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**Vertebrate taxonomic composition, species diversity, and paleoecology of two pliocene mid-latitude, inland-basin fossil assemblages: Panaca local fauna (Lincoln County, Nevada) and Hagerman local fauna (Twin Falls County, Idaho)**

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VERTEBRATE TAXONOMIC COMPOSITION, SPECIES DIVERSITY, AND  
PALEOECOLOGY OF TWO PLIOCENE MID-LATITUDE, INLAND-  
BASIN FOSSIL ASSEMBLAGES: PANACA LOCAL FAUNA  
(LINCOLN COUNTY, NEVADA) AND HAGERMAN LOCAL  
FAUNA (TWIN FALLS COUNTY, IDAHO)

by

Vicki Lynn Meyers

Bachelor of Science  
University of Wyoming  
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A thesis submitted in partial fulfillment of  
The requirements for the

**Master of Science in Geoscience  
Department of Geoscience  
College of Science**

**Graduate College  
University of Nevada, Las Vegas  
May 2011**

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## THE GRADUATE COLLEGE

We recommend the thesis prepared under our supervision by

**Vicki Lynn Meyers**

entitled

**Vertebrate Taxonomic Composition, Species Diversity, and  
Paleoecology of Two Pliocene Mid-Latitude, Inland-Basin Fossil  
Assemblages: Panaca Local Fauna (Lincoln County, Nevada) and  
Hagerman Local Fauna (Twin Falls County, Idaho)**

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**May 2011**



## ABSTRACT

### **Vertebrate Taxonomic Composition, Species Diversity, and Paleoecology of Two Mid-Latitude, Inland-Basin Fossil Assemblages: Panaca Local Fauna (Lincoln County, Nevada) and Hagerman Local Fauna (Twin Falls County, Idaho)**

by

Vicki Lynn Meyers

Dr. Stephen M. Rowland, Examination Committee Chair  
Professor of Geology  
University of Nevada, Las Vegas

I studied the sedimentology, species diversity, relative abundance, paleoenvironment, and paleoecology of the vertebrate fauna of the early Pliocene (Blancan Land Mammal Age) Panaca Formation of southeastern Nevada, and I compared these data with the slightly younger Hagerman fauna of south-central Idaho. The purpose of this study is to characterize the paleoecology and species diversity of mid-latitude inland basins during the Blancan Land Mammal Age, a time of climate change and immigrating taxa from Asia and South America. This study involved surface collecting and screenwashing of the Panaca Formation sediment in Meadow Valley, as well as a compilation of data from previous investigations.

About 500 specimens of large and small mammals, reptiles, and bird fossils were collected from 24 localities in this study. Nine genera of birds were identified for the first time, including *Cygnus*, *Anas*, *Rallus*, *Porzana*, *Callipepla*, *Spizella*, and *Buteo*. Forty-three genera of vertebrates are documented from the Panaca Formation, including *Sinocapra willdownsi*, which represents the earliest known caprine bovid in North America.

I compared the Panaca fauna with the Hagerman fauna, which has greater diversity. The Hagerman fauna has many more aquatic taxa: fish, turtles, birds, and mammals. The Panaca faunal assemblage has a larger number of lagomorphs, including the jackrabbit ecomorph *Lepoides lepoides*. The percentages of mammals in various trophic categories in the two localities are comparable, but Hagerman exhibits a greater number of carnivores. Lagomorphs display by far the highest relative abundance in number of identifiable specimens (NISP) calculations. Relative abundance comparisons suggest that different sampling methods preferentially sample different components of the fauna.

The Panaca and Hagerman Blancan ecosystems are interpreted to have been dominated by fluvial and floodplain environments in a seasonal climate of wet and dry periods, causing lake levels to fluctuate. The Hagerman climate was probably wetter and more temperate, while Panaca was more arid. The occurrence of environment-sensitive taxa and the strata suggest varied habitats within the ecosystem, including riparian, broad-leaf or brushy, and steppe habitats.

I propose that the Amboseli Basin of East Africa is a modern analog for the Blancan inland basins of the western North America. Modern bone assemblage studies of the Amboseli Basin suggest that species diversity and relative abundance of living herbivores is accurately recorded in the fossil record, thus supporting this method of fossil assemblage assessment.

