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Description, Taphonomy, and Paleoecology of the Late Pleistocene Peccaries (Artiodactyla: Tayassuidae) from Bat Cave, Pulaski County, Missouri

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(Artiodactyla: Tayassuidae) from Bat Cave, Pulaski County, Missouri

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ABSTRACT

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The late Pleistocene faunal assemblage from Bat Cave, central Ozarks, Missouri provides an opportunity to assess specific aspects of behavior, ecology, and ontogeny of the extinct peccary *Platygonus compressus*. All identifiable elements referable to this taxon were catalogued and examined, and a minimum number of individuals of 70 was determined for the sample. The presence of distinct, non-overlapping age groups suggests that *P. compressus* utilized Bat Cave on a seasonal basis. A predator-prey relationship with *Canis dirus*, the second most abundant vertebrate from the Bat Cave site, is also described in this study. Damage patterns suggest that the feeding patterns of *C. dirus* at Bat Cave were consistent with its extant relative, and that these predators would periodically enter the cave to hunt and/or scavenge peccaries. Overall, the fossil material from Bat Cave is virtually unweathered and represents one of the most extensive and well-preserved late Pleistocene faunas from the Ozarks.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The huge sample of peccary remains recovered from Bat Cave (BC), which have been referred to the late Pleistocene (Rancholabrean) taxon *Platygonus compressus*, provides the opportunity to examine the paleobiology of this species. Hawksley et al. (1973) identified 6,339 elements corresponding to a minimum of 98 individual peccaries from Bat Cave, making these by far the most numerous species recovered from the site. In spite of its abundance, however, the peccary remains at Bat Cave were never analyzed in any great detail. Instead, Hawksley et al. (1973) noted that detailed measurements and comparisons would be included in a proposed paper by Elaine Anderson and John Guilday, which was never published. Dr. Blaine Schubert has visited Bat Cave on several occasions to further assess the deposit. On these trips, additional peccary and other vertebrate remains were collected and a preliminary survey was conducted. Carnivoran modification and rodent damage was also noted on some of the peccary bones from the cave (Schubert, personal communication) but that information has not been published.

This thesis focuses on the Bat Cave peccary material collected by Hawksley et al. (1973). The Hawksley Collection is curated at the Illinois State Museum, and the material collected by Schubert is currently housed at East Tennessee State University. For the present study, the complete Bat Cave Hawksley collection was borrowed from the Illinois State Museum so that descriptive and taphonomic analyses were carried out.

Some of the fossils collected from the initial excavations were catalogued by Hawksley and students at Central Missouri State University (CMS). These fossils were eventually donated to the Illinois State Museum (ISM) for curation (Schubert, personal communication). A vast

number of the fossils remained uncatalogued and unidentified since the initial collection of the sample. Furthermore, many of the catalogued elements were misidentified, and the paired elements were never differentiated. Consequently, a major focus of this project was to catalogue these remains accurately, a process which first required thorough examination and description of all the peccary material.

The original minimum number of individuals for the Bat Cave *P. compressus* reported by Hawksley et al. (1973) was determined to be 98 based on 77 lower left canines and 21 upper left deciduous canines. However, that study did not elaborate how they differentiated the canines and examination revealed that some of the isolated dental material was misidentified. The MNI was therefore reevaluated in the present study. In addition, skeletal part representation and age demographics were recorded where possible.

Many of the peccary elements show bitemarks which are consistent with those of a large canid. Although Schubert (personal communication) had previously noted wolf-like bite damage on several of these bones, this has not been published. Thus, taphonomic analysis of the Bat Cave fauna was conducted to identify, assess, and describe the evidence of carnivore utilization on the peccary material. Additional taphonomic forces such as rodent gnawing, invertebrate damage, and weathering were also reported for the first time.

CHAPTER 2

BACKGROUND

Bat Cave, Missouri

Bat Cave is located 8km northwest of Waynesville in Pulaski County, Missouri in the

central Ozarks (Hawksley et al. 1973). It is one of several caves located in the Bear Ridge that

developed in Gasconade dolomite of Ordovician age. The Ozark Plateau is an uplifted region

that makes up about half the state of Missouri and portions of northern Arkansas, northeastern

Oklahoma, and southwestern Illinois (Figure 1). The core of this range existed as an island in the

Paleozoic seas, as evidenced by reef complexes which occur in the sedimentary layers

surrounding it (Unklesbay and Vineyard 1992). Dissolution has led to the formation of numerous

karst features such as springs, losing streams, sinkholes, and thousands of caves in the limestones

and dolomite bedrock, all of which characterize the region today (Vineyard and Feder 1974). The

Ozarks have remained unglaciated throughout the Quaternary and the region is presently covered

in thick, *Quercus*-dominated forests with mixtures of less abundant deciduous trees and a

grassland-forest ecotone which has been variable since the Pleistocene (King 1973; Thom and

Wilson 1980).

Figure 1. Location of Bat Cave in relation to the Ozark Plateau and Pulaski County, Missouri

Bat Cave itself was recognized for its paleontological potential as early as the late 1950s.

Portions of the cave were excavated throughout the 1960s by students and faculty from Central

Missouri State University (now University of Central Missouri). Excavations were primarily

under the guidance of Dr. Oscar Hawksley and focused on the section of the cave known as the

Bone Passage, though fossils were also recovered from Devil's Kitchen (Figure 2). The Bone

Passage is a low, narrow crawlway about 150m long. According to Hawksley et al. (1973), most

bones were found within the upper 30cm of a matrix with minimal moisture content, thus

forming an ideal environment for preservation of the fossils. Some bones were found in the

center of the floor and consisted of the more durable skeletal elements such as teeth. The

majority of the material, however, was apparently found along the sides of the passage.

Furthermore, there is evidence that the terminal end of the Bone Passage was once an entrance

that may have been utilized by ancient animals. According to Hawksley et al. (1973) the matrix there is wetter, indicating seepage of moisture from the outside. Hawksley et al. (1973) suggested in their report that the fossil animals found in the cave likely entered the cave voluntarily or were introduced there by a predator. They also noted that it was unlikely that the remains were deposited by water due to the relative lack of fluvial-action abrasion. Following his own excursions to Bat Cave, Dr. Blaine Schubert (personal communication) noted that a large portion of this deposit is still undisturbed and deserves further attention; the region closest to the potential Pleistocene entrance but farthest area to reach in current passageways.

Figure 2. Map of Bat Cave, Pulaski County, Missouri showing: (A) potential ancient entrance to Bone Passage, (B) Devil's Kitchen, (C) upper bluff entrance, (D) 3m drop-off in main passage, (E) passage junction, and (F & G) other current entrances. Redrawn from Hawksley et al. (1973).

Hawksley et al. (1973) identified about 45 terrestrial and semiaquatic vertebrate taxa, many of which are extant (Table 1), and based on this interpret the paleoecology as a well-watered forest-grassland ecotone with a strong taiga influence. Aquatic vertebrates from the Bat Cave fauna include hellbender salamander (*Cryptobranchus alleganiensis*), American beaver (*Castor canadensis*), and muskrat (*Ondatra zibethica*); the presence of which suggest that the site lay very near a substantial water source such as a stream (like the nearby Gasconade River). Open woodland and plains-adapted taxa include meadow vole (*Microtis pennsylvanicus*), eastern cottontail (*Sylvilagus floridanus*), snowshoe hare (*Lepus americanus*), and coyote (*Canis latrans*). Boreal forest taxa whose extant range limits lie far north of the site include yellow-cheeked vole (*Microtis xanthognathus*), northern bog lemming (*Synaptomys borealis*), and fisher (*Martes pennanti*). If these identifications are correct, the presence of these taxa suggest an overall cooler climate was present at the time of deposition. This climatic signal is supported by unpublished radiocarbon dates which indicate an age of last glacial maximum (Blaine Schubert, personal communication). Based on this date and the recorded paleofauna, the paleoenvironment immediately surrounding Bat Cave may be interpreted as an open forest habitat with *Pinus* and *Picea* being dominant and *Quercus* less so, as noted by King (1973). Other noteworthy extant vertebrates from the site include American black bear (*Ursus americanus*), red fox (*Vulpes vulpes*), and common raccoon (*Procyon lotor*). Extinct taxa include giant short-faced bear (*Arctodus simus*), dire wolf (*Canis dirus*), and flat-headed peccary (*Platygonus compressus*); the latter being not only the most abundantly represented taxon, but also the only ungulate reported from the site by Hawksley et al. (1973).

Table 1: List of Vertebrates Identified from the Bat Cave Site by Hawksley et al. (1973)

Taxon		NISP	MNI	Range
AMHPIBIA				
Caudata: Cryptobranchidae				
Cryptobranchus sp.	Hellbender salamander	3	1	P
Anura: Bufonidae				
Bufo sp.	Unidentified toad	1	1	
Anura: Ranidae				
Rana sp.	Unidentified frog	1	1	
REPTILIA				
Serpentes: Colubridae				
Pituophis sp.	Gopher snake			
Serpentes sp.	Unidentified snake			
AVES				
Passerine	Unidentified passerine bird	1	1	
MAMMALIA				
Insectivora: Soricidae				
Sorex cf. *S. cinereus*	Masked shrew	1	1	N
Sorex cf. *S. longirostris*	Southeastern shrew	1	1	
Blarina brevicauda	Short-tailed shrew	3	2	N
Chiroptera: Vespertilionidae				
Myotis cf. *M. lucifugus*	Little brown bat	1	1	P
Myotis cf. *M. griscescens*	Gray bat	10	3	P
Myotis sodalis	Indiana bat	1	1	P
Myotis spp.	Unidentified vespertilionid	10	7	
Pipistrellus subflavus	Pipistrelle	1	1	P
Eptesicus fuscus	Big brown bat	8	2	P
Lasiurus cf. *L. cinereus*	Hoary bat	3	1	P
Lasiurus cf. *L. borealis*	Red bat	3	2	P
Chiroptera spp.	Unidentified chiropterans	142		
Lagomorpha: Leporidae				
Sylvilagus floridanus	Eastern cottontail	30	3	P
Lepus americanus	Snowshoe hare	142	4	N
Rodentia: Sciuridae				
Marmota monax	Woodchuck	68	6	P
Tamias striatus	Eastern chipmunk	1	1	P
cf. *Tamias*	unidentified chipmunk	1	1	
Tamiasciurus cf. *T. hudsonicus*	Red squirrel	8	1	N
Rodentia: Geomyidae				
Geomys bursarius	Plains pocket gopher	15	3	P
Rodentia: Castoridae				
Castor canadensis	American beaver	3	1	1
Rodentia: Cricetidae				
Peromyscus sp.	White-footed mouse	12	3	P
Neotoma floridana	Eastern woodrat	44	5	P

Table 1 (continued)

Clethrionomys cf. *C. gapperi*	**Red-backed vole**	**1**	**1**	**N**
Microtis pennsylvanicus	Meadow vole	9	1	N
Microtis xanthognathus	Yellow-cheeked vole	26	4	N
Microtis sp. or *Pitymys*	Unidentified vole	9	2	
Microtis sp.	Unidentified vole	2		
Ondatra zibethica	Muskrat	1		
Synaptomys borealis	Northern bog lemming	1		
	Rodentia: Muridae			
Rattus sp.	Unidentified rat	1	1	
	Carnivora: Canidae			
Canis dirus	Dire wolf	177	6	E
Canis latrans	Coyote	5	2	P
Vulpes vulpes	Red fox	2	1	P
	Carnivora: Ursidae			
Arctodus simus	Giant short-faced bear	45	1	E
Ursus americanus	Black bear	1	1	P
	Carnivora: Procyonidae			
Procyon lotor	Common Raccoon	1	1	P
	Carnivora: Mustelidae			
Martes pennanti	Fisher	1	1	N
Mustela frenata	Long-tailed Weasel	1	1	P
	Carnivora: Felidae			
Lynx rufus	Bobcat	1	1	P
	Artiodactyla: Tayassuidae			
Platygonus compressus	Flat-headed Peccary	6339	98	E

N=extant range lies north of Missouri or Ozarks, E=extinct, P=occurs in the region in historic times. This table represents the original identifications, and does not address revisions in taxonomy, phylogenetic systematics, or potential misidentifications. The *Rattus* is considered to be a contaminent.

Differences Between Pigs and Peccaries

The family Tayassuidae (Palmer 1897), more commonly known as the peccaries, share a common ancestry and are superficially similar to true pigs (Suidae) in general appearance; both sharing a distinctive cartilaginous nasal disc used for digging through soft substrates (Sowls, 1997). However, the two families diverged very early in the Oligocene (Colbert 1980). Although fossil records show that peccaries were once present in Eurasia and Africa (Pearson 1927;

Colbert 1933; Hendy 1976), much of their evolutionary history has taken place in North America and they have been restricted to the Old World since the Pliocene (Scott 1913; Simpson 1950; 1980; Woodburne 1969a; 1969b). Pigs, on the other hand, are restricted to the Old World and there is no evidence of them ever being present in North America prior to European colonization (Simpson 1980).

A number of behavioral, anatomical, and ecological differences further differentiate the two families. Both pigs and peccaries have continually growing canines which occlude against each other, keeping them reasonably short in length and maintaining sharpened edges (Sowls 1997). In peccaries, however, the canines are oriented vertically and are concealed behind the lips when the mouth is closed (Simpson 1946; Sowls 1997). Pigs have true canine-tusks that protrude laterally and curve upward, remaining externally visible at all times (Simpson 1946). Because they are no longer contained behind closed lips, the tusks of some pig species may grow to quite impressive lengths and shapes. Extant peccaries possess 38 teeth with a consistent dental formula of I 2/3, C 1/1, P 3/3, M 3/3 (Simpson 1946; Wetzel 1977; Sowls 1997). Pigs are more variable in their dentition, having 34 to 44 teeth with a dental formula of I 1-3/3, C 1/1, P 2-4/2-4, M 3/3 (Simpson 1946). Compared to pigs, peccaries have more compact bodies with longer, more slender limb proportions for sustained running, as well as a vestigial tail composed of 6 to 9 caudal vertebrae (Sowls 1997).

Figure 3. Anterior view of the skulls of a pig, *Sus scrofa* ETVP 5260 (left), and a peccary, *Pecari tajacu* ETVP 5253 (right). Note the difference in the orientation of the canines. Those of the pig point laterally and upward, and would be permanently visible even with jaws occluded. Those of the peccary are more vertically-oriented, and as such would be concealed behind the lips during jaw occlusion. Photography by Aaron Woodruff.

Extant Peccaries

The collared peccary (*Pecari tajacu*) (Figure 4) is the smallest and most widely distributed of all extant peccaries; occurring from southern Texas, New Mexico, and Arizona in the United States, south through northwest Sonora in Mexico to Peru west of the Andes, and Santiago del Estero in Argentina east of the Andes (Oliver 1993; Gongora et al. 2011). Pleistocene-age fossils attributed to this species are also known from the southeastern United States (Hulbert et al. 2009), showing that its range was once even more expansive in the past. It is adapted to live in a wide variety of habitats including deserts, arid woodlands, oak woodlands,

and tropical rainforests (Oliver 1993; Sowls 1997). Diet varies in accordance to its range of habitats to include a wide variety of fruits, nuts, roots, tubers, and the edible parts of green plants.

Figure 4. Collared Peccary (*Pecari tajacu*) at Petencito Zoo, Santa Elena, Guatemala. Photography by Bernard Dupont, used with permission.

The white-lipped peccary (*Tayassu pecari*) (Figure 5) is also widely distributed, albeit to a lesser extent than the collared peccary. Its range extends from Veracruz and Oaxaca in southern Mexico, through Central America, and south to Ecuador west of the Andes, and Entre Rios in Argentina east of the Andes. It generally favors areas of higher rainfall and thicker bush cover than either the collared or Chacoan peccary (see below); occurring in tropical rainforests and savannas with ready access to a permanent water source such as a river, lake, or marsh (Oliver

1993). It is currently the only land mammal in the Neotropics that regularly forms large herds, which can number in the hundreds. White-lipped peccaries are more frugivorous than the other extant peccaries. Their diet comprises of fruits, seeds, and roots, but they will occasionally eat invertebrates, small vertebrates, fungi, and carrion (Oliver 1993).

Figure 5. White-lipped Peccary (*Tayassu pecari*) at Petencito Zoo, Santa Elena, Guatemala. Photography by Bernard Dupont, used with permission.

The Chacoan peccary (*Catagonus wagneri*) (Figure 6) has the most restricted distribution of any extant peccary. This species was first identified from subfossil remains from Santiago del Estero Province, Argentina, which were later described by Rusconi (1930). It was thought to have been extinct until living populations were discovered by Wetzel et al. (1975). The only true fossil record for this species comes from the Sopas Formation in Uruguay, a late Pleistocene

locality that lies far away from its known historic distribution (Gasparini et al. 2013). It currently

inhabits the semi-arid thorny forests of dry Chaco in western Paraguay, southeastern Bolivia, and

northern Argentina that have high temperatures and low rainfall year round (Mayer and Wetzel

1986; Oliver 1993; Gasparini et al. 2006; Gasparini et al. 2013).

Figure 6. Chacoan peccary (*Catagonus wagneri*) at Beardsley Zoo, Bridgeport, Connecticut. Photography by James Dowling-Healey, used with permission.

Flat-Headed Peccary (*Platygonus compressus*)

The flat-headed peccary (*Platygonus compressus*) was first identified in 1806 and was

fully described in the mid-19th century (LeConte, 1848). It was the most common North

American peccary species during the late Pleistocene and had a wide distribution, ranging from

east coast to west coast and from Canada to Mexico (Kurtén and Anderson 1980; Schmidt 2008).

It is particularly abundant in cave deposits around the United States (Hoare et al. 1964; Slaughter 1966; Davis 1969; Guilday et al. 1971; Hawksley et al. 1973; Wilson et al. 1975; Schubert and Mead 2012) (Figure 7), suggesting that such subsurface shelters were important to the ecology of this species.

