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

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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

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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 Leopards	Allopods	Animals taken into caves by predators	Extrinsic biogenic concentrations	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 pronghorn 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.

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.

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).

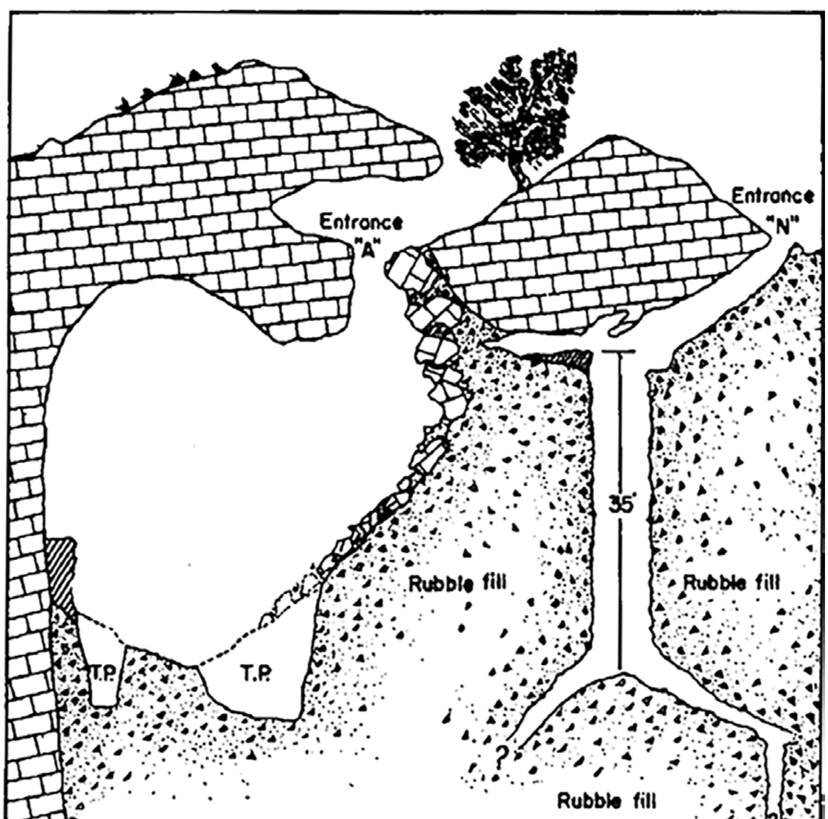

Figure 3. Cross section of Papago Springs Cave taken from Skinner, 1942: Fig. 1. The details of the cave fill sediments are oversimplified in this drawing. Czaplewski et al. (1999a) greatly clarified and amplified our understanding of those deposits. Entrance B of Skinner is not shown in this section.