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## CHAPTER 1

### INTRODUCTION

This study involves a comparison of two Pliocene vertebrate faunas belonging to the Blancan North American Land Mammal Age. North American Land Mammal Ages (NALMA) are time intervals characterized by distinctive assemblage of mammals that are distinguished from earlier and later assemblages (Lindsay, 1987; Woodburne, 2004) (Figure 1). These biochronologic units are defined by the presence of a number of mammalian index fossils, along with first and last appearances of certain mammal species (Lindsay, 1987). The Blancan NALMA is dated from 4.9 Ma to 1.9 Ma (Repenning, 1987; Lindsay et al., 2002). It is not formally divided, but often referenced as early, middle, and late Blancan.

During the three-million-year-long Blancan NALMA the global climate cooled off significantly, as recorded in a 1 per mil drop in oceanic  $\delta^{18}\text{O}$  values and the establishment of full-scale Northern Hemisphere ice sheets (Zachos et al., 2001). The attendant drop in sea level opened the Bering land bridge to immigrating Asian mammal taxa. During the same interval, the Panama Seaway between North and South America closed, opening the Panamanian land bridge to immigrants from South America (Zachos et al., 2001). Thus, the Blancan NALMA was a very dynamic interval; the ecological stage was being reset, and many taxonomic players were competing for roles in North America's emerging cooler-climate terrestrial communities.

