 1988, Locomotion, in Greenhall, A. M., and Schmidt, U., eds. Natural History of Vampire Bats: Boca Raton, CRC Press, p. 71-83.

Álvarez, T., 1972, Nuevo registro para el vampiro del Pleistoceno *Desmodus stocki* de Tlapacoya, Mexico: Anales de la Escuela Nacional de Ciencias Biológicas v. 19, p. 163-165.

Andrews, J. T., 2009, Wisconsinan (Weichselian, Würm) glaciation, in Gornitz, V., ed., Encyclopedia of Paleoclimatology and Ancient Environments: Dordrecht, Springer-Verlag, https://doi.org/10.1007/978-1-4020-4411-3_229

Arroyo-Cabrales, J., 1992, Sinopsis de los murciélagos fósiles de Mexico: Revista de la Sociedad Mexicana de Paleontología v. 5, p. 1-14.

Arroyo-Cabrales, J., and Ray, C. E., 1997, Revisión de los vampiros fósiles (Chiroptera: Phyllostomidae, Desmodontinae) de México, in Arroyo-Cabrales, J., and Polaco, Ó. J., eds., Homenaje al Profesor Ticul Álvarez: México, D. F., Instituto Nacional de Antropología e Historia, Coleccion Científica, p. 69-86.

Arroyo-Cabrales, J., and Polaco, O. J., 2003, Caves and the Pleistocene vertebrate paleontology of Mexico, in Schubert, B. W., Mead, J. I., and Graham, R. W., eds., Ice Age Cave Faunas of North America: Bloomington, Indiana University Press, p. 273-291.

Arroyo-Cabrales, J., and Polaco, O. J., 2008, Fossil bats of Mesoamerica: Arquivos do Museu Nacional, Rio de Janeiro v. 66, p. 155-160.

Auffenberg, W., 1963, The fossil snakes of Florida: Tulane Studies in Zoology v. 10, p. 131-216.

Auffenberg, W., 1976, The genus *Gopherus* (Testudinidae): part 1. Osteology and relationships of extant species: Bulletin of the Florida State Museum Biological Sciences v. 20, p. 47-110.

de Azcarate, T., 1980, Sociobiología y manejo del capybara *Hydrochoerus hydrochaeris*: Seville, Spain, Doñana, Acta Vertebrata, número especial v. 7 (6), p. 1-228.

Baker, R. J., O'Neill, M. B., and McAliley, L. R., 2003, A new species of desert shrew, *Notiosorex*, based on nuclear and mitochondrial sequence data: Occasional Papers, Museum of Texas Tech University no. 222, p. 1-12.

Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., and Lovette, I. J., 2015, New insights into New World biogeography: an integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies: Auk v. 132, p. 333-348.

Barquez, R. M., Mares, M. A., and Braun, J. K., 1999, The bats of Argentina: Special Publications Museum of Texas Tech University no. 42, p. 1-275.

Baskin, J., and Thomas, R., 2016, A review of *Camelops* (Mammalia, Artiodactyla, Camelidae), a giant llama from the middle and late Pleistocene (Irvingtonian and Rancholabrean) of North America: Historical Biology v. 28, p. 120-127.

Baumel, J. J., King, A. S, Lucas, A. M., Breazile, J. E., and Evans, H. E. (eds.), 1979, Nomina Anatomica Avium. An annotated anatomical dictionary of birds: London, Academic Press, 637 p.

Beck, D.D., 2005, Biology of Gila Monsters and Beaded Lizards: Berkeley, University of California Press.

Bertrand, D., 1950, Survey of contemporary knowledge of biogeochemistry 2. The biogeochemistry of vanadium: Bulletin of the American Museum of Natural History v. 94, p. 403-456.

Betancourt, J. L., Van Devender, T. R., and Martin, P. S., eds., 1990, Packrat Middens: the Last 40,000 Years of Biotic Change: Tucson, University of Arizona Press, 469 p.

Bever, G.S., 2005, Variation in the ilium of North American *Bufo* (Lissamphibia: Anura) its implications for species-level identification of fragmentary anuran fossils: Journal of Vertebrate Paleontology v. 25, p. 548-560.

Bickart, K. J., 1990, Recent advances in the study of Neogene fossil birds Part I. The birds of the late Miocene-early Pliocene Big Sandy Formation, Mohave County, Arizona: Ornithological Monographs no. 44, p. 1-72.

Bobrowiec, P.E.D., Lemes, M. R., and Gribel, R., 2015, Prey preference of the common vampire bat (*Desmodus rotundus*, Chiroptera) using molecular analysis: Journal of Mammalogy v. 96, p. 54-63.

Borry, M., Cordova, B., Perri, A., Wibowo, M., Honap, T. P., Ko, J., Yu, J., Britton, K., Girdland-Flink, L., Power, R. C., Stuijts, I., Salazar-García, D. C., Hofman, C., Hagan, R., Samdapawindé Kagoné, T., Meda, N., Carabin, H., Jacobson, D., Reinhard, K., Lewis, C., Kostic, A., Jeong, C., Herbig, A., Hübner, A., and Warinner, C., 2020, CoproID predicts the source of coprolites and paleofeces using microbiome composition and host DNA content: PeerJ v. 8, p. e9001.

Brattstrom, B. H., 1954, The fossil pit-vipers (Reptilia: Crotalidae) of North America: Transactions of the San Diego Society of Natural History v. 12, p. 31-46.

Bravo-Cuevas, V. M., Jiménez-Hidalgo, E., and Priego-Vargas, J., 2011, Taxonomía y hábito alimentario de *Equus conversidens* (Perissodactyla, Equidae) del Pleistoceno tardío (Rancholabreano) de Hidalgo, centro de Mexico: Revista Mexicana de Ciencias Geológicas v. 28, p. 65-82.

Bravo-Cuevas, V. M., Jiménez-Hidalgo, E., Cabral-Perdomo, M. A., and Priego-Vargas, J., 2013, Taxonomy and notes on the paleobiology of the late Pleistocene (Rancholabrean) antilocaprids (Mammalia, Artiodactyla, Antilocapridae) from the state of Hidalgo, central Mexico: Revista Mexicana de Ciencias Geológicas v. 30, p. 601-613.

Brennan, T.C., and Holycross, A. T., 2009, A Field Guide to Amphibians and Reptiles in Arizona: Phoenix, Arizona Game and Fish Department.

Brennan, T.C., Babb, R. D., and Rorabaugh, J. C., 2020, *Rhinocheilus lecontei*, in Holycross, H.T. and Mitchell, J. C., eds., Snakes of Arizona: Rodeo, New Mexico, ECO Publishing, p. 318-327.

Buckley, M., Lawless, C., and Rybczynski, N., 2019, Collagen sequence analysis of fossil camels, *Camelops* and cf. *Paracamelus*, from the Arctic and sub-Arctic of Plio-Pleistocene North America: Journal of Proteomics v. 194, p. 218-225.

Buecher, D. C., and Sidner, R. M., 1999, Bats of Kartchner Caverns State Park, Arizona: Journal of Cave and Karst Studies v. 61, p. 102-107.

Campbell, K. E. Jr., 1979, The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru: Life Sciences Contributions Royal Ontario Museum v. 118, p. 1-203.

Carbot-Chanona, G., Rivera-Velázquez, G., Jiménez-Hidalgo, E., and Reynoso, V. H., 2020, The fossil record of turtles and tortoises (Testudines) of Mexico, Central America and the Caribbean Islands, with comments on its taxonomy and paleobiogeography: a bibliographic review: Revista Mexicana de Ciencias Geológicas v. 37, p. 269-283.

Carpenter, M. C., 2003, Late Pleistocene Aves, Chiroptera, Perissodactyla, and Artiodactyla from Rampart Cave, Arizona. [M.S. thesis]: Flagstaff, Northern Arizona University.

Carpenter, M.C., and Mead, J.I., 2003, Late Pleistocene roadrunner (*Geococcyx*) from Kartchner Caverns State Park, southeastern Arizona: Southwestern Naturalist v. 48, p. 402-410.

Carranza, J., and Campo, D. R., 1982, Incidencias del murciélago hematófago *Desmodus rotundus* sobre los indígenas Yanomami de Venezuela: Doñana, Acta Vertebrados v. 7, p. 113.

Carrión, J. S., Scott, L., and Marais, E., 2006, Environmental implications of pollen spectra in bat droppings from southeastern Spain and potential for palaeoenvironmental reconstructions. Review of Palaeobotany and Palynology v. 140, p. 175-186.

Castellanos, A. X., and Banegas, G. A., 2015, Vampire bats bite lowland tapirs in Yasuni National Park, Ecuador: Tapir Conservation v. 24, p. 7.

Catenazzi, A., and Donelly, M. A., 2008, Sea lion *Otaria flavescens* as host of the common vampire bat *Desmodus rotundus*: Marine Ecology Progress Series v. 360, p. 285-289.

Ceballos, G. (ed.), 2014, Mammals of Mexico: Baltimore, Johns Hopkins University Press, 957 p,

Choate, J. R., and Hall, E. R., 1967, Two new species of bats, genus *Myotis*, from a Pleistocene deposit in Texas: American Midland Naturalist v. 78, p. 531-534.

Coblentz, D., 2005, The tectonic evolution of the Madrean Archipelago and its impact on the geoecology of the Sky Islands, Gottfried, G. J., Gebow, B. S., Eskew, L. G., and Edminster, C. B., compilers, Connecting Mountain Islands and Desert Seas: Biodiversity and Management of the Madrean Archipelago II: Tucson, United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Proceedings RMRS-P-36, p. 62-68.

Cockerell, T. D. A., 1930, An apparently extinct *Euglandina* from Texas: Proceedings of the Colorado Museum of Natural History v. 9, p. 52-53.

Colbert, E. H., 1950, The fossil vertebrates, in Haury, E. W., ed., The Stratigraphy and Archaeology of Ventana Cave Arizona: Tucson, University of Arizona Press, p. 126-156.

Coles, G. M., Gilbertson, D. D., Hunt, C. O., and Jenkinson, R. D. S., 1989, Taphonomy and the palynology of cave deposits: Cave Science v. 16, p. 83-89.

Coney, P. J., and Harms, T. A., 1984, Cordilleran metamorphic core complexes: Cenozoic extensional relics of Mesozoic compression: Geology v. 12, p. 550-554.

Connin, S. L., Betancourt, J., and Quade, J., 1998, Late Pleistocene C_4 plant dominance and summer rainfall in the southwestern United States from isotopic study of herbivore teeth. Quaternary Research v. 50, p. 179-193.

Cooper, A., Turney, C., Hughen, K. A., Brook, B. W., McDonald, H. G., and Bradshaw, C. J. A., 2015, Abrupt warming events drove late Pleistocene Holarctic megafaunal turnover: Science v. 349, p. 602-606.

Cox, C.L., Davis Rabosky, A. R., Holmes, I. A., Reyes-Velasco, J., Roelke, C. E., Smith, E. N., Flores-Villela, O., McGuire, J. A., and Campbell, J. A., 2018, Synopsis and taxonomic revision of three genera in the snake tribe Sonorini: Journal of Natural History 52:945-988.

Cox, C.L., Davis Rabosky, A. R., and Frost, D. R.,. 2020, *Sonora semiannulata*, in Holycross, H.T. and Mitchell, J. C., eds., Snakes of Arizona: Rodeo, New Mexico, ECO Publishing, p. 354-363.

Cruz, A. A., Arroyo-Cabrales, J., and Viñas-Vallverdú, R., 2009, Tortugas fósiles del Pleistoceno tardío de Santiago Chazumba, Oaxaca: Boletín de la Sociedad Geológica Mexicana v. 61, p. 225-232.

Czaplewski, N. J., and Peachey, W. D., 2003, Late Pleistocene bats from Arkenstone Cave, Arizona: Southwestern Naturalist v. 48, p. 597-609.

Czaplewski, N. J., J. I. Mead, C. J. Bell, W. D. Peachey, and T.-L. Ku. 1999, Papago Springs Cave revisited, part II: vertebrate paleofauna: Occasional Papers of the Oklahoma Museum of Natural History v. 5, p. 1-41.

Czaplewski, N. J., Mead, J. I., and Peachey, W. D., 2022, Late Pleistocene vertebrate fauna of Pyeatt Cave, Huachuca Mountains, Cochise County, Arizona: New Mexico Museum of Natural History and Science Bulletin v. 88, p. 301-329.

Dalquest, W. W., 1979, The little horses (genus *Equus*) of the Pleistocene of North America: American Midland Naturalist v. 101, p. 241-244.

Dalquest, W. W., and Stangl, F. B., Jr., 1984, The taxonomic status of *Myotis magnamolaris*, Choate and Hall: Journal of Mammalogy v. 65, p. 485-486.

Davis, G. H., 1980, Structural characteristics of metamorphic core complexes, southern Arizona, in Crittenden, M. D., Coney, P. J., and Davis, G. H., eds., Cordilleran Metamorphic Core Complexes: Geological Society of America Memoirs v. 153, p. 35-77.

Davis, G. H., Bos Orent, E., Clinkscales, C., Ferroni, F. R., Gehrels, G. E., George, S. W. M., Guns, K. A., Hanagan, C. E., Hughes, A. N., Iriondo, A., Jepson, G., Kelty, C., Krantz, R. W., Levenstein, B. M., Lingrey, S. H., Miggins, D. P., Moore, T. , Portnoy, S. E., Reeher, L. J., Wang, J. W., 2023, Structural Analysis and Chronologic Constraints on Progressive Deformation within the Rincon Mountains, Arizona: Implications for the Development of Metamorphic Core Complexes. Geological Society of America Memoir, vol. 222, p. 1-125. https:doi.org/10.1130/2023.1222(01)

Dorsey, S. L., 1977, A reevaluation of two new species of fossil bats from Innerspace Caverns: Texas Journal of Science v. 28, p. 103-108.

Drewes, H., 1977, Geologic map and sections of the Rincon Valley quadrangle, Pima County, Arizona: U. S. Geological Survey, Miscellaneous Investigations Series Map I-997.

Elias, S. A. (ed.), 2023, Introduction [et seq.]. Encyclopedia of Quaternary Sciences, 3rd edition. Available online as a Reference Module in Earth Systems and Environmental Sciences https://doi.org/10.1016/B978-0-323-99931-1.00095-7

Emslie, S. D., 1998, Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida Peninsula: Ornithological Monographs v. 50, p. 1-113.

Emslie, S. D., Speth, J. D., and Wiseman, R. N., 1992, The prehistoric Puebloan avifaunas from the Pecos Valley, southeastern New Mexico: Journal of Ethnobiology v. 12, p. 83-115.

Evans, S.E., 2008, The skull of lizards and tuatara, in Gans, C., ed., Biology of the Reptilia, Gaunt, A. S., and Adler, K., eds., The Skull of Lepidosauria, v. 20, Morphology: Lawrence, Kansas, Society for the Study of Amphibians and Reptiles, p. 1-347.

Feldner, J.J., Schuett, G. W., and Smith, C. F., 2016, Western massasauga, *Sistrurus tergeminus* (Baird and Girard 1853), in Schuett, G.W., Feldner, M. J., Smith, C. F., and Reiserer, R. S., eds., Rattlesnakes of Arizona, v 1: Rodeo, New Mexico, ECO Publishing, p. 701-734.

Ferreira, R. L., Martins, R. P., and Prous, X., 2007, Structure of bat guano communities in a dry Brazilian cave: Tropical Zoology v. 20, p. 55-74.

Freitas, M. B., Welker, A. F., Millan, S. F., and Pinheiro, E. C., 2003, Metabolic responses induced by fasting in the common vampire bat *Desmodus rotundus*: Journal of Comparative Physiology B, Biochemical, Systemic, and Environmental Physiology v. 173, p. 703-707.

Freitas, M. B., Passos, C. B. C., Vasconcelos, R. B., and Pinheiro, E. C., 2005, Effects of short-term fasting on energy reserves of vampire bats (*Desmodus rotundus*): Comparative Biochemistry and Physiology B, v. 140, p. 59-62.

Fricke, H. C., 2007, Stable isotope geochemistry of bonebed fossils: reconstructing paleoenvironments, paleoecology, and paleobiology, in Rogers, R. R., Eberth, D. A., and Fiorillo, A. R., eds., Bonebeds: Genesis, Analysis, and Paleobiological Significance: Chicago, University of Chicago Press, p. 437-490.

Frost, D. R., Grant, T., Faivovich, J., Bain, R. H., Haas, A., Haddad, C. F. B., De Sá, R. O., Channing, A., Wilkinson, M., Donnellan, S. C., Raxworthy, C. J., Campbell, J. A., Blotto, B. L., Moler, P., Drewes, R. C., Nussbaum, R. A., Lynch, J. D., Green, D. M., and Wheeler, W. C., 2006, The amphibian tree of life: Bulletin of the American Museum of Natural History, no. 297, p. 1-370.

Galetti, M., Pedrosa, F., Keuroghlian, A., and Sazima, I., 2016, Liquid lunch – vampire bats feed on invasive feral pigs and other ungulates: Frontiers in Ecology and Environment v. 14, p. 505-506.

Gauthier, J.A., Kearney, M., Maisano, J. A., Rieppel, O., and Behlke, A. D. B., 2012, Assembling the squamate tree of life: perspectives from the phenotype and the fossil record: Bulletin of the Peabody Museum of Natural History v. 53, p. 3-308.

Geanta, A., Tantau, I., Tamas, T., and Johnston, V. E., 2012, Palaeoenvironmental information from the palynology of an 800 year old bat guano deposit from Magurici Cave, NW Transylvania (Romania): Review of Palaeobotany and Palynology v. 174, p. 57-66.

Giurgiu, A., and Tamas, T., 2013, Mineralogical data on bat guano deposits from three Romanian caves: Studia UBB, Geologia v. 58, p. 13-18.

Gnocchi, A. P., and Srbek-Araujo, A. C., 2017, Common vampire bat (*Desmodus rotundus*) feeding on lowland tapir (*Tapirus terrestris*) in an Atlantic Forest remnant in southeastern Brazil: Biota Neotropica v. 17, p. e20170326. http://dx.doi.org/10.1590/1676-0611-BN-2017-0326

Gómez, R.O., and Turazzini, G. F., 2016, An overview of the ilium of anurans (Lissamphibia, Salientia), with a critical appraisal of the terminology and primary homology of main ilial features: Journal of Vertebrate Paleontology v. 36, p. 1-12.

Greenhall, A. M., 1972a, The biting and feeding habits of the vampire bat, *Desmodus rotundus*: Journal of Zoology, London v. 168, p. 451-461.

Greenhall, A. M., 1972b, The problem of bat rabies, migratory bats, livestock and wildlife: Transactions of 37th North American Wildlife and Natural Resources Conference, 12-15 March. Washington, D.C., Wildlife Management Institute.

Greenhall, A. M., 1988, Feeding behavior, in Greenhall, A. M., and Schmidt, U., eds., Natural History of Vampire Bats: Boca Raton, Florida, CRC Press, p. 111-131.

Greenhall, A. M., Joermann, G., Schmidt, U., and Seidel, M. R., 1983, *Desmodus rotundus*: Mammalian Species v. 202, p. 1-6.

Greenhall, A. M., Schmidt, U., and Lopez-Forment, W., 1969, Field observations on the mode of attack of the vampire bat (*Desmodus rotundus*) in Mexico: Anales del Instituto de Biología UNAM Serie Zoología v. 40, p. 245-252.

Griffith, G. E., Omernik, J. M., Johnson, C. B., and Turner, D. S., 2014, Ecoregions of Arizona (poster): U. S. Geological Survey Open-File Report 2014-1141, with map, scale 1:1,325,000. http://dx.doi.org/10.3133/ofr20141141

Guthrie, D. A., 1998. Analysis of avifaunal and bat remains from midden sites on San Miguel Island, in Power, D. M., ed., The California Islands: Proceedings of a Multidisciplinary Symposium: Santa Barbara, Santa Barbara Museum of Natural History, p. 689-702.

Harris, A. H., 1984a, *Neotoma* in the late Pleistocene of New Mexico and Chihuahua, in Genoways, H. H., and Dawson, M. R., eds., Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday: Pittsburgh, Carnegie Museum of Natural History Special Publication no. 8, p. 164-178.

Harris, A. H., 1984b, Two new species of late Pleistocene woodrats (Cricetidae: *Neotoma*) from New Mexico: Journal of Mammalogy v. 65, p. 560-566.

Harris, A. H., 1987, Reconstruction of mid-Wisconsin environments in southern New Mexico: National Geographic Research v. 3, p. 142-151.

Harris, A. H., 2014, Pleistocene Vertebrates of Southwestern USA and Northwestern Mexico: El Paso, University of Texas at El Paso Biodiversity Collections, website accessed at www.utep.edu/leb/pleistnm/

Harris, A. H., 2016, Pleistocene/Holocene faunas from the Trans-Pecos: Special Publications, Museum of Texas Tech University v. 65, p. 157-175.

Harris, A. H., and Crews, C. R., 1983, Conkling's roadrunner—a subspecies of the California roadrunner?: Southwestern Naturalist v. 28, p. 407-412.

Harris, A. H., and Porter, L. S. W., 1980, Late Pleistocene horses of Dry Cave, Eddy County, New Mexico: Journal of Mammalogy v. 61, p. 46-65.

Hayward, B. J., 1970, The natural history of the cave bat *Myotis velifer*: WRI-SCI (Western New Mexico University Research in Science) v. 1, p. 74.

Heintzman, P. D., Zazula, G. D., MacPhee, R. D. E., Scott, E., Cahill, J. A., McHorse, B.K., Kapp, J. D., Stiller, M., Wooller, M. J., Orlando, L., Southon, J., Froese, D. G., and Shapiro, B., 2017, A new genus of horse from Pleistocene North America: eLife https:doi.org/10.7554/eLife.29944

Heintzman, P. D., Zazula, G. D., Cahill, J. A., Reyes, A. V., MacPhee, R. D. E., and Shapiro, B., 2015, Genomic data from extinct North American *Camelops* revise camel evolutionary history: Molecular Biology and Evolution v. 32, p. 2433-2440.

Hibbard, C. W., 1963, The origin of the p3 pattern of *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus*: Journal of Mammalogy v. 44, p. 1-15.

Holman, J.A. 1965. Late Pleistocene herpetofauna from Missouri: Transactions of the Illinois Academy of Science 58:190-194.

Holman, J. A., 1979, A review of North American Tertiary snakes: Publications of the Museum, Michigan State University, Paleontological Series v. 1, p. 200-260.

Holman, J.A., 2000, Fossil Snakes of North America: Bloomington, Indiana University Press.

Holman, J.A., 2003, Fossil Frogs and Toads of North America: Bloomington, Indiana University Press.

Holmgren, C. A., Betancourt, J. L., and Rylander, K. A., 2006, A 36,000-yr vegetation history from the Peloncillo Mountains, southeastern Arizona, USA: Palaeogeography, Palaeoclimatology, Palaeoecology v. 240, p. 405-422.

Holycross, H.T., and J.C. Mitchell, J. C. (eds.), 2020, Snakes of Arizona: Rodeo, New Mexico, ECO Publishing.

Howard, H., 1929, The avifauna of Emeryville Shellmound: University of California Publications in Zoology, v. 32, p. 301-394.

Hunt, A. P., and Lucas, S. G., 2018, The record of sloth coprolites in North and South America: implications for terminal Pleistocene extinctions: New Mexico Museum of Natural History and Science v. 79, p. 277-298.

Hutchinson, G. E., 1950, Survey of existing knowledge of biogeochemistry 3. The biogeochemistry of vertebrate excretion: Bulletin of the American Museum of Natural History v. 96, p. 1-554.

Hutchison, J. H., 1967, A Pleistocene vampire bat (*Desmodus stocki*) from Potter Creek Cave, Shasta County, California: PaleoBios no. 3, p. 1-6.

Ibañez, C. J., 1981, Biología y ecología de los murciélagos del Hato "El Frío" Apure, Venezuela: Doñana, Acta Vertebrata v. 8, p. 1-271.

Jass, C. N., and Bell, C. J., 2010, Desert tortoises (*Gopherus agassizii*) from Pleistocene sediments in Cathedral Cave, White Pine County, Nevada: Southwestern Naturalist v. 55, p. 558-563.

Jiménez-Hidalgo, E., Carbot-Chanona, G., Guerrero-Arenas, R., Bravo-Cuevas, V. M., Safi Holdridge, G., and Israde-Alcántara, I., 2019, Species diversity and paleoecology of late Pleistocene horses from southern Mexico: Frontiers in Ecology and Evolution v. 7, p. 394. DOI: 10.3389/fevo.2019.00394

Jones, C. J., Fleharty, E. D., and Harris, A. H., 1960, Unusual habitats of grasshopper mice in New Mexico: Journal of Mammalogy v. 41, p. 275-276.

Jones, L.L., and R.E. Lovich, R. E., eds., 2009, Lizards of the American Southwest: Tucson, Rio Nuevo Publishers.

Joyce, W. G., and Bell, C. J., 2004, A review of the comparative morphology of extant testudinoid turtles (Reptilia: Testudines): Asiatic Herpetological Research v. 10, p. 53-109.

Jurestovsky, D.J., 2021, Small colubroids from the Late Hemphillian Gray Fossil Site, of northeastern Tennessee: Journal of Herpetology v. 55, p. 422-431.

Kays, R. W., and Wilson, D. W., 2002, Mammals of North America: Princeton, Princeton University Press, 240 p.

Kelly, T. S., Martin, R. A., Ronez, C., Cañón, C., and Pardiñas, U. F. J., 2022, Morphology and genetics of grasshopper mice revisited in a paleontological framework: reinstatement of Onychomyini (Rodentia, Cricetidae): Journal of Mammalogy v. 104, p. 3-28.

Kottkamp, S., Santucci, V. L., Tweet, J. S., Horrocks, R. D., and Morgan, G. S., 2022, Pleistocene vertebrates from Carlsbad Caverns National Park, New Mexico: New Mexico Museum of Natural History and Science Bulletin v. 88, p. 267-290.

Kunz, T. H., 1974, Feeding ecology of a temperate insectivorous bat (*Myotis velifer*): Ecology v. 55, p. 693-711.

Kunz, T. H., and Lumsden, L. F., 2003, Ecology of cavity and foliage roosting bats, in T. H. Kunz, T. H., and M. B. Fenton, M. B., eds., Bat Ecology: Chicago, University of Chicago Press, p. 3-89.

LaDuke, T. C., 1991, The fossil snakes of Pit 91, Rancho La Brea, California: Contributions in Science, Natural History Museum of Los Angeles County v. 424, p. 1-28.

Larson, L. M., 1930, Osteology of the California road-runner recent and Pleistocene: University of California Publications in Zoology v. 32, p. 409-428.

Lemm, J.M., 2009, Desert iguana, in Jones, L. L., and Lovich, R. E., eds., Lizards of the American Southwest: Tucson, Rio Nuevo Publishers, p. 131-134.

Lindsay, E. H., and Tessman, N. T., 1974, Cenozoic vertebrate localities and faunas in Arizona: Journal of the Arizona Academy of Science, v. 9, p. 3-24.

Long, C. A., and Martin, P. S., 1974, Death of American ground sloths: Science v. 186, p. 638-640.

Lord, R. D., Delpietro, H., and Lazaro, L., 1973, Vampiros que se alimentan de murciélagos: Physis, Seccion C, Asociación Argentina de Ciencias Naturales v. 32, p. 225.

Luna-Jorquera, G., and Culik, B. M., 1995, Penguins bled by vampires: Journal of Ornithology v. 136, p. 471-472.

Maher, L. J. Jr., 2006, Environmental information from guano palynology of insectivorous bats of the central part of the United States of America: Palaeogeography, Palaeoclimatology, Palaeoecology v. 237, p. 19-31.

Mann Fischer, G., 1951, Biología del vampiro: Biológica: Trabajos del Instituto de Biología "Juan Noe", Santiago de Chile, Universidad de Chile v. 12 & 13, p. 3-24.

Mantovan, K. B., Menozzi, B. D., Paiz, L. M., Sevá, A. P., Brandão, P. E., and Langoni, H., 2022, Geographic distribution of common vampire bat *Desmodus rotundus* (Chiroptera: Phyllostomidae) shelters: implications for the spread of rabies virus to cattle in southeastern Brazil: Pathogens v. 11(942), p. 1-10.

Marín-Leyva, A. H., Arroyo-Cabrales, J., García-Zepeda, M. L., Ponce-Saavedra, J., Schaaf, P., Pérez-Crespo, V. A., Morales-Puente, P., Cienfuegos-Alvarado, E., and Alberdi, M. T., 2016, Feeding ecology and habitat of late Pleistocene *Equus* horses from west-central Mexico using carbon and oxygen isotopes variation: Revista Mexicana de Ciencias Geológicas v. 33, p. 157-169.

Martin, R. E., Pine, R. H., and DeBlase, A. F., 2001, A Manual of Mammalogy with Keys to Families of the World, 3rd edition: Long Grove, Illinois, Waveland Press, 333 p.

McCord, R. D., 2002, Fossil history and evolution of the gopher tortoises (genus *Gopherus*), in Van Devender, T. R., ed., The Sonoran Desert Tortoise: Natural History, Biology, and Conservation: Tucson, Arizona-Sonora Desert Museum, p. 52-66.

McDonald, H. G., and Jefferson, G. T., 2008, Distribution of Pleistocene *Nothrotheriops* (Xenarthra, Nothrotheriidae) in North America, in Wang, X., and Barnes, L. G., eds., Geology and Vertebrate Paleontology of Western and Southern North America, Contributions in Honor of David P. Whistler: Los Angeles, Natural History Museum of Los Angeles County, Science Series no. 41, p. 313-331.

McNab, B. K., 1973, Energetics and the distribution of vampires: Journal of Mammalogy v. 54, p. 131-144.

Mead, J. I., Roth, E. L., Van Devender, T. R., and Steadman, D. W., 1984, The late Wisconsinan vertebrate fauna from Deadman Cave, southern Arizona: Transactions of the San Diego Society of Natural History v. 20, p. 247-276.

Mead, J.I., Arroyo-Cabrales, J., and Johnson, E., 1999, Pleistocene lizards (Reptilia: Squamata) from San Josecito Cave, Nuevo León, Mexico: Copeia v. 1999, p. 163-173.

Mead, J. I., Baez, A., Swift, S. L., Carpenter, M. C., Hollenshead, M., Czaplewski, N. J., Steadman, D. W., Bright, J., and Arroyo-Cabrales, J., 2006, Tropical marsh and savanna of the late Pleistocene in northeastern Sonora, México: Southwestern Naturalist v. 51, p. 226-239.

Mead, J.I., Schubert, B. W., Wallace, S. C., and Swift, S. L., 2012, Helodermatid lizard from the Mio-Pliocene oak-hickory forest of Tennessee, eastern USA, and a review of monstersaurian osteoderms: Acta Palaeontologica Polonica v. 57, p. 111-121.

Mead, J.I., Holte, S., White, R. S., and McCord, R., 2015, Early Pleistocene (Blancan) helodermatid lizards from Arizona, USA: Journal of Herpetology v. 49, p. 295-301.

Mead, J.I., and Steadman, D. W., 2017, Late Pleistocene snakes (Squamata: Serpentes) from Abaco, The Bahamas: Geobios v. 50, p. 431-440.

Mead, J.I., Czaplewski, N. J., and Smith, K. S., 2021, *Heloderma* (Helodermatidae; Squamata) from the Apache Local Fauna, Pleistocene, southwestern Oklahoma: Journal of Herpetology v. 55, p. 70-76.

Mead, J. I., Van Devender, T. R., Ferguson, G. M., and Hale, S., 2022, Late Pleistocene shrub-ox (*Euceratherium collinum*), Pontatoc Ridge Shelter, Santa Catalina Mountains, southeastern Arizona. Southwestern Naturalist v. 66, p. 102-113.

Miller, L., and DeMay, I., 1942, The fossil birds of California: an avifauna and bibliography with annotations: University of California Publications in Zoology v. 47, p. 47-142.

Moore, G., Tessler, M., Cunningham, S. W., Betancourt, J., and Harbert, R., 2020, Paleo-metagenomics of North American fossil packrat middens: past diversity revealed by ancient DNA: Ecology and Evolution v. 10, p. 2530-2544.

Morgan, G. S., and Harris, A. H., 2015, Pliocene and Pleistocene vertebrates of New Mexico: New Mexico Museum of Natural History and Science Bulletin v. 58, p. 233-427.

Morgan, G. S., Linares, O. J., and Ray, C. E., 1988, New species of fossil vampire bats (Mammalia: Chiroptera: Desmodontidae) from Florida and Venezuela: Proceedings of the Biological Society of Washington v. 101, p. 912-928.

Muchmore, W.B., and Pape, R. B., 1999, Description of an eyeless, cavernicolous *Albiorix* (Pseudoscorpionida: Ideoroncidae) in Arizona, with observations on its biology and ecology: Southwestern Naturalist v. 44, p. 138-147.

Murphy, J.C. 2018. Arizona's Amphibians and Reptiles. A Natural History and Field Guide: Book Services, USA.

Norell, M. A., 1989, Late Cenozoic lizards of the Anza-Borrego Desert, California: Contributions in Science, Natural History Museum of Los Angeles County v. 414, p. 1-31.

Nuñez, E. E., MacFadden, B. J., Mead, J. I., and Baez, A., 2010, Ancient forests and grasslands in the desert: diet and habitat of late Pleistocene mammals from north central Sonora, Mexico: Palaeogeography, Palaeoclimatology, Palaeoecology v. 297, p. 391-400.

de Oliveira, M. B., de Andrade, H. S. F., Cordeiro, J. L. P., and de Oliveira, L. F. B., 2022, Potential feeding event of *Priodontes maximus* (Cingulata: Dasypodidae) by *Desmodus rotundus* (Chiroptera: Desmodontinae) in the cerrado, western Brazil: Notas sobre Mamíferos Sudamericanos v. 4, p. 2-10. http://doi.org/10.31687/SaremNMS22.5.1

Olson, S. L., and Hilgartner, W. B., 1982, Fossil and subfossil birds from the Bahamas: Smithsonian Contributions to Paleobiology v. 48, p. 22-56.

Osborne, M. C., and Jass, C. N., 2008, The relationship of mineralogical data to paleontological questions: a case study from Cathedral Cave, White Pine County, Nevada: Journal of Cave and Karst Studies v. 70, p. 156-162.

Oswald, J. A., and Steadman, D. W., 2011, Late Pleistocene passerine birds from Sonora, Mexico: Palaeogeography, Palaeoclimatology, Palaeoecology v. 301, p. 56-63.

Pardiñas, U. F. J., and Tonni, E. P., 2000, A giant vampire (Mammalia, Chiroptera) in the late Holocene from the Argentinean pampas: paleoenvironmental significance: Palaeogeography, Palaeoclimatology, Palaeoecology v. 160, p. 213-221.

Parmley, D., and Holman, J. A., 2007, Earliest fossil record of a pygmy rattlesnake (Viperidae: *Sistrurus* Garman): Journal of Herpetology v. 41, p. 140-143.

Pasenko, M. R., and Agenbroad, L. D., 2012, Late Pleistocene mammalian fauna from Prescott Valley, west-central Arizona: Southwestern Naturalist v. 57, p. 74-86.

Peachey, W. D., 1993, Cave development in the structural domain of a metamorphic core complex: Arkenstone Cave, Pima County, Arizona: Southwest Regional conference, National Speleological Society, Midland, Texas, unpublished abstract with figure, p. 1-3.

Persons, T.B., and Drost., C. A., 2020, *Coluber constrictor*, in Holycross, H.T. and J.C. Mitchell, J. C., eds., 2020, Snakes of Arizona: Rodeo, New Mexico, ECO Publishing, p. 126-142.

Phillips, C. J., and Steinberg, B., 1976, Histological and scanning electron microscopic studies of tooth structure and thegosis in the common vampire bat, *Desmodus rotundus*: Occasional Papers the Museum Texas Tech University no. 42, p. 1-12.

Presch, W., 1969, Evolutionary osteology and relationships of the horned lizard genus *Phrynosoma* (family Iguanidae): Copeia v. 1969, p. 250-275.

Proctor, N. S., and Lynch, P. J., 1993, Manual of Ornithology Avian Structure and Function: New Haven, Yale University Press, 340 p.

Ray, C. E., Linares, O. J., and Morgan, G. S., 1988, Paleontology, in Greenhall, A. M., and Schmidt, U., eds. Natural History of Vampire Bats: Boca Raton, CRC Press, p. 19-30.

Rea, A., 1983, Once a River: Bird Life and Habitat Changes on the Middle Gila: Tucson, University of Arizona Press.

Reeve, W.L. ,1952, Taxonomy and distribution of the horned lizard genus *Phrynosoma*: University of Kansas, Science Bulletin v. 34, p. 817-915.

Reynoso, V.-H., and Montellano-Ballesteros, M., 2004, A new giant turtle of the genus *Gopherus* (Chelonia: Testudinidae) from the Pleistocene of Tamaulipas, Mexico, and a review of the phylogeny and biogeography of gopher tortoises: Journal of Vertebrate Paleontology v. 24, p. 822-837.

Rorabaugh, J.C., and Lemos-Espinal, J. A., 2016. A Field Guide to the Amphibians and Reptiles of Sonora, Mexico: Rodeo, New Mexico, ECO Publishing.

Rubio, M., 2010, Rattlesnakes of the United States & Canada. Rodeo, New Mexico, ECO Publishing.

Ryan, J., 2010, Mammalogy Techniques Manual: self-published by author, 293 p.

Sanchés-Cordeiro, V., Botello, F., Mangaña-Cota, G., and Iglesias, J., 2011, Vampire bats, *Desmodus rotundus*, feeding on white-tailed deer, *Odocoileus virginianus*: Mammalia v. 75, p. 91-92.

Sanchiz, B., 1998, Salientia. Encyclopedia of Paleoherpetology. Part 4: Frankfurt, Verlag Dr. Friedrich Pfeil.

Satoh, K., and Iwaku, F., 2006, Jaw muscle functional anatomy in northern grasshopper mouse, *Onychomys leucogaster*, a carnivorous murid: Journal of Morphology v. 267, p. 987-999.

Scarpetta, S.G., 2021, Iguanian lizards from the Split Rock Formation, Wyoming: exploring the modernization of the North American lizard fauna: Journal of Systematic Palaeontology v. 19, p. 221-251.

Schuett, G.W., Feldner, M. J., Smith, C. F., and Reiserer, R. S., eds., 2016, Rattlesnakes of Arizona. v. 1: Rodeo, New Mexico, ECO Publishing.

Shahack-Gross, R., Berna, F., Karkanas, P., and Weiner, S., 2004, Bat guano and preservation of archaeological remains in cave sites: Journal of Archaeological Science v. 31, p. 1259-1272.

Sidner, R., 1988, Colossal Cave and its importance to bats: Unpublished report submitted to Gene Laos, Director, Pima County Parks and Recreation Department, 8 p.

Simmons, N. B., Gunnell, G. F., and Czaplewski, N. J., 2020, Fragments and gaps, in Fleming, T. H., Dávalos, L. M., and Mello, M. A. R., eds., Phyllostomid Bats: A Unique Mammalian radiation: Chicago, University of Chicago Press, p.63-86.

Tihen, J.A., 1962, A review of New World fossil bufonids: American Midland Naturalist v. 68, p. 1-50.

Turner, D. C., 1975, The Vampire Bat: A Field Study in Behavior and Ecology: Baltimore, Johns Hopkins University Press.

Van Devender, T. R., 1990a, Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico, in Betancourt, J. L., Van Devender, T. R., and Martin, P. S., eds., Packrat Middens: the Last 40,000 Years of Biotic Change: Tucson, University of Arizona Press, p. 134-165.

Van Devender, T. R., 1990b, Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico, in Betancourt, J. L., Van Devender, T. R., and Martin, P. S., eds., Packrat Middens: the Last 40,000 Years of Biotic Change: Tucson, University of Arizona Press, p. 104-133.

Van Devender, T. R., 2001, Deep history and biogeography of La Frontera, in Webster, G. L., and Bahre, C. J., eds., Changing Plant Life of La Frontera: Observations on Vegetation in the United States/Mexico Borderlands: Albuquerque, University of New Mexico Press, p. 56-66.

Van Devender, T. R., 2007, Ice Ages in the Sonoran Desert: Pinyon pines and Joshua trees in the Dry Borders region, in Felger, R. S., and Broyles, B., eds., Dry Borders: Great Natural Reserves of the Sonoran Desert: Levan, University of Utah Press.

Van Devender, T.R., and Mead, J. I., 1978, Early Holocene and Late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens: Copeia v. 1978, p. 464-475.

Van Devender, T. R., and Spaulding, W. G., 1979, The development of vegetation and climate in the southwestern United States: Science v. 204, p. 701-710.

Van Devender, T. R., Moodie, K. B., and Harris, A. H., 1976, The desert tortoise (*Gopherus agassizii*) in the Pleistocene of the northern Chihuahuan Desert: Herpetologica v. 32, p. 298-304.

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

Vaughan, T. A., 1954, A new subspecies of bat (*Myotis velifer*) from southeastern California and Arizona: University of Kansas Publications Museum of Natural History v. 7, p. 507-512.

Villa-R., B., 1966, Los Murciélagos de Mexico: México, Universidad Nacional Autónoma de Mexico.

Villa-R., B., and Lopez-Forment, W., 1966, Cinco casos de depredación de pequeños vertebrados en murciélagos de México: Anales del Instituto de Biología v. 37, p. 187-193.

Voigt, C. C., and Kelm, D. H., 2006, Host preference of the common vampire bat (*Desmodus rotundus*; Chiroptera) assessed by stable isotopes: Journal of Mammalogy v. 87, p. 1-6.

Wagner, J. D. M., 2006, Speleothem record of southern Arizona paleoclimate, 54 to 3.5 ka: Ph.D. dissertation, Tucson, University of Arizona Department of Geosciences, 129 p.

Wagner, J. D. M., Cole, J. E., Beck, J. W., Patchett, P. J., Henderson, G. M., and Barnett, H. R., 2010, Moisture variability in the southwestern United States linked to abrupt glacial climate change: Nature Geoscience v. 3, p. 110-113.

Walker, F. M., Williamson, C. H. D., Sanchez, D. E., Sobek, C. J., and Chambers, C. L., 2016, Species from feces: order-wide identification of Chiroptera from guano and other non-invasive genetic samples: PLoS One v. 11(9), p. e0162342. Doi:10.1371/journal.pone.0162342

Walker, F. M., Tobin, A., Simmons, N. B., Sobek, C. J., Sanchez, D. E., Chambers, C. L., and Fofanov, V. Y., 2022, A fecal sequel: testing the limits of a genetic assay for species identification: PLoS One v. 14(11), p. e0224969. Doi:10.1371/journal.pone.0224969

Wilkinson, G. S., 1985, The social organization of the common vampire bat. I. Pattern and cause of association: Behavioral Ecology and Sociobiology v. 17, p. 111-121.

Wilkinson, G. S., 1988, Social organization and behavior, in Greenhall, A. M., and Schmidt, U., eds. Natural History of Vampire Bats: Boca Raton, CRC Press, p. 85-97.

Willerslev, E., Hansen, A. J., Binladen, J., Brand, T. B., Gilbert, M. T. P., Shapiro, B., Bunce, M., Wiuf, C., Gilichinsky, D. A., and Cooper, A., 2003, Diverse plant and animal genetic records from Holocene and Pleistocene sediments: Sciencexpress 10.1126/science.1084114

Williams, J. W., Grimm, E. C., Blois, J. L., Charles, D. F., Davis, E. B., Goring, S. J., Graham, R. W., Smith, A. J., Anderson, M., Arroyo-Cabrales, J., Ashworth, A. C., Betancourt, J. L., Bills, B. W., Booth, R. K., Buckland, P. I., Curry, B. B., Giesecke, T., Jackson, S. T., Latorre, C., Nicholas, J., Purdum, T., Roth, R. E., Stryker, M., and Takahara, H., 2018, The Neotoma Paleoecology Database, a multiproxy, international, community-curated data resource: Quaternary Research v. 89, p. 156-177.

Wimsatt, W. A., 1962, Responses of captive common vampires to cold and warm environments: Journal of Mammalogy v. 43, p. 185-191.

Wurster, C. M., McFarlane, D. A., and Bird, M. I., 2007, Spatial and temporal expression of vegetation and atmospheric variability from stable carbon and nitrogen isotope analysis of bat guano in the southern United States: Geochimica et Cosmochimica Acta v. 71, p. 3302-3310.

Wurster, C. M., Patterson, W. P., McFarlane, D. A., Wassenaar, L. I., Hobson, K. A., Athfield, N. B., and Bird, M. I., 2008, Stable carbon and hydrogen isotopes from bat guano in the Grand Canyon, USA, reveal Younger Dryas and 8.2 ka events: Geology v. 36, p. 683-686.

Zepeda Mendoza, M. L., Xiong, Z., Escalera-Zamudio, M., Runge, A. K., Théze, J., Streicker, D., Frank, H. K., Loza-Rubio, E., Liu, S., Ryder, O. A., Samaniego Castruita, J. A., Katzourakis, A., Pacheco, G., Taboada, B., Löber, U., Pybus, O. G., Li, Y., Rojas-Anaya, E., Bohmann, K., Baez, A. C., Arias, C. F., Liu, S., Greenwood, A. D., Bertelsen, M. F., White, N. E., Bunce, M., Zhang, G., Sicheritz-Pontén, T., and Gilbert, M. P. T., 2018, Hologenomic adaptations underlying the evolution of sanguivory in the common vampire bat: Nature Ecology and Evolution https://doi.org/10.1038/s41559-018-0476-8

Mary C. Carpenter and Jim I. Mead. *Vulpes Vuples* (Red fox) remains from Stanton's Cave, Grand Canyon National Park, Arizona. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 175-177. DOI:10.4311/2024LSC0104

VULPES VULPES (RED FOX) REMAINS FROM STANTON'S CAVE, GRAND CANYON NATIONAL PARK, ARIZONA

Mary C. Carpenter[1] and Jim I. Mead[2,C]

ABSTRACT

Stanton's Cave is a large solutional cavern in the eastern region of Grand Canyon National Park, Arizona. The cave is best known to Quaternary paleontologists for its abundant Late Pleistocene and early Holocene fossil remains of mammals, birds, and Archaic artifacts. Re-examination of the fossil vertebrate collection, housed at the Grand Canyon Museum Collections, has resulted in re-identification of two fox dentaries (GRCA 76272) that were originally published as *Urocyon cinereoargenteus* (gray fox). Morphometric and morphological comparisons presented here find the dentaries diagnostic to *Vulpes vulpes* (red fox) and not the gray fox. The remains are the first record of *Vulpes vulpes* from the Grand Canyon and may be the first fossil evidence of the species from Arizona.

INTRODUCTION

Stanton's Cave (elevation 927 m) at 44 m above the Colorado River in the eastern Colorado River corridor of the Grand Canyon (Grand Canyon National Park, GRCA), Arizona, is well known to Quaternary paleontologists and archaeologists for its numerous Late Pleistocene taxa such as the extinct Harrington's mountain goat (*Oreamnos harringtoni*), the extant bighorn sheep (*Ovis canadensis*), the extinct Merriam's teratorn (*Teratornis merriami*), and the extirpated but now reintroduced California condor (*Gymnogyps californianus*), along with unassociated archaeological split twig figurines that date to the middle to late Holocene (Mead, 1981; Euler, 1984; Rea and Hargrave, 1984). Excavation of the cave sediments in the late 1960s and early 1970s was under the direction of Dr. Robert C. Euler (deceased) who undertook archaeological and paleontological assessment of the deposits (Euler, 1984). Among the hundreds of skeletal specimens reported were two dentaries (lower jaws, GRCA 76272) identified as gray fox (*Urocyon cinereoargenteus*) (Olsen and Olsen, 1984). Re-examination of the two dentaries determined that the gray fox specimens were misidentified. Here we present the reanalysis of these specimens.

Three species of foxes live in Arizona today. The gray fox and kit fox (*Vulpes macrotis*) are relatively common, though of the two, the kit fox has a more restricted range (Cockrum, 1960; Hoffmeister, 1986). The red fox (*Vulpes vulpes*) is uncommon in Arizona, with all of its records occurring in the extreme northeastern corner of the state, within Apache and Navajo Counties (Hoffmeister, 1986). In a study of extant red foxes in this region, Mikesic and LaRue (2003) maintain that the red fox is more common than previously thought, at least in their study area of the Navajo Reservation in northeastern Arizona. However, they also state that the southern and western limits of the red fox in Arizona are unknown. Only the gray fox is known to occur today within or adjacent to the Grand Canyon (Bailey, 1935; Hoffmeister, 1971, 1986).

MATERIALS AND METHODS

The two fox dentaries from Stanton's Cave are curated by the National Park Service at GRCA and are stored in a field bag labeled, "From Packrat Nest (consolidated) adjacent to fig. [split twig figurine ?] find F.S. [Field Specimen] #13 in upper end of Antechamber #1. Depth of bone ca. 10-20 cm. June 18/19 [1969], L. Powers."

There was no direct radiometric age available for the fox specimens. The "post-Pleistocene levels above 20 cm in depth" is the only evidence for an age for the dentaries (Olsen and Olsen, 1984:52; see also Euler, 1984). However, packrats (*Neotoma* spp.; woodrats) are well known to collect plants, dung, bones, and other assorted small objects from their surroundings, no matter the age, and incorporate these items into their middens (nest debris accumulations). Phillips (1984) notes just such an event in Rampart Cave (western Grand Canyon), where a dung ball of the extinct Shasta ground sloth (*Nothrotheriops*) was recovered from a Holocene-age packrat midden, yet the specimen radiocarbon dated to the latest Pleistocene. Olsen and Olsen (1984:49) discuss various taphonomic factors affecting the composition of the Stanton's Cave deposits, stating, "In all probability, the majority of bone displacement may be attributed to bioturbation, primarily on the part of the wood rat (*Neotoma* sp. indet.)." Thus, it is plausible for the two fox specimens to be older than the depth association suggests. Traces of muscle tissue attached to the dentaries could be used for future radiocarbon dating.

Fossils cataloged as GRCA 76272 consist of an incomplete left dentary and an incomplete right dentary that clearly belong to one individual. Because of this, only one dentary was used for measurements (Fig. 1). Dentaries were

---

[1] Badlands National Park, Interior, SD 57750

[2] The Mammoth Site, Hot Springs, SD 57747, and Desert Laboratory on Tumamoc Hill, University of Arizona, Tucson, AZ 85745

[C] Corresponding author: jmead@mammothsite.org

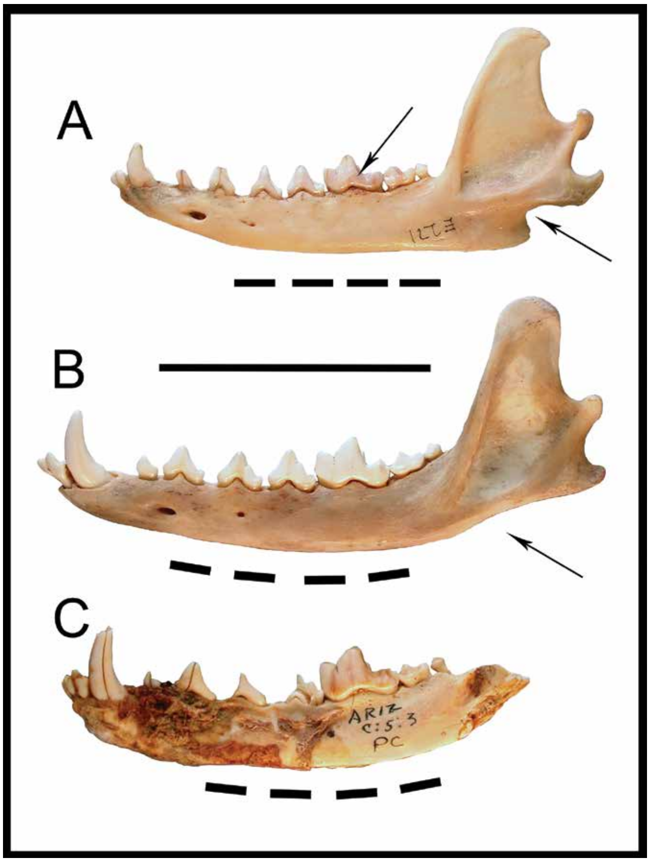


Figure 1. Left dentaries of foxes in labial view. A) modern Urocyon cinereoargenteus (gray fox), note the presence of notch in postero-ventral end of horizontal ramus (arrow), the straight ventral edge (dashed line), and the arrow to the m1 locating the protostylid (see text); B) modern *Vulpes vulpes* (red fox), note absence of postero-ventral notch (arrow versus that in A) and curved ventral edge (dashed line); C) GRCA 76272, note same characters exhibited in Vulpes vulpes and lack of characters exhibited in *Urocyon cinereoargenteus* (A).

Table 1. Alveolar length (mm) of the lower p1-m3. Comparing GRCA 76272 from Stanton's Cave, Grand Canyon, with modern fox specimens housed at the Mammoth Site, Hot Springs, South Dakota and Gray Fossil Site, East Tennessee State University, Tennessee.

Taxon	n=	Measurement
GRCA 76272	1	56.30
Vulpes vulpes (red fox)	5	54.87–64.57
Urocyon cinereoargenteus (gray fox)	6	43.67–51.00
Vulpes macrotis (kit fox)	5	42.75–47.53
Vulpes velox (swift fox)	1	49.37
Alopex lagopus (Arctic fox)	1	48.22

compared to modern specimens (now housed at the Mammoth Site, Hot Springs, SD; and the Gray Fossil Site, East Tennessee State University, TN) of five extant fox species: kit fox, gray fox, red fox, swift fox (*Vulpes velox*), and Arctic fox (*Alopex*) (Table 1, Fig. 1; taxonomy as used by Mercure et al., 1993).

The features used here to separate the gray fox from the red fox and other species are: 1) measurements of the alveolar length (mm) from the anterior alveolar edge of the lower first premolar (p1) through to the posterior alveolar edge of the lower third molar (m3); 2) the presence or absence of a distinctive notch in the postero-ventral end of the horizontal ramus (postero-ventral notch) (Fig. 1; see Tedford et al., 1995); 3) the curve or straightness of the ventral surface of the horizontal ramus (Fig. 1); and 4) the presence or absence of the protostylid on the postero-labial edge of the m1 protoconid (Fig. 1; Tedford et al., 1995; character 29) .

RESULTS

Measurements were taken of five species and compared to GRCA 76272 (Table 1). The dentaries of the kit, swift, and arctic foxes are characteristically smaller than that of the red fox and GRCA 76272 (Table 1). Measurement of GRCA 76272 is within the size range of red fox and is distinctly larger than that of the gray fox, smaller species of *Vulpes*, and *Alopex* (Table 1).

The GRCA 76272 dentary (Fig. 1C) is broken posteriorly, so the area where a postero-ventral notch would occur (as on *Urocyon*; Fig 1A) is not fully exhibited. However, the horizontal ramus continues far enough to prove no existence of a postero-ventral notch that is the characteristic in *Vulpes* spp. and *Alopex*.

On *Urocyon,* the ventral surface of the horizontal ramus is relatively straight antero-posteriorly until interrupted by the postero-ventral notch (Fig. 1A). This ventral surface of the horizontal ramus is conspicuously curved on species of *Vulpes* and *Alopex* (Fig. 1B) and the fossil specimen (Fig. 1C).

Urocyon has a protostylid on the posterolabial edge of the m1 protoconid (Fig. 1A), whereas *Vulpes* and the fossil specimen do not (Tedford et al., 1995; character 29).

Thus, given the four criteria mentioned above, GRCA 76272 is identified as a red fox and not *Urocyon*.

DISCUSSION

Kurtén and Anderson (1980) reported the red fox as an apparent late immigrant to North America, with no record antedating the Sangamonian Interglacial (greater than about 110,000 years old), except possibly in the far north (Alaska, Canada). More recent genetic work has revealed new information on the immigration of the red fox in North America (Aubry et al., 2009; Sacks et al., 2010, Statham et al., 2012). Their data suggest that the red fox first reached North America from Asia after dispersing across Beringia during a phase of the Illinoian Glaciation (Marine Isotope Stage 6, MIS), and during the following nearly 30,000 year-long Sangamonian Interglacial (approximately MIS 5e), it likely dispersed further south into the USA. During the continental Wisconsinan Glaciation (MIS 3 and 4) red fox populations separated in the far north from those further south resulting in two isolated populations, thus equating to a Holarctic clade and a Nearctic clade. The Holarctic clade was isolated in unglaciated portions of Alaska, the Yukon, and further west within Beringia. The Nearctic clade became isolated south of the ice sheets in the contiguous USA in forested western mountains, grasslands, and in the eastern region (Aubry et al., 2009; Statham et al., 2012).

The red fox has been documented in the fossil record from Late Pleistocene shoreline deposits of Lake Bonneville, Utah, in the eastern Great Basin (Nelson and Madsen, 1986), and in more than 25 late Rancholabrean-age sites from Arkansas, California, Colorado, Idaho, Missouri, New Mexico, Tennessee, Texas, Virginia, and Wyoming (Kurtén and Anderson, 1980; Harris, 1985; Harris, 2016). Despite this wide distribution, the fossil red fox has remained relatively unknown in the greater Southwest and into Sonora, Mexico (Mead et al., 2005; Harris, 2016).

CONCLUSIONS

Originally identified as *Urocyon cinereoargenteus* (gray fox) (Olsen and Olsen, 1984), morphometric and morphological data (Table 1, Fig. 1) presented here demonstrate that the two dentaries (GRCA 76262) from Stanton's Cave, eastern Grand Canyon belong to the red fox (*Vulpes vulpes*), not the gray fox. This finding is a significant addition to the paleobiological record of the Grand Canyon region, as well as that of Arizona. While the modern gray fox is common in the region today, the extant red fox is limited to the extreme northeastern portion of Arizona (Hoffmeister, 1986; Mikesic and LaRue, 2003) and is not known from the Grand Canyon (Mead et al., 2005). Although the fossil red fox has been documented from surrounding states and other regions in the greater Southwest (Kurtén and Anderson, 1980; Harris, 1985; Nelson and Madsen, Jr., 1986; Harris, 2016), the Late Pleistocene record in Arizona appears to be lacking this fox. Knowing this, we recommend that radiocarbon analysis be conducted on GRCA 76262. Although the two red fox dentaries could prove to be of the Late Pleistocene, we hypothesize that they will be middle to late Holocene in age. However, these specimens do represent the first record of red fox remains from the Grand Canyon and may be the first Pleistocene reported from Arizona.

ACKNOWLEDGMENTS

We thank the Grand Canyon National Park for allowing research in the park. Special thanks to: Colleen Hyde, GRCA Museum Collection manager for instigating this project and continued support; Sandra L. Swift for photographs and graphics assistance; David Mikesic, then Zoologist/Manager, Navajo Nation Zoological and Botanical Park and Dr. Jan Kamler, then Wildlife Conservation Research Unit, University of Oxford, United Kingdom, for early input on modern fox distributions in Arizona; and Meg Palevich for input on canid morphologies.

REFERENCES

Aubry, K.B., Statham, M.J., Sacks, B.N., Perrine, J.D., and Wisely, S.M., 2009, Phylogeography of the North American red fox: vicariance in Pleistocene forest refugia: Molecular Ecology, v. 18, p. 2668–2686. https://doi.org/10.1111/j.1365-294X.2009.04222.x

Bailey, V., 1935, Mammals of the Grand Canyon region: Grand Canyon Natural History Association, Natural History Bulletin, no. 1.

Cockrum, E.L., 1960, The recent mammals of Arizona: their taxonomy and distribution: University of Arizona Press, Tucson.

Euler, R.C., 1984, The archaeology, geology, and paleobiology of Stanton's Cave, Grand Canyon National Park, Arizona: Grand Canyon Natural History Association, Monograph no. 6, p. 1–141.

Harris, A.H., 1985, Late Pleistocene vertebrate paleoecology of the West: University of Texas Press, Austin.

Harris, A.H., 2016, Pleistocene vertebrates of southwestern USA and northwestern Mexico, University of Texas El Paso, accessed 6 March 2023. https:www.utep.edu/leb/pleistNM/taxaMamm/Vulpes.htm.

Hoffmeister, D.F., 1971, Mammals of Grand Canyon: University of Illinois Press, Urbana.

Hoffmeister, D.F., 1986, Mammals of Arizona: University of Arizona Press, Tucson.

Kurtén, B., and Anderson, E., 1980, Pleistocene mammals of North America: Columbia University Press, New York.

Mead, J.I., 1981, The last 30,000 years of faunal history within the Grand Canyon, Arizona: Quaternary Research, v. 15, p. 311–326. https://doi.org/10.1016/0033-5894(81)90033-8

Mead, J.I., Czaplewski, N.J., and Agenbroad, L.D., 2005, Rancholabrean (Late Pleistocene) mammals and localities of Arizona: *in* McCord, R.D., ed., Vertebrate paleontology of Arizona: Mesa Southwest Museum Bulletin, no. 11, p. 139–180.

Mikesic, D.G., and LaRue, C.T., 2003, Recent status and distribution of red foxes (*Vulpes vulpes*) in northeastern Arizona and Southeastern Utah: Southwestern Naturalist, v. 48, p. 624–634. https://doi.org/10.1894/0038-4909(2003)048<0624:RSADOR>2.0.CO;2

Mercure, A., Ralls, K., Koepfli, K.P., and Wayne, R.K., 1993, Genetic subdivisions among small canids: mitochondrial DNA differentiation of swift, kit, and arctic foxes: Evolution, v. 47, p. 1313–1328. https://doi.org/10.1111/j.1558-5646.1993.tb02157.x

Nelson, M.E., and Madsen, J. H., 1986, Canids from the Late Pleistocene of Utah: Great Basin Naturalist, v. 46, p. 415–420.

Olsen, J.W., and Olsen, S.J., 1984, Zooarchaeological analysis of small vertebrates from Stanton's Cave, Arizona: *in* Euler, R.C., ed., The archaeology, geology, and paleobiology of Stanton's Cave, Grand Canyon National Park, Arizona: Grand Canyon Natural History Association, Monograph no. 6., p. 48–57.

Phillips, A.M., 1984, Shasta ground sloth extinction: fossil packrat midden evidence from the western Grand Canyon: *in* Martin, P.S., and Klein, R.G., eds., Quaternary Extinctions: a prehistoric revolution: University of Arizona Press, Tucson, p. 148–158. https://doi.org/10.2307/j.ctv264f91j.12

Rea, A.M., and Hargrave, L.L., 1984. The bird bones from Stanton's Cave: *in* Euler, R.C., ed., The archaeology, geology, and paleobiology of Stanton's Cave, Grand Canyon National Park: Grand Canyon Natural History Association, Monograph no. 6, p. 77–91.

Sacks, B.N., Statham, M.J., Perrine, J.D., Wisely, S.M., and Aubry, K.B., 2010, North American montane red foxes: expansion, fragmentation, and the origin of the Sacramento Valley red fox: Conservation Genetics, v. 11, p. 1523–1539. https://doi.org/10.1007/s10592-010-0053-4

Statham, M.J., Sacks, B.N., Aubry, K.B., Perrine, J.D., and Wisely, S.M., 2012, The origin of recently established red fox populations in the United States: translocations or natural range expansions?: Journal of Mammalogy, v. 93, p. 52–65. https://doi.org/10.1644/11-MAMM-A-033.1

Tedford, R.H., Taylor, B.E., and Wang, X., 1995. Phylogeny of the Caninae (Carnivora: Canidae): the living taxa: American Museum Novitates, no. 3146.

Charles P. Bruce and Jim I. Mead. Quarternary badger (Mustelidae: *Taxidea*) from Snake Creek Burial Cave, Nevada. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 178-189. DOI:10.4311/2024PA0100

QUATERNARY BADGER (MUSTELIDAE: *TAXIDEA*) FROM SNAKE CREEK BURIAL CAVE, NEVADA

Charles P. Bruce[1] and Jim I. Mead[2,C]

ABSTRACT

We report on the fossils of the North American badger, *Taxidea taxus* (Carnivora) recovered from Snake Creek Burial Cave (SCBC), White Pine County, Nevada. The natural trap cave with its large funnel-shaped entrance at the base of the southern Snake Range, east-central Great Basin, contains deposits with radiocarbon ages that span from a median 8,709 cal yr BP to 48,028 cal yr BP. Skeletal remains of *Taxidea* are not overly abundant in the deposit compared to other more common carnivorans such as the canids (e.g., foxes). Measurements of the cranial and postcranial remains fall somewhere in the medium range relative to extant badger specimens. Thus, this badger appears to have been of the typical size of extant members and not a large variety emblematic of many Late Pleistocene mammals. Macrobotanical remains from packrat middens in the east-central Great Basin suggest that subalpine and montane conifers grew on the lower mountain slopes and valley bottoms above high lake stands of Lake Bonneville. Given the right substrate, select species of subalpine and montane conifers, along with sagebrush and other shrubs, likely formed a continuous or near-continuous belt from the Wasatch Front of Utah to the Sierra Nevada of California/Nevada. Continued work on the faunas and floras from caves and packrat middens in the Snake Range (e.g., Smith Creek, Ladder, Combustion, Cathedral, Arches Caves) and low in the valley (e.g., SCBC, Garrison Cave) will help in the reconstruction of the Late Pleistocene biotic communities above the high stands of Lake Bonneville and how the biotic communities, including the badger, adapted to climate change.

INTRODUCTION

The North American badger, *Taxidea taxus* (Schreber, 1778) (Carnivora: Mustelidae) is a mesocarnivore and a major component of extant North American prairies, shrublands, desert grasslands, among other communities (Long, 1973). It is the only living member of the subfamily Taxidiinae, which is the most basal subfamily within the crown group Mustelidae (Koepfli et al., 2008; Sato et al., 2012; Law et al., 2018). American badgers were once grouped within the Eurasian badger subfamily Melinae; however, it is now understood that "badgers" are a polyphyletic grouping of musteloids that tend to share similar ecologies and appearances, including the honey badger (Mellivorinae), the ferret badgers (Helictidinae), and the stink badgers (*Mydaus*; Mephitidae) (Owen, 2006; Sato, 2016).

The endemic *Taxidea taxus* is extant over most of central and western USA, extending south into central Mexico and north into western Canadian provinces (Long, 1973). Relevant to the study here is that the badger is common throughout the Great Basin, both in Nevada (Hall, 1946) and Utah (Durrant, 1952) (Fig. 1). The diet of extant *Taxidea* is predominantly rodents, especially fossorial ground squirrels (e.g., *Callospermophilus, Otospermophilus*, *Xerospermophilus*, following Helgen et al., 2009) and prairie dogs (*Cynomys*), but the badger is also exceedingly opportunistic (Linsdale, 1938; Long, 1973).

Taxidiine badgers have a poorly understood fossil record that makes the study of early members of the subfamily difficult, yet noteworthy. Two genera of extinct taxidiines are known exclusively from the Hemphillian North American Land Mammal Age (NALMA), *Chamitataxus* and *Pliotaxidea*; the earliest occurrence of *Taxidea* is from the late Hemphillian. For discussions on the earliest age for *Taxidea*, see Drescher (1939), Hall (1944), Stock (1948), Wagner (1976), and Owen (2006). In contrast to its earliest occurrence along with that of its ancestors, *T. taxus* is common in late Quaternary (Rancholabrean NALMA) fossil assemblages over much of the continent, albeit never abundant in any one locality (Harris, 1985). The presence of *T. taxus* in Quaternary fossil localities is often used to imply that the local setting was an open biome, with sandy to gravel-dominated substrates, yet it is scarce in marshy and clayey soil environs due to its digging habits (Hall, 1946; Long, 1973). Fossorial mammals, such as *Taxidea,* are known to be sensitive to environmental change (Rowe and Terry, 2014), thus, further understanding the Quaternary locations of this badger in the Great Basin is of biogeographical, if not also paleoenvironmental, interest. Here we present the fossil *Taxidea* from Snake Creek Burial Cave (SCBC), White Pine County, Nevada, east-central Great Basin.

---

[1] Department of Natural Resource Management, South Dakota State University, Rapid City, SD 57703

[2] The Mammoth Site, 1800 Hwy 18 BYP, Hot Springs, SD 57747; Desert Laboratory at Tumamoc Hill, University of Arizona, Tucson, AZ 85721

[C] Corresponding author: jmead@mammothsite.org

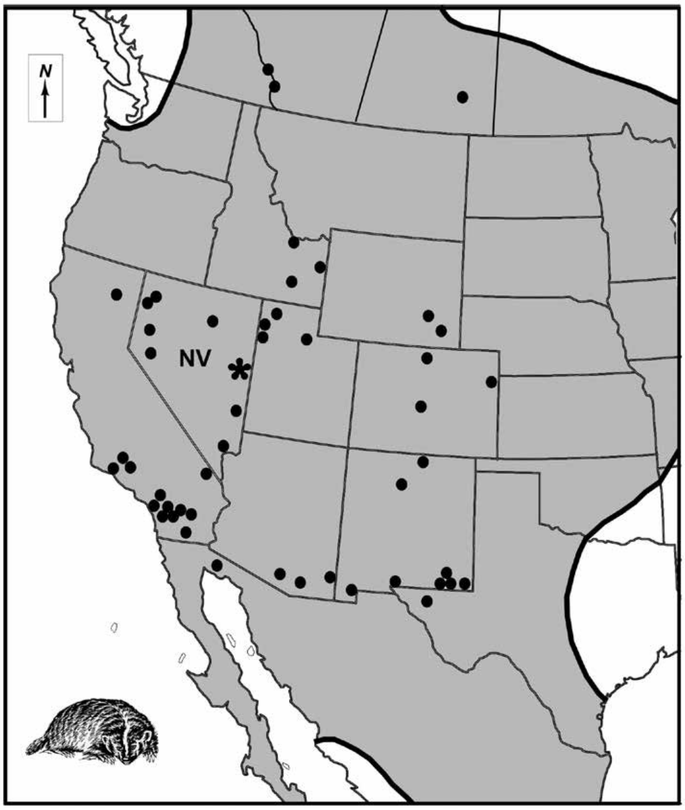


Figure 1. Western North American Pleistocene *Taxidea taxus* fossil localities as listed in Appendix 1. Present distribution of *Taxidea* covers most of the area on the map.

SNAKE CREEK BURIAL CAVE

SCBC is located at 1731 m elevation in a valley-bottom, open sagebrush setting just above and near the high stand of pluvial Lake Bonneville at its southwestern most extent to the southern Snake Range Mountains (Grayson, 1993; Reheis et al., 2014; Milligan and McDonald, 2017). When pluvial Lake Bonneville was at its highest stand during the Wisconsinan Glaciation (~18,000 yr BP; 1552 m; McGee et al., 2012) the beach was within about 5 km of the cave. The surface access to the cave begins as a large sinkhole that culminates to a hole that is approximately 0.5 by 1.0 m, which then drops 17 m to the sediment-filled room floor. The funnel-shaped sinkhole at the surface, and the bell-shaped free fall to the floor, have created a natural trap scenario for millennia (Mead and Mead, 1989).

Presence of extinct megafauna, such as *Camelops,* in this cave indicates a Rancholabrean NALMA for the deposit. Chronology of the fossil deposit continues to develop, but currently spans from approximately 8,700 to 48,000 calibrated radiocarbon years ago (see results).

Various taxonomic groups from the cave sediments are still in need of analysis and are ongoing. A nondescriptive presentation of the mustelid carnivores (including *Taxidea*) was presented in Mead and Mead (1985) and Mead and Mead (1989). Details about *Mustela* spp. were presented in an unpublished thesis by Fox (2014). The occurrence of the black-footed ferret (*Mustela nigripes*) was verified in Fox et al. (2017). Squamate reptiles were presented in Mead et al. (1989). Arvicoline rodents (voles) were presented in Bell and Mead (1998). A geometric morphometric study of a *Martes* (pine marten) cranium was part of an unpublished thesis (Meyers, 2007); a detailed presentation of all *Martes* cranial and postcranial remains from the deposit is ongoing. Canid remains were presented in an unpublished thesis (Palevich, 2005). Lagomorphs were analyzed for an unpublished thesis (Osterhaudt, 1999).

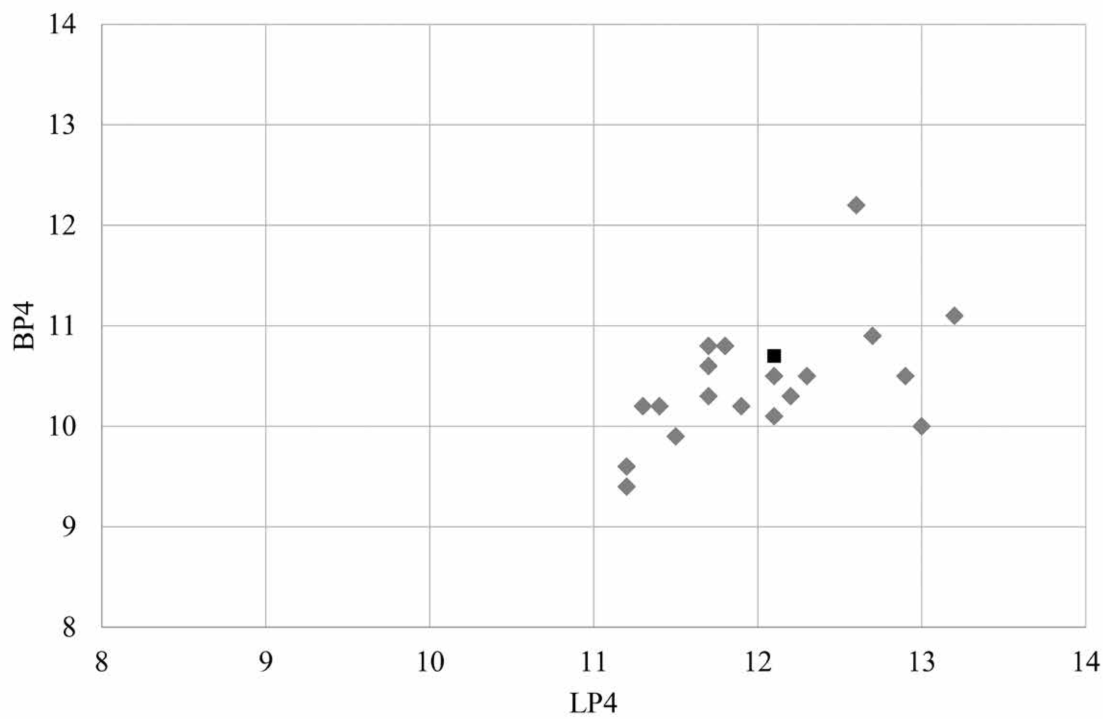


Figure 2. SCBC *Taxidea* upper fourth premolar length (LP4) vs. breadth (BP4) measurements (mm) compared to modern specimens. Square = SCBC; diamond = modern.

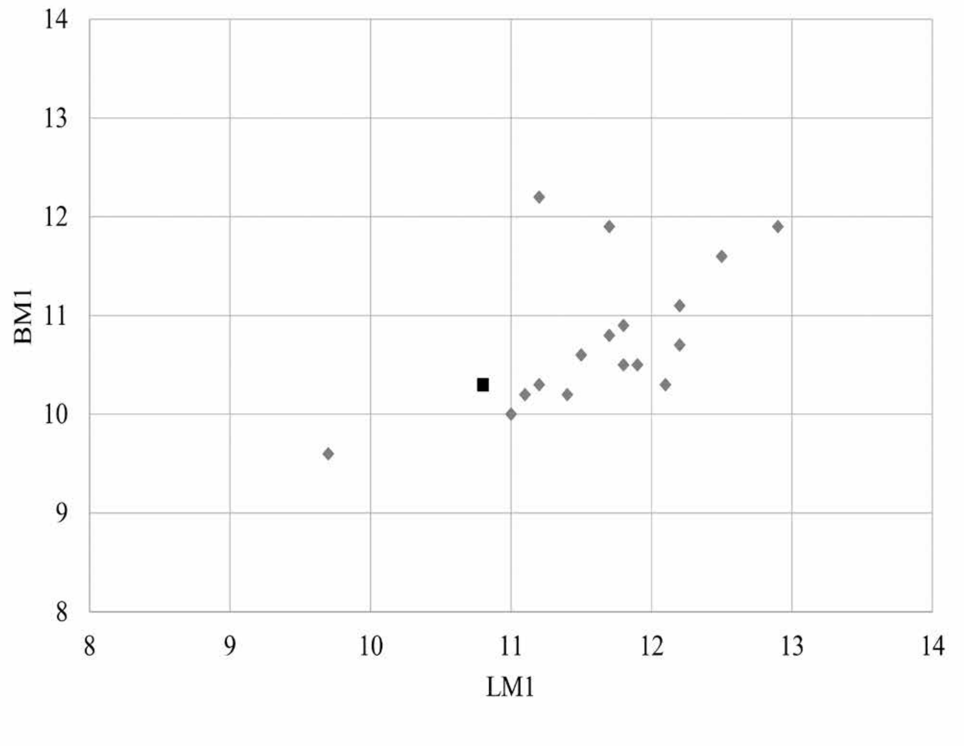


Figure 3. SCBC *Taxidea* upper first molar length (LM1) vs. breadth (BM1) measurements (mm) compared to modern specimens. Square = SCBC; diamond = modern.

Artiodactyl and horse fossils are the topic in an ongoing manuscript. Avian remains and additional radiocarbon dates were presented in Emslie and Mead (2023). Details about the *Taxidea* fossils are presented here.

METHODS

Fossils recovered from the excavations in 1984 and 1987 (see Mead and Mead, 1989) were curated into the collections of The Mammoth Site (Hot Springs, South Dakota; MSQ). The following specimens were recovered in the excavations. MSQ numbers are in parentheses. *Taxidea* skeletal elements consist of:1 L maxillary fragment with P4-M1 (10) (Fig. 7A, B); 2 mandible fragments including one L and one fused R+L fragment at symphysis (41-42); 2 R P4 and 2 L P4 (45-48); 2 axis (32-33) (Fig. 8); 2 pelvic fragments (49-50); 1 R humerus (11) (Fig. 7E, F); 4 R radius and 1 L radius, all immature, lacking proximal epiphyses (26, 34-37); 1 R and 2 L ulna, two lacking distal epiphyses (12, 43-44) (Fig. 7C, D); 3 R and 1 L femur, immature to lacking distal epiphyses (13, 19, 21, 27) (Fig. 8); 3 R tibia (38-40); 2 L astragalus (16, 53) (Fig. 8); 1 R and 2 L calcaneus (25, 51-52) (Fig. 8); 5 metacarpal (14, 18, 22); 1 metatarsal (15); 5 metapodial (24); 13 1st-2nd phalanx (17, 20, 23); 32 distal, 3rd phalanx (54-64) (Fig. 8).

There is limited literature that provides linear skeletal measurements of *Taxidea*. Measurement methods for postcrania used here are based on Von Den Driesch (1976) and Samuels et al. (2013). We found the measurement methods in Samuels et al. (2013) on the ulna to be more ideal for graphing length vs. width, thus we use their methods to supplement those of Von Den Driesch (1976) for this element. Measurements of the maxilla follow Anderson (1970). Identifications presented here are based on the analysis using morphological characters and linear measurements from comparative specimens.

Anatomical and skeletal abbreviations: BM1, breadth of the upper first molar; BP4, breadth of the upper fourth premolar; FBD, femur greatest breadth at distal end; FBP, femur greatest breadth of the proximal end; FGL, femur greatest length; FSD, femur smallest breadth of diaphysis; HBD, humerus greatest breadth at distal end; HBP, humerus greatest breadth of the proximal end; HGL, humerus greatest length; HSD, humerus smallest breadth of diaphysis; L, left; LM1, length of the upper first molar; LMTR, length maxillary tooth row; LP4, length of the upper fourth premolar; R, right; UAPD, ulna midshaft anteroposterior diameter; UDAP, ulna depth across the processus anconaeus; UGL, ulna greatest length; ULOL, ulna length of the olecranon process; and USDO, smallest depth of the olecranon.

Institutional abbreviation: LACM, Los Angeles County Museum, California; MSCC, Mammoth Site Comparative Collection, The Mammoth Site of Hot Springs, South Dakota; MSQ, Mammoth Site Quaternary, The Mammoth Site of Hot Springs, South Dakota; SDSM R, South Dakota School of Mines Recent, Rapid City, South Dakota; UCLA, University of California, Los Angeles, California; USNM, United States National Museum, Washington, DC.

RESULTS

Chronology for the SCBC deposit has expanded greatly since first presented in Mead and Mead (1989). New calibrated radiocarbon dates analyzed directly on select taxa are presented in Emslie and Mead (2023) and here, which illustrate that ages span from a median 8,709 cal yr BP to 48,028 cal yr BP (Table 1). A date directly on *Taxidea* is 37,045 cal yr BP.

Table 1. Radiometric ages from Snake Creek Burial Cave, White Pine County, Nevada, southern Snake Range. Notes include provenience from original excavation (year excavated followed by test pit number and level from surface; Mead and Mead, 1989). Abbreviations: *, U-Th age analysis, see reference; Lv, level; TR, this report. Calibration of AMS ages based on OxCal 4.4.

Species Dated	14C Age yr BP	Median Age Cal yr BP	Cal Age Range yr BP	Lab	Reference and Notes
Bat guano	7,860±130	8,709	9,011-8,411	Beta 22169	Mead and Mead, 1989; Unit II
Wood	9,460±160	10,755	11,190-10,338	Beta 24643	Mead and Mead, 1989; Unit III
Canis lupus wolf	10,085±25	11,653	11,815-11,600	UCIAMS 260201	TR; metacarpal; 87-1, Lv 3
Equus horse	15,100±700*	-	-	-	Mead and Mead, 1989; Unit III
Centrocercus sage-grouse	23,050±100	27,322	27,609- 27,190	UCIAMS 256740	Emslie and Mead, 2023, 87-3, Lv 1
Nyctea scandiaca snowy owl	30,680±240	35,028	35,498-34,544	UCIAMS 256737	Emslie and Mead, 2023; 87-1; Lv 6
Taxidea; badger	32,660±300	37,045	38,133-36,274	UCIAMS 260205	TR; metapodial; Unit III
Lynx rufus; bobcat	32,900±310	37,406	38,759-36,505	UCIAMS 260202	TR; p/4 from mandible; 87-1
Nyctea scandiaca; snowy owl	33,710±340	38,619	39,501-37,507	UCIAMS 256738	Emslie and Mead, 2023; 87-1, Lv 7
Centrocercus sage-grouse	35,019±410	40,182	40,949-39,395	UCIAMS 256739	Emslie and Mead, 2023; 87-1, Lv 5
Martes marten	45,300±1400	48,028	52,330-45,135	UCIAMS 260206	TR; m/1; Unit III

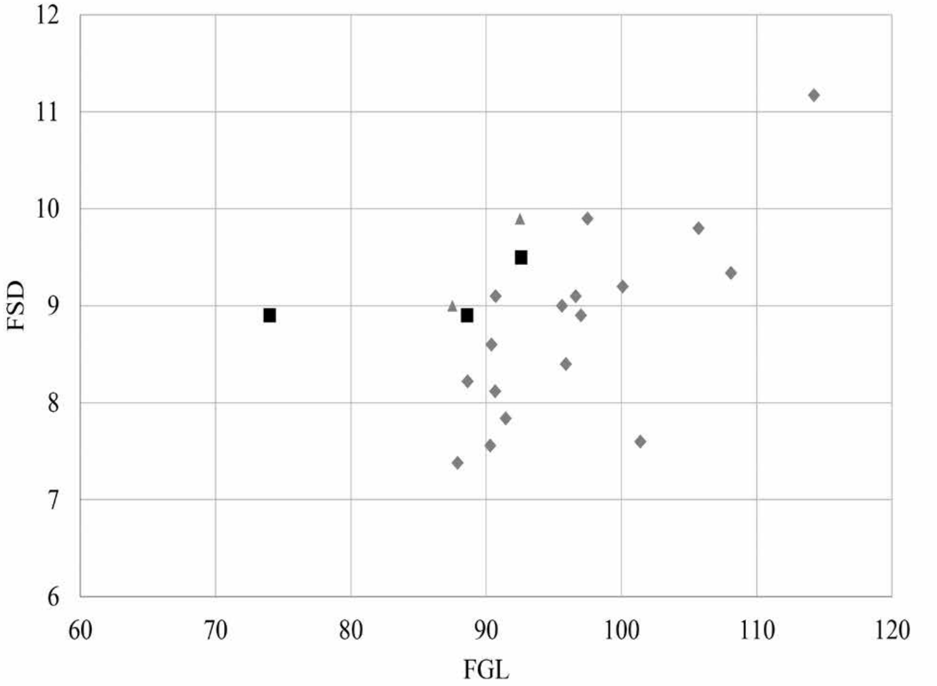


Figure 4. SCBC *Taxidea* femora greatest length (FGL) vs. smallest breadth of the diaphysis (FSD) measurements (mm) compared to modern specimens. Square = SCBC; diamond = modern; triangle = modern juvenile.

While presently confined to Eurasia, meline badgers inhabited North America in the pre-Pleistocene. For completeness, we compared the SCBC badger fossils to extant *Meles* and extinct North American melines using figures from Lavocat (1966), Wallace and Wang (2004), and Wolsan and Sotnikova (2013). Only two genera of meline badgers have been reported from North America, *Arctomeles* and *Ferinestrix*, which are known from cranial material that is early to middle Pliocene (Blancan NALMA; Tedford and Harington, 2003; Wallace and Wang, 2004; Wolsan and Sotnikova, 2013). The maxillary fragment from SCBC retains the upper left tooth row with P4, M1, and alveoli for P2-3 preserved. SCBC P4 is similar in size to the M1 in occlusal view, whereas the P4 of all melines is smaller than M1 (Wolsan and Sotnikova, 2013). SCBC P4 has a well-developed protocone, whereas all melines have a protocone that is small, ridge-like, or absent (Wolsan and Sotnikova, 2013). SCBC M1 is triangular in occlusal view similar to all known members of Taxidiinae (Owen, 2006). In contrast, the M1s of *Ferinestrix* and *Meles* are rectangular and that of *Arctomeles* is rhombus shaped. Additionally, SCBC M1 exhibits a labiolingually oriented crest formed by the epicrista that lies between the paracone and protocone, while the M1s of *Arctomeles*, *Ferinestrix*, and *Meles* share a complex anteroposteriorly oriented crest composed of the paraconule, protocone, and an elongate postprotocrista.

Cranial measurements of SCBC *Taxidea* fit well within the range of modern specimens (Table 2; Figs. 2 and 3). With the identification of the SCBC badger maxilla as taxidiine rather than meline, we compared SCBC badger skeletal material to another taxidiine badger, *Pliotaxidea*, using figures from Wagner (1976). The posterior margin of the SCBC M1 terminates in a blunt, rounded heel, rather than a sharp, elongate apex such as in *Pliotaxidea* (Wagner, 1976). Thus,

Table 2. Table of cranial measurements (mm) of *Taxidea taxus* from Snake Creek Burial Cave, White Pine County, Nevada, along with modern specimens. (*) denotes a minimal measurement from an unfused or fragmented element. (!) – denotes measurements from significantly worn teeth. Abbreviations in text.

Specimen	LP4	BP4	LM1	BM1	LMTR
MSQ 10	12.1	10.7	10.8	10.3	40.8
MSCC 10	11.2	9.6	11.2	10.3	39.0
MSCC 93	11.2!	9.4!	9.7!	9.6!	38.8!
MSCC 143	11.5	9.9	12.1	10.3	41.7
MSCC 388	11.7	10.6	11.9	10.5	40.6
MSCC 389	12.1	10.1	11.8	10.5	40.8
SDSM R 52	12.6	12.2	12.5	11.6	41.5
SDSM R 53	13.2	11.1	9.5!	11.5!	41.2
SDSM R 54	11.7	10.3	11.8	10.9	40.5
SDSM R 55	13.0*	10.0*	-	-	42.4
SDSM R 609	12.9	10.5	11.7	10.8	42.2
SDSM R 685	11.4	10.2	11.5	10.6	41.1
SDSM R 711	11.3	10.2	11.1	10.2	40.0
SDSM R 817	12.7	10.9	12.2	11.1	42.8
SDSM R 490	11.8	10.8	12.2	10.7	42.2
SDSM R244	11.8*	10.8	12.9	11.9	42.1
SDSM R 315	12.2	10.3	11.4	10.2	40.4
SDSM R 527	12.1	10.5	11.7	11.9	41.7
SDSM R 117688	11.7*	10.8	11.0	10.0	41.2
SDSM R 117689	11.9	10.2	11.2*	12.2	38.2
SDSM R 117690	12.3	10.5	-	10.9	-

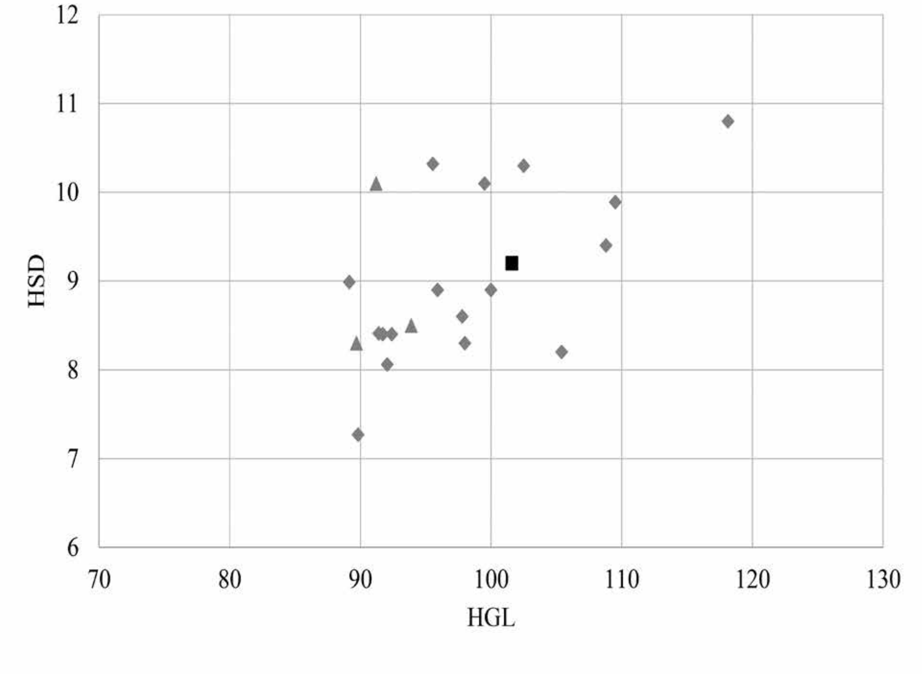


Figure 5. SCBC *Taxidea* humeri greatest length (HGL) vs. smallest breadth of the diaphysis (HSD) measure ments (mm) compared to modern specimens. Square = SCBC; diamond = modern; triangle = modern juvenile.

the SCBC specimen is identified as belonging to *Taxidea*.

Using modern comparative specimens and linear measurements (Tables 2–5), we were able to identify *Taxidea taxus* material from SCBC. Overall, the postcrania are short, stout, and that of a medium-sized carnivoran. We were able to rule out non-badger mustelids, as well as mephitids, based on the smaller size and more gracile postcrania of those taxa in relation to those of the badger. Additionally, we were able to rule out procyonids, canids, and felids based on the larger, longer, and thinner postcrania elements of those taxa.

For meline badgers, SCBC postcrania were only compared to *Meles* due to the lack of known North American meline postcrania. The SCBC badger humerus has a notably broad lateral supracondylar ridge that resembles the wide humeri of *Taxidea* rather than what is a comparably narrower humerus of *Meles*. The ulnae from SCBC have a long, protruding olecranon process, as observed on extant *Taxidea*, rather than the shorter morphology found on *Meles*. The badger phalanges and metapodials recovered from SCBC are particularly robust, an adaptation for heavy digging that can be attributed to *Taxidea*. Based on these characters, we propose that the SCBC badger specimens do not represent a late-surviving Quaternary North American meline badger.

Wagner (1976) states that the humerus of *Taxidea* has more developed deltoid and pectoral crests compared to *Pliotaxidea*, which is observed to be the case in the SCBC humerus (Fig. 7E–F). Based on these characters, we designated all SCBC badger skeletal remains as *Taxidea*. Additionally, the SCBC badger material shows no morphological evidence of being a distinct taxon from the only taxidiine badger species known from the Pleistocene, *Taxidea taxus;* and therefore, was designated as such.

The SCBC humerus (MSQ 11) fits within the upper size range of living juvenile *T. taxus*, making it a relatively large juvenile or immature individual (Table 4; Fig. 5; Fig. 8). The SCBC ulna (MSQ 12) is particularly large and robust compared to modern *Taxidea* specimens (Table 5; Fig. 6; Fig. 8), especially for an immature individual. MSQ 12 has a moderately long greatest length, but its depth is notably the greatest measurement of all other ulnae measured for this

Table 3. Table of measurements (mm) for the femur of *Taxidea taxus* from Snake Creek Burial Cave, White Pine County, Nevada, along with modern specimens. (*) – denotes a minimal measurement from an unfused or fragmented element. (/) denotes a measurement that was taken from fused and unfused elements of the same pair. Abbreviations in text.

Specimen	FGL	FSD	FBD	FBP
MSQ 19	92.6*	9.5	25*	31.2*
MSQ 21	92.8*	8.9	21.8*	27.8*
MSQ 13	74*	8.9	20.2*	24.9*
MSCC 389	100.1	9.2	24.3	29.2
MSCC 386	101.4	7.6	23.9	26.6
SDSM R 711	95.6	9	22.3	28.3
SDSM R 609	92.5*/97.5	9.9	21.1*/23.7	29.2
SDSM R 685	95.9	8.4	21.3	27.0
SDSM R 689	87.5*	9	20.6	24.8
SDSM R 468	105.7	9.8	23.4	30.1
SDSM R 817	97	8.9	22.5	27.1
MSCC 93	90.7	9.1	23.7	28.0
MSCC 10	90.4	8.6	24.1	28.8*
USNM 264140	114.2	11.17	27.16	-
LACM 52215	90.3	7.56	19.75	-
LACM 85731	91.4	7.84	19.77	-
UCLA 13768	96.6	9.1	23.03	-
UCLA 13974	90.6	8.12	21.56	-
UCLA 16002	87.8	7.38	19.93	-
UCLA 13971	88.6	8.22	21.28	-
UCLA 13057	108.1	9.34	23.48	-

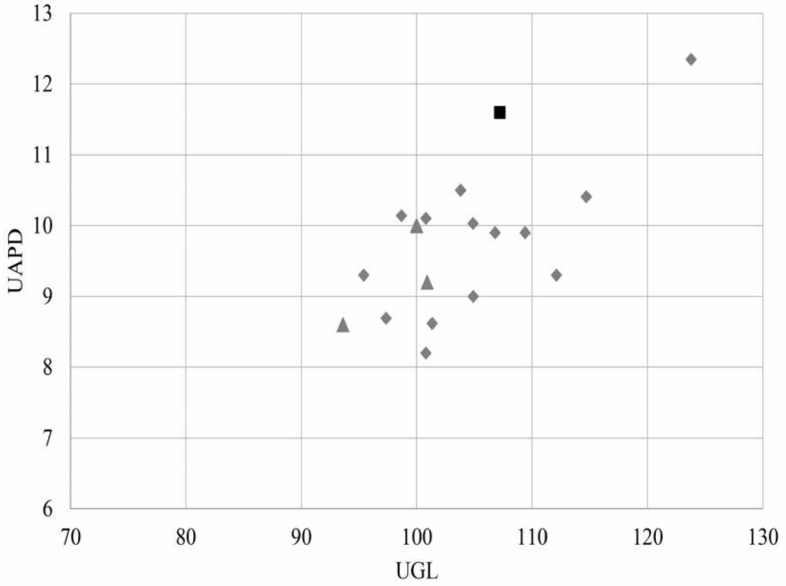


Figure 6. SCBC *Taxidea* ulnae greatest length (UGL) vs. midshaft mediolateral diameter (UAPD) measurements (mm) compared to modern specimens. Square = SCBC; diamond = modern; triangle = modern juvenile.

project. If the badger from SCBC had grown to maturity, based on its substantial ulna depth, it likely would have been a large individual.

There were three immature femora recovered. Measurements of SCBC femora are similar to modern specimens, except that MSQ 13 (small juvenile) is particularly shorter and thinner than both other fossil and modern specimens (Table 3; Fig. 4; Fig. 8). MSQ 21 is also from an immature individual, yet it has a distinctly robust anterior end, larger than typical adult badgers today (Fig. 8). All other SCBC skeletal measurements on *Taxidea* fall somewhere in the medium to small size range relative to extant badger specimens. Based on the overall measurements, most of the badgers recovered from SCBC appear to have been of typical size of the extant forms. The minimum number of individuals (MNI) of *Taxidea* recovered from SCBC is three based on three immature right radii from different proveniences (MSQ 34–36) and three immature right tibiae (MSQ 38–40).

DISCUSSION AND CONCLUSIONS

We present the analysis of the cranial and post-cranial remains of *Taxidea* from the Late Pleistocene deposits in SCBC. Calibrated radiocarbon ages analyzed directly on select avian and mammalian taxa confirm that the natural trap cave deposits represent the Wisconsinan pre-full glacial, late glacial, and earliest Holocene. Skeletal remains of *Taxidea* were not overly abundant in the deposit compared to other more common carnivorans, such as canids (e.g., foxes). The record of badger in SCBC is not surprising for both the Great Basin and the Intermountain West. Figure 1 displays the geographic distribution of Pleistocene-age localities (Table 6) yielding *Taxidea* (both *T. taxus* and *Taxidea* sp.) throughout western North America (see Harris 1985; https://www.utep.edu/leb/pleistNM/default.htm). All sites listed and shown in Figure 1 for western North America are within the historic range of *Taxidea* (Kyle et al., 2004); however, its range during the Late Pleistocene did extend further east than it occurs today (McDonald, 2002).

The immature state of most of the SCBC *Taxidea* remains is noteworthy and suggests to us that the avoidance of natural traps may be a learned behavior (White et al., 1984). However, the funnel-shaped sinkhole entrance is known to become coated with ice and snow during particularly harsh winter snowstorms, thus may have been more detrimental under select seasonal conditions (JIM field notes). *Taxidea* fossils from SCBC appear to indicate no notable size change in the species from the Pleistocene to today (Tables 2–5; Figs. 2–6), unlike several other extant Ice Age survivors,

Table 4. Table of measurements for the humerus of *Taxidea taxus* from Snake Creek Burial Cave, White Pine County, Nevada, along with modern specimens. Measurements in mm. (*) – denotes a minimal measurement from an unfused or fragmented element. (/) denotes a measurement that was taken from fused and unfused elements of the same pair. Abbreviations in text.