Figure 7. Known Rancholabrean sites which have yielded *Platygonus* fossils, represented by green circles (*P. compressus*) and green triangles (*P.* sp). Hollow stars denote the occurrence of *Platygonus* in cave deposits. Coordinate data recovered from the MIOMAP/FAUNMAP, 2011.

Compared to extant peccaries, *P. compressus* was highly specialized in a number of aspects (Figure 8). The Chacoan peccary (*Catagonus wagneri*), which currently resides in the

Gran Chaco region of South America, is thought to be the closest living relative of *P. compressus* (Mayer and Wetzel 1986). Both these species are somewhat specialized with many features that point to a preference for more open or lightly-wooded habitats such the development of relatively longer and more slender limbs for fast running (Kurtén and Anderson 1980; Sowls 1997). Both *Platygonus* and *Catagonus* have reduced the number of toes on their hindfeet to just two, instead of the more plesiomorphic three seen in other peccaries (Mayer and Wetzel 1986). In addition to this, *Platygonus* has lost the lateral toes on the manus, thus becoming fully didactyl (Guilday et al. 1971; Kurtén and Anderson 1980). Their eyes are also set higher up on the skull than other peccaries, an adaptation which is more extreme in *Platygonus* and is interpreted to reflect more derived long-range vision; making it easier to spot predators in open areas or while feeding on ground level vegetation (Guilday et al. 1971; Kurtén and Anderson 1980; Mayer and Wetzel 1986). In addition, the teeth have higher, zygolophodont cusps to handle more leafy plant matter than what is regularly ingested by other peccaries (Wetzel 1977; Kurtén and Anderson 1980; Mayer and Wetzel 1986); although those of *Catagonus* are proportionally larger and more robust than those of *Platygonus* (Guilday et al. 1971; Wetzel et al. 1975). The rostra of both genera are also deeper and house enlarged sinuses and complex turbinates which, at least in the extant *C. wagneri*, help to cope with dry, dusty air (Finch et al. 1972; Mayer and Wetzel 1986). *Platygonus compressus*, however, seems to be more associated with relatively well-watered localities (Kurtén and Anderson 1980), and thus heavily turbinated nostrils in this taxon may have been more of an adaptation for enhanced olfaction or to help warm and humidify incoming air during the winter months. Overall, *P. compressus* is generally thought of as a highly cursorial animal adapted to relatively open environments (Finch et al. 1972; Wetzel 1977; Kurtén and Anderson 1980).

Figure 8. Composite skeleton (A) and life reconstruction (B) of the flat-headed peccary, *Platygonus compressus*. Photography by Osborn at the American Museum of Natural History. Artwork by Aaron Woodruff, 2015.

Most past interpretations of the dental morphology of *P. compressus* have suggested that it was a browser (Holman 2001; Schmidt 2008). Kurtén and Anderson (1980) stated that "the hypsodont teeth were adapted to chew coarse vegetation, and the dentition suggests browsing habits." These early interpretations stem from observations of the post-canine dentition, which is more hypsodont even when compared to other *Platygonus* species. The molars, as noted above, further differ from the bunodont pattern seen in most peccary taxa and have become zygolophodont, with tall cusps adapted to crush hard browse. Finally, Schmidt (2008) performed low magnification dental microwear analysis of *P. compressus* and compared its profile to those of several extant grazers, mixed feeders, and browsers. The microwear profile of *P. compressus* was found to be most consistent with those of browsing herbivores.

Demographics

The huge *P. compressus* sample collected from Bat Cave provides the opportunity to obtain demographic and ontogenetic information about the population. Hawksley et al. (1973) noted in their report that various age groups from very young to very old animals are present in the sample. The three extant peccary species may be defined as territorial and highly social, existing in close knit herds that may hold the same home range over many generations (Bigler 1974; Taber 1991; Taber et al. 1993). Through phylogenetic bracketing it can be inferred that similar behavior was present in *P. compressus* (Witmer 1995). Further evidence to this end comes in the form of the shear abundance of *P. compressus* fossils at a given locality, often vastly outnumbering all other taxa (Kurtén and Anderson 1980), as well as a number of caves with extensive peccary trackways (Schubert, personal communication).
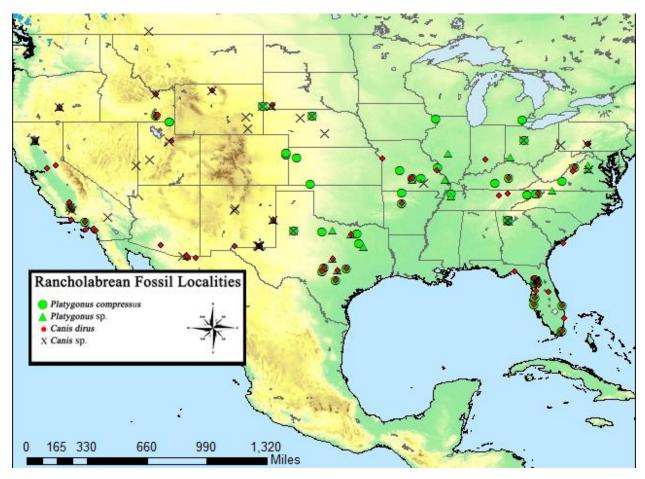
<u>Evidence of Predation</u>

As defined by Haynes (1983a), tooth marks are produced when an animal bites down on a bone, deforming it under pressure up to a point and leaving behind impressions on the bone surface. This is typically marked by fragments of cortical bone pushed inward and left embedded in the underlying trabecular bone (Schubert, personal communication) (Figure 9), which itself often becomes compacted under the pressure. Such marks are usually found on the proximal or distal ends of the long bones, ribs, pelvis, vertebrae, and sternebrae (Haynes 1980; 1982; 1983a). Furrows, scratches, or incisions may be produced when the animal moves its clenched teeth over the bone surface (Haynes 1980; 1982; 1983a). Such marks are generally most common on the ends of the remaining bone or bone fragments, especially on shaft fragments near the epiphyses where the predator's cheek teeth are commonly used to shear away cancellous or thin compact tissue (Haynes 1980; 1982; 1983a).

Carcass utilization by large carnivorans is surprisingly patterned with marked sequences, and family-level identification can be determined based on the diagnostic damage patterns left on compact bones (Haynes 1980; 1982; 1983a). In the case of wolf damage, this usually takes the form of circular puncturing-crushing impressions left by the premolars and carnassials (Figure 8). This damage pattern is the prevalent type observed among the Bat Cave peccary bones and supports the predator responsible as a large canid of the genus *Canis* as has been suggested by Schubert (personal communication). There is no evidence of large felid or ursid utilization; the former of which typically leave behind V-shaped cuts whereas the latter produces more of a grinding-crushing pattern. In comparison to hyenas (*Crocuta* and *Hyaena*) which have specialized durophagous dentition, wolves will spend much more time chewing on bones at killsites or dens, thus leading to characteristically differential tooth marking (Haynes 1983a).

Figure 9. Distal portion of a peccary humerus from Bat Cave showing the characteristic circular puncture marks made by a wolf carnassial. Scale bar = 1cm.

The dire wolf (*Canis dirus*) was a large, widely-distributed, hypercarnivorous canid of the late Pleistocene (Kurtén and Anderson 1980). It is the second most abundant vertebrate from the Bat Cave fauna, with Hawksley et al. (1973) reporting 177 identified elements and minimum of 6 individuals (based on four right metacarpal III and two left metacarpal III which vary considerably in length from the rights). This predator is therefore suspected to be the most likely culprit behind the bite marks left on the Bat Cave peccary bones. In addition to Bat Cave, dire wolf fossils are often found in the same fossil localities as flat-headed peccaries, many of which are cave sites (Hawksley et al. 1963; Slaughter 1966; Davis 1969; Guilday et al. 1971; Parmalee and Oeseh 1972; Schubert and Mead 2012), suggesting a possible predator-prey relationship between these two species which has never been described until the present study (Figure 10).

Figure 10. Known Rancholabrean sites which have yielded *Platygonus* (green circles and triangles) and *Canis dirus* (red circles). X symbols denote *Canis* specimens which have yet to be identified to species-level but are not attributable to extant taxa. Note the degree of overlap between *Platygonus* and *Canis*. Coordinate data recovered from MIOMAP/FAUNMAP, 2011.

Rodent Gnawing

In addition to predator modification, Schubert (personal communication) noted extensive rodent damage on many of the bones recovered from Bat Cave. Rodent gnaw marks on bony tissue occur as a series of paired, shallow grooves (Fiorello 1989) (Figure 11). It has been documented that rodents will opportunistically gnaw on bones and antlers to obtain the minerals required to sustain their hypselodont dentition and to help keep their incisors worn to a reasonable length (Klippel and Synstellien 2007).

Figure 11. Ventral view of an anterior peccary mandible fragment from Bat Cave which bares rodent gnaw marks along its medial surface. Scale bar = 1cm.

CHAPTER 3

METHODS

Abbreviations Used

BC (Bat Cave), **MC** (metacarpal), **MT** (metatarsal), **ETSU** (East Tennessee State University, **CMS** (Central Missouri State University; this institution is now named the University of Central Missouri), **ISM** (Illinois State Museum), **MNI** (minimum number of individuals), **NISP** (number of identified specimens), *Pe. tajacu* (*Pecari tajacu*), I (upper incisor), i (lower incisor), C (upper canine), c (lower canine), P (upper premolar), p (lower premolar), M (upper molar), m (lower molar).

Specimen Preparation

ISM catalogue numbers were given to each of the BC peccary fossils. The fossils were grouped together according to element, differentiated to left and right sides where applicable, and numbered accordingly. A base coat of B-98 was placed on each element over the area to be labeled. White acrylic paint was then applied to the treated area. ISM numbers were written on the marked areas using a black archival ink pen. The label was then covered by a single layer of B-72 for preservation. B-76 glue was used to repair those elements which had been broken during collection or preparation.

In several instances during preparation it was necessary to disassemble elements which had been previously and erroneously glued together during the initial CMS preparation (Figure 12). In these instances acetone was dripped in between individual elements to soften the glue so that it could be safely pulled apart. Multiple elements which were thought to be representative of

a single individual based on staining, articulation, and age were singled out, recorded, and stored together. Similarly, pathologic specimens within the sample were also noted.

Figure 12. A juvenile peccary forearm comprised of three separate elements (radius, ulna, and distal epiphysis) from three different individuals pieced together by CMS. This is one of several composite specimens from the Bat Cave peccary sample.

Demographic Assessment

Sexual Dimorphism—Sexual dimorphism in peccaries may be determined via certain measurements of the skull: greatest skull length, greatest skull width, ratio of skull length to skull with, and angle of the skull (Miller 1970; Sicuro et al. 2011). This method is not possible for the BC population because no intact skulls are preserved. Instead, the length and width of each m3 was measured and plotted against each other to test for bimodality. The Bat Cave measurements were then plotted together with similar measurements taken for *P. cumberlandensis* from the collections at University of Florida, a taxon that has been demonstrated to possess pronounced sexual dimorphism in its cranial morphology (Wright 1993). The m3s were selected for study because of their relative abundance and determinate growth. Although bimodality may be observed in peccary canines (Wright 1993), these teeth were not measured due to their semi-hypselodont nature, irregular placement of the enamel-dentine junction for isolated specimens, and age-related variability in basal width.

Age & Ontogeny—Age demographics for the BC peccary population were investigated first by referencing Kirkpatrick & Sowls (1962), in which the age-at-tooth eruption was recorded for the extant *Pe. tajacu* (Table 2). It is assumed that the age-at-eruption does not vary significantly between the extinct and extant taxa. For adult specimens with fully-erupted dentition, tooth wear was examined as a proxy for age. Special focus was placed on the m3 because it is the last of the permanent dentition to erupt (Kirkpatrick and Sowls 1962), and tends to be the most hypsodont tooth in the mouths of ungulates (Ozaki et al. 2009); making it a reliable indicator of physical maturity. Similar aging methods have been performed with extant white-tailed deer (Severinghaus 1949; Knight 2001; Cain and Wallace 2003); a taxon whose maximum life expectancy in the wild is comparable to that of extant peccaries. In addition, *O. virginianus* is a reasonable proxy for *P. compressus* because the two taxa are similar in terms of size and presumed browsing or mixed-feeding dietary regime (Kurtén and Anderson 1980; Schmidt 2008). Furthermore, the postcanine dental formula in cervids is the same as that of peccaries and have been demonstrated to erupt in the same sequence and at a similar rate (Kirkpatrick and Sowls 1962; Knight 2001; Cain and Wallace 2003), making these ungulates reasonable analogues for comparison with the BC peccaries.
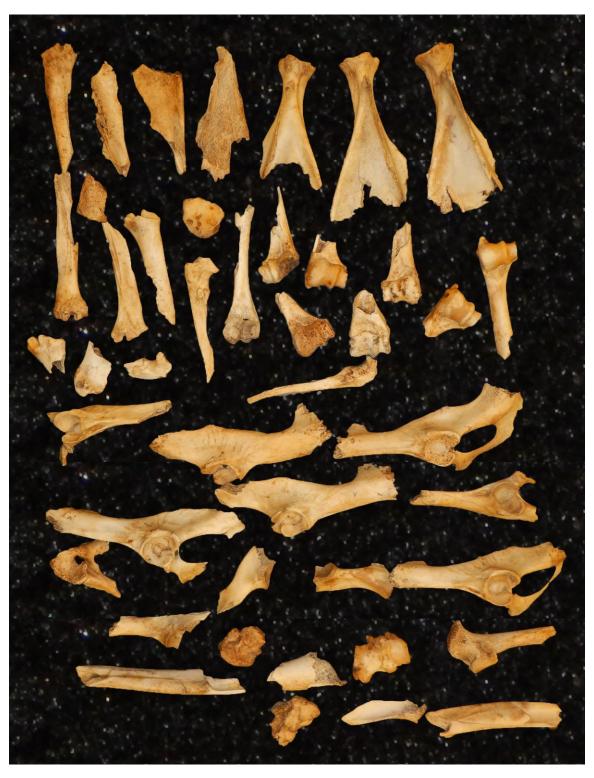
Table 2: Age of Tooth Eruption in Extant Peccaries

Tooth	Age (days)	Age (weeks)	Age (years)
di1	28-49	4-7	0.07-0.13
di2	45.5-91	6.5-13	0.12-0.25
dc1	At birth	At birth	At birth
dp2	21-35	3-5	0.05-0.1
dp3	14-21	2-3	0.03-0.06
dp4	28-52	4-7.5	0.07-0.14
i1	280-420	40-60	0.7-1.2
i2	364-504	52-72	1-1.4
c1	203-280	29-40	0.5-0.8
p2	462-581	66-83	1.2-1.6
p3	Not recorded	Not recorded	Not recorded
p4	Not recorded	Not recorded	Not recorded
m1	119-161	17-23	0.3-0.4
m2	252-350	36-50	0.7-0.96
m3	518-658	74-94	1.4-1.8

This table shows the age at which the lower dentition begin to erupt in the extant collared peccary, *Pecari tajacu*, depicted in days, weeks, and years. Adapted from Kirkpatrick & Sowls (1962).

Evidence of Predation

Comparative Sample— Wolf-eaten bones of white-tailed deer (*Odocoileus virginianus*), whose carcasses had been fed to captive gray wolves (*Canis lupus*), were used for direct comparison to the Bat Cave peccary material (Figure 13). These modern remains were collected from Bays Mountain Park in Kingsport, Tennessee by Blaine Schubert. In terms of linear measurements, many of the bones of white-tailed deer are roughly the same size, shape, and density as those of flat-headed peccary, particularly the upper limb and vertebral elements. This similarity makes the Bays Mountain Park deer material ideal subjects for comparison. To further assess the degree of damage, intact white-tailed deer bones from ETSU collections were also used for reference. Observations were then verified by referencing the work of Haynes (1980; 1982; 1983a; 1983b), who has done extensive work with bone damage inflicted by carnivorans.
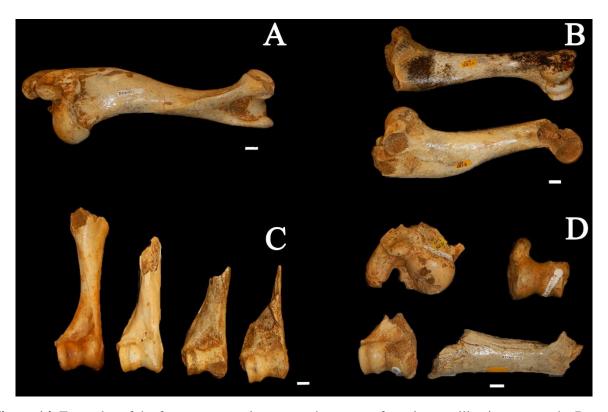
Figure 13. Wolf-eaten bones of white-tailed deer (ETVP 489) that were used as the comparative sample when identifying carnivore damage in the Bat Cave sample. The deer carcasses were road-killed animals which had been fed to the captive gray wolves at Bays Mountain Park in Kingsport, Tennessee.
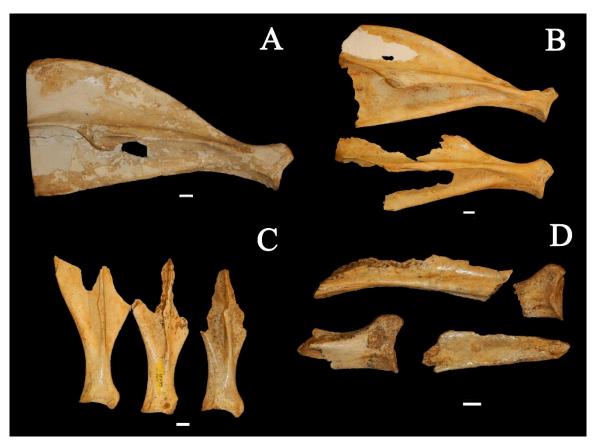
Stages of Utilization—To assess and categorize the degree to which bones were modified by carnivorans, a four-stage system loosely based on Behrensmeyer's weathering stages (1978) was established (Figure 14, 15, 16). By doing this, it is possible to observe the frequency and method in which particular skeletal elements are utilized, and to compare the results to the feeding patterns of extant predators. This method was used for all limb bones except the fibulae, patella, and those which comprise the manus and pes. Vertebral, rib, carpal, and tarsal elements were examined as well, but not to the same degree of scrutiny as the long bones due to their smaller size. Smaller scapular and cranial fragments were left out of the assessment as these are more likely to have been fragmented due to trampling over a period of time, although those elements which bear obvious signs of carnivore processing (i.e., scratch or gouge marks) are noted.