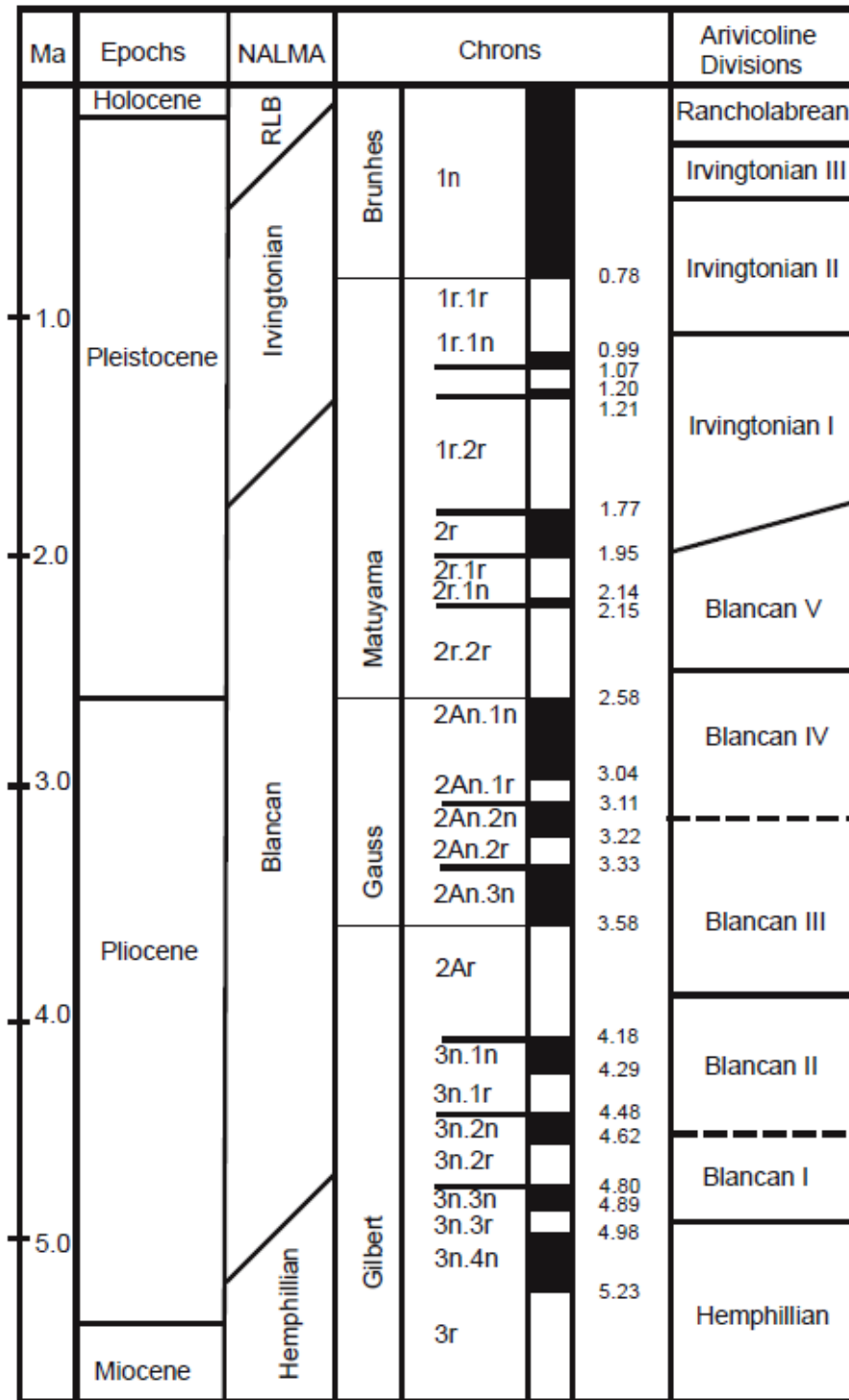


Figure 1. Temporal boundaries of the North American Land Mammal Ages and their subdivisions. Geomagnetic polarity time scale is from Berggren et al. (1995), and the arvicoline divisions are those proposed by Repenning (1987); Repenning et al. (1990). Dashed lines represent undefined temporal divisions. RLB = Rancholabrean. Modified from Bell et al. (2004).

As important as the Blancan NALMA was in the history of North American terrestrial ecosystems, the paleoecology and environment of the Blancan has not been well studied. Non-marine fossiliferous Blancan strata are known from a number of North American localities (Hibbard & Zakrzewski, 1972; Lindsay, 1978; Kelly, 1997; Morgan and Lucas, 2003; Bell et al., 2004), but only a few contain continuously fossiliferous strata (Bell et al., 2004). Furthermore, the early studies of these faunas have necessarily focused on taxonomy and geochronology. The time is now ripe to begin to compare Blancan faunas from different regions, as a crucial step toward understanding late Neogene ecosystem dynamics in North America.

The purpose of this study is to examine and compare the taxonomic composition, species diversity, paleoecology, and paleoenvironment of two Blancan, mid-latitude, inland-basin ecosystems: the Panaca faunal assemblage in the Panaca Formation of southeastern Nevada and the Hagerman faunal assemblage in the Glenns Ferry Formation of southern Idaho. The Hagerman fauna is a well-known Blancan assemblage that is suitable for comparison with the lesser studied Panaca faunal assemblage. I have compared these two assemblages for species diversity, depositional environment, and preservational bias. I was attracted to the Panaca Formation because of paleontologist Andrew Milner's discovery of a bone-rich layer northeast of the town of Panaca. Also, Mou (1999) recently completed a microvertebrate study of this formation with an emphasis on arvicoline rodents (voles). Mou's (1999) study established the precise age of the Panaca Formation, but it did not address paleoecological or

paleoenvironment questions. I selected the Hagerman local fauna for comparison with the Panaca Formation because it is a well-studied Blancan faunal assemblage.

The Panaca and the Hagerman faunas both occupied inland, mid-latitude, terrestrial basin settings. The latitudinal difference between them is 5°.

Evidence suggests that the Hagerman area experienced a wetter climate in the Pliocene than today (Thompson, 1991, 1996), providing a variety of habitats associated with meandering stream and lake ecosystems (McDonald et al., 1996). The Glenns Ferry Formation, within which the Hagerman fauna occurs, is a continuous stratigraphic section of floodplain, fluvial, and lacustrine sequences spanning approximately 1 million years (Figure 2). Previous studies of the



Figure 2. Photo of Glenns Ferry Formation strata on the southern portion of the Hagerman Fossil Beds National Monument. The Snake River can be seen on the right.

Panaca Formation identified horizontal lacustrine and fluvial basin-fill sediments, also spanning about one million years (Stock, 1921; Phoenix, 1948; Mead and Taylor, 2005). The Panaca strata display a change from lacustrine and fluvial sediments in the lower portion to eolian sediments above (Pederson, 1999, 2001) (Figure 3); this indicates a drying of the climate in southeastern Nevada over the depositional history of this formation.



Figure 3. Photo of Panaca Formation strata in northeastern Meadow Valley.

Sporadic Panaca studies have been conducted with regard to the taxa present, geologic setting, biochronological ages, and paleomagnetic dating, but previous researchers have not compared the Panaca fauna with other Blancan

faunas. I conducted my own field collection in the Panaca Formation in Meadow Valley, in addition to synthesizing the results of previous studies. The exposed Panaca Formation is slightly younger in Meadow Valley than in other nearby valleys (Reynolds and Lindsay, 1999). My field work in the Panaca Formation, together with two summer field internships at Hagerman Fossil Beds National Monument, provided experience at both localities.