Humerus	HGL	HSD	HBD	HBP
MSQ 11	101.6*	9.2	34.2	22*
MSCC 389	102.5	10.3	34.4	25.4
MSCC 386	105.4	8.2	32.6	23.1
SDSM R711	97.8	8.6	32.5	23
SDSM R609	91.2*/99.5	10.1	33.8	19.4*/22.4
SDSM R685	89.7*/98	8.3	32.3	18.4*/21.6
SDSM R689	93.9*	8.5	34.6	19*
SDSM R468	108.8	9.4	35.2	25.6
SDSM R817	100	8.9	31.5	23.8
MSCC 93	95.9	8.9	31.7	22.6
MSCC 10	92.4	8.4	33.8	24.7
USNM 264140	118.14	10.8	37.8	-
LACM 52215	91.72	8.4	28.73	-
UCLA 13768	95.54	10.32	30.74	-
UCLA 13974	91.4	8.41	30.71	-
UCLA 16002	89.82	7.27	28.75	-
LACM 85731	92.05	8.06	28.15	-
UCLA 13971	89.16	8.99	30.39	-
UCLA 13057	109.51	9.89	36.13	-

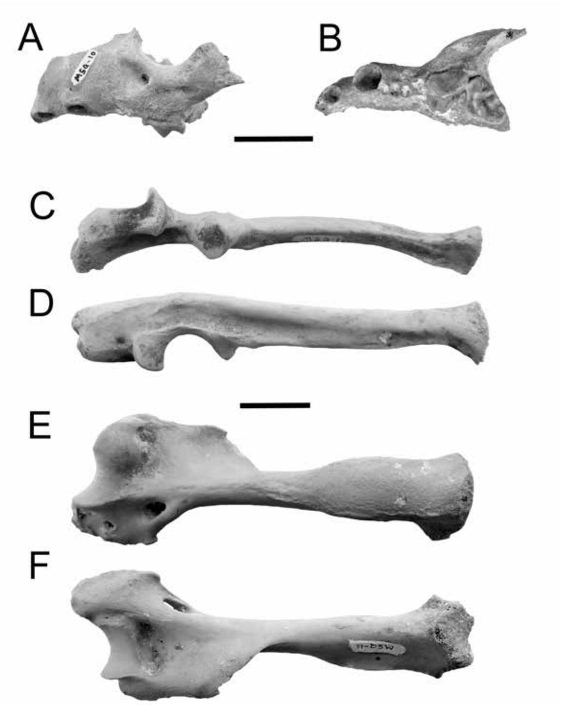


Figure 7. *Taxidea* cranial, humerus, and ulna from Snake Creek Burial Cave, White Pine County, Nevada. A, lateral and B, occlusal views of L maxillary fragment MSQ 10. C, anterior and D, lateral views of L ulna MSQ 12. E, anterior and F, posterior views of R humerus MSQ 11. Scale bars = 2 cm.

Table 5. Table of measurements for the ulna of *Taxidea taxus* from Snake Creek Burial Cave, White Pine County, Nevada, along with modern specimens. Measurements in mm. (*) – denotes a minimal measurement from an unfused or fragmented element. Abbreviations in text.

Ulna	UGL	UAPD	UDPA	USDO	ULOL
MSQ 12	107.2*	11.6	18.7	15.6	22.6
MSQ 44	111.7*	-	-	-	-
MSCC 389	109.4	9.9	17.1	12.5	19.5
MSCC 386	100.0*	10	17.3	14.2	20.1
SDSM R711	104.9	9	16.5	12.8	20.3
SDSM R609	103.8	10.5	16.7	12.5	19
SDSM R685	93.6*	8.6	15	11.7	19.3
SDSM R689	100.9*	9.2	17.1	13.4	20.4
SDSM R468	112.1	9.3	17.4	12.4	20.6
SDSM R817	106.8	9.9	15.3	11.5	20.3
MSCC 93	100.8	10.1	15.7	11.4	20.6
MSCC 10	100.8	8.2	16	12.7	19.4
USNM 264140	123.78	12.35	-	-	28.38
LACM 52215	101.33	8.62	-	-	18.26
UCLA 13768	104.88	10.03	-	-	21.15
UCLA 13974	98.68	10.14	-	-	22.67
UCLA 16002	97.34	8.69	-	-	18.45
UCLA 13971	95.41	9.3	-	-	16.57
UCLA 13057	114.71	10.41	-	-	24.73

such as *Bison*, *Martes*, *Ovis*, among others (Kurtén and Anderson, 1980). However, the sample size of badger is not ideal from SCBC. Further analysis of badger remains from additional caves should help to better understand the overall size range of Late Pleistocene *Taxidea* in the east-central Great Basin.

SCBC has not yielded fossils of *Cynomys*, thus badgers in this region would not have been preying on prairie dogs as they commonly do today elsewhere in the Intermountain West (Goodrich and Buskirk, 1998; Slobodchikoff et al., 2009). However, colonial ground squirrels, arvicoline voles, and other small rodent remains are plentiful, as well as lagomorphs in SCBC and other valley-bottom caves such as Crystal Ball Cave (60 km, 37 mi. north of SCBC; Heaton, 1987). In Nevada today, the badger is known to eat a variety of ground squirrels (*Urocitellus elegans*; *U. beldingi*; *U. townsendii*), pocket gophers (*Thomomys*), rabbits (*Lepus* and *Sylvilagus*), and various lizards (*Phrynosoma* and *Uta*) (Hall, 1946).

The environmental conditions of the Great Basin during the late Wisconsinan Glacial (~25,000 to 11,000 yr BP), Late Pleistocene, are unlike those observed there today. Alpine glaciers descended to below 2,800 m elevation in some of the larger mountain ranges (e.g., the southern Snake Range) while at the same time, pluvial lakes (such as Lake Bonneville) filled many of the extensive valley basins (Mifflin and Wheat, 1979; Benson and Thompson 1987; Grayson 1993, 2006; Reheis et al., 2014; Milligan and McDonald, 2017). Fossil plants for this period come from various lake and marsh deposits, along with dry caves and packrat middens (Thompson and Mead, 1982; Spaulding, 1990; Thompson, 1990).

Table 6. List of western North America localities that contain Quaternary *Taxidea* fossils. Assigned ages based on referenced author. Localities refer to dots in Figure 1.

Location	Locality Name	Age	Reference
Arizona			
	Papago Springs Cave	Late Pleistocene	Harris, 2008
	San Simon Fauna	Late Blancan	Harris, 2008
	Ventana Cave	Late Wisconsinan	Harris, 2008
California			
	Anza-Borego Desert State Park	Late Blancan to Irvingtonian	Harris, 2008
	Campbell Hill and Twentynine Palms Gravel Pit	Rancholabrean ? “Illinoinian”	Harris, 2008
	Carpinteria	Early Wisconsinan	Harris, 2008
	Diamond Valley Lake Local Fauna	Mid/Late Wisconsinan	Harris, 2008
	Kokoweef Cave	Late Wisconsinan/Holocene	Harris, 2008
	Maricopa	Late Wisconsinan	Harris, 2008
	McKittrick	Mid/Late Wisconsinan	Harris, 2008
	Mountain View Country Club	Late Wisconsinan	Harris, 2008
	Newberry Cave	Late Wisconsinan/Holocene	Harris, 2008
	Piute Ponds, Lake Thompson	Rancholabrean	Harris, 2008
	Pinto Basin JTNM	Early? Rancholabrean	Harris, 2008
	Potter Creek Cave	Early Holocene	Harris, 1985
	Rancho La Brea	Mid and Late Wisconsinan	Harris, 2008
	Schuiling Cave	Late Wisconsinan/Holocene	Harris, 2008
Colorado			
	Dutton	Late Pleistocene	Harris, 1985
	Chimney Rock Animal Trap	Late Wisconsin-Early Holocene	Hager, 1972
	Porcupine Cave	690,000 - 900,000 yrs	Anderson, 1996
Idaho			
	American Falls	”Probably Sangamonian”	Harris, 1985
	Booth Canyon		Akersten et al., 2002
	Moonshiner Cave	Post-glacial	Anderson, 1977
	Jaguar Cave	Late Pleistocene	Guilday and Adam, 1967
Nevada			
	Amy’s Rockshelter	Late Pleistocene	Miller, 1979
	Cathedral Cave	Mid-Late Pleistocene	Jass, 2007
	Centennial Parkway, Las Vegas Valley	Rancholabrean	Harris, 2008
	Hanging Rock Shelter	Late Pleistocene/Holocene	Grayson, 1988
	Hidden Cave	Holocene	Grayson, 1985
	Kachina Cave	Holocene	Miller, 1979
	Last Supper Cave	Late Pleistocene/Holocene	Grayson, 1988
	Mineral Hill Cave	Late Pleistocene/Holocene	Hockett and Dillingham, 2004
	O’Malley Shelter	Late Quaternary	Fowler et al., 1973
	Owl Cave #2	Late Quaternary	Turnmire, 1987
	Smith Creek Cave	Late Pleistocene	Harris, 1985

Location	Locality Name	Age	Reference
New Mexico			
	Big Manhole Cave	Mid/Late Wisconsinan	Harris, 2008
	Burnet Cave	Wisconsinan and Holocene	Harris, 2008
	Conkling Cavern	Late Wisconsinan/Holocene	Harris, 2008
	Dark Canyon Cave	Late Quaternary	Harris, 2008
	Dry Cave: Animal Fair	Late Pleistocene	Harris, 1985
	Dry Cave: Circus Route:	„Older than 11,880 on stratigraphic grounds”	Harris, 2008
	Dry Cave: Room of the Vanishing Floor	Early or Early/Mid Wisconsinan	Harris, 2008
	Isleta Cave 2	Late Wisconsinan and Holocene	Harris, 2008
	Jal	Late Wisconsinan	Harris, 2008
	Pendejo Cave	Late Quaternary	Harris, 2008
	San Antonio Cave	Medial Irvingtonian	Harris, 2008
	Shelter Cave	Mid/Late Wisconsinan/Holocene	Harris, 2008
	U-Bar Cave	Mid/Late Wisconsinan and Holocene	Harris, 2008
Oregon			
	Fossil Lake	„Probaly mid or possibly early Wisconsinan”	Harris, 1985
Texas			
	Sierra Diablo Cave	Mid/Late Wisconsinan/Holocene	Harris, 2008
Utah			
	Danger Cave	Late Pleistocene	Grayson, 1988
	Hogup Cave	Holocene	Aikens, 1970
	Silver Creek	Sangamonian	Harris, 1985
Wyoming			
	Bell Cave	Late Wisconsinan	Zeimens and Walker, 1974
	Horned Owl Cave	Late Pleistocene/Holocene	Harris, 1985
	Little Box Elder Cave	Late Wisconsinan and Holocene	Anderson, 1968, 1977
Alberta			
	Eagle Cave,	Late Pleistocene	Harrington, 2011
	Rats Nest Cave	Late Pleistocene	Harrington, 2011
Saskatchewan			
	Fort Qu’Appelle: (Bliss Gravel Pit-Echo Lake Gravel)	„Sangamonian (cf. Wisconsinan interstadial)”	Harris, 1985
	Saskatoon	Sangamonian or cf. Wisconsinan interstadial	Harris, 1985
Sonora			
	El Golfo	Irvingtonian	Harris, 2008

Macrobotanical remains from packrat middens suggest that subalpine and montane conifers grew on the lower mountain slopes and valley bottoms above high lake stands. Given the right substrate, select species of subalpine and montane conifers along with sagebrush and other shrubs, could have formed a continuous or near-continuous belt from the Wasatch Front of Utah to the Sierra Nevada of California/Nevada (Thompson, 1990). The recovery of sage-grouse from a number of caves in the region including SCBC suggest extensive stands of sagebrush and or sagebrush steppe in the valley (Emslie and Heaton, 1987; Grayson, 2006; Emslie and Mead, 2023). Taken together, this habitat description is what the badger inhabited above the Lake Bonneville shoreline, and below the level of glacial and periglacial zones of the highest peaks of the Snake Range. If there was a fairly continuous conifer-sagebrush steppe habitat east to west across the Great Basin, a number of mammalian species did not follow suite, indicating it was not a homogeneous biome across the Great Basin (see review in Grayson, 2006). Perhaps the Bonneville Basin provided a form of filter mechanism for select species, mainly montane mammals, such as the pika (*Ochotona*, Grayson, 1987, 2005). Each species reacted on its own to changes in climate from glacial to interglacial regimes (Brown, 1978; Grayson, 2006). As various species responded with change (extirpation, extinction, changes in mass, geographic distribution, skeletal morphology), the badger from the Great Basin did not seem to have necessitated such a response. Conversely, the Pleistocene *Taxidea* of Alaska, where they do not occur today, were distinctly larger (Anderson, 1977). Continued work on the faunas and floras from caves and packrat middens in the Snake Range (e.g., Smith Creek, Ladder, Combustion, Cathedral, Arches Caves) and low in the valley (e.g., SCBC, Garrison Cave) will help in the reconstruction of the Late Pleistocene biotic communities above the high lakes stands and how they adapted due to climate change to the current interglacial regime.

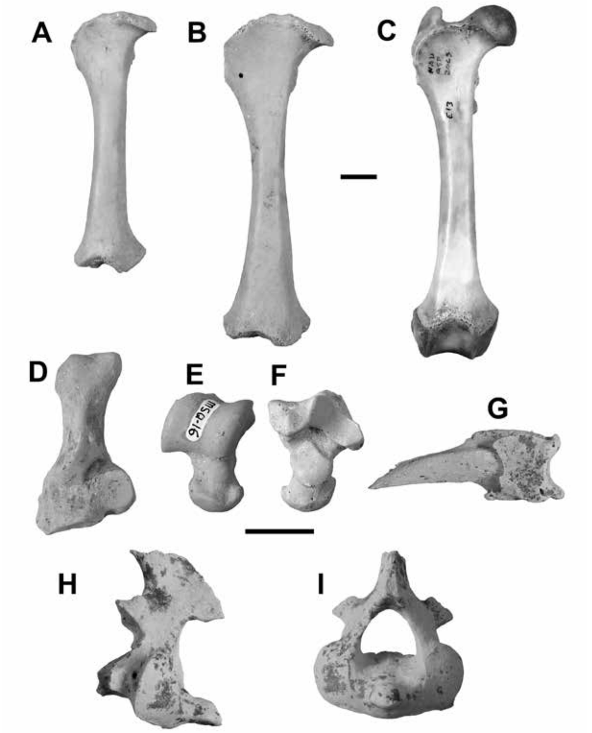


Figure 8. Taxidea postcranial elements from Snake Creek Burial Cave, White Pine County, Nevada. A, R juvenile femur (MSQ 13); B, R immature femur (MSQ 21); and C, R mature femur modern specimen (MSCC 389) anterior views. D, R calcaneus (MSQ 52) anterior (dorsal) view. E, anterior (dorsal) and F, posterior (plantar) views of L astragalus (MSQ 16). G, side view of distal (3rd) phalanx (MSQ 64). H, lateral and I, anterior views of axis (MSQ 32). Scale bars = 1 cm.

ACKNOWLEDGEMENTS

We thank N. Fox and the Museum of Geology, South Dakota School of Mines and Technology for allowing us to access the modern collections in the James E. Martin Paleontological Research Lab to measure badger skeletal remains. We thank S. Swift, S. Weaver, R. White, T. Fry, and the staff at The Mammoth Site of Hot Springs, South Dakota, for their help and support on the SCBC project. Thanks is given to S. Swift for producing Figures 1 and 8. We appreciate the in-depth discussions about Great Basin Pleistocene with C. Bell, S. Emslie, C. Jass, and L. Coats. We appreciate the continued support and discussions about the Great Basin with D. Powell (Ely Ranger District) and other staff of the USDA Forest Service. Thanks is given to J. Samuels and S. Wallace for discussions about badgers. We appreciate the editorial suggestions from two anonymous reviewers

REFERENCES

Aikens, C.M., 1970, Hogup Cave. University of Utah Anthropological Papers 93.

Akersten, W.A., Miller, S.J., and Repenning, C.A., 2002, The Booth Canyon Local Fauna, a depauperate mammalian assemblage from the Late Pleistocene of eastern Bonneville County, Idaho: *in* Akersten, W.A., Thompson, M.E., Meldrum, D.J., Rapp, R.A., and McDonald, H.G., eds., And Whereas…Papers on the vertebrate paleontology of Idaho honoring John A. White, Volume 2: Idaho Museum of Natural History Occasional Paper v. 37, p. 101–130.

Anderson, E., 1968, Fauna of the Little Box Elder Cave, Converse County, Wyoming: The Carnivora: University of Colorado Studies, Series in Earth Sciences, v. 6, p. 1–59.

Anderson, E., 1970, Quaternary evolution of the genus *Martes* (Carnivora, Mustelidae): ActaZoologica Fennica, v. 130, p. 1–132.

Anderson, E., 1977, Pleistocene Mustelidae (Mammalia, Carnivora) from Fairbanks, Alaska: Bulletin of the Museum of Comparative Zoology, v. 148, p. 1–21.

Anderson, E., 1996, A preliminary report on the Carnivora of Porcupine Cave, Park County, Colorado, *in* K.M. Stewart, and K.L. Seymour, editors, Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals. University of Toronto Press, Toronto, p. 259–282. https://doi.org/10.3138/9781487574154-014

Anderson, E., 2004. The Carnivora from Porcupine Cave, *in* Barnosky, A.D., ed., Biodiversity response to climate change in the Middle Pleistocene. The Porcupine Cave fauna from Colorado: Berkeley, California, University of California Press, p. 141–154. https://doi.org/10.1525/california/9780520240827.003.0013

Bell, C.J., and Mead, J.I., 1998, Late Pleistocene microtine rodents from Snake Creek Burial Cave, White Pine County, Nevada: Great Basin Naturalist, v. 58, p. 82–86.

Benson, L., and Thompson, R.S., 1987, The physical record of lakes in the Great Basin, *in* Ruddiman, W.F., and Wright, H.E., eds., North America and adjacent oceans during the last deglaciation: Boulder, Colorado, Geological Society of American, The geology of North America: v. K-3, p. 241–260. https://doi.org/10.1130/DNAG-GNA-K3.241

Brown, J.H., 1978, The theory of insular biogeography and the distribution of boreal birds and mammals, *in* Harper, K.T., and Reveal, J.L., eds., Intermountain biogeography: a symposium: Great Basin Naturalis Memoirs, v. 2, p. 209–227.

Drescher, A.B., 1939, A new Pliocene badger from Mexico: Bulletin of the Southern California Academy of Sciences, v. 38, p. 57–62.

Durrant, S.D., 1952, Mammals of Utah: University of Kansas Publications, Museum of Natural History, v. 6, p. 1–549.

Emslie, S.D., and Heaton, T.H., 1987, The late Pleistocene avifauna of Crystal Ball Cave, Utah: Journal of Arizona-Nevada Academy of Science, v. 21, p. 53–60.

Emslie, S.D., and Mead, J.I., 2023, Two new late Quaternary avifaunas from the east-central Great Basin with the description of a new species of *Falco*: Western North American Naturalist, v. 83, p. 33–50. https://doi.org/10.3398/064.083.0104

Fowler, D.D., Madsen, D.B., and Hattori, E.M., 1973, Prehistory of southeastern Nevada: Desert Research Institute Publications in the Social Science 6.

Fox, N.S., 2014, Analysis of Snake Creek Burial Cave *Mustela* fossils using linear and landmark-based morphometrics: implications for weasel classification and black-footed ferret conservation [MS thesis]: Johnson City, East Tennessee State University.

Fox, N.S., Wallace, S.C., and Mead, J.I., 2017, Fossil *Mustela nigripes* from Snake Creek Burial Cave, Nevada and implications for black-footed ferret paleoecology: Western North American Naturalist, v. 77, p. 137–151. https://doi.org/10.3398/064.077.0202

Goodrich, J.M., and Buskirk, S.W., 1998, Spacing and ecology of North American badgers (*Taxidea taxus*) in a prairie-dog (*Cynomys leucurus*) complex: Journal of Mammalogy, v. 79, p. 171–179. https://doi.org/10.2307/1382852

Grayson, D.K., 1985, The paleontology of Hidden Cave: birds and mammals, *in* Thomas, D.H., ed., The archaeology of Hidden Cave, Nevada: Anthropological Papers of the American Museum of Natural History 61, Part 1, p. 125–161.

Grayson, D.K., 1987, The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years: Journal of Mammalogy, v. 68, p. 359–375. https://doi.org/10.2307/1381475

Grayson, D.K., 1988, Danger Cave, Last Supper Cave, and Hanging Rock Shelter: the faunas: Anthropological Papers of the American Museum of Natural History 66, Part 1, 130 p.

Grayson, D.K., 1993, The desert's past. A natural prehistory of the Great Basin: Washington, D.C., Smithsonian Institution Press, p. 356.

Grayson, D.K., 2005, A brief history of Great Basin pikas: Journal of Biogeography, v. 32, p. 2101–2111. https://doi.org/10.1111/j.1365-2699.2005.01341.x

Grayson, D.K., 2006, The late Quaternary biogeographic histories of some Great Basin mammals (western USA): Quaternary Science Reviews, v. 25, p. 2964–2991. https://doi.org/10.1016/j.quascirev.2006.03.004

Guilday, J.E., and Adam, E.K., 1967, Small mammal remains from Jaguar Cave, Lemhi County, Idaho: Tebiwa, v. 10, p. 26-36.

Hager, M.W., 1972, A late Wisconsin-Recent vertebrate fauna from the Chimney Rock Animal trap, Larimer County, Colorado: University of Wyoming, Contributions to Geology, v. 11, p. 63–71.

Hall, E.R., 1944, A new genus of American Pliocene badger, with remarks on the relationships of badgers of the Northern Hemisphere: Carnegie Institute of Washington Publication v. 551, p. 11–23.

Hall, E.R., 1946, Mammals of Nevada: Berkeley, California, University of California Press, p. 710.

Harrington, C.R., 2011, Quaternary cave faunas of Canada: a review of the vertebrate remains: Journal of Cave and Karst Studies, v. 73, p. 162–180. https://doi.org/10.4311/jcks2009pa128

Harris, A.H., 1985, Late Pleistocene vertebrate paleoecology of the West: Austin, Texas, University of Texas Press, 293 p.

Harris, A.H., 2008, Pleistocene Vertebrates of Southwestern USA and Northwestern Mexico:https://www.utep.edu/leb/pleistNM/default.htm (accessed December 2023).

Heaton, T.H., 1987, Initial investigation of vertebrate remains from Snake Creek Burial Cave,White Pine County, Nevada: Current Research in the Pleistocene, v. 4, p. 107–109.

Helgen, K.M., Cole, F.R, Helgen, L.E., and Wilson, D.E., 2009, Generic revision in the Holarctic ground squirrel genus *Spermophilus*. Journal of Mammalogy, v. 90, p. 270–305. https://doi.org/10.1644/07-MAMM-A-309.1

Hockett, B., and Dillingham, E., 2004. Systematic paleontology of the Mineral Hill Cave carnivores, perissodactyls, and artiodactyls, *in* Hockett, B., and Dillingham, E., eds., Paleontological investigations at Mineral Hill Cave: U.S. Department of the Interior, Bureau of Land Management, Contribution to the Study of Cultural Resources, Technical Report no. 18, p. 18–60. https://doi.org/10.5962/bhl.title.153781

Jass, C.N., 2007, New perspectives on Pleistocene biochronology and biotic change in the east-central Great Basin: an examination of vertebrate fauna from Cathedral Cave, Nevada [Ph.D. dissertation]: Austin, Texas, University of Texas at Austin.

Koepfli, K.-P., Deere, K.A., Slater, G.J., Begg, C., Begg, K., Grassman, L., Lucherini, M., Veron, G., and Wayne, R.K., 2008, Multigene phylogeny of the Mustelidae: Resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation: BMC Biology, v. 6, p. 1–22. https://doi.org/10.1186/1741-7007-6-10

Kurtén, B., and Anderson, E., 1980, Pleistocene mammals of North America: New York, Columbia University Press, p 442.

Kyle, C.J., Weir, R.D., Newhouse, N.J., Davis, H., and Strobeck, C., 2004, Genetic structure of sensitive and endangered northwestern badger populations (*Taxidea taxus* and *T. t. jeffersonii*): Journal of Mammalogy, v. 85, p. 633–639. https://doi.org/10.1644/BRB-129

Lavocat, R., 1966, Faunes et flores préhistoriques de L'Europe Occidentale. Atlas de Préhistoire Tome III. Centre National de Recherche Scientifique [Prehistoric fauna and flora of Western Europe. Atlas of Prehistory Volume III. National Center for Scientific Research], Paris, 486 p.

Law, C.J., Slater, G.J., and Mehta, R.S., 2018, Lineage diversity and size disparity in Musteloidea: testing patterns of adaptive radiation using molecular and fossil-based methods: Systematic Biology, v. 67, p. 127–144. https://doi.org/10.1093/sysbio/syx047

Linsdale, J.M., 1938, Environmental responses of vertebrates in the Great Basin: American Midland Naturalist, v. 19, p. 1–206. https://doi.org/10.2307/2420430

Long, C.A., 1973, *Taxidea taxus*: Mammalian Species, v. 26, p. 1–4. https://doi.org/10.2307/3504047

McDonald, H.G., 2002, Second record of the badger *Taxidea taxus* (Schreber) from the Pleistocene of Kentucky and its paleoecological implications: Smithsonian Contributions toPaleobiology, v. 93, p. 77–82.

McGee, D., Quade, J., Edwards, R.L., Broecker, W.S., Cheng, H., Reiners, P.W., and Evenson N., 2012, Lacustrine cave carbonates: novel archives of paleohydrologic change in the Bonneville Basin (Utah, USA): Earth and Planetary Science Letters, v. 351, p. 182–194. https://doi.org/10.1016/j.epsl.2012.07.019

Mead, E.M., and Mead, J.I., 1989, Snake Creek Burial Cave and a review of the Quaternary mustelids of the Great Basin: Great Basin Naturalist, v. 49, p. 143–154.

Mead, J.I., and Mead, E.M., 1985, A natural trap for Pleistocene animals in Snake Valley, Eastern Nevada: Current Research in the Pleistocene, v. 2, p. 105–106.

Mead, J.I., Heaton, T.H., and Mead, E.M., 1989, Late Quaternary reptiles from two caves in the east-central Great Basin: Journal of Herpetology, v. 23, p. 186–189. https://doi.org/10.2307/1564031

Meyers, J.I., 2007, Basicranial analysis of *Martes* and the extinct *Martes nobilis* (Carnivora: Mustelidae) using geometric morphometrics [MS thesis]: Flagstaff, Northern Arizona University.

Mifflin, M.D., and Wheat, M.M., 1979, Pluvial lakes and estimated pluvial climates of Nevada: Nevada Bureau of Mines and Geology, Bulletin 94.

Miller, S.J., 1979, The archaeological fauna of four sites in Smith Creek Canyon, *in* Tuohy, D.R., and Rendal, D.L., eds., The archaeology of Smith Creek Canyon, eastern Nevada: Nevada State Museum, Anthropological Papers 17, p. 270–329.

Milligan, J., and McDonald, H.G., 2017, Shorelines and vertebrate fauna of Pleistocene Lake Bonneville, Utah, Idaho, and Nevada: Geology of the Intermountain West, v. 4, p. 181–214. https://doi.org/10.31711/giw.v4.pp181-214

Osterhaudt, J., 1999, A review of Quaternary Lagomorpha of the Great Basin and Snake Creek Burial Cave, Nevada [MS thesis]: Flagstaff, Northern Arizona University.

Owen, P.R., 2006, Description of a new Late Miocene American badger (Taxidiinae) utilizing high-resolution X-ray computed tomography: Palaeontology, v. 49, p. 999–1011. https://doi.org/10.1111/j.1475-4983.2006.00590.x

Palevich, M., 2005, Dental and cranial elements of canids from Snake Creek Burial Cave, White Pine County, Nevada [MS thesis]: Flagstaff, Northern Arizona University.

Reheis, M.C., Adams, K.D., Oviatt, C.G., and Bacon, S.N., 2014, Pluvial lakes in the great Basin of the western United States – a view from the outcrop: Quaternary Science Reviews, v. 97, p. 33–57. https://doi.org/10.1016/j.quascirev.2014.04.012

Rowe, R.J., and Terry, R.C., 2014, Small mammal responses to environmental change:integrating past and present dynamics: Journal of Mammalogy, v. 95, p. 1157–1174. https://doi.org/10.1644/13-MAMM-S-079

Samuels, J.X., Meachen, J.A., and Sakai, S.A., 2013, Postcranial morphology and the locomotor habits of living and extinct carnivorans: Journal of Morphology, v. 274, p. 121–146. https://doi.org/10.1002/jmor.20077

Sato, J.J., Wolsan, M., Prevosti, F.J., D'Elía, G., Begg, C., Begg, K., Hosoda, T., Campbell, K.L., and Suzuki, H., 2012, Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea): Molecular Phylogenetics and Evolution, v. 63, p. 745–757. https://doi.org/10.1016/j.ympev.2012.02.025

Sato, J.J., 2016, The systematics and taxonomy of the world's badger species—a review, *in* G. Proulx, G., and Do Linh San, E., eds., Badgers: systematics, biology, conservation and research techniques: Sherwood Park, Alberta, Alpha Wildlife Publications, p. 1–30.

Schreber, J.C., 1778, Die Säugthiere in Abbildungen nach der Natur, mit Beschreibungen: Walther'sch Kunst-und Buchhandlung [The mammals in illustrations after nature, with descriptions: Walther'sch Kunst-und Buchhandlung], v. 3, p. 520–589. [original not seen]

Slobodchikoff, C.N., Perla, B.S., and Verdolin, J.L., 2009. Prairie Dogs. Communication and community in an animal society. Harvard University Press, Cambridge, 264 p. https://doi.org/10.2307/j.ctv20hcvct

Spaulding, W.G., 1990, Vegetational and climatic development of the Mojave Desert: the last glacial maximum to the present, *in* Betancourt, J.L., Van Devender, T.R., and Martin, P.S., eds., Packrat middens. The last 40,000 years of biotic change: Tucson, Arizona, University of Arizona Press, p. 166–199. https://doi.org/10.2307/j.ctv21wj578.11

Stock, C., 1948, Restos de tejón (*Taxidea*), Pliocénico del occidente de Chihuahua: Boletín de la Sociedad Geológica Mexicana, v. 13, p. 69–76. https://doi.org/10.18268/BSGM1948v13n1a5

Tedford, R.H., and Harington, C.R., 2003, An Arctic mammal fauna from the early Pliocene of North America: Nature, v. 425, p. 388–390. https://doi.org/10.1038/nature01892

Thompson, R.S., 1990. Late Quaternary vegetation and climate in the Great Basin: *in* Betancourt, J.L., Van Devender, T.R., and Martin, P.S., eds., Packrat middens. The last 40,000 years of biotic change: Tucson, Arizona, University of Arizona Press, p. 200–239. https://doi.org/10.2307/j.ctv21wj578.12

Thompson, R.S., and Mead, J.I., 1982, Late Quaternary environments and biogeography in the Great Basin: Quaternary Research, v. 17, p. 39–55. https://doi.org/10.1016/0033-5894(82)90044-8

Turnmire, K.L., 1987, An analysis of the mammalian fauna from Owl Cave One and Two, Snake Range, east-central Nevada [M.S. thesis]: Orono, Maine, University of Maine.

Von Den Diesch, A., 1976, A Guide to the measurement of animal bones from archaeological sites: Harvard University, Cambridge, Massachusetts, Peabody Museum Bulletin, v. 1, p. 1–137.

Wagner, H., 1976, A new species of *Pliotaxidea* (Mustelidae: Carnivora) from California: Journal of Paleontology, v. 50, p. 107–127.

Wallace, S.C., and Wang, X., 2004, Two new carnivores from an unusual late Tertiary forest biota in eastern North America: Nature, v. 431, p. 556–559. https://doi.org/10.1038/nature02819

White, J.A., McDonald, H.G., Anderson, E., and Soiset, J.M., 1984, Lava blisters as carnivore traps: *in* Genoways, H.H. and Dawson, M.R. eds., Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday. Special Publication of Carnegie Museum of Natural History, v. 8, p. 241–256.

Wolsan, M., and Sotnikova, M., 2013, Systematics, evolution, and biogeography of the Pliocene stem meline badger *Ferinestrix* (Carnivora: Mustelidae): Zoological Journal of the Linnean Society, v. 167, p. 208–226. https://doi.org/10.1111/j.1096-3642.2012.00868.x

Zeimens, G., and Walker, D.N., 1974, Bell Cave, Wyoming: preliminary archaeological and paleontological investigations: *in* Wilson, M. ed., Applied geology and archaeology: the Holocene history of Wyoming, Geological Survey of Wyoming, Report of Investigations, v. 10, p. 88–90.

Jim I. Mead, Christopher N. Jass, Sandra L. Swift, and Sharon Weaver. Late Quaternary faunas from caves in the Black Hills, South Dakota. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 190-201. DOI:10.4311/2024PA0102

LATE QUATERNARY FAUNAS FROM CAVES IN THE BLACK HILLS, SOUTH DAKOTA

Jim I. Mead[1,2,*], Christopher N. Jass[1,3], Sandra L. Swift[1], and Sharon Weaver[1,4]

ABSTRACT

The dolomitic limestone Pahasapa Formation exposed in the Black Hills of South Dakota is well known to contain a multitude of caves and other karst features. In order to raise greater awareness of the Black Hills caves and karst fissures as a source of paleontologic data, we summarize the major Quaternary and Pliocene cave and karst localities which contain fossils. The Richmond Hill quarry provides at least eight fissures deposits which contain a diverse range of vertebrate and invertebrate fossils of the Pliocene. Nine caves (Don's Gooseberry Pit, Graveyard Cave, Jewel Cave, Parker's Pit, Persistence Cave, Rushmore Cave, Salamander Cave, Stagebarn Cave, and Wind Cave) contain late Quaternary age fossils. Many of these faunas are part of on-going study. A record of climate and environmental change is emerging from these caves which illustrates that the Black Hills have been part of the dynamic changes throughout the Quaternary.

INTRODUCTION

The Black Hills of southwestern South Dakota and northeastern Wyoming are a haven for cave and karst features as a result of extreme uplift and exposure of the Pahasapa Formation (=Madison, Redwall formations; Mississippian age). This massive dolomitic limestone is well known to contain a multitude of aquifers, springs, karst sinkholes, karst fissures, and caves with a range of extensive to short passageways (Palmer and Palmer, 1989; Palmer, 2016; Palmer et al., 2016). Collectively these caves, fissures, and sinkholes preserve a warehouse of information that record changing climatic and biotic communities throughout the Quaternary (Pleistocene [Ice Age] and Holocene; the most recent 2.58 million years of Earth history) in the Black Hills.

The unglaciated Black Hills represent a doubly plunging anticline (essentially a dome shape) formed by the Laramide Orogeny during the Late Cretaceous and Early Cenozoic (Karner, 1989; Lisenbee, 2010). The Black Hills encompass nearly 15,500 km^2 (6,000 mi^2) and rise more than 1,220 m (4,000 ft; [highest peak 2,207 m; 7,242 ft elevation]) above the surrounding northern Great Plains, essentially a forest-covered, mountainous island surrounded by a 'sea' of sagebrush and grasslands (Froiland, 1999; Larson and Johnson, 2007). The Belle Fourche and Cheyenne rivers bracket the Black Hills north and south, respectively (Fig. 1). They provide down-river riparian access to the Black Hills from the sagebrush steppe and shortgrass prairies from the north and west in Wyoming and Montana, and up-river riparian approach from the extensive mixed-grass and tall-grass prairies to the east (see related discussion in Buskirk, 2001). The geographic position of the Black Hills allows the isolated mountain mass to act as an island ecotone scenario for surrounding biomes (i.e., the grassland prairie habitats of the east and the shrublands and forests of the inter-mountain West. As fluctuations between glacial and interglacial climatic regimes occurred, the Black Hills were inhabited by plant and animal species with centers of distribution often much farther east, west, and north (Graham et al., 1987; Fulton et al., 2013; Jass et al., 2020). Because of their geographic position and the abundance of fossils in the caves, the Black Hills provide a unique opportunity to develop and test various biogeographic and ecological models. These fossil records also produce a 'natural' accumulation of flora and fauna not biased by the procurement by human cultures.

Caves in the Pahasapa Limestone exposed in the Black Hills often have multi-level passageways with a number of now-closed entrances characterized by old debris cones indicating the ancient nature of the enclosed sedimentary deposits (Palmer and Palmer, 1989). Many of the sedimentary deposits, some encased by flowstone, contain abundant vertebrate and invertebrate remains. In order to raise greater awareness of the Black Hills caves as an important source of paleontologic data, we summarize the major Quaternary and Pliocene cave and karst localities which contain fossils. Our summary is derived from existing publications, museum collections at the Mammoth Site of Hot Springs, SD and the South Dakota School of Mines and Technology, and previously unpublished field notes and laboratory data from the authors. The general locations of all sites are presented in Figure 1.

---

[1] Mammoth Site, 1800 Hwy 18 BYP, Hot Springs, SD 57747
[2] Desert Laboratory on Tumamoc Hill, University of Arizona, Tucson, AZ 85745; ORCID 0000-0002-4975-022X
[3] Royal Alberta Museum 9810-103A Ave, Edmonton, AB T5J 0G2
[4] Cave Discovery Initiative, 23679 Strato Rim Drive, Rapid City, SD 57702
*Corresponding author: jmead@mammothsite.org

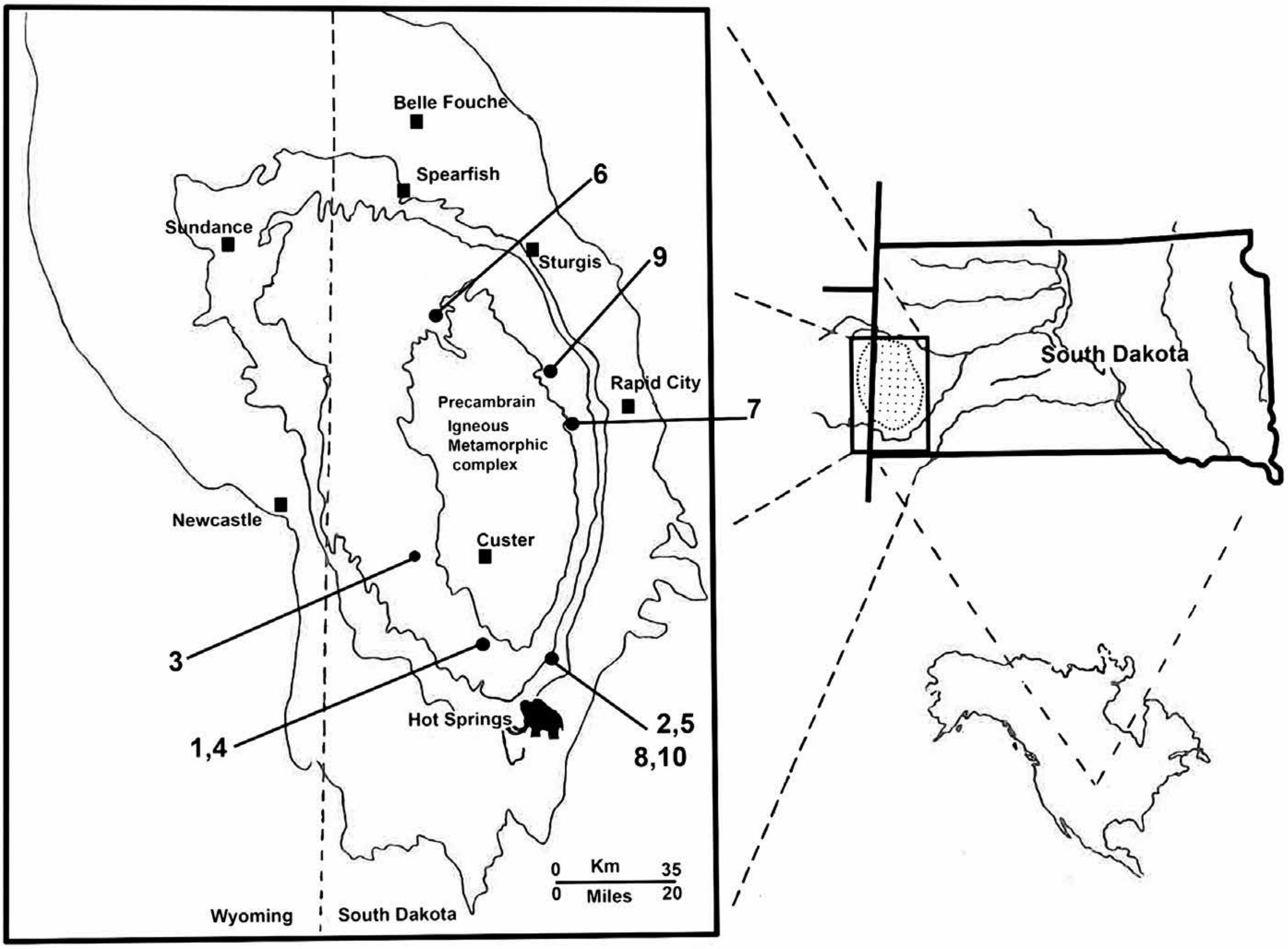


Figure 1. Map of the Black Hills illustrating general locations of cave sites with fossils discussed in text. 1, Don's Gooseberry Pit; 2, Graveyard Cave; 3, Jewel Cave; 4, Parker's Pit; 5, Persistence Cave; 6, Richmond Hill fissures; 7, Rushmore Cave; 8, Salamander Cave; 9, Stagebarn Cave; 10, Wind Cave.

ICE AGE CAVE LOCALITIES OF THE BLACK HILLS

The most studied cave/karst deposit with a paleontological record in the Black Hills is the Mammoth Site, a surface exposed filled karst sinkhole locality containing a large assemblage of mammoth (*Mammuthus*; ~60 individuals) remains in the town of Hot Springs (Fig. 1). Prior to the discovery and assessment of this locality, little was understood about the Late Pleistocene faunas of the Black Hills. The study of its fossils, stratigraphy, and chronology was initiated in 1974 (Agenbroad and Mead, 1994) and remains an active research center for Pleistocene deposits of the Black Hills and western North America. Initially the Mammoth Site deposits were thought to be about 26,000 years old based on radiocarbon dating using bone apatite. Errors were presumed based on the use of bone apatite, and thus more analyses were needed. More recently quartz and feldspar grains from high and low stratigraphic levels in the sinkhole deposit were assessed using optically stimulated luminescence (OSL). Luminescence ages (n=6) indicate that the fossil-bearing sediments span all of Marine Isotope Stage (MIS) 7 and MIS 6 and ended with complete infilling at the start of the interglacial age of MIS 5; approximately 255,00 to 130,000 years old (Shannon Mahan, in litt., March 2024). Details of the recovered fauna, flora, and geology can be found in the chapters within Agenbroad and Mead (1994).

Younger, Holocene faunas are known in archaeological contexts in rock shelters of the region (e.g., Beaver Creek Shelter: Abbott, 1989; Benton, 1990; Martin et al., 1993). Although those sites contain significant Quaternary records, our focus here is to highlight cave localities that are (or were) encountered as part of recreational and exploratory caving, and to emphasize the continued potential for recovery of significant paleontological data/sites within Black Hills cave systems likely to be explored by the recreational or professional caving community.

The number of caves known for the Black Hills is voluminous (Palmer et al., 2016) but research on fossil resources from these caves was intermittent prior to 2010 (e.g., Manganaro, 1994; Mead et al., 1996; Jass et al., 2002). Since that time, the evaluation of paleontological resources from Black Hills caves has evolved into a more concentrated effort to understand the Pleistocene record preserved in caves of the region (Pardi, 2010; Pardi and Graham, 2018; Jass et al., 2020; Mead et al., 2021). Presently, nine caves in the Black Hills are known to preserve late Quaternary paleontological records along with a series of karst fissures of Pliocene age. Some of these sites (e.g., Parker's Pit and Persistence Cave) form the basis of active, on-going field research, whereas others (e.g., Richmond Hill fissure fills) are partially described or are in exploratory stages in terms of paleontological research. Below, we summarize the present state of knowledge of each fossil locality. The chronological context for most localities is established using radiocarbon dating, typically on select, taxonomically important species. All radiocarbon dates presented here are calibrated typically using OxCal 4.4 program (either in the original publication or provided here) which produces an age presented as 'cal yr BP' (calibrated years before present). For specific details of individual radiocarbon dates, we provide the original reference(s) for those data.

Don's Gooseberry Pit

Don's Gooseberry Pit is a small natural trap cave positioned near the point of a flat ridge (approximately 1,665 m, 5,463 ft elevation) overlooking steep canyons to the north and east, within the Black Hills National Forest (Fig. 1). The cave is a vertical tube cave with a rectangular, modern entrance approximately 25 cm by 50 cm (Pardi and Graham, 2018:supplemental data). Today the cave is surrounded by an open ponderosa pine forest (Pardi and Graham, 2018).

Assessment of the cave was supervised by staff from the Illinois State Museum and the Pennsylvania State University. Excavation of the cave fill was initiated in 2003 and continued with short field seasons over many years until 2014. Preliminary analysis of rodents from the excavation was produced as a thesis by Pardi (2010). A thunderstorm in 2015 illustrated that much of the sediment in the cave is the result of surface sheet wash, mainly on the northeastern edge (field notes Don Brandborg; Pardi and Graham, 2018). The area within this tube-cave is not large enough to permit significant stratigraphic dip to deposited clastic layers; however, some cut-and-fill deposits were observed. Sedimentary matrix was wet screen washed through window mesh sieves (see details in Pardi and Graham, 2018).

Overall, the cave contains a diverse assemblage of mollusks, amphibians, reptiles, and mammals, including some that do not co-occur together today (non-analog). Detailed radiocarbon dating of non-analog species demonstrated severe mixing of the deposits. Thus, the presumed contemporaneity of a non-analog assemblage was refuted (Pardi and Graham, 2018). A list of the identified mammals was provided in Pardi and Graham (2018). Directly radiocarbon dated rodent specimens provide an age range for the deposit of 18,235 – 6,287 cal yr BP. Because of the mixed nature of the deposit, dating of the fauna requires directly radiocarbon dating each taxon in question (e.g., see details in Pardi and Graham, 2018).

Of paleoecological and biogeographical importance are specimens of Richardson's collared lemming (*Dicrostonyx richardsoni*), a lemming that today is tightly linked to the temperate shrub tundra environment near Hudson Bay, Canada (Kowalski, 1995; Pardi and Graham, 2018). Fossils of *Dicrostonyx* were radiocarbon dated directly yielding ages over 18,000 cal yr BP and were also sampled for aDNA analysis (Fulton et al., 2013; Pardi and Graham, 2018). Those records imply that during the Last Glacial Maximum at least the higher elevations of the Black Hills may have had a similar climate and vegetation community to the shrub tundra communities found much farther to the north today. Further study of the diverse fauna starting with the amphibians and reptiles is in progress.

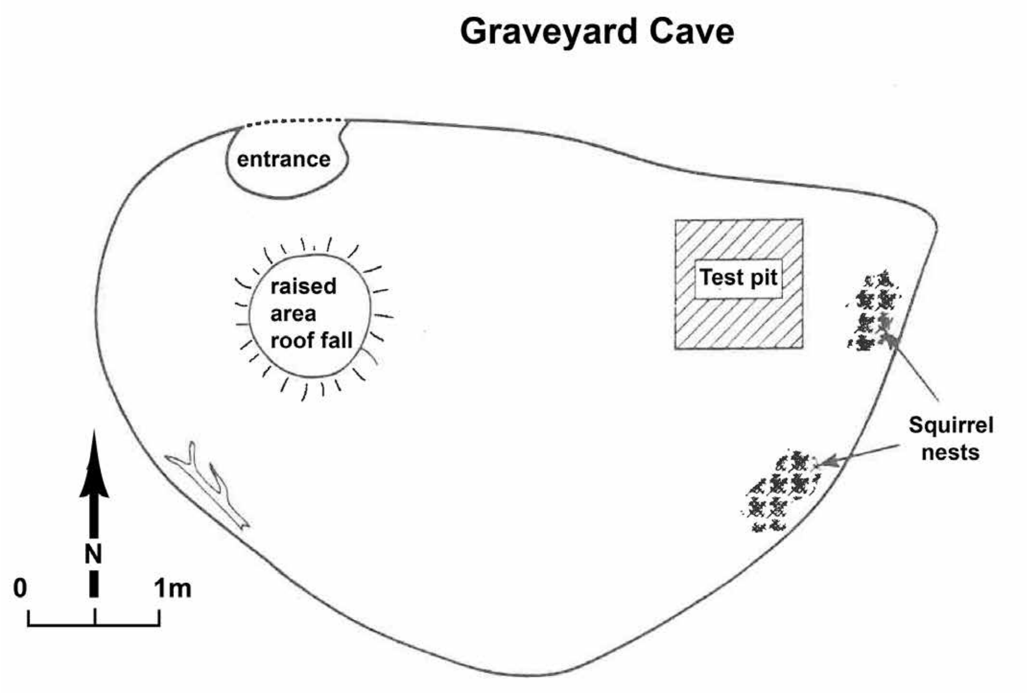
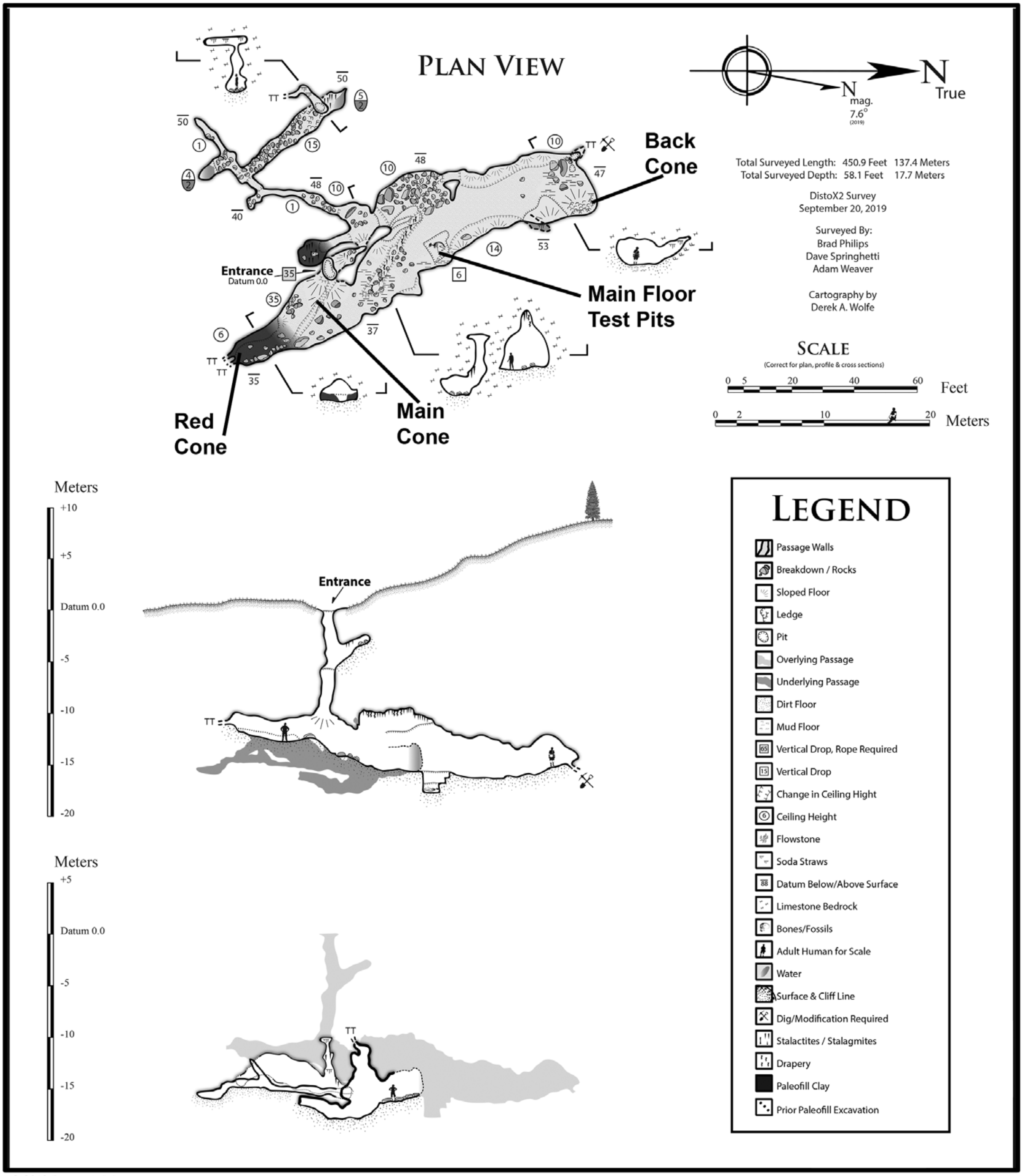


Figure 2. Map of Graveyard Cave (from Manganaro, 1994).



© 2019 Derek A. Wolfe

Figure 3. Map of Parker’s Pit locating the Red Cone, Main Cone, and the Main Floor test pits discussed in the text. Illustration for this article modified from official map provided by Adam Weaver.

Graveyard Cave

Graveyard Cave is a small, bowl-shaped cave situated at 1,355 m (4,457 m) elevation in Wind Cave National Park (Figs. 1). Vertebrates and mollusks dating to the late Holocene (2,547 – 2,037 cal yr BP) were recovered in a preliminary test pit excavation (Fig. 2) in the early 1990s for part of a master’s thesis (Manganaro, 1994). Terrestrial snails from the

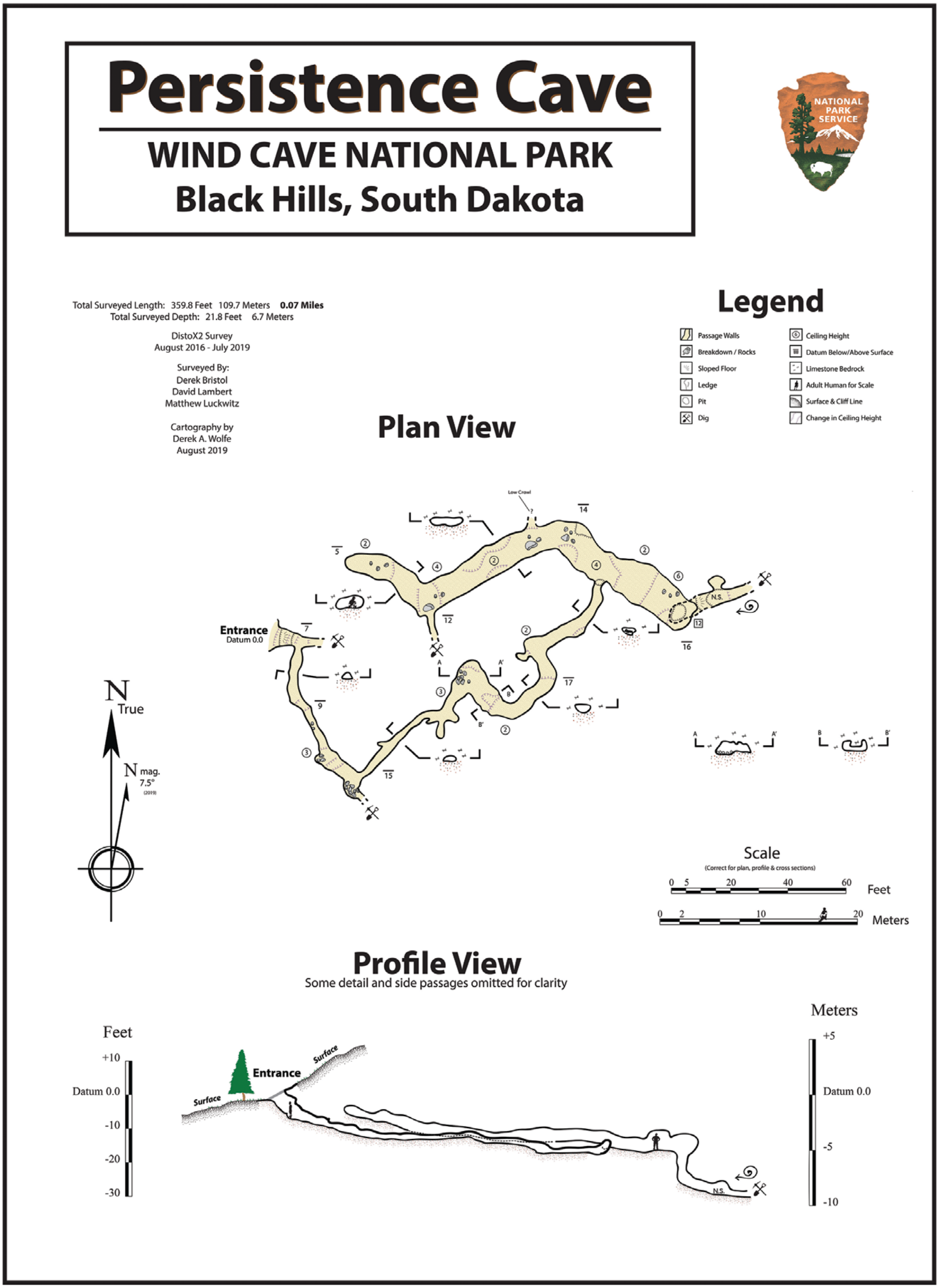


Figure 4. Map of Persistence Cave. Fossils are found in all the sediments that fill the cave system. Map provided by Marc Ohm, Wind Cave National Park.

locality were reported as part of a larger project that summarized Quaternary mollusk records from the southern Black Hills (Jass et al., 2002).

Jewel Cave

Jewel Cave (JECA) is located on the southwestern side of the Black Hills at 1,655 m (5,430 ft) elevation and is part of a national monument (Jewel Cave National Monument; Fig. 1). As with Wind Cave (see below), JECA contains limited amounts of clastic sediments likely to contain Quaternary fossils, except for a few constrained accumulations near the current entrance (Palmer, 2016). The cave has received extensive attention to its mineralogy, geology, passageway exploration, air flow, and hydrology (Conn, 1966; Conn and Conn, 1981; Wiles et al., 2009; Wiles, 2013, 2019). Staff from JECA requested an initial analysis of seemingly unfossiliferous cave sediments only to find out that there were fossils present (Agenbroad, field notes). An assemblage of vertebrate remains is known from an unpublished report, but the entire fauna is currently being reassessed by researchers at the Mammoth Site. The preliminary age range of the fauna is 3,819 – 185 cal yr BP and further radiocarbon dating will likely occur in conjunction with on-going fossil identifications.

Parker's Pit

Parker's Pit is a small limestone cave located near and at approximately the same elevation as Don's Gooseberry Pit in the Black Hills National Forest (Fig. 1). Excavations were overseen by Eric Grimm, Russ Graham, and other staff from the Illinois State Museum and the Pennsylvania State University. The current cave entrance is situated just below the crest of the ridge, and, as with Don's Gooseberry Pit, has a small surface catchment area which restricts how much plant debris and surface animal remains can be washed into the cave during rain storms. The entrance is a small opening with an approximately 14 m (45 ft) vertical drop to the top of a sloping debris cone below and serves as a natural trap today and likely did so during the Late Pleistocene. There is evidence of additional, entrances with older debris cones and associated faunas. These openings had different catchment areas and entrance scenarios versus the existing entrance. Paleontologically, the cave has two major debris cones from now-closed entrances (Red Cone, Main Cone; Fig. 3) that have been preliminarily assessed, and both contain a record of vertebrate and invertebrate remains (Graham et al., this volume). Graham et al. (this volume) have produced a preliminary overview about the fossil rodents from these two cones. The excavation of these two debris cones ceased in the early 2010s.

Since that time, work at Parker's Pit has focused on an extensive, seemingly continuous fossiliferous, clastic deposit on the Main Floor of the cave north of the Main Cone (Fig. 3). The extensive deposit at the center of the Main Floor is flat, and likely accumulated as runoff from the Main Cone debris. Excavations were initiated by Eric Grimm in 2013 in this area of the cave and continued to 2015, followed by a subsequent pause. Excavation resumed in 2017 under the coordination of researchers from the Mammoth Site and the Royal Alberta Museum. Excavations have proven fruitful for the recovery of a diverse fauna and an intact stratigraphic sequence acutely linked to both a detailed radiocarbon chronology (11,999 – 4,334 cal yr BP) and paleoenvironmental record enhanced with an analysis of isotopes (Rolfe Mandel, pers. com., 2024). Research on the Main Floor excavations is on-going.

Persistence Cave

Persistence Cave (PC) is a small cave in the Pahasapa Limestone, within Wind Cave National Park, in the southern Black Hills (Fig. 1). Initial work in PC by the National Park Service (NPS) was to further explore for new passageways. The cave is a sinuous, small tubular system mostly choked with sediments that entered via numerous short-lived small sinkhole openings along a ridgeline (Fig. 4). The initial request by the NPS in the early 2010s was to determine if cave sediments collected at the current entrance contained any fossils. Analysis by paleontologists originally at East Tennessee State University and now at the Mammoth Site (Mead, Swift) indicated that wet screen washing the cave deposit through 0.5 mm mesh sieves produced thousands of small mammal, amphibian, and reptile bones; fossils unobservable in the field when covered with a sediment coating. From the current and only known entrance, the cave immediately diverges into two narrow passages at the bottom of a short 2.6 m (8.5 ft) drop-in opening which acts as a natural trap for small species of animals.

One field season of excavation by a crew from the Mammoth Site occurred in the northern-most passageway and produced thousands of fossil remains. The main passageway, which emits strong wind in association with changes in barometric pressure, is being explored by park service personnel. Removal of sediments by the NPS from this lengthy passageway is primarily associated with exploration and has minimal or no stratigraphic control. As a result, all fossils determined to be of paleontological interest are directly radiocarbon dated. Because sediment removal continues from the cave, work is on-going in terms of identification and analysis. All sediments removed are wet screen washed through 500-600μm (0.5-0.6 mm) mesh sieves, dried, and sorted for plants, mollusks, and skeletal remains using a 10X microscope.

Nineteen radiocarbon dates directly on various taxa produced ages from greater than 44,000 cal yr BP to about 11,000 cal yr BP, with some indication that there may be a depositional hiatus. Five additional dates represent the

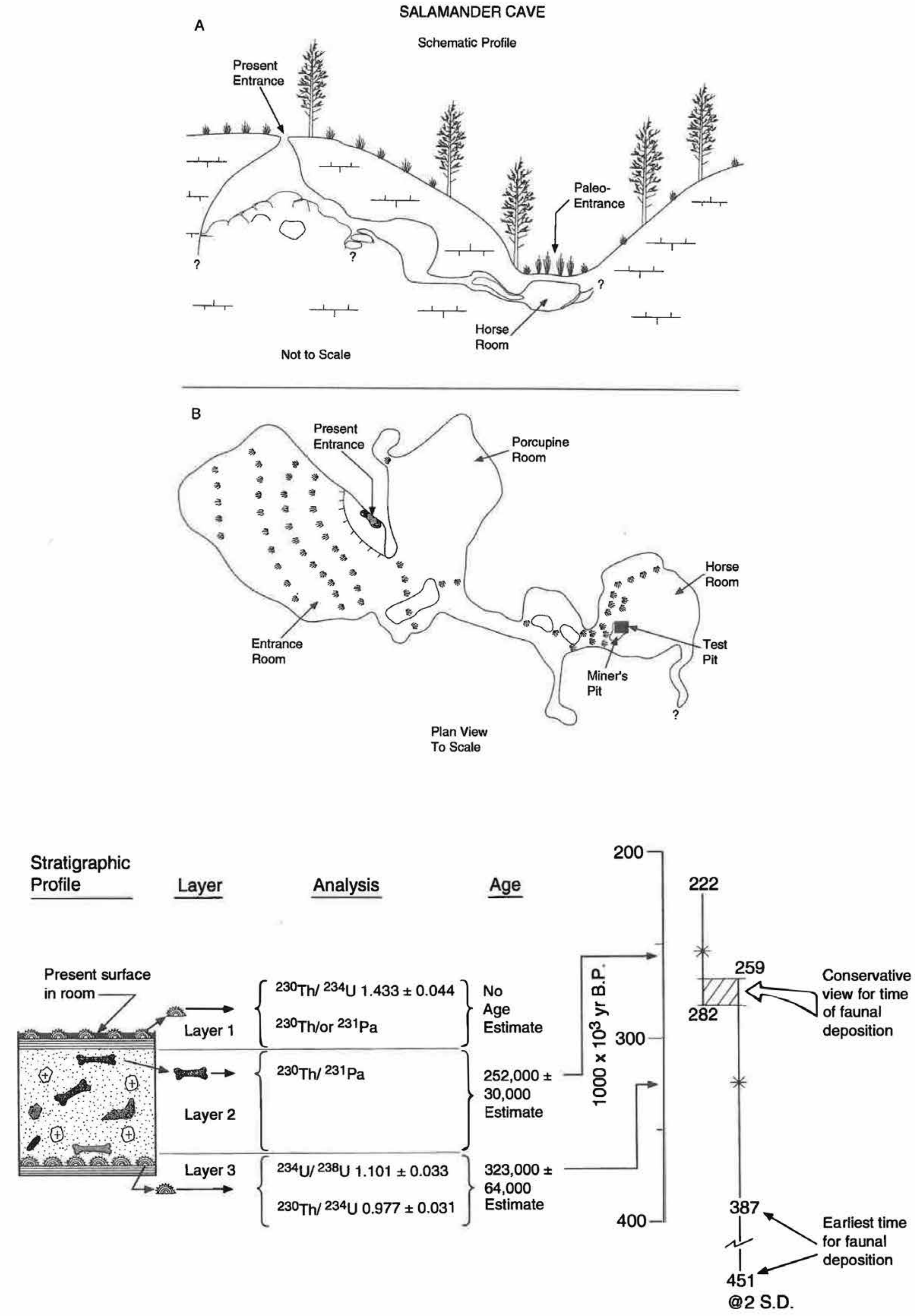


Figure 5. Schematic map of Salamander Cave in Wind Cave National Park showing the profile view, A, and the plan view B (from Mead et al., 1996). The chronological analysis of the deposits in the Horse Room is outlined in the graph showing the conservative estimate of 282 to 259 thousand years old based on U-series dates; older estimates are possible (Mead et al., 1996).

modern through the Holocene. Vole species recovered include heather vole (*Phenacomys* sp.), muskrat (*Ondatra* sp.), southern bog lemming (*Synaptomys cooperi*), red-backed vole (*Clethrionomys* sp. [=*Myodes*]; we follow Kryštufek et al., 2020), sagebrush vole (*Lemmiscus curtatus*), prairie vole (*Microtus ochrogaster*), and another unidentified meadow vole (*Microtus* sp.). The record supports an interpretation of a faunal turnover in the Late Pleistocene to early Holocene (Jass et al., 2020). Most of the faunal remains from the cave have yet to be completely studied but include a large, extinct form of bison, lizards, snakes, frogs, salamanders, fish, birds, mollusks, camel (*Camelops*), horse (*Equus*), bats, shrews, bear (*Ursus*), and other smaller carnivores. A few skeletal elements of the genus *Martes* (pine marten) were identified (Mead et al., 2021; see Wind Cave discussion below; see also Stagebarn Cave discussion). Considering the specimen from Wind Cave with the Persistence Cave specimen, most specimens are of the size of the extant pine martens (*Martes americana/caurina*), which are not known historically from the Black Hills. An additional jaw with teeth from PC is distinctly larger and within the size variation of the extinct noble marten (*M. nobilis*; Mead et al., 2021 and references within). The abundance of snake bones, especially of the rattlesnake (*Crotalus*) indicates that the cave was used as a hibernaculum for a long time. Descriptions of the amphibian and reptile fossils are in progress.

Richmond Hill

The quarry operation at the Richmond Hill Gold Mine in the northern Black Hills (8 km north of Lead, SD; Fig. 1) breached a number of small cave and fissure deposits containing Pliocene to early Pleistocene age fossils. Only two of the fissure deposits have been preliminarily assessed but approximately eight fossil sites have been removed and are now stored at the Museum of Geology, South Dakota School of Mines and Technology (SDSM&T). P. Bjork (SDSM&T) produced the initial excavations of two fissures but subsequent removal of the remaining fissures was conducted by James Martin (SDSM&T). The methodology used in recovering the fissure fill sediments is not currently available in publications. Carnivore species from the Unwily Coyote Site and the East-West Fissure Site indicate a Blancan North American Land Mammal Age for at least two of the sites (Bjork, 1997). Preliminary evaluations by CNJ and JIM on the arvicoline rodents, prairie dog (*Cynomys* sp.), pika (*Ochotona*), reptiles, and amphibians from these two fissure deposits have been conducted. These fissure fills provide the first and earliest record of pika in the Black Hills in addition to being the oldest known cave faunas for the region.

Rushmore Cave

Rushmore Cave is a privately-owned commercial walk-in cave at about 1,176 m (3,860 ft) elevation (Fig. 1). A 'grab-bag' of sediment samples from a few locations within the cave were assessed by researchers at the Mammoth Site and indicate that a Holocene age deposit of bats is preserved at the cave. Additional work is needed to evaluate the presence or absence of older, Pleistocene faunas. Presently, little is understood about the paleontological potential of this cave but the processed sediments hold great promise for a more expansive and focused study.

Salamander Cave

Salamander Cave is a small cave located in Wind Cave National Park (Fig. 1). Currently the cave has a 1.6 by 0.75 m entrance with a 6 m natural trap drop ending on an active debris cone. Live salamanders (*Ambystoma*) along with skeletal remains of rabbits, rodents, other small mammals, anurans (frogs and toads), and reptiles (snakes and lizards) were observed across the cone (J. Mead, pers. observation). A preliminary test of the cone produced thousands of skeletal remains that require further analysis; the chronology of the cone needs assessment but certainly contains records of the modern biota and likely contains at least a late Holocene record.

The cave also contains several larger rooms of which only two are being infilled via the current entrance (Fig. 5). The Porcupine Room is actively being infilled on one side via the current entrance but the opposite side of the room there is an older, fairly consolidated talus cone yet to be evaluated. A small corridor leading away from this room leads down into a back chamber called the Horse Room. Deposition into the Horse Room likely occurred from a previous entrance into the cave. A miner's test pit through the flowstone floor of the Horse Room exposed a mud, cobble, and bone unit, which was sampled in 1991 (Mead et al., 1996).

Details about the chronology and simple stratigraphy of the bone unit in the Horse Room indicate that the bone layer is no older than approximately 323,000 year old and no younger than 252,000 years old (Fig. 5; details in Mead et al., 1996). Multiple taxa are recorded from the bone unit including the extinct voles *Mictomys* cf. *M. meltoni*, *Microtus paroperarius*, and *Microtus* [*Terricola*] *meadensis*, a wolf (*Canis* cf. *C. dirus*; =*Aenocyon dirus*), a horse (*Equus*), and camel (*Camelops*). Additional taxa recovered include prairie dog (*Cynomys* sp.), pronghorn (Antilocapridae), and possibly snowshoe hare (*Lepus* cf. *L. americanus*), among other species of mammals. Presently, all are being reinvestigated. Fauna from the other rooms deserve further evaluation both in the lab and field.

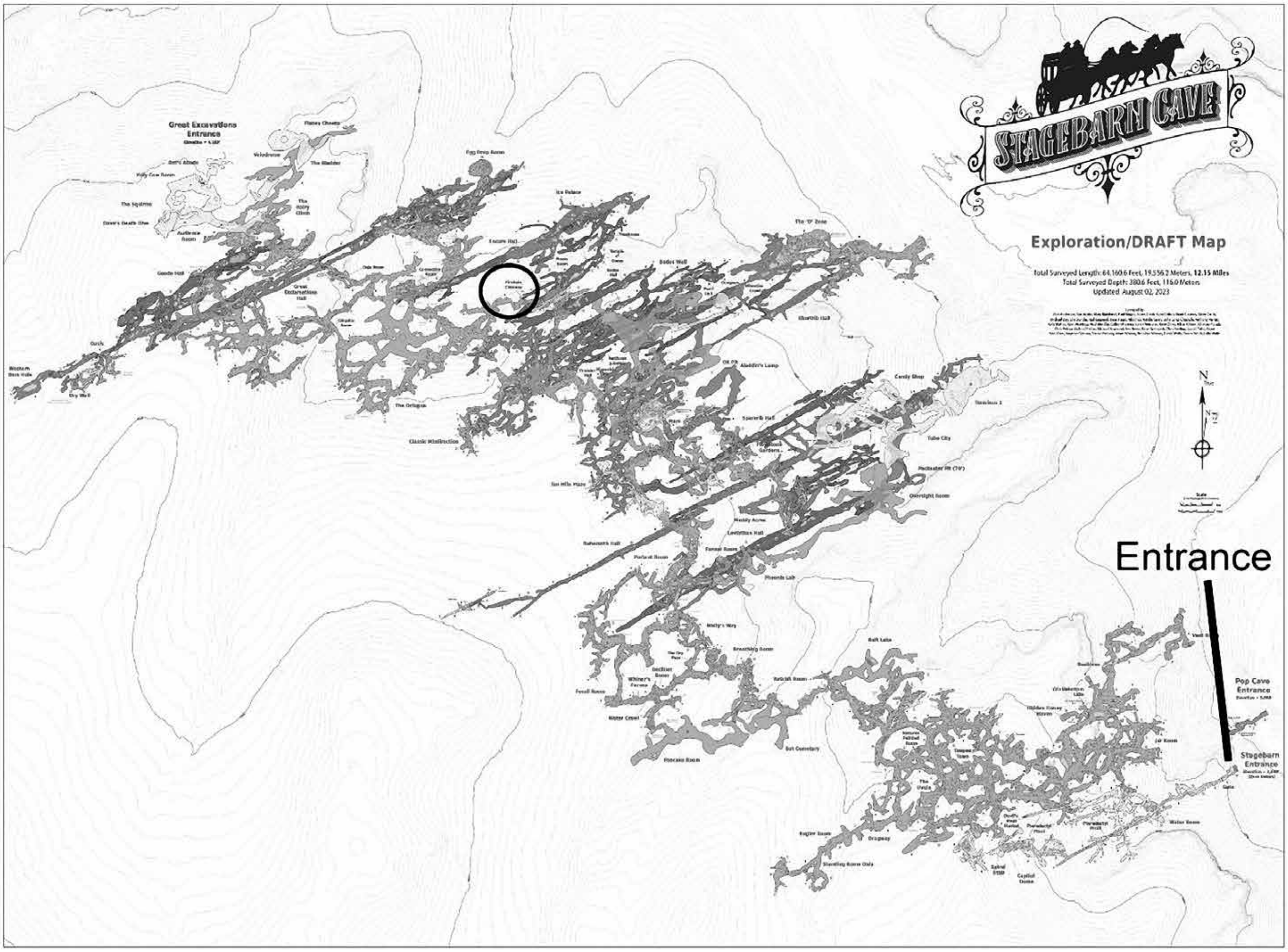


Figure 6. Map of Stagebarn Cave illustrating the 12+ miles of complex passageways, the main entrance, and the location (black circle) of the weasel and pine marten skeletons discussed in the text. Map provided by Adam Weaver.

Figure 7. Photograph of the left mandible of a pine marten (*Martes*) from Stagebarn Cave (circle in Fig. 6) as found in the cave. Note the adhering carbonate. Scale bar = 10 mm.

Stagebarn Cave

Stagebarn Cave (=Stagebarn Crystal Cave; 1,192 m; 3,910 ft elevation) is privately owned and is one of the longest caves in South Dakota (Fig. 1). A few of the passageways are known to contain multiple mammal carcasses of unknown identity and age but two have received detailed attention (Fig. 6).

A complete carcass of a small weasel was mapped in situ, removed, and is curated at the Mammoth Site. The carcass contained a coating of dermestid beetle larval castings (Coleoptera; scavengers of dead animals); some hair still adheres to the bones. Both the skull and the mandibles, as well as the postcranial elements are well preserved. Larval castings and vertebrae from the skeleton were radiocarbon dated and are modern, (UCIAMS 256729: 1.1776 modern fraction, dermestid egg casts; UCIAMS 260204: purified collagen content on bone: d13C -21.0, 1.1814 modern fraction; D14C 181.4). The mandibles have most of the cheek teeth (p2 – m1) in place, with only the m2 alveolus being edentulous.

The weasel tooth and mandible measurements were taken with digital calipers and follow the methodology of Anderson (1968). The length of the m1 is 5.1 mm and its width 2.2 mm. These measurements fit within the range for the long-tailed weasel (*Mustela frenata*) of both modern specimens (length = 4.5 – 5.6 mm; width = 1.4 – 2.0 mm) and fossils (length = 3.9 – 5.8 mm; width = 1.6 – 2.9 mm) recovered from Little Box Elder Cave, Wyoming (Anderson, 1968:table 9). The alveolar tooth row length, c – m2, is 15.3 mm for the Stagebarn Cave specimen which also fits within the range of modern populations (13.8 – 18.2 mm) and fossils from Little Box Elder Cave (13.1 – 17.0 mm) for *M. frenata* (Anderson, 1968). Although well within the size parameters of *M. frenata*, the size of the tooth and the tooth row from Stagebarn Cave is also congruent with the size of larger living males of the ermine (*M. erminea*) from Alaska; however, our measurements are not compatible with the fossil specimens of the typically smaller *M. erminea* or the minute least weasel (*M. nivalis*/*rixosa*) (Anderson, 1977). Both *M. frenata* and *M. erminea* live in various habitats of the Black Hills today (Turner, 1974). Based on the size of the specimen, and the consistency with modern and fossil data, we hypothesize that the Stagebarn Cave specimen is *M. frenata*.

Another complete carcass was mapped in situ, but only the left mandible and the left femur were removed, leaving most of the skeleton in situ in the cave. The bones of the skeleton are fragile, but all the teeth were preserved in the mandible (Fig. 7). The canine was removed for radiocarbon dating, producing a median age of 28,777 cal yr BP (range: 29,095 – 28,545 cal yr BP; 24,510±110 radiocarbon years old; UCIAMS 256736: d13C -19.6, D14C -952.7). Measurements taken from the mandible follow the methodology of Anderson (1970) as used in Mead et al. (2021) for fossil specimens of *Martes* from the Black Hills. The length of the m1 from Stagebarn Cave is 9.79 mm (reported as Lgm1 in Mead et al., 2021:table 1). This tooth in extant *Martes caurina* ranges from 8.1 – 10.9 mm, in *M. americana* ranges from 8.5 – 10.2 mm, and in the extinct *M. nobilis* ranges from 9.8 – 11.8 mm, including specimens from Little Box Elder Cave (WY) and Chimney Rock Animal Trap (CO) (see discussions in Anderson, 1968; Hager, 1972; Mead et al., 2021). These measurements imply that the Stagebarn Cave specimen could represent either of the two living North American species of pine martens. Neither species is indigenous to the Black Hills today, but it was introduced historically (Buskirk, 2001). However, the depth of the mandible (dorsoventral height below the posterior end of the m1) of the Stagebarn Cave specimen is 9.81 mm, indicating a stout jaw. Extant North American martens have a thinner mandible with both species having less than 8.7 mm for the depth of the mandible. The extinct *M. nobilis* is a more robust marten with a mandible depth of 7.9 – 11.0 mm (see discussion in Anderson, 1970; Mead et al., 2021 and references within). We hypothesize that the Stagebarn Cave marten specimen represents the extinct *M. nobilis,* which is also known locally from Persistence Cave (Mead et al., 2021; see discussion of Wind Cave). The implication is that this extinct, larger-than-present form of marten may have lived over most of the Black Hills during the Late Pleistocene. This hypothesis can be further tested by locating, measuring, and directly dating additional remains found in caves throughout the Black Hills.

Wind Cave

Wind Cave (Wind Cave National Park; Fig. 1) is a large cave system consisting of over 240 km (150 mi) of crisscrossing passageways with many corridors still to be explored, especially to the north. Exploration in new sections of the cave in 2019 produced the discovery of a complete skeletal carcass of a pine marten. The relatively dry passageway permitted the preservation of some hide, muscle tissue, and dermestid beetle debris. Direct radiocarbon dating of the carcass indicated that the animal died in that remote section of the cave system 11,182 – 10,779 cal yr BP years ago (for details, see Mead et al., 2021; and see discussion above: Persistence Cave). Other carcasses are known from the same and other distant passageways but have yet to be assessed. Isolated bones occur throughout the cave but have received little attention. A bison (*Bison bison*) leg bone with adjacent charcoal in the sediments produced a late-middle Holocene age (4658 – 4528 cal yr BP on charcoal). Given the extensive passageways in the cave system, with new corridors to be located, it is likely that there are deposits with significant faunal remains yet to be assessed.

DISCUSSION AND CONCLUSIONS

Caves are significant for the preservation of Quaternary faunas across North America (Jass and George, 2010). Fossil resources have been known from caves and karst deposits from the Black Hills for at least 50 years, yet compared to other geographic regions the number of known Quaternary fossil localities seems small compared to the extensive nature of the known cave systems. We suggest that this is largely an artifact of less focused attention to the presence of fossil resources, and the fact that Quaternary resources are often diagenetically unaltered (i.e., they may look like something that was trapped in a cave last year, versus thousands of years ago, and be dismissed as such).

A preliminary examination of the faunas from these caves have produced data that illustrates that the Black Hills have long been an ecotonal island influenced by distinct regional biomes to the east, west, and north. Pikas that live no closer than the higher elevations in the Big Horn Mountains approximately 80 km (150 mi) west in Wyoming today had no record of their fossil history in the Black Hills until the Richmond Hills discovery (Mead, 1987; Bjork, 1997). The record of voles and lemmings from a number of the caves illustrates that the Black Hills island has had considerable biotic turnover, as different taxa from north, west, east appear and disappear from the record through latter portions of the Quaternary (Pardi and Graham, 2018; Jass et al., 2020). The record of the pine marten from a number of caves, possibly representing two species, also points to this mountain island as a location where certain species once existed during previous glacial phases but have since become locally extirpated (until a historic re-introduction) (Mead et al., 2021, and above discussion). This may reflect a pattern of insular mountain mass occupation similar to other topographically high areas of western North America where the transition of glacial phases to interglacial phases resulted in some species becoming isolated at elevations, and ultimately leading to extirpation. Such a pattern was noted elsewhere at part of a complex theory about insular biogeography that has been a critical part of research on past climates and biotic community changes of the Intermountain West (Great Basin) (chapters in Harper and Reveal, 1978; Grayson, 1993; among others). Whether the Pleistocene record of the Black Hills mirrors biogeographic models observed elsewhere or represents a unique pattern of biological change requires further analysis. Much more work is needed on the existing faunas, and much remains to be discovered in cave systems of the Black Hills.

The records of cave localities and fossils summarized here illustrate that there is a wealth of Quaternary faunal remains preserved in Black Hills caverns, deposits which have much to contribute to our broader understanding of the natural history, environment, climate, and biogeography of the northern Great Plains region. Our hope is that by raising more awareness of the potential significance of those records, we continue to create collaborative endeavors with the larger caving community (be them private cavers or state and federal land managers) that explores Black Hills caves as well as caves of other surrounding regions. Bones situated on cave floors may be significantly older than they look and random bags of seemingly uninteresting looking, clastic cave sediments can often produce a wealth of fossil data. More of those finds will continue to help us understand the complex natural history of the Black Hills.

ACKNOWLEDGEMENTS

We dedicate this overview of caves and cave paleontology to Eric Grimm. We thank the many cavers, citizen scientists, and college students who continually work in caves and on the fossils found in those caves. We appreciate general discussions about Black Hills caves and their fossils with Larry Agenbroad, Eric Grimm, Russ Graham, Daniel Hanson, Roderic Horrocks, Rolfe Mandel, Marc Ohms, Blaine Schubert, Adam Weaver, and Michael Wiles. Adam Weaver is thanked for the Stagebarn and Parker's Pit cave maps and his enthusiasm towards the exploration of Black Hill caves; he sets an example for finding fossils in caves. We greatly appreciate Russ Graham and Eric Grimm for initiating the paleontological studies at Don's Gooseberry Pit and Parker's Pit and for forwarding the Parker's Pit project on to us for further study. We appreciate the extensive field work, field notes, and discussions from Don Brandborg, Angela Matthias, Melissa Pardi, and other crewmembers for fieldwork conducted at Don's Gooseberry Pit. Field and laboratory work on Parker's Pit has involved a small army of dedicated volunteers including: Jane Allard, Don and Nikkie Brandborg, Sue Brown, Bob and Jill Buck, Jim Cornette, Alex Gardner, Mark and Dena Hunter, William Jass, Steve and Brenda Johnson, Kierstan Leaf, Kelly Lubbers, Angela and Bill Matthias, Jim Ponnetta, Steve and Jessie Porter, Grace Self, Tim Voight, Sue Ware, Olga Potapova, and many others who provided logistical support in some form. We thank Brad Phillips, E. Clark Davis, and other staff of the US National Forest Service, Black Hills District, for their continuous permit support and the desire to understand the Quaternary cave resources of the Black Hills. Marc Ohms, Hollie Pucket, Tom Farrell, and additional staff of the Wind Cave National Park including the superintendents, along with Derek Jurestovsky, Jeff Martin, Rachel Short, Mary Carpenter, Josh Doby, and others including the many paleontological students of East Tennessee State University and the Museum of Geology, South Dakota School of Mines and Technology are thanked for the continuous work on and support of the research at Persistence Cave. Nate Fox of the Museum of Geology, South Dakota School of Mines and Technology and curation staff of Wind Cave National Park are thanked for their curation support of fossils from various caves mentioned in the text. Tom Hagen and Kevin Chase are appreciated for bringing our attention to the potential of fossils in Rushmore Cave. We thank Russ Graham and Gary Morgan for their reviews and editorial suggestions which greatly strengthened our manuscript.

REFERENCES

Abbott, J.P., 1989, The paleoecology of the Late and Post-Archaic section of the Beaver Creek Shelter (39CU779), Wind Cave National Park, Custer County, South Dakota. [MS Thesis]: Rapid City, South Dakota School of Mines and Technology.

Agenbroad, L.D., and Mead, J.I., eds., 1994, The Hot Springs Mammoth Site. A decade of field and laboratory research in paleontology, geology, and paleoecology: The Mammoth Site, Hot Springs, South Dakota.

Anderson, E., 1968, Fauna of the Little Box Elder Cave, Converse County, Wyoming: University of Colorado Studies, Series in Earth Sciences no. 6.

Anderson, E., 1970, Quaternary evolution of the genus *Martes* (Carnivora, Mustelidae): Acta Zoological Fennica, v. 130, p. 1–132.

Anderson, E., 1977, Pleistocene Mustelidae (Mammalia, Carnivora) from Fairbanks, Alaska: Bulletin of the Museum of Comparative Zoology, v. 148, p. 1–21.

Benton, R.C., 1990, the paleoecology of the Early and Middle Archaic sections of Beaver Creek Shelter (39CU779), Wind Cave National Park, Custer County, South Dakota: [MS Thesis]: Rapid City, South Dakota School of Mines and Technology.

Bjork, P.R., 1997, Pliocene cave and fissure deposits in the northern Black Hills of South Dakota with comments on the carnivores: Journal of Cave and Karst Studies, National Speleological Society Convention Abstracts, v. 59, p. 173.

Buskirk, S.W., 2001, Conservation assessment for the American marten in the Black Hills National Forest, South Dakota and Wyoming: Report on file, Black Hills National Forest, 1–56 p.

Conn, H., 1966, Barometric wind in Wind and Jewel Caves, South Dakota: National Speleological Society Bulletin, v. 28, p. 55–79.

Conn, H., and Conn, J., 1981, The Jewel Cave adventure. Fifty miles of discovery under South Dakota: Cave Books, St. Louis, Missouri.

Froiland, S.G., 1999, Natural history of the Black Hills and Badlands: Center for Western Studies, Augustana College, Sioux Falls, South Dakota.

Fulton, T.L., Norris, R.W., Graham, R.W., Semken, H.A., and Shapiro, B., 2013, Ancient DNA supports southern survival of Richardson's collared lemming (*Dicrostonyx richardsoni*) during the last glacial maximum: Molecular Ecology, v. 22, p. 2540–2548.

Graham, R.W., H.A. Semken, and M.A. Graham, eds., 1987, Late Quaternary mammalian biogeography and environments of the Great Plains and prairies: Illinois State Museum, Scientific Papers, no. 22.

Graham, R.W., Christine, J.A., and Semken, H.A., In Press, Taphonomic implication of ontogenetic distributions for field mice (*Peromyscus* spp.) populations from two debris cone deposits Parker's Pit, Black Hills, South Dakota: Journal of Cave and Karst Studies.

Grayson, D.K., 1993, The desert's past. A natural prehistory of the Great Basin: Smithsonian Institution Press, Washington.

Hager, M.W., 1972, A late Wisconsin-Recent vertebrate fauna from the Chimney Rock Animal trap, Larimer County, Colorado: University of Wyoming, Contributions to Geology, v. 11, p. 63–71.

Harper, K.T., and Reveal, J.L., 1978, Intermountain biogeography: a symposium: Great Basin Naturalist Memoirs, vo. 2, p. 1-268.

Jass, C.N., Mead, J.I., and Swift, S.L., 2020, Late Quaternary voles from Persistence Cave, Black Hills, South Dakota: Western North American Naturalist, v. 80, p. 521–530.

Jass, C.N., Mead, J.I., Morrison, A.D., and Agenbroad, L.D., 2002. Late Pleistocene mollusks from the southern Black Hills, South Dakota: Western North American Naturalist, v. 62, p. 129–140.

Jass, C.N., and George, C.O., 2010, An assessment of the contribution of fossil cave deposits to the Quaternary paleontological record: Quaternary International, v. 217, p.105–116.

Karner, F. R., 1989, Geological framework of the Black Hills and Bear Lodge Mountains: *in* Karner, F.R., ed., Volcanism and plutonism of Western North America: Devils Tower-Black Hills alkalic igneous rocks and general geology: Field trip T131 *in* Hanshaw, P.M., ed., Field trips for the 28th international geological congress. American Geophysical Union, Washington, D.C., p. 3–6.

Kowalski, K., 1995, Lemmings (Mammalia, Rodentia) as indicators of temperature and humidity in the European Quaternary: Acta Zoologica Cracoviensia, v. 38, p. 85–94.

Kryštufek, B., Tesakov, A.S., Lebedev, V.S., Bannikova, A.A., Abramson, N.I., and Shenbrot, G. 2020. Back to the future: the proper name for red-backed voles is *Clethrionomys* Tilesius and not *Myodes* Pallas. Mammalia, v. 84, p. 214-217.

Larson, G.E., and Johnson, J. R., 2007, Plants of the Black Hills and Bear Lodge Mountains: South Dakota State University, Brookings.

Lisenbee, A.L., 2010, The Black Hills uplift in its regional context: *in* Terry, M.P., Duke, E.F. and Tielke, J.A., eds., Geologic field trips in the Black Hills region, South Dakota: South Dakota School of Mines and Technology Bulletin, no.21, p. 202–207.

Manganaro, C.A., 1994, Graveyard Cave: a Holocene faunal record from the Black Hills of South Dakota [MS thesis]: Flagstaff, Northern Arizona University.

Martin J.E., Alex, R.A., Alex, L.M., Abbott, J.P., Benton, R.C., and Miller, L.F., 1993, The Beaver Creek Shelter (39CU779): a Holocene succession in the Black Hills of South Dakota: Plains Anthropologist, v. 38, Mem. 27, p. 17–36.

Mead, J.I., 1987, Quaternary records of pika, *Ochotona*, in North America. Boreas, v. 16, p. 165-171.

Mead, J.I., Manganaro, C., Repenning, C.A., and Agenbroad, L.D., 1996, Early Rancholabrean mammals from Salamander Cave, Black Hills, South Dakota: *in* Stewart, K.M., and Seymour, K.L., eds., Palaeoecology and Palaeoenvironments of Late Cenozoic mammals. Tributes to the Career of C.S. (Rufus) Churcher: Toronto, University of Toronto Press, p. 458–482.

Mead, J.I., Swift, S.L., Jass, C.N., Meyers, J.I., and Weaver, S.E., 2021, Late Pleistocene pine marten (*Martes*; Mustelidae) from the Black Hills, South Dakota: Northwestern Naturalist, v. 102, p. 109–119.

Palmer, A.N., 2016, Karst and caves of the Black Hills, South Dakota, USA: Boletin Geológico y Minero, v. 127, p. 67–78.

Palmer, A.N., and Palmer, M.V., 1989, Geologic history of the Black Hills caves, South Dakota: National Speleological Society Bulletin, v. 51, p. 72–99.

Palmer, A.N., Palmer, MV., and Paces, J.B., 2016, Geologic history of the Black Hill Caves, South Dakota: *in* Feinberg, J.M., Gao, Y., and Alexander E.C., eds., Caves and karst across Time: Geological Society of America Special Paper 516, p. 87–101.

Pardi, M.I., 2010, Paleoecology of the Late Pleistocene and Holocene rodents from Don's Gooseberry Pit, Black Hills, South Dakota [MS thesis]: State College, Pennsylvania State University.

Pardi, M.I., and Graham, R.W., 2018, Time averaging and late Quaternary ecological replacement in Don's Gooseberry Pit, South Dakota, USA: Quaternary Research, v. 89, p. 307–317.

Turner, R. W., 1974, Mammals of the Black Hills of South Dakota and Wyoming: University of Kansas, Museum of Natural History, Miscellaneous Publication, no. 60.

Wiles, M., 2013, Paleohydrology and the origin of Jewel Cave: *in* 20th National Cave and Karst Management Symposium: Report on file, US National Forest Service, Black Hills Forest Service, Custer, South Dakota, p. 33–40.

Wiles, M., 2019, Jewel Cave, South Dakota: *in* White, W.B., Culver, D.C., and Pan, T.P., eds., Encyclopedia of Caves (Third Edition): p. 577–587.

Wiles, M., Ohms, R.E., and Pflitsch, A., 2009, Cave climate studies and the potential extent of the Jewel Cave system: *in* Proceedings of the 15th International Congress of Speleology, Kerrville, Texas, July 19–26, 2009, Vol. 3, Contributed Papers for the International Congress of Speleology, p. 1723–1727.

Kevin L. Seymour. The Oregon Caves National Monument fossil jaguar and the paucity of fossil jaguars from the western USA.. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 202-215. DOI:10.4311/2024PA0105

THE OREGON CAVES NATIONAL MONUMENT FOSSIL JAGUAR AND THE PAUCITY OF FOSSIL JAGUARS FROM THE WESTERN USA.

Kevin L. Seymour[1]

ABSTRACT

The most northerly excavated partial skeleton of a fossil jaguar (*Panthera onca /augusta*) from the USA (Oregon Caves National Monument, or ORCA) is described, illustrated and identified. Most of the individual bones preserved as fossils are compared with those found in living puma (*Puma concolor*) and jaguar (*Panthera onca*) skeletons to demonstrate the identification characters for each element and to establish their identification as those of a fossil jaguar. The carbon date on this specimen dates to 38,620 +/- 440 years BP, making it the oldest dated jaguar specimen to date, and within the Rancholabrean land mammal age. Its dentition is about average in size for a Rancholabrean jaguar, but its canine teeth are larger, suggesting a male. Eight localities (including ORCA) containing specimens of fossil jaguar are identified from the western USA., whereas six others containing felid specimens purported to be jaguar are identified as other felids. Given that there was no apparent bias against the preservation of felids in the fossil record in the western USA, it is suggested that there was a relative lack of the preferred prey species in the west (peccaries, armadillos or species associated with water such as turtles, caimans, capybaras or tapirs) compared to the southeast USA, where fossil jaguars are more frequently found.

INTRODUCTION

The jaguar (*Panthera onca*), the largest living new world cat, was once part of the native fauna of the USA, with historical records from Arizona, New Mexico, California, Texas, and possibly a few other states (Brown, 1983; Hall and Kelson, 1969; Merriam, 1919). This species has a tenuous foothold in the USA with only a handful of recent records (Brown and López-González, 2001; McCain and Childs, 2008), consequently it is still on the USA Endangered Species list (Rogers, 1997). Pleistocene fossil material documents this species as being present throughout much of the southern and central USA, from West Virginia and Pennsylvania to Florida in the east, through Nebraska, Nevada and California in the west (Kurtén, 1973). In the fossil record, it is much more common in the east, especially from Florida where there are 37 known localities (Morgan and Seymour, 1997), with many fewer records from the west. The most northerly specimens recorded so far are a few scraps from Oregon (Lake Co. and Malheur Co.) with inexact locations, which are barely enough to document the presence of this species there. The Oregon Caves specimen, although located slightly further south than these previous Oregon records, is still the most northerly-known fossil jaguar skeleton in North America.

This paper documents the new specimen of fossil jaguar from the Oregon Caves National Monument (ORCA 2021), that was only briefly discussed by Roth (1996) and Seymour (2003). It is important to document this specimen, as fossil jaguar skeletons are exceedingly rare. As of 1993, only five localities have so far produced partial skeletons (Seymour, 1993), and all are from eastern USA or Texas and from caves. No complete fossil jaguar specimen has been recovered anywhere in North America.

A note about jaguar taxonomy is relevant here. As discussed by Seymour (1993), the larger Pleistocene form of the living jaguar has received various names. Some workers have considered this larger form to be a different subspecies from the living forms (naming it *Panthera onca augusta*), for example Simpson (1941) and Kurtén (1973), while others have considered it to be a different species (naming it *Panthera augusta*), for example McCrady et al. (1951), even while all acknowledge that there was probably genetic continuity between the fossil and living forms. Neither naming option is ideal. Naming it a different species would imply an extinction whereas naming it a different subspecies risks confusing geographic subspecies (variation at one time) with temporal subspecies (variation through time). For this reason, I prefer to use the informal lineage segment naming system as proposed by Martin (1993), resulting in the name *Panthera onca /augusta* for this form.

ABBREVIATIONS:

Institutional: AMNH: American Museum of Natural History, New York, New York
LABE: Lava Beds National Monument, Tulelake, California
LACM HC: Los Angeles County Museum, Hancock Collection (at the George Page Museum), Los Angeles, California
ORCA: Oregon Caves National Monument, Cave Junction, Oregon
NSM: Nevada State Museum, Carson City, Nevada
ROM: Royal Ontario Museum, Toronto, Ontario, Canada

---

[1] Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6. kevins@rom.on.ca

TMM: Texas Memorial Museum, Austin, Texas
UALP: University of Arizona Lab of Paleontology, Tucson, Arizona
UCMP: University of California, Museum of Paleontology, Berkeley, California
USNM: United States National Museum (Smithsonian), Washington, D.C.
UTEP: University of Texas at El Paso, El Paso, Texas.
MC: metacarpal; MT: metatarsal; MNI: minimum number of individuals.

LOCATION AND OCCURRENCE

Oregon Caves National Monument is located in southeastern Josephine County, within the northern Siskiyou mountains of south-west Oregon, Lat 42 05’ 53” N, Long 123 24’ 26’’ W. The monument itself is fairly small (about 488 acres or 1.97 sq km) consisting mostly of old-growth coniferous forest, dominated by Douglas Fir (*Pseudotsuga menziesii*). The entrance to the cave system is at about 1200 m elevation. The marble cave itself is about 5.6 km long, and harbors one of the largest assemblages of endemic cave-dwelling insects in the USA.