- Stage 0: An intact bone which shows now evidence of bite damage.

- Stage 1: For long bones, the shaft is intact but has attained bite damage and the epiphyseal ends may be partially or completely absent. For scapulae, the scapular spine is complete with portions of the fossae absent or bite damage to the distal end. For pelvises, a portion of the ilium or ischium may be absent but is otherwise mostly intact.

- Stage 2: For long bones, at least one of the epiphyseal ends is absent, along with a portion of the shaft. For scapulae, up to half of the scapular spine may be absent along with considerable portions of the spinous fossae. For pelvises, both the ilium and ischium are heavily damaged and mostly absent.

- Stage 3: For long bones, a bone which is so heavily damaged that only the epiphyseal end or a fragment of the shaft remains present. For scapulae, the scapular spine has been completely lost and only the distal neck or edge of the spinous fossae remain present. For
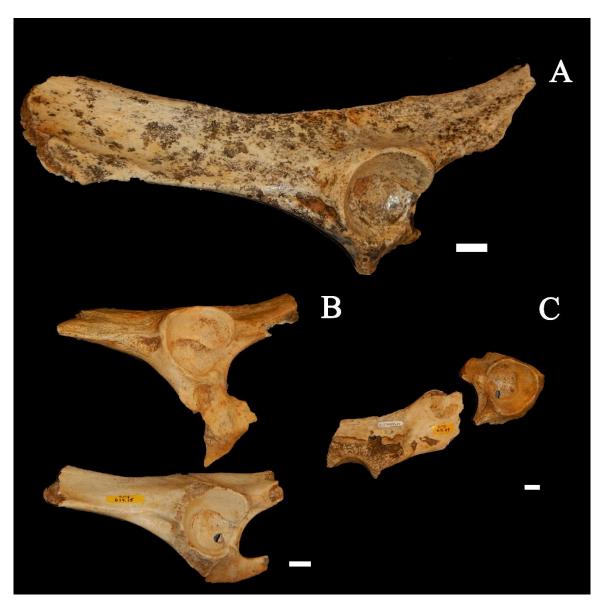
pelvises, consist only of the acetabulum and surrounding bone, or a broken ilium or

ischium.

Figure 14. Examples of the four stages used to assess the extent of carnivore utilization among the Bat Cave peccary long bones. (A) Stage 0 bones exhibit no evidence of carnivore damage, (B) Stage 1 bones retain an intact shaft with damaged or absent epiphyseal ends, (C) Stage 2 bones exhibit complete removal of one of the epiphyseal ends and part of the shaft, (D) Stage 3 bones exhibit complete destruction of the bone with only a shaft fragment or epiphyseal end remaining.

Figure 15. Examples of the four stages used to assess the extent of carnivore utilization to the Bat Cave peccary scapulae. (A) Stage 0 scapulae exhibit no evidence of carnivore damage, (B) Stage 1 scapulae retain a complete spine but have lost portions of the spinous fossae, (C) Stage 2 scapulae have lost portions of the spine in addition to the spinous fossae, (D) Stage 3 scapulae lack the scapular spine and have been reduced to the neck and glenoid fossae or fragment of the fossae.

Figure 16. Examples of the four stages used to assess the extent of carnivore utilization to the Bat Cave peccary pelvises. No examples of Stage 0, or fully intact peccary pelvises, are available from within the Bat Cave sample. (A) Stage 1 pelvises have minor damage to the ilium and/or ischium, (B) Stage 2 pelvises lack both the ilium and ischium, (C) Stage 3 pelvises consist only of the acetabulum and surrounding bone or the broken ilium or ischium.
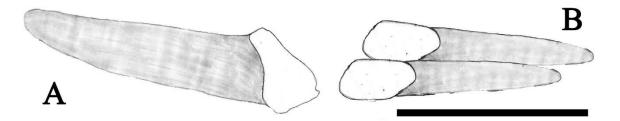
CHAPTER 4

BAT CAVE MATERIALS

The following is a summary of all the Bat Cave peccary material, all referable to the taxon

Platygonus compressus, which were identified, catalogued, and analyzed in the present study.

Supplementary tables are present in Appendix A, B, & C.
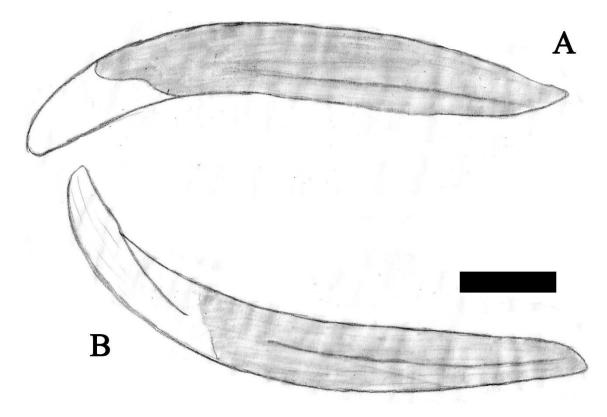
Isolated Dentition

     Deciduous incisors— Compared to extant peccaries, individuals of *P. compressus* have

incisors that are reduced both in size and in number; with two lower incisors instead of three.

The dI1 and dI2 of both the upper and lower jaws are similar in morphology and difficult to

differentiate from each other, thus both elements were grouped together and labeled accordingly.

There are 11 lower left (ISM 499236), 9 lower right (ISM 499237), 7 upper left (ISM 499238),

and 5 upper right (ISM 499239) isolated deciduous incisors (Figure 17).

Figure 17. Diagram of the left upper (A) and lower (B) deciduous incisors of *P. compressus* shown in anterior view. Scale bar = 1cm. Artwork by Aaron Woodruff.

     Deciduous canines— Upper and lower dC1 are oval-shaped in cross section. Lower dC1

are identifiable by the presence of the wear facet on its posterior-lingual surface which results

from occlusion with the upper dC1. The upper dC1 are, in turn, identifiable by the presence of

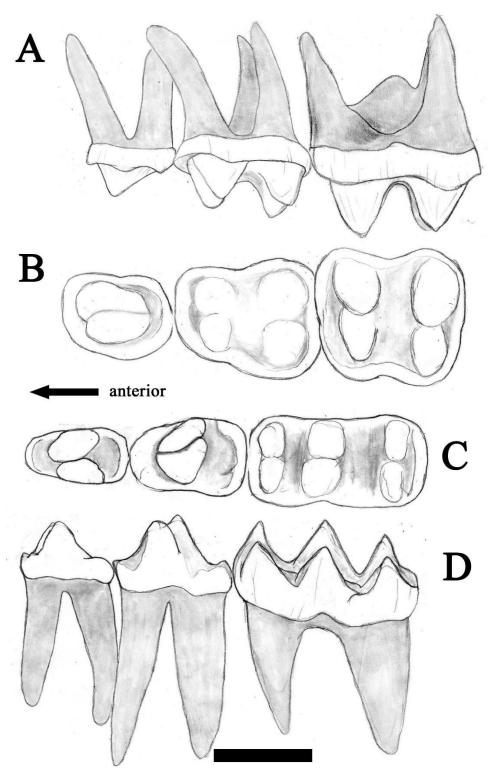the wear facet on its anterior tip of the crown. There are 11 lower left (ISM 499240), 9 lower

right (ISM 499241), 13 upper left (ISM 499242), and 21 upper right (ISM 499243) isolated

deciduous canines (Figure 18).

Figure 18. Diagram of the left upper (A) and lower (B) deciduous canines of *P. compressus* shown in labial view. Scale bar = 1cm. Artwork by Aaron Woodruff.
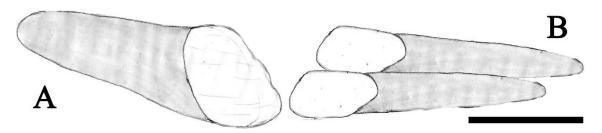
Deciduous premolars— Upper deciduous premolars are broader than those of the lower

jaw, which are more labio-lingually narrow (Figure 19). In general, the deciduous premolars are

more molariform than their permanent counterparts due to the absence of true molars. The dP2

differ in that they are less molariform than the other deciduous premolars, instead resembling the

permanent premolars in overall shape and function. There are two lower left (ISM 499244), two

lower right (ISM 499245), three upper left (ISM 499246), and one upper right (ISM 499247)

isolated dP2 from the BC peccary sample. Upper dP3 are molariform and trapezoidal in shape

whereas the lower dP3 is intermediate in form between a premolar and a molar; with a triangular

lateral profile and an expanded talonid basin for grinding. There are three lower left (ISM

499248), three lower right (ISM 499249), and two upper left (ISM 499250) isolated dP3. Upper

dP4 resembles a true molar very closely in its quadrate shape and in the arrangement of the cusps

(Lundelius 1960), differing from the M1 mainly in its noticeably smaller size. The lower dP4 is

elongated and has three transverse ridges that form six indistinct cusps (Lundelius 1960; Sowls

1997). There are six lower left (ISM 499252), six lower right (ISM 499253), three upper left

(ISM 499254), and four upper right (ISM 499255) isolated dP4.

Figure 19. Diagram of the left upper (A & B) and lower (C & D) deciduous cheek tooth row of *P. compressus* shown in labial and occlusial views. Note the molariform shape of the dP3 and dP4. Such features such as an elongated lower dP4 bearing six cusps and an upper dP3 with a trapezoidal shape are diagnostic characters within Tayassuidae. Anterior is to the left. Scale bar = 1cm and anterior is to the left. Artwork by Aaron Woodruff.
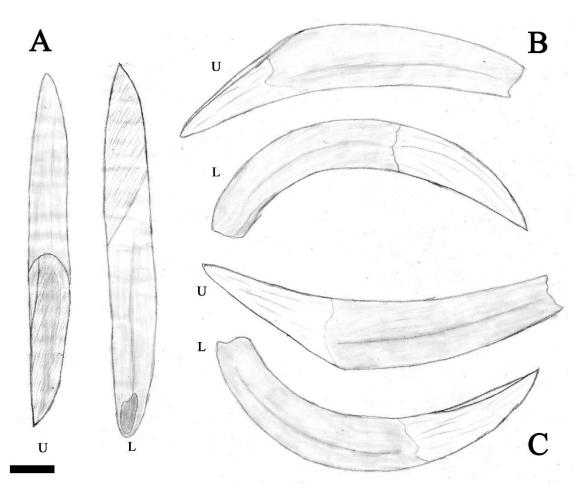
Permanent incisors—As with the deciduous incisors, the I1 and I2 are difficult to

differentiate beyond left and right side, and so both were grouped together accordingly. There are

45 lower left (ISM 499200), 39 lower right (ISM 499201), 18 upper left (ISM 499202), and 11

upper right (ISM 499203) identified permanent incisors (Figure 20).

Figure 20. Diagram of the left upper (A) and lower (B) permanent incisors of *P. compressus* shown in anterior view. The permanent incisors are distinguishable by their relatively larger size and more robust roots when compared to the deciduous incisors. The two lower incisors of *P. compressus* are small and closely spaced together. The upper I1 is enlarged but is proportionally smaller than that of extant taxa and the I2 may be vestigial or absent. Scale bar = 1cm. Artwork by Aaron Woodruff.

Permanent canines— Isolated permanent canines may be differentiated by several means

(Figure 21). The enamel is generally higher on the lingual side than it is on the labial side,

reflecting the slightly angled position of these teeth, thus assisting in the identification of isolated

teeth. In the initial unworn state, the C1 is elliptical in cross-section. As the C1 continues to

lengthen and begins to occlude with the c1, a large and flat wear facet develops on the anterior

surface of the crown with a distinctive series of parallel grooves running diagonally and

downward toward the lingual edge. Left and right C1 may therefore be differentiated by the

direction in which these grooves slope; a right-to-left downward slope indicates a right C1 and a

left-to right downward slope indicates the left C1. A secondary facet may also be present on the

proximal anterio-lingual surface. In the initial unworn state, the c1 are triangular in cross-section.

The C1 crown and roots are straighter, the c1 is more curved down its overall length. As it

lengthens and begins to occlude with the C1 a large, flat wear facet develops on the posterior

surface of the crown. Similarly to the C1, a series of parallel grooves run diagonally and upward

toward the lingual edge of the crown which can assist in identifying the tooth; a right-to-left

upward slope indicates a right c1 and a left-to-right upward slope indicates a left c1. A lateral

groove may also be present running down the lingual side of the root. A total of 200 isolated

permanent canines are documented from among the BC sample: 56 left lower (ISM 499204), 53

lower right (ISM 499205), 39 upper left (ISM 499206), and 52 upper right (ISM 499207),

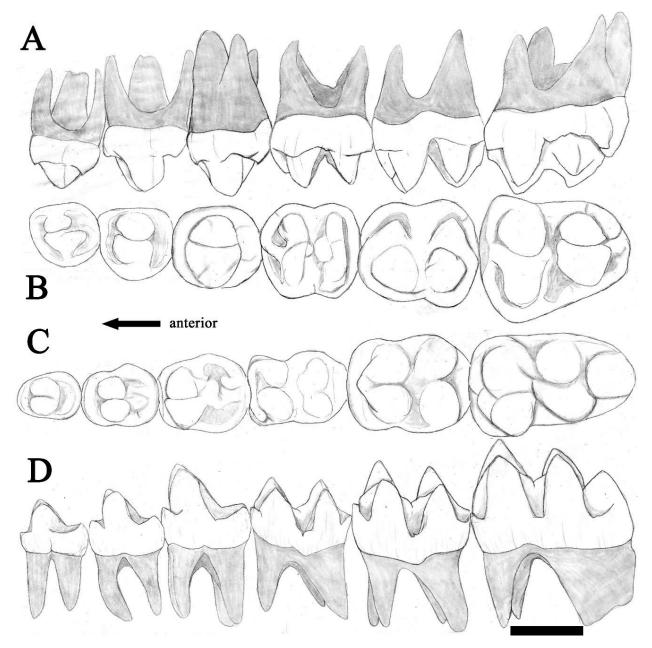making these the most numerous of all the isolated dental elements.

Figure 21. Diagram of the left upper (U) and left lower (L) permanent canines of *P. compressus* shown in occlusial (A), labial (B), and lingual (C) views. Apart from their larger size, permanent canines are characterized by their more pronounced wear facets. Unworn upper canines are elliptical in cross-section and have a relatively straight profile whereas unworn lower canines are triangular in cross-section and are more curved. Lefts and rights may be distinguished by the placement of the enamel-dentine junction on either side or by the slope of the linear scratches on the occlusial surfaces. Scale bar = 1cm. Artwork by Aaron Woodruff.

Permanent premolars—Unlike the deciduous premolars, the permanent premolars are not molariform and do not differ in overall shape (Figure 22). P2 are the smallest of the premolars and the smallest cheek teeth overall. There are six lower left (ISM 499208), four lower right (ISM 499209), four upper left (ISM 499210), and four upper right (ISM 499211) isolated permanent P2. P3 is intermediate in size between P2 and P4. There are four lower left (ISM 499212), eight lower right (ISM 499213), three upper left (ISM 499214), and nine upper right (ISM 499215) isolated permanent P3. P4 is the largest of the permanent premolars and the first to erupt. There are eight lower left (ISM 499216), seven lower right (ISM 499217), six upper left (ISM 499218), and six upper right (ISM 499219) isolated permanent P4.

Permanent molars— Upper and lower molars are easily distinguishable by the morphology of their roots. Upper molars are broader with labial roots which point vertically and lingual roots which point medially into the palate. Lower molars are transversely narrower with all roots pointing vertically into the dentaries. M1 is the smallest of the molars and the first to erupt. The upper M1 is very similar to the upper dP4 in shape and appearance, but the two may be distinguished by the latter's smaller size. There are 6 lower left (ISM 499220), 8 lower right (ISM 499221), 10 upper left (ISM 499222), and 9 upper right (ISM 499223) isolated M1. M2 is intermediate in size between M1 and M3. There are 15 lower left (ISM 499224), 13 lower right (ISM 499225), 8 upper left (ISM 499226), and 6 upper right (ISM 499227) isolated M2. M3 are the largest of the molars and the last teeth to erupt (Kirkpatrick and Sowls 1962). It is elongated by an enlarged hypoconulid that effectively functions as a fifth cusp. The width of this tooth is greatest across the anterior pair of cusps and taper posteriorly (Lundelius 1960). *Pe. tajacu* displays considerable variation in the number and placement of their accessory cusps. *Pl. compressus*, in contrast, displays more uniformity in the M3 with notable expansion of the

primary cusps and reduction of the accessory cusps. There are 8 lower left (ISM 499228), 14

lower right (ISM 499229), and 2 upper right (ISM 499231) isolated M3.

Figure 22. Diagram of the left upper (A & B) and lower (C & D) permanent cheek tooth rows of *P. compressus* shown in labial and occlusial views. Upper cheek dentition are characterized by their broader shape and by having lingual roots which point slightly laterally into the palate. In lower cheek teeth, the lingual cusps are generally higher whereas the opposite is true of the upper cheek teeth. Scale bar = 1cm and anterior is to the left. Artwork by Aaron Woodruff.

<u>Axial Skeleton</u>

Dentary—Peccaries exhibit a particularly strong fusion of the two dentaries which occurs very early in their development (personal observation). As a result, the anterior part of the mandible often survives as a single specimen as opposed to two separate halves split at the symphysis. For the purposes of this project, mandibles are defined as an intact mandibular symphysis with any portion of the right or left dentaries. However, where the mandibular symphysis is absent leaving only a single dentary and its associated dentition, the element will simply be referred to as either the left or the right dentary. A total of 22 mandibles (ISM 499097) are present, together with 35 left dentaries (ISM 499098) and 38 right dentaries (ISM 499099). Of the mandibles, only elements ISM 499097.1 and ISM 499097.2 are reasonably complete missing only the P2 and pieces of the angular process.