## CHAPTER 2

### BACKGROUND

#### 2.1 Panaca Study Area

##### 2.1.2 Previous Research

The term “Panaca beds” was first used by Chester Stock (1921) to describe fossil-bearing lacustrine sediments in Meadow Valley, Nevada. Phoenix (1948) later applied the name Panaca Formation to these beds, and he constructed the first geologic map of the Meadow Valley area. Tschanz and Pampeyan (1970) published “Geology and Mineral Deposits of Lincoln County,” in which they described the geologic units of Lincoln County. Tertiary units were further mapped and described by Ekren et al. (1977).

Phoenix (1948) and Ekren et al. (1977) characterized the Panaca Formation as lacustrine and eolian-or-alluvial deposits. However, Pederson et al. (2000a) argued that the formation is primarily eolian and fluvial, with minor amounts of calcareous and siliceous lacustrine/marsh deposits located in the basin center near the town of Panaca. Recent sedimentological research on the Panaca Formation has included the recognition of buried hillslope and colluvial sediments (Pederson, 1999; Pederson et al., 2000a, 2000b, 2001).

Stock (1921) collected fossil material in Meadow Valley for the University of California; he identified *Pliohippus* sp. (horse), as well as fragmentary remains of rhinocerotid and camelid species. Stock (1921) intended to use fossil material from the Panaca area to date the strata, but he was unable to collect enough material to clearly date the formation. Field work in Spring and Meadow valleys

was conducted in 1940-1941 by Guy Haxen and H.S. Gentry from the American Museum of Natural History (AMNH). Further field work in 1961 by AMNH collectors Ted Galusha and Robert Emery in the same area yielded a large number of fossils, which aided in the determination of the Blancan age for the Panaca Formation, but no results were published. Today these fossils are a part of the Frick Laboratories Collection at the AMNH, but much of the AMNH work on the Panaca Formation remains unpublished.

May (1981) used Panaca fossil material collected by the AMNH in his study of the genus *Repomys* (family Cricetidae), which is similar to a woodrat. He defined that genus's temporal and geographic distribution. White (1987, 1991) studied Panaca fossil material repositied at the AMNH to describe the systematics of lagomorphs and document the stratigraphic range of each taxon. He considered the Panaca lagomorph species to be characteristic of Blancan taxa. Mead and Taylor (2005) described a new North American species of sheep-like caprine bovid, *Sinocapra wilddownsi*, from the Blancan-age AMNH Panaca collections. This specimen represents the earliest known occurrence of bovids in North America.

Mou (1997, 1999) conducted the most extensive work on the Panaca fauna to date. She described several new species of arvicoline rodents (voles), including the first North American appearance of the genus *Mimomys*. She described the species *M. panacaensis* from the Panaca Formation. Examination of schmelzmuster (enamel microstructure) of *M. panacaensis* teeth led to the identification of primitive microstructure characteristics and the conclusion that



this species evolved from a species that immigrated from Eurasia (Mou, 1998; Bell et al., 2004). Other arvicoline species that have been recovered from the Panaca Formation include endemic species *Nevadomys fejfari*, *N. lindsayi*, and *N. downsi* (Mou, 1999). Mou (1999) also described a new genus of shrew, *Paranotiosorex panacaensis* from this formation. Mou (1999) used biochronology to demonstrate that the Panaca fauna belongs to the early Blancan land mammal age. Reynolds and Lindsay (1999) used the Panaca fauna from Lake, Spring, and Meadow valleys to determine the timing of basin fill. They concluded that the sedimentary fill within the three basins is not precisely the same age, so the faunas are not synchronous in age; the Panaca fauna in Meadow Valley is early Blancan, while the other two are Late Hemphillian (Reynolds and Lindsay, 1999).

Lindsay et al. (2002) used the Panaca fauna to determine the stratigraphic position of the boundary between the Hemphillian and Blancan land mammal ages in Nevada. They correlated the first appearance of the European arvicoline rodent genus *Mimomys* with the base of the Blancan land mammal age. Mou (1999) resolved the absolute age of the Hemphillian-Blancan boundary by sampling five sections in Meadow Valley for magnetostratigraphy. She used  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of ash layers to derive an age of 4.9 to 5.0 Ma for the age of the Blancan-Hemphillian boundary in the Panaca Formation.

No previous studies have focused on faunal diversity within the Panaca Formation, or its relationship to other Blancan faunas. A complete chronology of geological and paleontological studies of Meadow Valley can be found in Table 1.

Table 1. Chronology of researchers and studies conducted on the Panaca Formation in Lincoln County, Nevada. \*Fossil material list available at UCMP website at <http://www.ucmp.berkeley.edu/science/collections.php>; \*\*Frick (F:AM) collections are housed at the AMNH and fossil records are listed in the AMNH website at <http://research.amnh.org/paleontology/>; Miomap lists the specimens from UMCP, Frick (F:AM), and ULAP with extensive data at <http://www.ucmp.berkeley.edu/miomap/>. See page 24 for explanation of abbreviations.