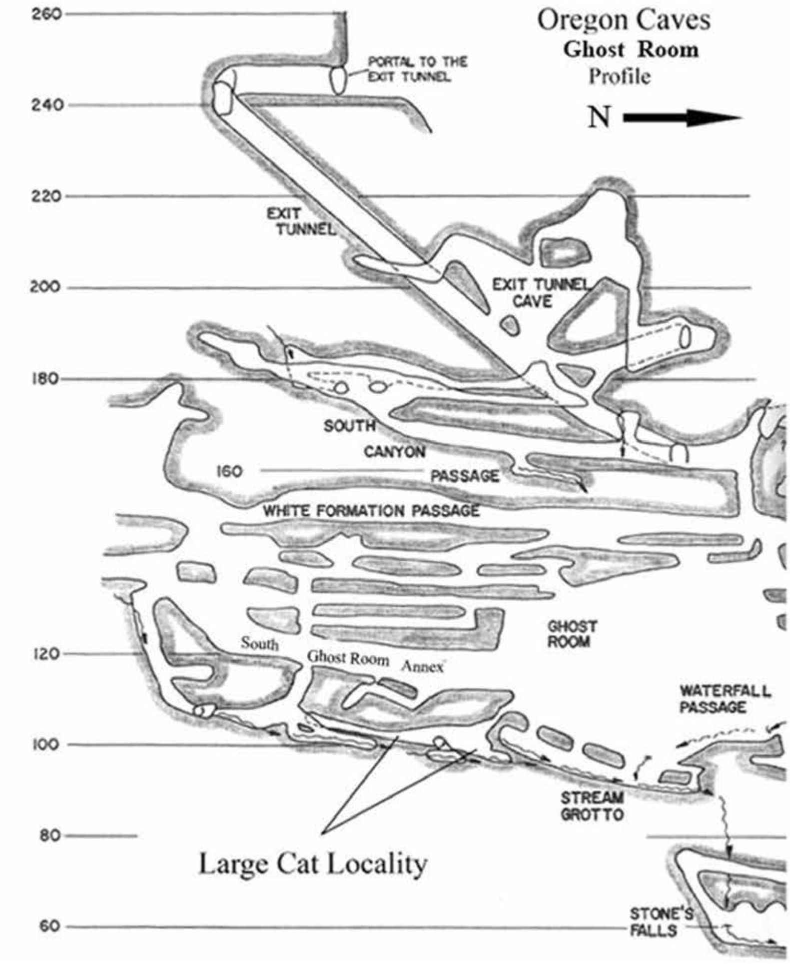


Figure 1. Cross section of a portion of the cave system at Oregon Caves National Monument. The numbers at the left measure depth in meters above the lowest point in the cave system. The jaguar specimen was recovered near the bottom of this diagram, below the Ghost room, labelled as “Large cat locality”. Diagram provided by Blaine Schubert.

The new fossil jaguar specimen (ORCA 2021) was found by Steve Knutson in August 1995 in a tight tunnel just down from a part of the cave called the Ghost Room (Fig. 1). The difficult access to the specimen made it hard to see for a positive identification and initially it was thought to be a bear, because of its large size and the fact that bear bones commonly have been found in other parts of this cave system. John Roth contacted Greg McDonald, then at Hagerman Fossil Beds National Monument in Idaho and requested that he work with the park to determine what animal the partial skeleton represented. Steve and Greg McDonald recovered the skull, jaws and a few long bones in 1997. The recovery of the skull and jaws allowed for an immediate identification as a large cat. The remainder of the skeleton was recovered on March 9, 1998 by Larry Coats, Blaine Schubert, and Jim Mead. Although most material was on the surface, some was coated with flowstone and was not possible to remove, some material was under water, and some was scattered in the crawl tunnel above the creek. Judging by the positioning of the bones, it is likely that the animal died in the crawl tunnel and that the material scattered slightly downhill from there (Blaine Schubert, pers. comm.).

GEOLOGICAL SETTING

A total of fourteen U-series dates on three different sample series were used as the basis for developing a speleothem growth chronology for the Oregon Caves flowstone (Turgeon and Lundberg, 2004). The Neptune’s Grotto flowstone series range between 359 and 122.9 ka, the Exit Tunnel Cave flowstone series range between 119.3 and 116.7 ka, and then another series ranges from 14.3 to 12.0 ka, and finally the White Formation Passage stalagmite dates between 3.9 ka and 2.3 ka (Turgeon and Lundberg, 2004). These dates represent when the cave formations were growing, mostly during mid to late Pleistocene interglacials, when excess moisture allowed the flowstones to grow.

Although the cave formations seem to have formed primarily earlier in the Pleistocene, the jaguar could have entered the cave at any time. It probably would have preferred to enter a drier rather than a wetter cave, judging from the evidence of jaguars in dry caves (Guilday and McGinnis, 1972). The carbon date indicates that the jaguar died in the cave during a time when the cave formations were not actively growing.

CARBON DATES ON JAGUAR SPECIMENS

Usually, the age of fossil jaguars is judged by the associated fossils preserved with them. No North American jaguar specimen appears to be older than about 1.6 million years old (Seymour, 1993) and all North American fossil jaguars are from the Pleistocene.

Previously only two accelerator mass spectrometry (AMS) carbon dates have been published for fossil jaguars, both published on Tennessee specimens (Corgan and Breitburg, 1996), although I attempted to obtain AMS carbon dates on two jaguar specimens from the Talara tar seeps, Peru (TO-B3649 and TO-B3650), but the impregnated tar prevented this. These dated Tennessee specimens are the two collected by Edward McCrady that were discussed by McCrady et al. (1951). The first (USNM 18262) was found in Little Salt River Cave, Franklin Co., Tennessee, and dates to 13,455 +/- 100 years BP (C-13 corrected; done on bone apatite; GX-20705-AMS). The second specimen, mentioned by McCrady et al. (1951) as being stored at the University of the South in Sewanee, Tennessee (where I examined the specimen in 1998), has since been transferred to USNM, and is now USNM 521280. This specimen, found in Johnson Cave, near Sparta, Putnam Co., Tennessee, dates to 28,855 +/- 300 years BP (C-13 corrected; done on bone gelatin; GX-20143-G).

An AMS carbon date on the L pelvis fragment of ORCA 2021 yielded a date of 38,620 **+/-** 440 years (C-13 corrected; done on bone apatite; TO-11167). This date should be considered a minimum age, as further research would be required to answer the question if the specimen is in fact older than this result. Regardless, ORCA 2021 is the oldest directly dated North American fossil jaguar specimen to date.

Description of the Oregon Caves specimen, ORCA 2021

The Oregon Caves jaguar skeleton is incomplete, although the individual bones are well preserved. Most elements are fragmented in some way, but 14 are complete, as follows: thoracic vertebra X, an anterior caudal vertebra (about caudal IX), right ulna, radius, calcaneum, MT II, and proximal phalanx of the same digit and the following elements from the left side: scapholunar, magnum, MC II, MC IV, MC V, navicular and MT III. This partial skeleton will be discussed below bone by bone.

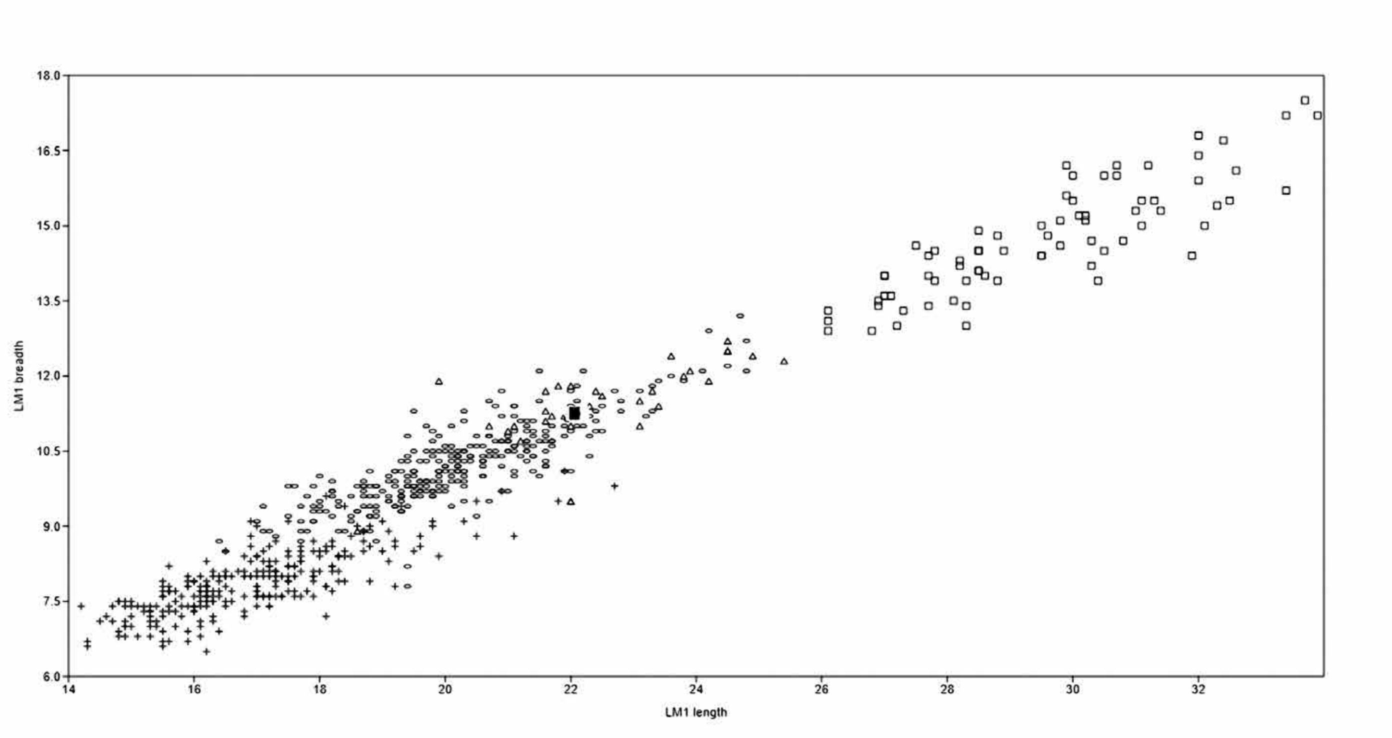


Figure 2. Bivaraiate graph plotting lower first molar length against lower first molar breadth for a selection of cats. Open squares represent Pa. atrox from North America, open ovals represent recent Pa. onca from both North and South America, open triangles represent fossil Pa. onca /augusta from North America, solid square represents ORCA 2021 and plus signs represent recent Pu. concolor from North and South America. Data from Seymour (1993) or Seymour (1999). Graph constructed using PAST (Hammer et al., 2001).

IDENTIFICATION

Identification of fragmentary fossil felid remains can be difficult (Schultz et al, 1985). Fortunately, ORCA 2021 is a partial, associated skeleton, with several complete elements available for comparison. These elements were compared directly with skeletal material of Recent *Puma concolor* (ROMVP R1510, ROMM 34.5.10.1), Recent *Panthera onca* (ROMVP R5703, ANSP 19349, FMNH 57199), fossil *Homotherium serum* (casts of TMM material) and fossil *Smilodon fatalis*, consisting of a series from Talara, Peru discussed by Kurtén and Werdelin (1990) and Seymour et al. (2018). The identification criteria discussed by Seymour (1983) were applied to confirm the identification. These criteria will be discussed below for each element. This specimen can be identified as *Panthera onca laugusta* using the system of informal lineage segments recommended by Martin (1993) and Seymour (1993).

Table 1 Comparison of the lengths of four teeth for a selection of fossil cats

Element length	ORCA	Rlb avg	Rlb N	Irv avg	Irv N
Upper carnassial (P4)	30.5	30.3	19	31.6	9
Lower carnassial (m1)	22.0	21.6	23	23.5	9
Upper canine (C)	21.2	20.6	16	21.5	10
Lower canine (c)	21.0	20.0	18	20.5	8

Abbreviations for Table: avg, average; C, upper canine; c. lower canine; Irv, Irvingtonian land mammal age; m, lower molar; N, samples size; ORCA, Oregon Cave National Monument; P, upper premolar; p, lower premolar; Rlb, Rancholabrean land mammal age. Specimen data from Seymour (1993).

DENTITION

The dentition clearly identifies this specimen as a non-machairodont cat. The canines are conical and the post-canine teeth do not angle posteriad as in the machairodonts. Almost the full dentition of ORCA 2021 has been preserved. The only teeth lacking from this specimen are left I1, right I1-2, right M1 and all lower incisors except right i3. Most publications on fossil cats discuss the dentition because the dental-bearing elements are taphonomically the most often preserved, however, individual felid teeth look very similar between species. The large size of the ORCA specimen and its robust teeth suggest a pantherine, but both *Puma* and *Miracinonyx* during the Pleistocene were larger than present-day *Pu. concolor*, and fossil lion, *Pa. atrox*, was also present in the area, so size alone is not necessarily a safe criterion for identification. Compared to *Pu. concolor*, p4 of *Pa. onca* is longer relative to m1, m1 is relatively broad (Hoffstetter, 1949), and Ic is relatively large whereas p3 is relatively small (Werdelin, 1983). Compared to *Pa. atrox*, size alone seems to be the major criterion for identification. For instance, in Fig 2, the lower first molar length is plotted against the lower first molar breath. There is no overlap between *Pa. onca* and *Pa. atrox*, but there is significant overlap between *Pu. concolor* and *Pa. onca* in both the length and width of the m1. However, for any given length, the breath of the m1 is relatively wider in *Pa. onca* and so this can be used to secure an identification. ORCA 2021 fits very nicely in the plot with the fossil and recent jaguar specimens found in North America.

Table 1 shows the measurements of selected teeth of ORCA 2021 compared to a sample of Rancholabrean jaguars and older Invingtonian jaguars (specimen list in Seymour, 1993). The carnassial teeth (P4 and m1) are the first to erupt in the adult dentition, and hence, these teeth are used when predicting body mass (Van Valkenburgh, 1990). The ORCA carnassials are very close to the Rancholabrean average, and smaller than the Irvingtonian average, as expected. However, the canines are larger than the Rancholabrean average, and closer to the average for the Irvingtonian jaguars. Since jaguars are particularly dimorphic in their canine size (Seymour, 1989; 1993), this indicates an animal with above average canine size for a Rancholabrean animal, which suggests a male.

Simpson (1941) stated that some North American fossil jaguar specimens had a relatively larger P2 compared to the largest living jaguar subspecies. Using a larger sample size of all living subspecies (N= 53) than was measured by Simpson (who used N= 8) gives the following P2 length data: average 6.9 mm, range 4.9 to 8.7 (Simpson's data were average 7.3, maximum of 7.7). ORCA 2021 has a P2 length of 7.7, which places it above average, but not out of the range of the living jaguar. This tooth might be considered vestigial in the living species, and so its slightly larger size on average in fossil jaguar is not unexpected but of dubious taxonomic significance.

SKULL

The skull is fragmented into several pieces, consisting of the two maxillae, the glenoid/mastoid/occipital region, several pieces of frontal and parietal and a number of smaller fragments.

Three portions of the posterior part of the skull are useful for the separation of *Pu. concolor* from *Pa. onca* (Seymour, 1999). The petrosal bones are exposed and easily visible due to the breakage of the skull. The disconfigured subarcuate fossa on the petrosal bone, as described and illustrated by Salles (1992: Fig 26) and Seymour (1999: Fig. 2-6), is an indication of a pantherine rather than *Puma*. The mastoid and paramastoid are well developed and well separated from each other, another jaguar character (Fig. 3; also Hoffstetter, 1949: #34, 35; Seymour, 1999: Fig. 2-4). Finally, the anterior entotympanic is extended into a narrow, finger-like projection (best seen on the left side of ORCA 2021), and the anterior ectotympanic is well developed anteriorly, contrasting the *Puma* condition (Fig. 3; also Hoffstetter, 1949: #39, 40; Seymour, 1999: Fig. 2-4). As discussed by Seymour (1999), all these characters show some variation but the character states present in ORCA 2021 are usually only present in *Pa*. *onca* rather than in *Pu*. *concolor*. In addition, pumas show a well-developed bregmatic process (finger-like extensions of the parietal growing anteriad on top of the frontal), a feature that is absent in ORCA 2021.

The differentiation of *Pa*. *atrox* from *Pa*. *onca* on skull morphology is more problematic. For instance, of the 57 characters utilized by Salles (1992) in his study of the skull morphology of the cat family, he listed only three characters that differentiate *Pa*. *leo* (a presumed close relative of *Pa*. *atrox,* although see Christiansen and Harris 2009) from *Pa*. *onca*. One is an internal sinus feature present only in *Pa*. *leo* (which does not appear to be present in the frontal fragment of ORCA 2021), another is the presence of a processus brevis on the malleus ear ossicle (which does appear to be present in ORCA 2021 as in *Pa. onca*; both the left malleus and an incomplete right malleus were preserved) and the third is the relative loss of the internal grooves on the upper canine in *Pa*. *onca*, which are present in all other pantherines. ORCA upper canines do not have grooves, as in *Pa*. *onca*.

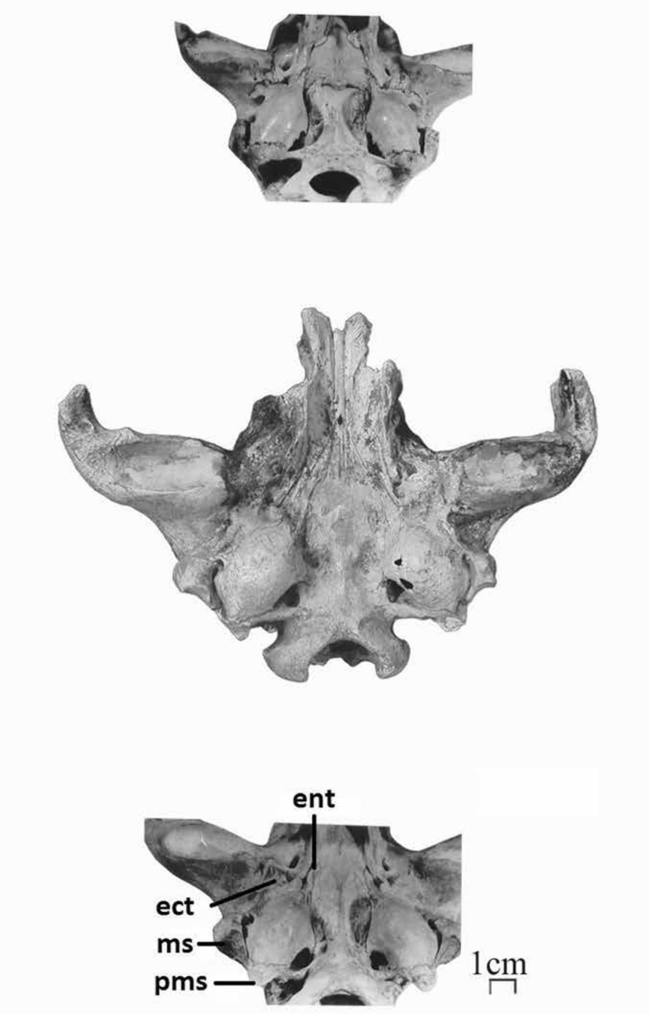


Figure 3. Ventral view of the skull to show the basicranium, anterior is at top. At top is Pu. concolor (ROMM 46326), in the middle is the fossil (ORCA 2921), at bottom is Pa. onca (FMNH 57199). Abbreviations: ect, anterior ectotympanic; ent, anterior entotympanic; ms, mastoid process; pms, paramastoid process.

Seymour (1983) suggested several other characters for the separation of *Pa*. *atrox* and *Pa*. *onca*, and all of them can be seen on ORCA 2021. However, it must be emphasized that these characters have not been examined yet on a series of skulls, and hence, the intraspecific variability is as yet unknown. Characters 4 through 7 are well-illustrated in Merriam and Stock (1932, Fig. 145). These include:

1. Lachrymal tubercle well developed in *Pa*. *onca*, weak or absent in *Pa*. *atrox*. ORCA 2021 is well developed, hence more like *Pa*. *onca*.
2. Mesopterygoid fossa strongly developed in *Pa*. *onca*, weakly developed in *Pa*. *atrox*. ORCA 2021 is weakly developed. I have seen a number of *Pa*. *onca* skulls with weakly developed fossae, so I do not put much trust in this character.
3. Infraorbital foramen relatively small in *Pa*. *onca*, large in *Pa*. *atrox*. In ORCA 2021, it is relatively large. I have seen wide variability in this character as well and tend not to trust it, until it has been quantified.
4. Auditory bulla more dome shaped in *Pa*. *onca*, more elongate in *Pa*. *atrox*. This character is rather difficult to quantify, but ORCA 2021 does appear to be more similar to *Pa*. *onca* than *Pa*. *atrox*.
5. Entotympanic process less developed in *Pa*. *onca*, more pronounced in *Pa*. *atrox*. ORCA 2021 is more like *Pa*. *onca*.
6. Bridge of bone anterior to the tympanohyal pit and stylomastoid foramen is flattened in *Pa*. *onca*, thicker in *Pa*. *atrox* (see Merriam and Stock 1932:197). ORCA 2021 is more like *Pa. onca*.

An additional character not discussed by Seymour (1983) is:

Postero-lateral palatal foramen is larger and placed more laterally in *Pa*. *atrox* than in *Pa*. *onca*. ORCA 2021 is more like *Pa*. *onca*.

In summary, 5 of the 7 characters demonstrate that ORCA 2021 is more similar to *Pa*. *onca* than to *Pa*. *atrox*. Although this confirms the identification as a fossil jaguar, it also indicates that characters 2 and 3 may be too variable to be used for the purpose of identification.

MANDIBLE

Other than the dentition, the mandible is a conservative element in felines. Although both halves are somewhat incomplete in ORCA 2021, the left is complete enough that the length can be measured, whereas the articular for the right half is separate from the main body and cannot be re-attached due to some missing bone.

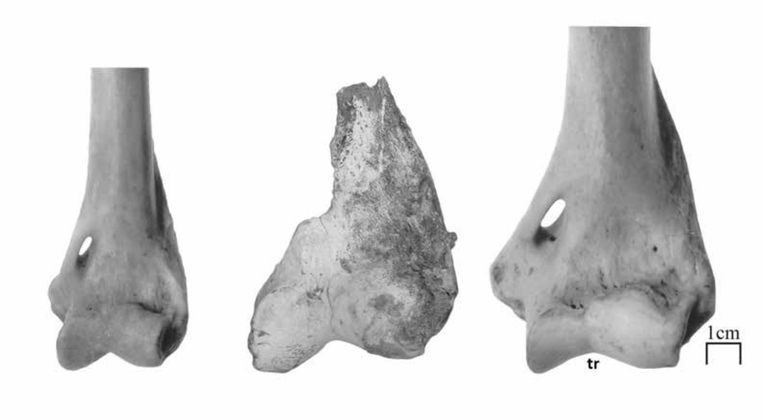


Figure 4. Anterior view of the distal part of the left hunerus. At left is *Pu. concolor* (ROMM 34.5.10.1), in the middle is the fossil (ORCA 2021) and at right is Pa. onca (FMNH 57199). Abbreviation: tr, trochlea.

The mental foramina are quite variable, but there are trends. Generally, they are relatively small in *Pa*. *onca*, and relatively large in *Pa*. *atrox*. The mental foramina of ORCA are relatively small as in *Pa*. *onca*.

LIMB AND FOOT BONES

The limb and foot bones of *Pa*. *atrox* are larger than those of *Pa*. *onca*, and so there should be little confusion between these two species, unless the material in question is fragmentary. However, the limb and foot bones of *Pu*. *concolor* and *Pa*. *onca* need to be carefully differentiated, as they can be similar in size. The morphological differences between the postcranial bones of these two species has not been discussed in any detail in the literature, other than in a thesis (Seymour, 1983). Here comparative descriptions of the elements preserved in ORCA 2021 are provided for the purposes of separating these two species, and identifying ORCA 2021. The source for these descriptions is Seymour (1983).

Figure 5. Top row is the anterior view of the proximal part of the left ulna, middle row is the lateral view of the proximal part of the left ulna and the bottom row is the lateral view of the distal part of the left ulna. Specimen numbers as in Figure 4. Abbreviations: b, bridge of bone; ol, olecranon process; sp, styloid process.

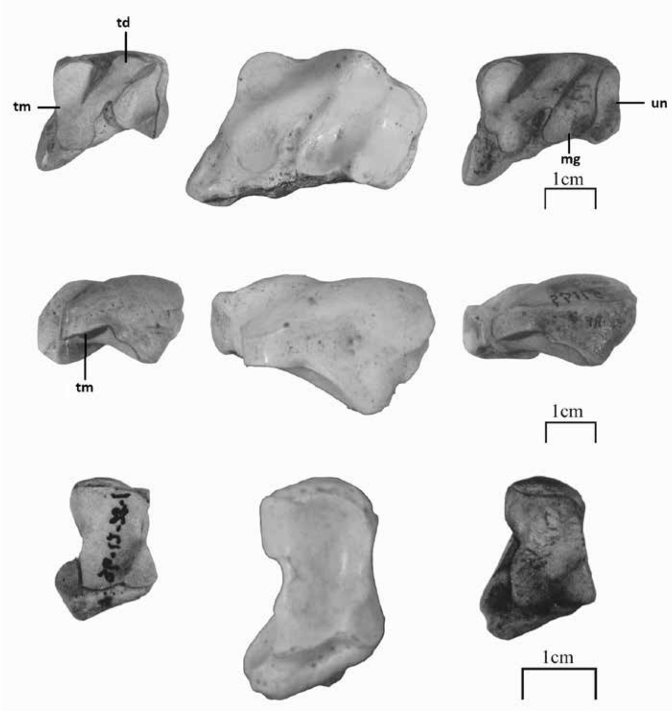


Figure 6. Top row is the distal view of the right scapholunar (flipped to appear left), middle row is the anterior view of the right scapholunar (flipped to appear left) and bottom row is the distal view of the right magnum (flipped to appear left), therefore lateral side is on the left. Specimen numbers as in Figure 4. Abbreviations: mg, articular surface for the magnum; td, articular surface for the trapezoid; tm, articular surface for the trapezium; un, articular surface for the unciform.

FORELIMB

The left humerus is broken into two pieces that cannot be re-attached, so the length of this element needs to be estimated, whereas the right humerus was not recovered. The trochlear notch on the distal end of the humerus is shallower in *Pa. onca* than in *Pu*. *concolor* (Fig. 4), and in this respect ORCA 2021 matches *Pa. onca*.

The left ulna is missing only a small portion of the distal end, whereas the right ulna is complete. Three characters that separate the ulna of *Pa*. *onca* from *Pu*. *concolor*: 1. The bridge of bone on the anterior face between the proximal extremity and the proximal end of the articulation for the humerus is broad, not narrow (Fig. 5, top row) 2. The posterior part of the olecranon process is squarish (not rounded) in outline, in lateral view (Fig. 5, middle row) 3. In lateral view, the notch between the styloid process and the articular surface for the radius is deeper than in the puma (Fig. 5, bottom row). All three characters of ORCA 2021 align with *Pa*. *onca*.

The left radius is represented by the proximal portion of the bone only, whereas the right radius is complete. The radius is one of the most conservative elements in felids,

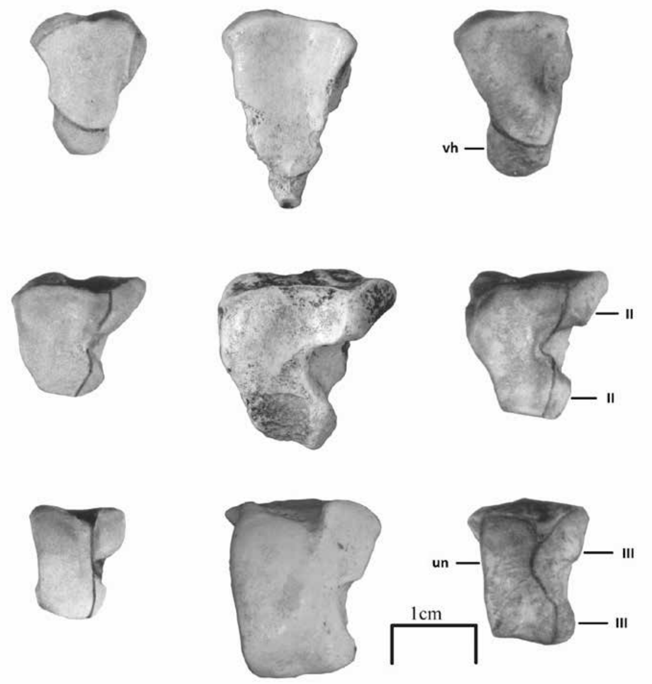


Figure 7. Top row is the proximal articular surface of the right metacarpal II (flipped to appear left, dorsal is at top and lateral is at left), middle row is the proximal articular surface of the right metacarpal III (flipped to appear left), bottom row is the proximal articular surface of the right metacarpal IV (flipped to appear left). Specimen numbers as in Figure 4. Abbreviations: II, articular surfaces for the articulation of metacarpal II; III, articular surfaces for the articulation of metacarpal III; un, articular surfaces for the unciform; vh, ventral hook.

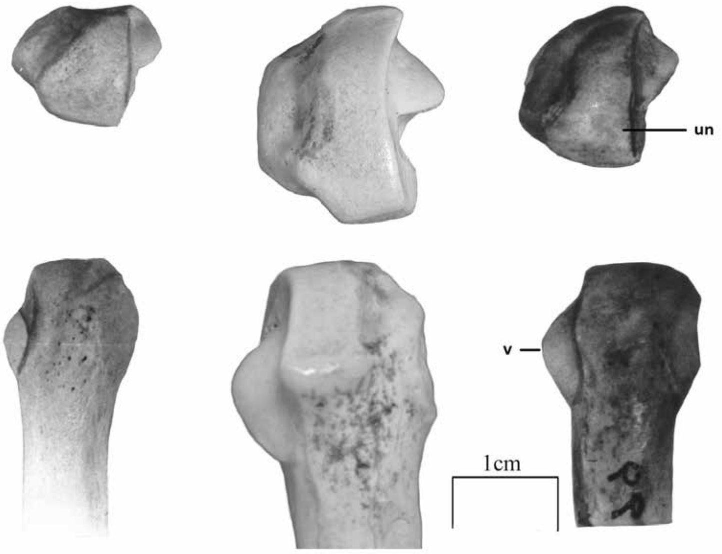


Figure 8. Top row is the proximal articular surface of the right metacarpal V (flipped to appear left, dorsal is at top and lateral is at left) and bottom row is the anterior view of the right metacarpal V (flipped to appear left). Specimen numbers as in Figure 4. Abbreviations: IV, articular facet for metacarpal IV; un, articular surface for the unciform.

often containing few or no characters, but three are listed here. The three characters that separate the radius of *Pa. onca* from *Pu. concolor* are: 1. The head is relatively larger, so that there is often a lip formed around the edge 2. the tubercle is elongate and aligned with the long axis of the bone and 3. the distal articular facet is larger and less elevated than in the puma. All three characters of ORCA 2021 align with *Pa. onca*, but are not illustrated here.

MANUS

From the manus, there is a complete left scapholunar and left magnum, as well as complete left MC II, IV and V, and an incomplete left MC III that is lacking the distal part. Since carpals and metacarpals are relatively diagnostic, each bone will be described separately.

The following characters separate the scapholunar of *Pa. onca* from that of *Pu. concolor*: 1. the unciform articular facet is angled less dorsad (almost vertical in puma; Fig. 6, top row) 2. the trapezoid and trapezium articular facets, although still angled dorsad as in the puma, are angled more laterad (Fig. 6 top row) 3. the most ventral end of the articular facet for the trapezium is broad (not narrow; Fig. 6, top row) 4. the articular facet for the magnum is not as deep as in puma (Fig. 6, top row) 5. the ventral end of the articular facet for the magnum is wider medio-laterally than in the puma (Fig. 6, top row) 6. the roughly rectangular protrusion of bone proximal to the articular facet for the trapezium is medio-laterally elongate (not dorso-ventrally thickened as in puma; Fig 6, middle row).

The following characters separate the magnum of *Pa. onca* from *Pu. concolor* (Fig 6, bottom row): 1. the lateral side has little or no indentation (well indented in puma) 2. the bone is more elongate in the dorso-ventral direction (less elongate in the puma).

The following character on the head of MC II separates *Pa. onca* from *Pu. concolor* (Fig. 7, top row): 1. the ventral hook on the proximal end is well developed, lengthening the head in a dorso-ventral direction.

The following characters on the head of MC III separate *Pa. onca* from *Pu. concolor* (Fig. 7, middle row): the head is more elongate in a dorso-ventral direction 2. the indentation between the two articular facets for MC II is relatively large.

The following characters on the head of MC IV separate *Pa. onca* from *Pu. concolor* (Fig. 7, bottom row): 1. the articular facets for MC III and unciform are not distinctly separated 2.the dorsal part of the articular facet for MC III is more elongate than in the puma 3. the indentation separating the two articular facets for MC III is dorso-ventrally shallow and wider than in puma 4. the outline of the ventral end is indented (rounded in puma).

The following characters on the head of MC V separate *Pa. onca* from *Pu. concolor* 1. the articular facet for the unciform is slightly elongated dorso-ventrally

(Fig. 8, top row) 2. in dorsal view, the ventral outline is rounded (straight in puma; Fig. 8, top row) 3. in anterior view, the articular facet for MC IV is larger and it extends further distally than in the puma (Fig. 8, bottom row).

Figure. 9. Anterior view of the distal part of the left femur (flipped to appear right). Specimen numbers as in Figure 4. Abbreviation: rs, rotular surface.

HIND LIMB

The right femur is represented by the distal end only, whereas the left femur is represented by the head and a separate piece of shaft. The most diagnostic character on the femur for the identification of *Pa. onca* is the shape of the patellar trochlea. In the jaguar (and in ORCA 2021), it is relatively wider and less deeply notched than in the puma (Fig. 9).

The left tibia is represented by the distal end only whereas the right tibia is represented by the proximal head only. In addition, there is only a piece of the shaft of the left fibula. Proportionally, the tibia of the jaguar is one of its most diagnostic elements, as it is relatively short and broad compared to the puma. However, all the good morphological features for separating jaguar from puma are on the unpreserved shaft, so the tibia is not illustrated here.

PES

There are two complete elements from the tarsus, the right calcaneum and left navicular.

The following characters separate the calcaneum of *Pa. onca* from *Pu. concolor*: 1. the neck is relatively short and stout (Fig. 10, top row) 2. the distal portion between the astragalar and cuboid articulations is shorter than in the puma (Fig. 10, top row) 3. the minor astragalar facet is laterally elongate and the protrusion of bone proximal to it is less well developed in a proximo-distal direction than in the puma (Fig. 10, middle row) 4. the groove for the peroneal tubercle is absent or not distinct (Fig. 10, middle row).

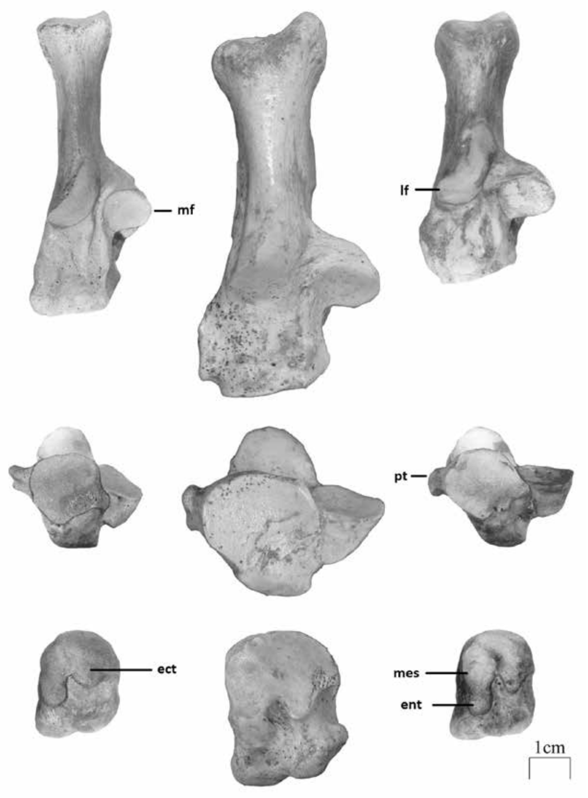


Figure 10. Top row is the dorsal view of the left calcaneum (flipped to appear right), middle row is the distal view of the left calcaneum (flipped to appear right) and the bottom row is the distal view of the left navicular. Specimen numbers as in Figure 4. Abbreviations: ect, articular surface for the ectocuneiform, ent, articular surface for the entocuneiform; lf, lateral facet; mes, articular surface for the mesocuneiform; mf, medial facet.

The following characters separate the navicular of *Pa. onca* from *Pu. concolor* (Fig. 10, bottom row): 1. the cuboid articular facet is not distinct and is flattened 2. the entocuneiforma and mesocuneiform articular facets are broadly joined (separated by a groove in puma) 3. the ventral extension of the ectocuneiform articular facet is well defined and raised.

From the metatarsus there are three complete elements, the right MT II and associated proximal phalanx, a left MT III, and an incomplete right MT IV.

The following characters separate the MT II of *Pa. onca* from *Pu. concolor* (Fig. 11, top row): 1. the articular facet for the mesocuneiform is only slightly indented on the lateral side (more clearly indented in puma) 2. the ventral portion of the proximal end is more elongated and curved to the lateral side than in the puma.

For the MT III, the following characters separate *Pa. onca* from *Pu. concolor*: 1. the lateral indentation on the proximal end is formed more dorsally (the lateral and medial indentations are opposite each other in puma; Fig. 11, second row) 2. On the lateral face, the plantar articulation for MT IV is only slightly raised (if at all) and not separated from the proximal articular surface (the ventral articulation in puma is raised and separated from the proximal articulation by a small bridge of bone; Fig. 11; third row) 3. On the lateral face, the two articular facets for MT IV are more widely separated than in puma (Fig. 11, third row).

For the MT IV, the following characters separate *Pa. onca* from *Pu. concolor*: 1. The ventral end of the proximal articular surface bears a strong groove, slanting laterally. This groove is also visible in lateral view, but it is lacking in puma 2. In medial view, the dorsal articular facet for MT III is placed more distally than in the puma (Fig. 11, bottom row) 3. In medial view, the ventral articular facet for MT III is placed more ventrally than in the puma (Fig. 11, bottom row).

Table 2 Comparison of the lengths of four bones for a selection of fossil cats

Element	ORCA	Rlb avg	N	Irv avg	N
Ulna L	270	266	2	293	1
Radius L	213	226	6	240	3
MT II L	91.0	86.7	6	99.5	5
MT IV L	103	101	12	112	5

Abbreviations for Table: avg, average; Irv, Irvingtonian land mammal age; L. length; N, samples size; ORCA, Oregon Cave National Monument; Rlb, Rancholabrean land mammal age). Specimen data from Seymour, 1993.

LIMB BONE SIZE

Using the limb bones, the overall size of this animal is average compared to other USA specimens of similar Rancholabrean age (Table 2), but smaller than older specimens of Irvingtonian age. There is no complete humerus, femur, tibia or fibula, so limb proportions cannot be calculated for ORCA 2021.

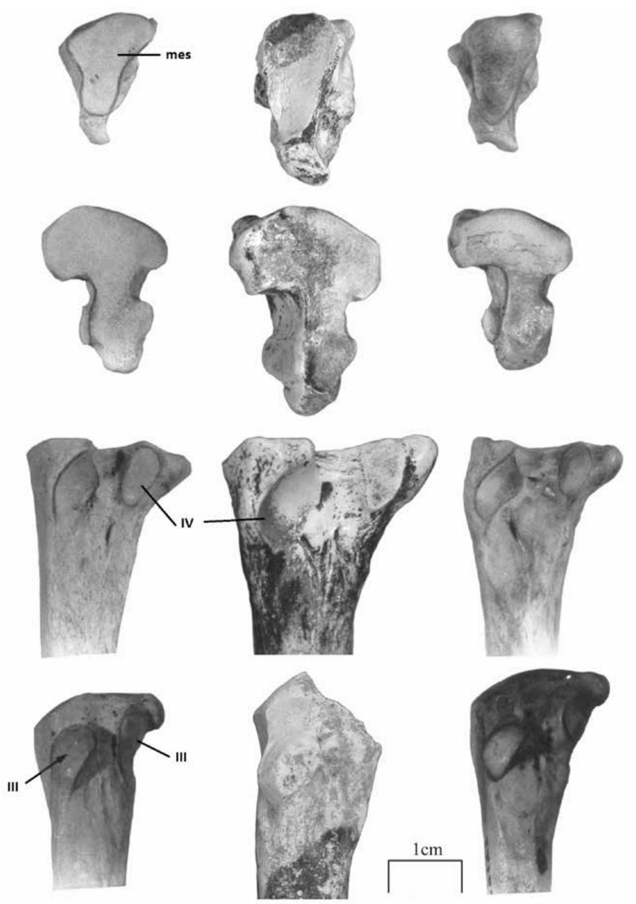


Figure 11. Top row is the proximal articular surface of the left metatarsal II (flipped to appear right, dorsal is at top, lateral is at right), second row is the proximal articular surface of the left metatarsal III (lateral is at left), third row is the lateral view of the left metatarsal III and bottom row is the medial view of the left metatarsal IV (flipped to appear right). Specimen numbers as in Figure 4. Abbreviations: III, facet for the articulation with metatarsal III; IV, facet for the articulation with metatarsal IV; mes, articular surface for the mesocuneiform.

VERTEBRAE AND GIRDLE ELEMENTS

Two vertebrae were recovered, a thoracic X and a caudal vertebra, about caudal IX.

Portions of both the right and left pelvis were collected, and a small sample from the left side was used for carbon dating.

MORPHOLOGICAL SUMMARY

In summary, this fossil specimen is average in overall size for a Rancholabrean fossil jaguar (*Panthera onca laugusta*), but the teeth are above average for a specimen of this age, suggesting that this partial skeleton probably represents a male.

REVIEW OF WESTERN JAGUARS

A summary of fossil jaguars in the USA was provided by Kurtén (1973) and updated by Seymour (1983; 1993); a summary of Seymour (1983) was presented in Arroyo-Cabrales (2002). The Florida records were briefly discussed by Morgan and Seymour (1997). None of these papers focused particularly on western USA jaguars. Here I provide an annotated list of the known fossil record of jaguars, or specimens purported to be jaguars, from the western USA (west of Texas). They are sorted into two groups, valid records and invalid records. All material was examined by the author unless noted otherwise. To date, the Oregon specimens are the most northerly jaguar specimens known in North America.

Valid *Panthera onca laugusta* records

Fossil Lake, Lake Co. Oregon

Material: UCMP 2979 distal portion of left radius, UCMP 26914 right metacarpal IV, UCMP 26966 right metatarsal IV.

Minimum number of individuals represented = 1

As summarized by Seymour (1993:348), this material was once thought to be Irvingtonian by Kurtén (1973:8) probably due to its large size. It is now considered to be younger, or Rancholabrean in age (Kurtén and Anderson, 1980:76). This locality was discussed by Elftman (1931) and Allison (1966). Two additional felid specimens from this locality are UCMP 26957 distal part of left tibia and UCMP 2980 an anterior thoracic vertebra, perhaps thoracic III. I cannot assign these latter two specimens to genus due to their incomplete nature, although the former appears closest to *Homotherium* sp.

“Oregon desert”, Oregon

Material: AMNH 8680 proximal part of ulna

Minimum number of individuals represented = 1

No more specific locality data is available for this specimen. It may derive from Lake Co. or Malheur Co. or another unknown locality.

Holden Cave, Shasta Co., California

Material: UCMP 130468 left metatarsal IV.

Minimum number of individuals represented = 1

This specimen is suspected to be Rancholabrean due to its associated fauna (H. Hutchison pers. comm.). It was originally part of UCMP 27308, a collection of *Ursus americanus* bones. Overall proportions plus all three jaguar characters identified by Seymour (1983) as diagnostic for MT IV confirm this identification.

Rancho La Brea tar pits, Los Angeles Co., California.

Material: All LACM HC material. 15 specimens found from five different pits, details were given by Jefferson (1983).

Minimum number of individuals represented = 5

Given the volume of carnivore material extracted from the Rancho La Brea tar pits, the few jaguar bones recovered speak to its rarity in the habitats represented by these deposits, or its ability to avoid being trapped in the sticky tar deposits. Bone collagen dates from the levels in the Hancock Park excavations that have yielded this jaguar material range in age from about 28.0 K to 11.6 K years BP (Jefferson, 1983; Marcus and Berger, 1984)

Irvington site 2, Alameda Co., California

Material: UCMP 71237, right dentary fragment with m1, a loose p4, and a p3 in a separate fragment.

Minimum number of individuals represented = 1

This specimen was discussed Kurtén (1973:6). The site was described by Savage (1951:219), and Lindsay et al. (1975) discussed the age of this site. Kurtén and Anderson (1980:27) note that a large *Smilodon* and an advanced *Mammuthus* occur at this site suggesting it might be younger than originally supposed. Schultz et al. (1985) state their suspicion that this site is late Irvingtonian in age. The tooth measurements fit very well with the Irvingtonian-aged jaguar from Hamilton Cave, West Virginia (USNM 299767) and the Rancholabrean-aged jaguar from Talara, Peru (ROM 2115), and the tooth morphology matches a cast of the Little Airplane Cave, Tennessee jaguar very well (ROM 4849). The dentary depth (dorso-ventrally) is small for a jaguar of this tooth size, due primarily to the fact that a subadult specimen is represented: p3 is still in the crypt and p4 was incompletely erupted when this individual died.

Smith Creek Canyon, White Pine Co., Nevada

Material: NSM 26WP46-1-09, left m1 lacking posterior root.

Minimum number of individuals represented = 1

According to Miller (1979:294), the presence of jaguar from this site is established by measurements (not given) on an isolated left m1. Other jaguar material apparently consists of a femur head, the distal end of a left femur, proximal end of an ulna, metatarsals, metacarpals, and first and third phalanges (Miller, 1979). I have been able to examine and confirm the identity only of the m1, whose length is 24.6 mm and width is 11.9 mm. The only other material located was the distal end of a metapodial (NSM 26WP46-2-09) that probably represents a left metatarsal IV fragment. This fragment is probably unidentifiable, but seems to match better with Pa. onca than Pu. concolor.

Dry Cave, Eddy Co., New Mexico

Material: All UTEP material. 7-1: left P3-4 in a maxillary fragment, right P4, left MC III, distal part of left MC II and distal part of right femur; 27-24 distal part of left MT II; 27-35 left MC III, right MT III and left MT IV; 27-42 left MC II; 27-43 phalanx one of right pes, digit III; 27-44 left MC I; 27-47 right MC III; 27-48 left maxilla with P3 and P4, right P4 in fragment of maxilla, right P3, 3 isolated incisors, phalanx one of right pes digit IV, and proximal part of right calcaneum.

Minimum number of individuals represented = 2

Both *Pu. concolor* and *Pa. onca* have been found in Dry Cave. So far the jaguar material is restricted to two sub-localities, South Chimney (UTEP 7), and Above Room of the Vanishing Floor (UTEP 27); MNI is one for each sub-locality.

Invalid records of *Panthera onca laugusta*

Delight (=Washtuckna Lake), Adams Co., Washington

Material: AMNH 8651, distal portion of left humerus, here identified as *Homotherium* sp.

Minimum number of individuals represented =1

Simpson (1941:22) identified this material as from Whitman Co. and considered this specimen to be large enough to be *Pa. atrox*, although he admitted it might be *Pa. onca*. Kurtén (1973:8) listed this specimen as a jaguar, and this assignment was followed by Kurtén and Anderson (1980:35) and Seymour (1983). The age of this locality is stated to be Irvingtonian or younger (Kurtén and Anderson, 1980). The locality was discussed by Matthew (1902) and Fry and Gustafson (1974). This is the most northerly record of purported jaguar. A re-examination of the single specimen reveals that it more correctly can be referred to *Homotherium* sp. for the following reasons: the lateral portion is greatly expanded, the medial portion projects in a bulbous way, the ectepicondylar foramen is placed more proximally on the shaft and the area just proximal to the lateral portion of the distal condyle is more indented. All but the second of these four characters can be seen illustrated in Figure 16 of Rawn-Schatzinger (1992).

In all these respects, this specimen is more similar to a cast of the Friesenhahn Cave, Texas, *Homotherium serum* (ROM 22631, cast of TMM 933-2206), than it is to available *Panthera* or *Smilodon* specimens.

Rome beds, Malheur Co., Oregon

Material: CIT VP 647 (now in LACM collection) right dentary fragment with roots of p3 and p4 and alveolus for lower canine, here identified as cf. *Panthera atrox*.

Minimum number of individuals represented = 1

The age of this specimen is unknown (Kurtén and Anderson, 1980:192); Kurtén (1973:5-6) guessed it might be Irvingtonian due to its size and northerly location, but these are hardly valid criteria. It was first discussed and illustrated by Merriam and Stock (1932:226-227; figure 152). Assessment of this specimen is difficult due to the lack of dentition, although overall conformation confirms the pantherine identification. By estimating the size of the teeth from the alveoli, and comparing these estimates with the tooth measurements presented in Seymour (1983), I conclude the following: the antero-posterior length of the lower canine (estimated at 25mm, but not estimated by Kurtén [1973]) is larger than any known specimen of *Pa. onca*, fossil or recent and about average for *Pa. atrox*; the p3 length (estimated at between 17.5 and 18.2 mm; Kurtén [1973] estimated an even larger 19 mm) is near the upper limit in size for *Pa. onca /augusta* and slightly below average for *Pa. atrox*; the p4 length (estimated at between 22.5 and 23.0 mm; Kurtén [1973] estimated an even larger 25 mm) is above average for *Pa. onca /augusta* and at the lower limit for *Pa. atrox*. In addition, the dentary depth at the diastema (45.8 mm; Kurtén [1973] estimated 45 mm) is at the upper limit for *Pa. onca /augusta* but average for *Pa. atrox*. We can conclude that this specimen represents either a *Pa. atrox* with a small p4, a *Pa. onca /augusta* with a record-sized canine, or another unknown pantherine; at this point I prefer the first of these possibilities. Kurtén (1973) made a case for the second of these possibilities, but also thought that this specimen aligned with the Curtis Ranch tooth which I suggest below represents cf. *Homotherium* sp.

Fossil Cave, Lava Beds National Monument, Siskiyou County, California

Material: LABE 2922 fragment of right P4

Minimum number of individuals represented =1

This single incomplete tooth was collected sometime in the 1930's and was said to be a jaguar left lower molar fragment. The symmetry of the cusp fragments indicates that it is actually a portion of the right upper carnassial, P4. The only parts of this tooth preserved are the anterior part of the metacone and posterior part of the paracone, hence no standard measurements can be collected from it. However, this tooth appears to be larger than living *Pa. onca*, and therefore, may represent *Pa. atrox*, but is probably too incomplete to be certain.

Curtis Ranch, Cochise Co., Arizona

Material: USNM 12865 right p4

Minimum number of individuals represented =1

This specimen was identified as jaguar by Kurtén (1973) and Kurtén and Anderson, (1980), but Seymour (1993) identified it as non-*Panthera*. Here I suggest it can be identified as cf. *Homotherium* sp. There are three other felid specimens from this locality, the first two of these were mentioned by Seymour (1993) as non-*Panthera*: USNM 12866 right calcaneum, USNM 12867 proximal part of left metatarsal III, and UALP 2479 fragment of left dentary. All three are here identified as *Miracinonyx* sp.

The age of this locality is now thought to be latest Blancan, or about 2.0 to 2.2 million years old (Morgan and White, 2005).

Algerita Blossom Cave, Eddy Co., New Mexico

Material: fragmentary metapodial UTEP

Minimum number of individuals represented =1

This specimen was reported by Harris (1993) as "*Panthera*?" but this identification has recently been rescinded by Harris and he now considers the specimen to represent *Puma*.

Pit N+W Animal Fair, Dry Cave, Eddy Co, New Mexico

Material: UTEP 122-665 Left upper P3

This specimen was reported by Harris (1993) as "*Panthera* cf. *onca*". I had examined this specimen in 1984 and had thought it was jaguar, but Harris' website now makes a case for this tooth to be *Pa. atrox* and I am inclined now to agree with him. It sits almost on the border between the two species but fits better as a very small *Pa. atrox* rather than a record-sized *Pa. onca /augusta*.

DISCUSSION

Fossil jaguars (*Pa. onca /augusta*) in North America tend to be larger than most living jaguars although there is overlap with the largest living subspecies from southern Brazil (Seymour, 1993). Geologically speaking, the older specimens tend to be larger than the younger ones (Seymour, 1993). This demonstrates a size change through time for this species. However, the whole animal did not change at the same rate. The limb bones shrunk proportionately more than did the teeth or skull, leaving the living species larger headed and shorter limbed than its oldest Pleistocene ancestors (Seymour, 1983; 1993). The taxonomic identification of these larger fossil jaguars is problematic as already noted. An increased sample size of North American fossil jaguar skeletons in the future might enable a re-consideration of these taxonomic issues.

On average in the living species, male jaguars are larger than females. Depending on the particular measurement, males average between 6% and 17% larger, a pattern called sexual dimorphism (Kurtén, 1973; Seymour, 1993). Jaguars are most dimorphic in their canines. Also, the largest living jaguars exist in the most southerly portions of the present range of this species, in southern Brazil and northern Argentina (subspecies *P. o. paraguensis*; Seymour, 1989).

The Oregon Caves individual appears to fit with the youngest fossil *Pa. onca /augusta* material, in that its limb and foot bones are relatively short, although its teeth are not that small. This suggests it might have been a male. Although there are some older faunal elements found in this cave, the proportions of this skeleton suggest that it may not belong with these. In other words, this animal came into the cave and died there at a later time than the rest of the material preserved in this cave.

GEOGRAPHICAL AND ECOLOGICAL CONSIDERATIONS

The earliest jaguars in North America may have been conspecific with the middle Pleistocene Eurasian *Pa. gombaszoegensis* (Hemmer, 1971; Kurtén, 1986) that apparently dispersed over the Bering land bridge to reach North America at that time or earlier (Johnson et al., 2006). More recent papers by European authors have taken to labelling this species *Pa. onca gombaszoegensis* to recognize this idea, but without morphological justification (for example Hemmer et al., 2003; Mol et al. 2011). The living species therefore can be considered a relict population of a once more widely distributed Holarctic form (Kurtén and Anderson, 1980; Kurtén, 1986). Obviously, these early jaguars would have survived on prey found in these regions, and so, even though we tend to think of the jaguar today as a more tropical-living form, their ancestors clearly were not.

Although living jaguars are reported from all habitat types within their range, including deserts, they live predominantly in areas with considerable plant cover, a water supply, and sufficient prey (Seymour, 1989). More than 85 prey species have been reported (Seymour, 1989), with a preference for diurnal terrestrial mammals with a body mass of > 1kg, although other kinds of prey are certainly taken (Emmons, 1987). Today, jaguars prefer peccaries, capybaras, pacas, agoutis, armadillos, caimans, and turtles (see references in Seymour, 1989). Most prey is taken in about the ratio of occurrence in an ecosystem, although jaguars in Peru were found to prey on peccaries more frequently than expected (Emmons, 1987). Indeed, this preference for peccaries is well-known and was used by Schultz et al. (1985) to suggest that the northerly distribution of the jaguar in the North American Pleistocene was limited by the occurrence of peccaries and perhaps also tapirs.

Where puma and jaguar ranges overlap, pumas tend to be more abundant in the drier areas and jaguars select wetter areas (Emmons, 1987; Schaller and Crawshaw, 1980). In contrast to puma, jaguars rarely take deer, although they may take brocket deer or marsh deer (Schaller and Vasconcelos, 1978; Watt, 1987). When beyond the range of these deer species, e.g. in Mexico, the White-tailed deer *Odocoileus virginianus* can be taken by both cats (Nuñez et al, 2000). There is broad overlap between the diet of jaguar and puma (Novack et al, 2005; Nuñez et al, 2000; Scognamillo et al., 2003). These two species can co-exist when the habitat is sufficiently heterogeneous or there is sufficient medium-sized prey for both species (Scognamillo et al., 2003). Also, pumas tend to have a broader food niche than jaguars, consuming smaller prey items more than the jaguar (Nuñez et al, 2000).

These two cat species co-occur in 10 out of the 15 Late Pleistocene fossil sites in Florida in which *Pu. concolor* is known [jaguar is much more common with 37 sites known in the Pleistocene of Florida; Morgan and Seymour (1997)]. This gives evidence that the broad overlap of habitat and prey use was probably present in the Pleistocene as well.

With these ecological parameters, it seems strange that the jaguar has been rarely recovered in the fossil record of the western USA, while it is much more common in the eastern USA. For the 11 western-most states [WA, OR, CA, ID, MT, WY, NV, UT, CO, AZ, NM] (and excluding Holocene localities), there are only 3 fossil jaguar records in the Faunmap database (although 8 are recorded here), while there are 19 *Pa. atrox* localities listed (5 considered questionable), 19 *Pu. concolor* localities (3 considered questionable), 20 *Lynx rufus* localities (3 questionable) and 13 *Smilodon* sp. localities (Graham and Lundelius, 1994). Therefore, it is apparent that the jaguar occurs in less than half as many fossil sites compared to most other fossil felids. Since jaguars exhibit a preference for entering caves in Appalachia (Guilday and McGinnis, 1972), then we would expect this species to be recovered in more western cave faunas.

Given that generally there was food and cover in the western USA, and not necessarily a bias against preserving felid specimens in the fossil record, we can conclude that Schultz et al. (1985) were most likely correct: that fossil jaguars are only rarely found north of the range of their preferred prey, peccaries, even though it is established that they will consume a wide variety of prey items. Schultz et al. (1985) provided a map showing the overall co-occurrence of fossil jaguar and fossil peccary ranges in North America. Even where the jaguar's range overlaps with peccary, though, such as Rancho la Brea, CA (where tens of thousands of bones of *Smilodon fatalis* and *Pa. atrox* also have been recovered) it is still relatively rare, with an MNI of only five for jaguar (Jefferson, 1983). All other locations in the western USA record an MNI of one, with the exception of Dry Cave, NM where there is evidence for two individuals in different parts of the cave system.

The importance of caves for the study of fossil cats

All five partial skeletons from Texas or eastern North America mentioned above were found in caves. In fact ,it is highly unusual for cat fossils found in regular deposits (fluvial, lacustrine, deltaic etc.) to consist of more than one tooth or bone. Six of 14 western sites discussed above were also found in caves including the ORCA site that produced ORCA 2021, the best western fossil jaguar skeleton known to date. More of this individual is still in the cave covered in flowstone. Associated bones or partial skeletons are the most useful when studying cat fossils, as individual teeth, for instance, can be tricky to identify because the teeth of different cats species are relatively simple and similar to each other. More jaguar material derived from caves is needed if we are to understand the full process of the size change that occurred in this lineage during the Pleistocene.

ACKNOWLEDGEMENTS

Thanks go to the collectors of ORCA 2021: Steve Knutson, Larry Coats, Blaine Schubert, Jim Mead and Greg McDonald. Greg McDonald got me involved with this project and Blaine Schubert gave me access to his field notes and provided Figure 1. John Roth (of ORCA) generously funded the carbon date. The following people either lent specimens or provided access to specimens, and I am grateful to all of them: Pat Holroyd (UCMP), Mary Merryman (LABE), Rachel Malloy (NSM), Art Harris (UTEP), Jeffrey Saunders (UALVP), Bob Purdy (USNM), Larry Barnes (LACM), John Alexander (AMNH), Chris Shaw (LACM HC). Sue Hobson assembled and manipulated the figures for which I am very grateful.

REFERENCES

Allison, I.S., 1966, Fossil Lake, Oregon: its geology and fossil faunas: Oregon State University Studies in Geology, v. 9, p. 1-48.

Arroyo-Cabrales, J., 2002, Registro fósil del jaguar: *in* Medellín, R.A. and others (compilers), El jaguar en el Nuevo milenio: Universidad Nacional Autónoma de México, p. 343-354.

Brown, D.E., and López-González, C.A., 2001, Borderland Jaguars: Tigres de la Frontera: Salt Lake City, University of Utah Press, 170 p.

Brown, D.F., 1983, On the status of the jaguar in the Southwest: Southwestern Naturalist, v. 28, p. 459-460.

Christiansen, P., and J.M. Harris, J.M., 2009, Craniomandibular morphology and phylogenetic affinities of *Panthera atrox*: implications for the evolution and paleobiology of the lion lineage: Journal of Vertebrate Paleontology, v. 29, p. 934-945.

Corgan, J., and Breitburg, E., eds., 1996, Tennessee's Prehistoric Vertebrates: Tennessee Division of Geology Bulletin, v. 84, p. 1-170.

Elftman, H.O., 1931, Pleistocene mammals of Fossil Lake, Oregon: American Museum Novitates, v. 481, p. 1-21.

Emmons, L.H., 1987, Comparative feeding ecology of felids in a Neotropical rainforest: Behavioral Ecology and Sociobiology, v. 20, p. 271-283.

Fry, W.E., and Gustafson, E.P., 1974, Cervids from the Pliocene of central Washington: Journal of Paleontology, v. 48, p. 375-386.

Graham, R.W., and Lundelius, E.L. Jr., 1994, Faunmap: a database documenting Late Quaternary distribution of mammal species in the United States: Illinois State Museum Scientific Papers, v. 25, pt. 2, p. 1-690.

Guilday, J.E., and McGinnis, H., 1972, Jaguar (*Panthera onca*) remains from Big Bone Cave Tennessee and east central North America: The National Speleological Society Bulletin, v. 34, p. 1-14.

Hall, E.R., and Kelson, K.R., 1969, The Mammals of North America: New York, Ronald Press Co., 1083 p.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001, PAST: Paleontological statistics software package for education and data analysis: Palaeontologia Electronica, v. 4, pt. 1, p. 1-9. Online at: http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Harris, A. H., 1993, Quaternary vertebrates of New Mexico, *in* Vertebrate Paleontology in New Mexico: New Mexico Museum of Natural History Bulletin, v. 2, p. 179-197.

Hemmer, H., 1971, Zur Charakterisierung und stratigrahischen Bedeutung von *Panthera gombaszoegensis* (Kretzoi, 1938): Neues Jahrbuch für Geologie und Paläontologie Monatschefte, v. 1971, p. 701-711.

Hemmer, H., Kahlke, R.-D., and Keller, T., 2003. *Panthera onca gombaszoegensis* (Kretzoi, 1938) from the Early Middle Pleistocene Mosbach Sands (Wiesbaden, Hessen, Germany) – a contribution to the knowledge of the variability and history of the dispersal of the jaguar: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 229, p. 31-60.

Hoffstetter, R.,1949, Les félins du Pléistocène de l'Équateur. I. Faune actuelle et methods de comparison: Travaux de l'Institut Français d'Études Andines, v. 1, p. 1-52.

Jefferson, G.T., 1983, First record of jaguar from the Late Pleistocene of California: Bulletin of the Southern California Academy of Sciences, v. 82, p. 95-98.

Johnson, W.E., Eizirik, E., Pecon Slattery, J., Murphy, W.J., Antunes, A., Teeling, E., and O'Brien, S.J., 2006, The late Miocene radiation of modern Felidae: a genetic assessment: Science, v. 311, p. 73-77.

Kurtén, B., 1973, Pleistocene jaguars in North America: Societas Scientiarum Fennica, Commentationes Biologicae, v. 62, p. 1-23.

Kurtén, B., 1986, Trans-Beringian carnivore populations in the Pleistocene, *in* Kontrimavichus, V.L., ed., Beringia in the Cenozoic Era: Rotterdam, A.A. Balkema, p. 349-355.

Kurtén, B., and Anderson, E., 1980, Pleistocene mammals of North America: New York, Columbia University Press, 442 p.

Kurtén, B., and Werdelin, L., 1990, Relationships between North and South American *Smilodon*: Journal of Vertebrate Paleontology, v. 10, p. 158-169.

Lindsay, E.H., Johnson, N.M., and Opdyke, N.D., 1975, Preliminary correlation of North American land mammal ages and geomagnetic chronology: University of Michigan Papers in Paleontology, v. 12, p. 111-119.

McCain, E.B., and Childs, J.L., 2008, Evidence of resident jaguars (*Panthera onca*) in the southwestern United States and the implications for conservation: Journal of Mammalogy, v. 89, p. 1-10.

McCrady, E., Kirby-Smith, H.T., and Templeton, H., 1951, New finds of Pleistocene jaguar skeletons from Tennessee caves: Proceedings of the United States National Museum, v. 101, p. 497-511.

Marcus, L.F., and Berger, R., 1984, The significance of radiocarbon dates for Rancho La Brea, *in* Martin, P.S., and Klein, R.G., eds., Quaternary Extinctions, a prehistoric revolution: Tucson, University of Arizona Press, p. 159-183.

Martin, R.A., 1993, Patterns of variation and speciation in Quaternary rodents, *in* Martin, R.A., and Barnosky, A.D., eds., Morphological Change in Quaternary Mammals of North America: New York, Cambridge University Press, p. 226-280.

Matthew, W.D., 1902, List of the Pleistocene fauna from Hay Springs, Nebraska: Bulletin of the American Museum of Natural History, v. 16, p. 317-322.

Merriam, J.C., 1919, Is the jaguar entitled to a place in the California fauna?: Journal of Mammalogy, v. 1, p. 38-40.

Merriam, J.C., and Stock, C., 1932, The Felidae of Rancho La Brea: Carnegie Institute of Washington Publication v. 422, p. 1-231.

Miller, S.J., 1979, The archaeological fauna of four sites in Smith Creek Canyon, *in* Tuohy, D.R., and Rendall, D.L., eds., The archaeology of Smith Creek Canyon, eastern Nevada: Nevada State Museum Anthropological Papers, v. 17, p. 271-329.

Mol, D., van Logchem, W., and de Vos, J., 2011, New record of the European jaguar, Panthera onca gombaszoegenis (Kretzoi, 1938), from the Plio-Pleistocene of Langenboom (The Netherlands): Cainozoic Research, v. 8, p. 35-40.

Morgan, G.S., and Seymour, K.L., 1997, Fossil history of the panther (*Puma concolor*) and the cheetah-like cat (*Miracinonyx inexpectatus*) in Florida: Bulletin of the Florida Museum of Natural History, v. 40, p. 177-219.

Morgan, G.S., and White, R.S. Jr., 2005, Miocene and Pliocene vertebrates from Arizona, *in* Heckert, A.B., and S.G. Lucas, S.G., eds., Vertebrate paleontology in Arizona: New Mexico Museum of Natural History and Science Bulletin, v. 29, p. 115-136.

Novack, A.J., Main, M.B., Sunquist, M.E., and Labisky, R.L., 2005, Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala: Journal of Zoology, London, v. 267, p. 167-178.

Nuñez, R., Miller, B., and Lindzey, F., 2000, Food habits of jaguars and pumas in Jalisco, Mexico: Journal of Zoology, London, v. 252, p. 373-379.

Rawn-Schatzinger, V., 1992, The scimitar cat *Homotherium serum* Cope: osteology, functional morphology and predatory behaviour: Illinois State Museum Reports of Investigations, v. 47, p. 1-80.

Rogers, J.G., 1997, Final Rule to Extend Endangered Status for the Jaguar in the United States, Document 97-19208, Federal Register 62(140), p. 39147-39157. Online at: http://endangered.fws.gov/r/fr97622.html

Roth, J., 1996, Fossil finds and the age of Oregon Caves: Crater Lake National Park Nature Notes, v. 27, p. 1-4. Online at: http:// www.nps.gov/crla/notes/vol27i.htm

Salles, L.O., 1992, Felid phylogenetics: extant taxa and skull morphology (Felidae, Aeluroidea): American Museum Novitates, v. 3047, p. 1-59.

Savage, D.E., 1951, Late Cenozoic vertebrates of the San Francisco Bay region: University of California Bulletin of the Department of Geological Sciences, v. 28, p. 215-314.

Schaller, G.B., and Crawshaw, P.G. Jr., 1980, Movement patterns of jaguar: Biotropica v. 12, p. 161-168.

Schaller, G.B., and Vasconcelos, J.M.C., 1978, Jaguar predation on capybara, Zeitschrift für Säugetierkunde, v. 43, p. 296-301.

Schultz, C.B., Martin, L.D., and Schultz, M.R., 1985, A Pleistocene jaguar from north-central Nebraska: Transactions of the Nebraska Academy of Sciences, v. 13, p. 93-98.

Scognamillo, D., Maxit, I.E., Sunquist, M., and Polisar, J., 2003, Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos: Journal of Zoology, London, v. 259, p. 269-279.

Seymour, K.L., 1983, The Felinae (Mammalia, Felidae) from the Late Pleistocene tar seeps at Talara, Peru, with a critical examination of the fossil and recent felines of North and South America [M.Sc. thesis]: Toronto, University of Toronto, 240 p.

Seymour, K.L., 1989, *Panthera onca*: Mammalian Species v. 340, p. 1-9.

Seymour, K.L., 1993, Size change in North American Quaternary jaguars, *in* Martin, R.A., and Barnosky, A.D., eds., Morphological Change in Quaternary Mammals of North America: New York, Cambridge University Press, p. 343-372.

Seymour, K.L., 1999, Taxonomy, morphology, palaeontology and phylogeny of the South American small cats (Mammalia: Felidae) [Ph.D. thesis], Toronto, University of Toronto, p. 929.

Seymour, K.L., 2003, The Oregon Caves fossil jaguar: National Park Service, Park Paleontology, v. 7, pt. 2, p. 3-4.

Seymour, K.L., Reynolds, A.R., and Churcher, C.S., 2018, *Smilodon fatalis* from Talara, Peru: Sex, Age, Mass, and Histology, *in* McDonald, H.G., Shaw, C., and Werdelin, L., eds., *Smilodon*: the Iconic Sabertooth: Baltimore, John's Hopkins University Press, p. 30-52.

Simpson, G.G., 1941, Large Pleistocene felines of North America: American Museum Novitates, v. 1136, p. 1-27.

Turgeon, S.C., and Lundberg, J., 2004, Establishing a speleothem chronology for southwestern Oregon: climatic controls and growth modeling, *in* Sasowsky, I.D., and Mylroie, J.E., eds., Studies of cave sediments: physical and chemical records: New York, Kluwer Academic/Plenum Publishers, p. 273-302.

Van Valkenburgh, B., 1990, Skeletal and dental predictors of body mass in carnivores, *in* Damuth, J. and MacFadden, B.J., eds., Body Size in Mammalian Paleobiology: New York, Cambridge University Press, p. 181-205.

Watt. E.M., 1987, A scatological analysis of parasites and food habits of jaguar (*Panthera onca*) in the Cockscomb Basin of Belize [M.Sc. thesis]: Toronto, University of Toronto, 90 p.

Werdelin, L., 1983, Morphological patterns in the skulls of cats: Biological Journal of the Linnean Society, v. 19, p. 375-391.

James C. Chatters, H. Gregory McDonald, Blaine W. Schubert, Joaquin Arroyo-Cabrales. Cenotes, caves, and sloths: Pleistocene sloth diversity on the Yucatan Peninsula, Mexico and Belize. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 216-224. DOI:10.4311/2024PA0106

CENOTES, CAVES, AND SLOTHS: PLEISTOCENE SLOTH DIVERSITY ON THE YUCATAN PENINSULA, MEXICO AND BELIZE

James C. Chatters,[1,2,C] H. Gregory McDonald,[3] Blaine W. Schubert,[4] and Joaquin Arroyo-Cabrales[5]

ABSTRACT

Exploration of both dry and submerged caves in the Yucatan Peninsula by cave divers has revealed a high diversity of Pleistocene giant ground sloths, representing all four families. Researchers working in the caves of Quintana Roo, Mexico, have identified up to five genera of sloths; a sixth genus is known from Belize. Three of the sloths, *Nohochichak xibalbahka*, *Xibalbaonyx oviceps*, and *X. exenferis* (if valid) are endemic to the peninsula. Preliminary dating indicates the genera were not all sympatric, with *Nothrotheriops* and a mylodontid occurring in the north during the last glacial maximum in what was likely an arid habitat, and with *Eremotherium* in forested central Belize. The northern part of the peninsula supported at least two megalonychids in earlier millennia in what was likely a more forested habitat. Better dating of known specimens is needed, along with stable isotope analyses, to clarify the history and ecology of sloths in the Yucatan.

INTRODUCTION

The recovery of fossil vertebrates from caves raises the question as to whether their presence results from a taphonomic process, such as being left by a predator, being carried in by another animal such as a packrat (*Neotoma* sp.), being transported into the cave after death by water, or falling into a natural trap; or from a behavioral process, including use of the cave as a den, shelter, or roost site. In the case of sloths, the strictly arboreal habits of the two living tree sloths, *Bradypus* and *Choloepus*, precludes caves as part of their ecology, so they cannot serve as a modern analog for the presence of fossil sloths in caves. Likewise, the other extant xenarthrans, anteaters, are not known to utilize caves, and while many armadillos burrow, they are also not commonly found in cave environments. In marked contrast, many different taxa of extinct ground sloths are commonly found preserved in caves in South, Central, and North America (McDonald, 2003). The presence of ground sloths in caves includes skeletal and dental material, and in some dry caves in arid environments there are also preserved large numbers of coprolites, suggesting that the cave served as a common latrine for multiple individuals. To date, all examples of ground sloth dung have been recovered from cave sites (Hunt and Lucas, 2018; Spaulding and Martin, 1979). This suggests that, for at least some ground sloths, caves (when available) played a critical role in their ecology. As caves may be present in many different types of habitats over a wide range of latitudes and different elevations, their role in the ecology of different ground sloth species probably varied considerably. Consequently, each association of a ground sloth with a cave needs to be considered on its own merits and context. The reasons for cave utilization in tropical habitats may differ from its purposes in a temperate zone.

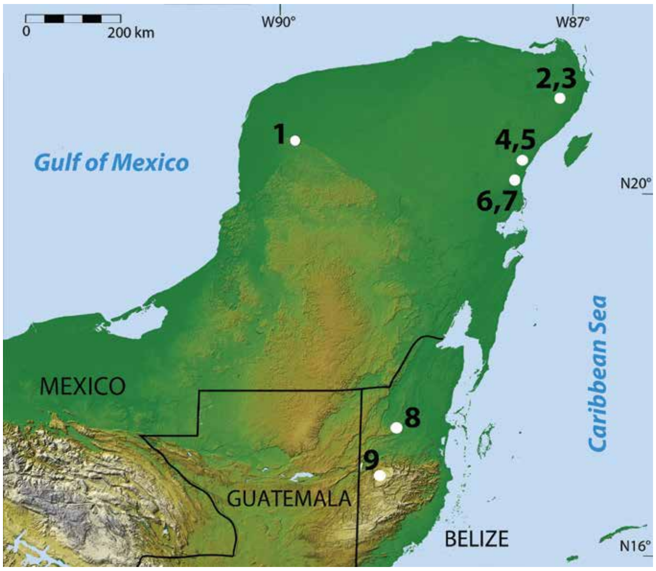


Figure 1. Map of the Yucatan Peninsula showing distribution of caves with sloths listed in Table 2 (white dots). (1) Aktun Spukil. (2) Cenote Zapote. (3) Cenote Tortugas. (4) Sistema Koox Baal. (5) Sistema Sac Actun. (6) Sistema Ox Bel Ha. (7) Sistema Chan Hol. (8) Aktun Lak. (9) Cara Blanca Cenotes.

The recent discovery and description of new taxa of extinct ground sloths from caves in the Yucatan Peninsula (McDonald et al., 2017; Stinnesbeck et al., 2017, 2021) has not only documented the greater diversity of ground sloths along with other Pleistocene taxa (Schubert et al., 2019) in the northern Neotropics, but also raises questions as to how the ecology of Central American ground sloths differed from that of their closest relatives living in more temperate envi-

---

[1] Applied Paleoscience, 10322 NE 190th Street, Bothell, WA 98011
[2] El Centro Investigador del Sistema Acuífero de Quintana Roo A.C., Carretera Federal Chetumal-Puerto Juárez km 269.5, 77733, Puerto Aventuras, Quintana Roo, Mexico
[3] 3309 Snowbrush Court, Fort Collins, CO 80521
[4] Center of Excellence in Paleontology and Department of Geosciences, East Tennessee State University, Johnson City, TN 37614
[5] Laboratorio de Arqueozoologia, Instituto Nacional de Antropología e História, Moneda # 16, Col. Centro 06060 Mexico, CDMX, Mexico
[C] Corresponding author: paleosci@gmail.com

ronments. Part of this question revolves around their presence in caves in tropical environments and whether the role played by caves in their natural history was similar to or different from that of ground sloths that lived in in more-temperate environments. For simplicity, all subsequent references to sloths pertain to ground sloths alone.

OVERVIEW OF SLOTHS FROM CAVES IN THE YUCATAN

Knowledge about the fossil record of the tropics is extremely limited, reflecting the high rate of decomposition of organic matter and general rarity of conditions that contribute to its preservation as fossils. One of the primary exceptions to this pattern occurs in tropical karstic regions when vertebrate remains accumulate in caves. An excellent example is the Yucatan Peninsula, which makes up Belize and parts of Guatemala and Mexico (Fig. 1). It is an approximately 181,000 km^2 area of low relief, almost entirely composed of porous limestone. Processes of cave development range from acidic water welling up in a semi-circle around the Chicxulub crater, which outlines the impact of an asteroid at the end of the Cretaceous Period, to primary cave development occurring at the fresh water/saline mixing zone during the elevated sea levels of marine isotope stage (MIS) 5e (Smart et al., 2006). This has resulted in the extensive karst and cave systems seen on the Yucatan Peninsula.

During glacial episodes, as growing ice masses elsewhere confined water on land, the water table of the Yucatan Peninsula was lower. While many of the caves in the Yucatan are flooded, they were air-filled when sea level was lower. Maximum exposure occurred during the last glacial maximum when sea level was 130 m below what it is today (Ludt and Rocha, 2015). This made many of the caves open and accessible to Pleistocene megafauna for most of the last 120,000 years, either as water sources, potential den sites, thermal refugia, or natural traps. With the subsequent decline of the glaciers and rise in sea level, many of these cave systems became flooded (Smart et al., 2006), reaching modern levels by around 5000 cal YBP (Collins et al., 2015). The development of scuba and improvements in technology for cave diving has permitted the exploration of these flooded caves. The discovery of a diversity of Pleistocene fauna has been a welcome byproduct. This includes new species (McDonald et al., 2017; Stinnesbeck et al., 2017, 2021) as well as taxa from South America not previously known to be present in North America (Schubert et al., 2019).

Table 1. Comparison of number of individuals of various taxonomic groups identified from caves in the Yucatan Peninsula documented by PHN and CINDAQ. Remains of humans are not included.

Taxonomic Group	No. of Individuals Identified to at Least the Family Taxon	Total No. of Individuals
Carnivora	36	37
Folivora	17	26
Perissodactyla	11	12
Proboscidea	7	7
Artiodactyla	5	5
Rodentia	2	2
Sirenea	1	1
Reptilia	3	3
Pisces	1	1
TOTAL	83	94

Ongoing exploration of caves and cave systems in the Yucatan consistently results in the discovery of new records of sloths, as well as other Pleistocene taxa. Given the logistical and skill challenges of cave diving and laws regulating fossil recoveries in Mexico, many new finds can only be documented photographically; voucher specimens might not be recovered. Two projects have systematically documented fossil finds within specific cave systems, permitting a quasi-quantitative record of the faunal assemblage. These are Proyecto Arqueológico Subacuatico Hoyo Negro (PHN), a project of the Subdirección de Arqueología Subacuática, Instituto Nacional de Antropología e História (SAS-INAH), and the cave documentation research of El Centro Investigador del Sistema Acuífero de Quintana Roo A.C. (CINDAQ), a non-governmental organization recognized by the 2001 UNESCO Convention on the Protection of Underwater Cultural Heritage. Most of what is reported here comes from those projects, with which we are affiliated and for which we provided some fossil identifications based on scaled, 3D photogrammetric models, and in the case of PHN, collected specimens. Both have addressed caves on the east coast of the peninsula, in the state of Quintana Roo, so most of what is known about ground sloths pertains to that region.

Contexts for these finds of fossil sloths vary considerably. Finds are usually of single, isolated individuals or genera, or of co-mingled, gnawed bones from more than one species found in what appear to be the dens of predatory or scavenging species. However, Hoyo Negro, an intensively studied site containing multiple sloth species, is a natural trap inside the Sac Actun Cave System. At Hoyo Negro, 20 species of medium-to-large mammals have been found, showing no sign of carnivore mediation. Included are the extinct sabertooth cat (*Smilodon fatalis*), a gomphothere (*Cuvieronius tropicus*), a short-faced bear (*Arctotherium wingei),* a canid (*Protocyon trogolodytes*), and sloths from three different families (Chatters et al.,

Figure 2. Photograph of a synsacrum and associated bones of *Nothrotheriops shastensis* partially covered with bat guano at 49 m BSL on the floor of Hoyo Negro, Sac Actun system, Quintana Roo, Mexico. Scale rod is colored in 10 cm intervals.

2014; Schubert et al., 2019). Sloths are represented by the Nothrotheriidae (*Nothrotheriops shastensis*), the Megalonychidae (*Nohochichak xibalbahkah*), cf. *Xibalbaonyx* sp., and the Mylodontidae. Extant species are also well-represented, including puma (*Puma concolor*), ocelot (*Leopardus pardalis*), collared peccary (*Pecari tajacu*), and white-nosed coati (*Nasua narica*).

When logistically feasible and if the discovery is of a rare, unique, or possibly new taxon, time and effort have been expended to obtain permits and recover diagnostic parts of a skeleton or even (on extremely rare occasions) the entire skeleton of an individual. That has been accomplished for Hoyo Negro, where voucher specimens of all taxa have been obtained, and for other cenotes where holotypes of two reported species of *Xibalbaonyx* have been obtained. In other cases, identifications are solely based on photographs or digital models. The list of taxa in Table 1 provides only a preliminary comparison of the relative frequency of the different taxa observed by the systematic work of CINDAQ and PHN. Thus, the accuracy of the identifications is limited depending on the skeletal element(s) observed, the degree of completeness, and the degree of exposure in the cave sediments. In many cases identification may be only to order or family rather than species or even genus. As shown in Table 1, sloths (listed there as Folivora) are more likely to be encountered in cave systems in the eastern Yucatan than any order other than carnivorans, but the record may be biased in two ways. First, many of the small carnivorans were found during the painstaking search of the Hoyo Negro site. They are rarely documented by divers in other settings, where an observer may traverse a passage more swiftly. If these are removed from consideration, sloths become the most common large animals recorded. Conversely, ground sloths are larger and more readily seen than all but the proboscideans and some perissodactyls. This, combined with a unique skeletal anatomy compared to other mammals in their size range, greatly facilitates their identification to at least order.

Table 2. List of caves and cenotes on the Yucatan Peninsula from which sloth remains have been published or documented by PHN and CINDAQ.

Taxon	Cave System or Cenote	No. Individuals	Reference or Project
Eremotherium laurillardi	Cara Blanca, Belize	1+	Larmon et al., 2019
Nothrotheriops shastensis	Aktun Lak, Belize	1	De Iuliis et al., 2015
Nothrotheriops shastensis	Chan Hol, Mexico	1	CINDAQ
Nothrotheriops shastensis	Ox Bel Ha, Mexico	2	CINDAQ
Nothrotheriops shastensis	Sac Aktun, Mexico	3	PHN
Nohochichak xibalbahka[h]a	Sac Aktun, Mexico	2	McDonald et al., 2017; PHN
Xibalbaonyx oviceps[a]	Cenote Zapoté, Mexico	1	Stinnesbeck et al., 2017
Xibalbaonyx exinferis[b]	Cenote Tortugas, Mexico	1	Stinnesbeck et al., 2021
cf. Xibalbaonyx[c]	Koox Baal, Mexico	2	Motyčka et al., 2013; CINDAQ
cf. Xibalbaonyx[c]	Sac Aktun, Mexico	3	PHN, CINDAQ
Miezonyx salvadorensis	Koox Baal, Mexico	1	CINDAQ
Mylodontidae sp.	Ox Bel Ha, Mexico	1	CINDAQ
Mylodontidae sp.	Sac Aktun, Mexico	1	PHN
cf. *Paramylodon*	Aktun Spukil, Mexico	1	Hatt, 1953; Mercer, 1896

a type locality for genus and species.
b type locality for species in existing genus.
c Similar to Xibalbaonyx, but these are adults whereas type specimens of both Xibalbonyx species are juveniles.
PHN: Proyecto Arqueológico Subacuático Hoyo Negro.
CINDAQ: El Centro Investigador del Sistema Aquífero de Quintana Roo A.C.

As well as being the most common group of large mammals identified in the caves in terms of individuals, the ground sloths are the most taxonomically diverse, with multiple genera and species documented to date by CINDAQ, PHN, and in publications (Table 2). Four genera, three of them represented by multiple individuals, have been found in Outland Cave of the Sac Actun system alone. Two skeletons are in the primary, submerged passages about 9–12 m below sea level, and six are in the trap of Hoyo Negro, a 60 m diameter circular collapse chamber that drops to depths up to 50 m below modern sea level (BSL).

Sloths in the shallow tunnels throughout the region usually are represented as articulated, yet often deteriorated, skeletons. In Hoyo Negro, most exhibit patterns indicative of disarticulation through decomposition in water and are in better condition, and lack evidence of carnivore consumption (Chatters et al., 2021). This demonstrates that most of the sloths had entered the caves on their own power, and the remains were not brought in by carnivores. We have, however, seen cases in the Ox Bel Ha and Koox Baal Cave Systems where sloth remains are commingled with those of other species and have marks characteristic of carnivore gnawing. These may have been the dens of carnivores.

Overall, sloth remains from the Yucatan include representatives of four families: Megalonychidae, Nothrotheriidae, Mylodontidae, and Megatheriidae. The megalonychid genus *Xibalbaonyx* and the nothrotheriid *Nothrotheriops* (Fig. 2) are the most common in the number of individuals. Notably, two megalonychid genera, *Nohochichak* and *Xibalbaonyx*, are relatively new to science, with *Nohochichak* (Fig. 3) thus far only known from the Yucatan (McDonald et al., 2017), while *Xibalbaonyx* is known from two species in the Yucatan and a third species from Jalisco, Mexico (Stinnesbeck et al., 2017, 2018, 2021). The megalonychid *Meizonyx*, formerly known only from the Irvingtonian land mammal age of El Salvador, has also been recently found from the terminal Pleistocene of Oaxaca, Mexico (McDonald et al., 2020). One specimen of this genus has also been provisionally recognized by us in a Quintana Roo cave.


Figure 3. Photograph of an articulated forearm of *Nohochichak xibalbahkah* on a wall of Hoyo Negro, 44 m below the water surface. Scale is in centimeters.

Nothrotheriops is best known from dry caves in the southwestern United States, so its presence in the tropics was not expected. *Nothrotheriops* are numerous in Quintana Roo, and there is a single record from a cave in Belize (De Iuliis et al., 2015) indicating that its range extended even farther south into the tropics. Based on recent finds referred to the genus, it may even have ranged as far south as Argentina (Brandoni and Vezzosi, 2019), but to date, the only nothrotheriid known from cave sites in South America, specifically Brazil, is *Nothrotherium* (Pujos, 2001).

A single mylodontid sloth is known from a shallow tunnel of Outland Cave. Although *Paramylodon*, which is well known from other sites in Mexico and the United States, has been previously reported from Actun Spukil, a cave in the northern part of the Yucatan Peninsula, the specimens are not diagnostic (Hatt, 1953; Mercer, 1896). Because a comprehensive study of that material has not been completed, identification of the mylodontid in this region as *Paramylodon* remains unsubstantiated.

McDonald (2002) reported 10 localities in Mexico for the megatheriid *Eremotherium*. Since that review, multiple new finds of this species have been described, increasing the number of localities to 19 (e.g. Gómez-Pérez and Carbot-Chanona, 2012; Carbot-Chanona et al., 2022). *Eremotherium* was a widespread taxon with a range extending north to the Atlantic coast of the United States and south into southern Brazil. Despite its wide distribution, it is primarily found in open terrestrial deposits, and while rarely found in caves, occurs frequently in cenotes or sinkholes over much of its range. During the last glacial maximum (26,000–20,000 years ago) when sea level was at its lowest, there was a concurrent lowering of the water table in the karst bedrock of the Yucatan Peninsula. The resulting reduction of surface water would have made cenotes attractive to wildlife, their depth and open surfaces providing access to the lower water table. Such sites would have also potentially served as traps for larger animals, such as *Eremotherium,* that may have been able to climb down to the water in the cenote but not back out. Currently, the only record of this sloth on the Yucatan Peninsula is from two of the Cara Blanca cenotes in Belize (Larmon et al., 2019). In one of these, remains of multiple individuals of *Eremotherium* are present on a ledge 21 m below the current water level. It is not known if this represents

Table 3. Approximate ages of the four taxa of ground sloth in the Hoyo Negro site, Mexico, and *Eremotherium* from Cara Blanca, Belize. All radiocarbon dates are on bioapatite; uranium-thorium date is from flowstone coating bone and is a minimum age. Estimated ages are computed based on an established reservoir effect, as described in the text.

Taxon	Dating Method	Lab and Specimen No.	Sampled Material	Radiometric Age	Age, cal YBP[a]	Estimated Age	MIS
Nothrotheriops 2	U-Th	UNAMQ-HN	flowstone	23,059 ± 134	23,330–22,790	23.3 YBP	2
Nothrotheriops 1	^{14}C	D-AMS 37546	orthodentin	23,355 ± 99	27,760–27,390	24.5 YBPc	2
Mylodontidae	^{14}C	D-AMS 27870	orthodentin	25,837 ± 112	30,500–29,621	26.9 YBPc	2
Eremotherium[b]	^{14}C	A3712	orthodentin	22,640 ± 120	27,300–26,780	27.0 YBPd	2
Nohochichak	^{14}C	D-AMS 25511	orthodentin	33,871 ± 289	39,030–37,370	34.4 YBPc	3
cf *Xibalbaonyx*	^{14}C	D-AMS 31907	bioapatite	38,386 ± 401	43,090–41,950	42.5 YBPc	3

a Calculated using IntCal 20 (Reimer et al., 2020).
b Larmon et al., 2019.
c Computed as median calibrated age minus 3200 (see text).
d No age correction can be applied.
UNAMQ: Universidad Nacional Autónoma de México, Querétaro campus.
D-AMS: DirectAMS, Inc., Seattle.

a time-averaged sample reflecting multiple entrapment events or a herd situation such as is described from other sites (Lindsey et al. 2020).

Accidental entrapment is also recorded for *Xibalbaonyx oviceps* and *X. exinferis*. The holotypes of both species are from cenotes El Zapote and Tortugas in Quintana Roo, Mexico, with openings on the surface connecting via a vertical chimney to an enlarged bell-shaped chamber (Stinnesbeck et al., 2017, 2021). For example, the diameter of the surface opening of cenote El Zapote is 8.5 to 10 m, and its lower chamber has a diameter of 40 m. The top of the debris cone below the opening is 35 m BSL and the bones of the disarticulated sloth were recovered between 50 m and 55 m BSL. In both cases, the animals likely fell through the opening, and even if they survived the fall, there was no means for climbing out. The type specimens of both species are juveniles as indicated by visible sutures of the skull and lack of fused epiphyses of the long bones.

The only two known specimens of *Nohochichak* were also entrapped in a bell-shaped chamber, albeit one located deep inside Outland Cave. This fate also befell other animals in Hoyo Negro (Chatters et al., 2021), including two Shasta sloths and two of what we infer to be adult members of the genus *Xibalbaonyx*.

DISCUSSION

Currently, five and possibly six genera of ground sloths are known from the Yucatan, giving it a greater diversity of Pleistocene sloths, with representatives of all four families, than any other region in North or Central America. Interestingly, two of the species of sloth found in the Yucatan Peninsula appear (for now) to be endemic to the area. *Meizonyx*, having thus far been found only in Oaxaca and Quintana Roo, appears to be endemic to southern Mexico and perhaps Central America. Two genera of sloths that have a greater distribution are *Nothrotheriops shastensis* and *Eremotherium laurillardi*, with ranges that extend north into the southern United States and south into South America. If the observed mylodontid is indeed *Paramylodon*, it has a similarly large range in North America.

The ecology of the sloth species that thus far appear to be endemic to the Yucatan and adjacent regions currently remains unknown. Out of all the sloths known from the Yucatan, only two genera that have been identified with certainty include species with a wide distribution and are known from multiple other sites outside of the Yucatan Peninsula. This allows some inference about their paleoecology. The two species are *Eremotherium laurillardi*, with a range that extends north into the United States along the Gulf Coast and eastern coastal plain and south into South America and southern Brazil, and *Nothrotheriops shastensis*, which in the late Pleistocene is primarily known from the southwestern United States. In the United States, the distributions of these two taxa are for the most part mutually exclusive in the late Pleistocene with one exception: the Nueces River fauna, Nueces County, Texas (Sagebiel, 2022). This is the eastern extreme of the range of *Nothrotheriops* and the westernmost record of *Eremotherium*. The fauna was recovered from sand-and-gravel, valley-fill deposits, so it is possible that it represents a time-averaged sample. There are no radiometric dates of either of these taxa from the site to confirm they were contemporaries. Likewise, while both genera are known from multiple sites in Mexico, *Eremotherium* by 19 records and *Nothrotheriops* by 10 records, the only locality where both taxa have been reported is Lago de Chapala, Jalisco, Mexico. The faunal remains reported from this site include taxa of Blancan, Irvingtonian, and Rancholabrean land mammal ages (Lucas, 2008), so again, while both taxa were present in the region, they may not have been contemporaries.

Given the significant differences in the ecology of the two sloths, with *Nothrotheriops* found primarily in desert habitat and with *Eremotherium* in subtropical to tropical forest (McDonald, 2021), it seems unlikely that they overlapped and were contemporaries on the Yucatan Peninsula. This is also indicated by the differences in their relative representation in the area, with multiple records of *Nothrotheriops* from cave sites, while *Eremotherium* is known only from two cenotes near the southern-most margin of the Yucatan Peninsula.

Diversity of the sloth fauna reflects the differences in the ecology of the various species, which allowed niche partitioning within the diverse tropical environment. During the late Pleistocene, the ranges of the various species probably shifted in response to changes in the distribution of the vegetation upon which sloths fed, which in turn, was responding to changes in the climate during the Pleistocene.

Precise radiometric dates on bone collagen are generally lacking from sloths and other fossil animals found in the Yucatan, but our ongoing studies in Hoyo Negro indicate some chronological patterning in the taxonomic composition of the local communities. Analysis of paired dates, matching radiocarbon dates on bone bioapatite, and actual ages of three animals from the site determined by both radiocarbon and uranium-thorium analyses indicates an approximately 3,200year reservoir (or diagenesis) effect, rendering the dates older due to dissolved inorganic carbon (Chatters, 2021). That chronological offset is valid for recomputing actual ages from bioapatite dates only for the approximate 23,000- to 10,000-year range from which it was computed and cannot be extrapolated to older materials with confidence. Subtracting that reservoir effect from bioapatite ages of older specimens can, however, provide approximate ages and enable an enhanced ordinal chronology (Table 3).

We can tentatively compare this chronology with the regional climatic record. *Nothrotheriops* and the mylodontid occupied the region later, likely during marine isotope stage (MIS) 2, whereas the megalonychids *Nohochichak* and cf. *Xibalbaonyx* were likely present earlier, apparently during MIS 3. According to Correa-Metrio et al. (2012), temperatures on the Yucatan Peninsula declined from 2.5 °C–3.5 °C below modern levels 84,000 years ago to 4 °C–5 °C below modern at the last glacial maximum. They infer that declining temperatures would have led to depression of the intertropical convergence zone southward, leading to lower cloud cover on the peninsula and hence dryer conditions. Given that *Nothrotheriops* tends to be found in desert environments and mylodontids in grasslands or open savannah (McDonald, 2021; Naples, 1989), it is likely the habitats of the peninsula were more open later in the late Pleistocene. Most megalonychids appear to have been browsers or at least mixed feeders (McDonald, 2022), so the earlier habitat was probably more forested. The *Eremotherium* from Belize dates approximately between the two groups, suggesting that a tropical forest habitat was available farther south in Central America even when more open vegetation appears to have prevailed in the northeastern Peninsula (Colinvaux, 1997). Central America is now highly diverse ecologically (Wallace, 1997; Janson, 2001), so it is possible, even likely, that several distinct, adjacent animal communities occupied the peninsula during different periods as climates changed. Marked fluctuations in the temperature record as well as precipitation during the late Pleistocene could mean sloth fauna frequently adjusted their geography during the time period the animal skeletons were collecting in regional caves.

In contrast to megatheriid and mylodontid sloths that are only infrequently found in caves, the remains of both megalonychid and nothrotheriid sloths are often found in caves and may be represented by multiple individuals, including adults and juveniles (McDonald, 2003). This suggests that when available, caves played an important role in the ecology for sloths in these families. The presence of juveniles of *Nothrotheriops* in Rampart Cave (Arizona) and San Josecito Cave (Nuevo León, México) (Couto, 1974) supports the idea that this species used caves for birthing or as dens to protect young from potential predators. McDonald (2003, 2022) suggested that, given the low basal metabolism and low body temperature of sloths, caves may have served as thermal refugia during seasonal extremes, particularly low temperatures. While seasonal low temperatures may not have been the issue on the Yucatan Peninsula like they would have been in temperate North America, caves could have provided a relatively cooler environment and prevented overheating during warmer seasons. A computer model of the seasonality temperature addressing the time represented by well-dated records of *Nothrotheriops* from dry caves in the United States does suggest caves may have also served as thermal refugia during summer high temperatures (McDonald, 2022).

While the proposed use of caves in temperate zones by sloths may not be fully applicable to explain the presence of sloths in caves in warmer subtropical to tropical zones, there is one distinctive feature of the Yucatan Peninsula during the late Pleistocene to consider, the availability of water. Given the absence of surface water on the karst platform of the Yucatan Peninsula for extended periods during the late Pleistocene, caves and cenotes may have provided the primary access to fresh water for the fauna. Such a scenario certainly can explain the presence of *Nothrotheriops* on the Yucatan Peninsula, given its close association with arid environments elsewhere in its range, but it raises questions about the ecology of other sloths. Based on other evidence, the megalonychids and megatheriids likely preferred habitats in which water was more abundant, or at least more readily available.

CONCLUSION

Over the last 30,000 years of the late Pleistocene, a high diversity of ground sloths utilized the Yucatan Peninsula. Up to six genera dwelled there in the range of plant communities that changed as temperatures and rainfall fluctuated. The preservation of sloth remains in a tropical environment was possible because of the karst systems of the region. During dry episodes and seasons, these animals were dependent on cenotes for fresh water, and sometimes this involved entry into the sinkholes. When water was at its lowest, freshwater would have been more limited and farther below ground level. Thus, the search for water would lead to entry into cave passages and deeper, more dangerous surface cenotes. The ongoing exploration of the flooded cave systems of the Yucatan and recovery and documentation of not only sloths, but also other Pleistocene vertebrates, remains provide a great opportunity for understanding the composition of mammalian communities and their dynamics as climates rapidly changed at the end of the Pleistocene.