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

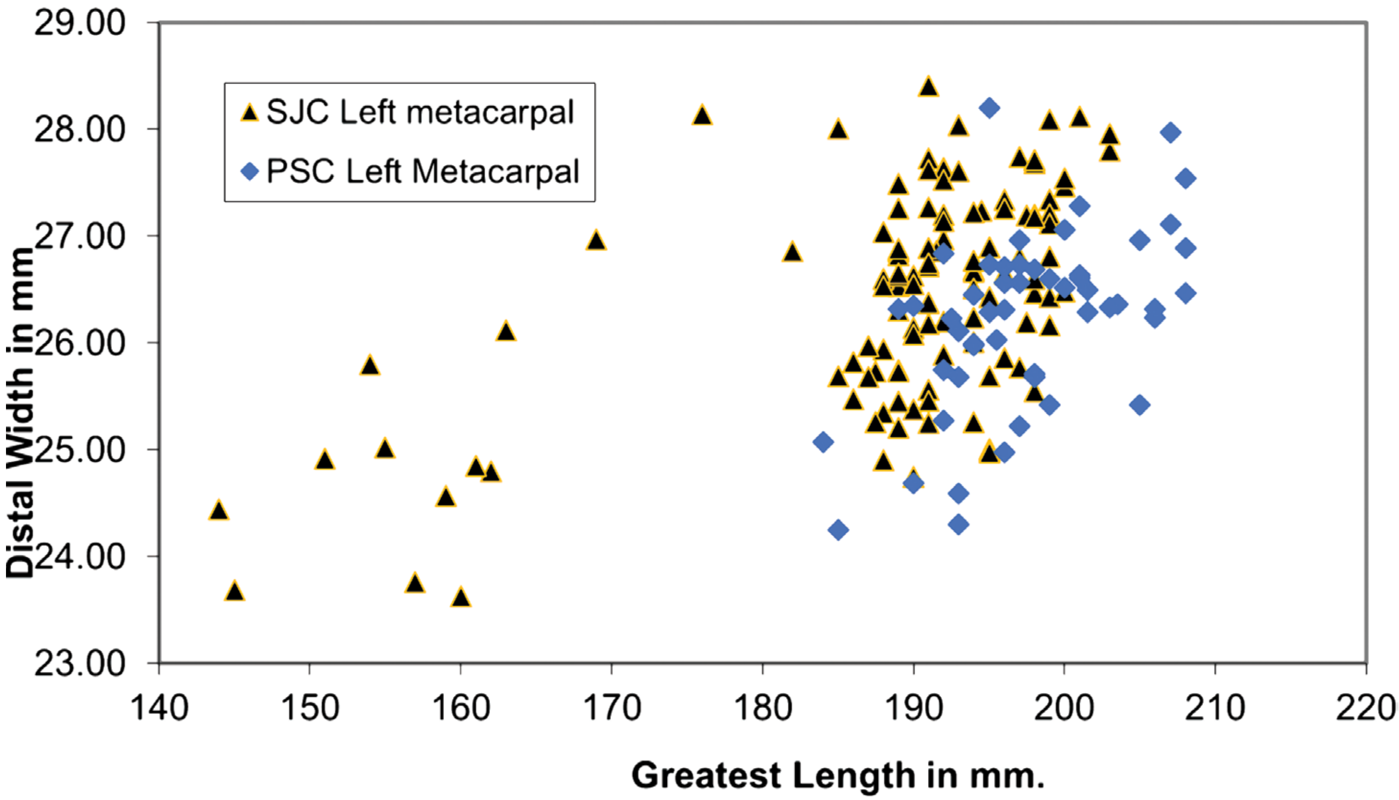

Figure 4. Bivariate plot of Greatest Length versus Distal Width of left metacarpals from San Josecito Cave (SJC) and Papago Springs Cave (PSC). The metacarpals from PSC are tightly clustered and the distribution is not bimodal. Those from SJC duplicate the tight PSC cluster, but show 13 individuals clearly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