Chronology of Panaca Researchers and Studies				
Year	Researchers	Publication Title or Work	Repository	Other Notes
1903	Spurr	Descriptive geology of Nevada south of fortieth parallel and adjacent portions of California		
1915	Carpenter	Ground water in southeastern Nevada		
1921	Stock	Later Cenozoic mammalian remains from Meadow Valley Region, southeastern Nevada	UCMP*	
1939	Stirton	The Nevada Miocene and Pliocene mammalian faunas as faunal units		
1940-1941	Haxen and Gentry	Field collection of Meadow and Spring valleys fossil material	Frick/AMNH**	No publications
1948	Phoenix	Geology and ground water of the Meadow Valley Wash drainage area, Nevada, above the vicinity of Caliente		
1956	MacDonald and Pelletier	The Pliocene mammalian faunas of Nevada, U.S.A.		Compilation of Nevada fauna
1961	Galusha and Emery	Field collection of Meadow and Spring valleys fossil material	Frick/AMNH**	No publications
1970	Tschantz & Pampeyan	Geology and Mineral Deposits of Lincoln County, Nevada		Bulletin 73
1977	Ekren et al.	Geologic map of Lincoln County, Nevada		Map with description
1981	May	<i>Repomys</i> (Mammalia: Rodentia, gen. nov.) from the late Neogene of California and Nevada	Frick/AMNH**	
1987	Repenning	Biochronology of microtine rodents of the United States		

Table 1 continued. Chronology of researchers and studies conducted on the Panaca Formation in Lincoln County, Nevada.

1987	White	The Archaeolaginae (Mammalia: Lagomorpha) of North America, excluding <i>Archaeolagus</i> and <i>Panolax</i>	Frick/AMNH**	
1991	White	North American Leporinae (Mammalia: Lagomorpha) from late Miocene (Clarendonian) to latest Pliocene (Blancan)	Frick/AMNH**	
1992-1997	Lindsay, Mou and Reynolds	Collaboration between UALP and SBCM and field collection	UALP & SBCM	
1996	Mou	A new arvicoline species (Mammalian: Rodentia) from the Pliocene Panaca Formation, southeast Nevada		Abstract/ Desert Research Symposium
1997	Mou	A new arvicoline species (Rodentia: Cricetidae) from the Pliocene Panaca Formation, southeast Nevada	UALP	
1998	Mou	Schmelzmuster of <i>Mimomys panacaensis</i>	UALP	
1999	Reynolds & Lindsay	Late Tertiary basins and vertebrate faunas along the Nevada-Utah border		Basin analysis based on mammals
1999	Mou	Biochronology and magnetostratigraphy of the Pliocene Panaca Formation, Southeast Nevada	UALP	PhD Dissertation
1999	Pederson	A long-term record of climate-controlled hillslope sedimentation		PhD Dissertation
2000	Pederson	Ancient hillslope deposits: Missing links in the study of climate controls on sedimentation		
2000	Pederson	Neogene through Quaternary hillslope records, basin sedimentation, and landscape evolution of southeastern Nevada		Field Guide 2
2001	Pederson	Comparing the modern, Quaternary, and Neogene records of climate-controlled hillslope sedimentation in southeast Nevada		

Table 1 continued. Chronology of researchers and studies conducted on the Panaca Formation in Lincoln County, Nevada.

2002	Lindsay et al.	Recognition of the Hemphillian/Blancan boundary in Nevada		Based on Cricetids
2005	Mead & Taylor	New species of <i>Sinocapra</i> (Bovidae, Caprinae) from the lower Pliocene Panaca Formation, Nevada, USA	F:AM**	
2006	Hollenshead & Mead	Early Pliocene <i>Crotaphytus</i> and <i>Gambelia</i> (squamata: Crotaphytidae) from the Panaca Formation of southeastern Nevada	UALP	
2009-2011	Meyers	Field work and collection in Meadow Valley	Nevada State Museum satellite repository at UNLV	Master's Thesis and field work

This compilation of previous research will assist future investigators in obtaining background information and locating Panaca collections.