When cave divers find animal remains, leave them undisturbed, and report them to the appropriate authorities of INAH, they are providing information of scientific value that ultimately can enable a better understanding of the reasons why ground sloth and other animal remains are often found in caves, whether intentional, accidental, or incidental, and their relative frequency. Once discoveries have been made, two additional steps are necessary: (1) good photography for 3-D modeling to enable preliminary identifications, and (2) authorized collection of specimens so that research can move forward. In demonstrating the presence of this important record, it is our hope that further support will be granted to collect vouchers of important specimens for museums and research. If this can be accomplished, it may ultimately enable us to understand the ecology of these extinct sloths and their contemporaries and reveal clues to the causes of their extinction.

Figure 4. Photograph of a skeleton of a mylodontid sloth in a 9-meter-deep passageway of Outland Cave, Sac Aktun Cave System, Quintana Roo, Mexico. For scale, the radius (white arrow at left) is 26 cm long and 9.5 cm wide.

ACKNOWLEDGEMENTS

We offer special thanks to Dr. Roberto Junco Sanchez and Helena Barba Meinecke, leaders of SAS-INAH and managers of the Hoyo Negro Project, and to Sam Meacham, Chris LeMaillot, Fred Devos, and Julien Fortin of CINDAQ, who readily shared their observations with us. Funding for the Hoyo Negro Project has come primarily from INAH, the Strauss Family Fund for Central American Research, Dr. Robert Lourie, National Geographic Society, DirectAMS, and anonymous donors. Alberto Nava, Alex Alvarez, Roberto Chávez Arce, and Sam Meacham recovered most of the underwater photographs and specimens from Hoyo Negro. The East Tennessee State University Center of Excellence in Paleontology, specifically Keila Bredehoeft and Chris Widga, provided three-dimensional scans of specimens and the former aided with fossil preparation. The Qualcomm Institute of the University of California, San Diego, and particularly Vid Petrovic and Dr. Dominique Rissolo, are responsible for three-dimensional virtual access to the Hoyo Negro Site, enabling many of the identifications. We also thank Salvador Estrada and Alex Jimenez for assistance in field/lab work and transporting specimens from the Yucatan to Mexico City. The photos in Figures 2 and 3 curtesy of Roberto Chavez-Arce and the photo in Figure 4 curtesy of Alberto Nava-Blank.

REFERENCES

Brandoni, D., and Vezzosi, R.I., 2019, *Nothrotheriops* sp. (Mammalia, Xenarthra) from the Late Pleistocene of Argentina: Implications for the dispersion of ground sloths during the Great American Biotic Interchange: Boreas, v. 48, p. 879–890, https://doi.org/10.1111/bor.12401.

Carbot-Chanona, G., Gómez-Pérez, L.E., and Coutiño-José, M.A., 2022, A new specimen of *Eremotherium laurillardi* (Xenarthra, Megatheriidae) from the Late Pleistocene of Chiapas, and comments about the distribution of the species in Mexico: Boletín de la Sociedad Geológica Mexicana, v. 74, article no. A070322, 12 p., https://doi.org/10.18268/BSGM2022v74n2a070322.

Chatters J.C., et al., 2014. Late Pleistocene human skeleton and mtDNA link Paleoamericans and modern Native Americans: Science, v. 344, p. 750–754, https://doi.org/10.1126/science.1252619.

Chatters J.C., Schubert, B.W., Petrovic, V., Nava-Blank, A., Rissolo, D., Arroyo-Cabrales, J., Arano-Recio, D., and Luna Erreguerena, P., 2021, Macrotafonomía de los restos humanos y faunísticos del Pleistoceno tardío en Hoyo Negro, Quintana Roo, México [Macrotaphonomy of late Pleistocene human and faunal remains from Hoyo Negro, Quintana Roo, Mexico], *in* Tiesler, V., Suzuki, S., and Periera, G., eds, Tratamientos Mortuorios del Cuerpo Humano: Perspectivas Tafonómicas y Arqueotanatológicas [Mortuary Treatments of the Human Body: Taphonomic and Archaeothanatological Perspectives]: Mexico City, Centro de Estudios Mexicanos y Centroamericanos, p. 211–239, https://tienda.cemca.org.mx/producto/tratamientos-mortuorios-del-cuerpo-humano-9872111672031/.

Chatters, J.C., 2021, Surmounting the problems of radiometric dating in the submerged caves of the Yucatan: The La Mina and Hoyo Negro examples: Geological Society of America Abstracts with Programs*,* v. 53, no. 6, https://doi.org/10.1130/abs/2021AM-366684.

Colinvaux, P., 1997, The history of forests on the isthmus from the ice age to the present, *in* Coates, A.G., ed, Central America: A Natural and Cultural History: New Haven, Yale University Press, p. 123–136, https://doi.org/10.2307/j.ctt1xp3sdf.11.

Collins, S.V., Reinhardt, E.G., Rissolo, D., Chatters, J.C., Nava Blank, A., and Luna Erreguerena, P., 2015, Reconstructing water level in Hoyo Negro, Quintana Roo, Mexico: Implications for early Paleoamerican and faunal access: Quaternary Science Reviews, v. 124, p. 68–83, https://doi.org/10.1016/j.quascirev.2015.06.024.

Correa-Metrio, A., Bush, M.B., Cabrera, K.R., Sully, S., Brenner, M., Hodell, D.A., Escobar, J., and Gilderson, T., 2012, Rapid climate change and nonanalog vegetation in lowland Central America during the last 86,000 years: Quaternary Science Reviews, v. 38, p. 63–75, https://doi.org/10.1016/j.quascirev.2012.01.025.

Couto, C. de P., 1974, The manus of *Nothrotheriops shastense* (Sinclair, 1905): Anais do XXVIII Congreso Brasileiro de Geologia, v. 2, p. 165–176, https://www.yumpu.com/pt/document/read/36422956/xxviii-congresso-sociedade-brasileira-de-geologia.

De Iuliis, G., McDonald, H.G., Stanchly, N., Spenard, J., and Powi, T.G., 2015, *Nothrotheriops shastensis* (Sinclair) from Actun Lak: First record of Nothrotheriidae (Mammalia, Xenarthra, Pilosa) from Belize: Ameghiniana, v. 52, p. 153–171, https://doi.org/10.5710/AMGH.05.11.2014.2821.

Gómez-Pérez, L.E., and Carbot-Chanona, G., 2012, Contribución al estudio de los megamamíferos del Pleistoceno tardío del municipio de Villaflores, Chiapas, México [Contribution to the study of megamammals from the late Pleistocene from the municipality of Villaflores, Chiapas, Mexico]: Lacandonia Revista de Ciencias UNICACH*,* v. 6, p. 31–41, https://www.researchgate.net/publication/258192653_Contribucion_al_estudio_de_los_megamamiferos_del_Pleistoceno_Tardio_del_municipio_de_Villaflores_Chiapas.

Hatt, R.T., 1953, Faunal and archaeological researches in Yucatan Caves: Cranbrook Institute of Science Bulletin, v. 33, p. 1–119.

Hunt, A.P., and Lucas, S.G., 2018, The record of sloth coprolites in North and South America: Implications for terminal Pleistocene extinctions, *in* Lucas, S.G., and Sullivan, R.M, eds., Fossil Record 6: New Mexico Museum of Natural History and Science Bulletin 79, p. 277–298, https://www.researchgate.net/publication/328676887_the_record_of_sloth_corprolites_in_north_and_south_america_implications_for_terminal_pleistocene_extinctions.

Jansen, T, 2001, Maya Nature: An Introduction to the Ecosystems, Plants, and Animals of the Mayan World: Guatemala, Vista Publications, 128 p.

Larmon, J.T., McDonald, H.G., Ambrose, S., DeSantis, L.R.G., and Lucero, L.J., 2019, A year in the life of a giant ground sloth during the last glacial maximum in Belize: Science Advances*,* v. 5, article no. eaau1200, 9 p., https://doi.org/10.1126/sciadv.aau1200.

Lindsey, E.L., Lopez Reyes, E.X., Matzke, G.E., Rice, K.A., and McDonald, H.G., 2020, A monodominant late-Pleistocene megafauna locality from Santa Elena, Ecuador: Insight on the biology and behavior of giant ground sloths: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 544, article no. 109599, 9 p., https://doi.org/10.1016/j.palaeo.2020.109599.

Lucas, S.G., 2008, Late Cenozoic fossil mammals from the Chapala rift basin, Jalisco, Mexico, *in* Lucas, S.G., Morgan, G.S. Spielmann, J.A., and Prothero, D.R., eds., Neogene Mammals: New Mexico Museum of Natural History and Science Bulletin, v. 44, p. 39–50, https://econtent.unm.edu/digital/collection/bulletins/id/624.

Ludt, W.B., and Rocha, L.A., 2015, Shifting seas: The impacts of Pleistocene sea-level fluctuations on the evolution of tropical marine taxa: Journal of Biogeography*,* v. 42, p. 25–38, https://doi.org/10.1111/jbi.12416.

McDonald, H.G., 2002, Fossil Xenarthra of México: A review, *in* Montellano-Ballesteros, M., and Arroyo-Cabrales, J., eds., Avances en los Estudios Paleomastozoológicos en México [Advances in Paleomastozoological Studies in Mexico]: Mexico City, Instituto Nacional de Antropología e Historia, p. 227–248, https://difusion.inah.gob.mx/compra-en-linea/catalogo-de-publicaciones/2538.html.

McDonald, H.G., 2003, Sloth remains from North American caves and associated karst features, *in* Schubert, B.W., Mead, J.I., and Graham, R.W, eds.*,* Ice Age Cave Faunas of North America: Bloomington, Indiana University Press and Denver Museum of Nature and Science, p. 1–16, https://iupress.org/9780253342683/ice-age-cave-faunas-of-north-america/.

McDonald, H.G., 2021, Yukon to the Yucatan: Habitat partitioning in North American late Pleistocene ground sloths (Xenarthra, Pilosa): Journal of Palaeosciences*,* v. 70, p. 237–251, https://doi.org/10.54991/jop.2021.17.

McDonald, H.G., 2022, Paleoecology of the extinct Shasta ground sloth, *Nothrotheriops shastensis* (Xenarthra, Nothrotheriidae): The physical environment, *in* Morgan, G.S., Baskin, J.A., Czaplewski, N.J., Lucas, S.G., McDonald, H.G., Mead, J.I., White, R.S., Jr., and Lichtig, A.J., eds., Late Cenozoic Vertebrates from the American Southwest: A Tribute to Arthur H. Harris: Bulletin of the New Mexico Museum of Natural History and Science, v. 88, p. 33–43, https://www.researchgate.net/publication/360731874_paleoecology_of_the_extinct_shasta_ground_sloth_nothrotheriops_shastensis_xenarthra_nothrotheridae_the_physical_environment.

McDonald, H.G., Arroyo-Cabrales, J., Alarcón-Durán, I., and Espinosa-Martínez, D.V., 2020, First record of *Meizonyx salvadorensis* (Mammalia: Xenarthra: Pilosa) from the late Pleistocene of Mexico and its evolutionary implications: Journal of Systematic Palaeontology, v. 18, p. 1829–1851, https://doi.org/10.1080/14772019.2020.1842816.

McDonald, H.G., Chatters, J.C., and Gaudin, T.J., 2017, A new genus of megalonychid ground sloth (Mammalia, Xenarthra) from the late Pleistocene of Quintana Roo, Mexico: Journal of Vertebrate Paleontology*,* v. 37, article no. e1307206, 14 p., https://doi.org/10.1080/02724634.2017.1307206.

Mercer, H.C., 1896, The Hill Caves of Yucatan: A Search for Man's Antiquity in the Caverns of Central America, Philadelphia, J. B. Lippincott, 183 p., https://archive.org/details/b24851528.

Motyčka, Z., Hutnan, D., and Husák, R., 2013, A Quest for the Secrets of Xibalba: Czech Republic, ZM Production, 113 p.

Naples, V.L., 1989, The feeding mechanism in the Pleistocene ground sloth, *Glossotherium*: Contributions to Science, v. 415, Los Angeles, Natural History Museum of Los Angeles County, 23 p., https://doi.org/10.5962/p.226818.

Pujos, F., 2001, Nouvelles données sur le genre *Nothrotherium* Lydekker, 1889, et validité des espèces *N. maquinense* Lund, 1839, et *N. escrivanense* Reinhardt, 1878 [New data on the genus *Nothrotherium* Lydekker, 1889, and validity of the species *N. maquinense* Lund, 1839, and *N. escrivanense* Reinhardt, 1878]: Geobios, v. 34, p. 349–356, https://doi.org/10.1016/S0016-6995(01)80081-4.

Reimer, P.J., et al., 2020, The IntCal20 northern hemisphere radiocarbon age calibration curve (0–55 cal kBP): Radiocarbon, v. 62, p. 725–757, https://doi.org/10.1017/RDC.2020.41.

Sagebiel, J.C., 2022, Xenarthrans from the Nueces River fauna, Upper Pleistocene of Nueces County, Texas, *in* Morgan, G.S., Baskin, J.A., Czaplewski, N.J., Lucas, S.G., McDonald, H.G., Mead, J.I., White, R.S., Jr., and Lichtig, A.J., eds., Late Cenozoic Vertebrates from the American Southwest: A Tribute to Arthur H. Harris: Bulletin of the New Mexico Museum of Natural History and Science, no. 88, p. 225–231, https://books.google.com/books/about/LATE_CENOZOIC_VERTEBRATES_FROM_THE_AMERI.html?id=ICKIEAAAQBAJ.

Schubert, B.W., Chatters, J.C., Arroyo-Cabrales, J., Samuels, J.X., Soibelzon, L.H., Prevosti, F.J, Widga, C., Nava, A., Rissolo, D., and Luna Erreguerena, P., 2019, Yucatán carnivorans shed light on the Great American Biotic Interchange: Biology Letters, v. 15, article no. 20190148, 6 p., https://doi.org/10.1098/rsbl.2019.0148.

Smart, P.L., Beddows, P.A., Coke, J., Doerr, S., Smith, S., and Whitacker, F.F., 2006, Cave development on the Caribbean coast of the Yucatan Peninsula, Quintana Roo, Mexico: Geological Survey of America, special paper 404, p. 105–128, https://doi.org/10.1130/2006.2404(10).

Spaulding, W.G., and Martin, P.S., 1979, Ground sloth dung of the Guadalupe Mountains, *in* Proceedings, Biological Investigations in the Guadalupe Mountains National Park, Texas, Lubbock, Texas, April 4–5, 1975: National Park Service Proceedings and Transaction Series 4, p. 259–269, https://www.nps.gov/parkhistory/online_books/gumo/gumo_biological_investigations.pdf

Stinnesbeck, S.R., et al., 2017, *Xibalbaonyx oviceps*, a new megalonychid ground sloth (Folivora, Xenarthra) from the Late Pleistocene of the Yucatán Peninsula, Mexico, and its palaeobiogeographic significance: Paläontologische Zeitschrift, v. 91, p. 245–271, https://doi.org/10.1007/s12542-017-0349-5.

Stinnesbeck, S.R., Frey, E., and Stinnesbeck, W., 2018, New insights on the palaeogeographic distribution of the Late Pleistocene ground sloth genus *Xibalbaonyx* along the Mesoamerican corridor: Journal of South American Earth Sciences, v. 85, p. 108–120, https://doi.org/10.1016/j.jsames.2018.05.004.

Stinnesbeck, S.R., Stinnesbeck, W., Frey, E., Avilés Olguín, J., and González González, A., 2021, *Xibalbaonyx exinferis* n. sp. (Megalonychidae), a new Pleistocene ground sloth from the Yucatán Peninsula, Mexico: Historical Biology, v. 33, p. 1952–1963, https://doi.org/10.1080/08912963.2020.1754817.

Wallace, D.R., 1997, Central American landscapes, *in* Coates, A.G, ed., Central America: A Natural and Cultural History: New Haven, Yale University Press, p. 72–96, https://doi.org/10.2307/j.ctt1xp3sdf.8.

Jim I. Mead, Sandra L. Swift, Nicolas J. Czaplewski, Kenneth L. Cole Middle Holocene flora and fauna from a ringtail *(Bassariscus, Carnivora)* den, western Grand Canyon, Arizona. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 225-238. DOI:10.4311/2024PA0108

MIDDLE HOLOCENE FLORA AND FAUNA FROM A RINGTAIL (*BASSARISCUS*, CARNIVORA) DEN, WESTERN GRAND CANYON, ARIZONA

Jim I. Mead[1,2, C], Sandra L. Swift[1], Nicolas J. Czaplewski[3], and Kenneth L. Cole[4]

ABSTRACT

Dietary remains recovered from *Bassariscus* (ringtail) midden deposits of middle Holocene age in the Weeping Cliffs, lower Grand Canyon, Arizona, indicate a diverse ringtail diet of plants and small vertebrates. Remains of fruits and seeds predominated among the plant parts, especially of hackberry, several cacti, and groundcherry. Highly fragmented remains of small vertebrates included anurans, lizards, snakes, bats, and rodents. Only one recovered vertebrate specimen exceeded 5 mm in length, necessitating meticulous morphological comparisons for taxonomic identifications, which were usually limited to generic level. Two radioisotopic dates on the middens range from ca. 7300 to 7900 cal yr BP. Vertebrate remains from the middens provide the first Quaternary records of amphibians (including *Anaxyrus* and *Hyla*/*Dryophytes*) and a bat (*Nyctinomops macrotis*) from the Grand Canyon. Rare, fragmentary specimens provide one of only two fossil records of *Dipsosaurus* in Arizona.

INTRODUCTION

The North American ringtail (Carnivora; Procyonidae; *Bassariscus astutus*) is a small to medium-sized (~1 kg) carnivore living today in arid, forested, and rocky habitats from southwestern Oregon south and east throughout most of the Intermountain West to Missouri, Texas, and south throughout most of Mexico (Poglayen-Neuwall and Toweill, 1988). Another similar living species of ringtail, *B. sumichrasti* (cacomistle), occurs in Central America north into southernmost Mexico (Pino et al., 2016). Fossils attributed to *Bassariscus* first appear in the Middle Miocene (Barstovian North American Land Mammal Age; Bever, 2003; Baskin, 2004; but see discussion in Koepfli et al., 2007) with additional early Neogene species from Washington and Oregon to Kansas and into the Southwest (Czaplewski, 1990; Bever, 2003; Gustafson, 2015; among others). Although the fossil history and skeleton of this small nocturnal carnivore have been assessed, its record of predation and consumption of the local biota is less well understood.

Quaternary-age vertebrates attributed to the collecting behavior of *Bassariscus astutus* are known from many caves including those in California (Mead et al., 2006; Stegner, 2015), Texas (Harris and Hearst, 2012), Arizona, New Mexico (Harris, 1985, 2013), Nevada (Emslie and Mead, 2023), and northern Mexico (White et al., 2010). In larger fossil cave deposits, the collecting behavior of the ringtail may be masked by other taphonomic scenarios such as at Papago Springs Cave, Arizona (Skinner, 1942; Czaplewski et al., 1999). Remains described as the extinct *B. sonoitensis* from Late Pleistocene deposits in Papago Springs Cave, southeastern Arizona, have been synonymized with the extant *B. astutus* (Skinner, 1942; Harris, 1990).

The Quaternary environmental history of the Grand Canyon has been reviewed showing that fossils of this age are typically found in caves (encompassing multiple taphonomic scenarios) and in isolated woodrat (packrat, *Neotoma*) middens within dry rock crevices (Phillips and Van Devender, 1974; Van Devender et al., 1977; Mead et al., 2003; Tweet et al., 2012; Mead et al., 2021). What has received much less attention has been the various deposits of vertebrates and plants that can be attributed to the ringtail. Large accumulations of Late Pleistocene fossils from the Grand Canyon are known from Rampart and Stanton Caves, localities where prior research has typically accented larger mammals and their dung (Mead, 1981), and a den comprising an accumulation of ringtail dung (coprolite debris accumulation; “latrinites” of Hunt and Lucas, 2012, 2021; here termed “ringtail midden”) was analyzed from Vulture Cave dating to the late Holocene (Mead and Van Devender, 1981). Here we report on the vertebrate and plant contents of a ringtail midden from a small crevice-cave positioned immediately above the alluvial terrace of the Colorado River, westernmost Grand Canyon. The Weeping Cliffs locality provides access to a riparian environment not previously sampled or preserved in other Grand Canyon cave deposits, and is one of the few direct dietary evidence records, thus making these finds noteworthy.

WEEPING CLIFFS, GRAND CANYON

The Weeping Cliffs (western Grand Canyon) are formed in the Muav Limestone, an exposure of cliffs along the Lower Granite Gorge of the Colorado River close to where the river exits the Grand Wash Cliffs of the Colorado Plateau (Fig. 1). Situated at 426 m elevation, the Weeping Cliffs contain small caves, overhangs, small shelters, and crevices. Prior to the development of Lake Mead reservoir in the 1930s, the position of the outcrop provided close access to sandy

---

[1] The Mammoth Site, 1800 Hwy 18 BYP, Hot Springs, SD 57747
[2] Desert Laboratory on Tumamoc Hill, 1675 W Anklam Rd, Tucson, AZ 85745
[3] Oklahoma Museum of Natural History, University of Oklahoma, Norman, OK 73072
[4] Deceased
[C] Corresponding author: jmead@mammothsite.org

floodplain and riparian environments along the Colorado River and to rocky talus slope and side-canyon habitats now with desert biota above the cliffs. The alluvial floodplain biotic community along the Colorado River became submerged and locally extirpated until approximately 2002 with the retreat of Lake Mead from the Grand Canyon (Fig. 1). Based upon the geomorphology of the river corridor, an enduring floodplain and associated habitat had previously bordered the Colorado River, possibly as far upriver as River Mile 237 (40 river miles [65 river km] from its exit at River Mile 277; L. E. Stevens personal communication, December 2023).

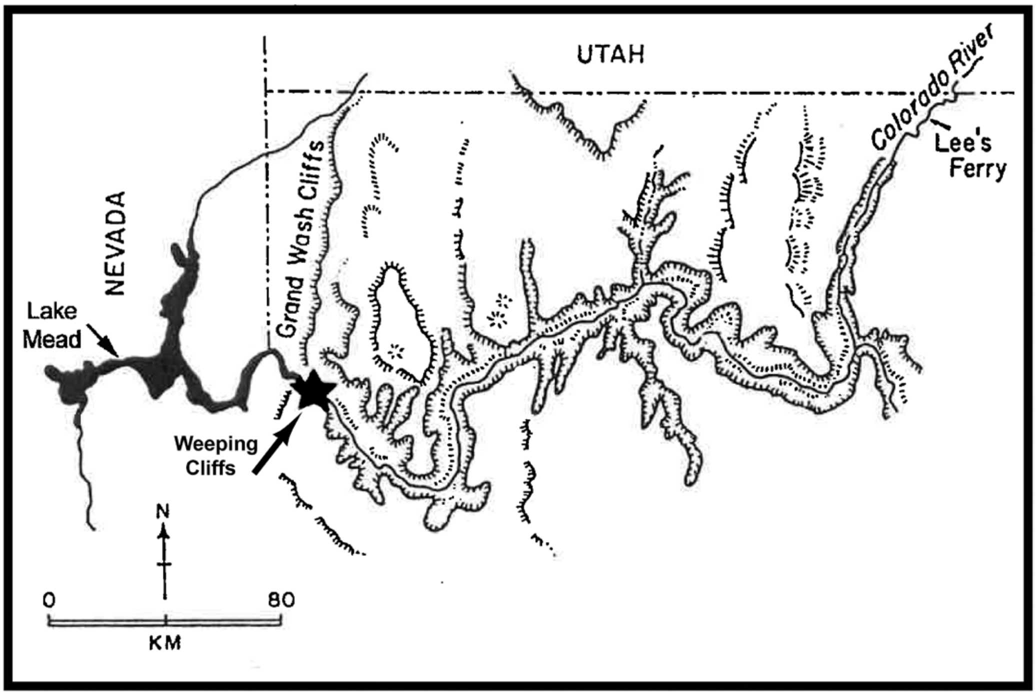


Figure 1. Map of Grand Canyon with location of Weeping Cliffs at the western, most down river location along the Colorado River. Other known cave sites with Late Pleistocene faunas nearby Weeping Cliffs (star) include Rampart, Muav, and Vulture Caves.

Today the local biotic community around the Weeping Cliffs contains plants and animals aligned with the Mojave and Sonoran deserts—many at the northern limits of their distributions. Well-known Late Pleistocene faunal localities near the Weeping Cliffs include Rampart Cave and Muav Caves (Wilson, 1942; Long and Martin, 1974; Van Devender et al., 1977), along with the more remote Vulture Cave (Mead and Phillips, 1981). Previous studies (Phillips, 1984; Phillips and Van Devender, 1974; Spaulding, 1990) provide details about the vegetation changes during the full and late Wisconsinan Glacial through the Holocene to today of this lower Grand Canyon region.

METHODS AND RESULTS

The Weeping Cliffs ringtail middens were found on a crevice-bearing ledge under an overhang about 65 m west of the Muav Caves. The moist alcove is unusual in that the northeast facing cliffs above provide shade and the name “Weeping Cliffs” suggests groundwater seepage, although none was observed at the time of collection. The alcove is further shaded by large trees of netleaf hackberry (*Celtis reticulata*) that occupy sites of groundwater seepage in this area (Phillips et al., 1987).

Limestone crevices and caves in the Grand Canyon, including the Weeping Cliffs with their horizontal and vertical crevices, have provided long-lasting shelters, protecting organic deposits such as the omnipresent packrat middens (organic debris piles dominated by plant remains) for thousands of years (chapters in Betancourt et al., 1990). Our report details the faunal and plant remains representing the diet of ringtails recovered from two ringtail middens that merge into a single unit within a crevice.

The Weeping Cliffs ringtail deposits are an accumulation of plant remains along with abundant, highly broken skeletal remnants. Most of the accumulation was cemented together presumably with the urine of the ringtail, analogous to the way that packrats solidify their middens with urine (amberat). We conducted no analysis to verify that ringtails cement their dung accumulations via continued urination, which may be more of a scent marking action (Barja and List, 2006). We have noted that packrat urine cement odor is distinctly different than that found in ringtail den accumulations. Multiple gallon-sized-bag masses of hardened ringtail midden were removed for our project. These middens were water-sieved through 0.5 mm mesh to remove the urine cement and then sorted by SLS for fossils using a 10x microscope. Plant macrofossils were identified by KLC, bat remains were identified by NJC, and other vertebrates were identified by JIM.

Due to their small size, the abundant plant fossils were not immediately evident during our crevice exploration. The collecting habits of packrats cause these rodents to construct their middens with abundant large plant macrofossils, many over 1 cm or more in length. In contrast, most of the plant macrofossils identified from the Weeping Cliffs ringtail middens were less than 2 mm in length. Many of these plant and vertebrate remains are damaged in such a way as to suggest that they may have passed through the digestive system of the ringtail, although we have no direct experimental evidence of the effects of ringtail mastication and digestion on plants. Significantly, modern ringtail dung accumulations and the Weeping Cliff middens also lack the voluminous remains of packrat dung pellets found in packrat middens; only the broken and fragmented remains of ringtail coprolites were observed.

All vertebrate remains are highly broken and sometimes etched. The extreme fragmentation suggests that the remains represent prey that was chewed by a small carnivore and do not exhibit the characteristics of raptor ingestion (e.g. , owl pellet). Only those skeletal remains that, although fragmented, exhibit diagnostic characters are identified and presented here. Identification to species typically was not conducted on these remains either due to the fragmented nature of the elements or because known characters providing specific rank identifications were not available.

To radiocarbon date the organics we used the Accelerator Mass Spectrometry (AMS) facility at the National Ocean Sciences AMS Facility, Woods Hole Oceanographic Institution; calibrations of the dates (cal yr BP) were assessed with OxCal 4.4, IntCal20. For the Weeping Cliffs 3a deposit, a single seed of *Opuntia* cf. *chlorotica* (prickly pear cactus) was dated to a median age 7,781 cal yr BP (95% confidence limits range: 7,925–7,666 cal yr BP; 6,950±65 radiocarbon yr BP, OS-33861). Weeping Cliffs 2 deposit was dated on plant debris mixed in with the ringtail dung to median age 7,460 cal BP (95% confidence limits range: 7,565–7,326 cal yr BP; 6,550±65 radiocarbon yr BP, OS-33862). Both dates indicate a middle Holocene age for the accumulation of the midden remains.

Plant Remains

The plant macrofossils identified from the middens (Table 1) all occur in the area today. The locality within 15 m of the fossils is in the shade of the netleaf hackberry trees, which were estimated to cover 70% of the immediate surrounding. Hackberry was by far the most common fossil in the ringtail midden. All the other plant macrofossils are of desert shrubs, herbs, and grasses that are now found just outside of this shaded refuge (Phillips et al., 1987). The predominant plant macrofossils recovered are the most fleshy, edible berries of these desert plants, suggesting that they had been collected as food. In contrast, packrat middens often contain more abundant thorns and spines, possibly collected to discourage predators, harvested but uneaten food plant foliage, and many other nonedible plant parts collected to make a shelter over the nesting area that contributes to security and thermoregulation of the packrat (Olsen, 1973; Vaughan, 1980).

Faunal Remains

All fossil remains are curated by the National Park Service, Grand Canyon National Park (GRCA), Arizona. In the taxonomic accounts below, the skeletal element listing is followed by parentheses that contain the specimen number for the GRCA archive along with the quantity of identifiable specimens. Abbreviations include: WP-2, Weeping Cliffs deposit sample 2; WP-3a, Weeping Cliffs deposit sample 3a. Given the Holocene age for the specimens, modern geographic distributions of locally extant amphibian and reptilian species played heavily into the identifications, although in select cases, other taxa well outside the modern range were considered. Terminology and characters used to describe the anuran (frog and toad) remains follows Bailon (1999) and Holman (2003). Descriptive terminology for the lizard remains usually follows Evans (2008). See text for the terminology and characters used to describe snake vertebrae, but typically follow Auffenberg (1963), Van Devender and Mead (1978), and LaDuke (1991).

SYSTEMATICS

Amphibia

Anura

Remains: WP-2: various highly fragmented postcranial bones of anurans were recovered but were not identifiable to a lower taxonomic level (125701).

Bufonidae

Anaxyrus (formerly *Bufo*) sp. (toad)

Remains: WP-2: frontoparietal (125702; 1).

Discussion: One fragment (3.5 mm long) of a left frontoparietal having a portion of the thickened medial ridge rugose and pitted on the dorsal side. This bone is thin and smooth on *Scaphiopus* and *Spea* (spadefoot toads); smooth and narrow on *Hyla* (*Dryophytes*) *arenicolor* (canyon tree frog) and *Pseudacris* (chorus frog). *Anaxyrus borealis* (western toad) and *A. debilis* (Chihuahuan green toad) have a predominantly smooth dorsal surface to the frontoparietal, but there is slight rugosity along the medial ridge; this is more pronounced on *A. woodhousii* (Woodhouse's toad) but still a ridge. *Anaxyrus cognatus* (Great Plains toad) has a heavily rugose medial ridge as found on the fossil. We did not compare the fossil with the extant *A. microscaphus* (Arizona toad), *A. retiformis* (Sonoran green toad), or *A. punctatus* (red-spotted toad, which occurs throughout the Grand Canyon corridor; Miller et al., 1982). Without more of the single fragmented bone, we are reluctant to identify the fossil to species, but given the morphological similarity, it is most similar to that of the Great Plains toad. Today, *A. cognatus* does not occur in the Grand Canyon or along this southwestern portion of the Colorado Plateau, whereas *A. woodhousii* does (Murphy, 2018). The fossils from the Weeping Cliffs represent the first Quaternary *Anaxyrus*, or of any amphibian, from the Grand Canyon (Olsen and Olsen, 1984; Mead, 2005).

Hylidae

Hyla sp. (treefrog)

Remains: WP-2: maxilla (125703; 6).

Discussion: All maxillae were highly fragmented with the largest specimen 2.5 mm long. Teeth are pedicellate, relatively narrow, and 0.5 mm high as found on *Hyla* (*Dryophytes*) *arenicolor* and *H. wrightorum*. These are the only tree frogs in this genus living in the Grand Canyon and elsewhere nearby today. We did not compare in detail with *Smilisca fodiens* or *Acris blanchardi*, which are other tree frogs found in Arizona but not within the Grand Canyon region today (Murphy, 2018). Teeth on the spadefoot toads (*Spea* and *Scaphiopus*) are typically wide at the base and short unlike those from the Weeping Cliffs. *Hyla arenicolor* was found living in wet canyons and springs near Weeping Cliffs (JIM field notes) and throughout the Grand Canyon corridor (Miller et al., 1982). These fossils from the Weeping Cliffs represent the first Quaternary *Hyla*/*Dryophytes* from the Grand Canyon (Olsen and Olsen, 1984; Mead, 2005)

Reptilia

Sauria

Lizards

Families and Genera Indeterminate

Remains: WP-2: dentaries, maxillae, vertebrae (125704, 20), premaxilla (125705, 1); WP-3a: dentaries, maxillae, vertebrae (125706, 15).

Discussion: These skeletal elements were too highly fragmented and etched by digestive acids to permit identifications.

Iguanidae

Dipsosaurus sp. (Desert Iguana)

Remains: WP-2: dentary (125707; 1 left), maxilla (125708; 1 left).

Discussion: The fragmented left dentary (125707) is 2.7 mm long, preserving the mandibular symphysis and one complete tooth, with space for an additional three teeth. The single preserved tooth flares up from the base to the apex, which encompasses 4, possibly 5 cusps; it has no single main cusp. The left maxilla fragment (125708) has a preserved tooth row length of 1.4 mm with two teeth. Both teeth flare from the base to the apex and are mediolaterally flattened. There is one central cusp with two lateral cusps and an incipient additional lateral cusp posteriorly (Fig. 2A).

Maxillary and dentary teeth of iguanine lizards are described by Edmund (1969) and in detail by de Queiroz (1987). For many iguanines, the maximum number of cusps per tooth is 4, comprising 1 large apical (median), up to 2 anterior cusps, and 1 posterior cusp. Tooth crowns become progressively more laterally compressed posteriorly in the tooth row. Greater cuspation on a tooth occurs on some other iguanines (much larger individuals than *Dipsosaurus*) such as *Ctenosaura* (spiny iguana), *Cyclura* (rock iguana), and *Sauromalus* (chuckwalla), with 5 to 10 cusps; *Iguana* (iguana) can have the greatest cuspation to the point that the teeth are serrated (see de Queiroz, 1987: Fig. 30; Avery and Tanner, 1971).

Today, the northern extent of this hot, xeric-adapted lizard appears to coincide with the distribution of *Larrea divaricata* (creosote bush) and with substrate conditions of loose sand and patches of firm ground with scattered rocks (Hulse, 1992). *Dipsosaurus* is not known from the Grand Canyon in historic times (Miller et al., 1982; Hulse, 1992; Holycross et al., 2022). There does not appear to have been any published, detailed survey of the sandy, desert flood plain area adjacent to the Colorado River in the Grand Canyon prior to its flooding with Lake Mead reservoir water in the 1930s. Given the present habitat requirements of *Dipsosaurus*, the recently flooded, now exposed riparian floodplain would have been the only suitable area for the species' prior existence in the lower Grand Canyon.

Fossils of *Dipsosaurus* are not common. The living *D. dorsalis* is known from the late Pliocene (Blancan North American Land Mammal Age) deposits in the Anza-Borrego Desert, California (Norell, 1989) and is reviewed in Mead and Self (manuscript). This desert lizard is recently recorded in the Late Pleistocene deposits in La Tetera Cave outside of Tucson, Arizona (Czaplewski et al., in press). The *Dipsosaurus* from Weeping Cliffs represents one of two Quaternary records in Arizona and the only record from within the Grand Canyon where it does not live today (Miller et al., 1982; Mead, 2005; Murphy, 2018).

Phrynosomatidae

Uta/*Cophosaurus*/*Holbrookia* indeterminate

Remains: WP-3a: dentary (125709; 1).

Discussion: The fragmented left dentary extends from near the mandibular symphysis to a length of 3.1 mm with 12 teeth. The Meckelian fossa is fused from just short of the symphysis, but the suture line is visible the entire length of the ventral side of the dentary. Teeth are parallel sided in medial view and end in a single blunt cusp. Some teeth have an incipient cusplet on both sides of the main cusp. Apices of teeth show a slight lateral flattening; anterior teeth are blunt pointed.

Teeth of *Callisaurus* (zebra-tailed lizard) are overall larger and thus omitted from consideration. *Petrosaurus* (banded rock lizard) has distinctly wide teeth with a triangular medial cusp and two adjacent smaller cusps, unlike the fossil. Teeth of *Urosaurus* (both *U. ornatus* [tree lizard] and *U. graciosus* [long-tailed brush lizard]) have relatively longer teeth that culminate in a longer pointed apex cusp, unlike the fossil. Teeth of *Cophosaurus* (greater earless lizard), *Holbrookia* spp. (lesser earless lizard), and *Uta* (side-blotched lizard) all have tooth and Meckelian suture morphology similar to that on the fossil; however, because the fossil is fragmented, we are unable to make a more definitive identification. Other sand lizards, *Uma* spp., are not considered due to their modern distributions, dissimilar habitats, and age of the fossil deposit.

Urosaurus and *Uta* are extant today throughout the Grand Canyon. *Callisaurus* is recorded from a single location at the Colorado River at the confluence of Diamond Creek, which may have been its access route. *Cophosaurus* and *Holbrookia* are not recorded from the Grand Canyon in historic times, although the latter lizard can be found on the Colorado Plateau around the Canyon (Miller et al., 1982; Murphy, 2018).

Sceloporus sp. (spiny lizard)

Remains: WP-2: dentary (125710, 1).

Discussion: A left dentary fragment 7 mm long from symphysis to distal break. The Meckelian fossa is open ventrally at the symphysis, then becomes oriented lingually to close at the seventh tooth. Fourteen teeth have highly dissolved lingual faces, but one apex shows an indication of a tricuspate apex. The size of the dentary is similar to the range of sizes in extant *Sceloporus* species having a snout-vent length greater than 55 mm (i.e. , not the small species of desert spiny lizards). Morphology appears most similar to a form of *Sceloporus* such as *S. occidentalis* or *S. magister* and others that live in and around the Grand Canyon (Murphy, 2018). Late Pleistocene records of *Sceloporus* are known from the Grand Canyon from various cave and packrat midden localities (Van Devender et al., 1977; Mead, 1981) and elsewhere in Arizona (Mead, 2005).

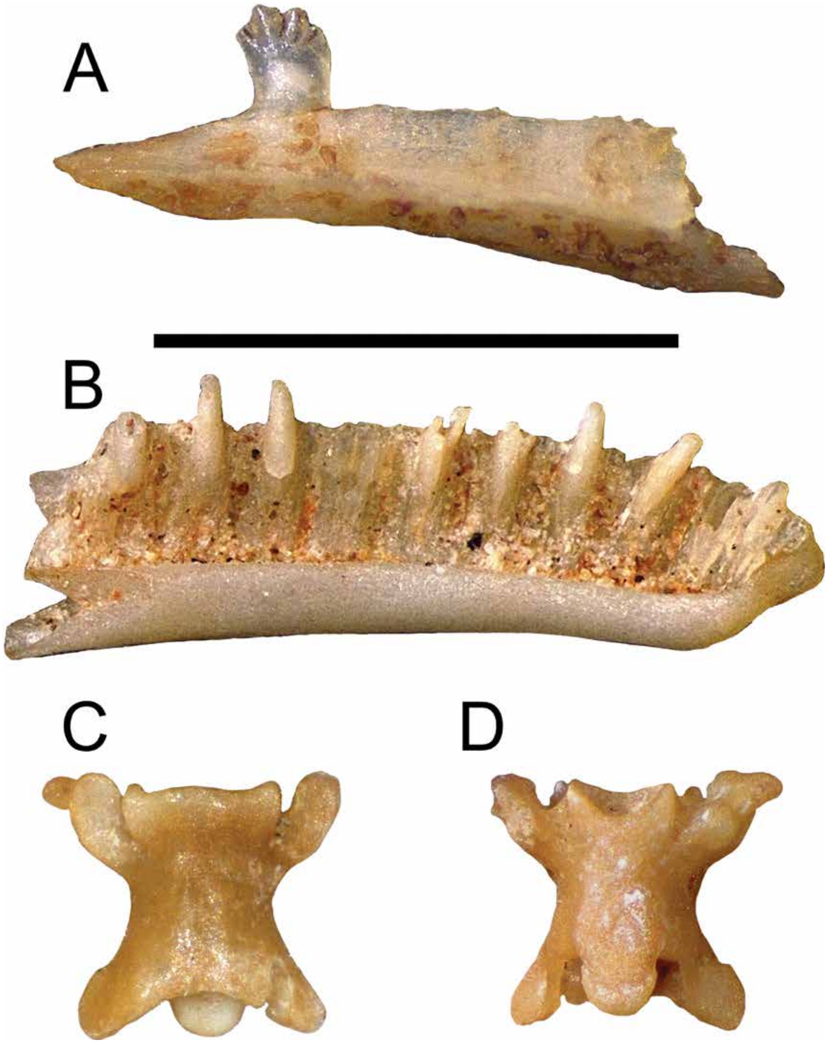


Figure 2. Selected reptile bones from the Weeping Cliffs ringtail midden locality. (A) fragmented dentary (GRCA 125707) belonging to *Dipsosaurus* (desert iguana). Although highly broken due to chewing by *Bassariscus*, the diagnostic tricuspate to multicuspate (shown here) pattern is preserved allowing identification, see text. (B) lingual view of the fragmented dentary (GRCA 125716) of *Coleonyx* (gecko). Vertebra of the scolecophidian snake, *Rena* (GRCA 125720) showing dorsal (C) and ventral (D) views, anterior is up. Note the extremely small adult size and the lack of a neural spine or hemal keel. Vertebra shown is the largest of several recovered vertebrae. Scale bar = 2 mm.

Crotaphytidae

Crotaphytus sp. (collared lizard)

Remains: WP-3a: dentary (125711, 3).

Discussion: Three dentary fragments are highly broken, but all contain teeth. The largest fragment is 1.6 mm long with three tricuspate teeth. The largest tooth is 0.5 mm wide at the base and only 1.0 mm tall. There is one distinct medial cusp and two less distinct lateral cusps. The size and robustness of the teeth suggest that the dentary belongs to *Crotaphytus*; no teeth show the curvature or pointed apex as appears on the related genus *Gambelia* (leopard lizard). Both *C. bicinctores* (Great Basin collared lizard) and *C. collaris* (eastern collared lizard), as well as *G. wislizenii* (long-nosed leopard lizard), are known today in and around the Grand Canyon (Miller et al., 1982; Murphy, 2018) and elsewhere in arid Arizona (Holycross et al., 2022). Late Pleistocene records of *Crotaphytus* are known from the Grand Canyon from various cave and packrat midden localities (Van Devender et al., 1977; Mead, 1981) and elsewhere in Arizona (Mead, 2005).

Gekkonidae

Coleonyx sp. (banded gecko)

Remains: WP-2: dentary (125716; 8, 4 left, 4 right), maxilla (125713; 2 right), premaxilla (125714; 2), frontal (125715; 1); WP-3a: dentary (125712; 3, 2 left, 1 right), maxilla (125717; 1 right).

Discussion: The dentaries of modern *Coleonyx* and the GRCA fossils have a fused (closed) Meckelian fossa and a wide dental shelf (gutter). Fragment lengths are from 1.2 to 2.0 mm for 125715, with the largest of eight in 125716 (Fig. 2B) being 4.3 mm as measured from the closed symphysis. Teeth of *Coleonyx* and the fossils are relatively tall and narrow on a wide dental shelf versus the condition observed on dentaries of *Xantusia* (night lizards). The fragmented maxillae (125717, 125713) (most complete is 3.2 mm long) have only a lateral orientation of the frontal process as in *Coleonyx* versus the condition in minute phrynosomatines in which the lateral orientation curves around more anteriorly to connect to the premaxilla process (e.g., *Urosaurus*, tree lizard). The Weeping Cliffs fossils lack the wide aspect of the premaxillary process and the longer more robust teeth of *Xantusia*. The fossil frontal (125715) has the midline fusion of the crista cranii forming a single covered frontal in palatal view, as found on modern *Coleonyx*. This contrasts with the open and paired characteristics to the frontals of *Xantusia*.

Today *C. variegatus* is a secretive, nocturnal lizard that lives in the hotter deserts of the Southwest, including throughout the Colorado River gorge of the Grand Canyon (Miller et al., 1982) and elsewhere in arid Arizona (Holycross et al., 2022). Although not a rare fossil in the Southwest, *Coleonyx* has been recovered in the Grand Canyon in deposits dating to the late Holocene and late Rancholabrean (Van Devender et al., 1977; Cole and Mead, 1981; Mead and Phillips, 1981; Mead and Van Devender, 1981; Mead, 2005). Its fossil record is typically found only in packrat middens and ringtail midden scats, although Norell (1986) recovered two specimens (of undefined age assignment) from accumulations in Kokoweef Cave, southern California.

Teiidae

Aspidoscelis sp. (whiptail lizard)

Remains: WP-2: dentary (125718, 1), frontal (125719, 1).

Discussion: The dentary (125718) fragment is 4.2 mm long with a closed Meckelian fossa closed on the ventral side of the bone. Six of the 10 teeth are bicuspate, which permits the identification as *Aspidoscelis* (formerly *Cnemidophorus*). The frontal fragment (125719) has an open groove at the cranial cristii in ventral view versus a shallow to no depression in the various sceloporine lizards. The dorsal surface on the fossil is fused but shows a suture line fusion for the two bones. There is some rugosity to the dorsal surface, and it lacks the distinct depression near the parietal suture found on *Sceloporus* (scaly lizards). The frontal is thin, smooth on the dorsal surface, and bowed on the various sand lizards, unlike the fossil. *Petrosaurus* has a frontal that is larger and more robust than the fossil. *Dipsosaurus* has a frontal about the same size as the fossil, but it is smoother and has a shallow groove between the cranial cristii, unlike the fossil. Anguid lizards such as *Elgaria kingii* (Arizona alligator lizard) has a frontal that is less diverging along the parietal/frontal suture, a deep groove between the cranial cristii that are highly expanded, and a more robust and textured dorsal surface than found on the fossil. Given these differences, we identify the frontal as that of a species of *Aspidoscelis*. We know of no characters of the frontal that permit identification of the species of this teiid, but it probably belonged to one of the many small species of the genus. At least twelve species are known to live in Arizona today, three of which occur in and around the Grand Canyon (Murphy, 2018). Late Pleistocene records of *Aspidoscelis* (recorded as *Cnemidophorus*) are known from the Grand Canyon from various cave and packrat midden localities (Van Devender et al., 1977; Mead, 1981) and elsewhere in Arizona (Mead, 2005).

Snakes

Leptotyphlopidae

Rena (Formerly *Leptotyphlops*; Threadsnake)

Remains: WP-2: vertebra (125720, 10).

Discussion: Ten vertebrae (two articulated) may represent a single individual. All are unique and readily identifiable as those of *Rena* in lacking the neural spine and the hypapophysis/hemal keel, and all are of an extremely small adult size (Fig. 2C and D; Mead, 2013).

Today *Rena humilis* (western thread snake, blind snake, or desert worm snake) is common in Arizona yet uncommon in the Grand Canyon (Fowlie, 1965; Miller et al., 1982; Wallach and Mitchell, 2020b). A second species, *Rena dissecta* (New Mexico thread snake) is known in southeastern Arizona and adjacent New Mexico (Wallach and Mitchell, 2020a). The occurrence of *Rena* in the Grand Canyon is not well understood, due likely to its secretive habits, but it is probably restricted to the desert environs of the river corridor similar to that previously discussed for the desert iguana. North American fossils of this tiny snake are rare and have been recovered only in Arizona (packrat middens) and New Mexico (owl roost and packrat midden; Van Devender and Worthington, 1977; Van Devender and Mead, 1978). The remains from Weeping Cliffs ringtail midden represent the first fossils for the Grand Canyon. We know of no vertebral characters that permit the identification to species, extant or fossil (Mead, 2013).

Colubridae

Sonora sp. (ground snake)

Remains: WP-2: vertebrae (125721, 3).

Discussion: Several small colubrid snakes have vertebrae that are similar to those of *Sonora*, including *Chilomeniscus* (sand snake), *Chionactis* (shovel-nosed snake), and *Hypsiglena* (night snake). The taxonomy of *Sonora* has been recently reinvestigated but does not seem to be fully resolved. Cox et al. (2018) place *Chionactis* and *Chilomeniscus* in the genus *Sonora*, which, according to these authors, now has at least 15 species. Here we will treat these genera as separate forms when examining the vertebrae and the vertebral characteristics.

Three vertebrae were recovered from the ringtail midden, 2 mid-trunk and 1 more cervical in position. Although all appear morphologically similar, only the characteristics of the largest are presented here. The large mid-trunk vertebra has a condyle length (cl) of 1.9 mm and a neural arch (na) width (naw) of 1.5 mm, thus a cl/naw ratio of 0.79. The na is slightly vaulted to not vaulted. The neural spine (ns) length is 1.3 mm, but its height cannot be determined due to breakage. Another of the vertebrae has its ns broken in part but shows enough to indicate that it was low. The zygosphene (z) is crenate as viewed from above and convex in anterior view. The accessory processes (ap) are directed laterally and are short and blunt pointed. There is no epizygapophyseal spine. The cotyle (ct) is round with a flat base (ventral). Two minute paracotylar foramina exist along with the paracotylar notches, but no ventrolateral cotylar processes occur. The hemal keel (hk) is a thin blade (gladiate; other vertebrae have an oblanceolate hk). The parapophysis is distinct from the diapophysis. The parapophysis is short, not protruding ventral to the ct. There are deep subcentral grooves alongside distinct subcentral ridges.

Van Devender et al. (1991a) determined that vertebrae of *Chionactis palarostris* (Sonoran shovel-nosed snake) differ, albeit slightly, from those of *C. occidentalis* (Mohave shovel-nosed snake; Van Devender and Mead, 1978). We feel that more data are needed about vertebral characteristics and potential variations between these two species along with a third Arizona shovel-nosed snake, *C. annulata* (resplendent shovel-nosed snake), as well as for all the species of *Sonora*, sensu lato.

Diadophis (ring-necked snake) has a long depressed na (cl=2.2 mm; naw=1.3; cl/naw=1.69; our data; see also LaDuke, 1991); thus, this snake is omitted from the fossil identification. Another small snake is *Tantilla* (black-headed snake) with vertebral characteristics similar to those for *Diadophis* (although smaller) and with long, thin, pointed ap (LaDuke, 1991), thus also differing from the fossil. *Hypsiglena* has a short, wide vertebra (cl=2.0 mm; naw=1.8 mm; cl/naw=1.11; our data; 1.18–1.3 from Van Devender and Mead, 1978). The prezygapophyseal facet shape and ap characters are not like those observed in the fossil (additional characters in Mead et al., 1984; Van Devender et al., 1991b). Thus, the fossil does not belong to *Hypsiglena*.

The vertebral characteristics of *Chilomeniscus* are not well represented in the literature; we present select data from both *C. cinctus* (banded sand snake; Arizona) and *C. stramineus* (of Baja California). The mid-trunk vertebra has the following characteristics: cl=1.4 mm, naw=1.0, and cl/naw=1.4. The z is crenate from above. The ap are directed laterally, are long, and robust. The ns is thin as on *Chionactis*. The hk is spatulate. The parapophyses drop below the ventral level of the ct, which is orbicular in shape. Vertebral characteristics for *Chionactis* from (Van Devender and Mead, 1978) are: ns is low, z is convex to crenate, ap are blunt pointed.

Given the characteristics of the mid-trunk vertebrae, as provided above from the literature and our data here, the fossils are most similar to *Chionactis* and *Sonora* and likely not *Chilomeniscus* or the other clearly different small snake vertebrae. Granted that molecular evidence argues for the synonymizing of *Chionactis* and *Chilomeniscus* with *Sonora* in the Sonorini (Grismer et al., 2002; Cox et al., 2018), our necessarily morphological approach suggests that the fossil is some form of *Sonora* (sensu lato) or of either *Chionactis* or *Sonora* (sensu stricto).

Three species of *Chionactis* live in Arizona today, *C. annulata* (resplendent shovel-nosed snake; Wood and Holycross, 2020a), *C. occipitalis* (Mohave shovel-nosed snake; Wood and Holycross, 2020b), and *C. palarostris* (Sonoran shovel-nosed snake; Wood and Holycross, 2020c; see also Fowlie, 1965; Rosen, 2007). None live in, around, or near the Grand Canyon today. However, *Sonora semiannulata* does occur in various locations in and around the Grand Canyon (Cox et al., 2020). As noted above, these authors recognize 15 species in the genus *Sonora*, that are distributed from central Mexico to the northwestern USA. It is doubtful that there will be definitive characteristics of the vertebrae that will permit the identification of isolated vertebrae to species or species-groups.

Late Pleistocene and Holocene *Chionactis* and *Sonora* vertebrae were recovered from packrat middens in southern Arizona in a reconstructed plant community containing *Larrea*-*Ambrosia* desert scrub intermixed with *Pinus* and *Juniperus* woodland species dating from 8,000 to 12,000 yr BP (Van Devender and Mead, 1978). Today *Chionactis* do not live within a woodland habitat but may live on the lower altitudinal edge of such a community (Miller et al., 1982; Mahrdt et al., 2001). It lives today in habitats similar to those occupied by *Dipsosaurus*. *Sonora* is found as a fossil in only a few places in the Grand Canyon (Mead, 1981) (now including the Weeping Cliffs record) and rarely elsewhere in Arizona (Mead, 2005). *Sonora semiannulata* lives today in open habitats, semiarid to arid environments, riparian zones, mixed *Juniper* to desert grasslands, and paloverde-saguaro habitats (Cox et al., 2020).

Mammalia

Vespertilionidae

Myotis sp. (bat)

Remains: WP-2 (125722): right upper first molar (M1).

Discussion: The tooth is in near-perfect condition, relatively easy to assign to genus *Myotis*, but alone it is not identifiable to species because of dental similarities across numerous species of the genus. Eight species of *Myotis* have been reported in the modern fauna within the Grand Canyon, *M. californicus, M. ciliolabrum, M. evotis, M. occultus, M. thysanodes, M. velifer, M. volans,* and *M. yumanensis* (Ruffner et al., 1978; Suttkus et al., 1978; Hoffmeister, 1986; Harvey et al., 2011). Generic characters that allow assignation to *Myotis* (following Gunnell et al., 2017) are: upper molars with very weak paraloph, short sloping postprotocrista, anteroposteriorly broad protofossa, and two narrow but distinct ectoflexi. The M1 measures 1.25 mm in anteroposterior length and 1.40 mm in transverse width.

There are few records of *Myotis* of Quaternary age from Grand Canyon deposits; the genus is recorded only in cave deposits of the eastern region (Olsen and Olsen, 1984; Emslie, 1988; Mead et al., 2021). In historic times, at least three species of bats (*Myotis* and *Tadarida*) have inhabited Bat Cave in the western Grand Canyon; ringtails also frequent this cave and are known to prey on the bats exiting the cave (Pape, 2014).

Molossidae

Nyctinomops macrotis (big freetail bat)

Remains: WP-2 (125723): Eleven isolated teeth, right C1, right P4, M1, M2, and M3, left M1, M2, and M3, right m1 and m3, left m2.

Discussion: Because there are no redundant teeth from this single sample, we assume that these 11 teeth represent a single individual bat that was consumed. Many teeth exhibit missing enamel likely through digestion, however, diagnostic characters are still discernible in remnants of enamel and in the underlying dentin. Most important for assigning the specimens to *N. macrotis* include the upper molar morphology; the upper molars show very long paralophs and metalophs extending from the bases of paracones and metacones all the way to the protocone apices on the upper M1s and M2s. These structures are shared derived features unique to the genus *Nyctinomops* (Czaplewski, 1997; Czaplewski et al., 2003). The lower teeth are also consistent with the morphology of *N. macrotis*. The large size of the teeth from Weeping Cliffs is that of *N. macrotis*, which is approximately twice the body mass of *N. femorosacca* (25–30 g for *N. macrotis* versus 10–14 g for *N. femorosacca*; Harvey et al., 2011), the only species of *Nyctinomops* so far reported from Grand Canyon cave deposits (Mead et al., 2021). However, living *N. macrotis* has been radio-tracked across parts of northern Arizona, including Marble Canyon and Kanab Canyon (Corbett et al., 2005), and almost certainly also occurs today in the lower Grand Canyon, including the Weeping Cliffs area. The only other molossids known in Grand Canyon and adjacent region are the common, smaller *Tadarida brasiliensis* and the even larger (than *N. macrotis*) *Eumops* sp. , both reported as fossils by Carpenter (2003) and Mead et al. (2021), or as part of the modern bat fauna by Hoffmeister (1971, 1986), Hoffmeister and Durham (1971), Ruffner et al. (1978), Suttkus et al. (1978), Rabe et al. (1998), Drost et al. (2000), and Pape (2014).

At least 11 genera of bats are known from Grand Canyon fossil deposits listed in Mead et al. (2021), but *Nyctinomops* is not among them. Although this bat lives in the region today, the report from Weeping Cliffs represents its first record as a fossil in Grand Canyon.

Rodentia

Cricetidae

Neotoma sp. (packrat, woodrat)

Remains: WP-2 (125724): M1 (1), M2 (3), M3 (1), m1 (1), m2 (3), m3 (1); WP-3a (125725): M2 (2), M3 (1), m1 (1), m2 (1), m3 (3).

Discussion: Many species of packrats live in and around the Grand Canyon today including (*Neotoma albigula* [white-throated woodrat], *N. cinerea* [bushytailed woodrat], *N. lepida* [desert woodrat], *N. mexicana* [Mexican woodrat], *N. stephensi* [Stephens' woodrat] (Hoffmeister, 1971, 1986). The identification of isolated woodrat teeth to species was not attempted due to the diversity of known occlusal patterns, inter- and intraspecies variability and overlap in dental characters, and the availability of complete toothrows for statistical significance (e.g., Harris, 1984, 2013).

Peromyscus/*Reithrodontomys* (deer mouse/mouse)

Remains: WP-2 (125726): isolated molars (67); WP-3a (125727): isolated molars (11).

Discussion: Six or seven species of *Peromyscus* and one of *Reithrodontomys* occur in and near GRCA in the modern fauna (Kays and Wilson, 2002). All have teeth that are morphologically similar qualitatively and overlap quantitatively. Although there have been attempts to distinguish some of them dentally (e.g., Hooper, 1957), their systematics and taxonomy have changed in the 76 years since that study, and its applicability today is thus compromised. The same caveats apply to teeth of these mice as mentioned above for *Neotoma*. We are unaware of dental characteristics to consistently identify isolated molars for all species within *Peromyscus/Reithrodontomys*.

Heteromyidae

Perognathus/*Chaetodipus*. (pocket mouse)

Remains: WP-2 (125728–125731): isolated cheek teeth (28); WP-3a (125732): isolated cheek teeth (15).

Discussion: About five species of *Perognathus* and two of *Chaetodipus* are known in the modern fauna of the GRCA area (Hoffmeister, 1986). Their teeth are qualitatively similar to one another, and the same caveats apply to teeth of these mice as mentioned above for *Neotoma*. We are unaware of dental characteristics to consistently identify isolated molars to species within *Perognathus* and *Chaetodipus*.

Table 1. Plant macrofossil contents from Weeping Cliffs ringtail middens lower Grand Canyon, Arizona. Radiocarbon dates are calibrated median age, see text.

Genus	Species	Family	Common Name	Fossil type and number of specimens
		WP-2 7,460 cal BP		
Celtis	*laevigata* var. *reticulata*	Ulmaceae	Netleaf hackberry	152 testa pieces; 30 exocarp pieces; 25 pedicels
Opuntia	*chlorotica*	Cactaceae	Pancake prickly pear	55 seed coats; 2 seeds
Echinocactus	*polycephalus*	Cactaceae	Cottontop cactus	40 seed pieces
Echinocereus	sp.	Cactaceae	Claretcup cactus	8 seeds
Ferocactus	*cylindraceus* var. *lecontei*	Cactaceae	California barrel cactus	5 seeds, 1 spine
Physalis	sp.	Solanaceae	Groundcherry	38 seeds
Cryptantha	*pterocarya*	Boraginaceae	Wingnut cryptantha	18 seeds
Dasyochloa	*pulchella*	Poaceae	Fluffgrass	6 florets
Bouteloua	sp.	Poaceae	Grama grass	1 floret
Senegalia (*Acacia*)	*greggii*	Fabaceae	Catclaw acacia	2 leaves
Phacelia	sp.	Hydrophyllaceae	Scorpionweed	2 seeds
Allionia	*incarnata*	Nyctaginaceae	Trailing allionia	1 seed coat piece
Astragalus	sp.	Fabaceae	Locoweed	1 seed
		WP-3a 7,781 cal yr BP		
Celtis	*laevigata* var. *reticulata*	Ulmaceae	Netleaf hackberry	3 twigs; 2 berries; 103 exocarp pieces; 20 pedicels
Echinocereus	sp.	Cactaceae	Claretcup cactus	12 seed pieces
Physalis	sp.	Solanaceae	Groundcherry	8 seeds
Senegalia (*Acacia*)	*greggii*	Fabaceae	Catclaw acacia	2 spines
Allionia	*incarnata*	Nyctaginaceae	Trailing allionia	2 seed coat pieces
Dasyochloa	*pulchella*	Poaceae	Fluffgrass	2 florets
Astragalus	sp.	Fabaceae	Locoweed	1 seed
Sphaeralcea	sp.	Malvaceae	Globemallow	1 seed coat piece

DISCUSSION AND CONCLUSIONS

Studies of the feces of extant *Bassariscus* from southern Mexico, islands in Baja California, northern California, Oregon, Utah, New Mexico, Texas, and elsewhere have shown that the ringtail is consistently an omnivore (Trapp, 1978; Poglayen-Neuwall and Toweill, 1988; Rodríguez-Estrella et al., 2000; among others). This nocturnal, small carnivore varies its diet from season to season, habitat to habitat, and includes a diverse array of food comprised of plants, arthropods, mammals, birds, herps, and scavenged carcasses (Alexander et al., 1994; Allen, 2013; among others). Single scats often include a variety of contents from plants to animals suggesting a smorgasbord approach to nightly eating. Ringtails also inhabit a variety of denning settings from bushes, trees, downed logs, caves, rock crevices, stumps, abandoned human-built structures (Gundermann et al., 2023), and including the active historic Desert Laboratory on Tumamoc Hill (Tucson, Arizona). Denning areas never seem to be occupied for a long time but are frequented often as latrines and scent marking areas (e.g., Barja and List, 2006; Harrison, 2012). Frequented latrines (here we call them ringtail middens) are accumulations of scats representing multiple eating episodes over time, and possibly over a number of seasons. The analysis of more ancient diets of ringtails is less well understood than modern (e.g., Alexander et al., 1994) but still supports an omnivorous diet as climate has changed through time (e.g., Mead and Van Devender, 1981).

The value of the study of scats and diet of extant *Bassariscus* is not only a better understanding of its modern ecology and habitat usage (Poglayen-Neuwall and Toweill, 1988; Gundermann et al., 2023), but as with the plant-collecting behavior of the packrat (Betancourt et al., 1990), provides a partial and detailed assessment of the local biota. Feces of the ringtail become a desirable resource for the reconstruction of past biotic communities, one where the biased fossil record is often not as all-inclusive as with modern studies. Fossils preserved in select locations are biased towards the taphonomic scenarios of that setting. Assessment of these fossil locations and the resulting reconstructions also can be biased by the analysis procedures of the researchers (such as a bias towards size of sieving of matrix or a taxonomic bias).

Ringtail middens are an unusual and neglected resource of micro-vertebrate and plant fossils, and the added value is that this carnivore selects a diverse set of prey that is typically nocturnal and small in size. Analysis of this resource mandates wet sieving through at least 500 µm mesh and sorting for skeletal and plant elements under low power microscope. For example, the minute vertebrae of an adult thread snake would have been lost using the often-used 1.0 mm or larger 1/16-inch (1.6 mm) screen.

Here we report on the scat contents (plant and vertebrate remains) based on the analysis of a ringtail midden from the lower Grand Canyon at the Weeping Cliffs and reconstruct the middle Holocene local biota of the area. Reconstructed Late Pleistocene and Holocene environments of this region have been based on many packrat middens that have produced a detailed, chronologically controlled succession of plant communities (Phillips and Van Devender, 1974; Phillips, 1984; Cole, 1990). Although packrat middens often contain micro-vertebrate remains (species that were either commensals in the packrat nest or that represent contents from raptor pellets or carnivore dung; Van Devender et al., 1977; Mead, 2005), packrat midden locations (dry shelters and caves) are typically situated well above the Colorado River riparian and floodplain environments.

The sandy, desert floodplain environment adjacent to the Colorado River extended up-canyon only a short distance (see above). This unusual habitat in the Grand Canyon was flooded and destroyed by the Lake Mead reservoir before being ecologically assessed in detail. The Weeping Cliffs ringtail midden locality is situated adjacent to this now-missing habitat. *Bassariscus* preyed on micro-vertebrates that inhabited this and other nearby communities and deposited these remains as scats in the dry cave crevices that have been preserved for many millennia. The Weeping Cliffs ringtail midden dates to the middle Holocene.

Plant remains are a common component in extant ringtail diets and include wood, leaves, moss, lichens, fruits, conifer scales, and seeds (Toweill and Teer, 1977; Alexander et al., 1994). The most common plant recovered from the Weeping Cliffs midden (Table 1) was the netleaf hackberry (*Celtis*), which grows at the locality today. Our study illustrates that the plant collecting habit of the ringtail is oriented towards just dietary needs (consumption) versus the catholic collection by the packrat. The ringtail can provide important data for reconstructing the local flora.

Today the anurans *Anxyrus*, *Hyla*, *Rana*, and *Scaphiopus* live adjacent to and in a variety of habitats throughout the Grand Canyon region along the river, active springs, and flowing side canyons (Miller et al., 1982). However, previous research failed to recover a fossil record of any anuran from the region. The Weeping Cliffs ringtail midden provides the first and only dated fossil anurans in the Grand Canyon (Mead, 1981). The nocturnal collecting habit of *Bassariscus* and the location of the Weeping Cliffs midden close to the river floodplain appears to have permitted the sampling of some anurans.

The Weeping Cliffs ringtail midden provides additional information about the existence of the gecko, *Coleonyx*, which is recorded in fossil packrat middens from the central Grand Canyon along with packrat middens near the Weeping Cliffs (Van Devender et al., 1977; Cole and Mead, 1981). The Weeping Cliffs ringtail midden provides the first evidence of the desert iguana (*Dipsosaurus*) in the Grand Canyon and one of the few for the arid Southwest (Mead and Self, in review). This lizard does not occur in the Grand Canyon today, although its habitat and the lizard likely occurred in the sandy floodplain a few miles upriver until it was inundated by the Lake Mead reservoir. The ringtail midden also provides evidence of the rare blind snake, *Rena*, from the Grand Canyon (Mead, 1981). Its fossil record is poor for the arid Southwest (Mead, 2005). The Weeping Cliffs ringtail midden also records the ground snake, Sonora. This snake was previously recorded from the nearby Vulture Cave,as well as in a few other Arizona localities (as Chionactis), but its late Quaternary distribution is still poorly understood (Van Devender et al., 1991a, b; Mead, 2005).

Ringtails are known to prey on a variety of amphibians, lizards, and snakes. In Oregon, *Bassariscus* rarely preyed on herp species (Alexander et al., 1994) but on Isla San José (Gulf of California), lizards, including the local *Dipsosaurus*, were a common food item (Rodríguez-Estrella et al., 2000). Small mammals, mainly rodents, are a typical prey item for *Bassariscus* for all dietary studies (Poglayen-Neuwall and Toweill, 1988), including the record from Weeping Cliffs. Winkler and Adams (1972) suggested that ringtail eating of bats might be limited to scavenging behavior. Certainly, the ringtail

Table 2. Vertebrate remains identified from the Weeping Cliffs ringtail middens, lower Grand Canyon, Arizona. Radiocarbon dates are calibrated median age, see text. Unkn, unidentifiable skeletal remains. Common names in text.

Taxon	WP-2: 7,460 cal BP	WP-3a: 7,781 cal yr BP
Unkn Anuran	X	-
Anaxyrus sp.	X	-
Hyla sp.	X	-
Unkn lizard	X	X
Dipsosaurus sp.	X	-
Uta/Cophosaurus/Holbrookia	-	X
Sceloporus sp.	X	-
Crotaphytus sp.	-	X
Coleonyx sp.	X	X
Aspidoscelis sp.	X	-
Rena sp.	X	-
Sonora sp.	X	-
Myotis sp.	X	-
Nyctinomops macrotis	X	-
Neotoma sp.	X	X
Peromyscus/Reithrodontomys	X	X
Perognathus/Chaetodipus	X	X

is known to scavenge carcasses such as the skunk, *Mephitis* (Allen, 2013). The two species of bats in the Weeping Cliffs ringtail midden are of interest as they include the first record of the big freetail bat (*Nyctinomops macrotis*) in the Grand Canyon. We do not know if the Weeping Cliffs ringtail captured the bat or if it scavenged a carcass, but ringtails are known to prey upon bats in the Grand Canyon (Pape, 2014) and elsewhere (Sparks et al., 2000). Bird remains and arthropods are common in the diet of modern ringtail (Poglayen-Neuwall and Toweill, 1988), however, the Weeping Cliffs ringtail midden does not record either of these groups as part of the sampled diet.

ACKNOWLEDGMENTS

We thank John Cannella for assisting with the collecting of the middens and Mary Carpenter for assistance with field logistics. We thank Jessa Fisher for helping with plant identifications. We thank Louella Colter, Marcella Coder, and Gary Nabhan of the Bilby Research Center, Center for Sustainable Environments, for their continued support of our projects in the Grand Canyon. Larry Stevens provided helpful discussions about Colorado River hydrology and geomorphology. Colleen Hyde and other personnel of GRCA provided collecting permits (GRCA-2000-SCI-0042), curation numbers, and continued support of our research in the park. Funding for the radiocarbon dates and field trip expenses was received as part of a USGS global change research program funding: “Past, recent, and 21st Century vegetation change of the arid Southwest” to KLC. We thank two anomalous reviewers for their suggestions.

REFERENCES

Alexander, L.F., Verts, B.J., and Farrell, T.P., 1994, Diet of ringtails (*Bassariscus astutus*) in Oregon: Northwestern Naturalist, v. 75, p. 97–101. https://doi.org/10.2307/3536831

Allen, M.L., 2013, Scavenging of a striped skunk (*Mephitis mephitis*) by a ringtail (*Bassariscus astutus*) in northern California: Northwestern Naturalist, v. 94, p. 79–81.https://doi.org/10.1898/12-18.1

Auffenberg, W., 1963, The fossil snakes of Florida: Tulane Studies in Zoology, v. 10, p. 131–216. https://doi.org/10.5962/bhl.part.4641

Avery, D.F., and Tanner, W.W., 1971, Evolution of the iguanine lizards (Sauria, Iguanidae) as determined by osteological and myological characters: Brigham Young University Science Bulletin, Biological Series, v. 12, p. 1–79.

Bailon, S., 1999, Différenciation ostéologique des anoures (Amphibia, Anura) de France: Fisches d’ostéologie animale pour l’archéologie, Série C [Osteological differentiation of anurans (Amphibia, Anura) from France: Animal osteology files for archaeology, Series C]: Varia, France.

Barja, I., and List, R., 2006, Faecal marking behavior in ringtails (*Bassariscus astutus*) during the nonbreeding period: spatial characteristics of latrines and single faeces: Chemoecology, v. 16, p. 219–22. https://doi.org/10.1007/s00049-006-0352-x

Baskin, J.A., 2004, *Bassariscus* and *Probassariscus* (Mammalia, Carnivora, Procyonidae) from the Early Barstovian (Middle Miocene): Journal of Vertebrate Paleontology, v. 24, p. 709–20. https://doi.org/10.1671/0272-4634(2004)024[0709:BAPMCP]2.0.CO;2

Betancourt, J.L., Van Devender, T.R., and Martin, P.S., eds., 1990, Packrat middens. The last 40,000 years of biotic change: Tucson, University of Arizona Press.

Bever, G.S., 2003, New record of *Bassariscus ogallalae* (Carnivora: Procyonidae) from the Ogallala group (Miocene) of Ellis County, Kansas, with comments on variation within *Bassariscus*: Southwestern Naturalist, v. 48, p. 249–56. https://doi.org/10.1894/0038-4909(2003)048<0249:NROBOC>2.0.CO;2

Carpenter, M.C., 2003, Late Pleistocene Aves, Chiroptera, Perissodactyla, and Artiodactyla from Rampart Cave, Grand Canyon, Arizona [Thesis]: Flagstaff, Northern Arizona University.

Cole, K.L., 1990, Late Quaternary vegetation gradients through the Grand Canyon: in Betancourt, J.L., Van Devender, T.R., and Martin, P.S., eds., Packrat middens. The last 40,000 years of biotic change: Tucson, University of Arizona Press, p. 240–58. https://doi.org/10.2307/j.ctv21wj578.13

Cole, K.L., and Mead, J.I., 1981, Late Quaternary animal remains from packrat middens in the eastern Grand Canyon, Arizona: Journal of the Arizona-Nevada Academy of Science, v. 16, p. 24–25.

Corbett, R.J.M., Chambers, C.L., Herder, M.J., and Leslie, E.F., 2005, Foraging patterns and roosting sites for female big free-tailed bats (*Nyctinomops macrotis*) in northern Arizona: Bat Research News, v. 46, p. 165–66

Cox, C.L., Davis Rabosky, A.R., Holmes, I.A., Reyes-Velasco, J., Roelke, C.E., Smith, E. N., Flores-Villela, O., McGuire, J.A., and Campbell, J.A., 2018, Synopsis and taxonomic revision of three genera in the snake tribe Sonorini: Journal of Natural History, v. 52, p. 945–88. https://doi.org/10.1080/00222933.2018.1449912

Cox, C.L., Davis Rabosky, A.R., and Frost, D.R., 2020, *Sonora semiannulata*: in Holycross, A.T., and Mitchell, J.C., eds., Snakes of Arizona: ECO Publishing, Rodeo, NM, p. 354–63.

Czaplewski, N.J., 1990, The Verde local fauna: small vertebrate fossils from the Verde Formation, Arizona: San Bernardino Museums Association Quarterly, v. 37, p. 1–39.

Czaplewski, N.J., 1997, Chiroptera: in Kay, R.F., Madden, R.H., Cifelli, R.L., and Flynn, J.J., eds., Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia: Washington, D.C., Smithsonian Institution Press, p. 410–31.

Czaplewski, N.J., Mead, J.I., Bell, C.J., and Peachey, W.D., 1999, Papago Springs Cave revisited, Part II: vertebrate paleofauna: University of Oklahoma, Norman, Occasional Papers of the Oklahoma Museum of Natural History, v. 5, p. 1–41.

Czaplewski, N.J., Mead, J.I., and Peachey, W.D., In Press. Late Pleistocene vertebrate fauna and bat guano deposit of La Tetera Cave, Arizona: Journal of Cave and Karst Studies.

Czaplewski, N.J., Morgan, G.S., and Naeher, T., 2003, Molossid bats from the late Tertiary of Florida with a review of the Tertiary Molossidae of North America. Acta Chiropterologica, v. 5, p. 61–74. https://doi.org/10.3161/001.005.0105

de Queiroz, K., 1987, Phylogenetic systematics of iguanine lizards. A comparative osteological study: University of California Publications, Zoology, v. 118, p. 1–203. https://doi.org/10.5962/bhl.title.4857

Drost, C.A., Petterson, J., and Leslie, E., 2000, Survey of bats along the Colorado River through Grand Canyon National Park: Final Report: Arizona Game and Fish, Heritage Grant I96031.

Edmund, A.G., 1969, Dentition: in Bellairs, A. d'A., and Parson, T.S., eds., Morphology A, v. 1, Gans, C., ed., Biology of Reptilia: London, Academic Press, p. 117–200.

Emslie, S.D., 1988, Vertebrate paleontology and taphonomy of caves in Grand Canyon, Arizona: National Geographic Research, v. 4, p. 128–42.

Emslie, S.D., and Mead, J.I., 2023, Two new late Quaternary avifaunas from the east-central Great Basin with the description of a new species of *Falco*: Western North American Naturalist, v. 83, p. 33–50. https://doi.org/10.3398/064.083.0104

Evans, S.E., 2008, The skull of lizards and tuatara: in Gans, C., Gaunt, A.S., and Adler, K., eds., Biology of Reptilia: the skull of Lepidosauria, v. 20, Morphology H.: Lawrence, KS, Society for the Study of Amphibians and Reptiles, p. 1–347.

Fowlie, J.A., 1965, The snakes of Arizona: Fallbrook, California, Azul Quinta Press.

Grismer, L.L., Wong, H., and Galina-Tessaro, P., 2002, Geographic variation and taxonomy of the sand snakes, *Chilomeniscus* (Squamata: Colubridae): Herpetologica, v. 58, p. 18–31. https://doi.org/10.1655/0018-0831(2002)058[0018:GVATOT]2.0.CO;2

Gundermann, K.P., Green, D.S., Buderman, F.E., Myers, C.H., Higley, J.M., Brown, R.N., and Matthews, S.M., 2023, Ecological characteristics of diural rest sites used by ringtails (*Bassariscus astutus*): Northwest Science, v. 96, p. 220–33. https://doi.org/10.3955/046.096.0306

Gunnell, G.F., Smith, R., and Smith, T., 2017, 33 million year old *Myotis* (Chiroptera, Vespertilionidae) and the rapid global radiation of modern bats: PLoS ONE, https://doi.org/10.1371/journal.pone.0172621.

Gustafson, E.P., 2015, *Bassariscus* from the early Pliocene of Washington: Northwest Science, v. 89, p. 129–35. https://doi.org/10.3955/046.089.0204

Harris, A.H., 1984, *Neotoma* in the Late Pleistocene of New Mexico and Chihuahua:
Special Publication of the Carnegie Museum of Natural History, v. 8, p. 164–78

Harris, A.H., 1985, Late Pleistocene vertebrate paleoecology of the West: Austin, University of Texas Press.

Harris, A.H., 1990, Taxonomic status of the Pleistocene ringtail *Bassariscus sonoitensis* (Carnivora): Southwestern Naturalist, v. 35, p. 343–46. https://doi.org/10.2307/3671953

Harris, A.H., 2013, Pleistocene vertebrates of southwestern USA and northwestern Mexico: Online ebook, Arthur H. Harris (utep.edu).

Harris, A.H., and Hearst, J., 2012, Late Wisconsin mammalian fauna from Dust Cave, Guadalupe Mountains National Park, Culberson County, Texas: Southwestern Naturalist, v. 57, p. 202–6. https://doi.org/10.1894/0038-4909-57.2.202

Harrison, R.L., 2012, Ringtail (*Bassariscus astutus*) ecology and behavior in central New Mexico, USA: Western North American Naturalist, v. 72, p. 495–506. https://doi.org/10.3398/064.072.0407

Harvey, M.J., Altenbach, J.S., and Best, T.L., 2011, Bats of the United States and Canada: Baltimore, Johns Hopkins University Press.

Hoffmeister, D.F., 1971, Mammals of Grand Canyon: Urbana, University of Illinois Press.

Hoffmeister, D.F., 1986, Mammals of Arizona: Tucson, University of Arizona Press.

Hoffmeister, D.F., and Durham, F.E., 1971, Mammals of the Arizona Strip including Grand Canyon National Monument: Museum of Northern Arizona Technical Series, no. 11, p. 1–44.

Holman, J.A., 2003, Fossil frogs and toads of North America: Bloomington, Indiana University Press.

Holycross, A.T., Brennan, T.C., and Babb, R.D., 2022, A field guide to amphibians and reptiles in Arizona: Phoenix, Arizona Game and Fish Department.

Hooper, E.T., 1957, Dental patterns in mice of the genus *Peromyscus*: University of Michigan, Miscellaneous Publications Museum of Zoology, no. 99, p. 1–64. https://doi.org/10.3998/mpub.12946845

Hulse, A.C., 1992, *Dipsosaurus dorsalis*: Catalogue of American Amphibians and Reptiles, no. 542, p. 1–6.

Hunt, A.P., and Lucas, S.G., 2012, Classification of vertebrate coprolites and related trace fossils: in Hunt, A.P., Milán, J., Lucas, S.G., and Spielmann, J.A., eds., Vertebrate coprolites: New Mexico Museum of Natural History and Science, Bulletin 57, p. 137–46.

Hunt, A.P., and Lucas, S.G., 2021, The ichnology of vertebrate consumption: dentalites, gastroliths and bromalites: New Mexico Museum of Natural History and Science, Bulletin, no. 87.

Kays, R.W., and Wilson, D.E., 2002, Mammals of North America: Princeton University Press.

Koepfli, K.-P., Gompper, M.E., Eizirik, E., Ho, C.-C., Linden, L., Maldonado, J.E., and Wayne, R.K., 2007, Phylogeny of the Procyonidae (Mammalia: Carnivora): molecules, morphology and the Great American Interchange: Molecular Phylogenetics and Evolution, v. 43, p. 1076–1095. https://doi.org/10.1016/j.ympev.2006.10.003

LaDuke, T.C., 1991, The fossil snakes of Pit 91, Rancho La Brea, California: Natural History Museum of Los Angeles County, Contributions in Science, v. 424, p. 1–28. https://doi.org/10.5962/p.226807

Long, A., and Martin, P. S., 1974, Death of American ground sloth: Science, v. 186, p. 638–40. https://doi.org/10.1126/science.186.4164.638

Mahrdt, C. R., Beaman, K. R., Rosen, P. C., and Holm, P. A., 2001, *Chionactis occipitalis*: Catalogue of American Amphibians and Reptiles, v. 731, p. 1–12.

Mead, J.I., 1981, The last 30,000 years of faunal history within the Grand Canyon, Arizona: Quaternary Research, v. 15, p. 311–26. https://doi.org/10.1016/0033-5894(81)90033-8

Mead, J.I., 2005, Late Pleistocene (Rancholabrean) amphibians and reptiles of Arizona: in Heckert, A.B., and Lucas, S.G., eds., Vertebrate paleontology in Arizona: New Mexico Museum of Natural History and Science, Bulletin 29, p. 1–16.

Mead, J.I., 2013, Scolecophidia (Serpentes) of the Late Oligocene and Early Miocene, North America, and a fossil history overview: Geobios, v. 46, p. 225–31. https://doi.org/10.1016/j.geobios.2012.10.016

Mead, J. I., and Phillips, A.M., 1981, The late Pleistocene and Holocene fauna and flora of Vulture Cave, Grand Canyon, Arizona: Southwestern Naturalist, v. 26, p. 257–88. https://doi.org/10.2307/3670906

Mead, J. I., and Van Devender, T.R., 1981, Late Holocene diet of *Bassariscus astutus* in the Grand Canyon, Arizona: Journal of Mammalogy, v. 62, p. 439–42. https://doi.org/10.2307/1380737

Mead, J. I., Roth, E.L., Van Devender, T.R., and Steadman, D.W., 1984, The Late Wisconsinan vertebrate fauna from Deadman Cave, southern Arizona: Transactions of the San Diego Society of Natural History, v. 20, p. 247–76. https://doi.org/10.5962/bhl.part.29007

Mead, J.I., Coats, L.L., and Schubert, B.W., 2003, Late Pleistocene faunas from caves in the eastern Grand Canyon, Arizona: in Schubert, B.W., Mead, J.I., and Graham, R.W., eds., Ice Age cave faunas of North America: Bloomington, Indiana University Press, p. 64–86.

Mead, J.I., McGinnis, T.W., and Keeley, J.E., 2006, A mid-Holocene fauna from Bear Den Cave, Sequoia National Park, California: Bulletin of the Southern California Academy of Science, v. 105, p. 43–58. https://doi.org/10.3160/0038-3872(2006)105[43:AMFFBD]2.0.CO;2

Mead, J.I., Tweet, J.S., Santucci, V.L., Tobin, J., Chambers, C.L., Thomas, S.C., and Carpenter, M.C., 2021, Pleistocene/Holocene cave fossils from Grand Canyon National Park - Ice Age (Pleistocene) flora, fauna, environments, and climate of the Grand Canyon, Arizona: in Santucci, V.L., and Tweet, J.S., eds., Grand Canyon National Park Centennial Paleontological Resources Inventory-A Century of Fossil Discovery and Research: Utah Geological Association, Special Publication 1, p. 221–40.

Mead, J. I., and Self, A.G., in review, Late Quaternary records of the desert iguana *Dipsosaurus* (Squamata, Iguanidae).

Miller, D.M., Young, R.A., Gatlin, T.W., and Richardson, J.A., 1982, Amphibians and reptiles of the Grand Canyon: Grand Canyon Natural History Association, Monograph 4, p. 1–144.

Murphy, J.C., 2018, Arizona's amphibians and reptiles. A natural history and field guide: Book Services.

Norell, M.A., 1986, Late Pleistocene lizards from Kokoweef Cave, San Bernardino County, California: Copeia, v. 1986, p. 244–46. https://doi.org/10.2307/1444921

Norell, M.A., 1989, Late Cenozoic lizards of the Anza Borrego Desert, California: Natural History Museum of Los Angeles County, Contributions in Science, v. 414, p. 1–31. https://doi.org/10.5962/p.208135

Olsen, J.W., and Olsen, S.J., 1984. Zooarchaeological analysis of small vertebrates from Stanton's Cave, Arizona: in Euler, R.C., ed., The archaeology, geology, and paleobiology of Stanton's Cave, Grand Canyon National Park, Arizona: Grand Canyon Natural History Association, Monograph 6, p. 47–57.

Olsen, R.W., 1973, Shelter-site selections in the white-throated woodrat, *Neotoma albigula*: Journal of Mammalogy, v. 54, p. 594–610. https://doi.org/10.2307/1378961

Pape, R.B., 2014, Biology and ecology of Bat Cave, Grand Canyon National Park, Arizona: Journal of Cave and Karst Studies, v. 76, p. 1–13. https://doi.org/10.4311/2012LSC0266

Phillips, A.M., 1984, Shasta ground sloth extinction: in Martin, P.S., and Klein, R.G., eds., Quaternary Extinctions: a prehistoric revolution: Tucson, University of Arizona Press, p. 148–57. https://doi.org/10.2307/j.ctv264f91j.12

Phillips, A.M., and Van Devender, T.R., 1974, Pleistocene packrat middens from the lower Grand Canyon of Arizona: Journal of the Arizona Academy of Science, v. 9, p. 117–19. https://doi.org/10.2307/40023611

Phillips, B.G., Phillips, A.M., and Schmidt Bernzott, M.A., 1987, Annotated checklist of vascular plants of Grand Canyon National Park: 1987: Grand Canyon Natural History Association.

Pino, J., Samudio, R., Gonzales-Maya, J.F., and Schipper, J., 2016, *Bassariscus sumichrasti*, cacomistle: The IUCN Red List of Threatened Species. Technical Report, e. T2613A45196645.

Poglayen-Neuwall, I., and Toweill, D.E., 1988, *Bassariscus astutus*. Mammalian Species, no. 327, p. 1–8. https://doi.org/10.2307/3504321

Rabe, M.J., Morrell, T.E., Green, H., deVos Jr. , J.C., and Miller, C.R., 1998, Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona: Journal of Wildlife Management, v. 62, p. 612–21. https://doi.org/10.2307/3802337

Rodríguez-Estrella, R., Rodríguez Moreno, A., and Grajales Tam, K., 2000, Spring diet of the endemic ring-tailed cat (*Bassariscus astutus insulicola*) population on an island in the Gulf of California, Mexico: Journal of Arid Environments, v. 44, p. 241–46. https://doi.org/10.1006/jare.1999.0579

Rosen, P.C., 2007, Reptiles and amphibians in arid southwestern Arizona and northwestern Sonora: in Felger, R.S., and Broyles, B., eds., Dry Borders. Great natural reserves of the Sonoran Desert: Salt Lake City, University of Utah Press, p. 310–37.

Ruffner, G.A., Czaplewski, N.J., and Carothers, S.W., 1978, Distribution and natural history of some mammals from the Inner Gorge of the Grand Canyon, Arizona: Journal of the Arizona-Nevada Academy of Science, v. 13, p. 85–91.

Skinner, M.F., 1942, The fauna from Papago Springs Cave, Arizona, and a study of *Stockoceros*: American Museum of Natural History, Bulletin 80, p. 143–220.

Sparks, D.W., Roberts, K.J., and Jones, C., 2000, Vertebrate predators on bats in North America north of Mexico: in Choate, J.R., ed., Reflections of a naturalist: papers honoring professor Eugene D. Fleharty: Hays, Kansas, Fort Hays Studies, Special Issue 1, p. 229–41.

Spaulding, W.G., 1990, Vegetational and climatic development of the Mojave Desert: the last glacial maximum to the present: in Betancourt, J.L., Van Devender, T.R., and Martin, P.S., eds., Packrat Middens: the last 40,000 years of biotic change: Tucson, University of Arizona Press, p. 166–99. https://doi.org/10.2307/j.ctv21wj578.11

Stegner, M.A., 2015, The Mescal Cave fauna (San Bernardino County, California) and testing assumptions of habitat fidelity in the Quaternary fossil record: Quaternary Research, v. 83, p. 582–87. https://doi.org/10.1016/j.yqres.2015.02.005

Suttkus, R.D., Clemmer, G.H., and Jones, C., 1978, Mammals of the riparian region of the Colorado River in the Grand Canyon area of Arizona: Occasional Papers of Tulane University Museum of Natural History 1978, p. 1–11.

Toweill, D.E., and Teer, J.G., 1977, Food habits of ringtails in the Edwards Plateau region of Texas: Journal of Mammalogy, v. 58, p. 660–63. https://doi.org/10.2307/1380015

Trapp, G., 1978, Comparative behavioral ecology of the ringtail and gray fox in southwestern Utah: Carnivore, v. 1, p. 3–32.

Tweet, J.S., Santucci, V.L., and Hunt, A.P., 2012, Inventory of packrat (*Neotoma* spp.) middens in national park service areas: in Hunt, A.P., Milan, J., Lucas, S.G., and Spielmann, J.A., eds., Vertebrate coprolites: New Mexico Museum of Natural History and Science, Bulletin 57, p. 355–68.

Van Devender, T.R., Phillips, A.M., and Mead, J.I., 1977, Late Pleistocene reptiles and small mammals from the lower Grand Canyon of Arizona: Southwestern Naturalist, v. 22, p. 49–66. https://doi.org/10.2307/3670463

Van Devender, T.R., and Worthington, R.D., 1977, The herpetofauna of Howell's Ridge Cave and the paleoecology of the northwestern Chihuahuan Desert: in Wauer, R.H., and Riskind, D.H., eds., Transactions of the symposium on the biological resources of the Chihuahuan Desert region United States and Mexico: National Park Service Transactions and Proceedings Series, no. 3, p. 85–106.

Van Devender, T.R., and Mead, J.I., 1978, Early Holocene and Late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens: Copeia, v. 1978, p. 464–75. https://doi.org/10.2307/1443613

Van Devender, T.R., Rea, A.M., and Hall, W.E., 1991a, Faunal analysis of late Quaternary vertebrates from Organ Pipe Cactus National Monument, Southwestern Arizona: Southwestern Naturalist, v. 36, p. 94–106. https://doi.org/10.2307/3672122

Van Devender, T.R., Mead, J.I., and Rea, A.M., 1991b, Late Quaternary Plants and Vertebrates from Picacho Peak, Arizona. Southwestern Naturalist, v. 36, p. 302–14. https://doi.org/10.2307/3671680

Vaughan, T.A., 1970. Woodrats and picturesque junipers: in Jacobs, L.L., ed. , Aspects of vertebrate history: essays in honor of Edwin Harris Colbert: Flagstaff, Museum of Northern Arizona Press, p. 387–401.

Wallach, V., and Mitchell, J.C., 2020a, *Rena dissecta*: in Holycross, A.T., and Mitchell, J.C., eds., Snakes of Arizona: Rodeo, NM, ECO Publishing, p. 62–68.

Wallach, V., and Mitchell, J.C., 2020b, *Rena humilis*: in Holycross, A.T., and Mitchell, J.C., eds., Snakes of Arizona: Rodeo, NM, ECO Publishing, p. 69–77.

White, R.S., Mead, J.I., Baez, A., and Swift, S.L., 2010, Localidades de vertebrados fósiles de Neógeno (Mioceno, Plioceno y Pleistoceno): Una evaluación preliminar de la biodiversidad del passado [Neogene Fossil Vertebrate Localities (Miocene, Pliocene, and Pleistocene): A Preliminary Assessment of Passad Biodiversity]: in Molina-Freaner, F.E., and Van Devender, T.R., eds., Diversidad biológica de Sonora [Biological Diversity of Sonora]: UNAM, México, p. 51–72.

Wilson, R.W., 1942, Preliminary study of the fauna of Rampart Cave, Arizona: Contributions to Paleontology, Carnegie Institution of Washington, v. 530, p. 169–85.

Winkler, W.G., and Adams, D.B., 1972, Utilization of southwestern bat caves by terrestrial carnivores: American Midland Naturalist, v. 87, p. 191–200. https://doi.org/10.2307/2423892

Wood, D.A., and Holycross, A.T., 2020a, *Chionactis annulate*: in Holycross, A.T., and Mitchell, J.C., eds., Snakes of Arizona: Rodeo, NM, ECO Publishing, p. 109–16.

Wood, D.A., and Holycross, A.T., 2020b, *Chionactis occipitalis*: in Holycross, A.T., and Mitchell, J.C., eds., Snakes of Arizona: Rodeo, NM, ECO Publishing, p. 117–21.

Wood, D.A., and Holycross, A.T., 2020c, *Chionactis palarostris*: in Holycross, A.T., and Mitchell, J.C., eds., Snakes of Arizona: Rodeo, NM, ECO Publishing, p. 122–25.

Espinasa, L., Espinasa-Pereña, R., Espinasa-Diamant, S., and Diamant, R. A fossil sloth skeleton from a cave in Quenetaro, Mexico. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 239-245. DOI:10.4311/2024PA0113

A FOSSIL SLOTH SKELETON FROM A CAVE IN QUERETARO, MEXICO

Espinasa, L.[1C,] Espinasa-Pereña, R.[2], Espinasa-Diamant, S.[3,] and Diamant, R.[4]

ABSTRACT

Over thousands of years, a pit within Cueva del Tesoro in Queretaro, Mexico, has functioned as a death trap for mammals. This has resulted in the accumulation of mammalian fossils. At the bottom of this pit there is an almost complete and articulated skeleton of a ground sloth (Xenarthra, Folivora, Nothrotheriidae), *Nothrotheriops shastensis*. Remains of other animals include partial remains of at least a second ground sloth, a bovid, and bats. Given the extreme fragility and brittle nature of the remains, no attempt was made to extract or excavate them. Here we report our results mainly through photographic documentation in situ, with particular emphasis on dentary elements.

INTRODUCTION

Caves are important environments for the preservation of fossils (Schubert et al., 2003). Some animals seek out caves as preferred habitats, and caves can also act as traps, resulting in the accumulation of fossils over thousands of years. The stable temperature and humidity of some caves can help to preserve fossils. Fossils can occur in many contexts, but among them, the remains of Pleistocene/Holocene animals that either entered, lived, or fell inadvertently into caves during their lives are of particular interest. Polaco and Butrón (1997) initially reported 14 caves in México where fossil vertebrate remains have been found. Six years later, Arroyo-Cabrales and Polaco (2003) recorded 18 different cave sites and described their fossil fauna, which represented more than half of the known Pleistocene fossil mammals of Mexico. More recently, Ferrusquía-Villafranca et al. (2017) and Bonilla (2018) mentioned 27 different cave sites with Pleistocene age materials. This number has increased in recent years by at least one cave and two cenotes (McDonald et al., 2017; McDonald et al., 2020; Stinnesbeck et al., 2021). Collaborations between cavers and paleontologists are bound to further increase this list (McDonald et al., 2020).

Mexico is key to understanding many aspects of the paleoecology and biogeography of ground sloths (Xenarthra, Folivora) in North America after their dispersal from South America during the Great American Biotic Interchange (McDonald, 2002). While most of the clade's evolutionary history is restricted to South America, during the late Miocene, some xenarthrans dispersed across the water barrier separating North and South America and became integrated into the North American fauna. Others entered North America following the formation of the Panamanian land bridge (McDonald, 2002). The geographic position of Mexico represents the southern portions of the temperate zone and northern portions of the tropics and is thus critical to a complete understanding of xenarthran zoogeography, paleoecology, and evolution, given that Mexico is the passageway for faunas dispersing between the Neotropics and the Nearctic.

The fossil record of xenarthrans in Mexico extends from the Hemphillian to Rancholabrean i.e., from the late Miocene to late Pleistocene (McDonald, 2002). Currently, ten genera of ground sloths have been reported from Mexico (Fig. 1A): *Pliometanastes, Zacatzontli, Megalonyx, Nohochichak, Nothrotheriops, Eremotherium, Glossotherium, Paramylodon, Xibalbaonyx,* and *Meizonyx* (McDonald, 2002; McDonald et al., 2020; Stinnesbeck et al., 2021).

A pit within a cave was explored by members of the Sociedad Mexicana de Exploraciones Subterraneas (SMES) in Queretaro, Mexico. At its bottom, a skeleton of a ground sloth was discovered, as well as bones from other vertebrates. A second expedition was then organized to photographically document the remains and assess their state of conservation. The purpose of this article is to report on its findings.

MATERIALS AND METHODS

Exploration and study of Cueva del Tesoro (20°58'23" N, 99° 40'21" W 1,303 masl), in the canyon of Barranco de Orduña, near the town of Rancho Quemado, Queretaro, Mexico is difficult to explore and requires technical caving expertise. The entrance of the cave is perched on the side of the canyon, 110 m above stream level and 200 m below the rim of the canyon, and single-rope-techniques must be employed to reach it. Once inside the cave, the first 170 m of terrain is mostly flat and very easy to traverse until, abruptly, a pit is encountered, the Sima de los Huesos (Fig. 1B-C). This pit is close to 50 m in depth. The pit has three sections: a 26 m vertical portion, a first landing step with a steep 12.6 m ramp, and a final 10 m vertical section to the bottom of the pit (Fig. 1C). Fossils were found on the landing step and ramp, as well as at the bottom of the pit.