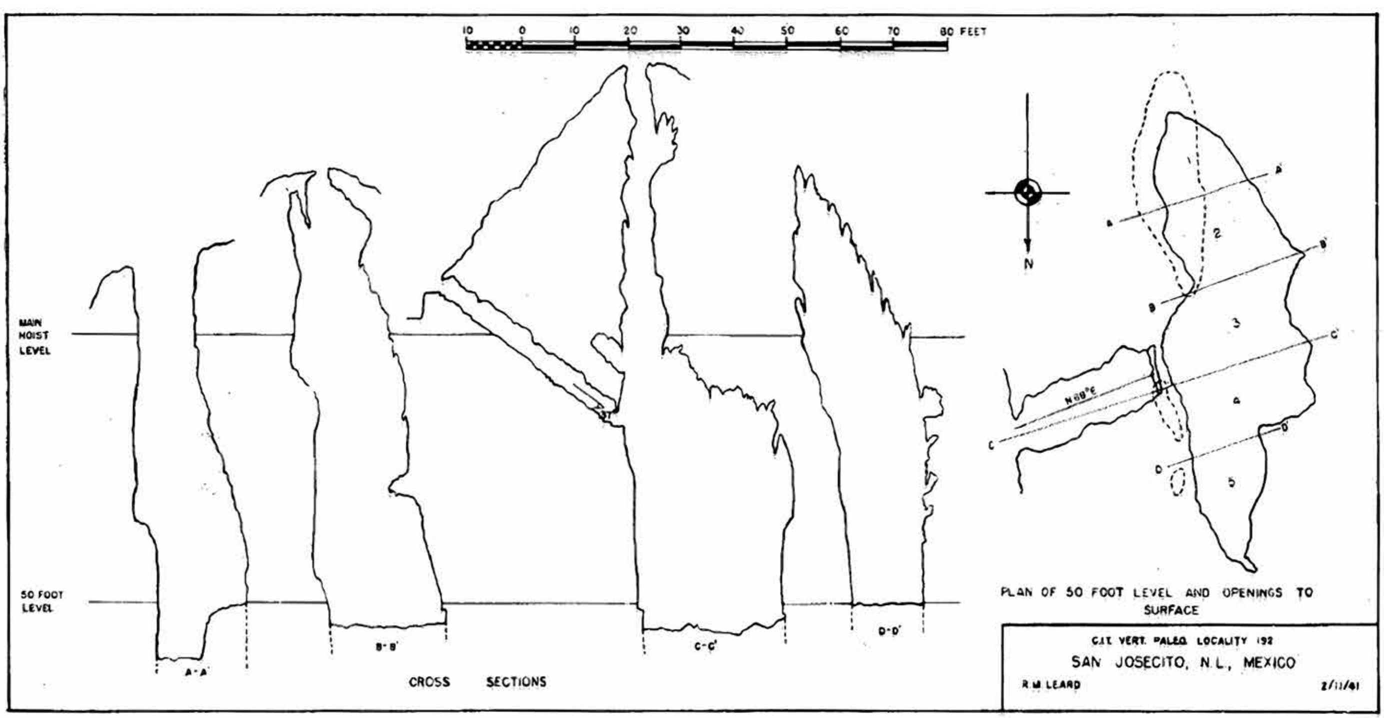

Figure 5. Sections and plan view of San Josecito Cave, Nuevo Leon, Mexico, taken from Stock, 1943.

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-

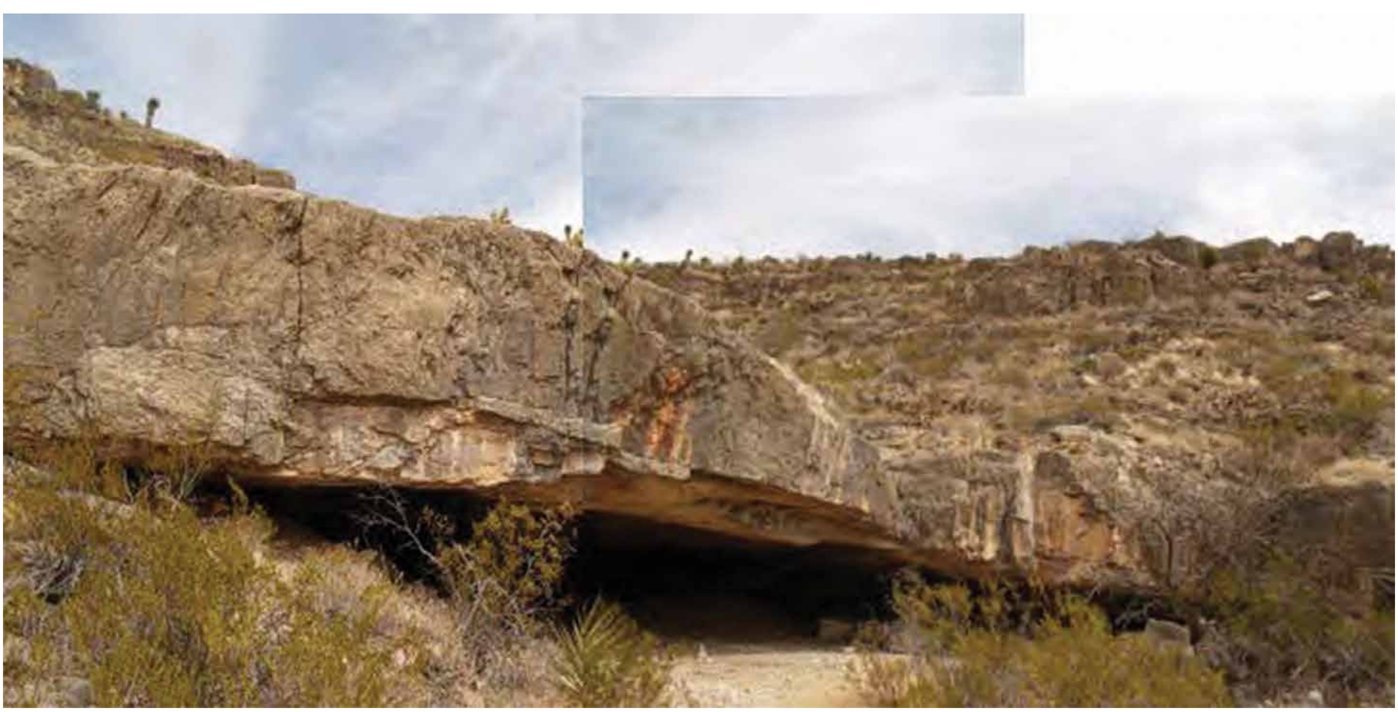

Figure 6. Shelter Cave, Doña Ana County, New Mexico. Photo courtesy of Arthur H. Harris.