Skull—The most complete skull from the BC peccary sample is a single specimen (ISM 499100.1) whose pieces are held together with plaster. From this specimen, much of the right and left facial area from the medial maxilla to the occipital condyle from the posterior maxilla to the auditory bullae respectively, as well as the internal system of turbinates (Figure 23). In addition to this, there are 3 other fused maxillae, 13 left maxillae (ISM 499101), and 13 right maxillae (ISM 499102), 19 of which retain intact but variable dentition. The remaining cranial material recovered from BC consists of moderate to small-sized bone fragments from various parts of the skull. Peccary skull bones appear to fuse relatively early during the lifespan starting at about 17 weeks of age with sutures being no longer visible by 2 years (Figure 24). This characteristic can make identification of individual cranial elements difficult, however there are 8 identifiable frontals (ISM 499103 and ISM 499104), 19 identifiable jugals (ISM 499105 and ISM 499106), 2 parietals (ISM 499209), 9 occiputs (ISM 499210), and 6 auditory bullae (ISM

499211 and ISM 499212). The remaining cranial elements are small, unidentifiable fragments which were left uncatalogued.
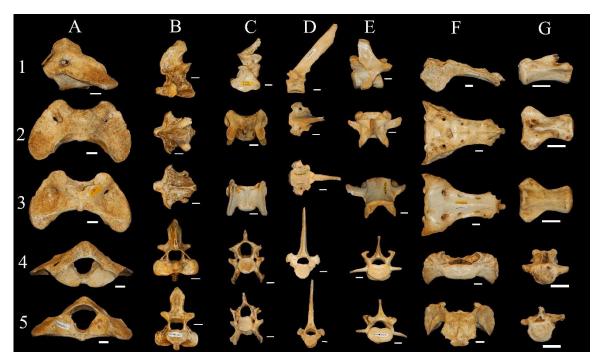

Figure 23. The most complete *P. compressus* skull from the Bat Cave sample, ISM 499101.1, in left (A) and right (B) lateral views.

Figure 24. Skulls belonging to a juvenile collared peccary ETVP 7229 (A) roughly 17 weeks in age alongside that of a young adult specimen ETVP 17584 (B) of about two years. Note that in the older individual the sutures are completely fused and are no longer visible. Specimens aged based on tooth eruption.

Vertebral Column—A total of 334 pre-sacral vertebrae have been identified (Figure 25).

There are 19 atlases (ISM 499175), 11 axises (ISM 499176), 62 other cervical vertebrae (ISM

499179). Thoracic vertebrae are characterized by rib facets. Given the large size and

demographic range of the BC sample, it has proven most practical to group the thoracic and

lumbar vertebrae under the number ISM 499183 and ISM 499184 respectively. There are a total

of 140 thoracic and 102 lumbar vertebrae. In mammals, the sacrum is the fusion of the five sacral

vertebrae and connects the vertebral column with the pelvic girdle. There are 22 peccary sacra

(ISM 499185).

Figure 25. Examples of vertebral elements from the Bat Cave peccary sample; (A) atlas, (B) axis, (C), cervical VI, (D) anterior thoracic, (E) lumbar, (F) sacrum, and (G) caudal vertebrae shown in lateral (1), dorsal (2), ventral (3), anterior (4), and posterior (5) views. Scale bars = 1cm.

Sternum, ribs, & costal cartilage—The sternum is a unit comprised of six segments

(Figure 26). A total of 46 sternebrae have been identified; there are 8 long and laterally

compressed first sternebra (ISM 499187), 6 second sternebra (ISM 499188) which have a

laterally compressed anterior end and a dorsoventrally compressed posterior end, 16 hourglass-shaped third sternebra (ISM 499189), 11 rounded fourth sternebra (ISM 499190), 4 fifth sternebra (ISM 499191), and 1 sixth sternebra (ISM 499192). 278 rib elements were identified by counting the articular ends. There are many more fragmentary rib elements which have yet to be counted. There are 54 specimens of costal cartilage from the BC sample.

Figure 26. Examples of each of the six sternal elements: first (ISM 499187.3, ISM 499188.1, ISM 499189.2, ISM 499190.4, ISM 499191.2, and ISM 499192.1) of *P. compressus* with a reconstruction of the intact sternum in lateral and ventral views. The anterior sternum is laterally compressed for the attachment of the pectoralis major muscle, while central elements bear facets on their lateral-ventral surfaces for the articulation of the costal cartilage. Scale bar = 1cm and anterior is to the left.

Appendicular Skeleton

Scapula—A total of 92 individual scapulae were catalogued; 50 left (ISM 499115) and 35 right (ISM 499114). These include nearly complete to fragmentary elements. Here, a full scapula is defined as having an intact or unbroken spine running the full length of the bone, although portions of the spinous fossae may be absent. Only four scapular specimens may be defined as such with ISM 499114.1 being the most complete among the sample, missing only a small fragment from its infraspinous fossa. This particular specimen is therefore the best subject to be used for comparative purposes. Among the scapulae, 24 specimens retain an intact glenoid fossa and neck but possess a broken scapular spine. Other elements include 11 glenoid fossae, 43 fragmented elements which lack the distal region, and 6 small elements belonging to fetal or newborn individuals (Figure 27). Other scapular elements are present, but these were so fragmentary that they were impossible to differentiate to side and therefore left uncatalogued.

Humerus—There are a total of 73 individual humeri; 38 left (ISM 499116) and 35 right (ISM 499117). Of these, seven elements were originally misidentified as femoral fragments by CMS, a mistake has been corrected as of this study. 10 of the humeri are reasonably complete with intact shafts and both epiphyses. Included among the sample are eight small specimens belonging to fetal or newborn individuals.

Radius & Ulna—In peccaries, the radius and ulna become fused by the time physical maturity is achieved (Sowls, 1998). Unfused elements can therefore be used to distinguish adult individuals from subadults and juveniles individuals. For this reason, both radius and ulna were treated as a single element for the purposes of this project. There are 83 identifiable radii/ulnae; 42 left (ISM 499118) and 41 right (ISM 499119) elements. Of these, five elements are reasonably complete retaining an unbroken shape. Another 19 elements consist of fused
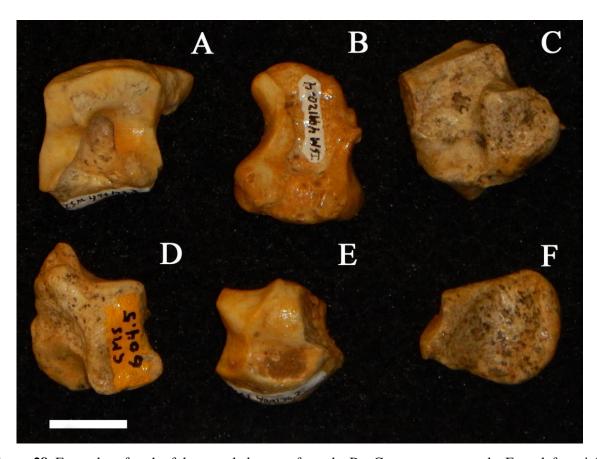
radii/ulnae which have been broken in various places. Also included within this sample are 15

unfused radii, 26 unfused ulnae, and 11 elements belonging to fetal or newborn individuals.

Figure 27. Examples of forelimb elements from the Bat Cave peccary sample; scapula ISM 499114.1 (A), humerus ISM 499117.1 (B), and radius/ulna ISM 499119.1 (C). Scale bar = 1cm.

Carpals—The carpus is comprised of eight small bones which lie between the forearm and metacarpals (Figure 28); scaphoid, lunar, cuneiform, pisiform, unciform, magnum, trapezoid, and trapezium. The following carpal elements have been identified;

- *Scaphoid*—15; 8 left (ISM 499120) and 7 right (ISM 499121).

- *Lunar*—12; 4 left (ISM 499122) and 8 right (ISM 499123).

- *Cuneiform*—11; 7 left (ISM 499124) and 4 right (ISM 499125).

- *Pisiform*—5; 4 left (ISM 499126) and 1 right (ISM 499127).

- *Unciform*—10; 3 left (ISM 499128) and 7 right (ISM 499129).

- *Magnum*—12; 7 left (ISM 499130) and 5 right (ISM 499131).

Figure 28. Examples of each of the carpal elements from the Bat Cave peccary sample. From left to right, top to bottom; lunar ISM 499122.2 (A), scaphoid ISM 499120.4 (B), unciform ISM 499128.1 (C), cuneiform ISM 499124.4 (D), magnum ISM 499130.2 (E), and pisiform ISM 499126.1 (F). Scale bar = 1cm.

Metacarpal III & IV—In peccaries, the third and fourth metacarpals do not fuse until the animal has reached a relatively advanced age. Thus, only four metacarpal pairs are fully fused forming a true cannon bone. These elements may therefore be interpreted as having come from relatively aged individuals. Other metacarpals are isolated, although many have been recognized as belonging to the same III-IV pair and were subsequently glued together. There are 9 left (ISM 499135) and 17 right (ISM 499136) metacarpal pairs are preserved. Also preserved are 15 left MC3 (ISM 499137), 12 left MC4 (ISM 499139), 17 right MC3 (ISM 499138), and 16 right MC4 (ISM 499140) isolated metacarpals which had not yet fused (Figure 29).

Figure 29. Example of a left metacarpal pair (ISM 499135.2) from the Bat Cave peccary sample. Scale bar = 1cm.

Pelvis—The two halves of the pelvis normally fuse at the symphysis, and this fusion is typically described as a single element. Among the BC material, however, no fully intact pelvises remain. At most, just the left or right halves of the pelvises remain. There are 26 left (ISM 499141) and 11 right (ISM 499142) peccary pelvis halves and fragments, making 37 in total (Figure 30).

Femur, Patella, & Tibia—There are a total of 92 individual femora; 48 (ISM 499143) left and 41 (ISM 499144) right. Of these, only one is reasonably complete retaining both epiphyses. Included among the sample are nine small specimens belonging to fetal or newborn individuals. In addition, there are 13 individual patella; 4 left (ISM 499167) and 9 right (ISM 499168). A total of 49 individual femora have also been identified; 21 (ISM 499145) left and 28 (ISM 499146) right. Of these, five are reasonably complete retaining both epiphyses.

Fibula—In peccaries, the fibula is a thin rod of bone which articulates with the proximal tibia and the calcaneus. When differentiating the left and right fibulae from each other, the distal articular end is the most useful. There are 18 left (ISM 499169) and 22 right (ISM 499170) distal fibulae. There are also 163 fibulae shaft fragments of various sizes which could not be confidently differentiated, and thus were left uncatalogued.

Figure 30. Examples of hindlimb elements from the Bat Cave peccary sample. From top to bottom; pelvis ISM 499142.1 (A), femur ISM 499144.1 (B), tibia ISM 499145.1 (C), and fibula ISM 499170.1 (D). Scale bar = 1cm.

Tarsals— The tarsus is comprised of six small bones which lie between the tibia and metatarsals (Figure 31): calcaneus, astragalus, navicular, cuboid, ectocuneiform, mesocuneiform, and entocuneiform. The following tarsal elements have been identified;

- *Calcaneus*—57; 30 left (ISM 499147) and 27 right (ISM 499148)

- *Astragalus*—52; 31 left (ISM 499149) and 21 right (ISM 499150).

- *Navicular*—17; 9 left (ISM 499151) and 8 right (ISM 499152).

- *Cuboid*—17; 7 left (ISM 499153) and 10 right (ISM 499154).

- *Ectocuneiform*—4; 1 left (ISM 499155) and 3 right (ISM 499156).

Figure 31. Examples of each of the tarsal elements from the Bat Cave peccary sample. From left to right, top to bottom; navicular ISM 499151.5 (A), astragalus ISM 499149.1 (B), ectocuneiform ISM 499155.1 (C), cuboid ISM 499153.4 (D), and calcaneus ISM 499147.2 (E). Scale bar = 1cm.

Metatarsal III & IV—As in MC3, MT3 is distinguishable from MT4 in having a proximal articular facet that is much broader and appears concave in anterior view. In peccaries, the MT3 and MT4 fuse together to form a single cannon bone by adulthood. Among the Bat Cave sample, 21 left (ISM 499161) and 17 right (ISM 499162) cannon bones are preserved. There are also 4 left MT3 (ISM 499163), 8 left MT4 (ISM 499165), 4 right MT3 (ISM 499164), and 5 right MT4 (ISM 499166) isolated juvenile metatarsals which had not yet fused (Figure 32).

Figure 32. Example of a left metatarsal pair (ISM 499161.3) from the Bat Cave peccary sample. Scale bar = 1cm

Phalanx—Peccaries, like all artiodactyls, have a stance in which the body weight is distributed through digit III and digit IV. As a result, many have undergone a reduction or complete loss of the lateral digits. Peccaries have hypertrophied digit III and IV with cloven hooves with digit II and/or digit V being reduced to shortened dewclaws which never contact the ground. Digit I is always absent. *P. compressus* has undergone further reduction of the digits becoming fully didactyl. For the BC sample, the phalanxes were unable to be differentiated to digit III, digit IV, manual, or pedal. The extent to which differentiation was able to be accurately carried out was to left and right digit. There are 164 proximal, 111 medial, and 87 distal phalanges.

CHAPTER 5

RESULTS AND OBSERVATIONS

<u>Bone Quality and Preservation</u>

Observations point to the Bat Cave site being an excellent environment for fossil preservation. All bones examined exhibit stage 1 weathering (Behrensmeyer 1978) with no evidence of bleaching, indicating that the sample was never exposed to extreme temperature fluctuations or direct sunlight which would accelerate the weathering process (Behrensmeyer 1978). The structural integrity of the bones has been substantially weakened due to leaching with many skeletal elements becoming very brittle with a consistency similar to that of porcelain. Otherwise, the bones retain their original shape and surface morphology with no deformation or warping, possibly due to the relatively young age of the site and relative lack of overlying sedimentation. Although the outer surface of most of the bones are stained by various minerals, the internal structure of recently broken elements is bright white in color, similar to the fresh condition. Overall, the condition of the bones suggests that they have remained in a relatively stable environment since the time of deposition.

<u>Skeletal Part Representation</u>

In the present study, about 2,700 elements out of the 6,300 noted by Hawksley et al. (1973) were complete enough for identification and all of these were catalogued with ISM numbers except for the ribs, of which 278 were counted based on the presence of the articular facet. Many other unidentifiable rib, cranial, and limb bone fragments remain to be examined. The following is a summary of the overall representation of particular skeletal elements within the BC peccary sample.

Dental Representation— Of all the isolated dentition, the permanent canines are by far the most numerous. This may be partly due to these teeth being the largest teeth in the jaws. The permanent incisors, which could not be differentiated to I1 or I2, are the second most abundant dental elements represented in the BC peccary sample. Isolated post-canine dentition are extremely rare, particularly the smaller premolars and first molars (Figure 33A). The deciduous dentition, although being far less abundant overall, mirror the permanent dentition in terms of relative abundance; the deciduous canines are the most numerous by a large margin, followed by the incisors, and with the post-canine dentition being much scarcer, numbering less than 10 per side per element (Figure 34A). When cranial and mandibular elements are factored into the tooth count, this basic pattern slightly adjusted with the addition of the emplaced post-canine dentition nearly doubling the relative abundance of these elements, although they are still not as numerous as the canines or incisors (Figure 33B, 34B).

Figure 33. Total representation of permanent dentition from the Bat Cave peccary sample; (top) isolated dentition only, (bottom) isolated and emplaced dentition.

Figure 34. Total representation of deciduous dentition from the Bat Cave peccary sample; (top) isolated dentition only, (bottom) isolated and emplaced dentition.

Postcranial Representation— The larger, proximal limb elements are among the most

numerous of all the postcranial elements, surpassed only by the vertebrae and phalanges. An

interesting inverse exists in the representation of metapodials of the forelimbs and hindlimbs; the

number of paired metacarpals is far fewer than the number of paired metatarsals, whereas there

the number of isolated metacarpals is much greater than that of isolated metatarsals. This

difference reflects the rate of fusion among these elements. In peccaries, the metatarsals tend to

fuse relatively early in life of the animal forming a single cannon bone (Sowls 1998). In contrast,

the metacarpals generally remain as separate elements and only fuse once the animal has reached

an advanced age (Sowls 1998). The smallest bones, particularly those which comprise the

carpals and tarsals, are represented in very low numbers; the scaphoid, lunar, cuneiform,

pisiform, unciform, magnum, navicular, and cuboid all being represented by 10 or fewer

individual elements per side. By contrast, the largest of the tarsal bones, the calcaneus and

astragalus, are much better represented in the sample with a combined 61 calcanei and 52

astragali (Figure 35).

Figure 35. Abundance of all paired postcranial elements from the BC peccary sample.

Collection bias—As noted above, many of the smaller elements are severely lacking in

number, particularly the smaller carpal and tarsal elements. The reason for this scarcity may be,

in part, due to collection bias during the original excavations of Bat Cave. During these excavations, bones were found mostly by surface collecting with some picking and screenwashing (Hawksley et al. 1973). In an interview with Blaine Schubert, Hawksley stated that much of the excavation work was performed using tools such as screwdrivers. The bones were then placed in simple containers, such as coffee cans, which were then packed with sediment for stability before being transported to the surface (Schubert, personal communication). This collection method generally favors the larger skeletal elements over those smaller ones.