### 2.1.2 Geographic Setting

The Panaca Formation is recognized in Meadow, Lake, and Spring valleys, as well as in the northeastern portion of the Caliente Caldera Complex of Lincoln County, Nevada and adjacent Iron County, Utah (Figure 4). These four areas of exposure represent four separate non-contiguous depositional basins during the Pliocene. I have concentrated on the northeastern portion of Meadow Valley, which is the most fossiliferous area. The study area is located north of Highway 319, east of Highway 93, and to the southwest of Black Hill within the Condor Canyon and Panaca USGS 7.5 minute series topographic quadrangles (Figure 4). This inland, mid-latitude basin is situated at approximately 37°47'5" north latitude and 114°23'3" west longitude. The elevation ranges from 4,750 to approximately 5,100 feet above sea level.

### 2.1.3 Geologic Setting

The Panaca Formation has been the subject of limited previous study and varying environmental interpretations (Stock, 1921; Phoenix, 1948; Tschanz and Pampeyan, 1970; Ekren et al., 1977; Mou, 1999; Pederson, 1999; Pederson et al., 2000a, 2000b, 2001). Lincoln County, which lies within the Basin and Range geologic province, contains abundant exposures of Paleozoic and Cenozoic rocks. During the Paleozoic Era, this portion of Nevada was a passive margin covered by shallow seas depositing mostly carbonate sediments. Mesozoic remnants are recognized by the generally north-striking central Nevada thrust