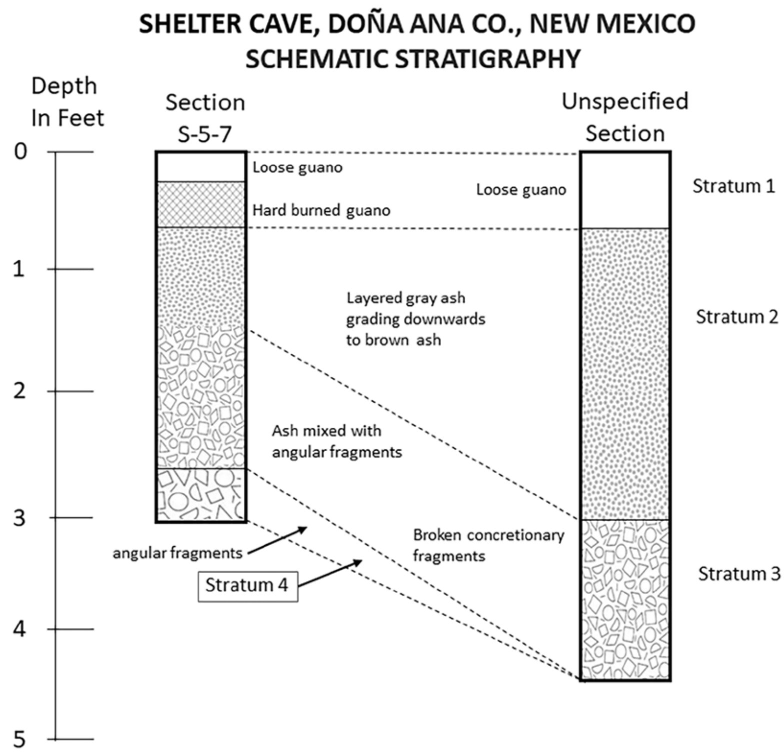

Figure 7. Schematic stratigraphic sections of Shelter Cave based on the excavator's field notes as quoted by Brattstrom (1964). The grouping of strata represents our interpretation of that data

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.

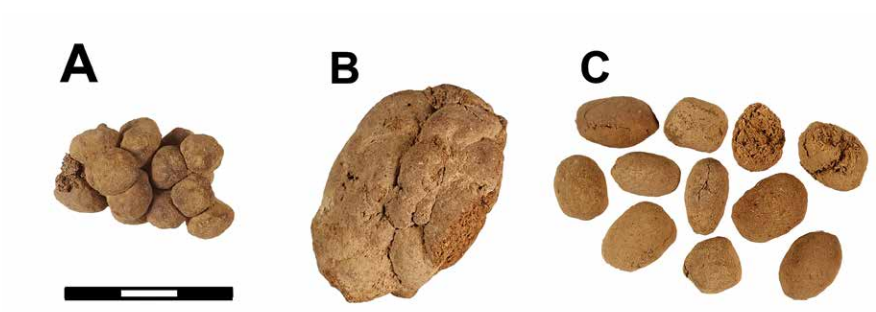

Figure 8. Antilocaprid dung from Shelter Cave and Dark Canyon Cave. A, Dark Canyon Cave, MSD-364; B and C, Shelter Cave. MSD-353, 354.

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.

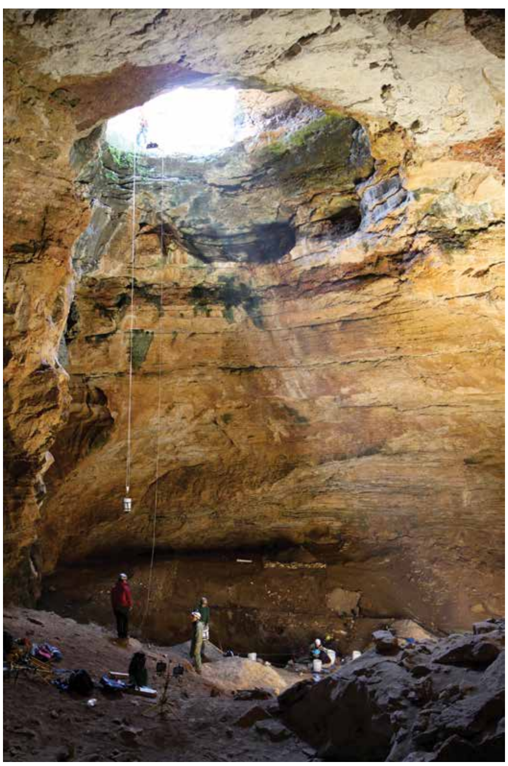

Figure 9. Natural Trap Cave, Wyoming. Photo courtesy of Justin S. Sipla, via Julie Meachen.