Preparation bias—1435 of 2652 (54.11%) of the elements examined had been previously catalogued by CMS. During the cataloguing process, the original preparators of the BC sample appear to have shown a preference for those elements which were relatively large with broad, flat surfaces. Another factor appears to have been the potential of particular elements to be utilized for MNI calculation. More numerous elements such as canines, phalanges, calcanei, astragali, and metatapodials are among the most frequently catalogued with each having a frequency of over 90% bearing the CMS label. In particular, 98.51% of permanent and 98.15% of deciduous canines bear CMS catalogue numbers. Other, larger elements within the sample were catalogued ranging in frequency from 89.47% for atlases to 41.3% for scapulae. A low number of mandibles, tibiae, radii/ulnae, and sacrums were cataloged prior to the present study ranging from 13.25% for radii/ulnae to 7.89% for dentaries. The remaining elements within the sample, mostly the smaller, isolated dental elements, were not catalogued prior to the present study.

Minimum Number of Individuals

The original MNI for the Bat Cave *P. compressus* reported by Hawksley et al (1973) was determined to be 98 based on 77 lower left canines and 21 upper left deciduous canines. The use

of the canines, the most abundant of all the dental elements, is the most effective means in determining the MNI of the BC peccary populations. However, the original study failed to elaborate on how Hawksley et al. (1973) differentiated the canines and some specimens have been found to be erroneously identified during the cataloguing process. For the present study, comparative morphological observations of the canines were carried out (summarized in Chapter 4) and the MNI was reevaluated based on these criteria.

Figure 36. Total number of isolated and emplaced canines from the BC peccary sample.

A total of 200 isolated permanent are documented; 56 lower left, 53 lower right, 39 upper left, and 52 upper right. With the inclusion of the rooted canines produces a total of 228 elements; 70 lower left, 64 lower right, 41 upper left, and 53 upper right. A total of 54 isolated dC1 are also documented; 11 lower left, 9 lower right, 13 upper left, and 21 upper right (Figure 36). The present study has demonstrated that lower left C1 remains the most numerous dental element despite having decreased from the estimation achieved by Hawksley et al. (1973). The number of upper right dC1 reported in the original report is determined to have been correct.

Therefore, a new MNI of 91 individuals may be obtained based on 70 lower left C1 and 21 upper left dC1. It should be noted, however, that a considerable number peccaries from BC are juveniles between the ages of 9 to 12 months old. At this age, peccaries may possess both permanent and deciduous canines although the latter are in the process of being lost. This fact raises a problem with the inclusion of both canines in the MNI calculation as it is possible that a single animal may have been counted twice. Therefore, a more conservative MNI estimate of 70 individuals based solely on the lower left canines is favored. This estimate may change after additional excavations are performed at the BC site.

Associated Materials

The following groups of elements are those which are believed to represent part of a single individual based on a number of elements including staining and articulation (Figure 37).

A. *ISM 499097.14 & ISM 499205.46*—An anterior mandible fragment and an isolated right lower canine. The mandible has the left canine in place but the right canine alveolus is empty. The isolated tooth closely matches the exiting tooth in size, age, and color and fits into the empty space.

B. *ISM 499097.6 & ISM 499204.38*—A mandible which retains most of the right dentary and an isolated left lower canine which matches it in coloration and fits perfectly within the alveolus.

C. *ISM 499097.10 & ISM 499205.44*—An anterior mandible fragment with an open right canine alveolus and an isolated right lower canine displaying the same staining along posterior surface.

D. *ISM 499098.29 & ISM 499099.1*—Left and right dentaries, both of which share the same length from the dP2 alveoli to the posterior M2 alveoli and share the same coloration.

Although ISM 499098.29 has lost its dentition, the dentition was clearly in the same stage of eruption as its counterpart based on the remaining M1 and M2 roots and alveolar depth. ISM 499098.29 appears to have been treated with a preservative agent by CMS based on its shiny appearance whereas ISM 499099.1 was not prior to this study.

E. *ISM 499097.15, ISM 499098.1, & ISM 499099.3*—Three mandibular fragments belonging to a young juvenile around one year of age. This assessment is based on all three elements having the same color staining and the dentition on the left and right toothrows are at the same stage of eruption and wear.

F. ISM 499097.16 & ISM 499098.2—An anterior mandible fragment with part of the left dentary of a yearling. Both elements appear to have been plastered together at one point and share the same speckled staining pattern.

G. *ISM 499116.10 & ISM 499118.3*—A left humerus, radius, and ulna which appear to be from the same individual based on their similar coloration and perfect articulation.

H. *ISM 499116.1, ISM 499118.1, ISM 499135.1, ISM 499147.1, ISM 499161.2*—A left humerus, radius, ulna, metacarpal pair, metatarsal pair, calcaneus, and medial phalanx. All are darker in color than other, comparable elements from the BC peccary sample and are also noticeably heavier. This may, in part, be due to the concretion which is still adhered to some of them. It appears that, while trying to remove this sediment, excavators and preparators at CMS inadvertently fractured the larger bones. None show signs of carnivore modification, suggesting that the individual was undisturbed after death and was relatively quickly covered over by sediment.

I. *ISM 499114.1, ISM 499119.1, ISM 499175.2, & ISM 499176.3*—Right scapula, radius, ulna, atlas, and axis. No evidence of predation is visible. White coloration suggests that

these elements remained at the surface after the soft tissue was removed until their recovery. Rodents appear to gnaw on some of the bones.

J. *ISM 499100.1 & ISM 499105.6*—A skull and isolated jugal which fits in place. Same color and staining.

Figure 37. Examples of elemental collections which may be representative of single individuals. Letters correspond to the above text. Scale bars = 1cm.

<u>Pathologies</u>

The following are elements of the BC peccary sample which exhibit bone pathology (Figure 38).

A. *ISM 499097.8*—A juvenile mandible which exhibits prominent swelling of the post-symphysis left dentary. The potential cause of this pathology has not yet been confirmed, but it is possibly the result of an infection within the bone.

B. *ISM 499122.4*—A left lunar which is highly deformed, possibly due to severe arthritis.

C. *ISM 499141.17*—A left pelvis with rugose, deformed bone surrounding the remaining acetabulum.

Figure 38. All elements from the Bat Cave peccary sample with bone pathology shown alongside comparable, healthy elements. (A) A left dentary with noticeable swelling possibly due to bone infection. (B) Highly deformed, possibly arthritic left lunar. (C) Left pelvic fragment with arthritic bone growth around the acetabulum. Scale bar = 1cm.

Sexual Dimorphism—The M3 measurements (Figure 39) failed to identify any notable

bimodality among the BC peccaries, thus confirming Wright's (1993) conclusion that *P.*

compressus displayed minimal sexual dimorphism in terms of size. Notable bimodality may be

noted in the *P. cumberlandensis* from the Leisey Shell Pit 1A site, with larger specimens inferred

to be males and the smaller specimens inferred to be females (Wright 1993). The Coleman II *P.*

cumberlandensis, however, are shown to plot well above the individuals recorded from Leisey

Shell Pit 1A. Such separation between two populations within a narrow geographic range is

somewhat unusual and may be attributable to temporal distinction or perhaps the presence of two

taxa.

Figure 39. Scatter plot showing the M3 measurements of the Bat Cave *Platygonus compressus* (orange circles) as compared to the Irvingtonian species *P. cumberlandensis* from Coleman II, Florida (red squares) and Leisey Shell Pit 1A, Florida (green triangles).

To determine sexual dimorphism among *P. compressus* a different approach is required. The mandibular keel has been described by Wagner (1903) who believed it to be a sexually dimorphic character, with those of males being particularly "strong and protuberant". Although this hypothesis is feasible, no comparative analysis has ever been performed to test this. Among the Bat Cave sample, 16 mandibles are preserved. One skull, 499097.2, which we hypothesize to be an older male based on its thickened canines, worn molars, and heavy muscle scarring, bears the most prominent mandibular keel. From the 8 juvenile mandibles in the sample, it appears that the keel begins as a rudimentary ridge which increases in prominence with age. A larger collection of intact mandibles is needed to test this hypothesis.

Age Demographics—On initial examination, it is readily evident that every age group from fetuses and newborn infants to elderly adult individuals are represented in the BC sample. On closer examination, the maturation of individuals and age at the time-of-death could be tracked using the eruption sequence as plotted by Kirkpatrick and Sowls (1962) and occlusial wear patterns. Particularly apparent among the younger individuals, clearly-definable age groups which show no observable overlap with one another could be established, each group being developmentally separated from each other by approximately 9 to 12 months based on Kirkpatrick and Sowls (1962). Similarly, 4 marked age groups can be observed among the collective limb elements based on size and fusion of the epiphyses (Figure 40). However, the dentition is recognized as the most useful part of the mammalian anatomy for the purposes of determining age (Severinghaus 1949; Spinage 1973; Skogland 1988; Kaiser et al. 2009). Using the dentition, 10 distinct age groupings were established and defined below (Figure 41, 42).

Figure 40. Examples of peccary humeri from Bat Cave which represent three non-overlapping age designations. From left to right: a neonate (ISM 499117.34), yearling (ISM 499117.4), and full grown specimen (ISM 499117.1) of unknown age. Scale bar = 1cm.

- *Newborn*—Only 3 specimens are attributable to this age group; ISM 499098.36, ISM

  499098.37, and ISM 499099.39. All appear to be within their first month of life, no older

  than 3 weeks, as indicated by their extreme small size and the erupting dP3. ISM

  499098.37 appears to be slightly older than ISM 499098.36 due to its larger size and

  more advanced state of eruption.

- *Year 1*—The lower C1 is only partially erupted and, as an isolated specimen, is hollow

  and very brittle. The dC1 alveoli are usually still present, but the teeth themselves may be

  absent. The dP4 is present with noticeable wear facets on its cusps. M1 is fully-erupted

76

and exhibits minor wear facets on the labial cusps. M2 is just beginning to erupt and may not yet have begun to emerge above the gumline. The muscle depressions of the angle are weakly-developed. Where the posterior portion of the lower jaw remains intact, the M3 bud may be visible within as is the case for ISM 499099.1. Based on these observations, 12 individuals have been placed within this age group.

- *Year 2*—The permanent C1, M1, and M2 have all fully erupted. M3 is just beginning to erupt and may not yet have begun to emerge above the gumline. The dP4 is still present, but has been worn smooth and is weakly rooted in the alveoli as it is gradually being replaced by the underlying P4. Similarly, the remaining deciduous premolars still remain present although the permanent premolars may be visible within the crypt where the anterior dentary is damaged, as is the case for ISM 499097.6, ISM 499097.8, ISM 499097.9, ISM 499097.10, ISM 499098.8, and ISM 499099.5. The M1 exhibits noticeable wear facets on the apicies. The M2 cusps retain intact apicies with no evidence of premortum pitting. The angle exhibits more prominent muscle depressions and greater depth than that of the previous age group, with some lateral flaring of the ventral edge beginning to take place. Based on these observations, 12 individuals have been placed within this age group.

- *Year 3*—P2 and M3 have now fully erupted, although the posterior base of the latter may still lie partially in the crypt. The lingual cusps of the M1 have been worn so that they form, level transverse ridges with a labial slope. Dentine is now visible. M2 now exhibits a similar to that of the year-2 M1 with noticeable wear facets on the apicies, particularly on the labial side. Any wear on the M3 is almost indistinguishable without magnification, particularly the hypoconulid. The lower C1, when present, shows minimal signs of

occlusion with the upper C1. Further deepening and thickening of the angle has taken place. Based on these observations, 12 individuals have been placed within this age group.

- *Year 4*—The M1 ridges are still distinguishable but have been worn down significantly. M2 now exhibits wear similar to that of the year-3 M1, forming transverse ridges with a labial slope. The M3 cusps have begun to wear but retain intact apicies with no evidence of premortum pitting. Based on these observations, 15 individuals have been attributed to this age group.

- *Year 5*—Deterioration of the M1 has progressed so that the anterior and posterior ridges have been worn almost smooth. The anterior and posterior M2 have been worn down further and some pitting may be evident. The M3 apicies have been worn considerably but are still distinguishable. Based on these observations, 9 individuals have been attributed to this age group.

- *Year 6*—M1 has now been worn almost completely smooth although there is still some separation between the anterior and posterior cusps. The anterior portion of M1 is worn down to the same level as the posterior edge of the P4 forming a single, continuous surface. M2 is now in a similar state of wear as the year-5 M1 with its anterior and posterior cusps still forming ridges but bearing pits which expose the dentine. The apicies of the M3 cusps have been worn so that an almost level ridge is formed. The hypoconulid has worn so that a concave depression now exists between it and the posterior cusps. Based on these observations, 7 individuals have been attributed to this age group.

- *Year 7*—M1 is now worn completely smooth with no discernable separation between the anterior and posterior cusps. M2 is almost worn smooth with some distinction between

78

the anterior and posterior cusps. The individual cusps of the M3 are still notable but have been worn down with heavy pitting. Based on these observations, 5 individuals have been attributed to this age group.

- *Year 8*—Based on two M3s bearing three distinct, smoothed basins in the former areas of the anterior cusps, posterior cusps, and hypoconulid, the latter having now been worn to the gumline on its posterior edge. M1 and M2 are worn smooth. A single M2 which has been worn almost completely smooth may also be attributable to this age group.

- *Year 9*—A single individual has been placed in this group based on a left lower M3 that has become completely worn smooth and dished out with no traces of individual cusps.

Figure 41. Ontogenic changes in the lower dentition of the Bat Cave *P. compressus*. Toothrows shown in right-lateral view. Scale bar = 1cm.

Figure 42. Age demographics of the Bat Cave peccary population.

Carnivore Damage

Most of the BC peccary bones display damage patterns that are identical to that of the Bays Mountain Park deer material, and both samples match the descriptions the detailed descriptions reported by Haynes (1980; 1982; 1983a; 1983b) regarding wolf bite damage on the bones of mid-sized ungulates. This confirms that the BC bones were processed by large canids, the most likely culprit being the dire wolf, the second most abundant vertebrate from the site. In association, linear spiral fractures are more common and indicate that predator utilization occurred soon after death and while the carcasses were relatively fresh, as opposed to a more stepped or jagged breakage which is more likely to occur if the bone was exposed to air for an extended period of time (Haynes 1982). The following is a summary of predator modifications observed among the BC material.

Limb Bones—Compared to the rest of the BC peccary material, predator modification is most frequent among the upper limb segments with at least 66.25% of scapula, 89.23% of

humeri, 73.61% of radii/ulnae, 89.19% of pelvises, 89.33% of femora, and 70.83% of tibiae

bearing the typical bite impressions and breakage patterns typical of wolf predation (Figure 43)

which ranges from minor (stage 1), moderate (stage 2), to extreme (stage 3). However, it must be

noted that predator modification could not be confirmed in a number of elements due to the

presence of secondary taphonomic forces such as rodent gnawing or trampling, which either

obscure or remove any evidence of bite damage that may have been present on the original bone.

These, along with all unfused epiphyses which lack diagnostic tooth impressions, were placed in

a separate category referred to as "undeterminable". About 33% of scapulae, 9% of humeri, 18%

of radii/ulnae, 8% of pelvises, 17% of femora, and 27% of tibiae fall under this distinction. The

overall severity of predator damage appears to decrease from the proximal segments toward the

distal segments (Figure 44), which also matches observations made by Haynes (1982; 1983) and

Hill (1989).

Figure 43. Frequency of predator-modified limb elements from the Bat Cave peccary sample.

Figure 44. Pie charts depicting the extent of predator modification observed among each respective collection of limb elements.

The scapulae and pelvises together exhibit greater proportions of stage 2 to stage 3 damage (Figure 45). Where the distal end is present, most of the modified scapulae exhibit puncture wounds to the scapular neck and fraying of the glenoid fossa. Others possess spinous

fossae with considerable portions having been removed. At minimum, all of the predator-modified BC peccary pelvises are broken at the symphysis and show removal of the anterior ilium. This particular element, however, is consistently one of the most heavily damaged of all the limb elements with only a single specimen (ISM 499142.1) being mostly complete with an intact obturator foramen and only the anterior rim of the ilium and posterior ischium being absent, and the remaining elements showing moderate to extreme damage. Among these are 16 elements which lack large portions of the ilium and ischium and 6 elements which consist only of the acetabulum and surrounding bone.

Figure 45. Examples of wolf-damaged scapulae (A) and pelvises (B) from the Bays Mountain Park deer comparative sample (ETVP 489) and the Bat Cave peccary sample (ISM 499114, ISM 499115, ISM 499141, and ISM 499142). In each case, the modern deer elements are on the left, and the fossil peccary material is on the right. Scale bar = 1cm.

In all documented cases of predation, the upper portions of the limbs are generally attacked first because of the larger muscle masses that are concentrated there (Haynes 1982), and the (Figure 46). The femora often show the most extensive damage compared to any of the other

long bones. Where the proximal femur is present, the greater trochanter is always absent and

gouge marks left by teeth is present on the femoral head when it is present. Frequently, both the

proximal and distal articular ends have been bitten off, leaving behind a hollow shaft. In other

instances, the proximal portion is eaten away to varying extents, leaving behind the distal

articular end which often bears quite large puncturing and shearing tooth impressions. The

humeri place second in terms of severity of predator modification, with the most frequent

damage being the destruction of the proximal articular surface and shaft to varying extents.

Figure 46. Examples of wolf-damaged humeri (A) and femora (B) from the Bays Mountain Park deer comparative sample (ETVP 489) and the Bat Cave peccary sample (ISM 499116, and ISM 499117, ISM 499143, ISM 499144). In each case, the modern deer elements are on the left, and the fossil peccary material is on the right. Scale bar = 1cm.

Damage to the medial limb elements tends to be less severe and relegated to the proximal

halves of these elements. Among the BC peccary sample, the forearms and tibiae appear to be

very comparable in terms of the severity of predator damage (Figure 47). The most frequent

damage observed among the ulnae is the puncturing or complete removal of the olecranon

process and the removal of the proximal end is the most common damage to the radius. Damage

to the tibiae typically consists of removal of the proximal condyles or tibial crest, or the absence of entire proximal portion.

Figure 47. Examples of wolf-damaged radii/ulnae (A) and tibiae (B) from the Bays Mountain Park deer comparative sample (ETVP 489) and the Bat Cave peccary sample (ISM 499118, ISM 499119, ISM 499145, and ISM 499146). In each case, the modern deer elements are on the left, and the fossil peccary material is on the right. Scale bar = 1cm.