---

[1] School of Science, Marist College, Poughkeepsie, New York, USA
[2] Sociedad Mexicana de Exploraciones Subterráneas, México respinasa@yahoo.com.mx
[3] Facultad de Ciencias, UNAM, México
[4] Lab. de Óptica Cuántica, Depto. de Física, Universidad Autónoma Metropolitana - Iztapalapa, México
[C] Corresponding author: Luis Espinasa luis.espinasa@marist.edu

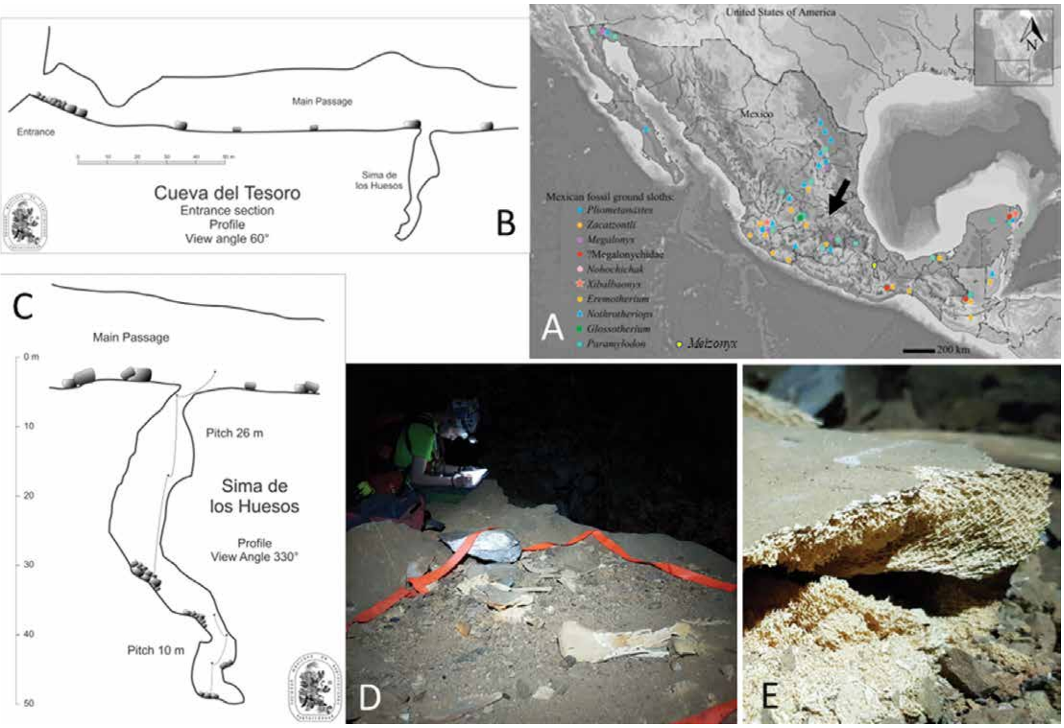


Figure 1. A; Map showing localities of ground sloths fossils in Mexico. Arrow points to the new locality of Cueva del Tesoro. Modified from Stinnesbeck (2020). B; Profile map of the area where the fossils were found in Cueva del Tesoro. Notice that a pit is encountered after flat, easily traversed galleries. C; Profile of the pit. Notice that a first landing step followed by a steep slope divides the pit. Fossils were found both in this step and at the bottom of the pit. D-E; Bones are extremely fragile and brittle. When disturbed, they break and pulverize.

The cave was mapped using the methods described in Ellis (1976), Dasher (1994), and Day (2002) by setting permanent stations along the cave passage, between which the distance was measured to the nearest millimeter with a Disto A5 laser rangefinder. Azimuth was measured to the nearest 0.5° using a Suunto KB-14 Compass, and inclination was measured to the nearest 0.5° using a Suunto PM-5 Inclinometer. At each survey station, distances to the left and right wall, ceiling and floor were also measured with the Disto A5 laser rangefinder. While recording these data, a scaled and properly oriented sketch of the cave passage was made in a hand-held notebook, in which passage shape detail, sedimentary fills, flowstone and calcite decorations, and any other data of interest were plotted. Survey data were processed using the Compass and CaveXO software to generate plan and profile views of the cave. Particularly detailed sketches were made of the areas of the cave where fossils were found (Fig. 1B-C).

The bottom of this pit had been explored previously by miners and/or cavers, as indicated by footprints. Regrettably, some of the fossils had been stepped on and destroyed (Fig. 1D). To prevent further accidental damage, areas with visible fossils on the surface were marked with orange flagging (Fig. 1D). Using a Samsung S21FE camera and an iPhone 12 Mini, iOS version 15.5, fossils were imaged in situ together with a 1 cm scale ruler or with a 1-inch-wide orange flagging tape for scale.

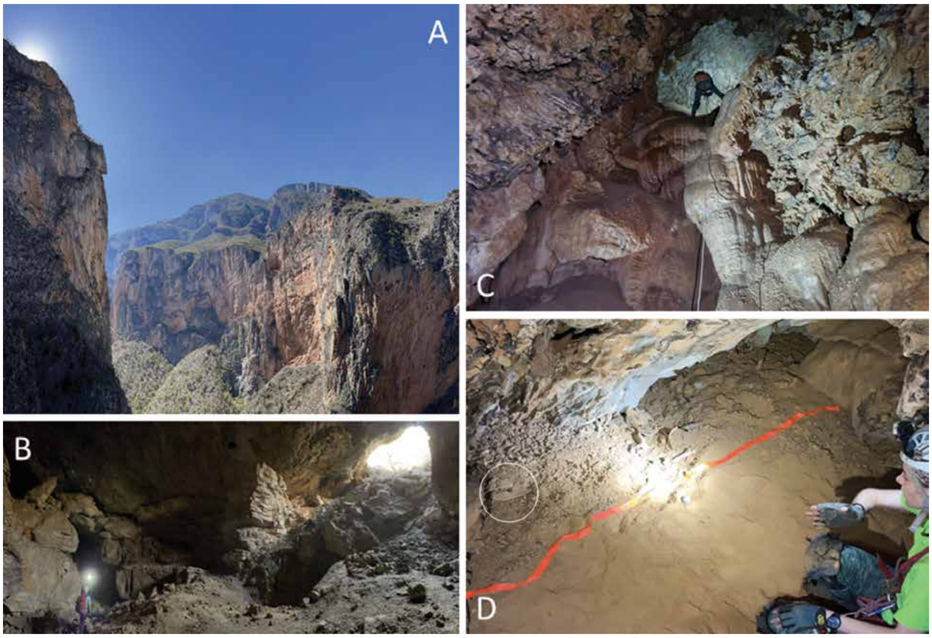


Figure 2. A; Barranco de Orduño canyon, where the cave is located. The entrance of the cave is behind the left clift. B; Entrance chamber. C; Sima de los Huesos pit. D; Assemblage of bones at the base of the pit. Circled in white is the skull of the ground sloth.

Visual inspection of the bones indicated that they were not permineralized or hardened in any way. Thus, they are extremely fragile and brittle. When fossils are disturbed, they turn easily into powdery dust (Fig. 1 E). Therefore, we decided to leave all bones in situ and no excavation was performed. Any future efforts to rescue the fossils will need to be done carefully, and the fossils will require considerable stabilization before they can safely be removed from the cave. The single exception was a claw of a ground sloth (Registered to the Instituto Nacional de Arqueología e Historia, Dirección de Registro Público de Monumentos y Zonas Arqueológicos e Históricos, Tramite INAH-03-001, No. de Oficio 401.3S.4-2023/1390), which was removed because it was on the ramp in the middle of the pit in a precarious position where it could easily be accidentally dislodged and destroyed. Also, it was not as fragile or brittle as most bones. This specimen was given the collection number CT-1 and is currently in the custody of the Sociedad Mexicana de Exploraciones Subterráneas A.C. (SMES).

Species identification from photographic material was done by H.G. McDonald, leading expert on fossil xenarthrans, and in particular, of fossil sloths from Mexican caves.

RESULTS

Cave description

The Barranco de Orduña is very steep with many vertical walls (Fig. 2A). The entrance of Cueva del Tesoro is perched a hundred meters above the floor of this canyon and 200 below the top of the cliff. It is difficult to access due to the steepness of the terrain. The main galleries of the cave have been extensively trampled by miners looking for the mineral cinnabar, to extract mercury. The cave has been mapped to 4,207 m and it has a single entrance. The 10 m wide entrance gives access to a large entrance chamber (Fig. 2B). Cave galleries follow. The first 170 m of passage is mostly flat and without obstacles. Ground sloths in the past and modern goats, whose skeletal remains are amply scattered throughout the cave, would have easily traversed its galleries. The exception is the Sima de los Huesos pit. After the initial flat 170 m of gallery, 105 m of which are in complete darkness, a pit adjoining one of the walls is abruptly encountered (Fig. 1B-C and 2C). Any animal traversing the cave could have stumbled into this unseen pit, making it a death trap. A mummified modern goat on the first step of the pit illustrates that this continues in the present. It is likely that the wide range of bones found in this pit are derived from a diverse array of mammals, ranging in age from the late Pleistocene to the Recent. Therefore, is an attritional, highly time-averaged sample.

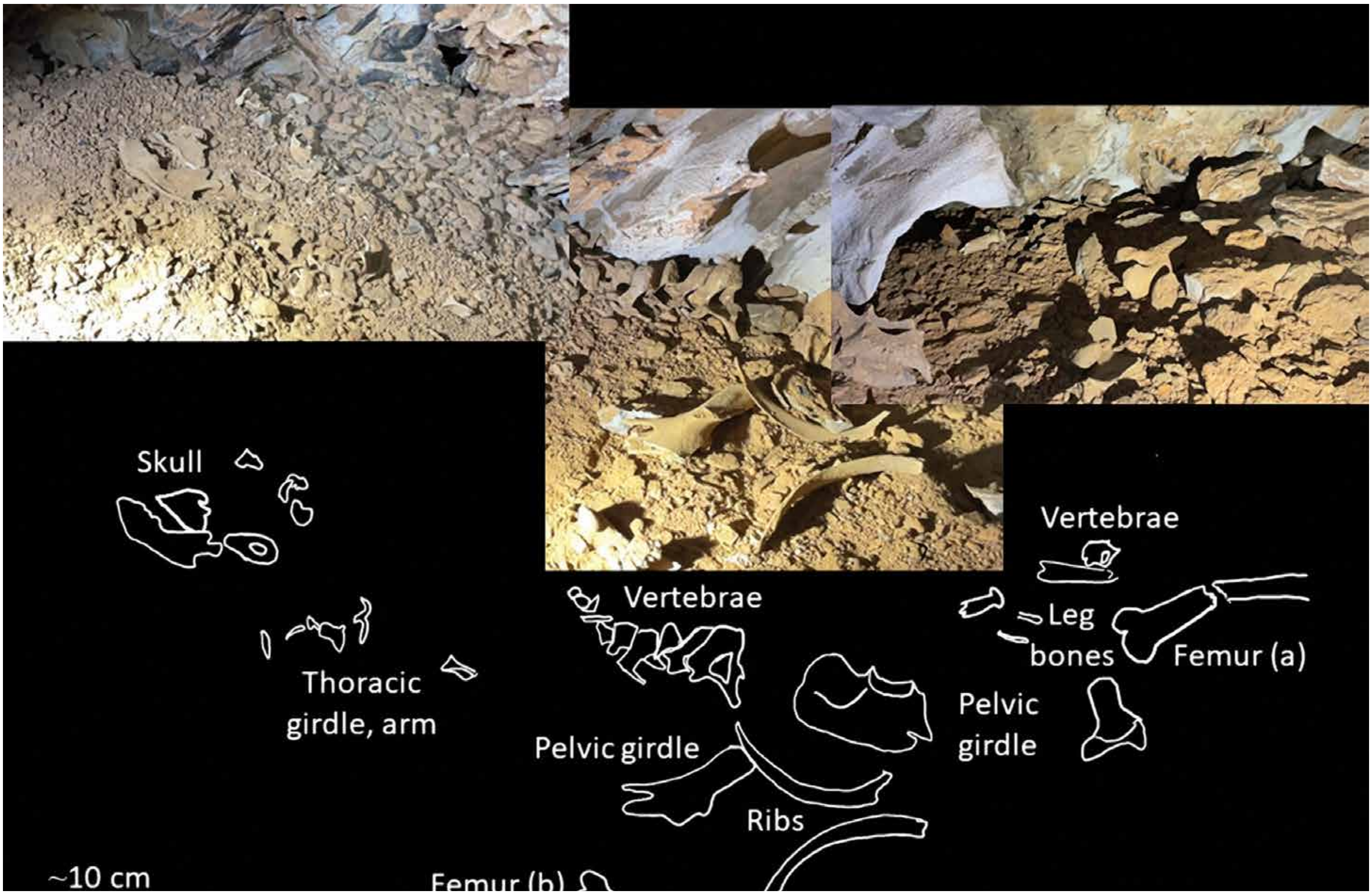


Figure 3. An almost complete skeleton of a ground sloth (Xenarthra) discovered at the bottom of the pit of Sima de lost Huesos. Bones are mostly in the position in which the animal laid when it died, when its skeleton was still articulated. In color (top) is a collage of photos showing bones in situ. In black and white (below) is a schematic representation of the above photo showing only the bones.

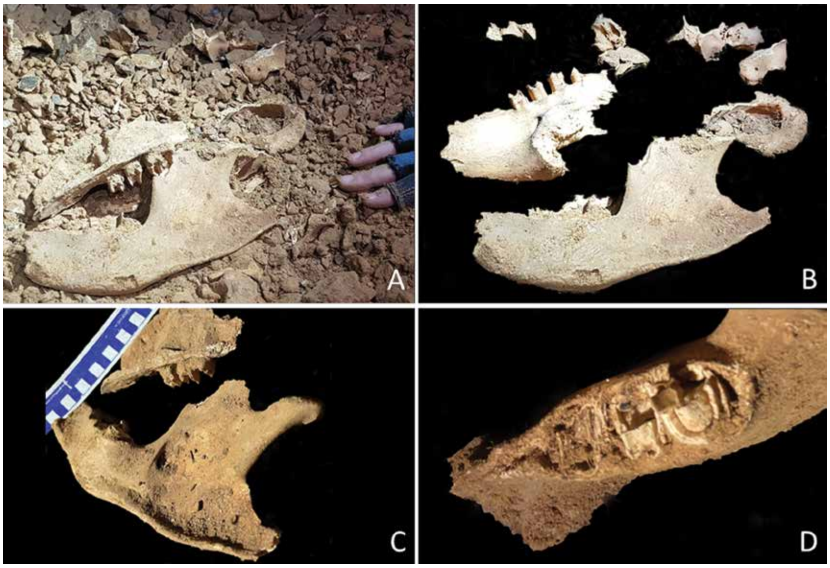


Figure 4. Cranium and mandible of ground sloth. A; Bones as preserved in situ. Left mandible, right internal side of maxilla, and fragments of skull are exposed. B; Bone fragments are isolated through photoshop for clarity. Maxilla and mandible shown in lateral view, with the former having been physically inverted, so that the dentition faces the top of the image and maxilla shows its external side. C; Left Mandible and right maxilla photographed from a different angle. Scale in centimeters. D. Occlusal view of left mandible showing fragments of the three molariform teeth.

It is likely that ground sloths would have gained access to the cave when the base of the canyon was not so deeply eroded. Vegetation growing in the canyon or on its walls at the time might also have allowed for easier access. A topographic map of the cave suggests it is extremely unlikely that in the past there was another entrance with a passage that gave easier access to the pit, because the cave transects perpendicular to the canyon walls, away from the cliff, and the top of the mountain plateau is 200 vertical meters above the entrance.

Field description of the deposits

At the bottom of the pit (Fig. 2C), a large assemblage of bones is present (Fig. 2D) and partially covered by gravel. Regrettably, some have been broken by falling rocks thrown into the pit by miners or by cavers descending into the pit. The main component of this bone assemblage is an almost complete skeleton of a ground sloth. Bones are mostly in the position in which the animal laid when it died, and its skeleton was still partially articulated (Fig. 3). The preserved remains of this individual includes the skull and mandible (Figs. 4-5), pectoral girdle and forelimb bones (Fig. 3), many vertebrae arranged as they were when articulated (Fig. 6A-B), pelvic girdle and ribs (Fig. 6C-D), and hindlimb bones (Fig. 7A-C). Some of the bones at the bottom of the pit belong to a different species of mammal. For example, there are two femurs (“a” and “b” in Fig. 3) of very different sizes, a small one (Fig. 6E) and a large one (Fig. 7C). The large one appears to belong to the nearly complete ground sloth skeleton.

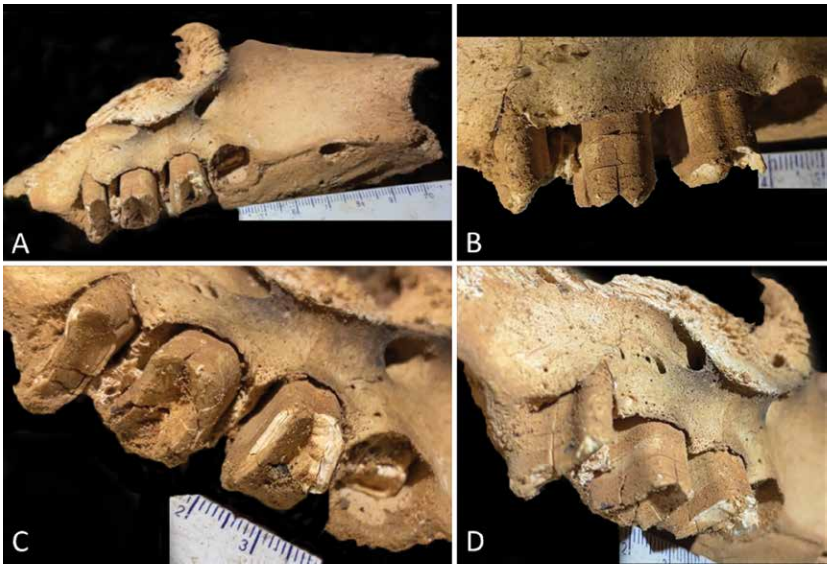


Figure 5. A; Right maxilla of ground sloth. B-D; Molariform maxillary teeth. in lateral (B), ventrolateral (C), and posteroventrolateral (D) views. Scales in centimeters and millimeters.

The skeleton was easily identified as belonging to a ground sloth because of its dental formula of 5/4 and its bilophodont molariform teeth (McDonald and De Iuliis, 2008; Gaudin and McDonald, 2008). The right maxilla has four molariform teeth and a socket for the caniniform tooth (Figs. 4B and 5). In the left mandible, the sockets for, and fragments of three molariform teeth, can be seen (Fig. 4D). Based on the photographic documentation and dental morphology in general, the sloth was identified as *Nothrotheriops shastensis* (McDonald and De Iuliis, 2008; Gaudin, 2004;). The presence of an alveolus for a caniniform is interesting but is atavistic and has been reported in *Nothrotheriops* before (McDonald, 1995), so it does not preclude the specimen from being assigned to *Nothrotheriops*.

Other bones could be found on the landing step and slope in the middle of the pit. Many of them are likely derived from modern goats. But there were other bones from larger animals. Regrettably, this landing step is where rocks and debris thrown in by miners landed when thrown into the pit. Rocks cover, and probably destroyed, most fossils. In this section of the cave, the 10 cm long claw of a ground sloth was also found (Fig. 7E). We assume it belongs to a second ground sloth whose remains are under the rocks and debris, with just a few fragments of the long bones showing between rocks.

On this landing step there is also at least the back of the skull and horns (Fig. 7D) of a *Bison sp.* (*Bison latifrons* or *Bison antiquus*?). From tip to tip, the horns measure about 40 cm. The skull is protected under a hollow at the side of the landing step, covered only by small pebbles, and luckily protected from the main destructive impact of rocks. We did not attempt to excavate it as it would still require considerable stabilization for its conservation.

The pit also preserves the remains of small vertebrates. Skulls and bones presumably from bats are included. They were not extracted for reasons mentioned before and no attempt at identification was made. Exoskeletons of beetles are also present. It remains to be determined if they are modern beetles, like those that can presently be found in the cave, or if they are the remains of insects that contributed to the decomposition of the ancient fauna.

Figure 6. A-D; Ground sloth. E; Femur of a smaller mammal. A-B; Aproximately nine vertebrae partially articulated and preserved in order. In B, several of the vertebrae have been isolated in Photoshop for clarity's sake in B, whereas in A they are photographed in situ. Also, in B thee thoracic vertebrae are shown in posteroventrolateral view, with the spinous processes facing the bottom of the image C; Pelvic girdle fragments. D; Pelvic girdle fragment and two ribs. E; Right femur of small mammal shown in posterior view.

DISCUSSION

Sloth remains from North American caves and associated karst features suggests they utilized caves in general (McDonald, 2003). The hypothesis that some ground sloths in Mexico passed part of their life in caves is supported by the findings of complete and articulated skeletons inside the cave systems of Quintana Roo (Stinnesbeck et al., 2021; McDonald et al., 2017). These articulated ground sloth skeletons discovered in deep parts of the caves, hundreds of meters from the nearest cenote entrance, suggest that these individuals died in situ and there was no secondary transport into the cave. The nearly complete and partially articulated skeleton found in Cueva del Tesoro further supports this notion. The location where the remains were found is 170 m from the entrance, well within the perpetual dark zone.

The topography of this cave likely enabled the accumulation of fossils over thousands of years, an inference confirmed by the presence of a sloth species that went extinct in North America at least 10,000 ybp at the end of the Pleistocene (McDonald, 2022). As noted above, any large mammal traversing the darkness of the cave could stumble into this unexpected death trap. It appears that at least two ground sloths, a large bovid, and many goats succumbed in this manner.

Remains of *Nothrotheriops* have been recovered from some 70 localities in the United States and Mexico (De Iuliis, 2015). They range in age from early Irvingtonian (ca. 1.7 Ma) to latest Rancholabrean (ca. 11Ma), with most records from the late Pleistocene (McDonald and Jefferson, 2008). The genus has two species; *N. texanus* and *N. shastensis*. Whereas both species have been described in the United States, the former is known from a single locality in Sonora, Northeast Mexico. On the contrary, *N. shastensis*' range extends throughout Mexico and as far south as Belize (De Iuliis et al., 2015). *Nothrotheriops shastensis* is commonly preserved in caves (McDonald, 2002; McDonald and Jefferson, 2008; McDonald et al., 2013). In Mexico, this species has been found in multiple caves including Bustamante Cave, Cerro de la Silla Cave, and San Josecito Cave in Nuevo Leon, Northeast Mexico, and La Presita Cave, in San Luis Potosi, Central Mexico (McDonald and Jefferson, 2008). San Luis Potosi is the neighboring state to Queretaro. To our knowledge, La Presita Cave, 200 km away, is the closest cave locality to Cueva del Tesoro with described remains of *N. shastensis*.

The small caniniform and the general dental morphology suggests that the Cueva del Tesoro articulated skeleton is a nothrotheriid sloth. Given the aforementioned biogeographic considerations, it supports the identification of the specimen as *N. shastensis*. Though *N. shastensis* has lost its caniniform, the tooth has been recorded in an early Pleistocene juvenile specimen of *N. texanus* (McDonald, 1995). Future studies may confirm that the specimen belongs to *N. shastensis* or may instead indicate that it pertains to some other nothrotheriid that retains the caniniform.

Recent revisions of the phylogenetic relationships of sloths based on DNA (Delsucet al., 2019) and palaeoproteomics (Presslee et al., 2019) have elucidated the broader relationships among sloths. Although these studies are important, sloth phylogeny is hardly a settled matter. The limited number of fossil specimens that preserve DNA or proteins means that resolution of the relationships for most sloth taxa will still have to be based primarily on morphology to determine the phylogenetic

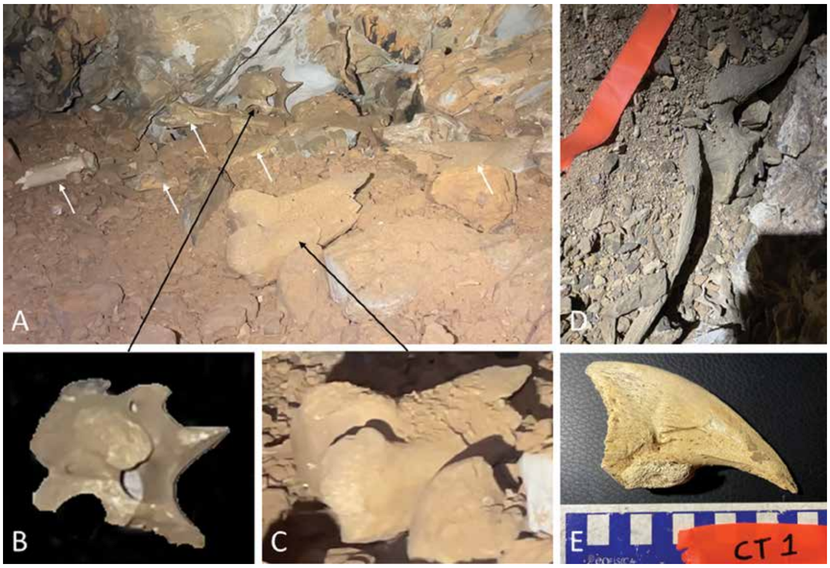


Figure 7. A-C; Bones of ground sloth at the bottom of the pit. D-E; Remains found on the first step and ramp in the middle of the pit. A; Arrows point at sloth remains predominately from hind limbs. Black arrows point at a cervical vertebra (B) and large femur (C). D; Skull and horns of a bovid. E; Claw of a ground sloth shown in lateral view. CT-1 Sociedad Mexicana de Exploraciones Subterráneas (SMES).

relationships of members of the clade in South, North, and Central America, as well as the Antillean taxa (McDonald et al., 2020). The relevance of the new discovery at Cueva del Tesoro lies in the completeness of the skeleton. Many studies rely on fragmentary material, such as fragmentary skulls with little to no associated other skeletal parts. The opportunity provided by having most of the skeleton of a single individual preserved will be of great value for comparative morphological and taxonomic studies.

Many interesting studies remain to be performed at this locality. Unfortunately, while the stable temperature and dry conditions have enabled the preservation of these bones over thousands of years, the bones have also become extremely fragile and brittle. Any future efforts to recover the fossils will require considerable stabilization of the bones prior to their removal. In their eagerness to extract interesting new bones, future scientists will have to be cautious not to destroy these valuable fossils. Conservation should be the priority.

ACKNOWLEDGEMENTS

We thank H.G. McDonald for the species identification based on the photographic material, and for his valuable advice on the manuscript. Julie Raines and Jordi Espinasa for proof-reading, and Marist College for partially supporting field work.

REFERENCES

Arroyo-Cabrales, J., and Polaco, O.J., 2003, Caves and the Pleistocene Vertebrate Paleontology of México. *In* Schubert, B.W., Mead, J.I., and Graham, R.W., Eds., Ice age cave faunas of North America, Bloomington, Indiana, University Press and Denver Museum of Nature & Science, p. 273–291.

Bonilla Díaz, C., 2018, Paleoecología del Pleistoceno tardío en la Cueva La Presita (San Luis Potosí, México): México, Benemérita Universidad Autónoma de Puebla, Tesis de Licenciatura, 57 p.

Dasher, G., 1994, On Station: National Speleological Society, Inc., USA., 242 p.

Day, A., 2002, Cave Surveying: British Cave Research Association, Cave Studies Series 11, Great Britain, 40 p.

Delsuc, F., Kuch, M., Gibb, G.C., Karpinski, E., Hackenberger, D., Szpak, J.G., Martınez, J.G., Mead, J.I., McDonald, H.G., MacPhee, R.D.E., Billet, G., Hautier, L., and Poinar, H.N., 2019, Ancient mitogenomes reveal the evolutionary history and biogeography of sloths: Current Biology, v. 29, p. 2031–2042. https://doi:10.1016/j.cub.2019.05.043

Ellis, B., 1976, Surveying Caves, British Cave Research Association, Great Britain, 88 p.

Ferrusquía-Villafranca, I., Arroyo-Cabrales, J., Johnson, E., Ruiz-González, J., Martínez-Hernández, E., Gama-Castro, J., de Anda-Hurtado, P., and Polaco, O.J., 2017, Quaternary Mammals, People, and Climate Change: A View from Southern North America. *In* Monks, G.G., ed., Climate Change and Human Responses: A Zooarchaeological Perspective, Vertebrate Paleobiology and Paleoanthropology, New York, Springer, p. 27–67. https://doi:10.1007/978-94-024-1106-5_3

Gaudin, T.J., and McDonald, H.G., 2008, Morphology-based investigations of the phylogenetic relationships among extant and fossil xenarthrans. In: Vizcaíno, S.F., and Loughry, W.J., eds. The biology of the Xenarthra. Gainesville: University of Florida Press, p. 24–36.

Gaudin. T.J., 2004, Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence: Zoological Journal of the Linnean Society, v.140, p. 255–305.

McDonald, H.G., 1995, Gravigrade xenarthrans from the early Pleistocene Leisey Shell Pit lA, Hillsborough County, Florida: Bulletin of the Florida Museum of Natural History, v. 37(11), pp.245-373.

McDonald, H.G., 2002, Fossil Xenarthra of Mexico: a review. Avances en los estudios paleomastozoológicos: México, DF, Instituto Nacional de Antropología e Historia, Serie Arqueología, 227-248 p.

McDonald, H.G., 2003, Sloth remains from North American caves and associated karst features. pp. 1-16 in Schubert, B.W., Mead J.I., and Graham R.W. (eds.). Ice Age Cave Faunas of North America, Indiana University Press and Denver Museum of Nature and Science.

McDonald, H.G., 2022, Paleoecology of the extinct Shasta ground sloth, *Nothrotheriops shastensis*, (Xenarthra, Nothrotheriidae): The physical environment: Bulletin New Mexico Museum of Natural History and Science, v. 88, p. 33-43.

McDonald, H.G., Arroyo-Cabrales, J., Alarcón-Durán, I., and Espinosa-Martínez, D.V., 2020, First record of *Meizonyx salvadorensis* (Mammalia: Xenarthra: Pilosa) from the late Pleistocene of Mexico and its evolutionary implications: Journal of Systematic Palaeontology, v. 18(22), p. 1829-1851.

McDonald, H.G., Chatters, J.C., and Gaudin, T.J., 2017, A new genus of megalonychid ground sloth (Mammalia, Xenarthra) from the late Pleistocene of Quintana Roo, Mexico: Journal of Vertebrate Paleontology, v. 37(3), 14 pp., https://doi:10.1080/02724634.2017.1307206,

McDonald, H.G., and De Iuliis, G., 2008, Fossil history of sloths. In: Vizcaino. S.F., Loughry, W.J., eds. The biology of the Xenarthra. Gainesville: University Press of Florida, p. 39–55.

Polaco, O., and Butrón, L., 1997, Mamíferos pleistocénicos de la cueva La Presita, San Luis Potosí, México. *In* Arroyo-Cabrales. J., and Polaco, O.J., 1997, Homenaje al Dr. Ticul Álvarez, Instituto Nacional de Antropología e Historia, Colección Científica, p. 279-296.

Presslee, S., Slater, G.J., Pujos, F., Forasiepi, A.M., Fischer, R., Molloy, K., Mackie, M., Olsen, J.V., Kramarz, A., Taglioretti, M., Scaglia, F., Lezcano, M., Lanata, J.L., Southon, J., Feranec, R., Bloch, J., Hajduk, A., Martin, F.M., Salas Gismondi, R., Reguero, M., de Muizon, C., Greenwood, A., Chait, B.T., Penkman, K., Collins, M., and MacPhee, R.D.E., 2019, Palaeoproteomics resolves sloth relationships: Nature Ecology & Evolution, v. 3, p. 1121–1130. https://doi:10.1038/s41559-019-0909-z

Schubert, B.W., Mead, J.I. and Graham, R.W. eds., 2003, Ice Age Cave Faunas of North America. Indiana University Press.

Stinnesbeck, S.R., Stinnesbeck, W., Frey, E., Aviles Olguin, J., and González, A.G., 2021, *Xibalbaonyx exinferis* n. sp. (Megalonychidae), a new Pleistocene ground sloth from the Yucatán Peninsula, Mexico: Historical Biology, v. 33(10), p. 1952-1963.

David A. Hubbard, Jr. and Frederick Grady. PRIOVAC: a paleontological resource inventory of Virginia caves. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 246-264. DOI:10.4311/2024PA0114

PRIOVAC: A PALEONTOLOGICAL RESOURCE INVENTORY OF VIRGINIA CAVES

David A. Hubbard, Jr.[1C] and Frederick Grady[2]

ABSTRACT

An inventory of the paleontological resources in Virginia caves was initiated by the authors in 1996. Invertebrate and vertebrate fossil occurrences in Virginia were examined to understand the range and scope of fossils present in caves to aid in determination as to what should constitute cave significance in the documentation of paleontological resources for Virginia's Significant Cave List. This cave study reviewed previously known vertebrate fossil sites and new vertebrate and invertebrate fossil sites before focusing on vertebrate fossil occurrences and the evidence of how they came to be deposited. As part of the inventory, to address the question of the percentage of Virginia caves that are paleontologically significant, 229 Virginia caves were examined to identify 100 caves with exposed non-human bones and/or teeth. Thirteen of the 100 caves yielded extinct or significant extirpated taxa, including one determined to have been excavated by E.D. Cope in 1867. Thirteen percent of the 100 bone caves examined or 5.7 % of the 229 study caves were documented as paleontologically significant. A selection of vertebrate cave fossils were radiocarbon dated and ranged in age from 11,986 +/- 76 to 39,300 +/- 1100 YBP. Uranium-thorium dating at one site suggests the fossil were older than 300,000 years and may be older than 450,000 YBP, indicating the age of this bone deposit is Pleistocene (Irvingtonian). A total of 43 cave sites were documented as paleontologically significant in the inventory and reported in Appendix C. PRIOVAC was recognized as an NSS Project from 2001 through 2006 and progress talks were presented at NSS Conventions in 1995, 1997, 1998, 2000, 2001, 2002, 2006, 2007, and a version of this summary in 2023 with abstracts published in the NSS Journal of Cave and Karst Studies and talks at the UIS Congresses in 1997 (Switzerland), 2001 (Brazil), and 2009 (US) published as papers in the UIS Proceedings. This paper is a summary report on PRIOVAC and the first publication of some of the bone dates and the U-Th dates.

BACKGROUND

The Commission on the Conservation of Caves was established in 1978 as a result of legislation initiated by members of the Virginia Region of the National Speleological Society, who were alarmed by the accelerated deterioration and vandalism of Virginia caves. Governor John Dalton made 11 appointments to the Commission to "study all problems incidental to cave use, protection, and conservation in Virginia (Lera, 2009)." Two important recommendations of this Commission were to establish a permanent cave commission and to strengthen the original Virginia Cave Protection Act of 1966 (Lera, 2009).

The Virginia Cave Protection Act (VCPA) of 1979 made it unlawful to disturb or damage caves and their contents, including cave surfaces, speleothems, speleogens, sediments, cave life, archaeological, historical and paleontological materials. The Act also established the Virginia Cave Commission as a permanent, governor appointed body. A primary responsibility assigned to the Cave Commission was to develop and maintain a list of significant caves in Virginia. Under the leadership of Dr. John Holsinger, the Annotated List of Significant Caves and Karst Areas in Virginia was completed in April 1980 (Holsinger, 1980). The criteria by which caves were evaluated for inclusion in this list are characterized by 11 scientific, economic, and caver perspective attribute categories: Archeological, Biological, Depth, Economic, Esthetic, Geological, Historical, Hydrological, Paleontological, Length, and Recreational. The list is a way of recognizing the most important caves in the Commonwealth of Virginia and is also a key to understanding how to protect these important caves and their resources. From the more than 2500 known Virginia caves, the initial Significant Cave List included 220 caves, of which only 10 were recognized under criteria within the Paleontological Category (Appendix A).

A PALEONTOLOGICAL INITIATIVE

The need for what would become the Paleontological Resource Inventory of Virginia Caves (PRIOVAC) was recognized in 1994, while author Hubbard was sorting through information on Virginia caves for an update of the Significant Caves List for Virginia. Members of the Virginia Cave Commission (renamed Virginia Cave Board in 1985), Virginia Speleological Survey, and other Virginia cavers had successfully recognized and documented many categories of significance for Virginia caves since the creation of the Significant Cave List. The Virginia Cave Protection Act delegated the authority to issue permits to excavate paleontological materials to the Virginia Historic Landmarks Commission

---

[1] 140 Woodlake Dr. Charlottesville, Virginia 22901-1330

[C] Corresponding Author: arcdadave@gmail.com

[2] Deceased

and specified that such field investigations be carried out under supervision of the Commissioner of Archaeology of the Virginia Research Center for Archaeology and the Virginia Historic Landmarks Commission. Unfortunately, the law enacted to protect cave resources also inhibited some legitimate efforts to study these resources, especially paleontological resources under the supervision of archaeologists.

The subsequent April 1985 list (Holsinger, 1985) of 224 significant caves only included 12 caves documented with criteria within the Paleontological Category (Appendix B). Considering that 135 caves were listed with criteria within the Biological Category, Virginia caves appeared in need of additional paleontological studies. Renewed interest in the paleontological resources of Virginia caves was kindled by the discovery of bear remains in Island Ford Cave in Alleghany County. Local youth encountered the remains in 1991, while digging open a passage (Hubbard and Grady, 1997). The 1995 NSS Convention in Blacksburg, Virginia presented an opportunity to both showcase the significant Virginia cave resources known by speleologists, but also encourage cavers to identify and report previously unrecognized cave resources. A paper on the fossil bone sites in Virginia (Grady, 1995) was prepared for the Convention Guidebook. A convention talk on the paleontological resources in Virginia caves was presented (Hubbard, 1997). Two goals of the presentation were: 1) stimulate caver awareness of the types of paleontological materials found in caves, and 2) initiate an aggressive program for documenting paleontological significance in Virginia caves. The subsequent dialog about paleontological resources in caves stimulated a team approach for simultaneously a) collecting appropriately and identifying animal remains to document important fauna and b) seek additional evidence to better understand the processes by which these animal remains came to be deposited and exposed. The success of the 1995 NSS Convention presentations prompted author Hubbard, a process-oriented geologist with the Virginia geological survey, to reach out to the second author, Grady, a paleontologist with the Smithsonian Institution who was actively working with paleontological cave resources in West Virginia, to further the paleontological studies in Virginia caves.

PALEONTOLOGICAL COLLECTION PERMITS

After passage of the Virginia Cave Protect Act of 1979, members of the Virginia Cave Commission unsuccessfully attempted to move the authority to issue permits for excavation of paleontological materials in caves away from archaeological agencies. The Commonwealth of Virginia entered into a cooperative arrangement with The Nature Conservancy to create the Virginia Natural Heritage Program in 1986. In 1988, the Natural Heritage Program came under the direction of the Virginia Department of Conservation and Recreation, which also oversaw the Virginia Cave Board. With the passage of The Virginia Natural Area Preserves Act in 1989, the Natural Heritage Program was empowered to conserve Virginia's biodiversity through inventory, protection and stewardship. Henceforth the Natural Heritage Program oversaw the issuing of cave collection permits for biospeleological inventories, and, with concurrence of the Director of the Department of Historical Resources, also archaeological, paleontological, prehistoric, and historic features. Starting in 1990, the senior author was issued cave collection permits for biospeleological inventories of Virginia caves and, between 1992 and 1995, cave collection permits for disturbed archaeological materials for the NSS recognized Marginella Burial Cave Project. In 1994, the authors were finally successful in having a cave collection permit issued to author Grady for excavation of the Island Ford Cave bear, subsequently identified as the extinct giant short-faced bear *Arctodus simus* (Grady, 1997).

PALEONTOLOGICAL DEPOSITS IN VIRGINIA CAVES

Paleontology is the study of prehistoric life preserved as fossils. The caves of Virginia are mostly solutional caves developed in carbonate rocks deposited from the Cambrian to Mississippian. Caves represent an important setting for fossil records because the sheltered alkaline environments of some Virginia caves permit better long-term preservation of bone and teeth than most of Virginia's surface sediment environments. Fossil remains may include extinct species that are no longer living today, as well as extant species that are still living today. Some species may span multiple geologic periods and examples of living species known from the fossil record that still exist elsewhere due to climatic shifts and are known as extirpated species where they no longer occur. The depositional settings of cave fossils are diverse. An excellent illustration of many cave fossil settings is provided by Sutcliffe (1976) and a modified illustration is provided in Alcover (1992). Cave fossil settings include deposits in the carbonate rocks in which the caves are dissolved and may be exposed in the cave walls, ceiling or floor. Wash-in of animal remains may represent whole or fragmental remains transported by erosional processes into cave openings or entrances or paleo-entrances, that may subsequently become choked with sediment. Vertical entrances and drops within caves have fatally injured or trapped the overly curious or inattentive visitors. Some animals may have briefly fed or sheltered in caves or utilized caves as den sites for hibernation and/or rearing their young, while depositing remains of their prey and occasionally their young or themselves if they perished in their den. Some raptors, such as owls, have utilized the twilight zones of caves as roosts, transporting prey into caves and sometimes harvesting cave bats and depositing bone bearing pellets. Woodrats gather food and nest materials from outside of caves into their middens, which often include mineral rich bones, teeth and other items that preserve tooth gnaw marks (Andrews, 1990; Schubert and Mead, 2019). Additional contributions can also result from other caves-using-animals such as bats, other rodents and birds, and salamanders.

Generally, cave sediments are stratigraphically deposited with the oldest sediments beneath younger sediments, such that remains of extinct or extirpated species are buried beneath younger sediments. Natural disruptions to this normal stratigraphic order that may expose older buried fossil bearing sediments include: burrowing animals and bear wallows, truncation and re-deposition by vadose waters, and stratigraphic mixing by deposition of transported ceiling passage sediments atop of floor sediments and erosion by epi-karstic waters. Human disruptions of sediment stratigraphy include mining for saltpetre (nitrates) and other materials, cave burials, and passage modifications for various other purposes, including cave commercialization, food storage, development of water supplies, and cave exploration.

PRIOVAC

The **P**aleontological **R**esource **I**nventory **O**f **V**irgini**A** **C**aves (PRIOVAC) began formally in early 1996. The inventory includes known and newly recognized paleontological resources. Both Grady and Hubbard were professional scientists and, in their spare time, cavers actively working to document cave resources. Grady mainly caved in West Virginia specializing in cave paleontology, whereas Hubbard primarily caved in Virginia working to document significant cave resources. The application for a cave collection permit to collect exposed non-human bone, teeth, and other fossil material from Virginia spelean environments for a paleontological inventory of the caves of the Commonwealth of Virginia was submitted on 23 January 1996. After numerous discussions of concerns about avoiding disturbances of archaeological resources, the cave collection permit was issued 1 November 1996.

Over a decade earlier, author Grady worked with fellow Smithsonian paleontologist Dr. Ralph Eshelman in a compilation of the “Quaternary vertebrate localities of Virginia and their avian and mammalian fauna.” They were invited to present their work at the Symposium on the Quaternary of Virginia in 1984. Eshelman and Grady (1986) documented 77 Virginia localities, of which 28 were cave or karst features that had yielded a record of an extinct or significant extirpated taxon. This work provided the bulk of the known cave paleontological resources to assess under PRIOVAC.

Because Hubbard was actively mapping the karst of southwestern Virginia and Grady was working in the Paleobiology Department in the Smithsonian Institution, the plan was for Hubbard to sample exposed paleontological deposits in caves and other karst environments and document the nature of the deposits, and for Grady to provide the identifications of the remains. Grady and Hubbard would then revisit paleontological resources determined to be significant based on the taxon or depositional environment.

ABBREVIATIONS

AA - University of Arizona’s NSF Arizona Accelerator Mass Spectrometry Laboratory, Tucson, Arizona.
CM – Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
MM - McMaster University, Hamilton, Ontario, Canada
USFS – United States Forest Service
USNM – National Museum of Natural History, Smithsonian Institution, Washington D.C.
VMNH – Virginia Museum of Natural History, Martinsville, Virginia

PALEONTOLOGICAL RECORDS PRIOR TO PRIOVAC

As noted above, Eshelman and Grady’s (1986) work provided 28 cave or karst features that had yielded record(s) of extinct or significant extirpated vertebrate taxon, which are listed below. A number of these caves were visited to examine their paleontological deposits and their depositional setting or context and are underlined. See the following section - The Virginia Cave Significance Criteria for the Paleontology Category **-** for a discussion on paleontological significance. All reported identifications and classifications follow the original publications.

Back Creek Caves No. 1 and 2, Bath County; Eshelman and Grady’s No.s 3 and 4 are actually rock shelters containing deposits dated as Late Pleistocene/early Holocene based on faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance include the records of the extinct peccary *Mylohyus* sp. (No. 1), and significant extirpated taxa: arctic shrew *Sorex arcticus* (No. 2), chipmunk *Tamias* (formerly *Eutamias)* sp. now *Tamias* sp. (No. 2), thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus*) *tridecemlineatus* (No.s 1 & 2), heather vole *Phenacomys intermedius* (No.s 1 & 2), yellow-cheeked vole *Microtus xanthognathus* (No.s 1 & 2), northern bog lemming *Synaptomys borealis* (No.s 1 & 2) (Guilday et al., 1977; Jones et al., 1984; Carnegie Museum of Natural History (CMNH) collection data; McDonald et al., 1998).

Clarks Cave, Bath County, Eshelman and Grady’s No. 11 has deposits from the Late Pleistocene based on the faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the first Virginia record of the extinct dire wolf *Aenocyon* (formerly *Canis)* cf. *C. dirus* and the significant extirpated taxa: Arctic shrew *Sorex arcticus*, New England cottontail *Sylvilagus transitionalis*, least chipmunk *Tamias* (formerly

Eutamias) *minimus*, thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus) tridecemlineatus*, heather vole *Phenacomys intermedius*, yellow-cheeked vole *Microtus xanthognathus*, northern bog lemming *Synaptomys borealis*, ermine *Mustela erminea* (Guilday et al., 1977; Jones et al., 1984; Grady, 1995; McDonald et al., 1998).

Darty Cave, Scott County, Eshelman and Grady's No. 17 has deposits from the Late Pleistocene based on the faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological importance includes the records of the significant extirpated heather vole *Phenacomys* sp. and caribou *Rangifer tarandus* (CMNH collection data; McDonald et al., 1998).

Earlys Cave (aka Earlys Pit), Wythe County, Eshelman and Grady's No. 20 has deposits from the Mid Pleistocene based on the faunal assemblage. Paleontological significance includes the records of the extinct ground sloth *Megalonyx* cf. *M. jeffersonii*, extinct complex-toothed horse *Equus* cf. *E. complicatus*, extinct tapir *Tapirus* sp. and extinct long-nosed peccary *Mylohyus* sp. (Cope, 1869a and b; Hay, 1923, Guilday, 1962a; Jones et al., 1984; Grady, 1995; McDonald et al., 1998). Note, the flat-headed peccary *Platygonus compressus* was mistakenly listed in Eshelman and Grady and is not found at this location.

Edinburg Fissure, Shenandoah County, Eshelman and Grady's No. 22 has deposits from the Late Pleistocene based on the faunal assemblage. Paleontological significance includes the records of the extinct tapir *Tapirus* sp., extinct peccary *Mylohyus* sp., extinct stag-moose *Cervalces* sp. and the extirpated yellow-cheeked vole *Microtus xanthognathus* (U. S. National Museum of Natural History (USNM) collection data; McDonald et al., 1998).

Eggleston Fissure, Giles County, Eshelman and Grady's No. 24 has deposits from the Late Pleistocene based on the faunal assemblage. Paleontological significance includes the records of the extirpated northern bog lemming *Synaptomys borealis*, and caribou *Rangifer tarandus* (CMNH collection data; McDonald et al., 1998).

Gardners Cave, Wythe County, Eshelman and Grady's No. 27 has deposits from the Late Pleistocene based on the faunal assemblage. Paleontological significance includes the record of the extinct peccary *Platygonus* sp. (Guilday, 1962b; USNM collection data; Grady, 1995; McDonald et al., 1998).

Gillespies Cliff Cave, Tazewell County, Eshelman and Grady's No. 28 has deposits of mixed Late Pleistocene and Holocene based on the faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the records of the extirpated yellow-cheeked vole *Microtus xanthognathus*, bog lemming *Synaptomys* sp. (CMNH collection data; McDonald et al., 1998).

Holston Vista Cave, Washington County, Eshelman and Grady's No. 30 has deposits from the Late Pleistocene/Holocene based on the faunal assemblage with owl roosts suggested as the possible depositional process. Paleontological significance includes the records of the extirpated arctic shrew *Sorex arcticus*, thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus) tridecemlineatus*, heather vole *Phenacomys* sp., yellow-cheeked vole *Microtus xanthognathus*, bog lemming *Synaptomys* cf. *S. borealis* (CMNH collection data; McDonald et al., 1998).

Jasper Saltpetre Cave, Lee County, Eshelman and Grady's No. 33 has deposits from the Mid Pleistocene based on the faunal assemblage. Paleontological significance includes the records of the extirpated pika *Ochotona* sp. and the northern bog lemming *Synaptomys borealis* (Guilday, 1979; Jones et al., 1984; CMNH collection data; Grady, 1995; McDonald et al., 1998).

Klotz Quarry Cave No. 5, Giles County, Eshelman and Grady's No. 35 has deposits from the Late Pleistocene based on the faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the records of the extirpated bog lemming *Synaptomys* sp. and caribou *Rangifer tarandus* (CMNH collection data; McDonald et al., 1998).

Lane Cave, Scott County, Eshelman and Grady's No. 37 has a deposit from the Late Pleistocene based on the occurrence of the extinct Jefferson's ground sloth *Megalonyx jeffersonii* (USNM 23734) (Holsinger, 1967; Grady, 1995; McDonald et al., 1998).

Loop Creek Quarry Cave, Russell County, Eshelman and Grady's No. 39 has deposits from the Late Pleistocene/early Holocene based on the faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the record of the extirpated ground squirrel cf. *Ictidomys* (*Spermophilus*) sp. and heather vole *Phenacomys* sp. (CMNH collection data; McDonald et al., 1998).

Luray Caverns, Page County, Eshelman and Grady's No. 40 produced a large cat specimen suspected to be from the Pleistocene. Hovey (1882) considered the remains to represent *Panthera* sp. or *Felis atrox* (now *Panthera atrox*), while McDonald et al. (1998) refers to this as the lion (*P. atrox*).

Meadowview Cave, Washington County, Eshelman and Grady's No. 41 has deposits from the Late Pleistocene based on the faunal assemblage. Paleontological significance includes the records of the extinct beautiful armadillo *Dasypus* cf. *D. bellus* and the extirpated heather vole *Phenacomys* sp. (Guilday and Parmalee, 1972; Jones et al., 1984; Klippel and Parmalee, 1984; CMNH collection data; McDonald et al., 1998).

Natural Chimneys Caves No. 1 & 2 (aka Brown's Cave and Cave of the Wooden Steps), Augusta County, Eshelman and Grady's No. 43 has deposits from the Mid Pleistocene based on the faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the records of the extinct giant beaver *Castoroides ohioensis*, extinct peccary *Mylohyus* sp. and significant extirpated taxa: arctic shrew *Sorex arcticus*, thirteen-lined ground squirrel *Ictidomys* (*Spermophilus*) *tridecemlineatus*, heather vole *Phenacomys* cf. *P. intermedius*, yellow-cheeked vole *Microtus xanthognathus*, northern bog lemming *Synaptomys borealis*, long-tailed weasel *Mustela* cf. *M. frenata*, and extralimital red squirrel *Tamiasciurus hudsonicus* (Guilday and Bender, 1960; Wetmore, 1962; Guilday, 1962b; Guilday and Parmalee, 1972; Jones et al., 1984; Fay, 1984; Anderson, 1984; Grady, 1995; McDonald et al., 1998).

Pembroke Railroad Cave No. 1, Giles County, Eshelman and Grady's No. 47 has a deposit from the Late Pleistocene based on faunal assemblage. Paleontological significance includes the records of the extinct peccary *Mylohyus* sp. and extinct fugitive deer *Sangamona*? sp. (CMNH collection data; McDonald et al., 1998).

Rass Hole (aka. Corbett's Cave), Highland County, Eshelman and Grady's No. 50 has a deposit from the Late Pleistocene based on the occurrence of the extinct peccary *Platygonus* sp. (CMNH collection data; McDonald et al., 1998).

Ripplemead Quarry Fissure, Giles County, Eshelman and Grady's No. 51 has deposits from the Late Pleistocene/Holocene based on faunal assemblage with owl roosts and natural accumulation recognized as the primary depositional processes. Paleontological significance includes the records of the extinct tapir *Tapirus* sp. and extinct peccary *Mylohyus* sp. (Weems and Higgins, 1977; Jones et al., 1984; Grady, 1995; McDonald et al., 1998).

<u>Skyline Caverns</u>, Warren County, Eshelman and Grady's No. 56 has a deposit from the Late Pleistocene based on faunal assemblage. Paleontological significance includes the record of the extinct peccary *Platygonus* sp. (USNM collection data; McDonald et al., 1998).

Strait Canyon Fissure, Highland County, Eshelman and Grady's No. 59 has deposits from the Late Pleistocene based on ^{14}C date of 29,870 +1800/-1400 yr B.P. with natural accumulation recognized as the primary depositional processes. Paleontological significance also includes the records of the extinct round-tailed muskrat *Neofiber leonardi*, extinct American mastodon *Mammut americanum*, extinct complex-toothed horse *Equus complicatus*, extinct Vero tapir *Tapirus* cf. *T. veroensis*, extinct long-nosed peccary *Mylohyus fossilis*, extinct woodland musk ox *Bootherium* (*Symbos cavifrons),* and the extirpated northern bog lemming *Synaptomys borealis*, heather vole *Phenacomys intermedius*, moose *Alces alces* (Guilday, 1982b; Jones et al., 1984; Fay, 1984; Anderson, 1984; CMNH and USNM collection data; Grady, 1995; McDonald et al., 1998, lists the musk ox as Harlan's Musk Ox *Bootherium bombifrons*).

Unknown, (cave ?), Clarke County, Eshelman and Grady's No. 63 is Late Pleistocene/Holocene based on faunal assemblage. Paleontological significance includes the record of the extirpated yellow-cheeked vole *Microtus xanthognathus* (USNM collection data; McDonald et al., 1998). Note: This record is included here with the addition of '(cave ?)' because author Grady recalls this material was encrusted with travertine indicative of a cave or karst environment.

Unnamed Cave, Smyth County, Eshelman and Grady's No. 65 has deposits from the Late Pleistocene/Holocene based on faunal assemblage. Paleontological significance includes the records of the extinct American mastodon *Mammut americanum* and extinct peccary *Platygonus* sp. (Radford University collection data; McDonald et al., 1998).

Vickers Cave, Washington County, Eshelman and Grady's No. 68 has deposits from the Pleistocene based on faunal assemblage. Paleontological significance includes the record of the extinct peccary *Platygonus vetus* (Guilday, 1971a; CMNH collection data; McDonald et al., 1998).

<u>Wills Cave</u> (aka Fraleys Cave), Washington County, Eshelman and Grady's No. 73 has deposits from the Late Pleistocene for records of the extinct tapir *Tapirus* sp. and peccary *Mylohyus* sp. (CMNH collection data; McDonald et al., 1998).

<u>Winding Stair Cave</u>, Scott County, Eshelman and Grady's No. 76 has deposits from the Late Pleistocene based on the records of the extinct tapir *Tapirus* sp. and extinct fugitive deer *Sangamona*? sp. (CMNH collection data; McDonald et al., 1998).

THE VIRGINIA CAVE SIGNIFICANCE CRITERIA FOR THE PALEONTOLOGY CATEGORY

All aspects of paleontological significance are of interest in documenting Virginia's Significant Caves. The Paleontological Category for significant caves and karst areas was defined as "caves that have yielded the skeletal remains of prehistoric animals and are thus important sites for fossil bone deposits; or caves containing pollen or old fills that can be dated and utilized as indicators of ancient climatic conditions or events (Holsinger, 1980)." As noted above, most of the Virginia caves are developed in carbonate rocks and many caves contain impressive arrays of the host rock invertebrate fossils displayed in ceilings, walls, floors, and specimens eroded from the limestone and secondarily concentrated in some cave sediments. Exceptional examples of host rock fossils may qualify as paleontologically significant and the listing of particular caves for the Paleontology Category. Studies of pollen or other plant material preserved in cave sediments also may qualify caves with exceptional records of past climatic biome documentation for the Paleontology Category listing. One of the ten caves listed for Paleontological significance in the 1980 List (Pig Hole, Appendices A & B) contains extensive ancient bat guano deposits. Ancient life is a key distinction in the qualification for the Paleontological Category with respect to the clause "ancient climatic conditions and events." A stratigraphic section of sediments preserving one or more magnetic reversals is geologically significant, but not necessarily paleontologically significant without reference to ancient life forms. Ancient climatic conditions defined by chemical signatures of sediments may qualify for the newer Atmospheric Category first recognized in 1997, but not necessarily the Paleontological Category. The original Paleontological Category definition referenced animal and plant evidence of ancient biome documentation, but neglected to include fungi, potist, and monera (bacteria) kingdom evidence, which may qualify as paleontologically significant.

Figure 1. In situ extinct *Mammuthus primigenius* lower third molar embedded in sediments in Endless Caverns.

The PRIOVAC project ultimately focused on the Pleistocene vertebrate fossils found in Virginia's caves. The presence of remains of one or more extinct vertebrate species constitutes a significant paleontological cave record with respect to the Virginia Significant Cave List. The finding of extirpated species remains in a cave is important for those species that now reside elsewhere due to climatic shifts and may also be considered paleontologically significant. Examples of extinct and extirpated species that disappeared from Virginia in the last couple centuries due to human impacts are not considered paleontologically significant in this work and include the extinct passenger pigeon *Ectopistes migratorius*, extirpated porcupine *Erethizon dorsatum*, extirpated grey wolf *Canis lupus*, and extirpated elk *Cervus elaphus*, unless those remains date as Pleistocene or older. Bison and black bear are two records that also are of interest paleontologically and records that date as Pleistocene or older may be considered significant. Trace fossil evidence such as bear wallows and large claw marks, which are indistinguishable between bear and large cats, are of interest paleontologically and those that date as Pleistocene or older may be considered significant.

SUPPLEMENTAL AND NEW PALEONTOLOGICAL FINDS IN VIRGINIA

Clarks Cave, Bath County, Eshelman and Grady's No. 11 is listed above; a PRIOVAC supplemental collection in May 1997 included 22 mammalian taxa, as well as several birds and snakes. Noteworthy fauna include the extirpated heather vole *Phenacomys intermedius*, extirpated yellow-cheeked vole *Microtus xanthagnathus*, and extirpated northern bog lemming *Synaptomys borealis* (mixed taxa USNM 609115).

Earlys Cave, Wythe County, Eshelman and Grady's No. 20 is listed above; contains remarkable evidence of Cope's (1869a, b) nineteenth century excavations and included pick and mattock marks through travertine layers and calcareous cemented sediment. Hay (1923) suggested these were Mid-Pleistocene deposits; however, considering Guilday's (1962) rejection of Cope's two new genera and five new species we believe these are Late Pleistocene deposits. PRIOVAC collections in June 1997 – May 1998 of these deposits included 18 taxa (including the extinct horse *Equus* sp.) from Earlys Cave (USNM 610270; Grady, 1992; Grady and Hubbard, 2000).

Earlys Pit, adjacent to the above cave is a separate site. PRIOVAC collections in June 1997 – May 1998 of these deposits, which we believe are Late Pleistocene, included the extinct horse *Equus* sp. (USNM 610271; Grady and Hubbard, 2000).

Endless Caverns, Rockingham County – In September 1996 caver/owner Wade Berdeaux recognized a tooth of the extinct wooly mammoth *Mammuthus primigenius* embedded in sediment in the non-commercial section of the cave and contacted the authors. The lower third molar (Fig. 1) was deposited by a debris flow through a former opening and exhibited only minor postmortem damage. The wear pattern indicates partial eruption and suggests the individual was in excess of 30 years in age at the time of death (Hubbard and Grady, 1997, 1999). The presence of a mammoth, a grazer, at this site, along the flank of Massanutten Mountain, may indicate the cave was overlain by a grassland or prairie habitat. Although there are other records of mammoth remains in Virginia, this is the first record from a cave (Grady et al., 1997). Approximately 110 m ESE from the historic entrance or approximately 85 m WNW from the former mammoth entrance, a bone excavated during commercial trail modifications was identified as the right humerus of the

Figure 2. Fred Grady with extinct *Arctodus simus* partial remains from Island Ford Cave at Smithsonian Institution in Chip Clark image.

flat-headed peccary *Platygonus compressus*; mixed taxa (USNM 610286) (Hubbard and Grady, 1997; site 81 in McDonald et al., 1998), but addition observation failed to locate addition remains of the peccary and evidence of a depositional context.

Island Ford Cave, Alleghany County - In 1991, NSS cavers Russ Carter, Dave Collings, and Tom Spina, with the help of the late Jack Hanner (a professor at Dabney S. Lancaster Community College) recovered an array of large bones that local youth had found digging open a passage approximately 220 m beyond the entrance. Subsequent excavations, under permit, yielded the partial skeleton of a giant short-faced bear *Arctodus simus* (USNM 521336) (Fig. 2). The remains were of a relatively small, but mature, adult and probably a female specimen (Grady, 1997; site 78 in McDonald et al., 1998). The individual may have died, possibly by drowning, during hibernation. Besides representing the first record of the species in Virginia, it appears to be one of the most complete specimens yet found (Hubbard and Grady, 1997). PRIOVAC investigators Hubbard and Grady attempted a radiocarbon bone date (AA45374) on a bone fragment of *A. simus*, but the sample contained insufficient collagen and only yielded a date of >29,000 YBP [AA45374]. Eventually, Dr. Blaine Schubert was able to date a tooth of *A. simus* from the cave as 34,080 +/-480 ^{14}C YBP (Grady and Schubert, 2007; Schubert, 2010 (Table 1). Based on a tip from Dr. Lynn Ferguson, Grady and Hubbard located a second bone matrix site (IF2a) that yielded an unerupted single tooth plate of a fetal extinct Mammoth *Mammuthus* sp.; remains of the extirpated thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus*) *tridecemlineatus*; extirpated vole *Phenacomys* sp.; extirpated prairie vole *Microtus* cf. *M. ochrogaster*; and extirpated yellow-cheeked vole *Microtus xanthognathus*. A ^{14}C date of 33,000 +/- 1,700 YBP [AA42514] was obtained from a bone fragment in IF2a. A third (IF2b) bone matrix site was initially thought to be a discontinuous segment of IF2a and yielded remains of the extirpated vole *Phenacomys* sp., but it subsequently dated older than IF2a: AA45375 yielded a ^{14}C date of 39,300 +/- 1,100 YBP. A fourth bone matrix site (IF3) yielded a molar of the extinct dire wolf *Aenocyon dirus*; remains of the extirpated thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus*) *tridecemlineatus*; extirpated heather vole *Phenacomys* sp.; extirpated prairie vole *Microtus* cf. *M. ochrogaster*. IF3 yielded a ^{14}C bone date of 11,986 +/-76 yr BP [AA45376] (Grady and Hubbard, 2009). Mixed taxa IF3 (USNM 610236).

Lane Cave, Scott County, Eshelman and Grady's No. 37 is listed above, the site where Jefferson's ground sloth *Megalonyx jeffersonii* was excavated (Holsinger, 1967). A large sliver of bone was found and collected from the sidewall of the sloth's excavation pit in a July, 1997 PRIOVAC supplemental collection. This fragment yielded a previously unpublished radiocarbon ^{14}C bone date of 28,700 +/-1000 YBP [AA42515].

Prince Albert Cave (Sugar Run System), Giles County - While the excavation of the giant short-faced bear *Artodus simus* in Island Ford Cave was underway, cavers Mike Ficco, Andrea and Mike Futrell made a paleontological discovery in a cave in Giles County. They found a fragmented tooth of the extinct American mastodon *Mammut americanum* (USNM 636277; Hubbard and Grady, 1997; site 79 in McDonald et al., 1998). The tooth was a lower third molar and was found in a fill of sandstone cobbles deposited by a sinking surface stream. The postmortem abrasion and damage to the tooth is significant and precludes a tooth-wear assessment of the age of the mastodon at the time of death.

Russells Reserve Cave, Bath County – In November of 2005, caver Phil Lucas approached us about a project cave with bear skulls and other skeletal remains. The other skeletal remains included the partial skull (Fig. 3) of a juvenile extinct tapir *Tapirus veroensis* (Graham and others, 2019; USNM 546112) and some of its post-cranial bones (Grady et al., 2006).

Winding Stair Cave, Scott County, Eshelman and Grady's No. 76 listed above, a PRIOVAC supplemental collection in March 1998 yielded the new record of an upper molar of Harlan's Musk Ox *Bootherium bombifrons* (Grady and Hubbard, 2001a; USNM 610272).

A PALEONTOLOGICAL EXPERIMENT: THE SEARCH OF 100 CAVES

The dominant motivation in forming PRIOVAC was to contribute to the paleontological knowledge of Virginia's caves, a category of significance with very little representation in the initial Virginia Significant Cave Listings of 1980 and 1985. We pondered the question of the percentage of known caves that have significant paleontological resources. The idea of searching 100 caves for paleontological significance was a start, except that our permit only allowed for collection of exposed, non-human, bone and teeth. Another complication was the nine-month delay in actually obtaining our permit; however, copies of Gilbert (1993) and Bass (1995) allowed the field inventory to begin, by osteological observation, rather than collection, through most of 1996. That goal of documenting 100 caves with exposed bone or teeth took five years and visits to 229 different Virginia caves to meet this goal.

Figure 3. In situ upside-down partial skull of a juvenile extinct *Tapirus veroensis*, above scale (in cm) and flagging tape, in Russells Reserve Cave in Phil Lucas image.

An elaboration on how the 229 caves were selected is related to the detail that simultaneous to the vertebrate collections, the living cave invertebrates were also collected in an otherwise unrelated biospeleological inventory. Cave selection included new caves found during karst mapping, known caves lacking a previous biospeleological inventory, and known caves with significant gaps in the known living invertebrate fauna. Bat and woodrat bones, as well as skeletal material still retaining flesh or fragmental bone without an epiphysis (terminal end), were considered inadequate to qualify a bone cave. Of those 100 bone caves, 13 yielded elements of extinct or significant extirpated vertebrate species and one historically known paleontologically significant cave was rediscovered. In simple statistical terms, 13 percent of the caves with exposed bones or teeth proved to be paleontologically significant and 5.7 percent of the 229 different caves, with or without exposed bone or teeth, were found to be paleontologically significant. This was a statewide survey rather than a localized study as the 100 caves were visited in 21 of the 27 karst counties of Virginia and the paleontologically significant caves were distributed over seven of the 27 karst counties.

Ten of these sites were newly recognized paleontological caves as follows:

Bush Handline Cave, Russell County, is a small cave about 18 m in length. A steep entrance slope yielded a tooth of the extinct Harlan's Musk Ox *Bootherium bombifrons* (USNM 610292; January 2000); probably a wash-in, but possibly a woodrat contribution to this Late Pleistocene deposit.

Campbell Cave, Wythe County, is 610 m long with stream and dry passages that were visited and mapped in conjunction with the Wythe County Cave Survey. An upper portion of an ulna of the extinct Leidy's peccary *Platygonus vetus* was collected in a paleo-stream passage (March 2000) along with horse *Equus* sp. (November 1999). The peccary element is Pleistocene in age and probably washed into the cave (USNM 610217).

Cedar Hill Cave, Rockingham County, Eshelman and Grady's No. 8 was not characterized as to age of the deposit and had no extinct or significant extirpated records in the USNM collections from its study, so is not listed above. In April 1999, – a partial tooth of an extinct musk ox *Bootherium* sp. (Grady and Hubbard, 2001a; USNM 636280) was collected; this record establishes that deposits associated with the entrance pit extend into the late Pleistocene.

Lost Lake Cave, Scott County, is a small cave previously used as a water source. A Late Pleistocene upper first or second molar of the extinct Vero tapir *Tapirus veroensis* (USNM 546116; May, 1997; Grady et al., 1998; site 83 in McDonald et al., 1998) was collected without a root, suggestive of possible transportation by a woodrat.

Melrose Caverns, Rockingham County, is a former commercial cave previously known as Virginia Caverns and Blue Grotto listed in McGill's (1933) Caverns of Virginia. An element of the extirpated heather vole *Phenacomys intermedius* was collected in March 2000. Subsequent surficial collections of the extirpated pocket gopher Geomys sp. and the extinct long-nosed peccary *Mylohyus fossilis* led us to request a permit to excavate a one by two-meter area of bone matrix in a wall niche. The site has yielded an assemblage of 47 vertebrate taxa including amphibians, fish, birds, reptiles, and mammals. The bone deposit appears to represent the den site of a small mammalian carnivore and possibly other contributors (Hubbard and Grady, 2001; USNM 610235). This Pleistocene aged deposit yielded the first Virginia record of the pocket gopher *Geomys* sp., an extirpated taxon that now lives in western, southwestern, and southern U.S. and the extirpated round tailed muskrat *Neofiber* cf. *N. alleni*, another form that now lives in the southern U.S. The Melrose fauna includes other extirpated forms that now live in the west: the prairie vole *Microtus ochrogaster* and the thirteen-lined ground squirrel *Ictidomys* (*Spermophilus*) *tridecemlineatus*; extirpated forms that now live in more northern areas: the heather vole *Phenacomys intermedius* and the northern bog lemming *Synaptomys borealis* and extinct long-nosed peccary *Mylohyus fossilis*. Another taxon of local significance is the hellbender salamander *Cryptobranchus alleghaniensis*, which is extirpated from the Potomac River Basin.

Figure 4. Cross sectioned 44 cm tall stalagmite with three marked locations for uranium-thorium dating of spar from Melrose Caverns fossil deposit.

The nearest *Geomys* sp. occurrence was a fossil record in New Trout Cave in Pendleton County, West Virginia. Lower levels of the New Trout Cave deposit date older than 30,000 years ago and contain *Geomys* sp. and *Cryptobranchus alleghaniensis*, but the yellow-cheeked vole *Microtus xanthognathus*, is not present. *Geomys* sp. and *Cryptobranchus alleghaniensis* have not been found in the upper levels of latest Pleistocene age, where the extirpated *Microtus xanthognathus* is relatively common (Grady and Hubbard, 2001b).

Two attempts to date the Melrose Caverns deposit failed when no collogen was found in the bone sample sent for AMS dating (AA40005; September 2000). A second bone date failed when too little collagen (0.18 %) was found in an AMS dating attempt (AA45377; October 2001). Subsequent excavation of the site fully exposed the base and then continued beneath the former location of an inactive stalagmite without changes in the taxa found. Both top and middle spar layers of the stalagmite had very low uranium but were uranium-thorium datable (Fig. 4). The top sample yielded an age of 373 +105/-54 ka and the middle sample an age of 382 +262/-72. These late Irvingtonian dates are previously unpublished and thought to represent the age of this significant bone matrix deposit.

Ruffners Cave No. 1, Page County, is the second largest cave in the county (Douglas, 1964: 350) and has two entrances. The 6 m pit entrance is the associated depositional setting for the Late Pleistocene lower canine and metatarsal elements of the extinct flat-headed peccary *Platygonus compressus* (Hubbard and Grady, 1997; February, 1996; site 80 in McDonald et al., 1998).

Slip Sliding Away Cave, Scott County, is a small cave with a 17 m slope – drop – slope entrance. A premolar of the extinct Vero tapir *Tapirus veroensis* (USNM 546115; March, 1997; Grady et al., 1998; site 82 in McDonald et al., 1998) could represent a wash-in or pit-fall environment for this Late Pleistocene site.

Starr Chapel Saltpetre Cave, Bath County is a large multi-mile long maze cave with a Pleistocene bone deposit based on faunal assemblage. Paleontological significance includes tooth fragments of the extinct American mastodon *Mammut americanum* (VMNH 121161); teeth of the extinct Vero tapir *Tapirus* cf. *T. veroensis* (VMNH 129850 and VMNH 129851); tooth of the extinct long-nosed peccary *Mylohyus fossilis* (VMNH 129852); tooth of the extirpated round-tailed muskrat *Neofiber* sp. (VMNH 121189); tooth of the extirpated pocket gopher *Geomys* sp. (VMNH 121077); a tooth fragment the caribou *Rangifer* cf. *R. tarandus* (VMNH 121156) documented by PRIOVAC collection data. The site was found during a mapping trip in September 1996 and confirmed on a subsequent Grady trip in July 1999 with the identification of a peccary tooth fragment and possible tapir tooth fragment. Collections were delayed until 2017 when US Forest Service permission and a Virginia cave collection permit were obtained. Further complications with curation specifications led to a shift in curation from the Smithsonian Institution to the Virginia Museum of Natural History in Martinsville, Virginia. The first publication of the initial surface collection, which remained cached in the cave for 18 years, plus shallow sampling of a one by two-meter area was reported in a poster at the 78th SVP meeting (Hastings, et al., 2018). The site remains under study.

Figure 5. Glove below molar fragment of an extinct *Mammut americanum* in Stewart Monk Cave.

Stewart Monk Cave, Russell County, is a small cave with a fissure entrance and sediment fills. A fragment of a molar (Fig. 5) of the extinct American mastodon *Mammut americanum* (USNM 610230) was collected in this Pleistocene wash-in site in April, 1999; a radiometric date was attempted on a fragment of the tooth root but failed when no collagen was found.

Unthanks Cave, Lee County, is a large cave with some steam passage that sumps closed for years at a time. The late caver Bill Keith had passed the Easter Pig Siphon and found a large leg bone protruding from a muddy streambed. Not knowing how long the siphon would remain open, he pulled the bone free of the mud and carefully padded and packed up the bone to move it beyond the sump area. The bone, a tibia, was found to be missing the proximal epiphysis (upper end) and was not identifiable. A September 1997 trip beyond the siphon relocated the site of the find and revealed the proximal end of the tibia, as well as the fragmental fibula, embedded in a gravel pocket in the limestone floor of the intermittent stream. The reassembled tibia and fibula (Fig. 6) were identified as from the extinct giant short-faced bear *Arctodus simus* (Hubbard and Grady, 2006; USNM 635774; site 84 in McDonald and others, 1998). A tibial spongy bone fragment yielded a previously unpublished radiocarbon ^{14}C bone date of 12,080 +/-130 YBP [AA40006].

Figure 6. Fred Grady holding reassembled tibia and fibula of an extinct *Arctodus simus* from Unthanks Cave.

Three additional paleontologically significant caves listed in the Supplemental and New Paleontological finds in Virginia section above were rediscovered during the 100 bone-cave search. They were known through literature and museum collections to Grady, but were unfamiliar to Hubbard during field work. An upper molar of the extinct Harlan's Musk Ox *Bootherium bombifrons* (USNM 610272) was collected in Winding Stair Cave in March 1997, after coaxing a nesting buzzard out of the entrance. This cave is also paleontologically significant for the occurrence of the extinct tapir *Tapirus* sp. and the extinct fugitive deer *Sangamona*? sp. documented by CMNM collection data noted in Eshelman and Grady (1986). Although not all consider buzzards raptors, the active nest, may suggest a raptor depositional context may have been viable in the past.

Earlys Cave contains remarkable evidence of Cope's (1869a, b) nineteenth century excavations and includes pick and mattock marks through travertine layers and calcareous cemented sediment; a single unerupted lower deciduous third or fourth premolar of the extinct horse *Equus* sp. was collected among 18 taxa (USNM 610270; Grady, 1992; Grady and Hubbard, 2000). Adjacent Earlys Pit contains similar paleontological deposits (USNM 610271; Grady and Hubbard, 2000) but without evidence of Cope's excavations. PRIOVAC collections in June 1997 – May 1998 of these deposits included the extinct horse *Equus* sp.

PRIOVAC DATING

Two different radiometric dating techniques were employed on PRIOVAC sites. Radiocarbon dating is the most economical of the two, but it can only date sites up to 50,000 YBP. A total of 10 bone and tooth specimens were submitted for ^{14}C dating in 2000-2001 through The University of Arizona's NSF Arizona Accelerator Mass Spectrometry (AMS) Laboratory. These specimens represent nine sites in six different caves. One sample was from historic times (Campbell Cave's horse), three samples failed to yield dates, but were believed older than 50,000 years based on the nature of these deposits (Stewart Monk Cave's Mastodon and two from Melrose Cave) and six sites in three caves were dated as late Pleistocene (Table 1). These six dates ranged from 11,986 +/- 76 [AA45376] to 39,300 +/- 1100 [AA45375] YBP and include previously unpublished dates for two extinct taxa: 12,080 +/- 1700 YBP [AA40006] for the Unthanks Cave giant short-faced bear *Arctodus simus* and 28,700 +/- 1000 YBP [AA42515] for the Lane Cave Jefferson's ground sloth *Megalonyx jeffersonii*. The Island Ford Cave giant short-faced bear *Arctodus simus*, would ultimately date older in Schubert's tooth date (34,080 +/-480 YBP; Grady and Schubert, 2007; Schubert, 2010) than our too low of collagen bone date of >29,900 YBP [AA45374].

Uranium-thorium dating of calcite formations assesses trace amounts of uranium precipitated from water and the radiometric decay products of the uranium. A calcite stalagmite that extended through 27 cm of the upper portions of the Melrose bone deposit was undermined and collected in the site excavation. The 44 cm by 6 to 7 cm speleothem was longitudinally sliced and spar sampled from basal, medial and top layers. U-Th dating by mass spectrometry was done through the McMaster University in Ontario, Canada (Table 2).

Table 1. PRIOVAC Radiocarbon Dates.

Sample #	Cave	Element	Submitted	% Collagen	δ13C	Date BP
AA37861	Stewart Monk Cave	Mammut tooth root	14-Apr-00	none	...	...
AA37862	Campbell Cave	Equus bone slice	14-Apr-00	...	-20.8	213 +34
AA40005	Melrose Caverns	bone fragment	15-Sep-00	none	...	...
AA40006	Unthanks Cave	Arctodus tibia spongy bone	15-Sep-00	2.38%	-19.2	12,080 +130
AA42514	Island Ford 2	bone fragment	5-Mar-01	?2.5%	-18.3	33,000 +1700
AA42515	Lane Cave	Megalonyx bone sliver	5-Mar-01	?1.3%	-21.5	28,700 +1000
AA45374	Island Ford 1A	Arctodus bone chip	4-Oct-01	0.70%	-18.8	>29,900
AA45375	Island Ford 2B	bone chip	4-Oct-01	...	-19.2	39,300 +1100
AA45376	Island Ford 3A	tooth root	4-Oct-01	...	-20.3	11,986 +76
AA45377	Melrose Caverns	snowshoe rabbit leg	4-Oct-01	0.18%	...	...

The age of the basal spar could not be determined accurately because the $230^{Th}/234U$ ratio was greater than 1.0, and suggestive of the presence of high detrital thorium. The very low basal U content was too low to allow the radiometric 230^{Th} signal to overwhelm the detrital 230^{Th} effects (Ford, 2002, pers. comm., 1 February 2002).

The two standard deviation error date margins are high because of the very low U content in all samples. The values of all three samples are similar, internally consistent and in proper stratigraphic order. The top and middle analyses allow us to conclude the formation is older than 300,000 years and may be older than 450,000 years (Ford, 2002, pers. comm., 28 February 2002).

DISCUSSION

The nature of the various paleontological resources found in Virginia caves and their characterization to document their level of significance is problematic. After examining various caves for significant host rock invertebrate fossils, Hubbard remained skeptical on how to document and differentiate significant examples. Sampling deposits of fossil shell lag for identification is more of a characterization of the fossil assemblage of a cave forming lithology. Many caves in Bath and Highland counties display impressive arrays of brachiopods and other invertebrate remains in Devonian and Silurian lithologies both *in situ* as wall, floor and ceiling displays and as weathered fossil shells in floor sediments. The differentiation of exceptional versus typical left us undecided. In contrast, a single cave in Lee County, displays up to two-inch long examples of an unidentified gastropod species weathered in relief like small hornet nests hanging from wall and ceiling rock that can be imaged for the documentation and is easily recognized as significant. Uncertain on how to justify examples of host rock invertebrate fossil displays as paleontologically significant, therefore, our project focused on documenting Pleistocene vertebrate fossils.

The Virginia karst, where the majority of our solutional caves occur, is a covered karst mantled by soils and unconsolidated sediments. Most caves in Virginia also contain accumulations of sediment that are typically stratigraphically layered with the youngest layers overlying older layers. The vertebrate fossil remains of extinct, extirpated, and extant fauna of late Pleistocene or earlier ages are usually buried under recent (Holocene) sediments less than 11,000 years old. We previously mentioned some of the natural disruptions to the normal stratigraphic order that can result in the exposure of older fossils, as well as human disruptions of sediment stratigraphy that may expose buried fossils. It is important to note that the sediments that overlay Pleistocene and older sediments are also important. These overlying sediments provide habitat for the invertebrate and many of the bacterial, fungal, and other fauna inhabiting the caves and may contribute to the understanding of the biological significance of the cave. Overlying sediments may also contain records of historic and prehistoric cave use.

Concerns by representatives of the Department of Historical Resources over potential damage to historic and prehistoric cave resources resulted in the nine-month delay in the issue of our primary study permit, restricting us to sampling only exposed non-human bone and tooth remains. With those concerns in mind, subsequent excavation permits were only requested when non-recent extinct taxon were found exposed in a bone matrix deposit. In caves elsewhere, human history may extend well into the Pleistocene potentially linking archaeological and paleontological interests in fossil bone sites.

Twilight-zone deposits of multiple species of small to medium sized vertebrates are typical of raptor roost sites. Dark zone deposits containing scores of vertebrate species typically are thought to characterize a den or lair site, unless the location is in a pit or beneath a former vertical or steep slope entrance. Most of these sites are probably very significant. In more than one of the caves

Table 2. PRIOVAC U-Th Dates

Sample	U content	234U/238U	230Th/234U	230Th/232Th	Age	Comment
Top	0.1143 ppm	1.1	0.999	82	372 ka +105/-54 ka	…
Middle	0.08 ppm	1.807	0.996	223	382 ka +262/-72 ka	…
Base	0.0744 ppm	1.132	1.649	38	could be >350 ka	230Th/234U >1.0

recognized in this paper, a single tooth record of an extinct species was recovered. Some finds can be characterized as a wash-in, erosional on a steep slope or possibly a woodrat contribution. In each of these cases, a cave contained a depositional environment that preserved remains of an identifiable extinct taxon. Even more importantly, because no excavation (other than to safely extract a partially exposed tooth) were performed at any of these single tooth sites, consequently we have no idea what other elements of the same species or others may remain buried *in situ*. Even in the cases where we suspect the tooth was transported by a woodrat based on the presence of gnaw marks, we have no idea how many other teeth or bone elements were cached and remain buried. Individual fossil evidence suggests peccaries, Jefferson's ground sloth and perhaps tapirs ventured beyond cave entrances into dark-zones, as do bears, porcupines and raccoons today. Individual teeth may have been transported within a cave by both biological agents (e,g;. woodrats) or nonbiological agents (i.e. erosional processes) within the cave. Our recognition of single tooth records of an extinct taxon as significant may be considered as tenuous by some, but they are paleontological records in an under investigated discipline within the cave sciences. If these occurrences were observed associated with any bone matrices suitable for excavation and clearly unrelated to historic or prehistoric human activities, permits would have been applied for as in three other sites documented herein.

It is interesting to note that the late Pleistocene date range of our ^{14}C dates 11,986 +/- 76 [AA45376] to 39,300 +/- 1100 YBP [AA45375] represent the range of dates over the four sites in Island Ford Cave. Initially we thought three of these sites represented erosional segments of a sprawling lair of the resident *Arctodus simus* or perhaps a short linage of multiple generations; however, dating revealed only one of these sites (2A, 33,000 +/-1700 YBP [AA42514]) is roughly contemporaneous with the bear (34,080 +/-480 YBP). The diversity of taxa found at these sites begs the question of what other predators contributed to these sites. The unidentified fish and amphibian taxa of these three bone matrix sites, curated in the Smithsonian Institution, potentially represent an interesting study of the aquatic vertebrate life, despite the prey bias, spanning over 40,000 years with comparison to the present vertebrate fauna inhabiting the adjacent Jackson River.

Because our work was limited to cave sites with exposed non-human bone and teeth, our study has only addressed the proverbial tip of the iceberg of the paleontological resources in only a few hundred caves. Based on the results of the 100 bone cave survey and the scarcity of cave paleontologists working within Virginia, we suspect the actual documentation of these resources will remain an order or two of magnitude underrepresented. Along with resource documentation, the conservation of cave resources is of importance. We still need to continue to recognize and document significant paleontological resources while respecting the significant ecosystems, as well as the archaeological resources associated with or adjacent to cave fossil deposits.

SUMMARY

The PRIOVAC project was initiated in 1996 to inventory known and newly recognized paleontological resources to contribute to a better understanding of the paleontological resources present in Virginia caves. Paleontological is one of the scientific, economic, and caver perspective attribute categories by which caves are evaluated for inclusion in Virginia's Significant Cave List. The list is a way of designating what the Virginia Cave Board and its designees consider the most important caves in the Commonwealth of Virginia and is also a key to understanding how best to protect these important caves. From its inception, the Significant Cave List was conceived to document our most important caves by recognition of their significance based on their scientific, natural and cultural attributes. From the more than 2500 known Virginia caves, the initial Significant Cave List from 1980 included 220 caves, of which only ten were recognized under the criteria within the Paleontological Category. Five years later, the Significant Cave List of 1985 included 224 caves, of which only 12 were recognized within the Paleontological Category. The PRIOVAC project considered the range of paleontological resources found in Virginia caves before focusing on Pleistocene vertebrate remains and documented the paleontological significance of seven of the ten caves in the 1980 listing and eight of the 12 caves in the 1985 listing mostly through the inventories of the known significant paleontological resources reported in Eshelman and Grady (1986).

With a series of cave collection permits, PRIOVAC investigators conducted field inventories of known and new paleontological resources in Virginia caves. The project considered the question of what percentage of Virginia caves contain significant paleontological resources. A plan to examine an additional 100 caves was modified considering the shift in the project focus to Pleistocene vertebrate remains and the limitation that cave collection permits only allowed sampling of exposed, non-human bones and teeth. A total of 229 caves were examined to identify 100 caves with exposed non-human bones and/or teeth, of which 13 yielded extinct or significant extirpated taxa, one of which was recognized as one studied by E.D. Cope in 1867. In other words, thirteen percent of the 100 bone caves examined or 5.7 % of all 229 caves revealed remains of paleontologically significant taxa.

In all, PRIOVAC documented the paleontological significance of the 28 cave sites reported in Eshelman and Grady (1986) along with another 15 paleontologically significant caves that are summarized in Appendix C of the Inventory of Cave and Karst Paleontological Resources. These 43 significant caves extend our knowledge in the Paleontology Category of cave significance to about one percent of the approximately 4,000 currently known Virginia caves.

Excavation permits were granted for one-to-two-meter areas of bone matrix sites in three caves with identified extinct and significant extirpated taxa, allowing the documentation of the very significant Pleistocene bone deposits in Island Ford Cave, Melrose Cave and Starr Chapel Saltpetre Cave (a U.S. Forest Service owned cave requiring a USFS permit).

Two different radiometric dating techniques were employed on nine sites in six different caves. Radiocarbon dating of six sites in three caves reveal they are Late Pleistocene in age and range from 11,986 +/- 76 [AA45376] to 39,300 +/- 1100 YBP [AA45375]. Four of these dates and this date range are from Island Ford Cave. All four sites were initially believed to represent isolated segments of a sprawling lair site of the Island Ford Cave giant short-faced bear *Arctodus simus*; however, radiocarbon dating revealed the actual bear remains and one of three distal bone matrix sites as roughly contemporary at 33,000 ±1700 YBP [AA42514].

Two other dates represent extinct taxa: 12,080 +/- 1700 YBP [AA40006] for the Unthanks Cave giant short-faced bear *Arctodus simus* and 28,700 +/- 1000 YBP [AA42515] for the Lane Cave Jefferson's ground sloth *Megalonyx jeffersonii*. Uranium-thorium dating of a 44 cm by 6 to 7 cm calcite stalagmite that extended through the upper 27 cm of the Melrose Caverns bone deposit yielded mid and upper formation spar dates of 382 ka +262/-72 ka and 372 ka +105/-54 ka, respectively and reveal much of this deposit, which extends well below the formation's base level, is older than 300,000 years and may be older than 450,000 YBP, dating this bone deposit as Pleistocene (Irvingtonian).

ACKNOWLEDGEMENTS

The PRIOVAC Project could not have been possible without the help of Larry Smith, now retired from the Virginia Department of Conservation and Recreation. Larry issued the cave paleontology collection permits and interfaced with the Virginia Department of Historic Resources. Funding for the PRIOVAC radiometric dates was facilitated by Stanley S. Johnson, former State Geologist and former head of the Virginia Division of Mineral Resources (now Virginia Energy's Geology and Mineral Resources Program). Mitzi deMartino of the NSF Arizona AMS Laboratory efficiently and cheerfully oversaw all communications, submissions and results for our ^{14}C dates. Dr. Derek Ford of McMaster University in Ontario, Canada expertly tested and explained the results of our speleothem uranium-thorium dating. The permitting for collections of the Starr Chapel Saltpetre Cave (SCSC) bone deposit probably would not have been issued without the intervention of Wil Orndorff (Virginia Natural Heritage Program), who subsequently became the principal permittee and assisted in the field work of the site. U.S. Forest Service personnel Steve and Carol Croy and Elizabeth McNichols facilitated SCSC permits and DWR wildlife biologist Rick Reynolds provided access to the SCSC key. Dr. Alexander Hastings facilitated the transition to the Virginia Museum of Natural History for the curation of the SCSC fossils and oversaw the identifications and reporting of the first two collections and assisted in the April 2017 collection. The late Dr Cliff Boyd, a human osteologist and co-permittee in the Marginella Burial Cave Project permits, accompanied us to Gardners Cave. Cavers Bill Keith, Paul Montgomery, Roddy Addington, Tom Spina, Phil Lucas, Dr. Lynn Ferguson, and Wade Berdeaux made significant contributions to the PRIOVAC project. Other cavers and folks who assisted with the Project include: Bob Alderson, Chris Alderson, Ted Andrews, Ron Anwarter, Pauline Apling, Gary Berdeaux, Jay Bird, Jeff Boarman, Kurt Buhlman. Ellen Burch, Russ Carter, Chip Clark, Todd Collier, Dave Collins, Mike Davis, Bob Denton, Nokie Faulkner, Katarina and Mike Ficco, Andrea Futrell, Mike Futrell, Jesse Giebell, John Graves, Jack Hanner, Don Harris, Scott Hesson, Robert Hicks, Chris Hobson, Bob Hoke, Gary Hoke, Dr. John Holsinger, Barry Horner, Linda Kingery, Benny Korsendorfer, Jim Logan, Tom Malabad, Andy Messer, Aaron Montgomery, Bill Murray, John Murray, Zenah Orndorff, Robert Peters, Chris Printz, Kimberly Smith, Mary Sue Socky, Greg Springer, Clay Stowers, John Taylor, Jimmy Thomas, Bob Thren, Janet Tinkham, Jim Washington, Trish Webb, Keith Wheeland, James Whisenhunt, and Joe Woodford. We are especially appreciative of the hundreds of cave owners who gave us permission to visit and sample their caves and made this study possible. We recognize the significant work of the late R.E. "Whitt" Whittemore, who collected bone matrix for many of the CMNH collections compiled by Eshelman and Grady (1986). Special thanks to Wil Orndorff, Dr. Blaine Schubert, Rick Toomey, Rodney Horrocks and Dr. Greg McDonald for reviewing this manuscript and their corrections and suggestions for its improvement.

This paper is dedicated to the memory of Dr. John R. Holsinger, a biospeleologist, who the authors consider as the Father of Virginia Speleology and to coauthor Fred Grady, who passed away prior to its submission for publication.

REFERENCES

Alcover, J.A., 1992, Fossils and Caves, *in* Camacho, A.I., ed., The Natural History of BioSpeleology, Monografias, Museo Nacional de Ciencias Naturales, p. 199-221.

Anderson, E., 1984, Review of the small carnivores of North America during the last 3.5 million years, *in* Genoways, H. H., and Dawson, M. R., eds., Contributions in Quaternary vertebrate paleontology: A volume in memorial to John E. Guilday: Carnegie Museum of Natural History, Special Publication 8, p. 257-266.

Andrews, P., 1990, Owls, Caves and Fossils, Natural History Museum Publications, London, 231 p.

Bass, W.M., 1995, Human osteology: A laboratory and field manual: Missouri Archaeological Society, Inc., Special Publication No. 2, 266 p.

Cope, E.D., 1869a, Synopsis of the extinct mammalia of the cave formations in the United States with observations on some Myriapoda found in and near the same, and on some extinct mammals of the caves of Anguilla, W. I., and of other localities: Proceedings of the American Philosophical Society, v. 11, p. 171- 192.

Cope, E.D., 1869b, Remarks on fossils from limestone caves of Virginia, Proceedings of the Academy of Natural Sciences of Philadelphia, v. 21, p. 3.

Douglas, H.H., 1964, Caves of Virginia: Virginia Cave Survey, Fall Church, Virginia, 761 p.

Eshelman, R.E. and Grady, F., 1986, Quaternary vertebrate localities of Virginia and their avian and mammalian fauna: Virginia Division of Mineral Resources, Publication 75, p. 43-70.

Fay, L.P., 1984, Mid-Wisconsinan and mid-Holocene herpetofaunas of eastern North America: A study in minimal contrasts, *in* Genoways, H.H. and Dawson, M.R., eds., Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday: Carnegie Museum of Natural History, Special Publications, v. 8, p. 14-19.

Gilbert, B.M., 1993, Mammalian osteology, Missouri Archaeological Society, Columbia, Missouri, 428 p.

Grady, F., 1992, More on Edward Drinker Cope's caving: Journal of Spelean History, v. 26, no. 1, p. 85-87.

Grady, F., 1995, Fossil bone sites in Virginia caves and karst, *in* Zokaites, C., ed., 1995 NSS Convention Guidebook, p. 179-181.

Grady, F., 1997, The first record of *Arctodus simus* from Virginia [abs.]: The Journal of Cave and Karst Studies, v. 59, no. 1, p. 58-59.

Grady, F., Baker, C., Hubbard, D.A., Jr., and Lucas, P., 2006, A Pleistocene tapir from a Virginia Cave [abs.]: The Journal of Cave and Karst Studies, v. 68, no. 3, p. 174.

Grady, F. and Hubbard, D.A., Jr., 2000, The Pleistocene fauna from Earlys Cave and Earlys Pit, Wythe County, Virginia [abs.]: The Journal of Cave and Karst Studies, v. 62, no. 3, p. 201.

Grady, F. and Hubbard, D.A., Jr., 2001a, The extinct muskox *Bootherium bombifrons* from caves in West Virginia and Virginia [abs.]: The Journal of Cave and Karst Studies, v. 63, no. 3, p. 117.

Grady, F. and Hubbard, D.A., Jr., 2001b, The Late Pleistocene fauna of Melrose Caverns, Virginia [abs.]: The Journal of Cave and Karst Studies, v. 63, no. 3, p. 117.

Grady, F. and Hubbard, D.A., Jr., 2002, The paleontological resource inventory of Virginia caves (PRIOVAC) is a new NSS Project [abs.]: The Journal of Cave and Karst Studies, v. 64, no. 3, p. 188-189.

Grady, F. and Hubbard, D.A., Jr., 2009, Fossil mammals from Island Ford Cave, Virginia, *in* Hubbard, D. and Hapka, R., eds., Archaeology and paleontology, Proceedings of the 15th International Congress of Speleology, Symposium Part 1, p. 86-89.

Grady, F., Hubbard, D.A., Jr., and Berdeaux, W., 1997, *Mammuthus primigenius* from Endless Caverns: The first cave record of a mammoth from Virginia [abs.]: The Journal of Cave and Karst Studies, v. 59, no. 3, p. 173-174.

Grady, F., Hubbard, D.A., Jr., and Holler, C., Jr., 1998, New finds of Pleistocene tapirs from Tennessee, Virginia, and North Carolina [abs.]: The Journal of Cave and Karst Studies v. 60, no. 3, p. 191.

Grady, F. and Schubert, B. W., 2007, A giant short-faced bear (*Arctodus simus*) from Island Ford Cave, Virginia [abs.]: The Journal of Cave and Karst Studies, v. 69, no. 3, p. 371.

Graham, R.W., Grady, F., and Ryan, T.M., 2019, Juvenile Pleistocene tapir skull from Russells Reserve Cave, Bath County, Virginia: Implications for cold climate adaptations. Quaternary International v. 530-531, p. 35-41.

Guilday, J.E., 1962a, Notes on Pleistocene vertebrates from Wythe County, Virginia: Annals of the Carnegie Museum v. 36, Art. 8, p. 77-86

Guilday, J.E., 1962b, The Pleistocene local fauna of the Natural Chimneys, Augusta County, Virginia: Annals Carnegie Museum, v. 36, Art. 9, p. 87-122.

Guilday, J.E., 1971, The Pleistocene history of the Appalachian mammal fauna, *in* Holt, P. C., ed., The distributional history of the biota of the southern Appalachians, part III, Vertebrates, Virginia Polytechnic Institute and State University, Research Division Monograph 4, p. 233-262.

Guilday, J.E., 1979, Eastern North American Pleistocene Ochotona (Lagomorpha: Mammalia): Annals Carnegie Museum, v. 48, Art. 24, p. 435-444.

Guilday, J.E., 1982, Dental variations in *Microtus xanthognathus*, *M. chrontorrhinus*, and *M. pennsylvanicus* (Rodentia: Mammalia): Annals Carnegie Museum, v. 51, Art. 11, p. 211-230.

Guilday, J.E. and Bender, M.S., 1960, Late Pleistocene records of the yellow-checked vole, *Microtus xanthognathus* (Leach): Annals of the Carnegie Museum, v. 35, p. 315-330.

Guilday, J.E. and Parmalee, P.W., 1972, Quaternary periglacial records of voles of the genus *Phenacomys* Merriam (Cricetidae: Rodentia); Quaternary Research, v. 2, p. 170-175.

Guilday, J.E., P.W. Parmalee, and Hamilton, H.W., 1977, The Clark's Cave bone deposit and the late Pleistocene paleoecology of the central Appalachian Mountains of Virginia: Bulletin, Carnegie Museum Natural History, v. 2, p. 1-87.

Hastings, A.K., D.A. Hubbard, Jr., F. Grady, R.G. Vodden and Khameiss, B., 2018, Newly collected material from Starr Chapel Cave reveals further presence of Pleistocene fauna in northwestern Virginia, USA: Society of Vertebrate Paleontology, 78th Annual Meeting, Albuquerque, New Mexico, Poster Session IV, B145.

Hay, O. P., 1923, The Pleistocene of North America and its vertebrated animals from the states east of the Mississippi River and from the Canadian provinces east of longitude 95 degrees. Carnegie Institution, Washington, Publication 322, 499 p.

Holsinger, J., 1967, Some bones and shields from a cave in SW Virginia: NSS News, v. 25, no. 11, p. 198-201.

Holsinger, J.R., 1980, Annotated list of significant caves and karst areas in Virginia, 55 p.