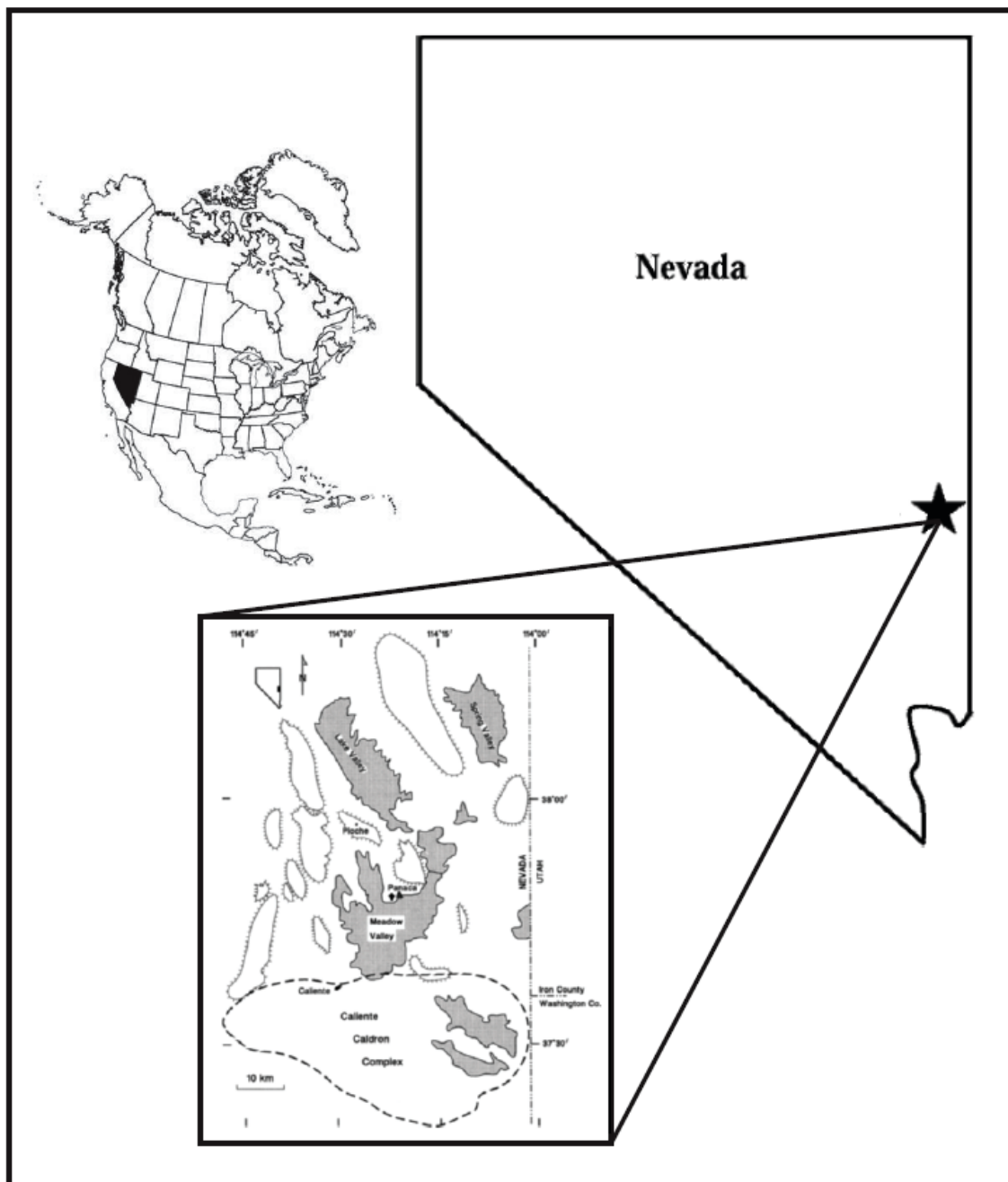


Figure 4. Star depicts location of the town of Panaca in Nevada. Insert map shows the location of the Panaca Formation outcrops in Lincoln County, Nevada in gray. Hachure areas depict highlands. Modified from Mou, (1999); Hollenshead and Mead, (2006).

belt and a series of folds and thrust faults in eastern Nevada, due to the Sevier orogeny (Taylor and Switzer, 2001). Cenozoic normal faulting associated with crustal extension formed elongated, north-south-oriented mountain ranges separated by wide, sediment-filled basins. Volcanism in Nevada migrated southward during the Eocene through Miocene epochs, ending with ignimbrite eruptions from calderas (Taylor et al., 1989; Axen et al., 1993). The ash-flow tuffs of the Indian Peak Caldera on the northern edge of Meadow Valley are 32-27 Ma (Late Eocene to Oligocene) (Best et al., 1989; Axen et al., 1993), while the Caliente Caldera ash flows on southern edge of Meadow Valley is dated at 26-15 Ma (Oligocene to early Miocene) (Axen et al., 1993). Meadow Valley extension and associated faulting occurred in the Pliocene Epoch (Taylor et al., 1989), creating a setting characterized by internal drainage and deposition in several adjacent, small extensional basins. The resulting basin-fill deposits are flat-lying with sediment derived from the surrounding uplands. Erosion and deposition in the basins was influenced by the distribution of Paleozoic limestone and the volcanic calderas (Reynolds and Lindsay, 1999). A fairly large internal basin lake is thought to have occupied Meadow Valley (Phoenix, 1948). Today, Meadow Valley drains into the Colorado River through Meadow Valley Wash (Tschanz and Pampeyan, 1970), but in the Pliocene there was no drainage outlet.

Tschanz and Pampeyan (1970) described the Panaca Formation as consisting of white, gray-green, light brown, and pink sand, silt, and clay. They interpreted these strata to represent a lacustrine depositional environment.





Ekren et al. (1977) described the Panaca and Muddy Creek formations as flat-lying, varicolored, tuffaceous siltstones, sandstones, and mudstones with locally thin beds of diatomite or diatomite-like ash and gravels (Figure 5). They dated the Panaca as Pliocene, based on mammal fossils.

Along the northeastern edge of the Meadow Valley basin, the Cambrian Highland Peak Limestone is exposed, unconformably overlain by the Panaca Formation (Figure 6). The basal Panaca beds consist of gray and tan siltstone and sandstone, and dark brown carbonaceous siltstone. Greenish-gray