Manus & Pes—Among the carpals and tarsals, the calcaneus is the most frequently and extensively damaged during carnivore feeding with 39.34% of elements showing signs of predator modification, the most frequent damage being the puncturing or complete removal of the distal portion, especially the epiphyseal end. Scratches and puncture damage are also commonly observed on the lateral and medial surfaces, and tooth abrasion may be present the proximal articular facets. 3.85% of astragali, the second most abundant carpal/tarsal elements after the calcanei, exhibit predator modification ranging form of small punctures, scratches, and cracks, to one particular specimen (ISM 499149.31) which appears to have been picked up by a predator and chewed for a period of time. The remaining carpals and tarsals show no signs of

damage apart from a single left scaphoid (ISM 499120.2). Predator modification is rare among the metapodials although it appears to be more frequent among the metatarsals; 12.9% of metatarsals show signs of predator modification as opposed to just 1.59% of metacarpals. Among the 383 phalanges, only two elements (ISM 499172.30 and ISM 499173.50) show damage that may be attributable to predator modification.

Skull & Mandible—Among the skull material, only the frontal fragments ISM 499103.2 and ISM 499103.3 bear surface gouge marks that may be directly attributable to predator feeding (Figure 48). All other cranial specimens are highly fragmented and do not bear such marks. However, it is noted by Haynes (1982) that wolves are capable of destroying much of the skull of a mid-sized ungulate, often leaving behind nothing but the toothrows. Although other forces may have acted upon the remains (see below), it cannot be ruled out that wolves were at least partially responsible for the overall lack of more complete cranial material for the BC peccary sample. When subjected to repeated biting by a large predator, the bones of the skull may be expected to shatter relatively more easily than the limb bones due to their relatively thin walls and general lack of internal buttressing, as opposed to the limb bones whose shafts require greater force to break and often retain their shape although sustaining obvious gouge and puncture wounds on the cancellous end regions.

Figure 48. Two *Platygonus compressus* frontal bone fragments (ISM 499103.2 & ISM 499103.3) which bare gouge marks that may be attributable to predator utilization. Scale bar = 1cm.

In contrast to the skulls, mandibular material is relatively well represented, although the majority of these demonstrate varying degrees of breakage that are consistent with canid utilization (Figure 49). When utilization is minimal, the angle of one or both dentaries' may be broken off once the throat has been opened and the tongue consumed (Haynes 1982). The mandibles may also be broken apart at or posterior to the symphysis or the lower borders of the dentary may be broken off (Haynes 1982). When the carcass is utilized particularly heavily, often the only parts of the mandible that remain are the lower tooth rows or isolated teeth (Haynes 1982; Munson 2013).

Figure 49. Examples of predator-modified mandibular elements of *Platygonus compressus* from Bat Cave.

Axial skeleton—During predator feeding, the relatively soft bones of the sternum are usually fully consumed (Haynes 1982) and this part of the skeleton is noticeably rare among the BC sample. Where it is present, certain sternal elements bear clear puncture wounds and breakage typical of canid feeding (Figure 50A, B). Similarly, the costal cartilage is usually consumed by feeding wolves, although some of the more ossified elements that remain bear similar puncture damage to that noted for the sternebrae (Figure 50C). Although the ribs were

not analyzed in detail, the majority of those examined have absent sternal ends, another pattern which is typical of wolf feeding (Haynes 1982).

Figure 50. Examples of predator-modified sternebrae (A & B) and costal cartilage (C) from the Bat Cave peccary sample. Scale bar = 1cm.

Vertebae—135 of 334 (40.42%) catalogued pre-sacral vertebrae bear one or more of the following signs of predator modification; visible puncture marks or tooth depressions, a sheared centrum, damage to one or both articular surfaces, broken neural spines, complete removal of the neural arch, and complete removal of the centrum (Figure 51, 52). In general, the cervical, thoracic, and lumbar vertebrae are comparable in terms of the overall frequency of particular damage patterns although the lumbar vertebrae appear to be the least frequently modified, possibly due to their larger size (Figure 53). Across all the pre-sacral vertebrae, damage to the neural spine is the most frequent damage observed followed closely by the occurrence of bitemarks in the form of pushed-in cortical bone. The peccary sacrums show particularly abundant signs of canid utilization, perhaps due to their articulation with the pelvis.

Figure 51. Column chart depicting the frequency at which specific damage patterns occur among predator-modified vertebral elements from the Bat Cave peccary sample.

Figure 52. Examples of predator-modified vertebrae. The left element is a white-tailed deer vertebra from the Bays Mountain Park (ETVP 489) comparative sample and the remaining two element are peccary vertebrae from the Bat Cave sample. Scale bar = 1cm.

Figure 53. Column chart depicting the frequency of predator-modified vertebral elements from the Bat Cave peccary sample.

Other Predators—Although dire wolf predation appears to be the primary agent for the damage inflicted on the BC peccary bones, closer examination of several of the catalogued specimens reveals shallower tooth impressions which are similar to those left by the wolves. These additional marks are, however, much smaller and fail to inflict any more severe damage to the bone. This implies that a smaller predator was present and was actively exploiting the peccary carcasses, perhaps after the wolves finished feeding. Based on the size of the bite impressions and the BC faunal assessment reported by Hawksley et al. (1973).

Other Biotic Taphanomic Factors

Rodent Modification—Rodent modification is frequently observed throughout the BC sample, varying from relatively minor and unnoticeable to extensive to the point at which the element has become highly deformed (Figure 54). On the limb bones, rodent gnawing is most frequently found in association with predator damage. Gnaw marks are concentrated around the edges of bone breakages. Sometimes the internal trabecular portion of a disembodied epiphysis

may be scooped out. Damage to skull and mandibular fragments is frequent, and is generally

concentrated along the toothrows. Often, this is so extensive that the underlying dental roots are

left exposed and partially removed. Among isolated teeth, rodent modification is frequently

evident on the dentine, whereas the harder enamel is left undamaged. In several instances, most

of the dentine portion of the tooth was removed, leaving behind only the tooth crown. Overall,

rodent modification appears to be most frequently encountered among bones which bear

thickened cortical tissue.

Figure 54. Examples of peccary humeri from Bat Cave (ISM 499116.10, ISM 499117.8, and ISM 499117.10) which bare varying degrees of rodent modification. Scale bar = 1cm.

Invertebrate Modification—A few remains from the BC peccary sample exhibit evidence of invertebrate utilization. These traces consist of shallow, circular pits and removal of the bone surface (Figure 55). Potential examples of invertebrate modification occur on mandibular elements ISM 499097.1 and ISM 499097.7, tibia ISM 499146.7, and radius/ulna ISM 499119.4, the latter two also appearing to be in a slightly more advanced state of weathering compared to the other tibiae, perhaps indicating that these spent more time at the surface and/or near the cave entrance where weathering processes are more extreme.

Figure 55. Examples of extant white-tailed deer (left; ETVP ##) and Bat Cave peccary (right; ISM 499119.4) limb elements which bare traces of invertebrate modification best attributable to dermestid beetles.

Trampling—The highly fragmented nature of many elements from the BC sample, many of which lack any discernable predator modification, may indicate that these bones tread upon, as could be expected if the native peccaries were utilizing the site regularly. Furthermore, Hawksley et al. (1973) noted that most of the larger elements were collected from the edges of the cave passage and smaller, more fragmentary remaining and isolated teeth were collected from the center. In a den or other such confined setting, it may be expected for debris to be actively or passively pushed out of the more heavily trafficked areas and toward the relatively less utilized

93

periphery (Haynes 1983). Smaller debris, particularly thin-walled skeletal elements, are more

likely to be broken up or pushed into by repeated trampling over a period of time with others

simply being pushed into the substrate (Haynes 1983).

CHAPTER 6

DISCUSSION

Behavioral Interpretations of the Bat Cave *Platygonus compressus*

Seasonal Behaviors—Previous authors have presented evidence of seasonal behavioral patterns in extinct mammal populations based on tooth eruption and wear patterns (e.g. Jefferson and Goldin 1989). However, the present study marks the first time this principle was applied to a fossil peccary population. Extant peccaries occur in close-knit herds which adhere to a set home range and territory over the course of many generations (Taber et al. 1993). Within this area, they will habitually travel to and utilize different locations at regular intervals and at particular times of the year to correspond with the availability of resources (Bigler 1974). Furthermore, the communal utilization of caves as a means of withstanding temperature extremes is well documented among extant taxa (Bissonette 1978; Schubert and Mead 2012). Phylogenetic bracketing (Witmer 1995) and mass accumulations of *P. compressus* at numerous fossil localities throughout North America (Hoare et al. 1964; Slaughter 1966; Davis 1969; Guilday et al. 1971; Hawksley et al. 1973; Wilson et al. 1975; Schubert and Mead 2012) suggests that these behaviors were true of this taxon as well.

The distinct age groupings reported from the BC peccary population, each spaced temporally by about 9 to 12 months, strongly suggests that 1) the cave site was utilized annually and on a seasonal basis, most likely during the winter months when such behavior would be most advantageous and 2) that reproduction for this taxon, at least within the BC locality, was a seasonal occurrence. Aseasonal reproduction is typical among ungulate populations occurring in the tropics and subtropics, which live under constant to near-constant warm temperatures,

precipitation, and food availability (Rutberg 1987; Gottdenker and Bodmer 1998). Under these conditions, breeding and birthing is often a year round occurrence with peaks at certain months (Rutberg 1987; Ramos et al. 2014). If such a reproductive strategy was utilized among the BC peccary population, we would expect intermediate growth stages between the age groupings identified in the present study.

Seasonal reproduction is a more practical strategy among ungulates occurring in areas of high seasonality, which are subjected to annual fluctuations in temperature, precipitation, and food availability. Cold, wet, and windy weather, combined with food scarcity and the reduced ability of lactating females to produce milk, have been shown to reduce the probability of survival for the newborns of many temperate and subarctic species (Slee 1971; Nowosad 1975; Dunbar 1980; Rutberg 1987; Cornell et al. 1998). Conception and birthing must therefore be synchronized so that offspring are born during periods where resources are more readily available and conditions are more favorable; thus ensuring that the young-of-the-year are able to gain large body size by autumn to increase the likelihood of winter survivorship (Dauphine and McClure 1974; Bunnell 1980; Clutton-Brock et al. 1982; Rutberg 1987; Cornell et al. 1998). This is demonstrated among the BC peccary population, for which the number of fetal and neonate individuals are extremely rare; whereas the number of yearling specimens being considerably more abundant.

The relative lack of very young juveniles under the age of nine months in the BC peccary population may suggest that these animals were not giving birth at the site under normal circumstances. Following the hypothesis that the local peccaries used the BC site as a winter shelter, it can be inferred that these animals would give birth in early to mid-spring when temperatures were more favorable and vegetation was in abundance. Extant herbivores which

live in highly seasonal environments follow the same general reproductive pattern; breeding

taking place during early- to mid-fall, gestation throughout the winter, and birthing taking place

from mid- to late-spring (Slee 1971; Dauphine and McClure 1974; Bunnell 1980; Dunbar 1980;

Rutberg 1987; Owen-Smith 1990; Cornell et al. 1998). The few late-term fetuses and infants

identified from the BC peccary sample may then represent early births, or perhaps indicate

occasional fluctuations in the annual climate which caused the animals to remain at the site

longer than usual.

Age Structure & Longevity—The age demographic obtained from the examination of the

BC peccary population shows that the composition of animals from one to four years of age was

relatively stable, with the number of individuals age five to nine years old gradually declining.

This trend matches demographic studies of extant peccaries (Ramos et al. 2014). As one may

expect, relatively young and healthy animals form the bulk of the population with older

individuals steadily dying off due to predation or complications associated with advanced age. In

mammals, dental wear is a major factor limiting longevity, with death occurring from the

inability to feed effectively and procure adequate nutrients (Skogland 1988; Kaiser et al 2009;

Ozaki 2009). Along with other ailments associated with old age such as arthritis, progressive

tooth wear makes older animals more likely to suffer during periods of food shortage as they are

less able to compete with their younger counterparts (Skogland 1988). For the BC peccary

population, this helps explain the downward trend of older adults beyond the age of four. The

maximum life expectancy for extant peccaries in the wild is about ten years with most animals

dying prior to this due to predation or other natural causes (Grzimek 1990; Owen-Smith 1990;

Cornell et al. 1998).

Predation & Other Biotic Taphonomic Forces

Causes of Bone Accumulation—Despite the high frequency of predator modification attributed to *Canis dirus*, the fact that *P. compressus* is the only ungulate to be recovered from the BC site (Hawksley et al. 1973) suggests that the site does not represent a wolf den, but rather a site in which peccaries would gather periodically and occasionally died. In a typical predator den or cache site, the disarticulated remains of multiple prey species are represented, often alongside the remains of multiple articulated remains of the predators which accumulated them over a period of time (Maguire et al. 1980; Hill 1989; Cruz-Uribe 1991; Mondini 2002; Pickering et al. 2004). The vast abundance of *P. compressus* remains, some of which have remained partially articulated, together with the scant remains of six dire wolves, two coyotes, and one red fox (Hawksley et al. 1973). It is therefore more likely that the local dire wolves were opportunistically entering the cave to either hunt live peccaries or to scavenge the carcasses of animals which died of natural causes. A similar bone accumulation of mountain goats (*Oreamnos americanus*) is reported by Jim Mead (personal communication) from a recent cave site in which grey wolves either killed or scavenged these animals inside the cave. Hunting of the BC peccaries by wolves is most likely to have taken place during late winter when they are likely to have been most vulnerable to predation. Smaller predators appear to have utilized the cave periodically and scavenged from any carcasses left behind. It is worth noting here that many of the smaller vertebrates represented at the site, such as American beaver and hellbender salamander (Hawksley et al. 1973), could have been transported there by smaller carnivores who would have utilized the cave when the peccaries were absent.

Feeding behavior of Canis dirus—Based on the taphonomic and faunal analysis of the remains it is hypothesized that the dire wolf was primarily responsible for carcass modification

on the peccaries at Bat Cave. From this, the feeding behavior of the dire wolf at Bat Cave is strikingly similar to the modifications inflicted on deer carcasses by gray wolves at Bays Mountain Park. As observed within the comparative sample, the proximal limb segments of the Bat Cave peccary bones appear to have been the most frequently utilized portions of the carcasses due to the larger muscle masses concentrated in these areas. The hindquarters in particular are the most heavily damaged elements among the BC sample. The relatively large size, laterally compressed nature, and close proximity to the upper limb segments make the calcaneus the most susceptible to predator modification among the carpals and tarsals. This may be due to the relatively large size of these bones compared to the other, smaller bones which comprise the wrists and ankles. Despite articulating directly to the tibia and being comparable to the calcanei in abundance and size, the astragali appear to be much more resistant to predator modification, most likely due to the compact and rounded shape of this element. The remaining bones which comprise the manus and pes are the least susceptible to predator modification because muscle attachment in this area is minimal, and could therefore be considered to be less palatable to feeding predators. Indeed, extant predators frequently ignore this part of the carcass completely often leaving the fully articulated limb extremity complete with skin (Haynes 1982).

It has been noted by Haynes (1982) that scavenged carcasses are utilized less fully and are abandoned more intact, whereas prey that is procured by the wolves themselves are consumed much more completely. The extreme damage and disarticulation noted in most of the BC peccary material seems to indicate that the dire wolves were actively hunting these animals more often than they took advantage of found carcasses. One possible exception in which wolves may fully utilize a scavenged carcass is during a period of relative food scarcity and when a particularly large number of wolves are involved during the feeding process. Social predators

generally consume the entire kill onsite when the carcass is relatively small or when a particularly large number of predators are involved. When a carcass is relatively large or if fewer feeding predators are involved, portions of the kill, most commonly the limbs (Haynes 1982; Hill 1989), may be removed and carried offsite to be consumed in relative privacy. The great abundance of limb elements are present among the Bat Cave sample suggests that the carcasses were not regularly being transported and supports the hypothesis that the wolf-eaten peccary bones were the result of wolves actively entering the cave to hunt or scavenge them.

Rodent Damage—Klippel and Synstellien (2007) demonstrated that rodent modification typically takes place between one and two years after death, long after the flesh has been removed from the bones. Furthermore, their study seems to imply that though omnivorous rodents are more likely to attack the fat-laden cancellous bone, more herbivorous rodents will tend to focus on the edge or on the protuberance of a bone after the fat has been leached away and where the cortices are thick. The pattern among the rodent modified elements from the BC sample suggest that the latter scenario occurred more frequently and is reinforced by the known presence of numerous herbivorous taxa such as eastern woodrat (*Neotoma floridana*). Also, rodent gnawing appears to be particularly pronounced around the edges of predator-inflicted bone breakages, perhaps due to these bones being broken into smaller fragments that are more manageable for gape of many rodents. Perhaps due to the relative thinness of the cortical bone in these elements, rodent modification to the skull and mandible is often particularly severe often leading to the damage and loss of teeth. Isolated teeth, in turn, appear to be highly sought after by rodents most likely due to the relatively high mineral content of the dentine.

Trampling—Trampling by ungulates includes inadvertent kicking and placement of the hoof directly upon an object on the surface of the ground (Haynes 1983). Impact damage due to

trampling is generally minimal when bones are whole and fresh, even after predators have removed the epiphyses. Dried or weathered bones, being much more brittle, tend to suffer much more impact damage and fracturing when subject to ungulate trampling (Haynes 1983). At minimum, trampled bones may simply be kicked several centimeters to several meters from their site of deposition. This typically occurs in high-traffic areas and partially explains why most of the bones collected from BC were collected from the sides of the cave. Most of the elements recovered from the cave center consisted of more enduring elements such as teeth. Continued trampling over a period of time often results in bones disappearing into the mud or being broken into ever smaller fragments. Skulls, ribs, vertebra, and scapulae may be crushed or splintered. Mandibles may be segmented into the ascending ramus, central cheek toothrow minus the lower border, and the forward part of the ramus. Pelvises may be broken in half or into several fragments, with bone surrounding the acetabulum surviving the longest. Spiral fractured long bones may develop additional linear fractures branching from the initial break. Even after subjected to particularly heavy carnivore utilization, individual elements are generally still identifiable. When secondarily subjected to trampling, however, elements may be reduced to unidentifiable chips and splinters. Such is the case observed among many of the BC peccary bones, many of which are so heavily fragmented that they were only identifiable as portions of long bone or skull.