Holsinger, J.R., 1985, Annotated list of significant caves and karst areas in Virginia, 251 p.

Hovey, H. C., 1882, Celebrated American caverns: Especially Mammoth, Wyandot, and Luray. Robert Clark and Company, Cincinnati, 228 p.

Hubbard, D.A., Jr., 1997, Is this cave paleontologically significant? [abs.]: The Journal of Cave and Karst Studies, v. 59, no. 1, p. 59.

Hubbard, D.A., Jr. and Grady, F., 1997, Vertebrate paleontological cave resources in Virginia, USA, *in* Hapka, R. Proceedings of the 12th International Congress of Speleology, 10th-17th August, La Chaux-de-Fonds, Switzerland, v. 3, p. 175-177.

Hubbard, D.A., Jr. and Grady, F., 1999, Mammoth tooth found in Endless Caverns, Virginia: Virginia Minerals, v. 45, no. 1, p. 1-3.

Hubbard, D.A., Jr. and Grady, F., 2001, Melrose Caverns: A late Pleistocene vertebrate locality in Virginia, U.S.A, *in* Speleology in the third millennium: Sustainable development of karst environments: Proceedings of 13th International Congress of Speleology, Brasilia, July 15-22, Brazil, v. 1, p. 237-240.

Hubbard, D.A., Jr. and Grady, F., 2006, Let those bones be: Lessons in paleontological context at Unthanks Cave, Virginia [abs.]: The Journal of Cave and Karst Studies, v. 68, no. 3, p. 174-175.

Jones, C. A., Choate, J. R., and Genoways, H. H., 1984, Phylogeny and paleobiogeography of short-tailed shrews (genus *Blarina*), *in* Genoways, H. H., and Dawson, M. R., eds., Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday: Carnegie Museum of Natural History, Special Publication 8, p. 56-148.

Klippel, W. E., and Parmalee, P. W., 1984, Armadillos in North American late Pleistocene contexts, *in* Genoways, H. H., and Dawson, M. R., eds., Contributions in Quaternary vertebrate paleontology: A volume in memorial to John E. Guilday: Carnegie Museum of Natural History, Special Publication 8, p. 149-160.

Lera, T., 2009, The Virginia cave protection act: A review (1966 – 2009): The Journal of Cave and Karst Studies, v. 71, no. 3, p. 204-209.

McDonald, J.N., Eshelman, R.E., Grady, F., and Hubbard, D.A., Jr., 1998, The late Wisconsinan mammalian fauna of Virginia, *in* Linzey, D.W., The mammals of Virginia: The McDonald & Woodward Publishing Company, p. 331-350.

McGill, W.M., 1933, Caverns of Virginia: Virginia Geological Survey Bulletin 35, Richmond, Virginia, 187 p.

Schubert, B.W., 2010, Late Quaternary chronology and extinction of North American giant short-faced bears (*Arctodus simus*), Quaternary International v. 217, p. 188-194.

Schubert, B.W. and Mead, J.I., 2019, Paleontology of caves, *in* White, W.B., Culver, D.C, and Pipan, T., eds., Encyclopedia of caves, Academic Press, Third Edition, p. 794-805.

Sutcliffe, A. J., 1976, Cave paleontology, *in* Ford, T.D. and Cullingford, C.H.D., eds., The science of speleology: Academic Press, London, p. 495-520.

Weems, R. E., and Higgins, B. B., 1977, Post Wisconsinan vertebrate remains from a fissure deposit near Ripplemead, Virginia: National Speleological Society Bulletin 39, p. 106-108.

Wetmore, A., 1962, Birds, *in* Guilday, J.E., ed., The Pleistocene local fauna of the Natural Chimneys, Augusta County, Virginia: Annals Carnegie Museum, v. 36, no. 9, p. 87-122.

APPENDIX A

Significant Caves List of 1980: Caves of Paleontological Significance
Natural Chimneys Cave No. 1, Augusta County:
Natural Chimneys Cave No. 2, Augusta County:
Clarks Cave, Bath County: excavation of Pleistocene bone deposits
Pig Hole, Giles County: (?)
Salamander Cave, Giles County: Pleistocene bear remains reported
Gilley Cave, Lee County: excavated paleontologically in the late 1800's (under the name Ely Cave)
Jasper Saltpetre Cave, Lee County:
Lane Cave, Scott County: nearly intact ground sloth (*Megalonyx jeffersoni*) excavated
Vickers Cave, Washington County: Pleistocene bone deposit
Wills (Fraleys) Cave, Washington County:

APPENDIX B

Significant Caves List of 1985: Caves of Paleontological Significance
Natural Chimneys Cave No. 1, Augusta County:
Natural Chimneys Cave No. 2, Augusta County:
Black Oak Cave: Bath County:
Clarks Cave, Bath County: excavation of Pleistocene bone deposits
Pig Hole, Giles County:
Salamander Cave, Giles County: Pleistocene bear remains reported
Corbett Cave, Highland County:
Gilley Cave, Lee County: excavated paleontologically in the late 1800's (under the name Ely Cave)
Jasper Saltpetre Cave, Lee County:
Lane Cave, Scott County: nearly intact ground sloth (*Megalonyx jeffersoni*) excavated
Vickers Cave, Washington County: Pleistocene bone deposit
Wills (Fraleys) Cave, Washington County:

APPENDIX C

PALEONTOLOGICALLY SIGNIFICANT VIRGINIA CAVE AND KARST SITES

Back Creek Caves No. 1 and 2, Bath County, are actually rockshelters with Late Pleistocene/early Holocene deposits based on faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance include the record of the extinct peccary *Mylohyus* sp. (No. 1), and the significant extirpated taxa: arctic shrew *Sorex arcticus* (No. 2); chipmunk *Tamias* (formerly *Eutamias)* sp. now *Tamias* sp. (No. 2); thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus) tridecemlineatus* (No.s 1 & 2); heather vole *Phenacomys intermedius* (No.s 1 & 2); yellow-cheeked vole *Microtus xanthognathus* (No.s 1 & 2); northern bog lemming *Synaptomys borealis* (No.s 1 & 2). Eshelman and Grady's no.s 3 and 4 (1986).

Bush Handline Cave, Russell County, is a small cave about 18 m in length. The cave yielded a Late Pleistocene tooth of the extinct Harlan's musk ox *Bootherium bombifrons* (USNM 619292; PRIOVAC January 2000); a wash-in or woodrat primary depositional process is suspected.

Campbell Cave, Wythe County, is 610 m long with stream and dry passages that were visited and mapped in conjunction with the Wythe County Cave Survey. A Pleistocene upper portion of ulna of the extinct Leidy's peccary *Platygonus vetus* (USNM 610217; PRIOVAC March 2000) is probably due to a wash-in depositional process.

Cedar Hill Cave, Rockingham County, contains a Late Pleistocene/early Holocene deposit with the pit entrance being the primary depositional process. Paleontological significance is due to a partial tooth of an extinct musk ox *Bootherium* sp. (USNM 636280; PRIOVAC April 1999.

Clarks Cave, Bath County, has deposits known as Late Pleistocene based on faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the first Virginia record of the extinct dire wolf *Aenocyon* (formerly *Canis)* cf. *C. dirus* and significant extirpated taxa: Arctic shrew *Sorex arcticus*; New

England cottontail *Sylvilagus transitionalis*; least chipmunk *Tamias (formerly Eutamias) minimus*; thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus) tridecemlineatus*; heather vole *Phenacomys intermedius*; yellow-cheeked vole *Microtus xanthognathus*; northern bog lemming *Synaptomys borealis*; ermine *Mustela erminea*. Eshelman and Grady's no. 11 (1986).

Corbett's Cave, See RASS Hole

Darty Cave, Scott County, has deposits from the Late Pleistocene based on faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological importance includes the records of the extirpated heather vole *Phenacomys* sp.; caribou *Rangifer tarandus*. Eshelman and Grady's no. 17 (1986).

Earlys Cave and Earlys Pit, Wythe County, have deposits recognized as Late Pleistocene based on faunal assemblage. Paleontological significance includes the record of an extinct ground sloth *Megalonyx* cf. *M. jeffersonii*; extinct complex-toothed horse *Equus* cf. *E. complicatus*; extinct tapir *Tapirus* sp.; extinct peccaries *Mylohyus* sp. Eshelman and Grady's no. 20 (1986), supplemental PRIOVAC collections June 1997 – May 1998 included extinct horse *Equus* sp. (Earlys Pit; USNM 610271; and 18 taxa (including the extinct horse *Equus* sp.) from Earlys Cave USNM 610270). Earlys Cave is earliest known cave site professionally investigated (8 September 1867 by E.D. Cope) for paleontological resources in Virginia.

Edinburg Fissure, Shenandoah County, has deposits from the Late Pleistocene based on faunal assemblage. Paleontological significance includes the records of the extinct tapir *Tapirus* sp.; extinct peccary *Mylohyus* sp.; extinct stag-moose *Cervalces* sp. and the extirpated yellow-cheeked vole *Microtus xanthognathus.* Eshelman and Grady's no. 22 (1986).

Eggleston Fissure, Giles County, has deposits from the Late Pleistocene based on faunal assemblage. Paleontological significance includes the records of the extirpated northern bog lemming *Synaptomys borealis*; caribou *Rangifer tarandus*. Eshelman and Grady's no. 24 (1986).

Endless Caverns, Rockingham County, has deposits recognized as Late Pleistocene based on faunal assemblage. Paleontological significance includes the lower third molar of the extinct wooly mammoth *Mammuthus primigenius* deposited by a debris flow through a former opening; right humerus of the extinct flat-headed peccary *Platygonus compressus* (USNM 610286; caver sourced with PRIOVAC) of unknown depositional process.

Gardners Cave, Wythe County, has deposits from the Late Pleistocene based on faunal assemblage. Paleontological significance includes the record of the extinct peccary *Platygonus* sp. Eshelman and Grady's no. 27 (1986).

Gillespies Cliff Cave, Tazewell County, has deposits from the mixed Late Pleistocene and Holocene based on faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the records of the extirpated yellow-cheeked vole *Microtus xanthognathus*; bog lemming *Synaptomys* sp. Eshelman and Grady's no. 28 (1986).

Holston Vista Cave, Washington County, has deposits from the Late Pleistocene/Holocene based on faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the records of the extirpated arctic shrew *Sorex arcticus*; thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus*) *tridecemlineatus*; heather vole *Phenacomys* sp.; yellow-cheeked vole *Microtus xanthognathus*; bog lemming *Synaptomys* cf. *S. borealis*. Eshelman and Grady's no. 30 (1986).

Island Ford Cave, Alleghany County, has Late Pleistocene deposits based on ^{14}C dating and faunal assemblage. Paleontological significance includes partial remains of a short-faced bear *Arctudus simus* (USNM 521336) representing the first record of the species in Virginia and dated 34,080 +/-480 ^{14}C YBP. PRIOVAC investigations found three additional deposits: a bone matrix site (IF2a) dated 33,000 +/- 1,700 YBP [AA42514] and yielded a unerupted single tooth plate of a fetal extinct Mammoth *Mammuthus* sp.; extirpated thirteen-lined ground squirrel *Ictidomys* (formerly Spermophilus) *tridecemlineatus*; extirpated vole *Phenacomys* sp.; prairie vole *Microtus* cf. *M. ochrogaster*; and yellow-cheeked vole *Microtus xanthognathus*. A second bone matrix site (IF2b) dated 39,300 +/- 1,100 YBP [AA45375] and yielded remains of the extirpated vole *Phenacomys* sp. A third bone matrix site (IF3) dated 11,986 +/-76 YBP [AA45376] and yielded a molar of the extinct dire wolf *Aenocyon dirus* (the second record of this species from the state); extirpated thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus*) *tridecemlineatus*; vole *Phenacomys* sp.; prairie vole *Microtus* cf. *M. ochrogaster*; (mixed taxa IF3, USNM 610236; PRIOVAC).

Jasper Saltpetre Cave, Lee County, has deposits from the Mid Pleistocene due to the paleontological significant records of the extirpated pika *Ochotona* sp. and northern bog lemming *Synaptomys borealis*. Eshelman and Grady's No. 33 (1986).

Klotz Quarry Cave No. 5, Giles County, has deposits from the Late Pleistocene based on faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the records of the extirpated bog lemming *Synaptomys* sp.; caribou *Rangifer tarandus*. Eshelman and Grady's No. 35 (1986).

Lane Cave, Scott County, has a deposit from the Late Pleistocene for a record of the extinct Jefferson's ground sloth *Megalonyx jeffersonii* (USNM 23734); Eshelman and Grady's No. 37 (1996) sourced; 1997 PRIOVAC supplemental collection of a bone sliver yielded a previously unpublished radiocarbon ^{14}C bone date of 28,700 +/-1000 YBP [AA42515].

Loop Creek Quarry Cave, Russell County, has deposits from the Late Pleistocene/early Holocene based on faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the records of the extirpated ground squirrel cf. *Ictidomys* (formerly *Spermophilus)* sp.; heather vole *Phenacomys* sp. Eshelman and Grady's No. 39 (1986).

Lost Lake Cave, Scott County, a small cave yielded a Late Pleistocene upper first or second molar of the extinct Vero tapir *Tapirus veroensis* (USNM 546116; PRIOVAC May, 1997) possibly transported by a woodrat.

Luray Caverns, Page County, has a deposit suspected as Pleistocene ? for a paleontologically significant record of the extinct large cat *Panthera* sp. indet. or *Felis atrox* (now *Panthera atrox*). Eshelman and Grady's No. 40 (1986).

Meadowview Cave, Washington County, has deposits from the Late Pleistocene based on faunal assemblage. Paleontological significance includes the records of the extinct beautiful armadillo *Dasypus* cf. *D. bellus* and the extirpated heather vole *Phenacomys* sp. Eshelman and Grady's No. 41 (1986).

Melrose Caverns, Rockingham County, is a former commercial cave previously known as Virginia Caverns and Blue Grotto, has Pleistocene (Irvingtonian) deposits based on Uranium-thorium dating and a faunal assemblage from a den site of a small mammalian carnivore and possibly other contributors. Additional Paleontological significance includes the extinct long-nosed peccary *Mylohyus fossilis*; the first Virginia record of the pocket gopher *Geomys* sp., extirpated taxa that now live in western and southwestern U.S. and other extirpated forms that now live in the west: prairie vole *Microtus ochrogaster* thirteen-lined ground squirrel *Ictidomys* (formerly *Spermophilus*) *tridecemlineatus*; extirpated forms that now live in more northern areas: heather vole *Phenacomys intermedius* and the northern bog lemming *Synaptomys borealis*; the hellbender salamander *Cryptobranchus alleghaniensis*, which is extirpated from the Potomac River Basin (mixed taxa USNM 610235; PRIOVAC). A stalagmite based in and extending through upper portions of the deposit yielded upper and mid-level spar samples dated as 373 +105/-54 ka and 382 +262/-72 ka, respectively.

Natural Chimneys Caves No. 1 & 2 (aka Brown's Cave and Cave of the Wooden Steps), Augusta County, has deposits from the Mid Pleistocene based on faunal assemblage with owl roosts recognized as the primary depositional process. Paleontological significance includes the records of the extinct giant beaver *Castoroides ohioensis*; extinct peccary *Mylohyus* sp. and records of the significant extirpated taxa: arctic shrew *Sorex arcticus*; thirteenth-lined ground squirrel *Ictidomys* (formerly *Spermophilus*) *tridecemlineatus*; heather vole *Phenacomys* cf. *P. intermedius*; yellow-cheeked vole *Microtus zanthognathus*; northern bog lemming *Synaptomys borealis*; long-tailed weasel *Mustela* cf. *M. frenata*; extralimital red squirrel *Tamiasciurus hudsonicus* cf. *T. h. tenduidens*. Eshelman and Grady's No. 43 (1986).

Pembroke Railroad Cave No. 1, Giles County, has a deposit from the Late Pleistocene based on faunal assemblage. Paleontological significance includes the records of the extinct peccary *Mylohyus* sp.; extinct fugitive deer *Sangamona*? sp. Eshelman and Grady's No. 47 (1986).

Prince Albert Cave, Giles County, yielded the Late Pleistocene washed-in fragmental tooth of the extinct American mastodon *Mammut americanum* (USNM 636277; caver sourced with PRIOVAC), a lower third molar.

RASS Hole (aka. **Corbett's Cave**), Highland County, has a deposit from the Late Pleistocene based on a record of the extinct peccary *Platygonus* sp. Eshelman and Grady's No. 50 (1986).

Ripplemead Quarry Fissure, Giles County, has deposits from the Late Pleistocene/ Holocene based on faunal assemblage with owl roosts and natural accumulation recognized as the primary depositional processes. Paleontological significance includes the records of the extinct tapir *Tapirus* sp.; extinct peccary *Mylohyus* sp. Eshelman and Grady's No. 51 (1986).

Ruffners Cave No. 1, Page County, is the second largest cave in the county and has two entrances. The 20-foot pit-fall entrance is the depositional setting for the lower canine and metatarsal elements of the extinct Late Pleistocene flat-headed peccary *Platygonus compressus* (PRIOVAC February, 1996).

Russells Reserve Cave, Bath County, has Late Pleistocene deposits, which yielded the paleontologically significant remains of a juvenile extinct Vero tapir *Tapirus veroensis* (USNM 546112; caver sourced with PRIOVAC).

Skyline Caverns, Warren County, has a deposit from the Late Pleistocene based on faunal assemblage. Paleontological significance includes the record of the extinct peccary *Platygonus* sp. Eshelman and Grady's No. 56 (1986).

Slip Sliding Away Cave, Scott County, is a small cave with a Late Pleistocene wash-in or pit-fall occurrence of a paleontologically significant premolar of the extinct Vero tapir *Tapirus veroensis* (USNM 546115; PRIOVAC March, 1997).

Starr Chapel Saltpetre Cave, Bath County is a large multi-mile long maze cave with a Pleistocene bone deposit based on faunal assemblage. Paleontological significance includes remains of the extinct American mastodon *Mammut americanum* (VMNH 121161); extinct the Vero tapir *Tapirus* cf. *T. veroensis* (VMNH 129850 and VMNH 129851); extinct long-nosed peccary *Mylohyus fossilis* (VMNH 129852); and the significant extirpated round-tailed muskrat *Neo-*

fiber sp. (VMNH 121189); pocket mouse *Geomys* sp. (VMNH 121077); caribou *Rangifer* cf. *tarandus* (VMNH 121156). PRIOVAC collections.

Stewart Monk Cave, Russell County, is a small cave with a fissure entrance and sediment fills. The cave yielded a paleontologically significant Pleistocene fragment of a molar of the extinct American mastodon *Mammut Americanum* (USNM 610230; PRIOVAC April 1999).

Strait Canyon Fissure, Highland County, has deposits from the Late Pleistocene based on ^{14}C date of 29,870 +1800/-1400 YBP with natural accumulation recognized as the primary depositional processes. Paleontological significance also includes the records of the extinct round-tailed muskrat *Neofiber leonardi*; extinct American mastodon *Mammut americanum*; extinct complex-toothed horse *Equus complicatus*; extinct Vero tapir *Tapirus* cf. *T. veroensis*; extinct long-nosed peccary *Mylohyus fossilis*; extinct woodland musk ox *Bootherium* (formerly *Symbos cavifrons*) *bombifrons*; and records of the significant extirpated northern bog lemming *Synaptomys borealis*; heather vole *Phenacomys intermedius*; moose *Alces alces*; McDonald et al. (1998) list the musk ox as Harlan's Musk Ox *Bootherium bombifrons.* Eshelman and Grady's No. 59 (1986).

Unknown, (cave ?), Clarke County, is Late Pleistocene/Holocene based on faunal assemblage. Paleontological significance includes the record of the extirpated yellow-cheeked vole *Microtus xanthognathus.* Eshelman and Grady's No. 63 (1986). Note: This record is included here with the addition of '(cave ?)' because Grady recalled this material was encrusted with travertine indicative of a cave or karst environment.

Unnamed Cave, Smyth County, has deposits from the Late Pleistocene/Holocene based on faunal assemblage. Paleontological significance includes records of the extinct American mastodon *Mammut americanum*; extinct peccary *Platygonus* sp. Eshelman and Grady's No. 65 (1986).

Unthanks Cave, Lee County, is a large cave with some stream passage that sumps closed for years at a time and contained a Late Pleistocene ^{14}C dated occurrence of the paleontologically significant extinct giant short-faced bear *Arctodus simus* (USNM 635774; caver sourced with PRIOVAC September, 1997), a spongy bone fragment of the tibia yielded a ^{14}C bone date of 12,080 +/-130 YBP [AA40006].

Vickers Cave, Washington County, has deposits from the Pleistocene (Illinoian?) based on faunal assemblage. Paleontological significance includes the record of the extinct peccary *Platygonus vetus*. Eshelman and Grady's No. 68 (1986).

Wills Cave, Washington County, has deposits from the Late Pleistocene for records of the extinct tapir *Tapirus* sp.; peccary *Mylohyus* sp. Eshelman and Grady's No. 73 (1986).

Winding Stair Cave, Scott County, has deposits from the Late Pleistocene based on the records of the extinct tapir Tapirus sp.; extinct fugitive deer *Sangamona*? sp. Eshelman and Grady's No. 76 (1986). A PRIOVAC supplemental collection yielded an upper molar of the extinct Harlan's musk ox *Bootherium bombifrons* (USNM 610272; March, 1998) and an active buzzard nest at the time of this collection may suggest a viable raptor depositional context in the past.

Gary S. Morgan and Nicholas J. Czaplewski. The North American fossil record of bats (Mammalia: Chiroptera) from cave and karst deposits. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 265-313. DOI:10.4311/2024PA0116

THE NORTH AMERICAN FOSSIL RECORD OF BATS (MAMMALIA: CHIROPTERA) FROM CAVE AND KARST DEPOSITS

Gary S. Morgan[1,C] and Nicholas J. Czaplewski[2]

Abstract

Bats are the group of mammals most closely associated with caves. More than half of the 45 living species of bats from temperate North America (NA) are cave-dwellers in the families Vespertilionidae, Molossidae, Phyllostomidae, and Mormoopidae. Bats that inhabit caves also die in caves, leaving their skeletons to become preserved in fossil deposits on the cave floor. During the latter half of the Pleistocene epoch (~10 ka to 1 Ma), bats have an excellent fossil record in NA caves, primarily vespertilionids of extant species. We recognize only two extinct species of vespertilionids, *Myotis rectidentis* (late Pleistocene) and *Corynorhinus alleganiensis* (middle Pleistocene). Two other extinct bats are known from late Pleistocene cave deposits in the US: a large vampire, *Desmodus stocki* (Phyllostomidae), in 8 caves in the southern US, 4 in Mexico, and 6 karst deposits in Florida, and the extinct mustached bat, *Pteronotus pristinus* (Mormoopidae) of Cuba, but is also known from a karst deposit in Florida. The record of bats from late Pleistocene cave deposits in Mesoamerica consists of 11 caves in Mexico and 1 in Belize. The only other extinct Pleistocene bat in Mesoamerica besides *Desmodus stocki* is the giant vampire, *D. draculae*, known from Loltún Cave in Mexico and Cebada Cave in Belize. A diverse fauna of Quaternary bats is known from several hundred cave deposits across the West Indies, including more extinct species (eight) than are found in Pleistocene deposits in continental NA: six extinct species from Cuba, *Pteronotus pristinus* and *Mormoops magna* (Mormoopidae; also known from Hispaniola) and *Artibeus anthonyi*, *Cubanycteris silvai*, *Phyllops silvai,* and *Phyllops vetus* (Phyllostomidae); *Tonatia saurophila* (Phyllostomidae) known only from Jamaica; and *Phyllonycteris major* (Phyllostomidae) from Puerto Rico, Antigua, and Marie Galante. There are also 18 living species of bats that underwent local extinction on one or more Antillean islands during the Holocene, including the extant vampire bat *Desmodus rotundus* in Cuba.

The oldest NA cave deposits containing fossil bats are early Pleistocene in age (~0.8–1.0 Ma) in West Virginia, Texas, Colorado, and New Mexico. NA bat fossil sites older than early Pleistocene are primarily paleokarst deposits (sinkholes, fissures, solution cavities) in peninsular Florida. The richest of these are: Inglis 1A (early Pleistocene, ~2 Ma), with 7 species, including the oldest NA record of *Desmodus* and the only eastern NA record of *Antrozous*; Thomas Farm (early Miocene,~18 Ma), a sediment-filled sinkhole/cave complex containing 9 species including *Primonatalus prattae*, the oldest named species in the strictly cave-dwelling family Natalidae, *Floridopteryx poyeri* in the Emballonuridae; and 3 extinct genera of vespertilionids, *Karstala*, *Miomyotis*, and *Suaptenos*; and two Oligocene (26–30 Ma) fissure fills, I-75 and Brooksville 2, with 7 species of bats, including *Koopmanycteris palaeomormoops*, the oldest member of Mormoopidae; 2 species of *Speonycteris* representing an extinct family (Speonycteridae) with Neotropical affinities; and *Oligopteryx floridanus* and *O. hamaxitos*, the earliest New World emballonurids. Although karstic deposits are widely distributed in NA, they mostly lack fossil bats, except in Florida. We suspect undiscovered Tertiary karst deposits with bats exist elsewhere in NA.

INTRODUCTION

Caves are well known as producers of vertebrate fossils around the world and through a substantial span of Earth history (Andrews, 1990; Simms, 1994; Harris, 2005; Lundelius, 2006), especially in the Quaternary (Jass and George, 2010; Schubert and Mead, 2012). We review the fossil record of bats (Mammalia: Chiroptera) in North America (NA) from caves and other karst deposits, from the early Oligocene (~30 million years ago [Ma])] through the end of the Pleistocene (~10 thousand years ago [ka]). Our review covers the entire North American continent from Alaska and Canada south to Panama and also includes the extensive fossil record of bats from caves in the West Indies. We focus mostly on the continental United States (US) because the record is more complete, including several hundred caves that have produced Pleistocene vertebrate faunas, many of which contain fossil bats (Martin, 1972; Kurtén and Anderson, 1980; Harris, 1985, 2023; FAUNMAP, 1994; Czaplewski et al., 2008). We note that Hawaii also has an important record of fossil bats from lava tube caves (Ziegler et al., 2016). However, Hawaii is considered part of Oceania so its fossil bat record is not discussed here. During the latter half of the Pleistocene (between about 10 ka and 1 Ma), bats have an excellent fossil record in NA caves, primarily insectivorous species in the family Vespertilionidae. We discuss several late Pleistocene cave deposits that have produced large samples of bats, including caves in Arizona, New Mexico,

---

[1] New Mexico Museum of Natural History, Albuquerque, NM 87104, USA
[2] Oklahoma Museum of Natural History, University of Oklahoma, Norman, OK 73072, USA
[C] Corresponding author: gary.morgan1@dca.nm.gov.

and Oklahoma. The record of fossil bats from Mesoamerica consists of about a dozen late Pleistocene cave deposits in Mexico and one in Belize. The West Indies has a rich Late Quaternary (late Pleistocene and Holocene) chiropteran record from caves (Morgan, 2001), including underwater caves with large fossil bat samples from Abaco in the Bahamas and the Dominican Republic (Steadman et al., 2007; Velazco et al., 2013; Soto-Centeno and Steadman, 2015). We are not aware of vertebrate fossils from caves in NA that are older than about 1 Ma. Older caves do exist, including several in Carlsbad Caverns National Park that are Miocene in age (~6–12 Ma) based on ^{40}Ar/^{39}Ar dates on sulfate minerals in cave deposits (Polyak et al., 1998), but these older caves do not contain fossil vertebrates. Older deposits containing abundant samples of bats, ranging in age from early Pleistocene to late Oligocene (~2 to 30 Ma), are known from Florida, but these are derived from karst features such as sinkholes, fissures, and solution cavities and not caves. In general, bats are more common and skeletally more complete as fossils in caves than in open sites, including fluvial, lacustrine, alluvial, and nearshore marine deposits (Kowalski, 1995; Eiting and Gunnell, 2009; Brown et al., 2019). However, the remarkable complete skeletons of bats in Eocene lake deposits from Messel in Germany and the Green River Formation in Wyoming are obvious exceptions (Smith et al., 2012; Rietbergen et al., 2023).

Figure 1A shows major regions of karst in the continental U. S. (Weary and Doctor, 2014). Many of these regions have caves containing Pleistocene deposits with bats and other vertebrates (Kurtén and Anderson, 1980; Harris, 1985), including (from east to west): Cenozoic marine limestones from Florida; Paleozoic carbonates in the Appalachian Mountains in Pennsylvania, Maryland, West Virginia, Virginia, Tennessee, Georgia, and Alabama; Paleozoic carbonates in western Kentucky, western Tennessee, and the Ozark Mountains in Missouri, Arkansas, and Oklahoma; Cretaceous limestones on the Edwards Plateau in Texas; and Paleozoic and Mesozoic carbonates in the Mountain West, including New Mexico, Arizona, Colorado, Utah, Nevada, and Wyoming. These are not the only areas in the continental US that have produced Pleistocene cave deposits with bats, with caves occurring in most states, including not only typical caves formed in carbonate rocks, but also caves formed as lava tubes or natural traps in areas with extensive volcanic deposits. An unusual type of karst occurs in the Southern Great Plains where the only modern caves are ephemeral, fast-eroding gypsum caves developed as salt-dissolution features in evaporite karst in Permian sandstone and siltstone formations (see Fig. 1; Johnson, 1989, 1996; Johnson and Neal, 2003). These gypsum caves in the Southern Great Plains have not yet produced Pleistocene vertebrate faunas.

Figure 1B indicates the distribution of carbonate rocks in NA, including not only the contiguous US but also Alaska, Canada, Mexico, Central America, and the West Indies (from a map of the global distribution of carbonate rocks; Ford and White, 2007; Hollingsworth et al., 2008). This map shows the widespread distribution of carbonate rocks in eastern and southern Mexico, in particular the Yucatán Peninsula, which also includes Belize and part of Guatemala, as well as more limited areas in Honduras, Nicaragua, and Costa Rica. Among the areas in Mesoamerica with extensive outcrops of carbonate rocks, the Sierra Madre Oriental in eastern Mexico and the Yucatán Peninsula in Mexico and Belize contain caves that have produced samples of fossil bats (Arroyo-Cabrales and Polaco, 2003; Czaplewski et al., 2003). This map also shows the four major islands in the Greater Antilles—Cuba, Hispaniola, Jamaica, and Puerto Rico—all of which have numerous carbonate caves containing fossil bats (Morgan, 2001; Dávalos and Turvey, 2012).

METHODS

We provide definitions of several terms we use in this paper (e.g., cave, karst, paleokarst) that may differ from the more traditional usage of these terms by cavers, cave geologists, and others. Our primary interest in this paper is how caves and karst features serve as natural cavities for the accumulation of vertebrate fossils, specifically bats. Online definitions (e.g., britannica.com; wikipedia.org) describe a cave as being a natural void in the ground that is large enough for a human to enter and usually extends to total darkness, to differentiate caves from rock shelters that are shallow and exposed to natural light and from fissures that are generally too small to allow human entry. This definition is especially important in Florida where caves containing vertebrate fossils are fairly uncommon, but karst-derived sinkholes, fissures, and solution cavities containing vertebrate fossils are commonplace. Caves normally form as underground voids by the dissolution of carbonate rocks through the action of weak carbonic acid and less commonly weak sulfuric acid. Less common types of caves include lava tubes formed in igneous rocks (e.g., basalt) and evaporite caves formed in gypsum. Karst is defined as a landform where the landscape is underlain by various types of carbonate rocks and is characterized by underground drainage and contains both caves and sinkholes and other karst-derived features (e.g., fissures, chimneys, solution cavities) that do not fit the definition of a cave. We also use the term paleokarst to refer to karst-derived features that formed in the geologic past.

We define several geographic regions here to eliminate any potential confusion regarding their usage. Our definition of North America (abbreviated throughout as NA) includes the entire North American continent, from Alaska and Canada south through the continental United States (US), Mexico, and Central America to Panama, including the West Indies. We recognize three major geographic subdivisions within North America: 1. Alaska, Canada, and the continental United States; 2. Mesoamerica (or Middle America), including Mexico and Central America; 3. West Indies. These

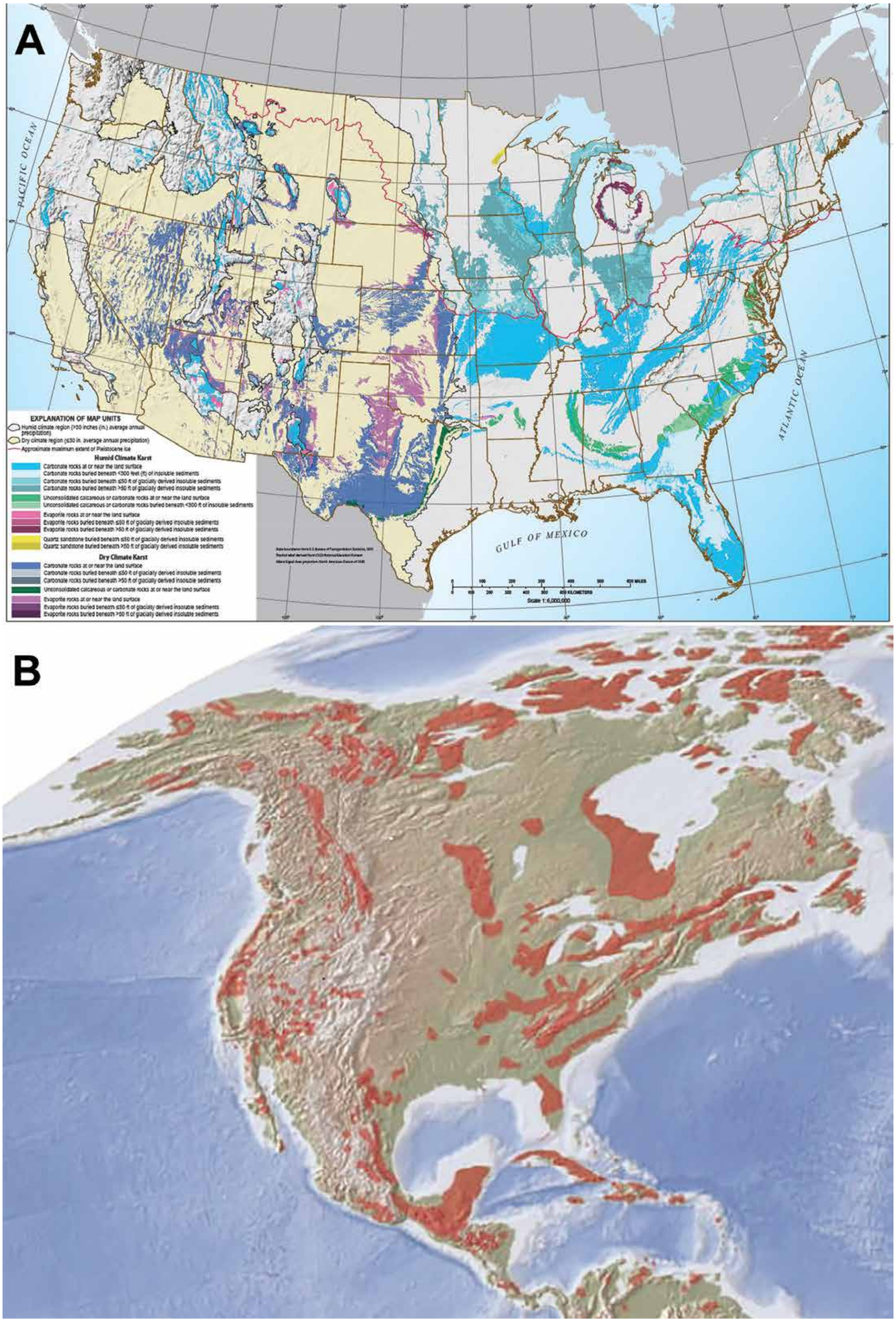


Figure 1. (A) Karst and potential karst areas in the contiguous United States (from Weary and Doctor, 2014). (B) North American distribution of carbonate rocks (from Ford and Williams. 2007; Hollingsworth et al., 2008).

three regions each have distinctive chiropteran faunas, with minimal overlap, and based on the fossil record, also had distinct bat faunas in the late Pleistocene. Within each of these three geographic regions, we discuss the occurrence of cave deposits containing fossil bats. We also recognize two biogeographic regions in NA, the Nearctic region and Neotropical region, with the boundary between these two regions located at approximately the Tropic of Cancer at 23° North latitude in central Mexico (Olson et al., 2001; Morrone, 2017; Morrone et al., 2022). The current Nearctic region is characterized by a boreal and temperate biota, occurring in the US, Canada, and northern Mexico. The current Neotropical region is characterized by a tropical biota and includes Mexico south of the Tropic of Cancer, Central America, the West Indies, and the tropical portion of South America (Morrone et al., 2022). The current bat fauna of Canada and the US consists primarily of insectivorous species in the family Vespertilionidae (33 species), most of which have temperate/Nearctic affinities. An additional 12 species in three other families, Phyllostomidae (4 species), Mormoopidae (1 species), and Molossidae (7 species), have primarily tropical/Neotropical affinities and occur at the northernmost limits of their geographic ranges in the southwestern US or Florida. Most of the 12 species with tropical affinities also occur in Mexico and farther south into Central America or the West Indies in the case of tropical species from Florida.

Figure 2. Bat fossils from late Pleistocene deposits in Three-Forks Cave in the Ozark Highland, Adair County, Oklahoma. (A) Finger is pointing to a cranium of the vespertilionid bat, *Myotis* sp., upside down and encrusted with flowstone. (B) A small jumble of bat wing bones in a muddy deposit on the floor of the cave.

Bats reach their greatest diversity or species richness in tropical regions (Hill and Smith, 1984; Nowak, 1994; Simmons, 2005), and this phenomenon is well illustrated in the transition from temperate/Nearctic to tropical/Neotropical bat faunas in the New World. A Neotropical chiropteran fauna characterizes central and southern Mexico (south of the Tropic of Cancer) and Central America, as well as the West Indies and the tropical regions of South America (López-Aguirre et al., 2018). The tropical bat fauna in Mesoamerica has a far larger number of species than does the bat fauna in temperate NA. For example, the modern chiropteran fauna of Mexico consists of about 140 species (Ceballos et al., 2014), and the bat fauna of northern Central America includes about 120 species (McCarthy et al., 1993), both of which are nearly three times the 45 species of mostly insectivorous bats that inhabit the US and Canada (Bradley et al., 2014). The Neotropical bat fauna also exhibits a much greater ecological diversity, with many species of fruit-eating and nectar-feeding bats (family Phyllostomidae, subfamilies Carolliinae, Glossophaginae, and Stenodermatinae), as well as bats that prey on other vertebrates (Phyllostomidae: Phyllostominae), including fish (Noctilionidae), and even feed on blood (Phyllostomidae: Desmodontinae). The Neotropical bat fauna occurs northward to the southern portion of the state of Tamaulipas along the Gulf of Mexico in northeastern Mexico, near the Tropic of Cancer (~23° N; Veracruzan province of Morrone et al., 2022), and extends somewhat farther north (~27° N) to the southern portion of the state of Sonora along the Gulf of California in northwestern Mexico (Pacific Lowlands province of Morrone et al., 2022). The West Indian islands have a very different bat fauna from the two other areas of NA, including many endemic genera and species, a result of their long isolation as oceanic islands (Baker and Genoways, 1978; Koopman, 1989; Morgan, 2001). The West Indian bat fauna is tropical in origin and is considered a subset of the Neotropical region (Antillean subregion of Morrone et al., 2022), mostly composed of endemic genera or species in the families Phyllostomidae, Mormoopidae, and Natalidae, as well as several species in the Molossidae that include both endemic Antillean species and species that also occur in Mexico and Central America.

We used absolute dates to determine the age of some cave and karst faunas, including radiocarbon (^{14}C) dates for sites younger than 50 ka or other types of radioisotopic dates (U-series, $^{40}Ar/^{39}Ar$, etc.) for sites older than 50 ka. We also relied on mammalian biochronology using the North American Land Mammal Ages (NALMA) for continental faunas from NA (chapters in Woodburne, 2004): Prothero and Emry (2004) for the late Eocene and early Oligocene (Chadronian, Orellan, and Whitneyan NALMAs); Tedford et al. (2004) for the late Oligocene through earliest Pliocene (Arikareean, Hemingfordian, Barstovian, Clarendonian, and Hemphillian NALMAs), with updated ages for the Arikareean from Albright et al. (2008); and Bell et al. (2004) for the early Pliocene through late Pleistocene (Blancan, Irvingtonian, and Rancholabrean NALMAs). Although we do not discuss vertebrate faunas from continental NA that are younger than late Pleistocene, many fossil bat faunas from the West Indies are Holocene in age and are discussed here. Most radiocarbon-dated cave faunas from the West Indies are either late Pleistocene or Holocene in age. However, only a small percentage of Antillean cave faunas have been ^{14}C dated; and therefore, we cannot be certain of their exact age. In the case of undated West Indian faunas, we use the more inclusive, but less precise, term “Late Quaternary” that includes both late Pleistocene and Holocene faunas. The system of NALMAs does not apply to the West Indies because the Antillean land mammal fauna is highly endemic, sharing no non-volant species with the NA continent (Morgan and Woods, 1986; Dávalos and Turvey, 2012), and only about 10 species of bats that are of little use in biochronology. Minimal change in bat faunas occurred during the late Pleistocene and Holocene in continental NA, including only three extinct species and a few additional species that occurred outside their current geographic ranges (i.e., extralimital). The situation is quite different in the West Indies where numerous species of bats either became extinct or underwent extirpation or local extinction on certain islands during the Late Quaternary, occurring during the post-Columbian period after the arrival of Europeans about 500 years ago (Morgan, 2001; Soto-Centeno and Steadman, 2015).

BATS FROM PLEISTOCENE CAVE FAUNAS IN NORTH AMERICA, EXCLUSIVE OF FLORIDA

As noted in the Methods section, we divide North America into three regions, continental US, Alaska, and Canada (temperate NA), Mexico and Central America or Mesoamerica (tropical NA), and the West Indies, each of which has a distinctive modern and late Pleistocene bat fauna, with only minimal overlap with the other regions. The majority of fossiliferous cave deposits containing bats from the continental US, Alaska, Canada, and Mexico are late Pleistocene (Rancholabrean) in age (Kurtén and Anderson, 1980). West Indian caves produce bat faunas that are either late Pleistocene or Holocene in age (i.e., Late Quaternary). No cave deposits containing bats from Mesoamerica or the West Indies are known to be older than late Pleistocene (10-250 ka; Morgan, 2001; Arroyo-Cabrales and Polaco, 2003). A limited number of older cave faunas with fossil bats, dating to the late early and middle Pleistocene (Irvingtonian NALMA; ~0.25-1.0 Ma), are known from the US. No Pleistocene cave deposits in NA older than late early Irvingtonian (>~1 Ma) are known to contain bats or other vertebrates. However, karst deposits in Florida, dating from the late Pleistocene (~10 ka) to the early Oligocene (~30 Ma), are known to contain important samples of fossil bats (Morgan and Hulbert, 2008; Morgan and Czaplewski, 2012, 2023). The Florida fossil bat record is reviewed separately because the record is dominated by karst deposits and covers a much longer period of time.

Chiroptera from Late Pleistocene (Rancholabrean NALMA) Cave Deposits in the US and Canada

Cave fossil deposits containing bat fossils are known throughout the United States from sites dating to the late Pleistocene Rancholabrean NALMA (Kurtén and Anderson, 1980; Harris, 1985, 2023; FAUNMAP, 1994). Several reviews of Rancholabrean vertebrates from US states contain information on fossil bats, including Arizona (Mead et al., 2005) and New Mexico (Harris, 1993; Morgan and Harris, 2015). US cave sites of late Pleistocene age from which significant samples of fossil bats have been reported include: New Paris Number 4, Pennsylvania (Guilday et al., 1964); Clark’s Cave, Virginia (Guilday et al., 1977); Robinson Cave (Guilday, 1967; Guilday et al., 1969) and Lookout Mountain Cave (Gaudin et al., 2011), Tennessee; Mammoth Cave, Kentucky (Jegla and Hall, 1962; Widga and Colburn, 2018); Brynjulfson Caves, Missouri (Parmalee and Oesch, 1972); Three-Forks Cave, Oklahoma (Czaplewski et al., 2018); Inner Space Cavern (aka Laubach Cave) (Choate and Hall, 1967; Dorsey, 1977) and Hall’s Cave (Toomey, 1993; Moroz et al., 2021), Texas; Carlsbad Cavern and Muskox Cave, New Mexico (Baker, 1963; Logan, 1981; Kottkamp et al., 2022); and Arkenstone Cave and La Tetera Cave, Arizona (Czaplewski and Peachey, 2003; Czaplewski et al., this volume). The Appendix lists all species of bats known from late Pleistocene (Rancholabrean) cave deposits in the US and Canada, and the most important cave sites in which these species have been identified. However, this list is not comprehensive, as it does not include all late Pleistocene records of bats.

Harington (2011) reviewed the late Pleistocene vertebrate record from caves in Canada, documenting 22 cave sites from four Canadian provinces and the Yukon (Appendix). Eight species of bats in the Vespertilionidae are reported from Canadian Pleistocene cave deposits, and 12 of the 22 faunas have a least 1 species of bat (Harington, 2011). January

Cave in Alberta has the richest fossil bat fauna with 5 species, and 3 caves have 4 species each, Laflèche Cave and Mine Cave in Quebec and Elba Cave in Ontario. There are no extinct species of bats from Canadian Pleistocene caves, and all the identified species occur within their current geographic ranges. Jass et al (2022) suggested that the limited record of Pleistocene bats and other vertebrates from caves in Canada might be related to the presence of glacial ice, or possibly to effects of deglaciation. The Alaskan cave record for bats is extremely poor. In a review of the vertebrate fauna from 15 Pleistocene and Holocene cave sites from Prince of Wales Island and other smaller islands in the Alexander Archipelago in southeastern Alaska, Heaton and Grady (2003) reported one species of bat, *Myotis* sp., from several of the caves. Only five species of bats have been recorded from the modern fauna of Alaska, all vespertilionids.

Several factors are worthy of note with regard to the late Pleistocene chiropteran record of temperate North America. This record comprises almost entirely living species, mostly Vespertilionidae that still inhabit the general vicinity of the cave where the fossil remains were found. One of the few late Pleistocene records of a bat occurring outside its current range (i.e., extralimital) is a partial skull of the California leaf-nosed bat, *Macrotus californicus*, (Phyllostomidae) identified from a fissure deposit near Terlingua in southwestern Texas, about 450 km northeast of the closest living population in Chihuahua, Mexico, and about 800 km east of its current eastern limit in southeastern Arizona (Ray and Wilson, 1979). The few extralimital records of bats in NA late Pleistocene cave deposits is surprising, especially considering that extralimital records of various species of rodents and shrews, and the resulting "nonanalog" or "disharmonious" faunas, are characteristic of many of these same late Pleistocene cave faunas (Semken et al., 2010). This may be related to the relatively limited availability of caves for roosting habitat, the greater dependence of many bats on caves, or the differing distributional patterns of NA bats compared to other small mammals. No species of bats are endemic to Canada or Alaska, and the chiropteran fauna becomes limited in diversity in more northerly latitudes, consisting of just a few vespertilionids (Wilson and Ruff, 1999; Simmons, 2005). By comparison, there are numerous species of rodents and shrews now restricted to boreal habitats in Alaska and Canada that extended their ranges southward during glacial intervals, where they co-occurred in cave deposits in the central and southeastern US with other species of small mammals from more temperate habitats that still occur in the vicinity of the caves, creating nonanalog or disharmonious faunas (Semken et al., 2010).

Although upwards of 10 extinct species of bats have been described from late Pleistocene cave deposits in temperate NA (Kurtén and Anderson, 1980), we only recognize two of those species as valid, *Desmodus stocki* and *Myotis rectidentis*, and consider the latter species questionable and in need of further taxonomic study. Stock's vampire bat, *Desmodus stocki* (Phyllostomidae), is the most distinctive of these extinct species. This extinct vampire bat was originally described from San Josecito Cave in northern Mexico (Jones, 1958) and is also known from 18 other late Pleistocene sites in NA, including 3 other cave sites in Mexico (Arroyo-Cabrales and Polaco, 2003), 9 cave deposits in the US from California to West Virginia (Appendix; Ray et al., 1988; Czaplewski and Peachey, 2003; Grady et al., 2002; Czaplewski et al., this volume), and 6 karst deposits in Florida (Morgan, 1991). *D. stocki* is larger and differs in several cranial and postcranial characters from the living common vampire bat, *D. rotundus* (Morgan, 1991), that currently has a tropical distribution from Mexico south through Central America and much of South America (Koopman, 1988). The US sites containing *D. stocki* are all well north of the current geographic range of *D. rotundus*, suggesting the extinct species was able to tolerate cooler winter temperatures than the living species, whose northward distribution is limited by the 10°C winter isotherm in Mexico (McNab, 1973). There are no fossil records of *D. rotundus* north of its current geographic range in Mexico. The extinction of *D. stocki* was almost certainly related to the extinction of the Pleistocene megafauna in NA and the disappearance of its primary food source, possibly the blood of ground sloths or other large xenarthrans such as glyptodonts or pampatheres (Morgan, 1991; McDonald and Jefferson, 2008; Morgan et al., 2025).

Another extinct bat species described from San Josecito Cave is the big-eared bat *Corynorhinus tetralophodon* (family Vespertilionidae). According to Handley (1955, p. 48), *C. tetralophodon* differs from the two living species of *Corynorhinus*—C. *rafinesquii* and *C. townsendii*—by having the… "M3 with a well-developed fourth commissure [= postmetacrista], almost equaling the third commissure [= premetacrista] in length." However, in a catalog of the type specimens of vertebrates from San Josecito Cave, Arroyo-Cabrales and Johnson (2002) synonymized *C. tetralophodon* with *C. townsendii*, a species of big-eared bat that still lives in northern Mexico, because they found the M3 postmetacrista is variably present in *C. townsendii*.

Choate and Hall (1967) described two new extinct species of *Myotis*—*M. magnamolaris* and *M. rectidentis*—based on mandibles from the late Pleistocene Laubach Cave (now Inner Space Cavern) in Texas. Dorsey (1977) and Dalquest and Stangl (1984) reevaluated the taxonomic status of *M. magnamolaris* and concluded that this species was conspecific with the living cave myotis *M. velifer*. Dorsey (1977) also determined that *M. rectidentis* was a valid species. We tentatively follow Dorsey's (1977) recognition of *M. rectidentis*, but also point out that in our experience, mandibles of NA species of *Myotis* are difficult to separate at the species level, as also noted by Gaudin et al. (2011) and others, especially when sample sizes are small.

We present several examples of Pleistocene caves in the US that have produced notable samples of fossil bats, mostly based on our field and research experience. Late Quaternary deposits in Three-Forks Cave in the Ozark Highland, Adair County, eastern Oklahoma, produced a large sample of bats represented by over 800 bones and isolated teeth (Czaplewski et al., 2018). Skeletal elements of bats are by far the most common fossils in the Three-Forks Cave deposits, all pertaining to the Vespertilionidae, and most representing the genus *Myotis*. At least four species of bats occurred as fossils in Three-Forks Cave: big brown bat, *Eptesicus fuscus*; gray bat, *Myotis grisescens*; one smaller unidentified species of *Myotis*; and tricolored bat (also known as the eastern pipistrelle or American perimyotis), *Perimyotis* (formerly *Pipistrellus*) *subflavus*. Figure 2 illustrates examples of bat fossils preserved in Three-Forks Cave. Several of these bats, including *E. fuscus* and *M. grisescens*, are represented by juvenile individuals indicating this cave has been a maternity roost for those species since the late Pleistocene (Czaplewski et al., 2018). Despite the relatively large sample of bat fossils from Three-Forks Cave, intra- and interspecies variation in body size (as reflected in isolated skeletal elements) underscores the difficulty in identification of related species of bats. This is particularly true for the common and speciose genus *Myotis*; the identification of *M. grisescens* is largely based on the single intact cranium in Figure 2A. Two of the bats identified as fossils in Three-Forks Cave, *P. subflavus* and *M. grisescens*, are presently listed federally as endangered species. This cave is typical of late Pleistocene cave deposits from NA containing large samples of bats in which all of the species preserved are cave dwellers, members of the Vespertilionidae, and still live in the general vicinity of the cave. Schubert (2010) provided a radiocarbon date of 34,063 rcybp for a tooth of the short-faced bear, *Arctodus simus*, from Three-Forks Cave. In addition to *A. simus*, the presence of three other extinct Pleistocene megafauna, the ground sloth, *Megalonyx jeffersonii*; the dire wolf, *Canis* (= *Aenocyon*) *dirus*; and a horse (Equidae), support a late Pleistocene (Rancholabrean) age for the Three-Forks chiropteran fauna.

Carlsbad Caverns National Park (National Park Service acronym CAVE) in Eddy County, southeastern New Mexico, contains at least three caves with large samples of fossil bats of Pleistocene age—Carlsbad Cavern, Muskox Cave, and Slaughter Canyon Cave (Baker, 1963; Logan, 1981; Morgan and Lucas, 2006; Kottkamp et al., 2022). The bats from Slaughter Canyon Cave are discussed in the following section on early and middle Pleistocene (Irvingtonian) bat faunas from NA. A large colony of the Mexican free-tailed bat, *Tadarida brasiliensis*, consisting of approximately a quarter million individuals (CAVE website), still inhabits Carlsbad Cavern, the main tourist cave in CAVE (Fig. 3A). Figures 3B and 3C illustrate two complete articulated skeletons of bats of unknown age but presumably Late Quaternary, preserved in flowstone in Carlsbad Caverns. Baker (1963) first mentioned the presence of numerous bat fossils in Carlsbad Caverns with the largest samples in the so-called "scenic rooms," including the Papoose Room and Mystery Room. Figure 4A shows a large accumulation of skulls and disarticulated postcranial skeletons of bats in the Papoose Room (Photo from Baker, 1963, fig. 4). Figures 4B and 4C illustrate disarticulated skulls, mandibles, and limb bones of bats attached by flowstone to the wall of the cave in a vertical fissure deposit near the natural entrance to Carlsbad Caverns This site has not been dated

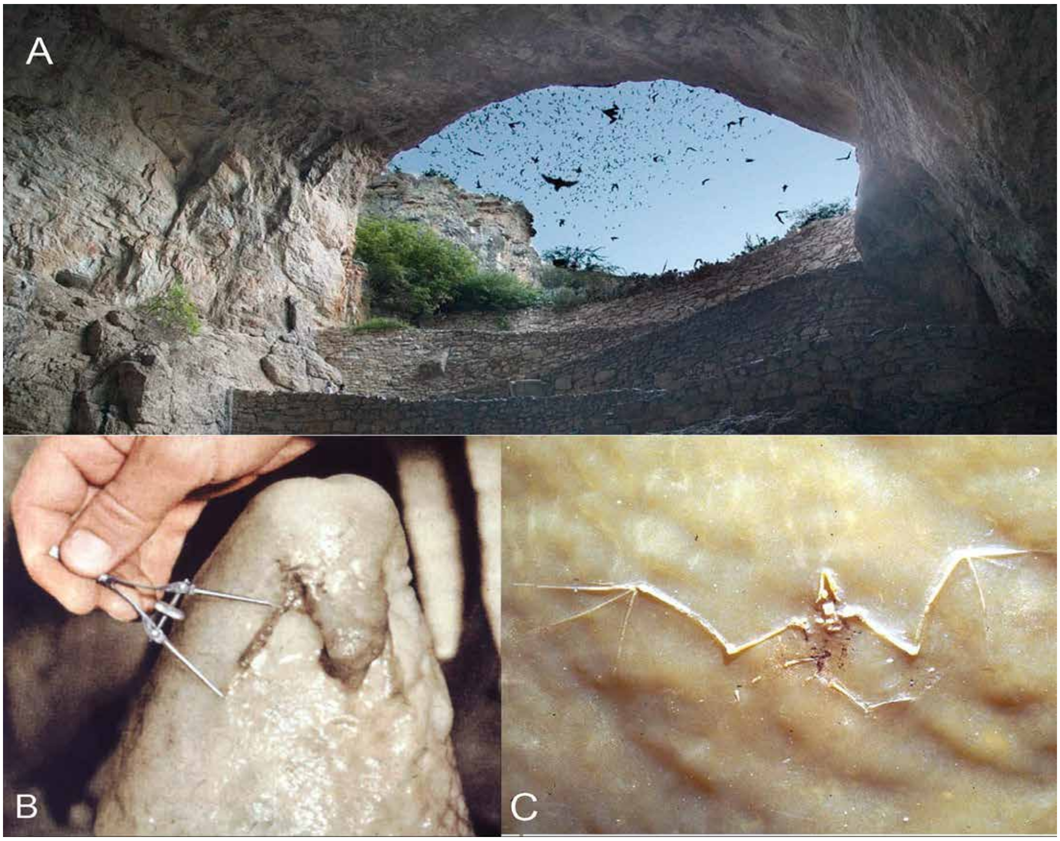


Figure 3. Carlsbad Cavern, Carlsbad Caverns National Park, Eddy County, New Mexico. (A) Carlsbad Cavern main entrance. Flight of Mexican free-tailed bats (*Tadarida brasiliensis*). (B, C) Bat skeletons preserved in flowstone, Carlsbad Cavern. (Photos courtesy of the National Park Service.)

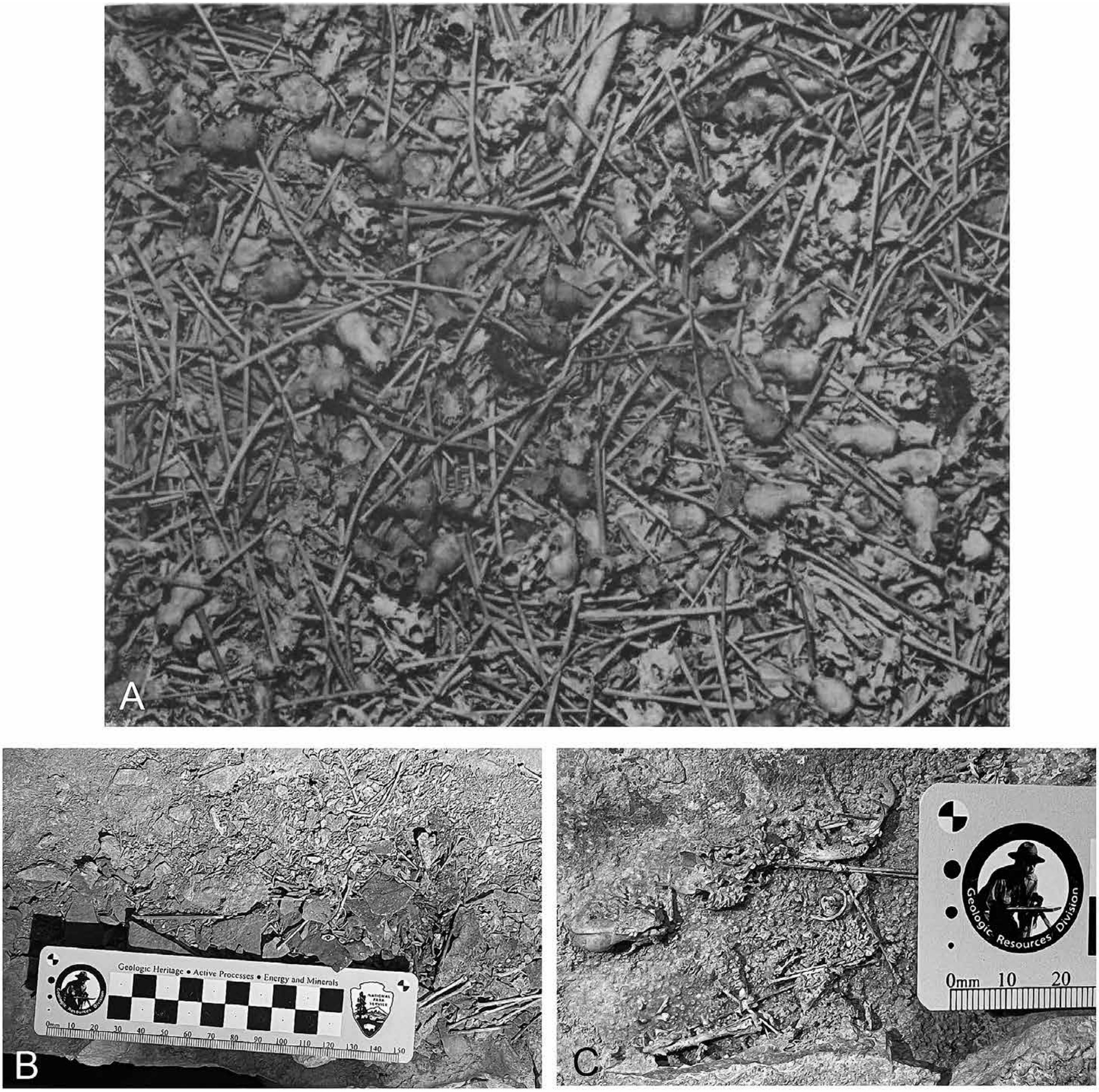


Figure 4. Carlsbad Cavern, Carlsbad Caverns National Park, Eddy County, New Mexico. (A) Accumulation of skulls and disarticulated skeletons of bats, Papoose Room (Photo from Baker, 1963). (B, C) Fossil bat skulls, mandibles, and limb bones (Vespertilionidae) in a vertical fissure deposit of Late Quaternary age near the natural entrance, attached to the cave wall with flowstone. (Photos courtesy of Rodney Horrocks (CAVE).)

but is probably late Pleistocene in age based on the discovery nearby of associated postcranial elements of the extinct American lion, *Panthera atrox* (Kottkamp et al., 2022). A locality in Lower Cave and another in the Big Room, both of which are in Carlsbad Cavern, contain guano deposits that have been radiocarbon-dated to approximately 50,000 rcybp and 35,000 rcybp, respectively (Jablonsky, NPS unpubl. reports, 1999, 2001; Kottkamp et al., 2022). These dates indicate that bats have inhabited Carlsbad Cavern for at least the past 50,000 years, if not considerably longer.

Muskox Cave has a sample consisting of several hundred partial skulls, mandibles, and limb bones of fossil bats, currently under study by GSM. Logan (1981) identified 6 species of bats from Muskox Cave, 5 vespertilionids—pallid bat, *Antrozous pallidus*; *Eptesicus fuscus*; *Myotis velifer*; fringed myotis, *Myotis thysanodes*; and Townsend's big-eared bat, *Plecotus* (=*Corynorhinus*) *townsendii*; and one molossid, *T. brasiliensis*, all living today in the Guadalupe Mountains in southeastern New Mexico. Radiocarbon dates on collagen from fossil bones in Muskox Cave range from 18,140 to 25,500 rcybp, indicating an age corresponding with the Last Glacial Maximum (LGM).

Over 4,700 skeletal elements of bats were recovered from a small deposit of Quaternary sediment in Arkenstone Cave, Pima County, Arizona (Czaplewski and Peachey, 2003; Fig. 5). These bat fossils belong to three species in two families—*Myotis thysanodes* and a small unidentified species of *Myotis* represent the Vespertilionidae, and an extinct species, *Desmodus stocki*, represents the Phyllostomidae. Most of the fossils (>4,000) represent an attritional accumulation beneath a late Pleistocene maternity colony of *M. thysanodes*, with most of the bones representing juvenile individuals (Czaplewski and Peachey, 2003). Although *M. thysanodes* no longer roosts at the elevation of Arkenstone Cave (~1,110 m), this species still occurs in the same general vicinity in southern Arizona but at somewhat higher elevations (1,200–2,100 m). The bat bones are too leached to provide a radiocarbon date, and no other age-diagnostic mammals were recovered from this cave. However, other records of *D. stocki* are from the late Pleistocene (Ray et al., 1988), supporting a late Pleistocene (Rancholabrean) age for the Arkenstone Cave deposit.

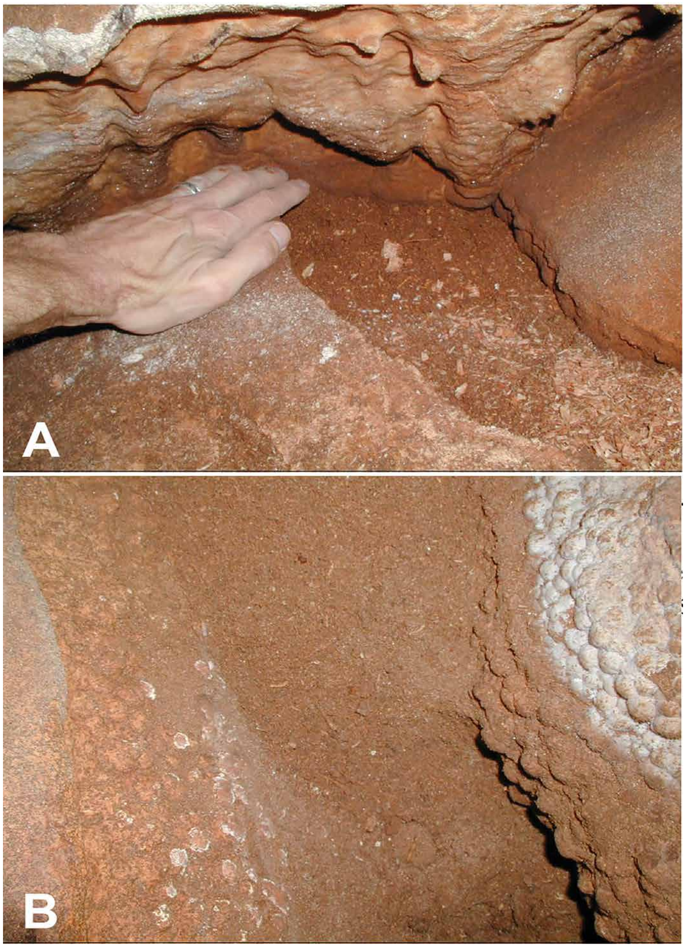


Figure 5. Quaternary deposit of bat bones in Arkenstone Cave, Arizona, including fringed myotis, *Myotis thysanodes*, and Stock's vampire bat, *Desmodus stocki.* (A) Excavation trench with a hand on the edge of the deposit. Several bones are visible as linear objects slightly paler than the bulk of the sediment. (B) Same trench, a closer view showing the pale linear bat limb bones and edentulous dentaries.

Chiroptera from Early and Middle Pleistocene (Irvingtonian NALMA) Cave Deposits in the US

Although there are a number of late early Pleistocene and middle Pleistocene (Irvingtonian; ~0.25–1.0 Ma) cave deposits in the US (Kurtén and Anderson, 1980), there are fewer than late Pleistocene (Rancholabrean) cave sites. No vertebrate-bearing cave deposits are known in NA that are older than about 1 Ma. This includes the earliest portion of the Pleistocene (~1.0–2.6 Ma), corresponding to the late Blancan (~1.6–2.6 Ma) and very early Irvingtonian (~1.0–1.6 Ma) NALMAs. NA Irvingtonian cave sites that have produced significant samples of fossil bats include (Appendix): Cumberland Cave, Maryland (Gidley and Gazin, 1938; Eshelman et al., 2025); Hamilton Cave, West Virginia (Repenning and Grady, 1988; Grady, personal communication); Conard Fissure, Arkansas (Brown, 1908); Fyllan Cave, Texas (Winkler and Gose, 2003); Porcupine Cave, Colorado (Barnosky, 2004; GSM, NJC, personal observations); and Slaughter Canyon Cave, New Mexico (Morgan and Lucas, 2006; Kottkamp et al., 2022). Gidley and Gazin (1938) listed only two species of bats from the middle Pleistocene (medial Irvingtonian) Cumberland Cave, *Eptesicus grandis* and *Corynorhinus alleganiensis*, both supposedly extinct species. In a review of the Cumberland Cave vertebrate fauna, Eshelman et al. (2025) identified more than 1,000 specimens of bats and added 5 species to the faunal list, including 4 vespertilionids, 2 species of *Myotis*, *M. grisescens* and the eastern small-footed bat *M. leibii*, *Perimyotis subflavus*, the red bat *Lasiurus borealis*, and one molossid, *Tadarida* sp. Brown (1908) reported several hundred specimens of bats from the medial Irvingtonian Conard Fissure, describing the extinct subspecies *Eptesicus fuscus grandis* and identifying the genus *Myotis*. As indicated by the site name, Conard Fissure is a karst fissure deposit, much like those described from Florida, and is not a cave with an opening to the surface. Conard Fissure clearly was a cave in the middle Pleistocene, as observed by the abundance of bat fossils and the presence of well-developed cave formations (Brown, 1908).

Slaughter Canyon Cave in CAVE contains sediment, as much as 3 m or more in thickness, mostly consisting of an ancient bat guano deposit that supported a commercial guano mining operation in the early to mid-20th century (Baker, 1963; Morgan and Lucas, 2006; Kottkamp et al., 2022; Figs. 6A, B). Slaughter Canyon Cave contains a phenomenal sample of bat fossils numbering in the tens of thousands (Hundreds of thousands? Millions?), mostly representing the extinct Constantine's free-tailed bat, *Tadarida constantinei* (Figs. 6C-G). Lawrence (1960) described *T. constantinei*, distinguishing this species from the living *T. brasiliensis* by its significantly larger size and several cranial characters.

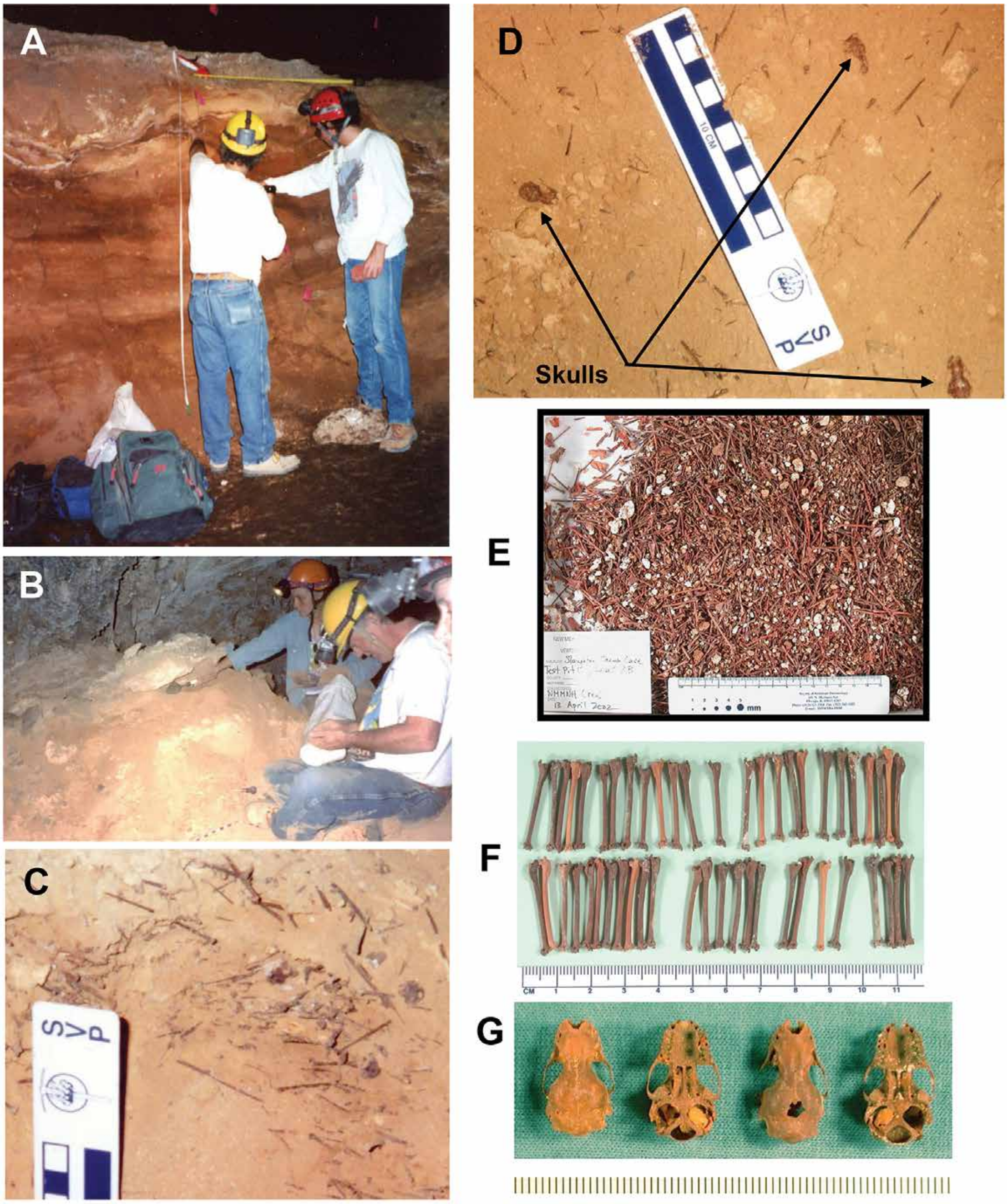


Figure 6. Slaughter Canyon Cave, Carlsbad Caverns National Park, New Mexico. This cave has produced a huge sample of bat fossils numbering in the tens of thousands of the extinct free-tailed bat, *Tadarida constantinei*, of middle Pleistocene age (Irvingtonian NALMA). (A) GSM (left) and Rick Toomey (right) measuring a section of ancient bat guano. (B) GSM (front) collecting a sample of *T. constantinei* fossils. Glenda Dawson (back) points to an overlying flowstone deposit with a U-series date of 206 to 212 ka. (C, D) In-place fossils of *T. constantinei*, including several skulls. (E) Sample of screenwashed concentrate from one bag of sediment (~10 kg) containing hundreds of bat fossils. (F) 50 complete humeri of *T. constantinei* from a single bag of sediment. (G) Four complete skulls of *T. constantinei*. (Photos in A-D courtesy of Patty Daw.)

Another factor supporting *T. constantinei* as a separate species is the presence in the Slaughter Canyon Cave deposits of a smaller species of *Tadarida* that appears to be conspecific with *T. brasiliensis* (Morgan and Lucas, 2006; Kottkamp et al., 2022). Although *T. constantinei* roosted in Slaughter Canyon Cave in large numbers in the middle Pleistocene, much like the modern colony of *T. brasiliensis* in Carlsbad Cavern, no bats have been observed roosting in this cave at present. Small numbers of fossils representing *Eptesicus fuscus* and two species of *Myotis* have also been identified from Slaughter Canyon Cave. Uranium-series dating of a flowstone overlying the fossil deposits in Slaughter Canyon Cave produced ages of 209 ka (Lundberg and McFarlane, 2006) and 212 ka (Polyak et al., 2006a), and U-series dates on other associated cave formations from this cave indicate a middle Pleistocene age (~0.5 Ma) that corresponds with a late Irvingtonian age for *T. constantinei* and the remainder of the vertebrate fauna (Polyak et al., 2006a). Records of an unidentified species of *Tadarida* larger than living *T. brasiliensis* are known from the medial Irvingtonian Hamilton Cave (Repenning and Grady, 1988; Grady, personal communication) and from a guano deposit in Mammoth Cave, Kentucky dated at >50 ka (Jegla and Hall, 1962; Widga and Colburn, 2015).

Only a few North American cave faunas are early medial Irvingtonian in age (~0.8-1.0 Ma), including Hamilton Cave (Repenning and Grady, 1988), Fyllan Cave (Winkler and Gose, 2003), Porcupine Cave (Barnosky, 2004; Barnoksy and Bell, 2004; Friedmann and Raynolds, 2004); and San Antonio Mountain (SAM) Cave, New Mexico (Rogers et al., 2000). Except for Hamilton Cave, paleomagnetic analyses of sediments in these caves document reversed polarity indicating referral to the Matuyama Chron, probably the uppermost reversed interval (subchron 1r.1r; 0.78–0.99 Ma). The biochronology of arvicoline (microtine) rodents from all four of these cave sites supports an early medial Irvingtonian age. Rogers et al. (2000, p. 96) reported "Chiroptera species indeterminate" from SAM Cave, a lava tube cave from high elevation (2,737 m) in the San Juan Mountains of northern New Mexico. Porcupine Cave in the Rocky Mountains of central Colorado also occurs at high elevation (2,900 m; Barnosky, 2004). Bats occur in several sites within Porcupine Cave but are unpublished. We have examined the Porcupine Cave bat sample, which consists of 56 specimens, mostly partial mandibles, maxillae, humeri, and other postcranial elements representing several species of *Myotis* that cannot be identified below the generic level. Winkler and Gose (2003) listed five species of bats from Fyllan Cave on the Edwards Plateau in central Texas, including *Pipistrellus* (*Perimyotis*) *subflavus* and another small unidentified vespertilionid, a "medium bat" similar in size to *Myotis velifer*, a molossid near *Tadarida brasiliensis*, and a larger bat similar in size to the hoary bat *Lasiurus* (*Aeorestes*) *cinereus*. Despite the name, Fyllan Cave is a karst deposit not a cave based on the site description and photos (Winkler and Gose, 2003), but it was almost certainly a functioning cave during the Irvingtonian when it was inhabited by bats.

Several extinct species of bats were described from Irvingtonian cave and karst deposits in NA, including the vespertilionids, *Eptesicus grandis* and *Corynorhinus alleganiensis*; the molossid, *Tadarida constantinei*; and the vampire bat *Desmodus archaeodaptes* from two early Irvingtonian karst deposits in Florida (see discussion below). *Eptesicus grandis* was originally described as the large, extinct subspecies *Eptesicus fuscus grandis* from Conard Fissure in Arkansas (Brown, 1908). Gidley and Gazin (1938) identified this species from Cumberland Cave in Maryland and elevated it to species status as *Eptesicus grandis*. Although Conard Fissure and Cumberland Cave are Irvingtonian in age, most other records of *E. grandis* are from late Pleistocene (Rancholabrean) cave deposits in the eastern US (Guilday, 1967). A detailed analysis of a remarkable sample of this species, consisting over 3,000 mandibles and nearly 90 partial skulls from the late Pleistocene Robinson Cave in Tennessee, led Guilday (1967) to synonymize *E. grandis* with the living NA species, *E. fuscus*. *Corynorhinus alleganiensis* was described from Cumberland Cave (Gidley and Gazin, 1933) and has not been reported from any other Pleistocene cave sites in NA. Although we tentatively regard *C. alleganiensis* as valid, this species has not undergone a rigorous taxonomic analysis.

Bats from Late Pleistocene Cave Deposits in Mexico and Central America

Arroyo-Cabrales and Polaco (2008) reviewed the fossil record of bats from Mesoamerica, documenting 17 sites, including 15 sites from Mexico, 1 from Belize, and 1 from El Salvador. Among these 17 sites, 12 are from caves and 5 are from open sites. All 12 of the cave sites, 11 from Mexico and 1 from Belize, are late Pleistocene (Rancholabrean) in age. Several of the late Pleistocene cave deposits from Mexico contain important and diverse samples of fossil bats (Appendix; Arroyo-Cabrales and Polaco, 2003, 2008). Nine species of bats were reported from San Josecito Cave in the state of Nuevo León in northeastern Mexico (Jones, 1958; Arroyo-Cabrales and Polaco, 2003, 2008). San Josecito Cave is the type locality of the large extinct vampire bat, *Desmodus stocki*, and the extinct big-eared bat, *Corynorhinus tetralophodon*, and has also produced a large sample of the Mexican long-nosed bat, *Leptonycteris nivalis*, a nectarivorous bat that feeds on the flowers of large columnar cacti and agaves (Handley, 1955; Jones, 1958). Both *D. stocki* and *L. nivalis* are in the endemic New World family Phyllostomidae, most species of which occur in the Neotropical region. Arroyo-Cabrales and Johnson (2008) synonymized *Corynorhinus tetralophodon* with the living species *C. townsendii*, that still lives in the general vicinity of San Josecito Cave, as does a newly named extant species, *Corynorhinus leonpaniaguae*, recently separated from *Corynorhinus mexicanus* (López-Cuamatzi et al., 2024). Cueva de la Boca in Nuevo León, Cueva de la Presita in San Luis Potosí, and a cave near Tlapacoya in the state of Mexico have also produced specimens of *D. stocki* (Ray et al., 1988; Arroyo-Cabrales and Polaco, 2003, 2008).

The late Pleistocene chiropteran fauna from Cueva de El Abra in the state of Tamaulipas in northeastern Mexico consists of 9 species, including several tropical forms typical of southern Mexico and Central America (Dalquest and Roth, 1970; Arroyo-Cabrales and Polaco, 2003, 2008). This cave is in the tropical lowlands of southeastern Tamaulipas, a region that documents the northernmost range of many species of Neotropical bats (Ceballos et al., 2014). Four species of Neotropical bats are represented by fossils from Cueva de El Abra, the emballonurid *Balantiopteryx io*, the frugivorous phyllostomid *Artibeus jamaicensis*, and the molossids *Nyctinomops aurispinosus* and *N. laticaudatus*. *B. io* from Cueva de El Abra represents one of the few extralimital records of bats from late Pleistocene cave deposits in Mexico, as this species now occurs no farther north than central Veracruz, several hundred kilometers south of Cueva de El Abra.

Two caves on the Yucatán Peninsula produced diverse samples of Late Quaternary bats: Loltún Cave or Gruta de Loltún in the state of Yucatán in Mexico (Arroyo-Cabrales and Alvarez, 2003; Arroyo-Cabrales and Polaco, 2003, 2008) and Cebada Cave in Belize (Czaplewski et al., 2003a). Most of the bats from Loltún Cave (15 species) and Cebada Cave (9 species) consist of tropical species that still inhabit southern Mexico and northern Central America. One notable exception is that both caves contain fossils of the giant extinct vampire bat, *Desmodus draculae*, a tropical species also recorded from caves in Venezuela and Brazil (Morgan et al., 1988; Czaplewski and Cartelle, 1998). Both *D. draculae* and *D. stocki* presumably fed upon the blood of one or more species of large mammals, possibly ground sloths, and became extinct at the end of the Pleistocene when their food sources also became extinct (Morgan, 1991; McDonald and Jefferson, 2008). These two extinct vampire bats have differing sizes: *D. draculae* is significantly larger than *D. stocki* and both species are larger than living *D. rotundus*. Together with their non-overlapping geographic ranges, *D. draculae* is restricted to the Neotropics from southern Mexico south to Brazil and *D. stocki* occurs from central Mexico to the southern US, this apparently reflects a difference in their prey species and perhaps their differing abilities to tolerate cooler temperatures.

Except for Cebada Cave, fossil bats are not reported from any other Pleistocene cave deposits from Belize and Guatemala south to Panama, in part owing to the overall rarity of caves in the predominantly volcanic terrane of Central America (Fig. 1B). Churcher (2020) reported a late Pleistocene (Rancholabrean) fauna from Extinction Cave in Belize, containing several extinct species of large mammals, including *Dasypus bellus*, *Panthera atrox*, *Tremarctos floridanus*, and *Equus conversidens*. However, the fauna from Extinction Cave did not include any bats or other small mammals, suggesting the site was not screened for microvertebrates. We suspect there are other caves with undiscovered late Pleistocene bat fossils from the carbonate terrain of Belize and northern Guatemala that forms the southeastern portion of the Yucatán Peninsula, probably including cenotes or underwater caves. Several fairly extensive cave systems are known from Central America, for example, Candelaria Caves and Grutas de Lanquín in Guatemala, Talgua Cave in Honduras, Terciopelo Cave and Venado Cave in Costa Rica, and Bayano Cave in Panama. However, to our knowledge, none of these caves have been systematically explored for Pleistocene vertebrate fossils. Pleistocene mammal faunas are known from most countries in Central America, including: Guatemala (Dávila et al., 2019; Lucas et al., 2021), Honduras (Webb and Perrigo, 1984; Lucas, 2008), El Salvador (Webb and Perrigo, 1984; Cisneros, 2005, 2008), Nicaragua (Lucas et al., 2008), Costa Rica (Lucas et al., 1997), and Panama (Gazin, 1957; Pearson, 2005; Lucas, 2014). However, these Central American Pleistocene faunas are mostly derived from open sites and mostly consist of large mammals, with no records of fossil bats. Webb and Perrigo (1984) illustrated a partial articulated skeleton tentatively identified as *Pteronotus parnellii* from the early Pleistocene (early Irvingtonian) Barranca del Sisimico LF in El Salvador. Although *P. parnellii* is member of the Mormoopidae and most species in this family are obligate cave dwellers (Smith, 1972), the skeleton from Barranca del Sisimico was derived from a diatomite representing a former lake deposit (Webb and Perrigo, 1984).

Chiroptera from Late Pleistocene and Holocene Cave Deposits in the West Indies

The West Indian islands have a remarkably robust record of fossil bats from cave deposits (Appendix; Morgan, 2001; Dávalos and Turvey, 2012) that date to the Late Quaternary (late Pleistocene or Holocene). Caves are abundant throughout Cuba, Jamaica, Hispaniola, and Puerto Rico, as well as the Bahamas and Cayman Islands, where widespread exposures of Cretaceous and Cenozoic carbonate rocks have been eroded into an extensive karst topography. This includes several hundred cave sites that have yielded Late Quaternary bats and other vertebrate fossils (Morgan and Woods, 1986; Morgan, 2001; Dávalos and Turvey, 2012). Abundant and diverse samples of Late Quaternary bats are known from caves on all four of the large Greater Antillean islands, including (Appendix): Cuba (Silva Taboada, 1974; 1979); Jamaica (Koopman and Williams, 1951; Morgan, 1993); Hispaniola (Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017), and Puerto Rico (Anthony, 1917, 1918, 1925; Choate and Birney, 1968). Substantial Late Quaternary bat faunas are also known from several smaller islands in the West Indies, including (Appendix): Abaco, Andros, and New Providence in the Bahamas (Morgan, 1989, 2001; Steadman et al., 2007; Soto-Centeno and Steadman, 2015); Grand Cayman and Cayman Brac in the Cayman Islands (Morgan, 1994); and Antigua (Steadman et al., 1984; Pregill et al., 1988) and Marie Galante in the Lesser Antilles (Stoetzel et al., 2016). Late Quaternary cave deposits in the West Indies have a much more diverse fossil record of the Chiroptera than does Mesoamerica. Furthermore, the Late Quaternary Antillean chiropteran fauna has also undergone more extensive extinctions and extirpations (local extinctions or island population losses) than in the late Pleistocene of continental North America.

The combined extant and Late Quaternary chiropteran fauna of the West Indies consists of 70 species (Appendix; Varona, 1974; Baker and Genoways, 1978; Silva Taboada, 1979; Koopman, 1989; Morgan, 2001; Tejedor, 2011; Dávalos and Turvey, 2012; Pavan and Marroig, 2016). Eight of these (11% of the bat fauna) are extinct species known only as Late Quaternary fossils: *Mormoops magna* and *Pteronotus pristinus* in the Mormoopidae; and *Artibeus anthonyi*, *Cubanycteris silvai*, *Phyllonycteris major*, *Phyllops silvai, Phyllops vetus,* and *Tonatia saurophila* in the Phyllostomidae. Four of these 8 extinct species, *A. anthonyi*, *C. silvai*, *P. silvai,* and *P. vetus,* are known only from Cuba (Woloszyn and Silva Taboada, 1977; Silva Taboada, 1979; Suárez and Diaz-Franco, 2003; Mancina and Garcia-Rivera, 2005). *Mormoops magna* occurred on both Cuba and Hispaniola (Silva Taboada, 1974; Velazco et al., 2013). *Pteronotus pristinus* was described from Cuba (Silva Taboada, 1974) and tentatively identified from a late Pleistocene karst deposit in southernmost Florida (Morgan, 1991). *Tonatia saurophila* is known only from Jamaica (Koopman and Williams, 1951).

Phyllonycteris major was originally described from Puerto Rico (Anthony, 1917, 1918) and has since been identified from two caves in the Lesser Antilles: a late Holocene cave deposit in Burma Quarry in Antigua (Pregill et al., 1988) and Holocene and late Pleistocene deposits from Blanchard Cave in Marie Galante (Stoetzel el al., 2016). *Tonatia saurophila* has a complicated taxonomic history, originally described as an extinct species known only from two caves in Jamaica (Koopman and Williams, 1951). Later, the name *T. saurophila* was applied to both the Jamaican fossils and a living species on the mainland, originally referred to the *T. bidens* complex, that occurs from Mexico to South America (Williams et al., 1995). Recently, two of the mainland forms in the *Tonatia bidens* complex, *T. bakeri* from Mexico and Central America and *T. maresi* from South America, were elevated to full species and *T. saurophila* was returned to its original status as an extinct species restricted to Late Quaternary cave deposits from Jamaica (Basantes et al., 2020). The eight extinct species of bats from the West Indies document more than twice the number of late Pleistocene bat extinctions that occurred in the far larger area of continental North America, from the US and Canada south to Panama, consisting of only three species: two species of vampire bats, *Desmodus draculae* and *D. stocki*; and the vespertilionid, *Myotis rectidentis*.

The West Indies experienced even more extensive extirpations of bat species, with 18 living species (29% of the extant Antillean bat fauna of 62 species) known to have undergone local extinction on one or more islands. Among those 18 species, two disappeared from the West Indies but still survive in Mesoamerica—a mormoopid, the ghost-faced bat *Mormoops megalophylla*; and a phyllostomid, the vampire bat, *Desmodus rotundus*. *M. megalophylla* has the most extensive West Indian distribution of these two species, with extirpated populations from Late Quaternary cave deposits in Cuba, Jamaica, Hispaniola, Abaco and Andros in the Bahamas, and Marie Galante in the Lesser Antilles (Silva Taboada, 1974; Morgan, 1989, 1993, 2001; Stoetzel et al., 2016), as well as peninsular Florida (Morgan, 1991, 2002). *D. rotundus* has been recorded in the West Indies from five Late Quaternary cave deposits in Cuba (Orihuela, 2011). A third extirpated species no longer found in the West Indies is a vespertilionid, the southeastern myotis, *Myotis austroriparius*, now restricted to Florida and the southeastern US, but tentatively identified from three Late Quaternary cave deposits on Abaco in the northern Bahamas (Morgan, 2001; Soto-Centeno and Steadman, 2015). There are currently no living species of *Myotis* found in the Greater Antilles or Bahamas. The identification of *M. austroriparius* from Abaco requires further study; as noted above, fragmentary fossils of *Myotis* are notoriously difficult to identify to species.

Among the other 15 West Indian bat species with extirpated populations on one or more islands, most of these occurred on smaller islands, including Abaco, Andros, and New Providence in the Bahamas; Grand Cayman and Cayman Brac in the Cayman Islands; and Anguilla, Antigua, Barbuda, and Marie Galante in the Lesser Antilles (Morgan, 2001). More than half of the species (8) that suffered local extinctions in the West Indies belong to two families of obligate cave-dwelling bats that reach their highest modern species diversity in the West Indies, Mormoopidae and Natalidae. Four of the 7 living species of mormoopids in the West Indies are known from one or more locally extinct populations, including the Antillean ghost-faced bat, *Mormoops blainvillei*, from caves on 8 islands where this species no longer occurs and 7 extirpated populations of Parnell's mustached bat, *Ptenonotus parnellii*. Four of the 8 extant species of Natalidae in the West Indies are also represented by extirpated island populations, including 7 locally extinct populations of a large species of funnel-eared bat previously referred to as either *Natalus stramineus* or *N. major*. Varona (1974) and Koopman (1989) recognized a single species of large *Natalus* in the West Indies, *N. stramineus*, whereas Morgan (2001) referred the large *Natalus* from the Greater Antilles to *N. major*. In a systematic review of the Natalidae, Tejedor (2011) recognized 3 large species in this genus from the Greater Antilles—*N. jamaicensis* from Jamaica, *N. major* from Hispaniola, and *N. primus* from Cuba, and restricted *N. stramineus* to the Lesser Antilles. Fossils representing extirpated populations of a large species of *Natalus* from Abaco, Andros, New Providence, Middle Caicos, and Grand Cayman were previously referred to *N. major* (Morgan, 2001). Following the systematic revision of the Natalidae (Tejedor, 2011), further study is required to determine the correct species identifications of the extirpated populations of a large *Natalus* in the Bahamas, Caicos Islands, and Cayman Islands. Several West Indian species in the Phyllostomidae also underwent rather widespread extirpations, including Waterhouse's leaf-nosed bat, *Macrotus waterhousii*, and the Greater Antillean long-tongued bat, *Monophyllus redmani*, both identified from fossils on five islands where these species no longer occur, and the Cuban fruit-eating bat *Brachyphylla nana* that became extinct on four islands.

The widespread disappearances of bats from certain islands in the West Indies during the Late Quaternary, including both species-level losses (extinctions) and population-level losses (extirpations), have been attributed to several causes, including reduction in island size as a result of rising sea level in the late Pleistocene, especially on smaller islands with low topography (e.g., Bahamas), flooding of low-lying caves also caused by rising sea level, and natural changes in climate and habitat (i.e., not human caused), most of which would have occurred during the late Pleistocene-Holocene transition from 11–9 ka (Morgan, 1999, 2001; Dávalos and Russell, 2012; Soto-Centeno and Steadman, 2015). Rising sea level and the flooding of caves that were dry during the late Pleistocene low sea level stand were certainly factors, as several underwater caves, also known as "blue holes" in the Bahamas, have produced samples of bat fossils, including Dan's Cave, Ralph's Cave, and Sawmill Sink on Abaco (Steadman et al., 2007; Soto-Centeno and Steadman, 2015; Fig. 7A) and

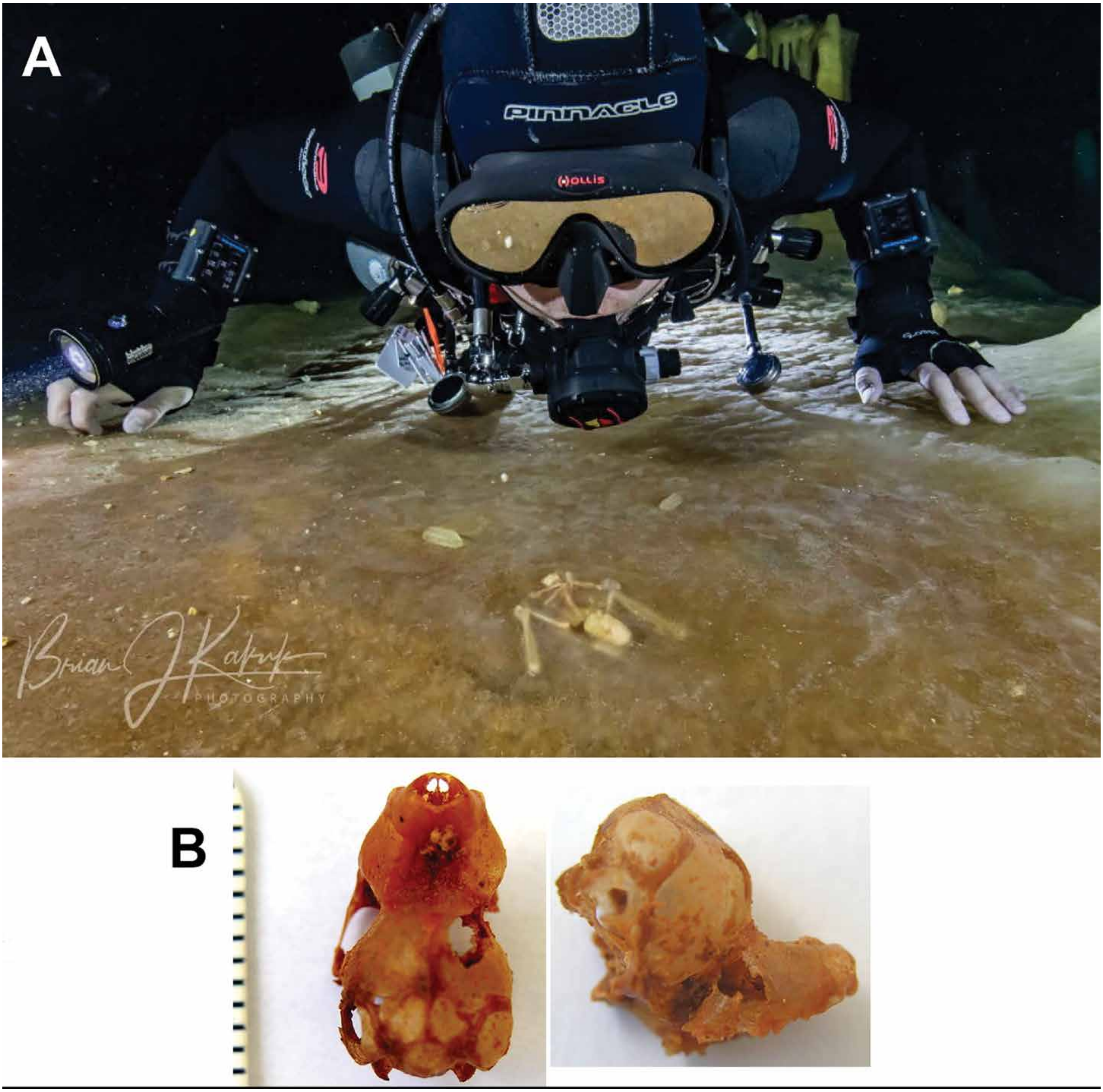


Figure 7. (A) Cave diver examining an articulated skeleton of a bat preserved in clear flowstone at a depth of 16 meters (52 feet) and a distance of 218 meters (715 feet) from the cave entrance, Ralph's Cave, Abaco, Bahamas (Photo courtesy of Brian J. Kakuk). (B) Fossil skull of a mormoopid bat, *Mormoops blainvillei*, dorsal view (left), lateral view (right), collected at depth of 18 meters and a distance of 91 meters from the cave entrance, Dan's Cave, Abaco, Bahamas. *Mormoops blainvillei* is now extralimital to the Bahamas (Skull photos courtesy of Nancy Albury).

Oleg's Bat Cave and Cueva de Lily in the Dominican Republic (Velazco et al., 2013; Fig. 8). Sawmill Sink produced four species of bats, including the vespertilionid, *Myotis austroriparius*, that no longer occurs in the Bahamas, from an owl roost deposit at a depth of 27–35 m below modern sea level. Bones from the owl roost in Sawmill Sink lack collagen so cannot be radiocarbon dated; however, the presence of a diverse terrestrial vertebrate fauna, including bats, birds, snakes, and lizards, at a depth of 35 m clearly indicates a late Pleistocene age older than 11 ka (Steadman and Franklin, 2015). Figure 7B illustrates a complete skull of the mormoopid bat, *Mormoops blainvillei*, now extirpated from the Bahamas, recovered from the floor of Dan's Cave on Abaco at a depth of 18 m and a distance of 91 m from the cave entrance. Although this skull has not been radiocarbon dated, *M. blainvillei* is an obligate cave dwelling bat that obviously inhabited Dan's

Figure 8. Flooded floor of Oleg's Bat Cave in the Dominican Republic, where numerous bat cranial and postcranial remains can be observed. Bat fossils were collected at this site from a depth of 8 m and about 15 m from the cave entrance (Photograph courtesy of Phillip Lehman. Reproduced from Velazco et al., 2013, with permission of the AMNH).