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….".

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; Gil-

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.

bert 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).

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.

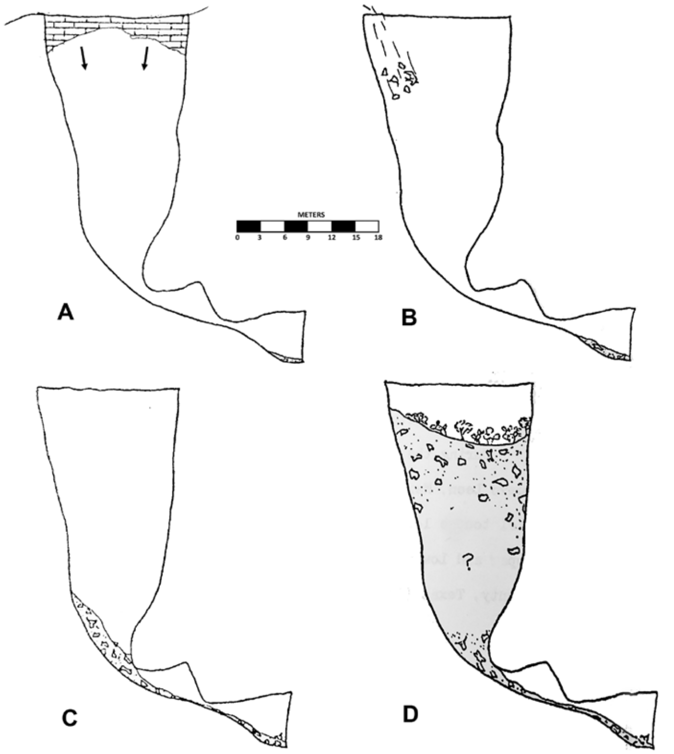

Figure 11. Schematic cross-sections showing the development of Muskox Cave. A, the collapse of the dome of the solution cavern to form a sinkhole; B, the pitfall entrapment of larger mammals; C, the filling of the cave with breakdown debris and sediments washing into the sinkhole; D, the filling of the 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.

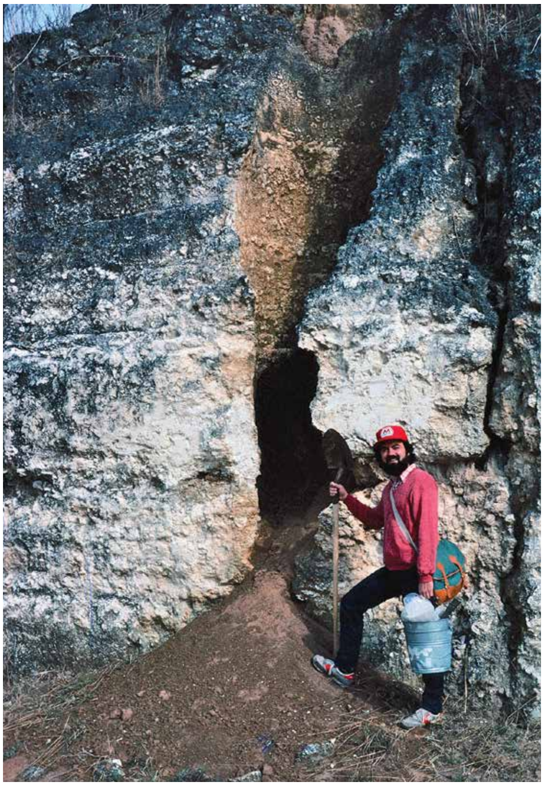

Figure 13. An example of the Florida cave and karst features. This shows a small, sediment-filled fissure in the Haile Quarry complex, near Newberry, Alachua County This site is much smaller than Inglis 1A but illustrates the geological context of the caves and fissures in the Eocene Ocala Limestone 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.

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