CHAPTER 7

CONCLUSIONS

- Examination of the Bat Cave peccary sample was undertaken to assess demographics, predator modification, and other taphonomic factors of the deposit.

- Maturation of individuals was assessed using tooth eruption sequence and occlusial wear patterns for all tooth-bearing mandibular elements and isolated lower dentition, which has demonstrated that all age groups are represented within the sample from unborn fetal to ~nine-year-old individuals.

- The presence of distinct, developmentally non-overlapping age groups suggest that *P. compressus* engaged in seasonal breeding behaviors, at least in the Bat Cave locality and other temperate regions. This finding suggests that caves were ecologically important to this species and offers insight into other *P. compressus* cave assemblages.

- At the time of deposition, the Bat Cave site appears to have served as a seasonal, communal shelter for local peccaries, most likely during winter.

- Demographic assessment of the Bat Cave peccary population suggests that younger individuals comprised the bulk of the population and individuals five and older gradually became less abundant.

- While the site was occupied by peccaries, dire wolves would occasionally enter the cave to hunt or scavenge them.

- Some peccaries, which were killed by wolves or by natural causes, were subsequently fed upon by smaller carnivorans and invertebrates.

- Many of the peccary bones from Bat Cave were modified by rodents long after the flesh had been removed.

- Smaller, often unidentifiable bone fragments which bare no evidence of predator modification may be attributable to continual trampling by peccaries.

- Small carnivorans appear to have utilized the cave site, perhaps when the peccaries were absent.

- The relatively stable environment within the Bone Passage region of Bat Cave served as an ideal preservational environment for late Pleistocene bones.

- Skeletal part representation suggests that a size-biased collection method was utilized. This supports historical documentation about the excavation and reflects difficulties in working in this area of the cave.

- Initial cataloguing of the Bat Cave peccary material by Central Missouri State University focused on those elements which were more numerous and potentially helpful in assessing MNI.

- The MNI for the Bat Cave peccaries has been revised from 98 to 70 individuals based on the number of lower left permanent canines.

- A larger sample of intact *P. compressus* mandibles is necessary to better assess sexual dimorphism in this taxon.

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APPENDIX A

Number of Identified Elements

Number of identified deciduous dental elements

Tooth	Lt Isolated	Lt Emplaced	Lt Total	Rt Isolated	Rt Emplaced	Rt Total
Lower dI1-2	0	0	**0**	0	0	**0**
Upper dI1-2	0	0	**0**	0	0	**0**
Lower dC1	11	0	**11**	9	0	**9**
Upper dC1	13	0	**13**	21	0	**21**
Lower dP2	2	2	**4**	2	0	**2**
Upper dP2	3	0	**3**	1	0	**1**
Lower dP3	3	2	**5**	3	1	**4**
Upper dP3	2	1	**3**	0	0	**0**
Lower dP4	6	2	**8**	6	3	**9**
Upper dP4	3	2	**5**	4	1	**5**

Number of identified permanent dental elements

Tooth	Lt Isolated	Lt Emplaced	Lt Total	Rt Isolated	Rt Emplaced	Rt Total
Lower I1-2	45	2	**47**	39	0	**39**
Upper I1-2	18	0	**18**	11	0	**11**
Lower C1	56	14	**70**	53	11	**64**
Upper C1	39	2	**41**	52	1	**53**
Lower P2	6	3	**9**	4	4	**8**
Upper P2	4	0	**4**	4	3	**7**
Lower P3	4	13	**17**	8	11	**19**
Upper P3	3	1	**4**	9	3	**12**
Lower P4	8	14	**22**	7	16	**23**
Upper P4	6	3	**9**	6	4	**10**
Lower M1	6	18	**24**	8	17	**25**
Upper M1	10	5	**15**	9	7	**16**
Lower M2	15	18	**33**	13	16	**29**
Upper M2	8	4	**12**	6	7	**13**
Lower M3	8	12	**20**	14	19	**33**
Upper M3	0	4	**4**	2	6	**8**

Number of identified postcranial elements

Element	Left	—	Right	Total
Scapula	42		50	92
Humerus	38		35	73
Radius/Ulna	42		41	83
Scaphoid	8		8	16
Lunar	4		8	12
Cuneiform	7		4	11
Pisiform	4		1	5
Unciform	3		7	10
Magnum	7		5	12
Trapezoid	0		0	0
Trapezium	0		0	0
Metacarpal pair	9		7	16
Metacarpal III	15		17	32
Metacarpal IV	12		16	28
Pelvis	25		11	36
Femur	48		44	92
Tibia	21		28	49
Fibula	18		22	40
Calcaneus	31		30	61
Astragalus	31		21	52
Navicular	9		9	18
Cuboid	7		10	17
Metatarsal pair	24		17	41
Metatarsal III	5		6	11
Metatarsal IV	5		6	11
Patella	9		4	13
Prox. Phalanges	82		82	164
Med. Phalanges	53		58	111
Dist. Phalanges	48		40	88
Atlas		19		19
Axis		10		10
Other Cervicals		58		58
Thoracic Vert.		140		140
Lumbar Vert.		102		102
Sacrum		22		22
Caudal Vert.		25		25
1st Sternbra		8		8
2nd Sternebra		6		6
3rd Sternebra		15		15

4th Sternebra	11	**11**
5th Sternebra	4	**4**
6th Sternebra	1	**1**
Ribs	278	**278**
Isolated Fibulae	163	**163**
Costal Cartilage	54	**54**

Catalogue Numbers

ISM catologue number assignments

ISM #	Element	ISM #	Element	ISM #	Element
499097	Mandible	499148	Rt Calcaneus	499203	Rt Upper I1-2
499098	Lt Dentary	499149	Lt Astragalus	499204	Lt Lower C1
499099	Rt Dentary	499150	Rt Astragalus	499205	Rt Lower C1
499100	Skull/Palate	499151	Lt Navicular	499206	Lt Upper C1
499101	Lt Maxilla/Premaxilla	499152	Rt Navicular	499207	Rt Upper C1
499102	Rt Maxilla/Premaxilla	499153	Lt Cuboid	499208	Lt Lower P2
499103	Lt Frontal	499154	Rt Cuboid	499209	Rt Lower P2
499104	Rt Frontal	499155	Lt Ectocuneiform	499210	Lt Upper P2
499105	Lt Jugal	499156	Rt Ectocuneiform	499211	Rt Upper P2
499106	Rt Jugal	499157	Lt Mesocuneiform	499212	Lt Lower P3
499107	Lt Squamosal	499158	Rt Mesocuneiform	499213	Rt Lower P3
499108	Rt Squamosal	499159	Lt Entocuneiform	499214	Lt Upper P3
499109	Nasal	499160	Rt Entocuneiform	499215	Rt Upper P3
499110	Parietal	499161	Lt Cannon Bone	499216	Lt Lower P4
499111	Occiput	499162	Rt Cannon Bone	499217	Rt Lower P4
499112	Auditory Bulla	499163	Lt Metatarsal III	499218	Lt Upper P4
499114	Lt Scapula	499164	Rt Metatarsal III	499219	Rt Upper P4
499115	Rt Scapula	499165	Lt Metatarsal IV	499220	Lt Lower M1
499116	Lt Humerus	499166	Rt Metatarsal IV	499221	Rt Lower M1
499117	Rt Humerus	499167	Lt Patella	499222	Lt Upper M1
499118	Lt Radius/Ulna	499168	Rt Patella	499223	Rt Upper M1
499119	Right Radius/Ulna	499169	Lt Fibula	499224	Lt Lower M2
499120	Lt Scaphoid	499170	Rt Fibula	499225	Rt Lower M2
499121	Rt Scaphoid	499171	Lt Proximal Phalanx	499226	Lt Upper M2
499122	Lt Lunar	499172	Rt Proximal Phalanx	499227	Rt Upper M2
499123	Rt Lunar	499173	Lt Medial Phalanx	499228	Lt Lower M3
499124	Lt Cuneiform	499174	Rt Medial Phalanx	499229	Rt Lower M3
499125	Rt Cuneiform	499175	Lt Distal Phalanx	499230	Lt Upper M3
499126	Lt Pisiform	499176	Rt Distal Phalanx	499231	Rt Upper M3
499127	Rt Pisiform	499177	CV1 (Atlas)	499236	Lt Lower dI1-2
499128	Lt Unciform	499178	CV2 (Axis)	499237	Rt Lower dI1-2
499129	Rt Unciform	499179	CV3-4	499238	Lt Upper dI1-2
499130	Lt Magnum	499180	CV5	499239	Rt Upper dI1-2
499131	Rt Magnum	499181	CV6	499240	Lt Lower dC1

499132	Lt Trapezoid	**499182**	CV7	**499241**	Rt Lower dC1
499133	Rt Trapezoid	**499183**	TV1-13	**499242**	Lt Upper dC1
499134	Lt Trapezium	**499184**	LV1-5	**499243**	Rt Upper dC1
499135	Lt Cannon Bone	**499185**	Sacrum	**499244**	Lt Lower dP2
499136	Rt Cannon Bone	**499186**	Caudal vertebrae	**499245**	Rt Lower dP2
499137	Lt MC3	**499187**	1st Sternebra	**499246**	Lt Upper dP2
499138	Rt MC3	**499188**	2nd Sternebra	**499247**	Rt Upper dP2
499139	Lt MC4	**499189**	3rd Sternebra	**499248**	Lt Lower dP3
499140	Rt MC4	**499190**	4th Sternebra	**499249**	Rt Lower dP3
499141	Lt Pelvis	**499191**	5th Sternebra	**499250**	Lt Upper dP3
499142	Rt Pelvis	**499192**	6th Sternebra	**499251**	Rt Upper dP3
499143	Lt Femur	**499193**	Costal Cartilage	**499252**	Lt Lower dP4
499144	Rt Femur	**499194**	Ribs	**499253**	Rt Lower dP4
499145	Lt Tibia	**499200**	Lt Lower I1-2	**499254**	Lt Upper dP4
499146	Rt Tibia	**499201**	Rt Lower I1-2	**499255**	Rt Upper dP4
499147	Lt Calcaneus	**499202**	Lt Upper I1-2		

Frequency of elements bearing the CMS catalogue

Element	%	Element	%
Metacarpal Pair	100%	Humerus	67.12%
C1	98.51%	Magnum	66.67%
dC1	98.15%	Metatarsal III	63.63%
Metatarsal Pair	97.56%	Scapula	41.30%
Astragalus	96.15%	Radius/Ulna	13.25%
Cuboid	94.12%	Sacrum	9.09%
Proximal Phalanges	93.90%	Tibia	8.16%
Metacarpal III	93.75%	Unciform	8%
Distal Phalanges	93.10%	Dentary	7.89%
Patella	92.30%	M2	4.76%
Calcaneus	91.80%	M3	4.17%
Lunar	91.67%	dI1-2	0%
Metatarsal IV	90.90%	dP2	0%
Atlas	89.47%	dP3	0%
Pelvis	89.19%	dP4	0%
Medial Phalanges	89.19%	I1-2	0%
Navicular	88.89%	P2	0%
Fibula	87.50%	P3	0%
Lumbar Vertebrae	86.27%	P4	0%
Metacarpal IV	85.71%	M1	0%
Axis	81.81%	Pisiform	0%
Scaphoid	80%	Trapezoid	0%
Other Cervicals	77.42%	Trapezium	0%
Mandible	72.72%	Caudal Vertebrae	0%
Cuneiform	72.72%	Sternebrae	0%
Thoracic Vertebrae	72.14%	Costal Cartilage	0%
Femur	71.74%	Ribs	0%

Summary of Limb Elements

Scapulae

Scapula	Left	Right	Total
Complete spine	1	3	4
Incomplete spine	15	9	24
Glenoid fossa	7	8	15
Fragmented	24	19	43
Fetal/Neonate	3	3	6
Total	50	42	92

Humeri

Humerus	Left	Right	Total
Complete element	6	4	10
Absent proximal shaft	11	8	19
Distal end only	4	7	11
Proximal end only	9	11	20
Shaft fragment	4	1	5
Fetal/Neonate	4	4	8
Total	38	35	73

Radii & ulnae

Radius/Ulna	Left	Right	Total
Complete element	4	1	5
Incomplete element	8	11	19
Unfused epiphysis	4	3	7
Isolated radius	7	8	15
Isolated ulna	13	13	26
Fetal/Neonate radius	4	4	8
Fetal/Neonate ulna	2	1	3
Total	42	41	83

Femora

Femur	Left	Right	Total
Complete element	0	1	1
Incomplete element	3	1	4
Proximal end only	7	6	13
Distal end only	16	13	29
Unfused proximal epiphysis	6	9	15
Shaft	11	10	21
Fetal/Neonate	5	4	9
Total	48	44	92

Tibiae

Tibia	Left	Right	Total
Complete element	2	3	5
Proximal end only	6	10	16
Distal end only	3	3	6
Shaft w/ distal end	4	6	10
Shaft w/ distal end	6	6	12
Fetal/Neonate	0	0	0
Total	21	28	49

APPENDIX D

Demographic Assessment

Lower M3 measurements

Specimen	Taxon (site)	Length (mm)	Width (mm)
UF 12090	*Platygonus cumberlandensis* (Coleman II)	25.28	15.11
	Platygonus cumberlandensis (Coleman II)	26.88	15.6
UF 12089	*Platygonus cumberlandensis* (Coleman II)	25.92	15.47
	Platygonus cumberlandensis (Coleman II)	27.83	15.67
UF 12086	*Platygonus cumberlandensis* (Coleman II)	26.04	14.94
UF 87819	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	23.74	14.09
UF 63907	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	21.74	13.46
UF 67178	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	22.1	13.85
UF 67177	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	23.75	15.01
UF 87835	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	22.11	13.66
UF 86918	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	21.82	13.45
UF 63909	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	23.61	14.47
UF 63904	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	21.79	12.81
UF 67176	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	23.99	14.91
UF 81551	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	21.37	13.48
UF 65262	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	21.46	13.27
UF 87794	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	20.37	12.36
UF 87772	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	22.88	13.67
UF 80821	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	24.42	14.41
UF 82218	*Platygonus cumberlandensis* (Leisey Shell Pit 1A)	24.07	15.25
ISM 499097.1	*Platygonus compressus* (Bat Cave)	20.46	12.98
ISM 499097.2	*Platygonus compressus* (Bat Cave)	21.95	12
ISM 499097.3	*Platygonus compressus* (Bat Cave)	21.73	13.24
ISM 499097.4	*Platygonus compressus* (Bat Cave)	21.97	12.5
ISM 499097.5	*Platygonus compressus* (Bat Cave)	22.28	12.65
ISM 499097.6	*Platygonus compressus* (Bat Cave)	22.8	12.77
ISM 499097.7	*Platygonus compressus* (Bat Cave)	20.64	11.35
ISM 499098.3	*Platygonus compressus* (Bat Cave)	20.74	12.62
ISM 499098.4	*Platygonus compressus* (Bat Cave)	20.83	11.74
ISM 499098.5	*Platygonus compressus* (Bat Cave)	21.84	12.54
ISM 499098.6	*Platygonus compressus* (Bat Cave)	20.71	12.69
ISM 499098.7	*Platygonus compressus* (Bat Cave)	20.12	12.73
ISM 499098.15	*Platygonus compressus* (Bat Cave)	23.03	12.93
ISM 499098.16	*Platygonus compressus* (Bat Cave)	21.24	12.74

ISM 499099.1	*Platygonus compressus* (Bat Cave)	21.69	11.61
ISM 499099.6	*Platygonus compressus* (Bat Cave)	20.98	13.2
ISM 499099.7	*Platygonus compressus* (Bat Cave)	21.71	12.73
ISM 499099.8	*Platygonus compressus* (Bat Cave)	21.63	13.14
ISM 499099.11	*Platygonus compressus* (Bat Cave)	22.82	13.71
ISM 499099.12	*Platygonus compressus* (Bat Cave)	22.4	12.78
ISM 499099.13	*Platygonus compressus* (Bat Cave)	21.74	13.05
ISM 499099.19	*Platygonus compressus* (Bat Cave)	22.88	12.79
ISM 499099.20	*Platygonus compressus* (Bat Cave)	22.11	13.53
ISM 499099.21	*Platygonus compressus* (Bat Cave)	20.85	12.54

APPENDIX E

Predator Damage Assessment

Frequency of predator damage to scapulae

Stage 0	Stage 1	Stage 2	Stage 3	Indeterminable
ISM 499114.1	ISM 499115.1	ISM 499115.3	ISM 499115.17	ISM 499115.9
	ISM 499115.2	ISM 499115.4	ISM 499115.18	ISM 499115.12
	ISM 499114.2	ISM 499115.5	ISM 499115.19	ISM 499115.13
	ISM 499114.3	ISM 499115.6	ISM 499115.20	ISM 499115.27
		ISM 499115.7	ISM 499115.21	ISM 499115.29
		ISM 499115.8	ISM 499115.22	ISM 499115.30
		ISM 499115.10	ISM 499115.23	ISM 499115.31
		ISM 499115.11	ISM 499115.24	ISM 499115.32
		ISM 499115.14	ISM 499115.25	ISM 499115.33
		ISM 499115.15	ISM 499115.26	ISM 499115.34
		ISM 499115.16	ISM 499115.28	ISM 499115.36
		ISM 499114.5	ISM 499115.35	ISM 499115.38
		ISM 499114.6	ISM 499115.37	ISM 499115.39
		ISM 499114.9	ISM 499115.41	ISM 499115.40
		ISM 499114.10	ISM 499115.44	ISM 499115.42
		ISM 499114.11	ISM 499115.47	ISM 499115.43
		ISM 499114.13	ISM 499114.12	ISM 499115.45
			ISM 499114.14	ISM 499115.46
			ISM 499114.15	ISM 499114.4
			ISM 499114.16	ISM 499114.7
			ISM 499114.17	ISM 499114.8
			ISM 499114.18	ISM 499114.23
			ISM 499114.19	ISM 499114.24
			ISM 499114.20	ISM 499114.25
			ISM 499114.21	ISM 499114.27
			ISM 499114.22	ISM 499114.28
			ISM 499114.26	ISM 499114.29
			ISM 499114.35	ISM 499114.30
			ISM 499114.36	ISM 499114.31
			ISM 499114.37	ISM 499114.32
			ISM 499114.38	ISM 499114.33
			ISM 499114.39	ISM 499114.34