Cave when it was a dry cave during a period of lower sea level in the late Pleistocene. Dan's Cave also contains extensive cave formations (stalactites, stalagmites, etc.) that form only under subaerial conditions but are now 18 m or more underwater. Fossils representing five extirpated species of bats from Ralph's Cave on Abaco, including three obligate cave dwellers, *Pteronotus parnellii*, *Monophyllus redmani*, and *Natalus primus*, late Holocene in age, with AMS radiocarbon dates ranging from 1,820 to 4,220 YBP (Soto-Centeno and Steadman, 2015). These dates are considerably younger than the major rise in sea level and changes in climate and vegetation that occurred during the late Pleistocene to the early Holocene transition (between 11 and 9 ka), suggesting these local bat extinctions were probably related to the arrival of humans and subsequent habitat changes in the Bahamas in the late Holocene (Soto-Centeno and Steadman, 2015). Oleg's Bat Cave in the Dominican Republic produced a remarkable sample of Late Quaternary bats, with 11 species represented by thousands of fossils, including hundreds of complete skulls recovered from the cave floor 8 m underwater and about 15 m from the cave entrance (Fig. 8). The bat fauna from Oleg's Bat Cave includes one extinct species, *Mormoops magna*, otherwise known only from Cuba, and one species that no longer occurs on Hispaniola, *Pteronotus macleayii* (Velazco et al., 2013); both are mormoopids, a family in which almost all living species are obligate cavernicoles (Smith, 1972; Morgan et al., 2019).

FOSSIL BATS FROM CENOZOIC CAVE AND KARST DEPOSITS IN FLORIDA

Fossil bats from cave and karst deposits in Florida are treated in a separate section because the record consists primarily of fossils from karst deposits not caves. The Florida record also covers a much longer period of time than elsewhere in North America, beginning in the early Oligocene (~30 Ma) and extending to the end of the Pleistocene (10 ka). The region that is now the Florida peninsula was submerged until the Oligocene, and as a result, much of northern peninsular Florida is underlain by Eocene and Oligocene marine limestones. Florida first emerged above sea level in the early Oligocene, and throughout the remainder of the Cenozoic, the peninsula fluctuated between submerged and emergent depending upon changes in sea level. During this time period, the highly soluble Paleogene limestones of northern Florida were acted upon by both chemical and physical erosional processes to develop one of the most extensive karst terrains in North America (Lane, 1986; Florea, 2008). The map in Figure 9 shows the distribution of limestone in Florida and the associated karst terrain. Areas with limestone at or near the surface (in red) have well developed karst solution features, as do areas with a moderate covering of clastic sediments (in gold). Most of the cave and karst fossil deposits in Florida are located in the areas of either red or gold on this map.

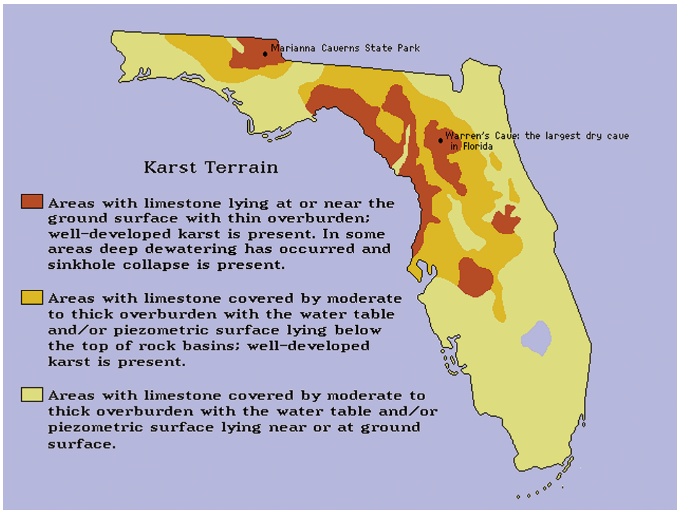


Figure 9. Map of Florida showing the karst terrain. Most Florida fossil faunas containing abundant bats are former cave deposits and are located in areas with well-developed karst (indicated by red and gold on this map). (Map courtesy of the Florida Speleological Society.)

The north Florida karst geomorphic province is well known for the abundance of fossil deposits containing terrestrial vertebrates occurring in current or former caves and other paleokarst features (Morgan and Hulbert, 2008). Karst deposits of terrestrial origin generally consist of sands and clays filling solution features such as sinkholes, fissures, and isolated sediment pockets, and often contain large samples of both small and large terrestrial vertebrates. The presence of bat fossils in many of these karst deposits is especially diagnostic, suggesting they represent the remnants of former cave systems. The same erosional processes that originally formed caves in the Florida peninsula eventually destroyed most of them. With the collapse of the caves, their contained sediments and fossils became buried, and the caves were no longer accessible from surface entrances. The limestones in northern Florida are mined commercially for road bedding and other construction purposes, which has resulted in the discovery of most of these karst fossil deposits. Vertebrate paleontologists from the Florida Museum of Natural History (FLMNH) regularly survey active commercial limestone mines in search of clay- and sand-filled fissures and sinkholes containing fossils (Fig. 10). More than 150 vertebrate fossil sites of karst origin are known from the Florida peninsula, including many deposits that contain bats (Morgan and Hulbert, 2008; Morgan and Czaplewski, 2012, 2023). Nowhere else in North America are karst-derived vertebrate fossil deposits of Cenozoic age found in such abundance in a limited geographic region. Moreover, we suspect only a small percentage of these buried fossiliferous karst deposits have been uncovered within the past century through mining operations.

Chiroptera from Late Pleistocene (Rancholabrean) Cave and Karst Deposits in Florida

The process of cave formation and destruction/collapse in Florida appears to have occurred rather rapidly in geologic time. Dry caves in Florida containing surficial deposits that have produced vertebrate fossils are exclusively late Pleistocene in age (<250 ka) and are referred to the Rancholabrean based on the presence of *Bison* or other mammals typical of this NALMA (Morgan and Hulbert, 1995). Late Pleistocene subaerial cave sites (i.e., not underwater) containing vertebrate fossils that retain an opening to the surface, fitting the definition of a cave, are not numerous in Florida, including fewer than 10 sites, the best known of which are: Surprise Cave, Alachua County; Eichelberger Cave and Mefford Cave, Marion County; and Saber-tooth Cave, Citrus County, all located in the Florida peninsula; and Peccary Tooth Cave near Florida Caverns State Park in Jackson County in the Florida panhandle (Simpson, 1928; Webb, 1974; Morgan and Hulbert, 2008; Gillette and Means, personal communication). Only two of those cave sites, Surprise Cave and Peccary Tooth Cave, contain substantial bat faunas (Appendix). The fossil bats from these caves mostly consist of vespertilionids that still occur in Florida, although the presence of the gray bat *Myotis grisescens* in Surprise Cave is extralimital, about 300 km southeast of the southernmost current record of this species in Jackson County in the Florida panhandle (Marks and Marks, 2006).

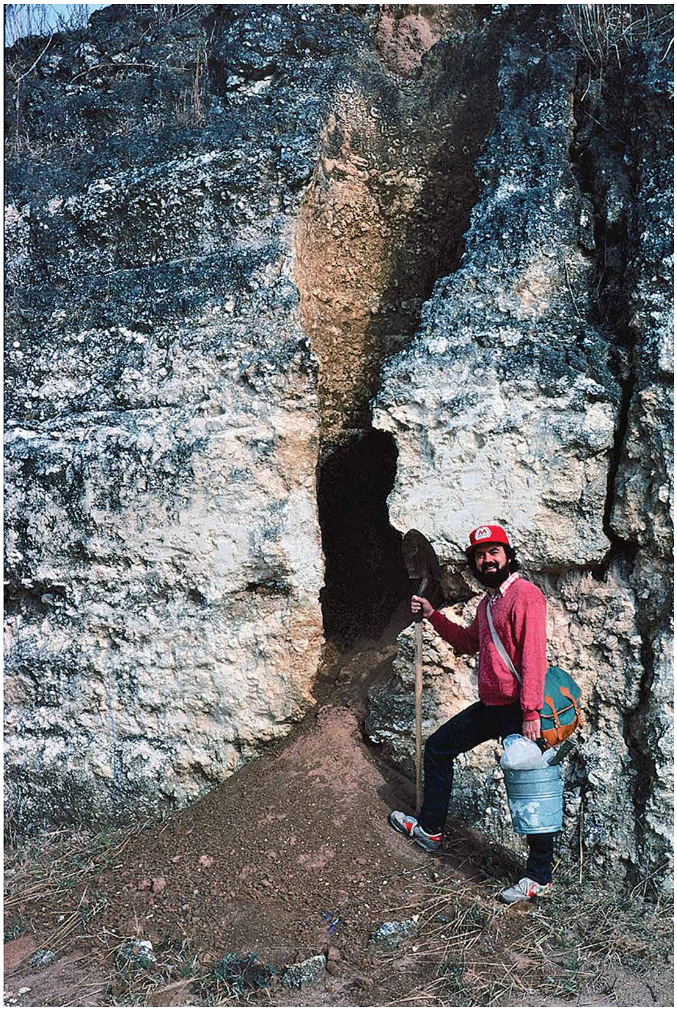


Figure 10. Karst fissure deposit, Haile Quarry complex, Alachua County, Florida. Reddish brown sands and clays deposited in a former cave contained late Pleistocene vertebrate fossils, including bats. The fissure is formed in the marine Eocene Ocala limestone. GSM for scale.

Groundwater levels are generally high in Florida and many caves are submerged (Scott et al., 2004). No dry caves currently occur in the southern third of the Florida peninsula and the Florida Keys (Morgan, 2002). Many of these underwater caves and springs would have been subaerial during the late Pleistocene low sea level stand (maximum of ~120 m below current sea level) that corresponded with lower regional water tables. Sea level began rising in the late Pleistocene and reached its current level in the early Holocene, flooding many previously dry caves and cave/spring complexes in Florida. Underwater caves greatly outnumber dry caves in northern Florida (Scott et al., 2004). Beginning in the 1960s, paleontologists from the FLMNH began working with scuba divers throughout northern Florida to recover vertebrate fossils from rivers, springs, underwater caves, and water-filled sinkholes (Webb, 1974). These underwater sites have mostly produced large vertebrates, but a few are known to contain late Pleistocene deposits with bats, including Devil's Den in

Levy County (Martin and Webb, 1974) and Rock Springs in Orange County (Ray et al., 1963; Wilkins, 1983). Both sites were subaerial caves when they were inhabited by bats in the late Pleistocene during a period of lower sea level and correspondingly lower regional water tables.

In the early 1960s, scuba-diving paleontologists H. K. Brooks and Clayton Ray recovered late Pleistocene vertebrates in Devil's Den, a water-filled sinkhole/cave complex with a lateral passage at about 20 m in depth. Devil's Den has produced a large sample of Rancholabrean fossils, in particular several skeletons of the extinct Florida cave bear, *Tremarctos floridanus* (Kurtén, 1966), as well as four species of bats, *Myotis* cf. *austroriparius*, *M. grisescens*, *Pipistrellus* (*Perimyotis*) *subflavus*, and yellow bat cf. *Lasiurus* (*Dasypterus*) *intermedius* (Martin and Webb, 1974). As with the record of *M. grisescens* from Surprise Cave, the Devil's Den record of the gray bat is several hundred kilometers south and east of its current southernmost occurrence in the Florida Caverns area near Marianna in the Florida panhandle (Marks and Marks, 2006). In 1957, Jack Todd recovered fossil vertebrates from Rock Springs, an underwater spring and cave complex (Ray et al., 1963; Wilkins, 1983; Morgan, 1991, 2002). Rock Springs has produced over 25 species of both small and large mammals (Wilkins, 1983) and a remarkable sample of fossil birds, with over 1,000 specimens representing 35 species (Woolfenden, 1959). Rock Springs has produced two species of cave-dwelling bats, the extralimital mormoopid, *Mormoops megalophylla*, and *Myotis austroriparius*. *M. megalophylla* is no longer found in Florida or elsewhere in the eastern US. It is primarily a tropical American species, occurring as far north as southwestern Texas. We are certain that further exploration of underwater caves in Florida will continue to yield important samples of fossil vertebrates, including bats.

More than 25 separate late Pleistocene karst deposits have been documented from the Haile Quarry complex in Alachua County, northern peninsular Florida, an area covering several square kilometers with more than 20 commercial limestone quarries. FLMNH paleontologists have assigned each of these quarries a number (e.g., Haile 7), and within a quarry each separate karst deposit is given a letter (e.g., Haile 7C is the third named karst deposit within Haile Quarry 7). The Haile Quarry complex also contains several older middle and early Pleistocene (Irvingtonian and Blancan) and late Miocene (Hemphillian) karst deposits containing vertebrate fossils (see next section). Other areas of the Florida peninsula with numerous fossiliferous late Pleistocene karst deposits include: Arredondo (11 sites) and Kanapaha (6 sites) in Alachua County; Reddick (7 sites) in Marion County; Lecanto (3 sites) in Citrus County; Coleman (5 sites) in Sumter County; and 2 sinkhole sites, Cutler Hammock and Monkey Jungle Hammock, in Dade County, southernmost peninsular Florida (Webb, 1974; Morgan. 1991, 2002; Emslie and Morgan, 1995; Morgan and Hulbert, 2008).

Florida late Pleistocene (Rancholabrean) karst deposits document several species of extinct and extralimital species of bats (Appendix), and in this regard, the Florida record bears more similarity to the Late Quaternary bat record of the West Indies than to the remainder of continental North America. The large extinct vampire bat, *Desmodus stocki*, occurs in four late Pleistocene karst deposits in northern peninsular Florida, Arredondo 2, Haile 1A, and Haile 11B in Alachua County; and Reddick 1 in Marion County (Morgan, 1991). This large vampire bat was originally described as *Desmodus magnus* from Reddick 1 (Gut, 1959), but has since been shown to be a synonym of *D. stocki* (Hutchison 1967; Morgan, 1991), described the previous year from San Josecito Cave in northern Mexico (Jones, 1958), and also known from about a dozen other late Pleistocene caves sites in the southwestern US and Mexico (Ray et al., 1988). A second extinct species, the mormoopid, *Pteronotus pristinus*, occurs in Monkey Jungle Hammock, a late Pleistocene sinkhole deposit in southernmost Florida, (Morgan, 1991, 2002). *P. pristinus* is otherwise known only from Late Quaternary cave deposits in Cuba (Silva Taboada, 1974), and represents the only record of the tropical genus, *Pteronotus*, in the US. Late Pleistocene extralimital records of bats from Florida include two other primarily tropical species, the mormoopid, *Mormoops megalophylla*, and the large molossid, *Eumops underwoodi*. *M. megalophylla* has been identified from three Florida late Pleistocene karst-derived deposits, Rock Springs in Orange County in central Florida, an underwater cave, as described above (Ray et al., 1963; Wilkins, 1983; Morgan, 1991); and two karst sinkhole deposits, Cutler Hammock and Monkey Jungle Hammock in Dade County in the southernmost peninsula (Morgan, 1991, 2002). *M. megalophylla* no longer occurs in Florida, with the closest mainland (overland) population from southwestern Texas about 2,000 km west of Florida. As noted above, there are also six extirpated populations of *M. megalophylla* from the West Indies where this mainland Neotropical species also no longer occurs. It is possible (likely?) that the Florida late Pleistocene population of *M. megalophylla* dispersed from the West Indies, probably Cuba or the northern Bahamas (Abaco and Andros), which are only a few hundred kilometers east (Bahamas) or south (Cuba) of southern peninsular Florida. The origin of the extirpated populations of *M. megalophylla* from both Florida and the West Indies could eventually be determined through the analysis of ancient DNA. The Cutler Hammock and Monkey Jungle Hammock sinkholes were both part of extensive cave systems in the late Pleistocene based on the abundance of cavernicolous bats in these deposits, including the vespertilionids, *Eptesicus fuscus* and *Myotis austroriparius*, and the mormoopids, *M. megalophylla* and *P. pristinus* (Morgan, 1991, 2002). These two vespertilionids no longer occur in the southern third of the Florida peninsula because they require caves for roosting, and this region now lacks dry caves. A living species of a large molossid, Underwood's bonneted bat, *Eumops underwoodi*, was identified from Lecanto 2A, a late Pleistocene karst deposit in central Florida (Morgan, 1991). *E. underwoodi* is primarily a tropical bat and is no longer found

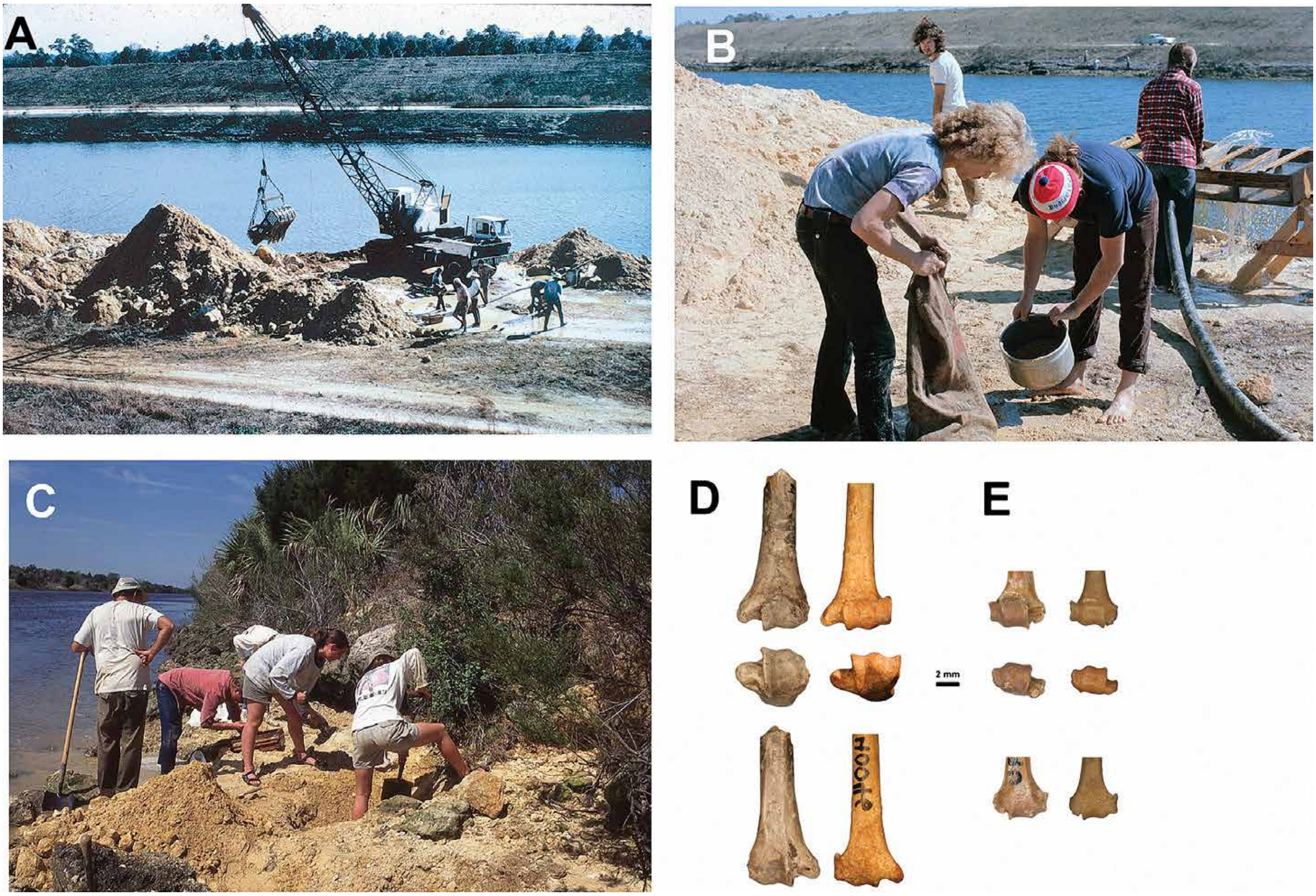


Figure 11. Inglis fossil sites, along the now-abandoned Cross-Florida Barge Canal, Citrus County, Florida, early Pleistocene (late Blancan NALMA). (A, B) Field crew working the Inglis 1A site. (A) Dragline removing in-place sediment from Inglis 1A. (B) Field crew screenwashing sediments from Inglis 1A. (C) Field crew excavating the Inglis 1C site. (Photos in A, B courtesy of David Webb; photo in C courtesy of Steven Emslie.) (D) Distal ends of the humerus of vampire bats, genus *Desmodus*, in anterior, distal, and posterior views, from top to bottom: *D. archaeodaptes*, Inglis 1A (right) and *D.* aff. *draculae*, El Breal de Orucual, late Pliocene/early Pleistocene of Venezuela (left) (Photos from Czaplewski and Rincon, 2020). (E) Distal ends of the humerus of pallid bats, genus *Antrozous*, in anterior, distal, and posterior views, from top to bottom: *Antrozous* sp. from Inglis 1A (left) and modern specimen of *A. pallidus* (right).

in Florida, now occurring from southern Arizona to Nicaragua. We hypothesize that an overland dispersal route from the southwestern United States of about 2,500 km is more likely than the somewhat shorter (~1,500 km) but overwater dispersal route across the Gulf of Mexico from southeastern Mexico or northern Central America.

Chiroptera from Early and Middle Pleistocene (Blancan and Irvingtonian) Karst Deposits in Florida

No cave deposits in Florida are older than late Pleistocene, but there are more than 25 karst-derived vertebrate faunas of early to middle Pleistocene age (Blancan and Irvingtonian NALMAs) from peninsular Florida, several of which represent former cave deposits based on the abundance of bats, as well as geologic and taphonomic features of the sites (Morgan and Hulbert, 2008), including Coleman 2A, Haile 16A, Haile 21A, and Inglis 1A (Appendix). The late Irvingtonian (~0.25–0.5 Ma) Coleman 2A LF from Sumter County in central Florida is a sinkhole deposit that produced three extant species of cave-dwelling vespertilionid bats, *Myotis austroriparius*, *Pipistrellus* (=*Perimyotis*) *subflavus*, and Rafinesque's big-eared bat, *Plecotus* (=*Corynorhinus*) *rafinesquii*, all of which still live in the Florida peninsula (Martin, 1974). Two early Pleistocene (early Irvingtonian, ~1.0–1.6 Ma) karst deposits, Haile 16A and Haile 21A, are sinkholes or fissures in the Haile Quarry complex in Alachua County, both of which produced fossils of the extinct vampire bat, *Desmodus archaeodaptes*, with Haile 21A as the type locality. This vampire is a smaller species than the late Pleistocene *D. stocki*, similar in size to the living *D. rotundus* but differing in several cranial characters (Morgan et al., 1988). Haile 16A and Haile 21A also produced large samples of *M. austroriparius*, indicating these two karst deposits originally formed as caves.

The most diverse NA chiropteran fauna of early Pleistocene age (late Blancan) is from Inglis 1A, a karst deposit located along the now-abandoned Cross-Florida Barge Canal in Citrus County, about 10 km inland from the Florida Gulf Coast. The site consisted of layers of sand and clay filling a large solution cavity in limestone of the marine Eocene

Inglis Formation. Figures 11A–C show field crews excavating and screenwashing the Inglis 1A site and the nearby Inglis 1C site of similar age and origin (Ruez, 2002). Inglis 1A documents the earliest known occurrence of the vampire bat, *Desmodus archaeodaptes* (Fig. 11D), together with six genera of vespertilionid bats, *Antrozous* (Fig. 11E), *Corynorhinus*, *Eptesicus*, *Lasiurus*, *Myotis*, and *Perimyotis* (Morgan, 1991). The abundance of cave-dwelling bats, in particular species of *Corynorhinus*, *Myotis*, and *Perimyotis*, indicates the Inglis 1A site was a part of an extensive cave system in the early Pleistocene. Inglis 1A documents the only Blancan record of the big-eared bat genus *Corynorhinus* and one of only two Blancan sites with *Perimyotis*. The Inglis 1A record of *Antrozous* represents the first occurrence of this genus in eastern North America. The closest modern record of the pallid bat, *Antrozous pallidus*, is in central Texas more than 1,500 km west of the Florida peninsula, although a related subspecies or species, *Antrozous pallidus koopmani* or *A. koopmani*, occurs in Cuba (Silva Taboada, 1976, 1979; Silva and Vela, 2009; García and Mancina, 2011; Orihuela et al., 2020a, b). Morgan and Emslie (2010) documented a number of extralimital mammals and birds from Inglis 1A that had western affinities, including *Antrozous* and the jackrabbit, *Lepus*.

The late Blancan Inglis 1A and early Irvingtonian Haile 16A sites are notable for their diverse faunas of large mammals of South American origin that participated in the Great American Biotic Interchange (GABI), including (Webb, 1976; McDonald, 2005; Morgan, 2005): three genera of ground sloths, *Eremotherium*, *Megalonyx*, and *Paramylodon*; the pampathere or giant armadillo, *Holmesina*; and a large, extinct species of the extant armadillo genus *Dasypus*. Additional GABI species from these two faunas include: the giant, flightless predatory bird, *Titanis*, a member of the otherwise endemic South American family Phorusrhacidae; the large glyptodont, *Glyptotherium*; and the capybara, *Neochoerus*, in Inglis 1A and the smaller glyptataeline glyptodont, *Pachyarmatherium*, in Haile 16A. Morgan (1991) hypothesized that *Desmodus*, a phyllostomid bat of South American origin, dispersed into NA as a participant in the GABI after the connection of North and South America at the Panamanian Isthmus at about 5 Ma, arriving in Florida in the early Pleistocene (~ 2 Ma) at Inglis 1A, following its favored prey species, probably ground sloths or other large xenarthrans, northward.

Chiroptera from Oligocene and Miocene Karst Deposits in Florida

North American fossil deposits of karst origin that contain bats of Miocene and Oligocene age are known almost exclusively from peninsular Florida (Czaplewski et al., 2008; Morgan and Czaplewski, 2012, 2023). The taphonomy of these karst deposits, which include sinkhole fills, fissure deposits, and isolated sediment pockets in solution cavities, as well as the frequent presence of bat fossils, indicates their prior existence as caves. Florida early Miocene and Oligocene (~18–30 Ma) karst deposits provide important data pertaining to the mid Cenozoic chiropteran fauna of southeastern NA, including the earliest New World representatives of several families of Neotropical bats: sac-winged bats (Emballonuridae), ghost-faced and mustached bats (Mormoopidae), and funnel-eared bats (Natalidae), as well as the extinct family Speonycteridae. All of these bats indicate a warmer tropical to subtropical climate in Florida during the Oligocene and early Miocene. The oldest cave-dwelling bats in NA (~26–30 Ma) were also members of these same four families. The richest pre-Pleistocene bat faunas from Florida are from three karst sites, the early Oligocene I-75, late Oligocene Brooksville 2, and early Miocene Thomas Farm (Czaplewski et al., 2003b; Morgan and Czaplewski, 2003, 2012, 2023; Czaplewski and Morgan, 2012; Morgan et al., 2019). These sites are discussed here from oldest to youngest.

The I-75 site was discovered in a roadcut on Interstate Highway 75 (I-75) in Gainesville, Alachua County, northern peninsular Florida, and was destroyed by road-building activities shortly thereafter. The fossiliferous sediments in the I-75 site consisted of massive, dark, silty clays, deposited in a small karst solution feature 5 m in diameter and 2 m deep, developed in marine Eocene limestone. Considering the small size of the fossiliferous deposit, the I-75 site has a diverse vertebrate fauna composed of about 35 terrestrial and freshwater species: toads, salamanders, turtles, lizards, snakes, and about 20 species of mammals, including seven species of bats (Patton, 1969; Hayes, 2000; Czaplewski and Morgan, 2012; Morgan and Czaplewski, 2012, 2023; Morgan et al., 2019). Mammalian biochronology confirms that I-75 is the oldest land vertebrate fauna known from Florida, dating to the early Oligocene (late Whitneyan NALMA; 30–31 Ma; Patton, 1969; Prothero and Emry, 2004; Morgan and Czaplewski, 2023). Most of the bats from I-75 belong to families now found in the New World tropics but no longer occur in Florida, including: an extinct genus and two new species of Emballonuridae, *Oligopteryx floridanus* and *O. hamaxitos*, representing the earliest known Neotropical members of the family (Morgan and Czaplewski, 2023); an extinct genus and species, *Koopmanycteris palaeomormoops*, of Mormoopidae, the oldest known member of this family (Morgan et al., 2019); and an indeterminate genus and species representing the earliest record of the family Natalidae (Morgan and Czaplewski, 2003). An extinct genus and two new species identified from I-75, *Speonycteris aurantiadens* and *S. naturalis*, belong to the extinct family Speonycteridae that also has Neotropical affinities and, together with the mormoopid, *Koopmanycteris*, are the oldest known members of the superfamily Noctilionoidea (Czaplewski and Morgan, 2012). The abundance of bats in the I-75 LF, in particular, the Mormoopidae, which are primarily obligate cave-dwelling species (Smith, 1972), the abundance of other small terrestrial vertebrates, and the karst structure of the fossil deposit, all strongly indicate this site originally formed in a cave.

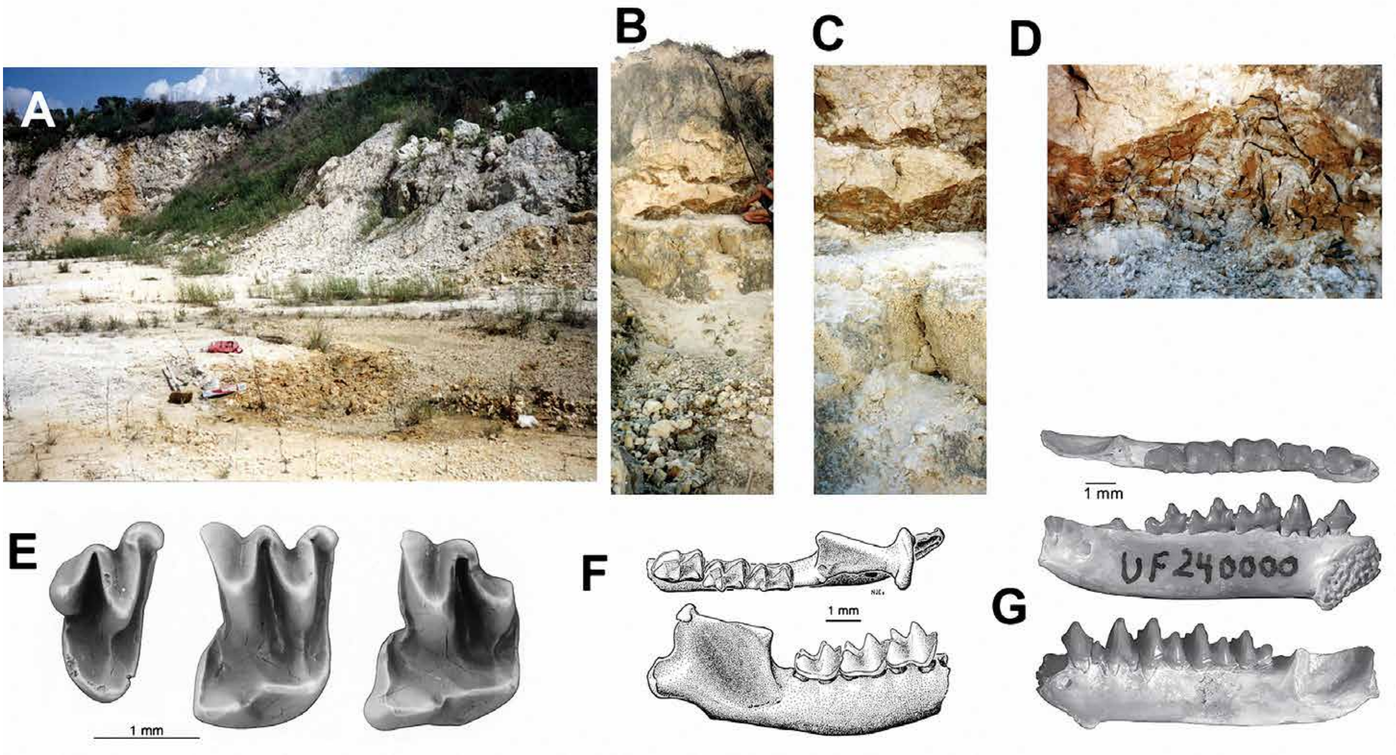


Figure 12. Brooksville 2 Quarry, Hernando County, Florida. (A) Overview of the Brookville 2 Quarry. (B–D) Series of three photos showing the same fissure deposit in the Brooksville Quarry, with each photo a closer view (from left to right). (Photos A–D courtesy of Glynn Hayes.) (E) Occlusal views of three upper molars of *Oligopteryx floridanus*, an extinct genus and species of Emballonuridae (Photos from Morgan and Czaplewski, 2023). (F) Mandible in occlusal view (top) and lateral view (bottom) of *Koopmanyteris palaeomormoops,* oldest member of the Mormoopidae (Illustrations from Morgan et al., 2019). (G) Mandible in occlusal, medial, and lateral views, from top to bottom, of *Speonycteris aurantiadens* in the extinct family Speonycteridae and oldest member of the Neotropical Noctilionoidea (Photos from Czaplewski and Morgan, 2012).

The Brooksville 2 site was discovered in a limestone quarry near Brooksville, Hernando County, central Florida (Fig. 12A). The site consists of clays and sands filling several small karst solution features or fissure deposits developed in the marine Oligocene Suwannee Limestone (Hayes, 2000; Figs. 12B-D). Although specimens of larger vertebrates were found on the surface, FLMNH field crews collected the fossils primarily by screenwashing because of the abundance of microvertebrates. The vertebrate assemblage from Brooksville 2 consists of frogs, lizards, snakes, and a diverse fauna of both large and small mammals, including five species of bats (Hayes, 2000; Czaplewski and Morgan, 2012; Morgan et al., 2019; Morgan and Czaplewski, 2023). The mammalian biochronology of the Brooksville 2 LF indicates a late Oligocene age (early Arikareean NALMA; 26-28 Ma; Hayes, 2000). Four of the five species of bats from Brooksville 2 are the same species with tropical affinities found at I-75: the emballonurids, *Oligopteryx floridanus* (Fig. 12E) and *O. hamaxitos*; the mormoopid, *Koopmanycteris palaeomormoops* (Fig. 12F); and the speonycterid, *Speonycteris aurantiadens* (Fig. 12G), all of which were described as new genera and species from Brooksville 2 (Czaplewski and Morgan, 2012; Morgan et al., 2019; Morgan and Czaplewski, 2023). As with I-75, the abundance of bats, particularly the mormoopid, *Koopmanycteris*; the abundance of small terrestrial vertebrates; and the karst origin of the solution features and sediments, all point to the Brooksville site having formed as a cave.

The Thomas Farm site near Bell in Gilchrist County, northern peninsular Florida, is the best known and most diverse early Miocene (early Hemingfordian NALMA; ~18 Ma) vertebrate fauna in eastern NA. The site consists of clays and sands filling a 30 m-deep, vertical-walled sinkhole, developed in marine Eocene limestone (Pratt, 1989, 1990; Figs. 13A-C). Thomas Farm has produced a diverse vertebrate fauna of about 90 species, with more than 20 species of large mammals and nearly 70 species of small vertebrates consisting of frogs and toads, salamanders, lizards, snakes, one of the largest Miocene avifaunas in NA, shrews, rodents, and a large sample of bats (Pratt, 1989, 1990; Czaplewski and Morgan, 2000; Morgan and Czaplewski, 2003, 2012, 2023). Many of the small vertebrates appear to have been deposited in a former cave system developed in the wall of the sinkhole (Fig. 13C), either as a coprocoenosis derived from the scat of small mammalian carnivores, the pellets of raptorial birds, or through the natural accumulation of carcasses on a cave floor in the case of the bats (Pratt, 1989). Thomas Farm has the largest bat sample from any Tertiary fossil deposit in NA, with more than 3,000 identified specimens (University of Florida/

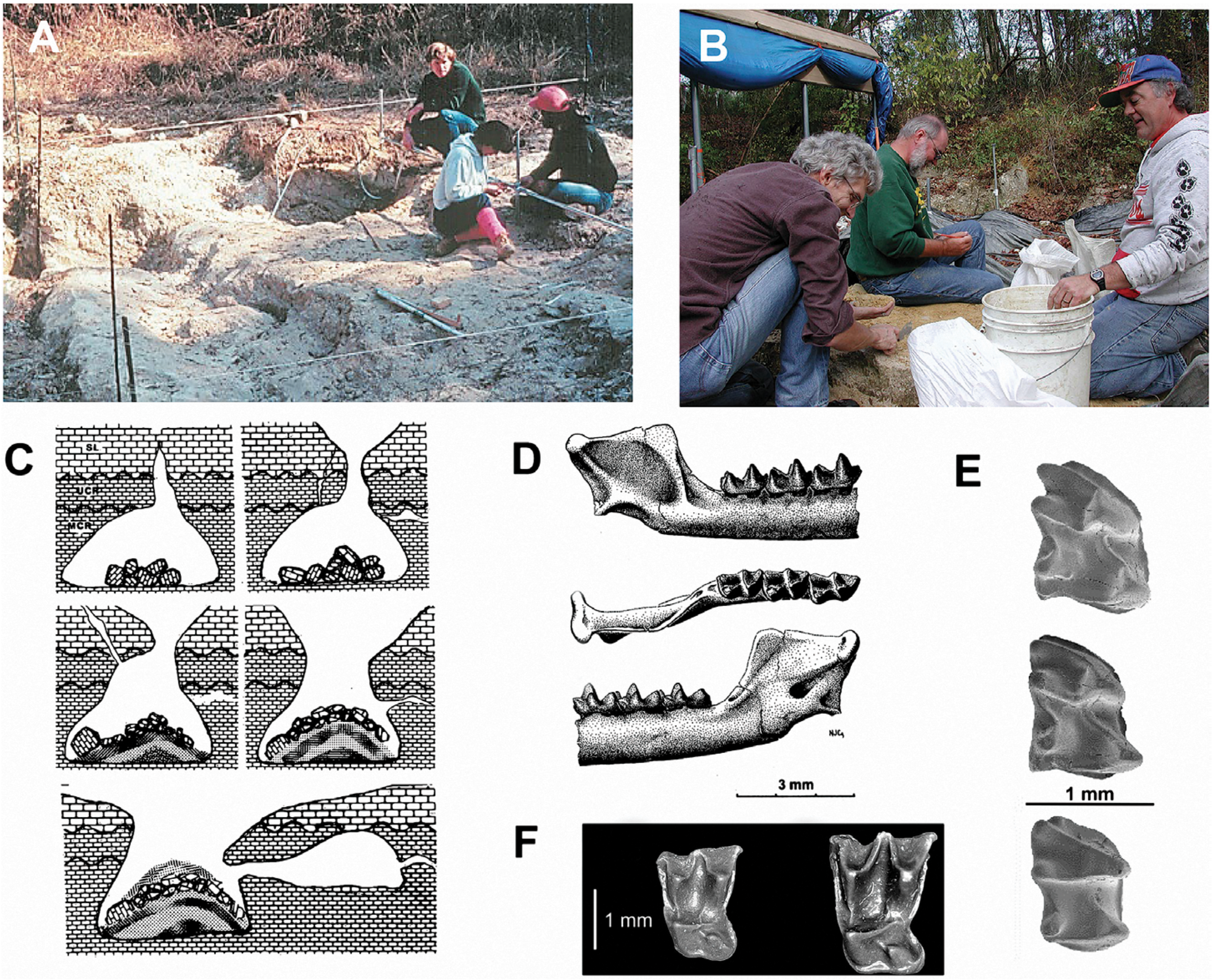


Figure 13. Thomas Farm site, a karst sinkhole-cave complex, Gilchrist County, Florida, early Miocene, (early Hemingfordian). (A) Steven Emslie (top), Ann Pratt (left), and GSM (right) excavating the Thomas Farm site (Photo courtesy of Richard Hulbert). (B) NJC (left), Arthur Poyer (center), and GSM (right) collecting sediments to screenwash for fossil bats (Photo courtesy of Erika Simons). (C) Schematic cross-sections showing how the Thomas Farm site formed as a 30 m deep sinkhole in Eocene marine limestone. Lowermost cross-section shows a cave in the wall of the sinkhole. Layers of sand and clay filled the sinkhole, including cave sediments with bat fossils (Illustrations from Pratt, 1990). (D) Type mandible of *Primonatalus prattae*, in lateral, occlusal, and medial views, from top to bottom, an extinct genus and species of bat in the endemic Neotropical family Natalidae (Illustrations from Morgan and Czaplewski, 2003). (E) Occlusal views of three lower molars of *Floridopteryx poyeri*, a new genus and species of bat in the tropical family Emballonuridae (Photos from Morgan and Czaplewski, 2023). (F) Occlusal views of upper molars of two undescribed species of Molossidae (Photos from Czaplewski et al., 2003b).

FLMNH vertebrate paleontology database) representing at least nine species. Four of the Thomas Farm bats belong to families with Neotropical affinities: an extinct genus and species of Natalidae, *Primonatalus prattae* (Morgan and Czaplewski, 2003; Fig. 13D); an extinct genus and species of Emballonuridae, *Floridopteryx poyeri* (Morgan and Czaplewski, 2023; Fig. 13E); and two undescribed species of Molossidae (Czaplewski et al., 2003b; Fig 13F). The other five species belong to the Vespertilionidae, three of which are extinct genera and species known only from Thomas Farm, *Karstala silva*, *Miomyotis floridanus*, and *Suaptenos whitei* (Lawrence, 1943; Czaplewski and Morgan, 2000). The remarkable sample of bats, in particular the natalid *Primonatalus prattae*, a member of an endemic Neotropical family (Natalidae) in which all living species are obligate cave dwellers (Morgan and Czaplewski, 2003; Tejedor, 2011), supports data from the geology, taphonomy, and remainder of the vertebrate fauna that Thomas Farm formed, at least in part, as an extensive cave system.

The I-75, Brooksville 2, and Thomas Farm sites provide important data on the deep-time evolution of the North American chiropteran fauna, including the earliest records of the taxonomic diversity and community structure of NA mid-Cenozoic bats (between 18 and 30 Ma). The Oligocene I-75 and Brooksville 2 faunas document the oldest members of several endemic Neotropical bat families, as well as the earliest evidence of cave-dwelling bats in the New World. Although there are older bats in NA from several Eocene faunas, these fossils are from non-karst depositional environments, mostly from lacustrine or lake sediments, and thus, we are not able to determine if they may have been cave-roosting species. However, at least one Eocene species of archaic bat of indeterminate family, *Vielasia sigei,* has been found abundantly preserved in cave sediments in a locality in France, indicating that some bats had already adopted caves by about 50 Ma (Hand et al., 2023), and other bat fossils are widely known from Eocene karstic deposits elsewhere in Europe as well as in Africa and Asia (e.g., Sigé & Legendre, 1983; Maitre, 2014; Ravel et al., 2013, 2016). The Florida Oligocene (~26-30 Ma) chiropteran faunas from I-75 and Brooksville 2 are composed almost exclusively of species with tropical affinities (Emballonuridae, Mormoopidae, and Speonycteridae), whereas the early Miocene (~18 Ma) bat fauna from Thomas Farm is 10 million years younger and about evenly divided between species with tropical (Emballonuridae, Natalidae, Molossidae) and temperate (Vespertilionidae) affinities. The transition from a mostly tropical chiropteran fauna in Florida in the Oligocene to a combination of tropical and temperate species in the early Miocene, was followed by the disappearance of tropical bats in Florida by the middle Miocene. (Morgan and Czaplewski, 2023). As noted above, a few extralimital species of bats with tropical affinities are recorded from Florida late Pleistocene faunas.

There is a long gap in the fossil record of bats in Florida after the Thomas Farm site, extending from the early Miocene to the end of the Pliocene (~18–2.6 Ma), during which there are no sites of karst origin that contain extensive chiropteran faunas, suggesting a lack of former cave deposits during this time interval. The sparse sample of bats from Florida middle Miocene through Pliocene sites consists entirely of vespertilionids (Morgan and Czaplewski, 2012). There are numerous vertebrate faunas of karst origin in northern peninsular Florida during this time period, particularly the late Miocene (Clarendonian and Hemphillian NALMAs; ~7–10 Ma), including: Love Bone Bed, McGehee Farm, Haile 19A, Mixson's Bone Bed, Tyner Farm, and Withlacoochee River 4A. These sites formed in a limestone karst terrain but not in caves, including sinkhole ponds, nearshore marine or estuarine lagoonal or deltaic deposits, fluvial deposits, natural traps, or other taphonomic settings that contained few or no bats (Morgan and Hulbert, 2008). The geologic explanations for the lack of karst deposits of cave origin in Florida from the middle Miocene through the late Pliocene are varied but would have included high water tables during periods of high sea level that would have flooded caves, periods of even higher sea level that would have completely submerged the Florida peninsula, and the deposition of a thick overburden of clastic sediments (clays and sands) overlying the Paleogene carbonate bedrock that would have impeded cave and karst development.

FUTURE DIRECTION OF RESEARCH ON NORTH AMERICAN FOSSIL BATS

Late Pleistocene cave deposits containing bats and other vertebrate fossils are common throughout North America, as reviewed above, and additional fossiliferous caves continue to be found as cavers and cave paleontologists explore caves throughout the continent. Early to middle Pleistocene (Irvingtonian) cave deposits are much less common in NA, and very few sites of this age with significant bat samples have been discovered over the past several decades. Prior to the early Pleistocene (early Irvingtonian; ~1 Ma), cave deposits with Tertiary vertebrate fossils are unknown anywhere in NA and fossiliferous karst deposits are rare, except in Florida. Unlike the Pleistocene record, most Tertiary fossil sites from NA containing bats, once again exclusive of Florida, occur in open or non-karst depositional settings, including paleosol, alluvial, fluvial, or lacustrine deposits, and mainly consist of small samples of fragmentary specimens, rather than larger samples of better-preserved bat fossils typical of caves and karst depositional environments (Czaplewski et al., 2008). An exception is the earliest known bats from NA that consist of several remarkably complete skeletons from early Eocene (~50-52 Ma) lake deposits in the Green River Formation of Wyoming (Jepsen, 1966; Simmons et al., 2008; Rietbergen et al., 2023). Fossil bats occur sporadically in western NA in the Eocene, Oligocene, Miocene, and Pliocene, almost all of which are from non-karst deposits (Czaplewski et al., 2008). Bats older than late Pleistocene are unknown from the West Indies, and only a few pre-late Pleistocene records of bats are known from Mesoamerica, none of which are from cave or karst deposits.

As we have documented for Florida, former caves now preserved as various types of karst features, such as sinkholes, fissures, or solution cavities, often preserve sediments that contain fossils of bats. Because of an abundance of fossil-bearing karst deposits, ranging in age from early Oligocene to late Pleistocene, Florida has the richest fossil chiropteran record in North America (Czaplewski et al., 2008; Morgan and Hulbert, 2008). However, for reasons still unclear to us, similar karst deposits containing vertebrate fossils are rare or absent elsewhere in NA, particularly during the Tertiary. Conard Fissure in Arkansas is a notable middle Pleistocene (Irvingtonian) karst fissure deposit containing an abundant bat fauna (Brown, 1908). As described by Winkler and Gose (2003), the early Pleistocene (early/medial Irvingtonian) Fyllan Cave site in Texas consists of sediments preserved in a small solution cavity representing a former cave developed in Cretaceous limestone in an abandoned quarry. Prior to the Irvingtonian, there are only a handful of early Quaternary and Tertiary karst deposits in NA, outside of Florida, that contain vertebrate fossils and even fewer that contain bats. Considering the widespread occurrence of potential karst areas throughout the US (Fig. 1), the paucity of Tertiary karst deposits containing vertebrate fossils in puzzling, especially taking into account the widespread occurrence throughout southern Europe of Tertiary karst sites containing bats (Sigé and Legendre, 1983; Gunnell and Simmons, 2005).

It is also worth noting that pre-late Pleistocene cave and karst deposits containing bats are unknown from South America, which is a major contributing factor to the poor Tertiary chiropteran record on that continent (Morgan and Czaplewski, 2012, 2023). However, the potential for such sites in South America has been hinted at by previous researchers (Hartenberger et al., 1984). The famous fossiliferous beds of late Paleocene age at low elevation near the Brazilian coast at Itaboraí have such potential and have produced diverse notometatherians and eutherians, including microvertebrates (Bergqvist et al., 2008), but are apparently too old to preserve bats. No large-scale historical geological settings and situations similar to the bat-rich Florida peninsula or Quercy phosphorites and other fissure fillings in Europe are known in South America, but perhaps small areas of karstified limestone similar to those of the continental interior (such as NA sites mentioned below) could occur along the Andean cordillera where the limestones have been uplifted and abut Paleogene or Neogene sedimentary rocks? Perhaps searching by remote sensing such as the approach explored by Anemone et al. (2011a, 2011b) and Emerson and Anemone (2012) would help?

The distribution of karst terrain across the Earth's continents is uneven (Williams and Ford, 2006) and could partly explain the presence or absence of cave- or karst-related bat fossils in each. Although we have not systematically or even cursorily examined these deposits or why they bear or lack vertebrate fossils including bats, we mention a few of the more notable Tertiary karst deposits on other continents that have produced important samples of fossil bats. The rich record from southern Europe is mentioned above. The famous Riversleigh World Heritage Area in Australia consists of an extensive region of limestone with karst deposits that holds a treasure-trove of Oligocene and Miocene vertebrate fossils including a high diversity of fossil bats (e.g., Hand and Kirsch, 2003; Hand et al., 2005, and references therein). Less well searched but fossiliferous karstic rocks and formations of Cenozoic age also occur in many parts of Africa including the circum-Mediterranean region, like those in southern Europe (Gunnell et al., 2016). Fossil bats are known from Neogene deposits in Angola, Botswana, and Namibia in southwestern Africa, with the most notable being the Otavi Mountain karst in Namibia that has produced large and diverse samples of Miocene bats (e.g., Pickford et al., 1994; Rosina and Pickford, 2019). Karst deposits in Asia have also produced fossil bats (e.g., Ravel et al., 2013).

We briefly mention two late Pliocene or early Pleistocene (Blancan) karst deposits containing vertebrate fossils in western North America. The Blancan Anita LF was derived from a karst fissure deposit in the Permian Kaibab Limestone in the Val Verde Copper Mine, Coconino County, northern Arizona (Hay, 1921). The Anita fauna was collected in the early 1900s, long before the advent of screenwashing, so very small vertebrates, such as bats and shrews, are absent from the fauna. However, the abundance of rabbits from Anita (Hay, 1921; GSM, personal observation), as well as the occurrence of three species of medium-sized rodents, two sciurids, and the woodrat, *Neotoma*, suggests that smaller mammals, including bats, were probably present in the Anita fissure deposit but were not collected. Unfortunately, the Anita site no longer exists. The Richmond Hill fissure deposits, from a gold mining region in the northern Black Hills, Lawrence County, southwestern South Dakota, have produced a Blancan mammal fauna, including small vertebrates (Guthrie, 2005; J. Mead and N. Fox, personal communication). Jim Mead, Chris Jass, and Nate Fox are planning further work on the small vertebrate fauna from the Richmond Hill fissure deposits (see Mead et al., this volume). We are hopeful these sites may eventually produce Pliocene or early Pleistocene (Blancan) bats.

Within the past few decades, two latest Miocene or earliest Pliocene (latest Hemphillian NALMA) karst deposits have been discovered in the continental interior of eastern North America, the Gray Fossil Site in Tennessee and the Pipe Creek Sinkhole in Indiana. These two sites were discovered in the same way most Florida karst sites were first found, by excavation with heavy equipment. The Gray Fossil Site was uncovered during the construction of a road and the Pipe Creek Sinkhole was found in a commercial mining operation. Since their initial discovery, both sites have been carefully excavated by paleontologists and both contain diverse samples of small mammals and other small vertebrates collected by screenwashing. The Gray Fossil Site is a sinkhole pond or lake that formed in the Appalachian Valley and Ridge karst region composed of Paleozoic carbonate rocks. The Gray Fossil Site has produced a diverse latest Hemphillian vertebrate fauna (Wallace and Wang, 2004; Hulbert et al., 2009), including two species of vespertilionid bats: one tentatively referred to the living species, *Eptesicus fuscus*, one of the most common and widespread bats in NA, and a second smaller bat indeterminate at the genus and species levels (Czaplewski, 2017). Excavation and screenwashing for microvertebrates are ongoing at the Gray Fossil Site, so there is the potential for the recovery of additional bat specimens.

The Pipe Creek Sinkhole in Indiana is a sinkhole developed in a Silurian reef deposit in which a cave formed and then collapsed, eventually resulting in a sinkhole pond containing both freshwater and terrestrial vertebrates (Farlow et al., 2001). The Pipe Creek Sinkhole contains abundant microvertebrates, including a diverse rodent fauna with small cricetids and one species of each of rabbit and shrew (Farlow et al., 2001; Martin et al., 2002; Czaplewski et al., 2012).

Unfortunately, the Pipe Creek Sinkhole deposit appears to have been mined out and did not yield any bat fossils (J. O. Farlow, personal communication). We are not aware of any NA Eocene, Oligocene, or early- to middle-Miocene karst sites with vertebrate fossils, outside of Florida, although the NA Tertiary record of karst fossil deposits is surely incomplete.

In comparison with the remainder of the North American continent, which has fewer than 10 Tertiary karst deposits containing vertebrate fossils, the Florida peninsula has more than 30 vertebrate-fossil-bearing paleokarst deposits of Oligocene and Miocene age (none are known from the Pliocene) and another 20 sites of early Pleistocene age (late Blancan and early Irvingtonian) (Morgan and Hulbert, 2008). The geologic circumstances that have led to the development of an extensive karst terrain in Florida are discussed above and have resulted in an abundance of both dry and submerged caves, springs, and various types of paleokarst deposits such as sinkholes, solution cavities, and fissures (Lane, 1986; Florea, 2008; Fig. 9). Factors that have resulted in the discovery of large numbers of paleokarst fossil sites in Florida include: extensive commercial limestone mining operations in northern peninsular Florida, regular surveys of these mines by paleontologists from the FLMNH, a large contingent of avocational paleontologists who are continually scouring the Florida landscape in search of new fossil sites, the popularity of scuba diving in Florida rivers and springs, and a dedicated cadre of experienced cave divers.

A major underexploited source of fossil bats in NA is from underwater caves, which are numerous in Florida, the Yucatán Peninsula of Mexico, Belize, and Guatemala, and on islands throughout the Greater Antilles and Bahamas. Dan's Cave, Ralph's Cave, and Sawmill Sink on Abaco in the Bahamas (Fig. 7) and Oleg's Bat Cave in the Dominican Republic (Fig. 8) demonstrate the tremendous potential of underwater caves to produce large and well-preserved samples of fossil bats and other vertebrates (Steadman et al., 2007; Velazco et al., 2013; Soto-Centeno and Steadman, 2015). Other islands in the Bahamas, including Acklins, Andros, Eleuthera, Grand Bahama, and Mayaguana, contain underwater caves or blue holes that have produced fossils of extinct or extirpated tortoises, crocodiles, and rodents, and could potentially yield fossil bats (Morgan and Albury, 2013). We know from discussions with cave divers that underwater caves exist on other West Indian islands (e.g., Cuba, Puerto Rico, and Grand Cayman), but these caves have not been systematically explored for fossils. Several underwater caves or cenotes in the Yucatán Peninsula of Mexico have produced well-preserved samples of large mammals of late Pleistocene age, including ground sloths and carnivores from Hoyo Negro in the state of Quintana Roo (McDonald et al., 2017; Schubert et al., 2019), as well as bats (Cruz et al., 2024).

Late Pleistocene vertebrate fossils have been known from underwater caves and springs of karst origin in Florida since the 1930s, following the discovery of a skeleton of the American mastodon, *Mammut americanum*, in Wakulla Springs in the Florida Panhandle south of Tallahassee by Herman Gunter of the Florida Geological Survey. Beginning in the 1950s and 1960s, with the early development and refinement of scuba diving techniques, and continuing to the present, paleontologists from the FLMNH have worked with a large contingent of scuba divers to systematically survey the rivers, springs, sinkholes, and underwater caves of peninsular Florida for vertebrate fossils (Webb, 1974). Many rivers in Florida, including the Aucilla River, Ichetucknee River, Ocklawaha River, Peace River, Santa Fe River, St. Johns River, and Waccasassa River, among others, have produced large samples of late Pleistocene vertebrate fossils, some of which are derived from what are now underwater caves or karst deposits. However, for various reasons, including the difficulty in collecting fossils underwater using scuba gear, most of the fossil samples from Florida rivers consist of large mammals and other large vertebrates, with only limited samples of small vertebrates and few bats. Many Florida underwater sites in rivers and springs are either not of karst origin, or if karst in origin (e.g., sinkhole ponds/lakes), do not represent former dry caves and would not be expected to contain fossil bats.

Only three underwater fossil sites in Florida have been systematically collected for smaller vertebrates. The late Pleistocene (Rancholabrean) Page-Ladson site in the Aucilla River in the eastern Florida Panhandle produced a diverse sample of fish, amphibians, reptiles, birds, and small mammals, but no small rodents, shrews, moles, or bats (Webb and Simons, 2006). The absence of small vertebrates in the Page-Ladson fauna was almost certainly a result of the collecting technique in which unconsolidated sediments were "vacuumed" from the bottom of the Aucilla River using a dredge and then washed though a ¼-inch screen. Mammals in the size category of rabbits, squirrels, muskrats, and porcupines were collected using this technique (Webb and Simons, 2006), but few vertebrates smaller than ¼ inch, such as frogs, lizards, passerine birds, cricetid rodents, and bats, were recovered. Moreover, the late Pleistocene depositional setting of the Page-Ladson site in the Aucilla River was a sinkhole pond, which was probably not conducive to the preservation of bat fossils (Webb and Simons, 2006). The two Florida late Pleistocene underwater sites that have produced bats, Devil's Den and Rock Springs, are both underwater caves, not river deposits, as described in more detail above.

Most of the fossiliferous karst deposits in Florida have been discovered during commercial mining operations, as was three of the four Tertiary fossil sites from elsewhere in the US. The Pliocene Anita Fauna in Arizona was found in a fissure deposit in a copper mine, the Pliocene Richmond Hill fissure deposits in South Dakota occur in a gold mining region, and the latest Miocene/earliest Pliocene Pipe Creek Sinkhole is a sinkhole representing a former cave uncovered during limestone mining operations. Other karst sites have been uncovered during road building operations, including the latest Miocene/earliest Pliocene Gray Fossil Site in Tennessee and the early Oligocene I-75 Fauna in Florida, named for Interstate Highway 75 whose construction near Gainesville, Florida, led to the discovery of this site. Initial excavations for the now-abandoned Cross-Florida Barge Canal in the 1960s led to the discovery of 15 early Pleistocene (Blancan) karst sites near Inglis, just inland from the Florida Gulf Coast, Inglis sites 1A-1L and 2A-2C, all of which consist of sinkholes or fissure deposits developed in the marine Eocene Inglis Formation (Fig. 11). Other Florida Tertiary karst sites were uncovered during farming activities, including the Miocene Thomas Farm, McGehee Farm, and Tyner Farm.

However, not all early Pleistocene and Tertiary karst fossil deposits in Florida have been discovered essentially at random through mining, construction, or farming activities. A number of Florida karst sites were discovered during a systematic paleontological survey of Florida rivers by FLMNH paleontologists using scuba (Webb, 1974), including the late Oligocene Cow House Slough, late Miocene Withlacoochee River 4A, and several early Pleistocene sites in the Santa Fe River (Santa Fe River 1, 1B, 4, 8, 8A, 8C). Several important Florida karst deposits were discovered by avocational paleontologists who were scuba diving in search of fossils in Florida rivers, including the early Miocene Miller site, which has a small sample of bats in the families Molossidae and Vespertilionidae (Andreas Kerner, personal communication), and the early Pleistocene Waccasassa River 9A and Withlacoochee River 1A sites (Hulbert, 2010). Although these various types of karst sites are located in Florida, most of these field methods could be used to discover karst sites in other places in NA, particularly in areas with suitable karst geology (Figs.1A, B).

FINAL COMMENTS

We would like to make a plea to cavers, cave paleontologists, cave geologists, cave conservationists, scuba divers, and avocational paleontologists to help discover new cave and karst fossil sites in North America. A nationwide network of dedicated cavers, particularly groups associated with the National Speleological Society, find new cave fossil deposits on a regular basis. However, most of these sites occur in caves and the fossil deposits are late Pleistocene in age, improving the already robust record of NA late Pleistocene cave faunas. Older pre-Pleistocene cave and karst sites are of particular interest to our research because they may contain bat faunas composed of new genera or species that would help us better understand the earlier evolution of the NA chiropteran fauna, particularly cave-dwelling species. These older bat faunas may also be found in caves, but often occur in karst features representing former caves that are not found in a current cave environment. Examples of older pre-late Pleistocene fossil deposits in caves often consist of indurated breccias or other types of consolidated sediments that occur in the ceiling or in fissures in the walls of caves, not in unconsolidated sediments on the cave floor. Examples of older cave deposits are found in Jamaica where fossils of the large extinct rodent, *Clidomys*, were recovered from indurated breccias preserved in the ceiling of several caves, including Slue's Cave near Lluidas Vale in the Worthy Park area (Morgan and Wilkins, 2003). Uranium-series dates ranging from 100–200 ka on flowstones associated with indurated breccia deposits containing *Clidomys* fossils in two other Jamaican caves, Worthy Park Cave and Wallingford Roadside Cave, document among the oldest dated cave deposits in the West Indies (MacPhee et al., 1989; McFarlane et al., 1998). Fossils of *Clidomys* do not occur in younger Late Quaternary sediments on the floor of Jamaican caves, indicating the older breccia deposits sample a fauna that became extinct before the end of the Pleistocene. Even older cave breccias from the island of St. Barthélemy in the northern Lesser Antilles have yielded fossils of the extinct giant caviomorph rodent, *Amblyrhiza inundata*, with bracketing uranium-thorium dates providing an age of ~500 ka for these specimens (McFarlane et al., 2014). Similar breccia deposits older than late Pleistocene surficial sediments occur in caves elsewhere in the West Indies and probably the US as well.

Karst deposits of Pliocene age and older are more difficult to locate because they are usually found outside of caves, occurring in a variety of different geologic features in areas with karst geology (Figs. 1A, B). The Gray Fossil Site in Tennessee is a good example of a rich fossil deposit occurring in an area typified by karst geology. It is very likely that other buried sinkhole pond or lake deposits, and probably fissure deposits as well, occur in this vast region of karst geology extending from Pennsylvania, Maryland, and West Virginia, south through Virginia and Tennessee to northern Georgia and Alabama. This same region is well known for caves containing late Pleistocene fossil deposits (see above), and we suspect that, as in Florida, older caves containing vertebrate fossils of Tertiary age probably existed in the Appalachians but have since collapsed through erosional processes. It is likely that mining, road building, and other construction activities in the Appalachian region will lead to more opportunistic discoveries of Tertiary fossil sites of karst origin, similar to the Gray Fossil Site. These same factors also apply to other major karst regions in the US with caves that have produced late Pleistocene cave faunas, including western Kentucky and Tennessee; the Ozark region of Arkansas, Missouri, and Oklahoma; and the Edwards Plateau of central Texas. We suspect these other regions in the US may eventually produce older, karst-derived Tertiary fossil sites containing bats. In the tropical regions of NA,

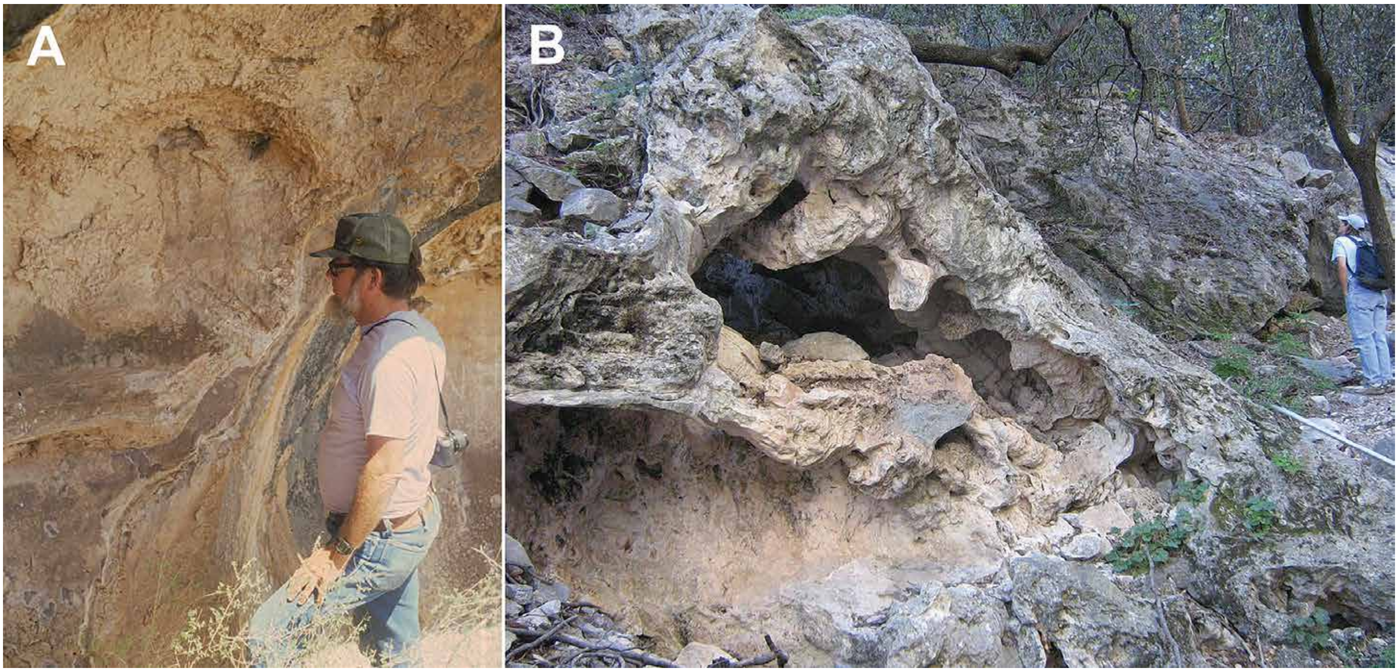


Figure 14. Paleocave remnants in southern Arizona. (A) Geologist and caver Bill Peachey in front of an ancient cave now open to the surface, showing stratified deposits (at left) reflecting former pools that could potentially yield bat fossils, Rincon Mountains. (B) Part of a former cave of unknown age, now exposed to the surface, Scheelite Canyon Trail, Huachuca Mountains.

extensive karst regions with caves exist in the Yucatán Peninsula of Mexico, Belize, and Guatemala, and throughout the larger islands in the West Indies. Late Quaternary cave faunas are common in these regions that could potentially produce older pre-late Pleistocene cave faunas, such as those mentioned above from Jamaica and St. Barthélemy, as well as older Tertiary vertebrate faunas from various types of karst features.

We mention several examples of North American karst deposits in which we regard the occurrence of vertebrate fossils as a definite possibility, even though fossils have yet to be found in these deposits. Polyak et al. (1998, 2006b) reported the occurrence of sulfate minerals, including alunite, in several caves in Carlsbad Caverns National Park (CAVE) that were produced from sulfuric acid speleogenesis. This is the process that formed the large caves in CAVE, including Carlsbad Cavern and Lechuguilla Cave, rather than the more common carbonic acid cave-forming process. ^{40}Ar/^{39}Ar dates on alunite deposits in caves in CAVE range in age from about 4 to 12 Ma, indicating these caves formed sometime between the early Pliocene and the middle Miocene (Polyak et al., 1996, 2006b). All vertebrate fossils currently known from CAVE are Pleistocene in age (Kottkamp et al., 2022), with the oldest fossils being middle Pleistocene (medial/late Irvingtonian, ~0.5 Ma) from Slaughter Canyon Cave. However, based on the ages indicated by these mineral deposits, considerably older sediments of Pliocene or Miocene age containing vertebrate fossils may eventually be found in CAVE.

Photos in Figure 14 show examples of former caves, now exposed at the surface, in southern Arizona. Sites like these could potentially hold ancient deposits with bats or other fossils. Figure 14A is a photo of geologist and caver Bill Peachey in front of a former cave of unknown age in the Rincon Mountains of southern Arizona now represented by a karst feature open to the surface, showing stratified deposits reflecting former pools. Interestingly, Peachey and NJC found evidence of modern bat use of this overhang as a night roost, consisting of guano and bits of stamen filaments and anthers from flowers visited by local Mexican long-tongued bats, *Choeronycteris mexicana*. Figure 14B shows a small, shelf-like stratified carbonate deposit in the Huachuca Mountains, also in southern Arizona, that were not searched, but many modern caves occur in the same mountain range and from this paleocave remnant we infer the possibility of others there. Karst deposits such as these sites in southern Arizona that represent former caves could potentially yield bat fossils, as have Tertiary karst deposits in Florida. The key is learning to recognize the various types of karst deposits, including geographic regions where they would be most likely to occur (See Fig. 1), and then surveying these areas in search of vertebrate fossil deposits.

Conservation Paleobiology and the North American Fossil Record of Bats

In closing, we note the emergence of the field of conservation paleobiology and the potential ability of bat fossils to demonstrate relatively deep-time presence of extant species and changes in evolving species, biodiversity, species distributions, and faunal composition through time and space. The fossil record of bats in caves can have important conservation implications. A simple record of a species in a cave can show its long-term usage (for perhaps tens of thousands of years if in a stratigraphic sequence, or at least once since the Pleistocene) of the cave, justifying the preservation of the cave as a means to conserve the bat species. Theoretical biogeographic work (e.g., McGuire and Davis, 2014; Dietl et al., 2015; Jablonski and Shubin, 2015; Kemp and Hadly, 2016) can use ecological niche modeling, temporal range shifts, community- or species-level distribution changes, or paleoclimatic data to predict future pressures on a species or cave locality due to climatic changes during the Quaternary existence of a cave to inform cave management that might benefit the species inhabiting the cave. New discoveries of fossil bats may potentially add important information to these emerging fields of paleontological study.

Shelter is one of the most important resources for the survival of most animal species. Caves and rock crevices are but one type of diurnal roosting resources for bats (as well as tree bark, foliage, tree hollows, and other types of roosts [Kunz, 1982; Voss et al., 2016]). Nevertheless, these types of shelters are one of the most important for western hemisphere temperate zone bats, primarily in the families Vespertilionidae and Molossidae. This dependence emphasizes the importance of preserving caves and karstic crevices as roosting habitat for extant species. Of the bat species in NA that are currently considered imperiled or vulnerable (14 of 17 in Canada; 33 of 45 in US; 49 of 142 in Mexico; O'Shea et al. 2018; NABCA 2023), at least 31 of 45 species (~69%) in the US and Canada use caves, mostly for either day-roosting, hibernation, or night-roosting (compiled from Harvey et al. 2011). Although the fossil record of bats is relatively weak, caves and karstic fissures are particularly effective at preserving fossils of bats and other vertebrates (Andrews, 1990). The fossil record in these shelters, where available, provides a deep historical perspective on cave-dependence of many bat species. Appropriately, the conservation of bats, caves, and cave fossils are parts of the National Speleological Society's ethic of conserving all cave resources (Hildreth-Werker and Werker, 2006; Toomey, 2006).

ACKNOWLEDGMENTS

We have both spent a substantial portion of our professional careers studying fossil bats from caves and karst deposits. The list of colleagues who have helped with our field work and research on caves and karst deposits through the US and West Indies is too long to credit everyone here, but we feel it is important to thank our colleagues whose help has been particularly significant. GSM wishes to thank Nancy Albury, Carol Belski, Carol Bordegaray, Sybil Burger, Patty Daw, Glenda Dawson, Steven Emslie, Ralph Eshelman, Richard Franz, Frederick Grady, Glynn Hayes, Rodney Horrocks, Richard Hulbert, Patricia Jablonsky, Brian Kakuk, Margaret Langworthy, Gregory McDonald, Rachel Montenegro, Lannois Neely, Dale Pate, Art Poyer, Ann Pratt, Dave Steadman, Barbara and Reed Toomey, and Rickard Toomey, III. NJC would like to thank several of the same people, as well as Bill Peachey, Chris Bell, Tom Bethard, Steve Carothers, Cástor Cartelle, Cheryl and Jessica Czaplewski, Kyle Davies, Bob Emry, Jim Farlow, Francisco Goin, Richard Kay, Jen Larsen, Alvie Laverty, Ernie Lundelius, Richard Madden, Bill and Julie May, Jim Mead, Chuck Minckley, Bob and Esty Pape, Mary Poteet, Ascanio Rincon, George Ruffner, Clayton and Sylvia Russell, Marcelo Sanchez-Villagra, Blaine Schubert, Kent Smith, Steve Smith, Marcelo Tejedor, Rick Warner, Steve Willsey, and the late Bill Puckette and Sheridan Stone. For allowing us to reproduce their photographs, we thank Steven Emslie, Glynn Hayes, Rodney Horrocks, Richard Hulbert, Brian Kakuk, Phillip Lehman, and Erika Simons. In particular, Brian Kakuk and Phillip Lehman shared their spectacular photographs of bat fossils from underwater caves in Abaco in the Bahamas (BK) and the Dominican Republic (PL). Thanks to Jessica Czaplewski for help in compiling cave usage numbers. We are grateful to Jim Mead and Sharon Holte Weaver, the organizers of the symposium on cave and karst paleontology at the 2022 National Speleological Society annual meeting in Rapid City, South Dakota, and Mead and Gregory McDonald, the co-editors of this volume, for inviting us to participate in the symposium and to contribute a paper. Joaquin Arroyo-Cabrales, Chris Jass, and Jim Mead provided helpful reviews of our paper.

We dedicate this paper to the memory of our friend and colleague, Fred Grady, a talented caver and cave paleontologist who helped GSM collect and prepare large samples of bat fossils from Tobago. Fred was best known for collecting and preserving vertebrate fossils from Pleistocene cave deposits in West Virginia, including an early Pleistocene sample of the free-tailed bat, *Tadarida*, from Hamilton Cave and the northernmost fossil record of the vampire bat, *Desmodus stocki*, in eastern North America from Little Trout Cave. Fred's passing leaves a void in the field of cave paleontology that cannot be filled.

REFERENCES

Albright, L.B., III, Woodburne, M.O., Fremd, T., Swisher, C.C., MacFadden, B.J., and Scott, G.R., 2008, Revised chronostratigraphy and biostratigraphy of the John Day Formation (Turtle Cove and Kimberly members), Oregon, with implications for updated calibration of the Arikareean North American Land Mammal Age: Journal of Geology, v. 116, p. 211–237. https://doi.org/10.1086/587650

Álvarez, T., 1972, Nuevo registro para el vampiro del Pleistoceno *Desmodus stocki* de Tlapacoya, Mexico: Anales de la Escuela Nacional de Ciencias Biológicas [New record for the Pleistocene vampire Desmodus stocki from Tlapacoya, Mexico: Annals of the National School of Biological Sciences] v. 19, p. 163–165.

Andrews, P., 1990, Owls, Caves, and Fossils: Chicago, University of Chicago Press, 231 p.

Anemone, R.L., Conroy, G.C., and Emerson, C.W., 2011a, GIS and paleoanthropology: incorporating new approaches from the geospatial sciences in the analysis of primate and human evolution: Yearbook of Physical Anthropology, v. 54, p. 19–46.

https://doi.org/10.1002/ajpa.21609

Anemone, R., Emerson, C., and Conroy, G., 2011b, Finding fossils in new ways: an artificial neural network approach to predicting the location of productive fossil localities: Evolutionary Anthropology, v. 20, p. 169–180. https://doi.org/10.1002/evan.20324

Anthony, H.E., 1917, Two new fossil bats from Porto Rico: Bulletin of the American Museum of Natural History, v. 37, p. 565–568.

Anthony, H.E., 1918, The indigenous land mammals of Porto Rico, living and extinct: Memoirs of the American Museum of Natural History (new series), v. 2, no. 2, p. 333–435.

Anthony, H.E., 1925, Mammals of Porto Rico, living and extinct–Chiroptera and Insectivora: Scientific Survey of Porto Rico and the Virgin Islands: v. 9, pt. 1, p. 1–96, pl 1–15. New York: New York Academy of Sciences.

Arroyo-Cabrales, J., and Alvarez, T., 2003, A preliminary report of the Late Quaternary mammals from Loltún Cave, Yucatán, Mexico; *in* Schubert, B.W., Mead, J.I. and Graham, R.W., eds., Ice Age cave faunas of North America: Bloomington, Indianapolis, and Denver Museum of Nature and Science, Indiana University Press, p. 262–272.

Arroyo-Cabrales, J., and Johnson, E., 2002, Catálogo de los ejemplares tipo procedentes de Cueva de la San Josecito, Nuevo León, México: Revista Mexicana de Ciencias Geológicas [Catalogue of the type specimens from Cueva de la San Josecito, Nuevo León, Mexico: Revista Mexicana de Ciencias Geológicas], v. 20, no. 1, p. 79–93.

Arroyo-Cabrales, J., and Polaco, O.J., 2003, Caves and the Pleistocene vertebrate paleontology of Mexico. *in* Schubert, B.W., Mead, J.I. and Graham, R.W., eds., Ice Age Cave Faunas of North America: Bloomington, Indianapolis, and Denver Museum of Nature and Science, Indiana University Press, p. 273–291.

Arroyo-Cabrales, J., and Polaco, O.J., 2008, Fossil bats from Mesoamerica: Arquivos do Museu Nacional [National Museum Archives], Rio de Janeiro, v. 66, no.1, p. 155–60.

Baker, J.K., 1963, Fossilization of bat skeletons in the Carlsbad Caverns: National Speleological Society Bulletin, v. 25, p. 37–44.

Baker, R.J. and Genoways, H.H., 1978, Zoogeography of Antillean bats; *in* Gill F.B., ed., Zoogeography in the Caribbean, The 1975 Leidy Medal Symposium, Academy of Natural Sciences of Philadelphia, Special Publication no. 13, p. 53–97.

Barnosky, A.D., ed., 2004, Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado: Berkeley, University of California Press, 385 p. https://doi.org/10.1525/california/9780520240827.001.0001

Barnosky, A.D., and Bell, C.J., 2004, Age and correlation of key fossil sites in Porcupine Cave; *in* Barnosky, A.D., ed., Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado: Berkeley, University of California Press, p. 64–73. https://doi.org/10.1525/california/9780520240827.003.0007

Basantes, M., Tinoco, N., Velazco, P.M., Hofmann, M.J., Rodríguez-Posada, M.E., and Camacho, M.A., 2020, Systematics and taxonomy of *Tonatia saurophila* Koopman & Williams, 1951 (Chiroptera, Phyllostomidae): ZooKeys, no. 915, p. 59–86. https://doi.org/10.3897/zookeys.915.46995

Bell, C.J., Lundelius, E.L., Jr., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez, D.R., Jr., Semken, H.A., Jr., Webb, S.D., and Zakrzewski, R.J., 2004, The Blancan, Irvingtonian and Rancholabrean mammal ages; *in* Woodburne, M.O., ed., Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology: New York, Columbia University Press, p. 232–314. https://doi.org/10.7312/wood13040-009

Bergqvist, L.P., Mansur, K., Rodrigues, M.A., Rodrigues-Francisco, B.H., Perez, R.A.R., and Beltrão, M.C., 2008. Itaboraí Basin, State of Rio de Janeiro—the cradle of mammals in Brazil; *in* Winge, M., Schobbenhaus, M., Souza, C., C.R.G., Fernandes, A.C.S., Berbert-Born, M., and Queiroz, E.T., eds., Sítios Geológicos e Paleontológicos do Brasil [Geological and Paleontological Sites of Brazil] SIGEP 123: CPRM, Brasılia, Brazil, p. 413–432.

Bradley, R.D., Ammerman, L.K., Baker, R.J., Bradley, L.C., Cook, J.A., Dowler, R.C., Jones, C., Schmidly, D.J., Stangl, F.B., Jr., Van Den Bussche, R.A., and Würsig, B., 2014, Revised checklist of North American mammals north of Mexico, 2014: Museum of Texas Tech University, Occasional Papers, no. 327, p. 1–27.

Brown. B., 1908, The Conard Fissure, a Pleistocene bone deposit in northern Arkansas: with descriptions of two new genera and twenty new species of mammals: Memoirs of the American Museum of Natural History, v. 9, pt. 4, p. 157–208.

Brown, E.E., Cashmore, D.D., Simmons, N.B., and Butler, R.J., 2019, Quantifying the completeness of the bat fossil record: Palaeontology v. 2019, p. 1–20. https://doi.org/10.1111/pala.12426

Carpenter, M.C., 2004, Late Pleistocene Aves, Chiroptera, Perissodactyla, and Artiodactyla from Rampart Cave, Arizona: Unpublished M.S. thesis, Flagstaff, Northern Arizona University.

Ceballos, G., Arroyo-Cabrales, J., and Vazquez, D., 2014, Order Chiroptera; in Ceballos, G., ed., Mammals of Mexico: Baltimore, Johns Hopkins University Press, p. 667–838.

Choate, J.R., and Birney, E.C., 1968, Sub-recent Insectivora and Chiroptera from Puerto Rico, with the description of a new bat of the Genus *Stenoderma*: Journal of Mammalogy, v. 49, p. 400–412. https://doi.org/10.2307/1378198

Choate, J.R., and Hall, E.R., 1967, Two new species of bats, genus *Myotis*, from a Pleistocene deposit in Texas: American Midland Naturalist, v. 78, p. 531–534. https://doi.org/10.2307/2485251

Churcher, C.S., 2020, Pleistocene mammals from Extinction Cave, Belize: Canadian Journal of Earth Sciences, v. 57, p. 366–376. https://doi.org/10.1139/cjes-2018-0178

Cisneros, J.C., 2005, New Pleistocene vertebrate fauna from El Salvador: Revista Brasileira de Paleontologia [Brazilian Journal of Paleontology], v. 8, p. 239–255. https://doi.org/10.4072/rbp.2005.3.09

Cisneros, J.C., 2008. The fossil mammals of El Salvador: New Mexico Museum of Natural History and Science, Bulletin 44, p. 375–380.

Cope, E.D., and Mercer, H.C., 1897-1901, Vertebrate remains from Port Kennedy bone deposit: Journal of the Academy of Natural Sciences of Philadelphia, (series 2), v. 11, p. 193–289.

Cruz, J.A., Arroyo-Cabrales, J., Schubert, B.W., Chatters, J.C., Samuels, J.X., and Gunnin, R.D., 2024, Small vertebrates from Hoyo Negro and their palaeoecological importance: 12th NAPC (North American Paleontology Conference) 2024, 17-21 June, Ann Arbor, Michigan, University of Michigan, abstract, p. 163

Czaplewski, N.J., 2017, First report of bats (Mammalia: Chiroptera) from the Gray Fossil Site (late Miocene or early Pliocene), Tennessee: USA. PeerJ 5:e3263. https://doi.org/10.7717/peerj.3263

Czaplewski, N.J., and Cartelle, C., 1998, Pleistocene bats from cave deposits in Bahia, Brazil. Journal of Mammalogy, v. 79, p. 784–803. https://doi.org/10.2307/1383089

Czaplewski, N.J., Farlow, J.O., and Argast, A., 2012, A fossil shrew (Mammalia, Soricidae) from the Pipe Creek Sinkhole (late Neogene: Hemphillian), Indiana. Proceedings of the Indiana Academy of Science, v. 12, p. 79–86.

Czaplewski, N.J., Krejca, J., and Miller, T.E., 2003a, Late Quaternary bats from Cebada Cave, Chiquibul Cave System, Belize: Caribbean Journal of Science, v. 39, p. 23–33.

Czaplewski, N.J., Mead, J.I., Bell, C.J., Peachey, W.D., and Ku, T.L., 1999, Papago Springs Cave revisited, part II: vertebrate paleofauna: Occasional Papers of the Oklahoma Museum of Natural History v. 5, p. 1–41.

Czaplewski, N.J., Mead, J.I., and Peachey, W.D., 2022, Late Pleistocene vertebrate fauna of Pyeatt Cave, Huachuca Mountains, Cochise County, Arizona: New Mexico Museum of Natural History and Science Bulletin v. 88, p. 301–329.

Czaplewski, N.J., Mead, J.I., and Peachey, W.D., this volume, Late Pleistocene vertebrate fauna and bat guano deposit of La Tetera Cave, Arizona, USA: Journal of Cave and Karst Studies

Czaplewski, N.J., and Morgan, G.S., 2000, A new vespertilionid bat (Mammalia: Chiroptera) from the early Miocene (Hemingfordian) of Florida, USA: Journal of Vertebrate Paleontology, v. 20, p. 736–742. https://doi.org/10.1671/0272-4634(2000)020[0736:ANVBMC]2.0.CO;2

Czaplewski, N.J., and Morgan, G.S., 2012, New basal noctilionoid bats (Mammalia: Chiroptera) from the Oligocene of subtropical North America; *in* Gunnell, G.F. and Simmons N.B., eds., Evolutionary History of Bats: Fossils, Molecules, and Morphology: Cambridge, Cambridge University Press, p. 162–209. https://doi.org/10.1017/CBO9781139045599.006

Czaplewski, N.J., Morgan, G.S., and McLeod, S.A., 2008. Chapter 12. Chiroptera; *in* Janis, C.M., Gunnell, G.F., and Uhen, M.D., eds., Evolution of Tertiary Mammals of North America, Vol. 2: Small Mammals, Xenarthrans, and Marine Mammals: Cambridge, Cambridge University Press, p. 174–197. https://doi.org/10.1017/CBO9780511541438.013

Czaplewski, N.J., Morgan, G.S., and Naeher, T., 2003b, Molossid bats from the Late Tertiary of Florida with a review of the Tertiary Molossidae of North America: Acta Chiropterologica, v. 5, p. 61–74. https://doi.org/10.3161/001.005.0105

Czaplewski, N.J., and Peachey, W.D., 2003, Late Pleistocene bats from Arkenstone Cave, Arizona: Southwestern Naturalist, v. 48, p. 597–609. https://doi.org/10.1894/0038-4909(2003)048<0597:LPBFAC>2.0.CO;2

Czaplewski N.J., Puckette, W.L., and Russell, C., 2002, A Pleistocene tapir and associated mammals from the southwestern Ozark Highland. Journal of Cave and Karst Studies, v. 64, p. 97–107.

Czaplewski, N.J., and Rincon, A.D., 2020, A giant vampire bat (Phyllostomidae, Desmodontinae) from the Pliocene-Pleistocene El Breal de Orocual asphaltic deposits (tar pits), Venezuela: Historical Biology. https://doi.org/10.1080/08912963.2020.1800684

Czaplewski, N.J., Rogers, K.J., and Russell, C., 2018, Late Pleistocene vertebrates from Three-Forks Cave, Adair County, Oklahoma Ozark Highland: Journal of Cave and Karst Studies, v. 80, no. 2, p. 1–16. https://doi.org/10.4311/2017PA0118

Dalquest, W.W., and Roth, E., 1970, Late Pleistocene mammals from a cave in Tamaulipas, Mexico: Southwestern Naturalist, v. 15, p. 217–230. https://doi.org/10.2307/3670350

Dalquest, W.W., Roth, E., and Judd, F., 1969, The mammal fauna of Schulze Cave, Edwards County, Texas: Bulletin of the Florida State Museum, v. 13, p. 204–276. https://doi.org/10.58782/flmnh.kqdk9637

Dalquest, W.W., and Stangl, F.B., Jr., 1984, The taxonomic status of *Myotis magnamolaris*, Choate and Hall: Journal of Mammalogy, v. 65, p. 485–486. https://doi.org/10.2307/1381098

Dávalos, L.M., and Russell, A.L., 2012, Deglaciation explains bat extinction in the Caribbean: Ecology and Evolution, v. 2, p. 3045–3051. https://doi.org/10.1002/ece3.399

Dávalos, L.M., and Turvey, S.T., 2012, West Indian mammals: the old, the new, and the recently extinct; *in* Patterson, B.D. and Costa, L.P. eds., Bones, Clones, and Biomes: The History and Geography of Recent Neotropical Mammals: Chicago, University of Chicago Press, p. 157–202. https://doi.org/10.7208/chicago/9780226649214.003.0009

Dávila, S.L., Stinnesbeck, S.R., Gonzalez, S., Lindauer, S., Escamilla. J., and Stinnesbeck, W., 2019, Guatemala's Late Pleistocene (Rancholabrean) fauna: Revision and interpretation: Quaternary Science Reviews, v. 219, p. 277–296. https://doi.org/10.1016/j.quascirev.2019.07.011

Dietl, G.P., Kidwell, S.M., Brenner, M., Burney, D.A., Flessa, K.W., Jackson, S.T., and Koch, P.L., 2015, Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration: Annual Review of Earth and Planetary Science v. 43, p. 79–103. https://doi.org/10.1146/annurev-earth-040610-133349

Dorsey, S.L., 1977, A reevaluation of two new species of fossil bats from Inner Space Caverns: Texas Journal of Science, v. 28, p. 103–108.

Ebersole, J.A., and Ebersole, S.M., 2011, Late Pleistocene mammals of Alabama: a comprehensive faunal review with 21 previously unreported taxa: Alabama Museum of Natural History Bulletin 28, p. 1–69.

Eiting, T.P., and Gunnell, G.F., 2009, Global completeness of the bat fossil record: Journal of Mammalian Evolution, v. 16, p. 151–173. https://doi.org/10.1007/s10914-009-9118-x

Emerson, C.W., and R.L. Anemone, 2012, An artificial neural network-based approach to identifying mammalian fossil localities in the Great Divide Basin, Wyoming: Remote Sensing Letters, v. 3, p. 453–460. https://doi.org/10.1080/01431161.2011.621463

Emslie, S.D., 1988, Vertebrate paleontology and taphonomy of caves in Grand Canyon, Arizona: National Geographic Research, v. 4, p. 128–142.

Emslie, S.D., and Morgan, G.S., 1995, Taphonomy of a Late Pleistocene carnivore den, Dade County Florida; *in* Steadman, D.W. and Mead, J.I., eds., Late Quaternary Environments and Deep History: A Tribute to Paul S. Martin: The Mammoth Site of Hot Springs, South Dakota, Scientific Papers, v. 3, p. 65–83.

Eshelman, R.E., Bell, C.J., Graham, R.W., Semken, H.A., Jr., Withnell, C.B., Scarpetta, S.G., James, H.F., Godfrey, S.J., Mead, J.I., Hodnett, J.P., and Grady, F.V., 2025, Middle Pleistocene Cumberland Bone Cave Local Fauna, Allegany County, Maryland: A systematic revision and paleoecological interpretation of the Irvingtonian, Middle Appalachians, USA: Smithsonian Contributions to Paleobiology.

Farlow, J.O., Sunderman, J.A., Havens, J.J., Swinehart, A.L., Holman, J.A., Richards, R.L., Miller, N.G., Martin. R.A., Hunt, R.M., Jr., Storrs, G.W., Curry, B.B., Fluegeman, R.H., Dawson. M.R, and Fling, M.E,T, 2001, The Pipe Creek Sinkhole biota, a diverse Late Tertiary continental fossil assemblage from Grant County, Indiana: American Midland Naturalist, v. 145, p. 367–378. https://doi.org/10.1674/0003-0031(2001)145[0367:TPCSBA]2.0.CO;2

FAUNMAP Working Group, 1994, FAUNMAP: A database documenting Late Quaternary distributions of mammal species in the United States: Illinois State Museum, Scientific Papers, v. 25 (no. 1 and 2), 690 p.

Florea, L.J., 2008, Geology and hydrology of karst in west-central and north-central Florida; *in* Florea, L.J., ed., Caves and karst of Florida. A Guidebook for the 2008 NSS National Convention, Lake City, Florida, National Speleological Society, Huntsville, Alabama, p. 225–239.

Ford, D.C., and Williams, P., 2007. Karst hydrogeology and geomorphology. Hoboken, John Wiley and Sons, 562 p. https://doi.org/10.1002/9781118684986

Friedmann, S.J., and Raynolds, R.G., 2004, Magneostratigraphic constraints on the age of Pleistocene fossiliferous strata in Porcupine Cave's DMNH Velvet Room excavation *in* Barnosky, A.D., ed., Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado: Berkeley, University of California Press, p. 57–63. https://doi.org/10.1525/california/9780520240827.003.0006

García Rivera, L., and Mancina, C.A., 2011, Murciélagos insectívoros [Insectivorous bats]; *in* Borroto-Páez, R., and Mancina, C. A., eds., Mamíferos en Cuba [Mammals in Cuba:]: Vasa, Finland: UPC, p. 140–165.

Garton, E.R., and Grady, F.V., 1980, The late Pleistocene fauna of New Trout Cave, Pendleton County, West Virginia: Proceedings of the West Virginia Academy of Science, v. 52, p. 14.

Gaudin, T.J., Miller, A.N., Bramblett, J.L., and Wilson, T.P., 2011, Holocene and late Pleistocene bat fossils (Mammalia: Chiroptera) from Hamilton County, TN, and their ecological implications: Southeastern Naturalist: v. 10, p. 609–628. https://doi.org/10.1656/058.010.0403

Gazin, C.L., 1957, Exploration for the remains of giant ground sloths in Panama: Smithsonian Institution, Annual Report, 1956, p. 341–354.

Gidley, J.W., and Gazin, C.L., 1933, New Mammalia in the Pleistocene fauna from Cumberland Cave: Journal of Mammalogy, v. 14, p. 343–357. https://doi.org/10.2307/1373954

Gidley, J.W., and Gazin, C.L., 1938, The Pleistocene vertebrate fauna from Cumberland Cave Maryland: Smithsonian Institution, United States National Museum, Bulletin 171, p. 1–99. https://doi.org/10.5479/si.03629236.171.i

Grady, F., 1988, A preliminary account of the Pleistocene mammals from Patton Cave, Monroe County, West Virginia: National Speleological Society Bulletin, v. 50, p. 9–16.

Grady, F., 1991, Fossil Chiroptera from two West Virginia caves: Bulletin of the National Speleological Society, v. 53, p. 122.

Grady, F., Arroyo-Cabrales, J., and Garton, E.R., 2002, The northernmost occurrence of the Pleistocene vampire bat *Desmodus stocki* Jones (Chiroptera: Phyllostomatidae: Desmodontinae) in eastern North America: Smithsonian Contributions to Paleobiology, no. 93, p. 73–75. https://doi.org/10.5479/si.00810266.93.73

Guilday, J.E., 1961, *Plecotus* from the Pennsylvania Pleistocene: Journal of Mammalogy, v. 42, p. 402–403. https://doi.org/10.2307/1377048

Guilday, J.E., 1967, Notes on the Pleistocene big brown bat *Eptesicus grandis* (Brown): Annals of Carnegie Museum, v. 39, p. 105–114. https://doi.org/10.5962/p.330857

Guilday, J.E., and Hamilton, H.W., 1978, Ecological significance of displaced boreal mammals in West Virginia caves: Journal of Mammalogy, v. 59, p. 176–181. https://doi.org/10.2307/1379886

Guilday, J.E., Hamilton, H.W., Anderson, E., Parmalee, P.W., Faulkner, C.H., Hill, F.C., and Van Dam, G.H., 1978, The Baker Bluff Cave Deposit, Tennessee, and the late Pleistocene faunal gradient: Bulletin of Carnegie Museum of Natural History no. 11, p. 1–67. https://doi.org/10.5962/p.228590

Guilday, J.E., Hamilton, H.W., and McCrady, A.D., 1969, The Pleistocene vertebrate fauna of Robinson Cave, Overton County, Tennessee: Palaeovertebrata, v. 2, p. 25–75. https://doi.org/10.18563/pv.2.2.25-75

Guilday, J.E., Martin, P.S., and McCrady, A.D., 1964, New Paris No. 4: A late Pleistocene cave deposit in Bedford County, Pennsylvania: Bulletin of the National Speleological Society, v. 26, no. 4, p. 121–194.

Guilday, J.E., Parmalee, P.W., and Hamilton, H.W., 1977, The Clark's Cave bone deposit and the late Pleistocene paleoecology of the Central Appalachian Mountains of Virginia: Bulletin of Carnegie Museum of Natural History, no. 2, p. 1–88. https://doi.org/10.5962/p.228581

Gunnell, G.F., and Simmons, N.B., 2005, Fossil evidence and the origin of bats: Journal of Mammalian Evolution, v. 12, p. 209–246. https://doi.org/10.1007/s10914-005-6945-2

Gunnell, G.F., Winkler, A.J., Miller, E.R., Head, J.J., El-Barkooky, A.N., Gawad, M.A., Sanders, W.J., and Gingerich, P.D., 2016, Small vertebrates from Khasm El-Raqaba, late middle Miocene, Eastern Desert, Egypt. Historical Biology, v. 28, p. 159–171. https://doi.org/10.1080/08912963.2015.1014354

Gut, H.J., 1959, A Pleistocene vampire bat from Florida: Journal of Mammalogy, v. 40, p. 534–538. https://doi.org/10.2307/1376270

Guthrie, R.E., 2005, Paleontology and paleoecology of the Coyote Ledge locality (Blancan), Richmond Hill fissure fills, Lawrence County, South Dakota, USA: Unpublished Master's Thesis, South Dakota School of Mines, Rapid City, South Dakota.

Hand, S., Archer, M., and Godthelp, H., 2005, Australian Oligo-Miocene mystacinids (Microchiroptera): upper dentition, new taxa and divergence of New Zealand species. Geobios, v. 38, p. 339–352. https://doi.org/10.1016/j.geobios.2003.11.005

Hand, S.J., and Kirsch, J.A.W., 2003, *Archerops*, a new annectant hipposiderid genus (Mammalia: Microchiroptera) from the Australian Miocene. Journal of Paleontology, v. 77, p. 1139–1151. https://doi.org/10.1666/0022-3360(2003)077<1139:AANAHG>2.0.CO;2

Hand, S.J., Maugoust, J., Beck, R.M.D., and Orliac, M.J., 2023, A 50-million-year-old, three-dimensionally preserved bat skull supports an early origin for modern echolocation: Current Biology, https://doi.org/10.1016/j.cub.2023.09.043

Handley, C.O., Jr., 1955, A new Pleistocene bat (*Corynorhinus*) from Mexico: Journal of the Washington Academy of Sciences, v. 45, p. 48–49.

Harington, C.R., 2011, Quaternary cave faunas of Canada: a review of the vertebrate remains: Journal of Cave and Karst Studies, v. 73, p. 162–180. https://doi.org/10.4311/jcks2009pa128

Harris, A.H., 1985, Late Pleistocene Vertebrate Paleoecology of the West: Austin, University of Texas Press, 293 p.

Harris, A.H., 1987, Reconstruction of Mid-Wisconsin environments in southern New Mexico: National Geographic Research, v. 3, p. 142–151.

Harris, A.H., 1993, Quaternary vertebrates of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 2, p. 179–197.

Harris, A.H., 2003, The Pleistocene vertebrate fauna from Pendejo Cave; *in* MacNeish, R.S., and Libby, J.G., eds., Pendejo Cave: University of New Mexico Press, Albuquerque, p. 36–65.

Harris, A.H., 2005, Caves as unique resources for Pleistocene vertebrate faunas: New Mexico Museum of Natural History and Science, Bulletin 28, p. 249–253.

Harris, A.H., 2024, Pleistocene Vertebrates of Southwestern USA and Northwestern Mexico: Website accessed on 2/20/2023 at: www.utep.edu/leb/pleistnm/.

Hartenberger, J.-L., Megard, F., and Sigé, B., 1984, Faunules à rongeurs de l'Oligocène inférieur à Lircay (Andes du Pérou central); datation d'un episode karstique; intérêt paléobiogéographique des remplissages tertiaires en Amérique du Sud. Comptes Rendus Academie des Sciences [Lower Oligocene rodent falcons at Lircay (Andes of central Peru); dating of a karst episode; paleobiogeographic interest of Tertiary fillings in South America. Academy of Sciences Proceedings], Paris, v. 299, p. 565–568.

Harvey, M.J., Altenbach, J.S., and Best, T.L., 2011, Bats of the United States and Canada: Johns Hopkins University Press, Baltimore.

Hawksley, O., Reynolds, J.F., and Foley, R.L., 1973, Pleistocene vertebrate fauna of Bat Cave, Pulaski County, Missouri: Bulletin of the National Speleological Society, v. 35, p. 61–87.

Hay, O.P., 1921, Descriptions of species of Pleistocene Vertebrata, types or specimens of most of which are preserved in the United States National Museum: Proceedings of the United States National Museum, v. 59, p. 599–642. https://doi.org/10.5479/si.00963801.59-2391.599

Hayes, F.G., 2000, The Brooksville 2 Local Fauna (Arikareean, latest Oligocene): Hernando County, Florida: Bulletin of the Florida Museum of Natural History, v. 43, p. 1–47. https://doi.org/10.58782/flmnh.isca2513

Heaton, T.H., 1985, Quaternary paleontology and paleoecology of Crystal Ball Cave, Millard County, Utah: with emphasis on mammals and description of a new species of fossil skunk: Great Basin Naturalist, v. 45, p. 337–390. https://doi.org/10.5962/bhl.part.4433

Heaton, T.H., and Grady, F., 2003, The late Wisconsin vertebrate history of Prince of Wales Islands, southeast Alaska; *in* Schubert, B.W., Mead, J.I. and Graham, R.W., eds., Ice Age Cave Faunas of North America: Bloomington, Indianapolis, and Denver Museum of Nature and Science, Indiana University Press, p. 17–53.

Hildreth-Werker, V., and Werker, J.C., eds., 2006, Cave Conservation and Restoration: National Speleological Society, Inc., Huntsville, Alabama.

Hill J.E., and Smith, J.D., 1984; Bats, a Natural History: London, British Museum (Natural History), 243 p.

Hockett, B.S., 2000, Paleobiogeographic changes at the Pleistocene-Holocene boundary near Pintwater Cave, southern Nevada: Quaternary Research, v. 53, p. 263–269. https://doi.org/10.1006/qres.1999.2116

Hollingsworth, E., Brahana, V., Inlander, E., and Slay, M., 2008, Karst regions of the World (KROW): global karst datasets and maps to advance the protection of karst species and habitats worldwide; *in* Kuniansky, E.L., ed., U.S. Geological Survey Karst Interest Group Proceedings: Bowling Green, Kentucky, 27-29 May 2008. U.S. Geological Survey Scientific Investigations Report 2008-5023, Reston, Virginia, p. 17-24. https://doi.org/10.3133/sir20085023

Hulbert, R.C., Jr., 2010, A new early Pleistocene tapir (Mammalia: Perissodacytla) from Florida, with a review of Blancan tapirs from the state: Bulletin of the Florida Museum of Natural History, v. 49, p. 67–126. https://doi.org/10.58782/flmnh.ezjr9001

Hutchison, J.H., 1967, A Pleistocene vampire bat (*Desmodus stocki*) from Potter Creek Cave, Shasta County, California: Paleobios, no. 3 p. 1–6.

Jablonski, D., and Shubin, N.H., 2015, The future of the fossil record: paleontology in the 21st century: Proceedings of the National Academy of Sciences USA, v. 112, p. 4852–4858. https://doi.org/10.1073/pnas.1505146112

Jablonsky, P.L., 1999, Carbon-14 analysis of Chiroptera specimens and guano deposits, Carlsbad Cavern, Carlsbad Caverns National Park: unpublished report to the National Park Service, on file at CAVE.

Jablonsky, P.L., 2001, Continuation of Chiroptera guano analysis utilizing carbon-14 dating techniques: unpublished report to the National Park Service, on file at CAVE.

Jansky, K., Schubert, B.W., and Wallace, S.C., 2016, Geometric morphometrics of dentaries in *Myotis*: species identification and its implications for conservation and the fossil record. Northeastern Naturalist, v. 23, p. 184–194. https://doi.org/10.1656/045.023.0115

Jans-Langel, C.M., and Semken, H.A., Jr., 2003, Paleoecological interpretation of late Holocene and late Pleistocene micromammal faunules from Duhme Cave, eastern Iowa; *in* Schubert, B.W., Mead, J.I., and Graham, R.W., eds., Ice Age Cave Faunas of North America: Bloomington, Indianapolis, and Denver Museum of Nature and Science, Indiana University Press, p. 119–148.

Jass, C.N., and George, C.O., 2010, An assessment of the contribution of fossil cave deposits to the Quaternary paleontological record: Quaternary International, v. 217, p. 105–116. https://doi.org/10.1016/j.quaint.2009.11.008

Jefferson, G.T., 1982, Late Pleistocene vertebrates from a Mormon Mountain cave in southern Nevada: Bulletin of the Southern California Academy of Sciences, v. 81, p. 121–127.

Jegla, T.C., and Hall, J.S., 1962, A Pleistocene deposit of the free-tailed bat in Mammoth Cave, Kentucky: Journal of Mammalogy, v. 43, p. 477–481. https://doi.org/10.2307/1376910

Jepsen, G.L., 1966, Early Eocene bat from Wyoming: Science, v. 154, p. 1333–1339. https://doi.org/10.1126/science.154.3754.1333

Johnson, K.S., 1989, Salt dissolution, interstratal karst, and ground subsidence in the northern part of the Texas panhandle; *in* Beck, B.F., ed., Proceedings of the 3rd Multidisciplinary Conference on Sinkholes: Rotterdam: Balkema, p. 115–121.

Johnson, K.S., 1996, Gypsum karst in the United States. International Journal of Speleology, v. 25, p. 183–193. https://doi.org/10.5038/1827-806X.25.3.13

Johnson, K.S., and Neal, J.T., 2003, Evaporite karst and engineering/environmental problems in the United States: Oklahoma Geological Survey Circular 109, US Geological Survey and National Cave and Karst Research Institute, National Park Service, 353 p. http://ogs.ou.edu/docs/circulars/C109.pdf

Jones, J.K., Jr., 1958, Pleistocene bats from San Josecito Cave, Nuevo Leon, Mexico: University of Kansas Publications, Museum of Natural History, v 9, no. 14, p. 389–396.

Jones, W.K., and White, W.B., 2012, Karst; *in* White, W. and Culver, D., eds., Encyclopedia of Caves. 2nd edition: New York, Academic Press, p. 430–438. https://doi.org/10.1016/B978-0-12-383832-2.00061-X

Kemp, M.E., and Hadly, E.A., 2016, Rocking Earth's biodiversity cradle: challenges, advances, and prospects for conservation paleontology in the tropics: Journal of Vertebrate Paleontology. https://doi.org/10.1080/02724634.2016.1179640

Koopman, K.F., 1955, A new subspecies of *Chilonycteris* from the West Indies and a discussion of the mammals of La Gonâve: Journal of Mammalogy, v. 36, p. 109-113. https://doi.org/10.2307/1375730

Koopman, K.F., 1958, A fossil vampire bat from Cuba: Breviora, no. 90, p. 1–4.

Koopman, K.F., 1988, Systematics and distribution; *in* Greenhall, A.M., and Schmidt, U., eds. Natural History of Vampire Bats: Boca Raton, Florida, CRC Press, p. 7–17. https://doi.org/10.1201/9781351074919-2

Koopman, K.F., 1989, A review and analysis of the bats of the West Indies; *in* Woods, C.A., ed., Biogeography of the West Indies: Past, Present, and Future: Gainesville, Florida, Sandhill Crane Press, p. 635–644.

Koopman, K.F., and Williams, E.E., 1951, Fossil Chiroptera collected by H. E. Anthony in Jamaica, 1919–1920: American Museum Novitates, no. 1519, p. 1–29.

Kottkamp, S., Santucci, V.L., Tweet, J.S., Horrocks, R.D., and Morgan, G.S., 2022, Pleistocene vertebrates from Carlsbad Caverns National Park, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 88, p. 267–290.

Kowalski, K., 1995, Taphonomy of bats (Chiroptera): Geobios, v. 18, p. 251–256. https://doi.org/10.1016/S0016-6995(95)80172-3

Kunz, T.H., 1982, Roosting ecology of bats; *in* Kunz, T.H., ed., Ecology of Bats: Plenum Publishing Corporation, New York, p. 1–55. https://doi.org/10.1007/978-1-4613-3421-7_1

Kurtén, B., 1966, Pleistocene bears of North America: 1. Genus *Tremarctos*, spectacled bears: Acta Zoologica Fennica, v. 115, p. 1–120.

Kurtén, B., and Anderson, E., 1980, Pleistocene Mammals of North America: New York, Columbia University Press, 442 p.

Lane, E., 1986, Karst in Florida: Florida Geological Survey, Special Publication 29, p. 1–100.

LaSalle, P., 1984, Geological setting and preliminary faunal report for the St-Elzéar Cave, Quebec, Canada; *in* Genoways, H.H., and Dawson, M.R., eds., Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday: Special Publication of Carnegie Museum of Natural History no. 8, p. 332–346.

Lawrence, B., 1943, Miocene bat remains from Florida, with notes on the generic characters of the humerus of bats: Journal of Mammalogy, v. 24, p. 356–369. https://doi.org/10.2307/1374836

Lawrence, B., 1960, Fossil *Tadarida* from New Mexico: Journal of Mammalogy, v. 41, p. 320–322. https://doi.org/10.2307/1377489

Logan, L.E., 1981, The mammalian fossils of Muskox Cave, Eddy County, New Mexico; *in* Beck, B.F., ed., Proceedings of the Eight International Congress of Speleology, v. 1, p. 159–160.

López-Aguirre, C., Hand, S.J., Laffan, S.W., and Archer, M., 2018, Phylogenetic diversity, types of endemism and the evolutionary history of New World bats. Ecography, v. 41, p. 1–12. https://doi.org/10.1111/ecog.03260

López-Cuamatzi, I.L., Ortega, J., Ospina-Garcés, S.M., Zúñiga, G., MacSwiney, G.M.C., 2024, Molecular and morphological data suggest a new species of big-eared bat (Vespertilionidae: *Corynorhinus*) endemic to northeastern Mexico: PLoS One, v. 19, p. e0296275. https://doi.org/10.1371/journal.pone.0296275

Lucas, S.G., 2008, Pleistocene mammals from Yeroconte, Honduras: New Mexico Museum of Natural History and Science, Bulletin 44, p. 403–407.

Lucas, S.G., 2014, Late Pleistocene mammals from El Hatillo, Panama: Revista Geológica de América Central, v. 50, p. 139–151.

Lucas, S.G., Alvarado, G.E., and Vega, E., 1997, The Pleistocene mammals of Costa Rica: Journal of Vertebrate Paleontology, v. 17, p. 413–427. https://doi.org/10.1080/02724634.1997.10010985

Lucas, S.G., Garcia, R., Espinosa, E., Alvarado, G.E., Hurtado de Mendoza, L., and Vega, E., 2008, The fossil mammals of Nicaragua: New Mexico Museum of Natural History and Science, Bulletin 44, p. 417–429.

Lucas, S.G., Romero, J.E., Vásquez, O.J., and Alvarado, G.E., 2021, The fossil vertebrates of Guatemala: Revista Geológica de América Central [Geological Journal of Central America], v. 66, p. 1–32. https://doi.org/10.15517/rgac.v66i0.48590

Lundberg, J., and McFarlane, D.A., 2006, A minimum age for canyon incision and for the extinct molossid bat, *Tadarida constantinei*, from Carlsbad Caverns National Park, New Mexico: Journal of Cave and Karst Studies, v. 68, p. 115–117.

Lundelius, E.L., 2006, Cave site contributions to vertebrate history. Alcheringa: An Australian Journal of Palaeontology, v. 30, p. 195–210. http://dx.doi.org/10.1080/03115510609506863

MacPhee, R.D.E., Ford, D.C., and McFarlane, D.A., 1989, Pre-Wisconsinan mammals from Jamaica and models of Late Quaternary extinction in the Greater Antilles: Quaternary Research, v. 31, p. 94–106. https://doi.org/10.1016/0033-5894(89)90088-4

Maitre, E., 2014, Western European middle Eocene to early Oligocene Chiroptera: systematics, phylogeny and palaeoecology based on new material from the Quercy (France): Swiss Journal of Palaeontology, v. 133, p. 141–242. https://doi.org/10.1007/s13358-014-0069-3

Mancina, C.A., and Garcia-Rivera, L., 2005, New genus and species of fossil bat (Chiroptera: Phyllostomidae) from Cuba: Caribbean Journal of Science, v. 41, p. 22–27.

Marks, C.S., and Marks, G.E., 2006, Bats of Florida: University Press of Florida, Gainesville, 176 p.

Martin, R.A., 1972, Synopsis of Late Pliocene and Pleistocene bats of North America and the Antilles: American Midland Naturalist, v. 87, p. 326–335. https://doi.org/10.2307/2423565

Martin, R.A., 1974, Fossil mammals from the Coleman IIA Fauna, Sumter County; *in* Webb, S.D. ed., Pleistocene Mammals of Florida: Gainesville, University Presses of Florida, p. 35–99.

Martin, R.A., Goodwin, H.T. and Farlow, J.O., 2002, Late Neogene (Late Hemphillian) rodents from the Pipe Creek Sinkhole, Grant County, Indiana: Journal of Vertebrate Paleontology, v. 22, p. 137–151. https://doi.org/10.1671/0272-4634(2002)022[0137:LNLHRF]2.0.CO;2

Martin, R.A., and Webb, S.D., 1974, Late Pleistocene mammals from the Devil's Den Fauna, Levy County; *in* Webb, S.D. ed., Pleistocene Mammals of Florida: Gainesville, University Presses of Florida, p. 114–145.

McCarthy, T.J., Davis, W.B., Hill, J.E., Jones, J.K., Jr., and Cruz, G.A., 1993, Bat (Mammalia: Chiroptera) records, early collectors, and faunal lists for northern Central America: Annals of Carnegie Museum, no. 62, p. 191–228. https://doi.org/10.5962/p.226650

McDonald, H.G., 2005, Paleoecology of extinct xenarthrans and the Great American Biotic Interchange: Bulletin of the Florida Museum of Natural History, v. 45, p. 313–333. https://doi.org/10.58782/flmnh.zrar3244

McDonald, H.G., Chatters, J.C., and Gaudin, T.J., 2017, A new genus of megalonychid ground sloth (Mammalia, Xenarthra) from the late Pleistocene of Quintana Roo, Mexico: Journal of Vertebrate Paleontology. https://doi.org/10.1080/02724634.2017.1307206

McDonald, H.G., and Jefferson, G.T., 2008, Distribution of Pleistocene *Nothrotheriops* (Xenarthra, Nothrotheriidae) in North America: Natural History Museum of Los Angeles County, Science Series, no. 41, p. 313–331.

McFarlane, D.A., Lundberg, J., Flemming, C., MacPhee, R.D.E., and Lauritzen, S.-E., 1998, A second pre-Wisconsinan locality for the extinct Jamaican rodent *Clidomys* (Rodentia: Heptaxodontidae), Caribbean Journal of Science, v. 34, p. 315–317.

McFarlane, D.A., Lundberg, J. and Maincent, G., 2014, New specimens of *Amblyrhiza inundata* (Rodentia: Caviomorpha) from the Middle Pleistocene of Saint Barthélemy, French West Indies: Caribbean Journal of Earth Science, v. 47, p. 15–19.

McGuire, J.L., and Davis, E.B., 2014, Conservation paleobiogeography: the past, present, and future of species distributions: Ecography, v. 37, p. 1092–1094. https://doi.org/10.1111/ecog.01337

McNab, B.K., 1973, Energetics and the distribution of vampires: Journal of Mammalogy, v. 54, p. 131–144. https://doi.org/10.2307/1378876

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

Mead, J.I., Jass, C.N., Swift, S.L,. and Weaver, S., this volume, Late Quaternary faunas from caves in the Black Hills, South Dakota: Journal of Cave and Karst Studies.

Mead, J.I., and Mikesic, D.G., 2001, First fossil record of *Euderma maculatum* (Chiroptera: Vespertilionidae), eastern Grand Canyon, Arizona. Southwestern Naturalist, v. 46, p. 380–383. https://doi.org/10.2307/3672439

Mead, J.I., Roth, E.L., Van Devender, T.R., and Steadman, D.W., 1984, The late Wisconsinan vertebrate fauna from Deadman Cave, southern Arizona: Transactions of the San Diego Society of Natural History v. 20, p. 247–276. https://doi.org/10.5962/bhl.part.29007

Morgan, G.S., 1989, Fossil Chiroptera and Rodentia from the Bahamas, and the historical biogeography of the Bahamian mammal fauna; *in* Woods, C.A., ed., Biogeography of the West Indies: Past, Present, and Future: Gainesville, Florida, Sandhill Crane Press, p. 685–740.

Morgan, G.S., 1991, Neotropical Chiroptera from the Pliocene and Pleistocene of Florida: Bulletin of the American Museum of Natural History, v. 206, p. 176–213.

Morgan, G.S., 1993, Quaternary land vertebrates of Jamaica; *in* Wright, R.M., and Robinson, E., eds., Biostratigraphy of Jamaica: Geological Society of America, Memoir 182, p. 417–442. https://doi.org/10.1130/MEM182-p417

Morgan, G.S., 1994, Late Quaternary fossil vertebrates from the Cayman Islands; *in* Brunt, M.A., and Davies, J.E., eds., The Cayman Islands: Natural History and Biogeography: Dordrecht, Netherlands, Kluwer Academic Publishers, p. 465–508. https://doi.org/10.1007/978-94-011-0904-8_22

Morgan, G.S., 1999, Late Pleistocene climatic change and Neotropical bat extinctions: Current Research in the Pleistocene, v. 16, p. 133–134.

Morgan, G.S., 2001, Patterns of extinction in West Indian bats; *in* Woods, C.A., and Sergile, F.E., eds., Biogeography of the West Indies: Patterns and Perspectives, Second ed.: Boca Raton, Florida, CRC Press, p. 369–407. https://doi.org/10.1201/9781420039481.ch20

Morgan, G.S., 2002a, Late Rancholabrean mammals from southernmost Florida, and the Neotropical influence in Florida Pleistocene faunas: Smithsonian Contributions to Paleobiology, no. 93, p. 15–38.

Morgan, G.S., 2002b, Pleistocene vertebrate fossils from Slaughter Canyon Cave, Carlsbad Caverns National Park: Park Paleontology, v. 6, p. 5.

Morgan, G.S., 2005, The Great American Biotic Interchange in Florida: Bulletin of the Florida Museum of Natural History, v. 45, p. 271–311. https://doi.org/10.58782/flmnh.pkqn7297

Morgan, G.S., and Albury, N.A., 2013, The Cuban crocodile (*Crocodylus rhombifer*) from Late Quaternary fossil deposits in the Bahamas and Cayman Islands: Bulletin of the Florida Museum of Natural History, v. 52, no. 3, p. 161–236. https://doi.org/10.58782/flmnh.zlxt6519

Morgan, G.S., and Czaplewski, N.J., 2003, A new bat (Chiroptera: Natalidae) from the early Miocene of Florida, with comments on natalid phylogeny. Journal of Mammalogy, v. 84, p. 729–752. https://doi.org/10.1644/1545-1542(2003)084<0729:ANBCNF>2.0.CO;2

Morgan, G.S., and Czaplewski, N.J., 2012; Evolutionary history of the Neotropical Chiroptera: the fossil record. *in* Gunnell, G.F., and Simmons, N.B. eds., Evolutionary History of Bats: Fossils, Molecules, and Morphology: Cambridge, Cambridge University Press, p. 105–161. https://doi.org/10.1017/CBO9781139045599.005

Morgan, G.S., and Czaplewski, N.J., 2023, New bats in the tropical family Emballonuridae (Mammalia: Chiroptera) from the Oligocene and early Miocene of Florida: Bulletin of the Florida Museum of Natural History, v. 60(3), p. 133–234. https://doi.org/10.58782/flmnh.wefq4531

Morgan, G.S., Czaplewski, N.J., and Simmons. N.B., 2019, A new mormoopid bat from the Oligocene (Whitneyan and Arikareean) of Florida, and phylogenetic relationships of the major clades of Mormoopidae (Mammalia: Chiroptera): Bulletin of the American Museum of Natural History, no. 434, p. 1–141. https://doi.org/10.1206/0003-0090.434.1.1

Morgan, G.S., and Emslie, S.D., 2010. Tropical and western influences in vertebrate faunas from the Pliocene and Pleistocene of Florida: Quaternary International, v. 217, p. 143–158. https://doi.org/10.1016/j.quaint.2009.11.030

Morgan. G.S., and Harris, A.H., 2015, Pliocene and Pleistocene vertebrates of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 68, p. 233–427.

Morgan, G.S., and Hulbert, R.C., Jr., 2008, Cenozoic vertebrate fossils from paleokarst deposits in Florida; *in* Florea, L.J., ed., Caves and Karst of Florida: A Guidebook for the 2008 NSS National Convention, Lake City, Florida. National Speleological Society, Huntsville, Alabama, p. 248–271.

Morgan, G.S., Linares, O.J., and Ray, C.E., 1988, New species of fossil vampire bats (Mammalia, Chiroptera, Desmodontidae) from Florida and Venezuela: Proceedings of the Biological Society of Washington, v. 101, p. 912–928.

Morgan, G.S. and Lucas, S.G., 2006, Pleistocene vertebrates from southeastern New Mexico: New Mexico Geological Society, Guidebook 57, p. 317–335. https://doi.org/10.56577/FFC-57.317

Morgan, G. S., McDonald, H. G., and Czaplewski, N. J., 2025, Possible Coevolution of Vampire Bats (Chiroptera:Phyllostomidae: Desmodus) and Large Xenarthrans (Cingulata,Pilosa) in North America and South America During the Quaternary: Quaternary https://doi.org/10.3390/quat9010002

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

Morgan, G.S., and Wilkins, L., 2003, The extinct rodent *Clidomys* (Heptaxodontidae) from a Late Quaternary cave deposit in Jamaica: Caribbean Journal of Science*,* v. 39, p. 34–41.

Morgan, G.S., and Woods, C.A., 1986, Extinction and the zoogeography of West Indian land mammals: Biological Journal of the Linnean Society, v. 28, p. 167–203. https://doi.org/10.1111/j.1095-8312.1986.tb01753.x

Moroz, M., Jackson, I.S.C., Ramirez, D., and Kemp, M.E., 2021, Divergent morphological responses to millennia of climate change in two species of bats from Hall's Cave, Texas, USA: PeerJ 9:e10856 http://doi.org/10.7717/peerj.10856.

Morrone, J.J., 2017, Neotropical biogeography: Regionalization and evolution: Boca Raton, Florida, CRC Press, Taylor and Francis Group, 282 p. https://doi.org/10.1201/b21824

Morrone, J.J., Escalante, T., Rodríguez-Tapia, G., Carmona, A., Arana, M., and Mercado-Gómez, J.D., 2022, Biogeographic regionalization of the Neotropical region: New map and shapefile: Anais da Academia Brasiliera Ciencias, v. 94. https://doi.org/10.1590/0001-3765202220211167

North American Bat Conservation Alliance (NABCA), 2023, State of the bats North America: https://www.batcon.org/stateofthebats.

Nowak, R.M., 1994, Walker's Bats of the World: Baltimore, Johns Hopkins University Press, 287 p.

Olson, D.M. et al., 2001, Terrestrial ecoregions of the world: a new map of life on Earth. BioScience, v. 51, p. 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Orihuela, J., 2011, Skull variation of the vampire bat *Desmodus rotundus* (Chiroptera: Phyllostomidae): Taxonomic implications for the Cuban fossil vampire bat *Desmodus puntajudensis*. Chiroptera Neotropical. v. 17, p. 963–976.

Orihuela, J., Pérez Orozco, L., Álvarez Licourt, J.L., Viera Muñoz, R.A., and Santana Barani, C., 2020b, Late Holocene land vertebrate fauna from Cueva de los Nesofontes, western Cuba: stratigraphy, chronology diversity, and paleoecology. Palaeontologia Electronica v. 23, no. 3, p. a57. https://doi.org/10.26879/995

Orihuela, J., Viñola, L.W., and Viera, R.A., 2020, New bat records from Cuba with emphasis on the province of Matanzas: Novitates Caribaea, v. 15, p. 96–116. https://doi.org/10.33800/nc.vi15.218

O'Shea, T.J., Cryan, P.M., and Bogan, M.A., 2018, United States bat species of concern: a synthesis: Proceedings of the California Academy of Sciences, Series 4, v. 65, p. 1–79.

Parmalee, P.W., 1967, A recent cave bone deposit in southwestern Illinois: National Speleological Society Bulletin, v. 29, p. 119–147.

Parmalee, P.W., and Oesch, R.D., 1972, Pleistocene and Recent faunas from the Brynjulfson Caves, Missouri: Illinois State Museum Reports of Investigations, no. 25, p. 1–43.

Parmalee, P.W., Oesch, R.D., and Guilday, J.E., 1969, Pleistocene and recent vertebrate faunas from Crankshaft Cave, Missouri: Illinois State Museum, Reports of Investigations, no. 14, p. 1–37.

Patton, T.H., 1963, Fossil vertebrates from Miller's Cave, Llano County, Texas: Texas Memorial Museum Bulletin 7, p. 1–41.

Patton, T.H., 1969, An Oligocene land vertebrate fauna from Florida: Journal of Paleontology, v. 43, p. 543–546.

Pavan, A.C., and Marroig, G., 2016, Integrating multiple evidences in taxonomy: species diversity and phylogeny of mustached bats (Mormoopidae: *Pteronotus*): Molecular Phylogenetics and Evolution, v. 103, p. 184–198. https://doi.org/10.1016/j.ympev.2016.07.011

Pearson, G.A., 2005, Late Pleistocene megafaunal deposits of the Isthmus of Panama and their paleoenvironmental implications: Caribbean Journal of Science, v. 41, p. 1–13.

Pickford, M., Mein, P., and Senut, B., 1994, Fossiliferous Neogene karst fillings in Angola, Botswana and Namibia. Suid-Afrikaanse Tydskrif vir Wetenskap, v. 90, p. 227–230.

Polyak, V.J., Asmerom, Y., and Rasmussen, J.B.T., 2006a, Old bat guano in Slaughter Canyon Cave: New Mexico Geological Society, Guidebook 57, p. 23–24.

https://doi.org/10.56577/FFC-.23

Polyak, V.J., McIntosh, W.C., Provencio, P.P., and Güven, N., 1998, Age and origin of Carlsbad Caverns and related caves from ^{40}Ar/^{39}Ar of alunite: Science, v. 279, p. 1919–1922. https://doi.org/10.1126/science.279.5358.1919

Polyak, V.J., McIntosh, W.C., Provencio, P.P., and Güven, N., 2006b, Alunite and natroalunite tell a story–the age and origin of Carlsbad Cavern, Lechuguilla Cave, and other sulfuric-acid type caves of the Guadalupe Mountains: New Mexico Geological Society, Guidebook 57, p. 203–209. https://doi.org/10.56577/FFC-57.203

Pratt, A.E., 1989, Taphonomy of the microvertebrate fauna from the early Miocene Thomas Farm locality, Florida (U.S.A.). Palaeogeography, Palaeoclimatology, and Palaeoecology, v. 76, p. 125–151. https://doi.org/10.1016/0031-0182(89)90107-7

Pratt, A.E., 1990, Taphonomy of the large vertebrate fauna from the Thomas Farm locality (Miocene, Hemingfordian), Gilchrist County, Florida. Bulletin of the Florida Museum of Natural History, v. 35(2), p. 35–130. https://doi.org/10.58782/flmnh.dlja4398

Pregill, G.K., Steadman, D.W., Olson, S.L., and Grady F.V., 1988, Late Holocene fossil vertebrates from Burma Quarry, Antigua, Lesser Antilles: Smithsonian Contributions to Zoology, no. 463, p. 1–27. https://doi.org/10.5479/si.00810282.463

Pregill, G.K., Steadman, D.W., and Watters, D.R., 1994, The Quaternary vertebrate fauna of the Lesser Antilles: Historical components of Caribbean biogeography: Bulletin of Carnegie Museum of Natural History, no. 30, p. 1–51. https://doi.org/10.5962/p.240776

Prothero, D.R., and Emry, R.J., 2004, The Chadronian, Orellan, and Whitneyan North American Land Mammal Ages; *in* Woodburne, M.O., ed., Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology: New York, Columbia University Press, p. 156–168. https://doi.org/10.7312/wood13040-007

Ravel, A., Adaci, M., Bensalah, M., Charruault, A.-L., Essid, E.M., Ammar, H.K., Marzougui, W., Mahboubi, M., Mebrouk, F., Merzeraud, G., Vianey-Liaud, M., Tabuce, R., and Marivaux, L., 2016, Origine et radiation initiale des chauves-souris modernes : nouvelles découvertes dans l'Éocène d'Afrique du Nord: Geodiversitas [Origin and Initial Radiation of Modern Bats: New Discoveries in the Eocene of North Africa: Geodiversitas], v. 38, p. 355–434. http://dx.doi.org/10.5252/g2016n3a3

Ravel, A., Marivaux, L., Qi, T., Wang, Y.-Q., and Beard, K.C., 2013, New chiropterans from the middle Eocene of Shanghuang (Jiangsu Province, coastal China): new insight into the dawn horseshoe bats (Rhinolophidae) in Asia. Zoologica Scripta, v. 43, p. 1–23. https://doi.org/10.1111/zsc.12027

Ray, C.E., Olsen, S.J., and Gut, H.J., 1963, Three mammals new to the Pleistocene fauna of Florida, and a reconsideration of five earlier records: Journal of Mammalogy, v. 44, p. 373–395. https://doi.org/10.2307/1377207

Ray, C.E., Linares, O.J. and Morgan, G.S., 1988, Paleontology; *in* Greenhall, A.M, and Schmidt, U., eds, Natural History of Vampire Bats: Boca Raton, Florida, CRC Press, p. 19–30. https://doi.org/10.1201/9781351074919-3

Ray, C.E., and Wilson, D.E., 1979, Evidence for *Macrotus californicus* from Terlingua, Texas: The Museum, Texas Tech University, Occasional Papers, no. 57, p. 1–10. https://doi.org/10.5962/bhl.title.156529

Repenning, C.A., and Grady, F.V., 1988, The microtine rodents of the Cheetah Room Fauna, Hamilton Cave, West Virginia, and the spontaneous origin of *Synaptomys*: U.S. Geological Survey Bulletin 1853, p. 1–32.

Reynolds, R.E., Reynolds, R.L., Bell, C.J., Czaplewski, N.J., Goodwin, H.T., Mead, J.I., and Roth, B., 1991, The Kokoweef Cave faunal assemblage; *in* Reynolds, R.E., ed., Crossing the borders: Quaternary studies in eastern California and southwestern Nevada: San Bernardino County Museum Association, Redlands, MDQRC Special Publication, p. 97–103.

Rietbergen, T.B., van den Hoek Ostende, L.W., Aase, A., Jones, M.F., Medeiros, E.D., and Simmons, N.B., 2023, The oldest known bat skeletons and their implications for Eocene chiropteran diversification. PLoS One, v. 18(4), p. e0283505. https://doi.org/10.1371/journal.pone.0283505

Rogers, K.L., Repenning, C.A., Luiszer, F.G., and Benson, R.D., 2000, Geologic history, stratigraphy, and paleontology of SAM Cave, north-central New Mexico: New Mexico Geology, v. 22, p. 89–100, 113–117. https://doi.org/10.58799/NMG-v22n4.89

Rosina, V.V., and Pickford, M., 2019, Preliminary overview of the fossil record of bats (Chiroptera, Mammalia) from the Miocene sites of Otavi Mountainland (northern Namibia). Communications of the Geological Survey of Namibia, v. 21, p. 48–58.

Ruez, D.R., Jr., 2002, Mammalian taphonomy of the early Irvingtonian (late Pliocene) Inglis 1C Fauna (Citrus County, Florida): Southeastern Geology, v. 41, p. 159–168.

Sagebiel, J.C., 2010, Late Pleistocene fauna from Zesch Cave, Mason County, Texas: Quaternary International, v. 217, p. 159–174. https://doi.org/10.1016/j.quaint.2009.11.029

Santucci, V.L., Kenworthy, J., and Kerbo, R., 2001, An inventory of paleontological resources associated with National Park Service caves: Geologic Resources Division Technical Report NPS/NRGRD/GRDTR-01/02

Scott, T.M., Means, G.H., Meegan, R.P., Means, R.C., Upchurch, S.B., Copeland, R.E., Jones, J., Roberts, T., and Willet, A., 2004, Springs of Florida: Florida Geological Survey, Bulletin 66, 658 p.

Schubert, B.W., 2003, A late Pleistocene and early Holocene mammalian fauna from Little Beaver Cave, central Ozarks, Missouri; *in* Schubert, B.W., Mead, J.I., and Graham, R.W., eds., Ice Age Cave Faunas of North America: Bloomington, Indianapolis, and Denver Museum of Nature and Science, Indiana University Press, p. 149–200. https://doi.org/10.2979/1982.0

Schubert, B.W., 2010, Late Quaternary chronology and extinction of North American giant short-faced bears (*Arctodus simus*): Quaternary International, v. 217, p. 188−194. https://doi.org/10.1016/j.quaint.2009.11.010.

Schubert, B.W., Chatters, J.C., Arroyo-Cabrales, J., Samuels, J.X., Soibelzon, L.H., Prevosti, F.J., Widga, C., Nava, A., Rissolo. D., and Erreguerena, P.L., 2019, Yucatán carnivorans shed light on the Great American Biotic Interchange: Biology Letters, v. 15 (6 pages): 20190148. http://dx.doi.org/10.1098/rsbl.2019.0148.

Schubert, B.W., and Mead, J.I., 2012, Paleontology in caves: *in* White, W.B., and Culver, D.C., eds., Encyclopedia of Caves: Chennai, Academic Press, p. 590–598. https://doi.org/10.1016/B978-0-12-383832-2.00087-6

Semken, H.A. Jr., 1961, Fossil vertebrates from Longhorn Cavern, Burnet County, Texas: Texas Journal of Science, v. 13, p. 290–310.

Semken, H.A., Jr., Graham, R.W., and Stafford, T.W., Jr., 2010, AMS ^{14}C analysis of Late Pleistocene non-analog faunal components from 21 cave deposits in southeastern North America: Quaternary International, v. 217, p. 240–255. https://doi.org/10.1016/j.quaint.2009.11.031

Sigé, B., and Legendre, S., 1983, L'histoire des peuplements de chiroptères du Bassin Méditerranéen: L'apport comparé des remplissages karstiques et des dépôts fluviolacustres. Mémoires de Biospéologie [The history of bat populations in the Mediterranean Basin: The comparative contribution of karst fillings and fluviolacustrine deposits. Memoirs of Biospeology], v. 10, p. 209–225.

Silva Taboada, G., 1974, Fossil Chiroptera from cave deposits in central Cuba, with description of two new species (genera *Pteronotus* and *Mormoops*) and the first West Indian record of *Mormoops megalophylla*: Acta Zoologica Cracoviensia, v. 19, p. 33–73.

Silva Taboada, G., 1976, Historia y actualización taxonómica de algunas especies Antillanas de murciélagos de los géneros *Pteronotus*, *Brachyphylla*, *Lasiurus*, y *Antrozous* (Mammalia: Chiroptera). Poeyana [History and taxonomic update of some West Indian species of bats of the genera Pteronotus, Brachyphylla, Lasiurus, and Antrozous (Mammalia: Chiroptera). Poeyana], v. 153, p. 1–24.

Silva Taboada, G., 1979, Los Murciélagos de Cuba: La Habana, Cuba, Editorial Academia [The Bats of Cuba: Havana, Cuba, Editorial Academia], 423 p.

Silva Taboada, G., and Vela Rodríguez, H., 2009, Actualización taxonómica y distribucional de los murciélagos de Cuba. El Explorador [Taxonomic and distributional update of bats in Cuba. The Explorer], v. 61, p. 1–5.

Simmons, N.B., 2005, Order Chiroptera; *in* Wilson, D.E., and Reeder, D.M., eds., Mammal Species of the World: A Taxonomic and Geographic Reference: Baltimore, Johns Hopkins University Press, p. 312–529.

Simmons, N.B., Gunnell, G.F., and Czaplewski, N.J., 2020, Fragments and gaps: the fossil record; *in* Fleming, T.H., Dávalos, L.M., and Mello, M.A.R., eds., Phyllostomid Bats: A Unique Mammalian radiation: Chicago, University of Chicago Press, p. 63–86. https://doi.org/10.7208/chicago/9780226696263.003.0005

Simmons, N.B., Seymour, K.L. Habersetzer, J., and Gunnell, G.F., 2008, Primitive Early Eocene bat from Wyoming and the evolution of flight and echolocation: Nature, v. 451, p. 818–821. https://doi.org/10.1038/nature06549

Simms, M.J., 1994, Emplacement and preservation of vertebrates in caves and fissures. Zoological Journal of the Linnean Society, v. 112, p. 261–283. https://doi.org/10.1006/zjls.1994.1042

Simpson, G.G., 1928, Pleistocene mammals from a cave in Citrus County, Florida: American Museum Novitiates, no. 328, p. 1–16.

Sinclair, W.J., 1904, The exploration of the Potter Creek Cave. University of California Publications, American Archaeology and Ethnology, v. 2, p. 1–27.

Sinclair, W.J., 1905, New Mammalia from the Quaternary caves of California. University of California Publications in Geology. v. 4, p. 145–161.

Skinner, M.F., 1942, The fauna of Papago Springs Cave, Arizona, and a study of *Stockoceros*; with three new antilocaprines from Nebraska and Arizona: Bulletin of the American Museum of Natural History v. 80, p. 143–220.

Smith, J.D., 1972, Systematics of the chiropteran Family Mormoopidae. University of Kansas Museum of Natural History, Miscellaneous Publication, no 56, p. 1–132.

Smith, T., Habersetzer, J., Simmons, N.B., and Gunnell, G.F., 2012, Systematics and paleobiogeography of early bats; *in* Gunnell, G.F., and Simmons, N.B., eds., Evolutionary History of Bats: Fossils, Molecules and Morphology: Cambridge, Cambridge University Press, p. 23–66. https://doi.org/10.1017/CBO9781139045599.003

Soto-Centeno J.A., Simmons, N.B., and Steadman, D.W., 2017, The bat community of Haiti and evidence for its long-term persistence at high elevations: PLoS ONE 12(6): e0178066. https://doi.org/10.1371/journal.pone.0178066

Soto-Centeno, J.A., and Steadman, D.W., 2015, Fossils reject climate change as the cause of extinction of Caribbean bats: Scientific Reports, 5:7971. https://doi.org/10.1038/srep07971

Steadman, D.W., and Franklin, J., 2015, Changes in a West Indian bird community since the late Pleistocene: Journal of Biogeography, v. 42, p. 426–438. https://doi.org/10.1111/jbi.12418

Steadman, D.W., Franz, R., Morgan, G.S., Albury, N.A., Kakuk, B., Broad, K., Franz, S.E., Tinker, K., Pateman, M.P., Lott, T.A., Jarzen, D.M., and Dilcher, D.L., 2007, Exceptionally well preserved late Quaternary plant and vertebrate fossils from a blue hole on Abaco, The Bahamas. Proceedings of the National Academy of Sciences. USA, v. 104, p. 19897–19902. https://doi.org/10.1073/pnas.0709572104

Steadman, D.W., Mead, J.I., Bright, R.C., Force, C., 1994, Late Quaternary plants and animals from Rattlesnake Cave, Snake River Plain, Idaho: Environmental Science and Research Foundation, Idaho Falls, Foundation-001, p. 1–34.

Steadman, D.W., Pregill, G.K., and Olson, S.L., 1984, Fossil vertebrates from Antigua, Lesser Antilles: evidence for late Holocene human-caused extinctions in the West Indies: Proceedings of the National Academy of Sciences, v.81, p. 4448–4451. https://doi.org/10.1073/pnas.81.14.4448

Stoetzel, E., Royer, A., Cochard, D., and Lenoble, A., 2016, Late Quaternary changes in bat palaeobiodiversity and palaeobiogeography under climatic and anthropogenic pressure: new insights from Marie-Galante, Lesser Antilles: Quaternary Science Reviews, v. 143, p. 150–174. http://dx.doi.org/10.1016/j.quascirev.2016.05.013.

Suárez, W., and Diaz-Franco, S., 2003, A new fossil bat (Chiroptera: Phyllostomidae) from a Quaternary cave deposit in Cuba: Caribbean Journal of Science, v. 39, p. 371–377.

Tedford, R.H., Albright, L.B., III, Barnosky, A.D., Ferrusquia-Villafranca, I., Hunt, R.M., Jr., Storer, J.E., Swisher, C.C., III, Voorhies, M.R., Webb, S.D., and Whistler, D.P., 2004, Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs); *in* Woodburne, M.O., ed., Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology: New York, Columbia University Press, p. 169–231. https://doi.org/10.7312/wood13040-008

Tejedor, A., 2011, Systematics of funnel-eared bats (Chiroptera: Natalidae): Bulletin of the American Museum of Natural History, no. 353, p. 1–140. https://doi.org/10.1206/636.1

Toomey, R.S., III, 1993, Late Pleistocene and Holocene faunal and environmental changes at Hall's Cave, Kerr County, Texas: Unpublished PhD Thesis, Austin, Texas, University of Texas at Austin.

Toomey, R.S., III, 2006, Paleontology in cave conservation and restoration – archived antiquity; *in* Hildreth-Werker, V., and Werker, J.C., eds., Cave Conservation and Restoration: National Speleological Society, Inc., Huntsville, Alabama, p. 83–92.

Toomey, R.S., III, Blum, M.D, and Valastro, S., 1993, Late Quaternary climates and environments of the Edwards Plateau, Texas: Global and Planetary Change v. 7, p. 299–320. https://doi.org/10.1016/0921-8181(93)90003-7

Varona, L.S. 1974, Catálogo de los Mamíferos Vivientes y Extinguidos de las Antillas: Habana, Cuba, Academia de Ciencias de Cuba [Catalogue of Living and Extinct Mammals of the Antilles: Havana, Cuba, Cuban Academy of Sciences], 139 p.

Velazco, P.M., O'Neill, H., Gunnell, G.F., Cooke, S.B., Rimoli, R., Rosenberger, A.L., and Simmons, N.B., 2013, Quaternary bat diversity in the Dominican Republic: American Museum Novitates, no. 3779, p. 1–20. https://doi.org/10.1206/3779.2

Voss, R.S., Fleck, D.W., Strauss, R.E., Velazco, P.M., and Simmons, N.B., 2016, Roosting ecology of Amazonian bats: evidence for guild structure in hyperdiverse mammalian communities: American Museum Novitates, no. 3870, p. 1–43. https://doi.org/10.1206/3870.1

Weary, D.J., and Doctor, D.H., 2014, Karst in the United States: A digital map compilation and database: U.S. Geological Survey Open-File Report 2014–1156, 23 p. https://dx.doi.org/10.3133/ofr20141156.

Webb, S.D., 1974, Chronology of Florida Pleistocene mammals; *in* Webb, S.D., ed., Pleistocene Mammals of Florida: Gainesville, Florida, University Presses of Florida, p. 5–31.

Webb, S.D., 1976, Mammalian faunal dynamics of the Great American Interchange: Paleobiology, v. 2, p. 220–234. https://doi.org/10.1017/S0094837300004802

Webb, S.D., and Perrigo, S.C., 1984, Late Cenozoic vertebrates from Honduras and El Salvador: Journal of Vertebrate Paleontology, v. 4, p. 237–254. https://doi.org/10.1080/02724634.1984.10012006

Webb, S.D., and Simons, E., 2006, Vertebrate paleontology; in Webb, S.D., ed., First Floridians and Last Mastodons: The Page-Ladson Site in the Aucilla River: Dordrecht, Netherlands, Springer, p. 215–246. https://doi.org/10.1007/978-1-4020-4694-0_8

Widga, C., and Colburn, M., 2015, Paleontology and paleoecology of guano deposits in Mammoth Cave, Kentucky, USA: Quaternary Research, v. 83, p. 427–436. http://dx.doi.org/10.1016/j.yqres.2015.01.008

Wilkins, K.T., 1983, Pleistocene mammals from the Rock Springs Local Fauna, central Florida: North Carolina State Museum of Natural History, Brimleyana, no. 9. p. 69–82.

Williams, P.W., and Ford, D.C., 2006, Global distribution of carbonate rocks [map]; *in* Pfeffer, K.-H., ed., Karst, International Atlas of Karst Phenomena, Union Internationale de Spéléologie: International Association of Geomorphologists 6th International Conference, Zaragoza 2005-Karst papers: Berlin, Stuttgart: Gebruder Bontraeger. Zeitschrift für Geomorphologie [Journal of Geomorphology], Supplement, v. 147, Sheets 18-21. ISBN 978-3-443-21147-9.

Williams, S.L., Willig, M.R., and Reid, F.A., 1995, Review of the *Tonatia bidens* complex (Mammalia: Chiroptera), with descriptions of two new subspecies: Journal of Mammalogy, v. 76, p. 612–626. https://doi.org/10.2307/1382370

Wilson, D.W., and Ruff, S., eds., 1999, The Smithsonian Book of North American Mammals: Washington, Smithsonian Institution Press, 750 p.

Wilson, R.W., 1942, Preliminary study of the fauna of Rampart Cave, Arizona: Contributions to Paleontology, Carnegie Institution of Washington, v. 530, p. 169–185.

Winkler, A.J., and Gose, W., 2003; Mammalian fauna and paleomagnetics of the middle Irvingtonian (early Pleistocene) Fyllan Cave and Kitchen Door localities, Travis County, Texas; *in* Schubert, B.W., Mead, J.I. and Graham, R.W., eds., Ice Age Cave Faunas of North America: Bloomington, Indianapolis, and Denver Museum of Nature and Science, Indiana University Press, p. 215–261.

Woloszyn, B.W., and Silva Taboada, G., 1977, Nueva especie fósil de *Artibeus* (Mammalia: Chiroptera) de Cuba, y tipificación preliminar de los depósitos fosilíferos Cubanos contentivos de mamíferos terrestres: Poeyana [New fossil species of Artibeus (Mammalia: Chiroptera) from Cuba, and preliminary typing of Cuban fossil deposits containing terrestrial mammals: Poeyana], v. 161, p. 1–17.

Womochel, D.R., and Barnett, W.S., 1980, Field Trip Number 3: The Pleistocene vertebrate assemblage of Little Bear Cave, Colbert County, Alabama; *in* Tull, J.F., ed., Field Trips for the Southeastern Section of the Geological Society of America, Birmingham, Alabama, March 27-30, 1980, p. 69–76.

Woodburne, M.O., (ed.), 2004, Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology: New York, Columbia University Press. https://doi.org/10.7312/wood13040

Woolfenden, G.E., 1959, A Pleistocene avifauna from Rock Spring, Florida: Wilson Bulletin, v. 71. p. 183–187.

Ziegler, A.C., Howarth, F.G., and Simmons, N.B., 2016, A second endemic land mammal for the Hawaiian Islands: a new genus and species of fossil bat (Chiroptera: Vespertilionidae): American Museum Novitates, no. 3854, p. 1–52. https://doi.org/10.1206/3854.1

Appendix. Species list of Cenozoic bats (Mammalia: Chiroptera) from cave and karst deposits in North America. This list is divided into the same geographic and chronologic sections as in the text. Fossil bats from caves are separated into three geographic regions: US and Canada, Mesoamerica (Mexico and Central America), and the West Indies. Fossil bats from Florida are listed separately because most of the fossil sites are karst deposits not caves. The order of families follows Simmons (2005). Within a family (subfamily for the Phyllostomidae), the genera and species are listed in alphabetical order. Extinct taxa are indicated by a dagger (†). The type locality for an extinct species is indicated by an asterisk (*). Extralimital records of a species are indicated by the pound sign (#). Quaternary records are not comprehensive; records published as "genus and species indet", "Chiroptera indet.", and "bat sp." are not included except for Oligocene-Miocene records. Abbreviations: indet. (indeterminate, refers to fossils that are too incomplete for a positive identification to a higher taxonomic level than indicated below); NALMA (North American Land Mammal Age).

Age and Geography Family, genus, species	Localities[1]	Age & NALMA	References
LATE PLEISTOCENE, Canada and US except Florida			
Phyllostomidae			
Macrotus californicus.	TEXAS: Terlingua fissure filling	Late Pleistocene, Rancholabrean	Ray & Wilson, 1979; Ray et al., 1988; Simmons et al., 2020
Desmodus †stocki	ARIZONA: Arkenstone Cave, La Tetera Cave, Rampart Cave; CALIFORNIA: Potter Creek Cave; NEW MEXICO: U-Bar Cave; TEXAS: Sierra Diablo Cave, Terlingua fissure filling; WEST VIRGINIA: New Trout Cave	Late Pleistocene, Rancholabrean	Sinclair, 1904, 1905; Wilson, 1942; Hutchison, 1967; Ray & Wilson, 1979; Garton & Grady, 1980; Harris, 1987, 2024; Ray et al., 1988; Grady et al., 2002; Czaplewski & Peachey, 2003; Carpenter, 2004; Czaplewski et al., this volume;
Molossidae			
Eumops sp.	ARIZONA: Rampart Cave	Late Pleistocene, Rancholabrean	Carpenter, 2004
?*Nyctinomops*	NEW MEXICO: Dry Cave[2]	Late Pleistocene, Rancholabrean	Harris, 2024
Tadarida brasiliensis	ARIZONA: Bat Cave, Rampart Cave; KENTUCKY: Mammoth Cave; NEW MEXICO: Carlsbad Cavern, Dry Cave[1], U-Bar Cave; WEST VIRGINIA: Hamilton Cave; TEXAS: Hall's Cave, Lower Sloth Cave, Schulze Cave	Late Pleistocene, Rancholabrean	Dalquest et al., 1969; Harris, 1987, 2024; Grady, 1991; Toomey, 1993; Carpenter, 2004; Schubert & Mead, 2012; Moroz et al., 2021; Kottkamp et al., 2022
Vespertilionidae			
Antrozous pallidus	NEVADA: Pintwater Cave; NEW MEXICO: Conkling Cavern, Dark Canyon Cave, Dry Cave[1], Howell's Ridge Cave, Isleta Cave No. 1, Muskox Cave, Pendejo Cave, Sierra Diablo Cave, U-Bar Cave; TEXAS: Dust Cave, Upper Sloth Cave; UTAH: Crystal Ball Cave	Late Pleistocene, Rancholabrean	Sinclair, 1904, 1905; Skinner, 1942; Hutchison, 1967; Jefferson, 1982; Heaton, 1985; Harris, 1987, 2003, 2024; Emslie, 1988; Reynolds et al., 1991; Czaplewski et al., 1999; Hockett, 2000; Mead et al., 2004, 2005
Corynorhinus rafinesquii	TENNESSEE: Lookout Mountain Cave	Late Pleistocene, Rancholabrean	Gaudin et al., 2011

Corynorhinus townsendii	ARIZONA: Bida Cave, Kartchner Cavern, Papago Springs Cave, Sandblast Cave, and Skull Cave; IDAHO: Rattlesnake Cave; NEVADA: a Mormon Mountain cave; NEW MEXICO: Carlsbad Cavern, Dry Cave[1], Muskox Cave, U-Bar Cave; TEXAS: Dust Cave, Lower Sloth Cave	Late Pleistocene, Rancholabrean	Skinner, 1942; Jefferson, 1982; Harris, 1987, 2024; Emslie, 1988; Steadman et al., 1994; Czaplewski et al., 1999; NJC unpublished; Mead et al., 2005; Kottkamp et al., 2022
?*Corynorhinus townsendii*	UTAH: Crystal Ball Cave	Late Pleistocene, Rancholabrean	Heaton, 1985
Corynorhinus sp.	ILLINOIS: Meyer Cave; KENTUCKY: Mammoth Cave; MISSOURI: Crankshaft Cave; NEW MEXICO: Dry Cave[1], U-Bar Cave; PENNSYLVANIA: Frankstown Cave, Hamilton Cave; TENNESSEE: Baker Bluff Cave, Cave Without a Name, Lookout Mountain Cave; VIRGINIA: Clark's Cave; WEST VIRGINIA: New Trout Cave, Hamilton Cave	Late Pleistocene, Rancholabrean	Guilday, 1961; Parmalee, 1967; Parmalee et al., 1969; Guilday et al., 1977, 1978; Garton & Grady, 1980; Harris, 1987, 2024; Grady, 1991; Grady et al., 2002; Gaudin et al., 2011; Schubert & Mead, 2012
Eptesicus fuscus	CANADA: QUEBEC: Mine Cave, Laflèche Cave, ONTARIO: Elba Cave, Dickson Cacve, ALBERTA: Eagle Cave; US: ALABAMA: ACb-2, ACb-3, & ACb-4 Caves, Little Bear Cave; ARIZONA: Bida Cave, Pyeatt Cave, Stanton's Cave; ILLINOIS: Meyer Cave; KENTUCKY: Mammoth Cave; MISSOURI: Bat Cave, Brynjulfson Caves 1 & 2, Crankshaft Cave; NEVADA: a Mormon Mountain cave; NEW MEXICO: Carlsbad Cavern, Dry Cave[1], Howell's Ridge Cave, Muskox Cave, Sierra Diablo Cave, U-Bar Cave; OKLAHOMA: Three-Forks Cave; PENNSYLVANIA: Hamilton Cave; TENNESSEE: Baker Bluff Cave, Cave Without a Name, Lookout Mountain Cave; TEXAS: Dust Cave, Fowlkes Cave, Hall's Cave, Lower Sloth Cave, Miller's Cave, Schulze Cave, Upper Sloth Cave, Zesch Cave; VIRGINIA: Clark's Cave; WEST VIRGINIA: Hoffman School Cave, New Trout Cave	Late Pleistocene, Rancholabrean	Patton, 1963; Parmalee, 1967; Dalquest et al., 1969; Parmalee et al., 1969; Parmalee & Oesch, 1972; Hawksley et al., 1973; Guilday et al., 1977, 1978; Guilday & Hamilton, 1978; Garton & Grady, 1980; Womochel & Barnett, 1980; Jefferson, 1982; Harris, 1987, 2024; Emslie, 1988; Grady, 1991; Toomey, 1993; Grady et al., 2002; Mead et al., 2005; Sagebiel, 2010; Ebersole & Ebersole, 2011; Gaudin et al., 2011; Harington, 2011; Schubert & Mead, 2012; Czaplewski et al., 2018, 2022; Moroz et al., 2021; Kottkamp et al., 2022
Eptesicus cf. *fuscus*	PENNSYLVANIA: New Paris No. 4 Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1964
cf. *Eptesicus fuscus*	MISSOURI: Little Beaver Cave	Late Pleistocene, Rancholabrean	Schubert, 2003
Euderma maculatum	ARIZONA: Marble Canyon Cave	Late Pleistocene, Rancholabrean	Mead & Mikesic, 2001
Lasionycteris noctivagans	CANADA: QUEBEC: Mine Cave; ALBERTA: Eagle Cave, Rats Nest Cave; US: OKLAHOMA: Sassafras Cave	Late Pleistocene, Rancholabrean	Czaplewski et al., 2002; Harington, 2011
Lasiurus blossevillii	NEW MEXICO: Carlsbad Cavern	Late Pleistocene, Rancholabrean	Kottkamp et al., 2022; Harris, 2024
Lasiurus borealis	KENTUCKY: Mammoth Cave; WEST VIRGINIA: New Trout Cave, Patton Cave, Hamilton Cave	Late Pleistocene, Rancholabrean	Garton & Grady, 1980, 1988, 1991; Grady et al., 2002; Schubert & Mead, 2012
Lasiurus cf. *borealis*	MISSOURI: Bat Cave; VIRGINIA: Clark's Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1977; Hawksley et al., 1973
Lasiurus borealis or *L. seminolus*	TENNESSEE: Lookout Mountain Cave	Late Pleistocene, Rancholabrean	Gaudin et al., 2011
Aeorestes cinereus	CANADA: ALBERTA: Eagle Cave; US: KENTUCKY: Mammoth Cave; NEW MEXICO: Carlsbad Caverns, Dry Cave[1], Pendejo Cave; TEXAS: Schulze Cave	Late Pleistocene, Rancholabrean	Dalquest et al., 1969; Harris, 2003, 2024; Schubert & Mead, 2012; Kottkamp et al., 2022

Aeorestes cf. *cinereus*	MISSOURI: Bat Cave	Late Pleistocene, Rancholabrean	Hawksley et al., 1973
Lasiurus sp.	NEW MEXICO: Dry Cave[1]	Late Pleistocene, Rancholabrean	Harris, 2024
cf. *Myotis*	ARIZONA: Deadman Cave	Late Pleistocene, Rancholabrean	Mead et al., 2004, 2005
Myotis austroriparius	KENTUCKY: Bat Cave	Late Pleistocene, Rancholabrean	Jansky et al., 2016
Myotis californicus	NEW MEXICO: Dry Cave[1]	Late Pleistocene, Rancholabrean	Harris, 2024
Myotis ciliolabrum	CALIFORNIA: Kokoweef Cave; NEW MEXICO: Carlsbad Cavern; TEXAS: Lower Sloth Cave	Late Pleistocene, Rancholabrean	Reynolds et al., 1991; Kottkamp et al., 2022; Harris, 2024
Myotis californicus or *M. ciliolabrum*	NEW MEXICO: Dry Cave[1]; TEXAS: Dust Cave	Late Pleistocene, Rancholabrean	Harris, 2024
Myotis ciliolabrum or *M. melanorhinus*	IDAHO: Rattlesnake Cave	Late Pleistocene, Rancholabrean	Steadman et al., 1994
Myotis evotis	NEW MEXICO: Dry Cave[1]	Late Pleistocene, Rancholabrean	Harris, 2024
Myotis cf. *evotis*	TEXAS: Schulze Cave	Late Pleistocene, Rancholabrean	Dalquest et al., 1969
Myotis grisescens	KENTUCKY: Bat Cave, Mammoth Cave; MISSOURI: Crankshaft Cave; OKLAHOMA: Three-Forks Cave; TENNESSEE: Lookout Mountain Cave; WEST VIRGINIA: New Trout Cave	Late Pleistocene, Rancholabrean	Parmalee et al., 1969; Garton & Grady, 1980; Grady et al., 2002; Gaudin et al., 2011; Schubert & Mead, 2012; Jansky et al., 2016; Czaplewski et al., 2018
Myotis cf. *grisescens*	MISSOURI: Bat Cave, Brynjulfson Caves 1 & 2; WEST VIRGINIA: Hoffman School Cave	Late Pleistocene, Rancholabrean	Parmalee & Oesch, 1972; Hawksley et al., 1973; Guilday & Hamilton, 1978
Myotis keenii	CANADA: QUEBEC: Trou Otis & Spéos de la Fée Caves; ONTARIO: Elba Cave, Dickson Cave	Late Pleistocene-early Holocene, Rancholabrean-Recent	Harington, 2011
Myotis leibii	KENTUCKY: Bat Cave, Mammoth Cave; TENNESSEE: Cave Without a Name, Lookout Mountain Cave; WEST VIRGINIA: New Trout Cave	Late Pleistocene, Rancholabrean	Garton & Grady, 1980; Grady et al., 2002; Gaudin et al., 2011; Schubert & Mead, 2012; Jansky et al., 2016
Myotis lucifugus	CANADA: QUEBEC: St-Elzéar Cave, Mine Cave, Laflèche Cave; ONTARIO: Elba Cave, Kelso Cave, Mt. Nemo Cave;, ALBERTA: Rats Nest Cave; US: ALABAMA: ACb-2, ACb-3, & ACb-4 Caves, Little Bear Cave; KENTUCKY: Bat Cave, Mammoth Cave	Late Pleistocene, Rancholabrean	Womochel & Barnett, 1980; Ebersole & Ebersole, 2011; Harington, 2011; Schubert & Mead, 2012; Jansky et al., 2016
Myotis cf. *lucifugus*	CANADA, QUEBEC: Saint-Elzéar Cave; MISSOURI: Bat Cave, Crankshaft Cave; PENNSYLVANIA: New Paris no. 4 Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1964; Parmalee et al., 1969; Hawksley et al., 1973; LaSalle, 1984
Myotis †*rectidentis*	TEXAS: *Laubach Cave/Innerspace Cavern	Late Pleistocene, Rancholabrean	Choate & Hall, 1967; Dorsey, 1977; Dalquest & Stangl, 1984
Myotis cf. *rectidentis*	NEW MEXICO: Dry Cave[1]	Late Pleistocene, Rancholabrean	Harris, 2024
Myotis septentrionalis	CANADA: QUEBEC: Mine Cave, Laflèche Cave; ONTARIO: Elba Cave; US: KENTUCKY: Bat Cave, Mammoth Cave; PENNSYLVANIA: New Paris No. 4 Cave; TENNESSEE: Cave Without a Name, Lookout Mountain Cave; WEST VIRGINIA: Patton Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1964; Grady, 1988; Gaudin et al., 2011; Harington, 2011; Schubert & Mead, 2012; Jansky et al., 2016
Myotis sodalis	KENTUCKY: Bat Cave, Mammoth Cave; MISSOURI: Bat Cave	Late Pleistocene, Rancholabrean	Hawksley et al., 1973; Schubert & Mead, 2012; Jansky et al., 2016

Myotis cf. *sodalis*	MISSOURI: Crankshaft Cave	Late Pleistocene, Rancholabrean	Parmalee et al., 1969
	ARIZONA: Arkenstone Cave, Bida Cave, Papago Springs Cave, Pyeatt Cave; CALIFORNIA: Kokoweef Cave; NEW MEXICO: Dry Cave[1], Isleta Cave no. 1, Muskox Cave; TEXAS: Lower Sloth Cave	Late Pleistocene, Rancholabrean	Skinner, 1942; Emslie, 1988; Reynolds et al., 1991; Czaplewski et al., 1999, 2022; Czaplewski & Peachey, 2003; Mead et al., 2005; Harris, 2024
Myotis velifer including *Myotis velifer* †*magnamolaris*	ARIZONA: Kartchner Cavern, Papago Springs Cave; NEW MEXICO: Carlsbad Cavern, Dark Canyon Cave, Dry Cave[1], Muskox Cave, Pendejo Cave, U-Bar Cave; TEXAS: Fowlkes Cave, Hall's Cave, *Laubach Cave/Innerspace Cavern, Lower Sloth Cave, Miller's Cave, Schulze Cave, Upper Sloth Cave, Zesch Cave	Late Pleistocene, Rancholabrean	Skinner, 1942; Patton, 1963; Choate & Hall, 1967; Dalquest et al., 1969; Dorsey, 1977; Dalquest & Stangl, 1984; Harris, 1987, 2003, 2024; Toomey, 1993; Czaplewski et al., 1999; NJC unpublished; Sagebiel, 2010; Moroz et al., 2021; Kottkamp et al., 2022
Myotis cf. *velifer*	ARIZONA: La Tetera Cave	Late Pleistocene, Rancholabrean	Czaplewski et al., this volume
Myotis volans	CANADA: ALBERTA: Eagle Cave; NEW MEXICO: Carlsbad Cavern	Late Pleistocene, Rancholabrean	Harington, 2011; Kottkamp et al., 2022; Harris, 2024
Myotis yumanensis	NEW MEXICO: Carlsbad Cavern	Late Pleistocene, Rancholabrean	Kottkamp et al., 2022; Harris, 2024
Myotis sp.	CANADA: ALBERTA: Eagle Cave; BRITISH COLUMBIA: Charlie Lake Cave, Pellucidar II Cave; US: ALABAMA: ACb-2, ACb-3, & ACb-4 Caves, Little Bear Cave; ALASKA: Multiple caves of Prince of Wales Island; ARIZONA: Arkenstone Cave, Bida Cave, Kartchner Cavern, Papago Springs Cave, Pyeatt Cave, Sandblast Cave and Skull Cave, Stanton's Cave; CALIFORNIA: Antelope Cave; IDAHO: Rattlesnake Cave; ILLINOIS: Meyer Cave; IOWA: Duhme Cave; MISSOURI: Bat Cave, Brynjulfson Caves 1 & 2, Little Beaver Cave; NEVADA: a Mormon Mountain cave; NEW MEXICO: Algerita Blossom Cave, Carlsbad Cavern, Conkling Cavern, Dark Canyon Cave, Dry Cave[1], Pendejo Cave, Sierra Diablo Cave, Slaughter Canyon Cave, U-Bar Cave; OKLAHOMA: Sassafras Cave, Three-Forks Cave; WEST VIRGINA: Hamilton Cave, New Paris No. 4 Cave; TENNESSEE: Baker Bluff Cave, Cave Without a Name, Lookout Mountain Cave; TEXAS: Fowlkes Cave, Lower Sloth Cave, Zesch Cave; UTAH: Crystal Ball Cave; VIRGINIA: Clark's Cave; WEST VIRGINIA: Hoffman School Cave, Mandy Walters Cave, New Trout Cave, Patton Cave	Late Pleistocene, Rancholabrean	Skinner, 1942; Guilday et al., 1964, 1977, 1978; Parmalee, 1967; Parmalee & Oesch, 1972; Hawksley et al., 1973; Guilday & Hamilton, 1978; Garton & Grady, 1980; Womochel & Barnett, 1980; Jefferson, 1982; Heaton, 1985; Harris, 1987, 2003, 2024; Emslie, 1988; Grady, 1988, 1991; Reynolds et al., 1991; Steadman et al., 1994; Czaplewski et al., 1999, 2002, 2018, 2022; Grady et al., 2002; Czaplewski & Peachey, 2003; Heaton & Grady, 2003; Jans-Langel & Semken, 2003; Schubert, 2003; Mead et al., 2005; Sagebiel, 2010; Ebersole & Ebersole, 2011; Gaudin et al., 2011; Harington, 2011; Kottkamp et al., 2022
Nycticeius humeralis	ALABAMA: ACb-2, ACb-3, & ACb-4 Caves, Little Bear Cave; TENNESSEE: Baker Bluff Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1978; Womochel & Barnett, 1980; Ebersole & Ebersole, 2011
Parastrellus hesperus	ARIZONA: Sandblast Cave and Skull Cave	Late Pleistocene, Rancholabrean	Emslie, 1988

Perimyotis subflavus	CANADA: QUEBEC: Laflèche Cave; ONTARIO: Mt. Nemo Cave; US: ILLINOIS: Meyer Cave; IOWA: Duhme Cave; KENTUCKY: Mammoth Cave; MISSOURI: Bat Cave, Brynjulfson Caves 1 & 2; OKLAHOMA: Sassafras Cave, Three-Forks Cave; PENNSYLVANIA: Hamilton Cave; TENNESSEE: Baker Bluff Cave, Cave Without a Name, Lookout Mountain Cave; TEXAS: Schulze Cave; VIRGINIA: Clark's Cave; WEST VIRGINIA: Hoffman School Cave, New Trout Cave, Patton Cave	Late Pleistocene, Rancholabrean	Parmalee, 1967; Dalquest et al., 1969; Parmalee & Oesch, 1972; Hawksley et al., 1973; Guilday & Hamilton, 1978; Guilday et al., 1978; Garton & Grady, 1980; Grady, 1988, 1991; Czaplewski et al., 2002, 2018; Grady et al., 2002; Jans-Langel & Semken, 2003; Gaudin et al., 2011; Harington, 2011; Schubert & Mead, 201
Perimyotis cf. *subflavus*	MISSOURI: Crankshaft Cave; PENNSYLVANIA: New Paris no. 4 Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1964; Parmalee et al., 1969
Perimyotis sp.	ALABAMA: Little Bear Cave; MISSOURI: Little Beaver Cave	Late Pleistocene, Rancholabrean	Womochel & Barnett, 1980; Schubert, 2003
?*Perimyotis* sp.	ALABAMA: ACb-2, ACb-3, & ACb-4 Caves	Late Pleistocene, Rancholabrean	Ebersole & Ebersole, 2011
early/middle PLEISTOCENE[3]			
Canada & US except Florida			
Phyllostomidae			
Desmodus sp.	KENTUCKY: Mammoth Cave	middle Pleistocene, late Irvingtonian	Jegla & Hall, 1962; Santucci et al., 2001; Schubert & Mead, 2012
Molossidae			
Tadarida sp.	KENTUCKY: Mammoth Cave; MARYLAND: Cumberland Cave; WEST VIRGINIA: Hamilton Cave	middle Pleistocene, medial and late Irvingtonian	Jegla & Hall, 1962; Repenning & Grady, 1988; Santucci et al., 2001; Schubert & Mead, 2012; Widga & Colburn, 2015; Eshelman et al., 2025
Tadarida †*constantinei*	NEW MEXICO: *New Cave/Slaughter Canyon Cave	middle Pleistocene, medial Irvingtonian	Lawrence, 1960; Morgan, 2002b; Lundberg & McFarlane, 2006; Kottkamp et al., 2022
Tadarida cf. *brasiliensis*	TEXAS: Fyllan Cave	early Pleistocene, early Irvingtonian	Winkler & Gose, 2003; This paper
Vespertilionidae			
Lasiurus borealis		middle Pleistocene, medial Irvingtonian	Eshelman et al., 2025
?*Myotis* sp.	PENNSYLVANIA: Port Kennedy Cave	Pleistocene, medial Irvingtonian	Cope &Mercer, 1897–1901
Myotis sp.	COLORADO: Porcupine Cave; NEW MEXICO: Slaughter Canyon Cave; TEXAS: Fyllan Cave	early to middle Pleistocene, early to medial Irvingtonian	Winkler & Gose, 2003; This paper
Myotis cf. *grisescens*	MARYLAND: Cumberland Cave	middle Pleistocene, medial Irvingtonian	Gidley & Gazin, 1933, 1938; Eshelman et al., 2025
Myotis leibii	MARYLAND: Cumberland Cave	middle Pleistocene, medial Irvingtonian	Eshelman et al., 2025
Corynorhinus †*alleganiensis*	MARYLAND: *Cumberland Cave	middle Pleistocene, medial Irvingtonian	Gidley & Gazin, 1933, 1938

Eptesicus fuscus †grandis	ARKANSAS: Conard Fissure; MARYLAND: *Cumberland Cave	middle to late Pleistocene, Irvingtonian	Brown, 1908; Gidley & Gazin, 1933, 1938
Eptesicus fuscus	NEW MEXICO: Slaughter Canyon Cave	middle Pleistocene, medial Irvingtonian	This paper
Perimyotis subflavus	MARYLAND: Cumberland Cave	middle Pleistocene, medial Irvingtonian	Eshelman et al., 2025
Perimyotis sp.	TEXAS: Fyllan Cave	early Pleistocene, early Irvingtonian	Winkler & Gose, 2003
LATE PLEISTOCENE, Mesoamerica (Mexico & Belize)			
Emballonuridae			
Balantiopteryx io	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Peropteryx macrotis	YUCATÁN: Gruta de Loltún	Late Pleistocene/Holocene	Arroyo-Cabrales & Álvarez, 2003
Mormoopidae			
Mormoops megalophylla	NUEVO LEÓN: Cueva de San Josecito; SAN LUIS POTOSÍ: Cueva de La Presita; YUCATÁN: Gruta de Loltún, Actún Spukil	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003
Pteronotus mexicanus[4]	YUCATÁN: Gruta de Loltún, Actún Spukil	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003
Phyllostomidae[5]			
Macrotinae			
Macrotus californicus	SAN LUIS POTOSÍ: Cueva de La Presita	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Desmodontinae			
Desmodus cf. *draculae*	YUCATÁN: Gruta de Loltún	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Álvarez, 2003
Desmodus †draculae	BELIZE: Chiquibul Cave System, Cebada Cave	Late Pleistocene & Holocene	Czaplewski et al., 2003
Desmodus rotundus	YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003
Desmodus †stocki	MEXICO: Cerro de Tlapacoya Cave; NUEVO LEÓN: Cueva de La Boca; *Cueva de San Josecito; SAN LUIS POTOSÍ: Cueva de La Presita	Late Pleistocene, Rancholabrean	Ray et al., 1988; Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003
Diphylla ecaudata	YUCATÁN: Gruta de Loltún	Late Pleistocene/Holocene	Arroyo-Cabrales & Álvarez, 2003
Phyllostominae			
Chrotopterus auritus	YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003
Mimon cozumelae	YUCATÁN: Actún Spukil	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Tonatia bakeri	BELIZE: Chiquibul Cave System, Cebada Cave	Holocene?	Czaplewski et al., 2003
Tonatia sp.	QUINTANA ROO: Hoyo Negro cenote	Late Pleistocene, Rancholabrean	Cruz et al., 2024
Glossophaginae			
Choeronycteris mexicana	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Glossophaga soricina	YUCATÁN: Gruta de Loltún	Late Pleistocene/Holocene	Arroyo-Cabrales & Álvarez, 2003

Leptonycteris nivalis	NUEVO LEÓN: Cueva de San Josecito; TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970; Arroyo-Cabrales & Polaco 2003
Leptonycteris yerbabuenae	SAN LUIS POTOSÍ: Cueva de La Presita	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco 2003
Carolliinae			
Carollia subrufa or *C. brevicauda*	BELIZE: Chiquibul Cave System, Cebada Cave	Late Pleistocene/Holocene	Czaplewski et al., 2003
Stenodermatinae			
Artibeus jamaicensis	TAMAULIPAS: Cueva de El Abra; YUCATÁN: Gruta de Loltún, Actún Spukil	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970; Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003;
Artibeus lituratus	BELIZE: Chiquibul Cave System, Cebada Cave	Late Pleistocene/Holocene	Czaplewski et al., 2003
Artibeus sp.	QUINTANA ROO: Hoyo Negro cenote	Late Pleistocene, Rancholabrean	Cruz et al., 2024
Centurio senex	BELIZE: Chiquibul Cave System, Cebada Cave	Holocene?	Czaplewski et al., 2003
Chiroderma villosum	YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003
Dermanura sp.	BELIZE: Chiquibul Cave System, Cebada Cave	Holocene?	Czaplewski et al., 2003
Sturnira lilium	YUCATÁN: Gruta de Loltún; BELIZE: Chiquibul Cave System, Cebada Cave	Late Pleistocene/Holocene	Arroyo-Cabrales & Álvarez, 2003; Czaplewski et al., 2003
Molossidae			
Eumops perotis	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Nyctinomops aurispinosus	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Nyctinomops laticaudatus	TAMAULIPAS: Cueva de El Abra; YUCATÁN: Gruta de Loltún	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970; Arroyo-Cabrales & Álvarez, 2003;
Tadarida brasiliensis	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Tadarida cf. *brasiliensis*			
Tadarida sp.	CHIHUAHUA: Cueva Jiménez	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003; Harris, 2024
Vespertilionidae			
Aeorestes cinereus	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Antrozous pallidus	CHIHUAHUA: Cueva Jiménez	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Corynorhinus townsendii[6]	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Handley, 1955; Jones, 1958; Arroyo-Cabrales & Polaco, 2003;
Dasypterus ega	BELIZE: Cebada Cave, Chiquibul Cave System; YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene, Rancholabrean	Arroyo-Cabrales & Álvarez, 2003; Czaplewski et al., 2003
Dasypterus intermedius	YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003; Simmons et al., 2020
Eptesicus furinalis	YUCATÁN: Gruta de Loltún, Actún Spukil	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003
Eptesicus fuscus	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Johnson, 2002
Lasionycteris cf. *noctivagans*	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Lasiurus blossevillii	BELIZE: Chiquibul Cave System, Cebada Cave; NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene & Holocene, Rancholabrean	Arroyo-Cabrales & Johnson, 2002; Czaplewski et al., 2003

Myotis californicus	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Johnson, 2002; Arroyo-Cabrales & Polaco, 2003
Myotis thysanodes	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Johnson, 2002; Arroyo-Cabrales & Polaco, 2003
Myotis sp.	CHIHUAHUA: Cueva Jiménez; SAN LUIS POTOSÍ: Cueva de La Presita; TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970; Arroyo-Cabrales & Polaco, 2003; Harris, 2024
LATE QUATERNARY[7] West Indies			
Noctilonidae			
Noctilio leporinus	Barbuda; Cuba; Puerto Rico	Late Quaternary[5]	Silva Taboada, 1979; Morgan, 2001
Mormoopdidae			
Mormoops blainvillei	Anguilla#, Antigua#, Bahamas#: Abaco, Exuma, New Providence; Barbuda#; Cuba; Gonâve#; Guadeloupe: Marie-Galante#; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Koopman, 1955; Pregill et al., 1988, 1994; Morgan, 2001; Velazco et al., 2013; Stoetzel et al., 2016
Mormoops †magna	Cuba*; Hispaniola (DR)	Late Quaternary	Silva Taboada, 1974; Velazco et al., 2013
Mormoops megalophylla#	Bahamas: Abaco, Andros; Cuba; Guadeloupe: Marie-Galante#; Hispaniola (DR); Jamaica	Late Quaternary	Morgan, 2001; Silva Taboada, 1974; Stoetzel et al., 2016
Pteronotus macleayi	Bahamas#: New Providence; Cuba; Guadeloupe: Marie-Galante#; Hispaniola (DR)	Late Quaternary	Morgan, 1989, 2001; Silva Taboada, 1974, 1979; Velazco et al., 2013; Stoetzel et al., 2016
Pteronotus parnellii[4]	Antigua#; Bahamas#: Abaco, New Providence: Cayman Islands#: Grand Cayman; Cuba; Guadeloupe: Marie-Galante#; Jamaica	Late Quaternary	Pregill et al., 1988; Morgan, 1994, 2001; Soto-Centeno & Steadman, 2015; Stoetzel et al., 2016
Pteronotus portoricensis	Puerto Rico	Late Quaternary	Morgan, 2001
Pteronotus †pristinus	Cuba*	Late Quaternary	Silva Taboada, 1974
Pteronotus pusillus	GonÂve#, Hispaniola (DR, H)	Late Quaternary	Koopman, 1955; Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Pteronotus quadridens	Bahamas#: Abaco, Andros, New Providence; Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Phyllostomidae[5]			
Macrotinae			
Macrotus waterhousii	Anguilla#, Bahamas: Abaco, Andros, Exuma, New Providence; Barbuda#; CAICOS ISLAMDS: Middle (=Grand) Caicos#; Cayman Islands: Cayman Brac, Grand Cayman; Cuba; Gonâve#; Hispaniola (DR, H); Puerto Rico#, St. Martin#	Late Quaternary[1]	Koopman, 1955; Pregill et al., 1994; Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Desmodontinae			
Desmodus rotundus#	Cuba	Late Quaternary	Koopman, 1958; Orihuela, 2011

Phyllostominae			
Tonatia †saurophila	Jamaica	Late Quaternary	Koopman & Williams, 1951
Glossophaginae			
Brachyphylla cavernarum	Antigua; Guadeloupe: Marie-Galante; Puerto Rico	Late Quaternary	Pregill et al., 1988; Morgan, 2001; Stoetzel et al., 2016
Brachyphylla nana	Bahamas#: Andros; CAICOS ISLANDS: Middle (=Grand) Caicos; Cayman Islands: Cayman Brac#, Grand Cayman; Cuba; Hispaniola (DR, H); Jamaica#	Late Quaternary	Koopman & Williams, 1951; Silva Taboada, 1979; Morgan, 1989, 1994, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Erophylla bombifrons	Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Erophylla sezekorni	Bahamas: Abaco, Andros, Exuma, New Providence; Cayman Islands: Cayman Brac, Grand Cayman; Cuba; Jamaica	Late Quaternary	Silva Taboada, 1979; Morgan, 1989, 1994, 2001
Glossophaga soricina	Jamaica	Late Quaternary	Koopman & Williams, 1951
Monophyllus plethodon	Antigua; Guadeloupe: Marie-Galante; Puerto Rico#	Late Quaternary	Choate and Birney 1968; Morgan, 2001; Stoetzel et al., 2016
Monophyllus redmani	Bahamas#: Abaco, Andros, New Providence; CAICOS ISLANDS: Middle (=Grand) Caicos; Cayman Islands#: Grand Cayman; Cuba; Gonâve#; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Phyllonycteris aphylla	Jamaica	Late Quaternary	Koopman & Williams, 1951
Phyllonycteris †major	Antigua; Guadeloupe: Marie-Galante; Puerto Rico	Late Quaternary	Pregill et al., 1984; Morgan, 2001; Simmons et al., 2020; Stoetzel et al., 2016
Phyllonycteris poeyi	Bahamas#: Abaco, New Providence; Cayman Islands#: Cayman Brac; Cuba; Hispaniola (DR, H)	Late Quaternary	Silva, 1979; Morgan, 1989, 1994, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Stenodermatinae			
Ardops nichollsi	Guadeloupe: Marie-Galante	Late Quaternary	Stoetzel et al., 2016
Ariteus flavescens	Jamaica	Late Quaternary	Koopman & Williams, 1951
Artibeus †anthonyi	Cuba	Late Quaternary	Silva Taboada, 1979; Morgan, 2001
Artibeus jamaicensis	Cuba; Gonâve; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Koopman, 1955; Silva Taboada, 1979; Morgan, 2001
†*Cubanycteris silvai*	Cuba	Late Quaternary	Mancina & García-Rivera, 2005
Phyllops falcatus	Cuba, Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Phyllops †silvai	Cuba	Late Quaternary	Suárez & Díaz-Franco, 2003
Phyllops †vetus	Cuba	Late Quaternary	Morgan, 2001
Stenoderma rufum	Puerto Rico	Late Quaternary	Choate & Birney, 1968
Natalidae			Tejedor, 2011
Chilonatalus macer	Cayman Islands#: Grand Cayman; Cuba	Late Quaternary	Morgan, 2001; Tejedor, 2011

Chilonatalus micropus	Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Tejedor, 2011; Velazco et al., 2013; Soto-Centeno et al., 2017
Chilonatalus tumidifrons	Bahamas: Andros, Cat#, Exuma#, New Providence#	Late Quaternary	Morgan, 1989, 2001
Natalus jamaicensis	Jamaica	Late Quaternary	Koopman & Williams, 1951; Tejedor, 2011;
Natalus major[8]	Guadeloupe: Marie-Galante#; Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Tejedor, 2011; Stoetzel et al., 2016; Soto-Centeno et al., 2017
Natalus primus	Bahamas#: Abaco, Andros, Eleuthera, New Providence: Caicos Islands: Middle (=Grand) Caicos#; Cayman Islands#: Grand Cayman; Cuba	Late Quaternary	Morgan, 2001; Tejedor, 2011
Natalus stramineus[8]	Guadeloupe: Marie-Galante	Late Quaternary	Stoetzel et al., 2016
Nyctiellus lepidus	Bahamas: Andros#, Exuma; Cuba	Late Quaternary	Silva Taboada, 1979; Morgan, 2001
Molossidae			
Molossus molossus	Antigua; Guadeloupe: Marie-Galante; Jamaica;	Late Quaternary	Koopman & Williams, 1951; Pregill et al., 1988; Stoetzel et al., 2016
Nyctinomops macrotis	Cuba; Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Soto-Centeno et al., 2017
Tadarida brasiliensis	Antigua; Bahamas: Abaco, New Providence#; Cayman Islands: Grand Cayman; Cuba; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Morgan, 2001; Soto-Centeno et al., 2017
Vespertilionidae			
Aeorestes cinereus	Hispaniola (H)	Late Quaternary	Soto-Centeno et al., 2017
Antrozous koopmani[9]	Cuba	Late Quaternary	Silva Taboada, 1979; Morgan, 2001; Orihuela et al., 2020
Dasypterus insularis	Cuba; Hispaniola (DR#)	Late Quaternary	Silva Taboada, 1979; Morgan, 2001
Eptesicus fuscus	Bahamas: Abaco, Andros, Exuma New Providence; Cayman Islands: Grand Cayman, Cayman Brac; Cuba; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Lasiurus minor	Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Soto-Centeno et al., 2017
Lasiurus pfeifferi	Cuba	Late Quaternary	Silva Taboada, 1979; Morgan, 2001
Myotis cf. *austroriparius#*	Bahamas: Abaco	Late Pleistocene	Morgan, 2001; Soto-Ceteno & Steadman, 2015
Florida Karst Deposits[10] **Late Pleistocene**			
Phyllostomidae			
Desmodus †stocki	Arredondo 2A, Haile 1A, Haile 11B, Reddick 1A, 1B, 1C	Late Pleistocene, Rancholabrean	Morgan, 1991

Mormoopidae			
Mormoops megalophylla#	Cutler Hammock, Monkey Jungle Hammock, Rock Springs	Late Pleistocene, Rancholabrean	Ray et al., 1963; Wilkins, 1983; Morgan, 1991, 2002
Pteronotus †*pristinus*	Monkey Jungle Hammock	Late Pleistocene, Rancholabrean	Morgan, 1991, 2002
Molossidae			
Eumops floridanus	Monkey Jungle Hammock	Late Pleistocene, Rancholabrean	Martin, 1977; Morgan, 1991, 2002
Eumops underwoodi#	Lecanto 2A	Late Pleistocene, Rancholabrean	Morgan, 1991
Tadarida brasiliensis	Monkey Jungle Hammock, Reddick 1A	Late Pleistocene, Rancholabrean	Morgan, 1991
Vespertilionidae			
Eptesicus fuscus	Arredondo 2A, Cutler Hammock, Monkey Jungle Hammock, Reddick 1	Late Pleistocene, Rancholabrean	Morgan, 1991
Lasiurus borealis/*L. seminolus*	Monkey Jungle Hammock, Reddick 1	Late Pleistocene, Rancholabrean	Morgan, 1991
Dasypterus intermedius	Arredondo 2A, Devil's Den, Haile 11B, Reddick 1	Late Pleistocene, Rancholabrean	Martin & Webb, 1974; Morgan, 1991
Myotis austroriparius	Arredondo 2A, Cutler Hammock, Devil's Den, Reddick 1, Rock Springs	Late Pleistocene, Rancholabrean	Martin & Webb, 1974; Morgan, 1991
Myotis grisescens	Devil's Den, Surprise Cave	Late Pleistocene, Rancholabrean	Martin & Webb, 1974; This paper
Nycticeius humeralis	Cutler Hammock, Monkey Jungle Hammock	Late Pleistocene, Rancholabrean	Morgan, 1991
Perimyotis subflavus	Devil's Den, Haile 11B, Lecanto 2A, Reddick 1	Late Pleistocene, Rancholabrean	Martin & Webb, 1974; Morgan, 1991
Florida Karst Deposits Early and Middle Pleistocene			
Phyllostomidae			
Desmodus †*archaeodaptes*	Inglis 1A Haile 16A, Haile 21A*	early Pleistocene, late Blancan early Pleistocene, early Irvingtonian	Morgan et al., 1988
Vespertilionidae			
Antrozous sp.#	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Corynorhinus rafinesquii	Coleman 2A	middle Pleistocene, late Irvingtonian	Martin, 1974
Corynorhinus sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Eptesicus sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Lasiurus sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Myotis cf. *austroriparius*	Haile 16A, Haile 21A Coleman 2A	early Pleistocene, early Irvingtonian middle Pleistocene, late Irvingtonian	Morgan, 1991 Martin, 1974
Myotis sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Perimyotis subflavus	Coleman 2A	middle Pleistocene, late Irvingtonian	Martin, 1974

Perimyotis sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Florida Karst Deposits Oligocene and Miocene			
Emballonuridae			
†*Floridopteryx poyeri*	Thomas Farm*	early Miocene, early Hemingfordian	Morgan & Czaplewski, 2023
†*Oligopteryx floridanus*	I-75 Brooksville 2*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Morgan & Czaplewski, 2023
†*Oligopteryx hamaxitos*	I-75 Brooksville 2*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Morgan & Czaplewski, 2023
†*Karstopteryx gunnelli*	Buda*	latest Oligocene, late Arikareean	Morgan & Czaplewski, 2023
†Speonycteridae[11]			
†*Speonycteris aurantiadens*	I-75 Brooksville 2*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Czaplewski & Morgan, 2012
†*Speonycteris naturalis*	I-75*	early Oligocene, Whitneyan	Czaplewski & Morgan, 2012
Mormoopidae[5]			
†*Koopmanycteris palaeomormoops*	I-75 Brooksville 2*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Morgan et al., 2019
Natalidae			
†*Primonatalus prattae*	Thomas Farm*	early Miocene, early Hemingfordian	Morgan & Czaplewski, 2003
genus and species indet.	I-75	early Oligocene, Whitneyan	Morgan & Czaplewski, 2003
Molossidae			
Tadarida/*Mormopterus* sp. indet. 1	Thomas Farm	early Miocene, early Hemingfordian	Czaplewski et al., 2000b
Tadarida/*Mormopterus* sp. indet. 2	Thomas Farm	early Miocene, early Hemingfordian	Czaplewski et al., 2000b
genus & species indet.	Brooksville 2	late Oligocene, early Arikareean	Czaplewski et al., 2000b
Vespertilionidae			
†*Karsta silva*	Thomas Farm*	early Miocene, early Hemingfordian	Czaplewski & Morgan, 2000
†*Miomyotis floridanus*	Thomas Farm*	early Miocene, early Hemingfordian	Lawrence, 1943
†*Suaptenos whitei*	Thomas Farm*	early Miocene, early Hemingfordian	Lawrence, 1943
lasiurine, undesc. genus & species	Thomas Farm	early Miocene, early Hemingfordian	Morgan & Czaplewski, 2023
plecotine, undesc. genus & species	Thomas Farm	early Miocene, early Hemingfordian	Morgan & Czaplewski, 2023
genus & species indet.	I-75	early Oligocene, Whitneyan	Morgan & Czaplewski, 2023

---

[1] States of the US and Mexico are in upper case letters, as are Belize in Central America. Because our paper focuses primarily on continental North America and there are several hundred cave sites in the West Indies that have produced fossil bats, we do not list individual cave sites in the West Indies, only the islands on which the bat species have been reported. See Morgan (2001) for references to most of the individual cave sites from which these species are known, with more recent updates in Dávalos and Turvey (2012), Velazco et al. (2013), Soto-Centeno and Steadman (2015), Stoetzel et al (2016), and Soto-Centeno et al. (2017).

[2] Dry Cave, New Mexico, US, includes sublocalities published as Animal Fair, Balcony Room, Bison Chamber, Harris' Pocket, Lost Valley, Room of the Vanishing Floor, and Sabertooth Camel Maze (Harris, 1985; 2024).

[3] We recognize the subdivisions of the Irvingtonian NALMA of Bell et al. (2004) as follows: Irvingtonian I (=early Irvingtonian), 0.85-1.72 Ma; Irvingtonian II (=medial Irvingtonian), 0.4-0.85 Ma; Irvingtonian III (=late Irvingtonian). 0.4-0.15 Ma.

[4] Pavan and Marroig (2016) recognized eight species formerly included within the species *Pteronotus parnellii*, two of which occur in Mesoamerica, *P. mexicanus* and *P. mesoamericanus*, and three of which occur the West Indies, *P. parnelii* s.s., *P. portoricensis,* and *P. pusillus*. *P. parnellii*, as recognized by Pavan and Marroig (2016), occurs only in Cuba and Jamaica, with fossil records from both islands noted here. No member of the *P. parnellii* species group occurs at present in the Bahamas, Cayman Islands, or Lesser Antilles, so we have left the fossil records from these islands under *P. parnellii*, until they can be studied further to determine their correct species allocation.

[5] We subdivide the Phyllostomidae into subfamilies following Baker et al. (2016). The order of subfamilies follows the phylogeny in Baker et al. (2016); genera and species within each subfamily are in alphabetical order.

[6] Originally described as an extinct species, *Corynorhinus tetralophodon* (Handley, 1955), but synonymized with *C. townsendii* by Arroyo-Cabrales and Johnson (2002).

[7] For the West Indies only, both late Pleistocene and Holocene fossil bats are combined under the broader time category of Late Quaternary, with most fossil bats from this region probably Holocene in age. The few bat bones from the West Indies that have been directly radiocarbon dated are Holocene (e.g., seven species of bats from Ralph's Cave, Abaco, Bahamas with ^{14}C AMS dates ranging from 1,810–3,740-yr BP; Soto-Centeno and Steadman, 2015). Late Pleistocene dates ranging from 11,348–34,600 yr BP were associated with fossil bats from Blanchard Cave, Marie-Galante, but the dates were analyzed using guano not bat bones (Stoetzel et al., 2016).

[8] Varona (1974) and Koopman (1989) recognized a single species of large *Natalus*, *N. stramineus*, from the West Indies. Morgan (2001) limited *N. stramineus* to the Lesser Antilles and recognized a larger species, *N. major*, from the Greater Antilles. Tejedor (2011) split the large species of *Natalus* from the West Indies into four species, *N. jamaicensis* from Jamaica, *N. major* from Hispaniola, *N. primus* from Cuba, and *N. stramineus* from the Lesser Antilles. Tejedor (2011) referred extirpated populations of a large *Natalus* from the Bahamas, Middle (=Grand) Caicos, and Grand Cayman to *N. primus.*

[9] We recognize *Antrozous koopmani* as a valid species following Orihuela et al. (2020). Other publications consider *A. koopmani* to be a subspecies of the mainland *A. pallidus* (Simmons, 2005).

[10] Late Pleistocene deposits from Florida include bats from one underwater cave (Devil's Den), one underwater spring (Rock Springs), and one dry cave (Surprise Cave). All other Florida fossil sites listed here are karst deposits.

[11] The extinct family Speonycteridae and the extant family Mormoopidae, together with the extant families Phyllostomidae, Noctilionidae, and Thyropteridae are placed in the superfamily Noctilionoidea.

GUIDE TO AUTHORS

The *Journal of Cave and Karst Studies* is a multidisciplinary journal devoted to cave and karst research. The Journal is seeking original, unpublished manuscripts concerning the scientific study of caves or other karst features. Authors do not need to be members of the National Speleological Society, but preference is given to manuscripts of importance to North American speleology.

LANGUAGES: The *Journal of Cave and Karst Studies* uses American-style English as its standard language and spelling style. A second abstract in another language will be considered when room allows and is determined necessary. In the case of proper names, the *Journal* tries to accommodate other spellings and punctuation styles. In cases where the Editor-in-Chief finds it appropriate to use non-English words outside of proper names (generally where no equivalent English word exist), the *Journal* italicizes them. Common abbreviations, i.e., e.g., et al., etc. should appear in normal text. Authors are encouraged to write for our combined professional and amateur readerships. Spell out first use of acronyms.

CONTENT: Each paper will contain a title, the authors' names and addresses, an abstract, and the text of the paper, including a summary or conclusions section. Acknowledgments and references are to follow the text. Manuscripts should be limited to 6,000 words and no more than 10 figures and 5 tables. Larger manuscripts may be considered, but the Journal reserves the right to charge processing fees for larger submissions.

ABSTRACTS: An abstract stating the essential points and results is required. The abstract is to be a summary, not a promise of what topics are covered in the paper.

STYLE: The *Journal* consults The Chicago Manual of Style on most general style issues.

REFERENCES: References to previously published work should be followed by the relevant author's name and date in parentheses. All cited references are to be listed alphabetical at the end of the manuscript with senior author's last name first, followed by date of publication, title, publisher, volume, and page numbers. Geological Society of America format should be used (see http://www.geosociety.org/gsa/gsa/pubs/Ref-Guide-Examples). Please do not abbreviate periodical titles. Web references are acceptable when deemed appropriate. The references should follow the style of: Author (or publisher), year, Webpage title: Publisher (if a specific author is available), full URL (e.g., http://www.usgs. gov/citguide.html), and the date the website was accessed in brackets. If there are specific authors given, use their name and list the responsible organization as publisher. Citations within the text should read: (Author, Year).

SUBMISSION: Manuscripts are to be submitted via the PeerTrack submission system at https://www.editorialmanager.com/jcks. Additional instructions are provided at that address. You will be prompted to establish a login and password, after which you will enter information about your manuscript and upload your manuscript, tables, and figure files. Manuscript files can be uploaded as DOC, WPD, RTF, TXT, or LaTeX. Note: LaTeX files should not use any unusual style files; a LaTeX template and BiBTeX file may be obtained from the Editor-in-Chief. Table files can be uploaded as DOC, WPD, RTF, TXT, XLS, or LaTeX files and figure files can be uploaded as TIFF, AI, EPS, or CDR files. The including of supplementary materials should be minimized. Supplemental data or other materials (e.g. video clips) may be placed on the Journal's website at the discretion of the Editor-in-Chief. The data used within a paper must be made available upon request during the review process.

FIGURES: Figures and lettering must be neat and legible. A list of figures and their captions should be provided at the end of the text or as a separate document and not within the figure. Figures should be numbered in sequence and referred to in the text by inserting (Fig. x). Most figures will be reduced; hence, the lettering should be large. Photographs must be sharp and high contrast. Figures must have a minimum resolution of 300 dpi for acceptance. Please minimize the use of JPEG images.

TABLES: See https://caves.org/wp-content/uploads/2022/01/JCKS_Tables.pdf. for table layout guidelines.

MEASUREMENTS: All measurements will be in the International System of Units (SI or metric) except when quoting historical references. Other units will be allowed where necessary if placed in parentheses following the SI units.

DISCUSSIONS: Critical discussions of papers previously published in the Journal are welcome. Authors will be given an opportunity to reply. Discussions and replies must be limited to a maximum of 1000 words and discussions will be subject to review before publication. Discussions must be within 12 months after the original article appears.

COPYRIGHT AND AUTHOR'S RESPONSIBILITIES: The submitted work should represent original work of the author(s) that has not been previously published. It is the author's responsibility to clear any copyright or acknowledgement matters concerning text, tables, or figures used from others. Authors should address sensitive or legal issues such as landowner and land manager concerns or policies, verify that the work was conducted using necessary permissions and permits, and minimize the disclosure of sensitive features and cave locations.

PROCESS: Submitted manuscripts are assigned to the appropriate Associate Editor and sent out to at least two experts in the field for review. Reviewed manuscripts are then returned to the author for consideration of the referees' remarks and revision, where appropriate. Revised manuscripts are returned to the Associate Editor who then recommends acceptance or rejection. The Editor-in-Chief makes final decisions regarding publication. Upon acceptance, the senior author will be sent one set of PDF proofs for review prior to publication.

Journal of Cave and Karst Studies

Volume 87 Number 4 December 2025

CONTENTS

Visit us at www.caves.org/pub/journal