Frequency of predator damage to humeri

Stage 0	Stage 1	Stage 2	Stage 3	Indeterminable
ISM 499116.1	ISM 499116.2	ISM 499116.9	ISM 499116.18	ISM 499116.27
	ISM 499116.3	ISM 499116.10	ISM 499116.19	ISM 499116.28
	ISM 499116.4	ISM 499116.11	ISM 499116.20	ISM 499117.18
	ISM 499116.5	ISM 499116.12	ISM 499116.21	ISM 499117.27
	ISM 499116.6	ISM 499116.13	ISM 499116.22	ISM 499117.28
	ISM 499116.7	ISM 499116.14	ISM 499116.23	ISM 499117.29
	ISM 499116.8	ISM 499116.15	ISM 499116.24	ISM 499117.30
	ISM 499117.1	ISM 499116.16	ISM 499116.25	ISM 499117.31
	ISM 499117.2	ISM 499116.17	ISM 499116.26	
	ISM 499117.3	ISM 499117.7	ISM 499116.29	
	ISM 499117.4	ISM 499117.8	ISM 499116.30	
	ISM 499117.5	ISM 499117.9	ISM 499116.31	
	ISM 499117.6	ISM 499117.10	ISM 499116.32	
		ISM 499117.11	ISM 499116.33	
		ISM 499117.12	ISM 499116.34	
			ISM 499117.13	
			ISM 499117.14	
			ISM 499117.15	
			ISM 499117.16	
			ISM 499117.17	
			ISM 499117.19	
			ISM 499117.20	
			ISM 499117.21	
			ISM 499117.22	
			ISM 499117.23	
			ISM 499117.24	
			ISM 499117.25	
			ISM 499117.26	

Frequency of predator damage to radii and ulnae

Stage 0	Stage 1	Stage 2	Stage 3	Indeterminable
ISM 499118.1	ISM 499118.3	ISM 499118.6	ISM 499118.8	ISM 499118.13
ISM 499118.2	ISM 499118.5	ISM 499118.7	ISM 499118.9	ISM 499118.14
ISM 499118.4	ISM 499118.16	ISM 499118.17	ISM 499118.10	ISM 499118.20
ISM 499118.15	ISM 499118.24	ISM 499118.18	ISM 499118.11	ISM 499118.21
ISM 499119.1	ISM 499118.27	ISM 499118.19	ISM 499118.12	ISM 499118.33
ISM 499119.31	ISM 499119.2	ISM 499118.22	ISM 499118.23	ISM 499119.12
	ISM 499119.3	ISM 499118.25	ISM 499118.28	ISM 499119.13
	ISM 499119.4	ISM 499118.26	ISM 499118.29	ISM 499119.14
	ISM 499119.5	ISM 499119.6	ISM 499118.30	ISM 499119.15
	ISM 499119.17	ISM 499119.7	ISM 499118.31	ISM 499119.16
	ISM 499119.18	ISM 499119.8	ISM 499118.32	ISM 499119.27
	ISM 499119.19	ISM 499119.9	ISM 499118.34	ISM 499119.35
		ISM 499119.10	ISM 499118.35	
		ISM 499119.11	ISM 499118.36	
		ISM 499119.20	ISM 499119.22	
		ISM 499119.21	ISM 499119.23	
		ISM 499119.26	ISM 499119.24	
		ISM 499119.28	ISM 499119.25	
			ISM 499119.29	
			ISM 499119.30	
			ISM 499119.32	
			ISM 499119.33	
			ISM 499119.34	
			ISM 499119.36	

Frequency of predator damage to pelvises.

Stage 0	Stage 1	Stage 2	Stage 3	Indeterminable
	ISM 499142.1	ISM 499141.1	ISM 499141.13	ISM 499141.22
		ISM 499141.2	ISM 499141.14	ISM 499141.25
		ISM 499141.3	ISM 499141.15	
		ISM 499141.4	ISM 499141.17	
		ISM 499141.5	ISM 499141.18	
		ISM 499141.6	ISM 499141.19	
		ISM 499141.7	ISM 499141.20	
		ISM 499141.8	ISM 499141.21	
		ISM 499141.9	ISM 499141.23	
		ISM 499141.10	ISM 499141.24	
		ISM 499141.11	ISM 499142.5	
		ISM 499141.12	ISM 499142.6	
		ISM 499141.16	ISM 499142.7	
		ISM 499142.2	ISM 499142.8	
		ISM 499142.3	ISM 499142.9	
		ISM 499142.4	ISM 499142.10	
			ISM 499142.11	
			ISM 499142.12	

Frequency of predator damage to femora

Stage 0	Stage 1	Stage 2	Stage 3	Indeterminable
	ISM 499143.1	ISM 499143.8	ISM 499143.13	ISM 499143.16
	ISM 499143.2	ISM 499143.9	ISM 499143.14	ISM 499143.19
	ISM 499143.3	ISM 499143.10	ISM 499143.15	ISM 499143.32
	ISM 499143.4	ISM 499143.11	ISM 499143.17	ISM 499143.36
	ISM 499143.5	ISM 499143.12	ISM 499143.18	ISM 499143.43
	ISM 499143.6	ISM 499144.2	ISM 499143.20	ISM 499144.14
	ISM 499143.7	ISM 499144.3	ISM 499143.21	ISM 499144.17
	ISM 499144.1	ISM 499144.4	ISM 499143.22	ISM 499144.28
		ISM 499144.5	ISM 499143.23	ISM 499144.29
		ISM 499144.6	ISM 499143.24	ISM 499144.30
		ISM 499144.7	ISM 499143.25	ISM 499144.32
		ISM 499144.8	ISM 499143.26	ISM 499144.33
		ISM 499144.11	ISM 499143.27	ISM 499144.34
		ISM 499144.38	ISM 499143.28	ISM 499144.35
		ISM 499144.39	ISM 499143.29	
			ISM 499143.30	
			ISM 499143.31	

			ISM 499143.33	
			ISM 499143.34	
			ISM 499143.35	
			ISM 499143.37	
			ISM 499143.38	
			ISM 499143.39	
			ISM 499143.40	
			ISM 499143.41	
			ISM 499143.42	
			ISM 499144.9	
			ISM 499144.10	
			ISM 499144.12	
			ISM 499144.13	
			ISM 499144.15	
			ISM 499144.16	
			ISM 499144.18	
			ISM 499144.19	
			ISM 499144.20	
			ISM 499144.21	
			ISM 499144.22	
			ISM 499144.23	
			ISM 499144.24	
			ISM 499144.25	
			ISM 499144.26	
			ISM 499144.27	
			ISM 499144.31	
			ISM 499144.36	
			ISM 499144.37	
			ISM 499144.40	

Frequency of predator damage to tibiae

Stage 0	Stage 1	Stage 2	Stage 3	Indeterminable
ISM 499145.1	ISM 499145.2	ISM 499145.4	ISM 499145.10	ISM 499145.7
	ISM 499145.3	ISM 499145.8	ISM 499145.11	ISM 499145.15
	ISM 499145.5	ISM 499145.9	ISM 499145.12	ISM 499145.16
	ISM 499145.6	ISM 499145.21	ISM 499145.13	ISM 499145.18
	ISM 499146.1	ISM 499146.6	ISM 499145.14	ISM 499145.20
	ISM 499146.2	ISM 499146.7	ISM 499145.17	ISM 499146.9
	ISM 499146.3	ISM 499146.8	ISM 499145.19	ISM 499146.10
	ISM 499146.4	ISM 499146.11	ISM 499146.18	ISM 499146.14
	ISM 499146.5	ISM 499146.12	ISM 499146.19	ISM 499146.17
		ISM 499146.13	ISM 499146.20	ISM 499146.23
		ISM 499146.15	ISM 499146.21	ISM 499146.24
		ISM 499146.16	ISM 499146.22	ISM 499146.25
			ISM 499146.28	ISM 499146.26
				ISM 499146.27

Predator damage patterns observed among cervical vertebrae

Specimen ID	Visible punctures	Sheared centrum	Damaged articular surface	Broken neural spine	Absent neural arch	Absent centrum
ISM 499177.2	✓					
ISM 499177.4				✓		
ISM 499177.5	✓			✓		
ISM 499177.6				✓		
ISM 499177.7				✓		
ISM 499177.8	✓			✓	✓	
ISM 499177.9	✓			✓		
ISM 499177.10	✓			✓		
ISM 499177.11	✓			✓		
ISM 499177.12	✓		✓	✓		
ISM 499177.13	✓			✓		
ISM 499177.14	✓		✓	✓		
ISM 499177.15	✓		✓	✓		
ISM 499177.16	✓			✓	✓	✓

Specimen ID	Visible punctures	Sheared centrum	Damaged articular surface	Broken neural spine	Absent neural arch	Absent centrum
ISM 499178.3	✓			✓		
ISM 499178.4	✓			✓		
ISM 499178.5	✓		✓	✓		
ISM 499178.7	✓		✓	✓		
ISM 499178.8	✓			✓		
ISM 499178.10	✓				✓	
ISM 499178.11	✓	✓	✓	✓		
ISM 499179.3	✓			✓		
ISM 499179.4	✓		✓	✓		
ISM 499179.7	✓			✓		
ISM 499179.8	✓					
ISM 499179.10	✓	✓	✓	✓		
ISM 499179.12	✓	✓	✓	✓		
ISM 499179.13	✓	✓	✓	✓		
ISM 499179.14	✓		✓	✓		
ISM 499179.23						
ISM 499179.24		✓	✓	✓		
ISM 499179.26		✓	✓	✓		
ISM 499179.27	✓	✓		✓		
ISM 499179.28	✓	✓		✓		
ISM 499179.29	✓				✓	✓
ISM 499180.4			✓	✓		
ISM 499180.5	✓	✓	✓	✓		
ISM 499180.6	✓		✓	✓		
ISM 499182.11	✓	✓	✓	✓		
ISM 499182.12	✓	✓	✓	✓		

Predator damage patterns observed among thoracic vertebrae

Specimen ID	Visible punctures	Sheared centrum	Damaged articular surface	Broken neural spine	Absent neural arch	Absent centrum
ISM 499183.4			✓	✓		
ISM 499183.5	✓		✓	✓		
ISM 499183.7			✓	✓		
ISM 499183.9			✓	✓		
ISM 499183.11	✓			✓		

ISM 499183.12				✓		
ISM 499183.13	✓		✓	✓		
ISM 499183.14	✓		✓	✓		
ISM 499183.17	✓			✓		
ISM 499183.18				✓		
ISM 499183.22			✓			
ISM 499183.24				✓		
ISM 499183.27				✓		
ISM 499183.28	✓		✓	✓		
ISM 499183.29				✓		
ISM 499183.35	✓			✓		
ISM 499183.36	✓			✓		
ISM 499183.40	✓			✓		
ISM 499183.41	✓			✓		
ISM 499183.44	✓			✓		
ISM 499183.49			✓	✓		
ISM 499183.51				✓		
ISM 499183.53	✓		✓	✓		
ISM 499183.54	✓		✓	✓		
ISM 499183.55	✓		✓	✓		
ISM 499183.58	✓	✓	✓	✓		
ISM 499183.59	✓		✓	✓		
ISM 499183.60	✓	✓	✓	✓		
ISM 499183.61	✓		✓			
ISM 499183.62	✓		✓		✓	
ISM 499183.63			✓			
ISM 499183.64	✓	✓	✓	✓		
ISM 499183.65	✓		✓	✓		
ISM 499183.68				✓		
ISM 499183.73	✓			✓		
ISM 499183.75	✓		✓	✓		
ISM 499183.76		✓				
ISM 499183.78	✓		✓	✓		
ISM 499183.82		✓	✓	✓		
ISM 499183.88	✓			✓		
ISM 499183.91	✓			✓		
ISM 499183.92			✓	✓		
ISM 499183.95			✓	✓		
ISM 499183.96				✓		
ISM 499183.98	✓			✓		
ISM 499183.103	✓		✓	✓		

Specimen ID						
ISM 499183.104		✓	✓	✓		
ISM 499183.106	✓	✓		✓		
ISM 499183.107	✓	✓		✓		
ISM 499183.110			✓	✓		
ISM 499183.111	✓					
ISM 499183.113		✓	✓	✓		
ISM 499183.114	✓		✓	✓		
ISM 499183.115		✓	✓	✓		
ISM 499183.118	✓	✓	✓	✓		
ISM 499183.119			✓	✓		
ISM 499183.124	✓			✓		✓
ISM 499183.126	✓			✓		✓
ISM 499183.127	✓	✓	✓	✓		
ISM 499183.129	✓			✓		✓
ISM 499183.130				✓		✓
ISM 499183.131	✓			✓		✓
ISM 499183.133	✓			✓		✓

Predator damage patterns observed among lumbar vertebrae

Specimen ID	Visible punctures	Sheared centrum	Damaged articular surface	Broken neural spine	Absent neural arch	Absent centrum
ISM 499184.4	✓			✓		
ISM 499184.10	✓		✓	✓		
ISM 499184.11	✓			✓		
ISM 499184.20	✓			✓		
ISM 499184.21			✓	✓		
ISM 499184.22	✓	✓	✓	✓		
ISM 499184.23				✓		
ISM 499184.25	✓			✓		
ISM 499184.26			✓	✓		
ISM 499184.27	✓		✓	✓		
ISM 499184.31	✓	✓	✓	✓		
ISM 499184.32	✓		✓	✓		
ISM 499184.33	✓			✓		
ISM 499184.34	✓			✓		

ISM 499184.35		✓	✓	✓		
ISM 499184.36	✓			✓		
ISM 499184.42	✓			✓		
ISM 499184.43				✓		
ISM 499184.50	✓			✓		
ISM 499184.52	✓			✓		
ISM 499184.55	✓		✓	✓		
ISM 499184.66	✓	✓	✓	✓		
ISM 499184.73	✓			✓		
ISM 499184.84	✓			✓		
ISM 499184.85	✓		✓	✓		
ISM 499184.91	✓	✓	✓	✓		
ISM 499184.92	✓	✓	✓	✓		
ISM 499184.93	✓			✓		✓
ISM 499184.94	✓		✓	✓		
ISM 499184.97	✓	✓	✓		✓	
ISM 499184.99	✓	✓	✓		✓	
ISM 499184.101	✓				✓	

VITA

AARON L. WOODRUFF

Education:
2016 M. S. Geosciences with concentration in Paleontology, advised by Blaine W. Schubert PhD, East Tennessee State University, Johnson City, Tennessee

2012 B. S., Biology with specialization in wildlife conservation, Fort Valley State University, Fort Valley, Georgia

Research Interests:
Morphology and paleoecology of Cenozoic mammals

Niche stratification and hierarchy of extant and extinct mammals

Late Pleistocene paleofaunas and ecosystems prior to human colonization

How ecosystems change over time and how animals adapt to handle these changes

Predator-prey dynamics and interspecies relationships

Paleoart and reconstruction

Employment:
2014-2015: Graduate Assistant: ETSU Museum of Natural History & Gray Fossil Site

2015-Present: Graduate Research Assistant at ETSU. Working with Dr. Blaine Schubert on the paleobiology of peccaries from Bat Cave, Missouri

Field Experience:
2015: Excavations at Natural Trap Cave, Wyoming

2014-Present: Excavations at Gray Fossil Site, Tennessee

2012: Limnology data collection in Peach County, Georgia

Committees:
2015-Present: Assistant Professor Search Committee: ETSU Department of Geosciences

Affiliations:
American Society of Mammalogists

Society of Vertebrate Paleontology

Southeastern Association of Vertebrate Paleontology

Don Sundquist Center of Excellence in Paleontology

East Tennessee State University & General Shale Natural History Museum

Conferences and Posters: Evidence of predation by Dire Wolves (*Canis dirus*) on the late
                                     Pleistocene Flat-headed Peccary (*Platygonus compressus*)
                                     from Bat Cave, Missouri. Society of Vertebrate
                                     Paleontology Meeting, 2015
                              A preliminary report on the peccaries (*Platygonus compressus*) at
                                     Bat Cave, Pulaski County, Missouri. Southeastern
                                     Association of Vertebrate Paleontology Meeting, 2015

Articles in Preparation: Predation by dire wolves, *Canis dirus* (Carnivora: Canidae) on the
                                     extinct flat-headed peccary, *Platygonus compressus*
                                     (Artiodactyla: Tayassuidae) from Bat Cave, Missouri

                             The osteology and eco-morphological assessment of the extinct

                                     peccary *Platygonus compressus*

                             Seasonal denning behavior and population dynamics of the late
                                     Pleistocene peccary *Platygonus compressus* (Artiodactyla:
                                     Tayassuidae) from Bat Cave, Missouri
                             Reassessment of the late Pleistocene vertebrate fauna of Bat Cave,
                                      Pulaski County, Missouri with comments on the
                                     paleoclimate and paleoecology of the site
                             Using species distribution modeling and fossil data to predict the
                                     current and future potential distributions of extant peccaries
                                     (Artiodactyla: Tayassuidae)
                             A revised facial reconstruction of sabertoothed predators with
                                     respect to mandibular morphology
                             A review of the Sebecidae (Archosauria: Mesoeucrocodylia)