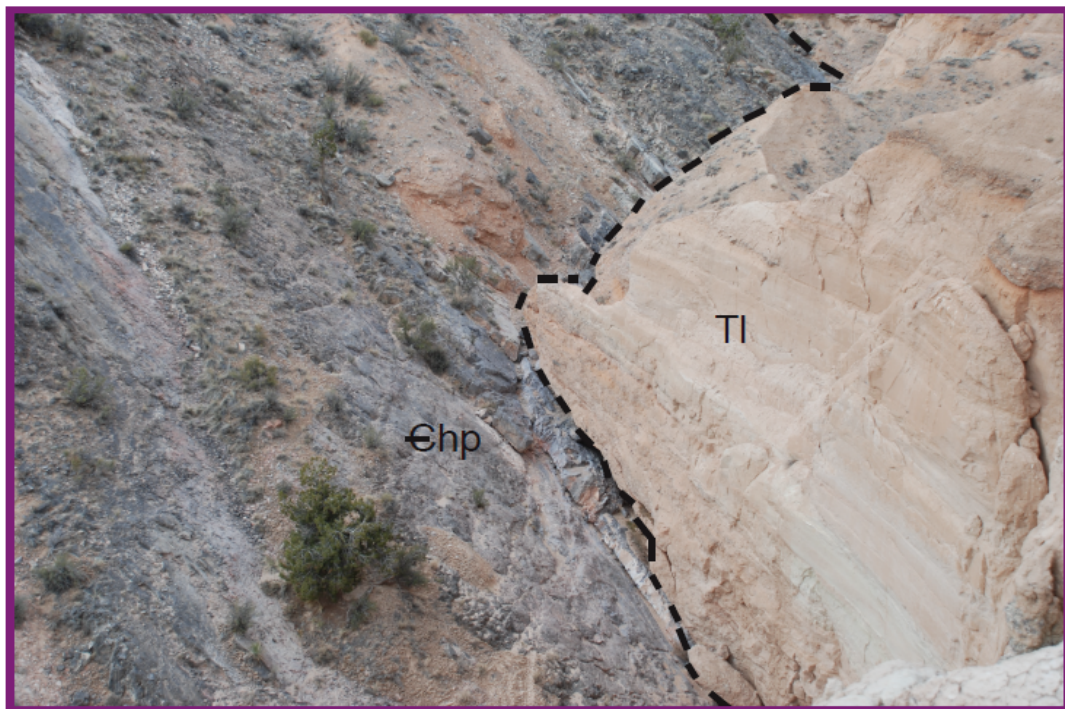


Figure 6. Photo of Cambrian Highland Peak Limestone (€hp) unconformably overlain by Pliocene sediments of Panaca (TI) colluvium, sandstone, and siltstone.

lacustrine sediments occur in conspicuous outcrops directly adjacent to the town of Panaca. Mou (1999) reported gastropods and ostracods in these sediments,

and she stated that most fossil sites within the Panaca Formation occur on the margin of the Meadow Valley basin.

Pederson (1999) differed from previous researchers; he interpreted the Panaca as predominantly fluvial and eolian deposition, with minor amounts of calcareous and siliceous lacustrine sediments at the basin center. He concluded that the basin is largely unfaulted, retaining its depositional dip. He interpreted the slight dip to be due to basin-center sagging. Pederson et al. (2000a, 2000b, 2001) identified colluvium wedges in the fluvial and eolian strata on the basin margins. The basin margins are composed of imbricated pebble-to-cobble conglomerate within a light reddish-brown, clayey-silt matrix. They interpreted these lithologies to be the product of fluctuating amounts of coarse colluvium due to climatic change and associated fluctuations in precipitation.

#### 2.1.4 Age of the Panaca Formation

The age of the Panaca Formation has been determined from two lines of evidence: biostratigraphy and magnetostratigraphy. Faunal evidence points to the oldest Panaca sediments as Hemphillian land mammal age, but most of the Panaca local fauna represents an early Blancan land mammal age (Mou, 1999; Reynolds and Lindsay, 1999). Reynolds and Lindsay (1999) reviewed Meadow Valley fossil specimens and determined that rhinocerotid specimens recovered from a site near the center of the basin indicate a Hemphillian age, but they concluded that other large and small mammals from Meadow Valley represent a Blancan land mammal age. Mou (1999) discussed six taxa within the Panaca Formation in Meadow Valley that support the conclusion that the Panaca local

fauna age is early Blancan, with the exception of the rhinocerotid collected by Stock (1921).

Mou (1999) used magnetostratigraphy to correlate and date four sections within Meadow Valley. Two major fossil localities in the exposed section of the Panaca Formation were dated mid-Gilbert geochron. Figure 7 shows the placement of two Panaca fossil localities within the Geomagnetic Polarity Time Scale (GPTS); the figure also shows the position of the Hagerman Fossil Beds within the Glens Ferry Formation. This analysis, along with an  $^{40}\text{Ar}/^{39}\text{Ar}$  ash date of  $4.64 \pm 0.03$  Ma, permitted Mou to date the Hemphillian-Blancan boundary to be 4.95 Ma in Meadow Valley. This boundary occurs near the bottom of the exposed portion of the Panaca Formation in Meadow Valley (Figure 7). Ashes higher in the section were analyzed by R. Shroba of the USGS, but they were too fine-grained to be isotopically dated (Mou, 1999). No studies have determined the age of the top of the Panaca Formation as the sediments are eolian. These sediments do not preserve a paleomagnetic signature, nor do they contain volcanic ash beds.

## 2.2 Hagerman Fossil Beds Study Area

### 2.2.1 Previous Research

Vertebrate fossils in the Hagerman, Idaho area were discovered in the 1920s by rancher Elmer Cook (Gazin, 1936; Graham, 2009). Geologist H. T. Stearns of the United States Geological Survey alerted the United States National Museum (USNM) of Cook's discovery of fossil horse material (Gazin,

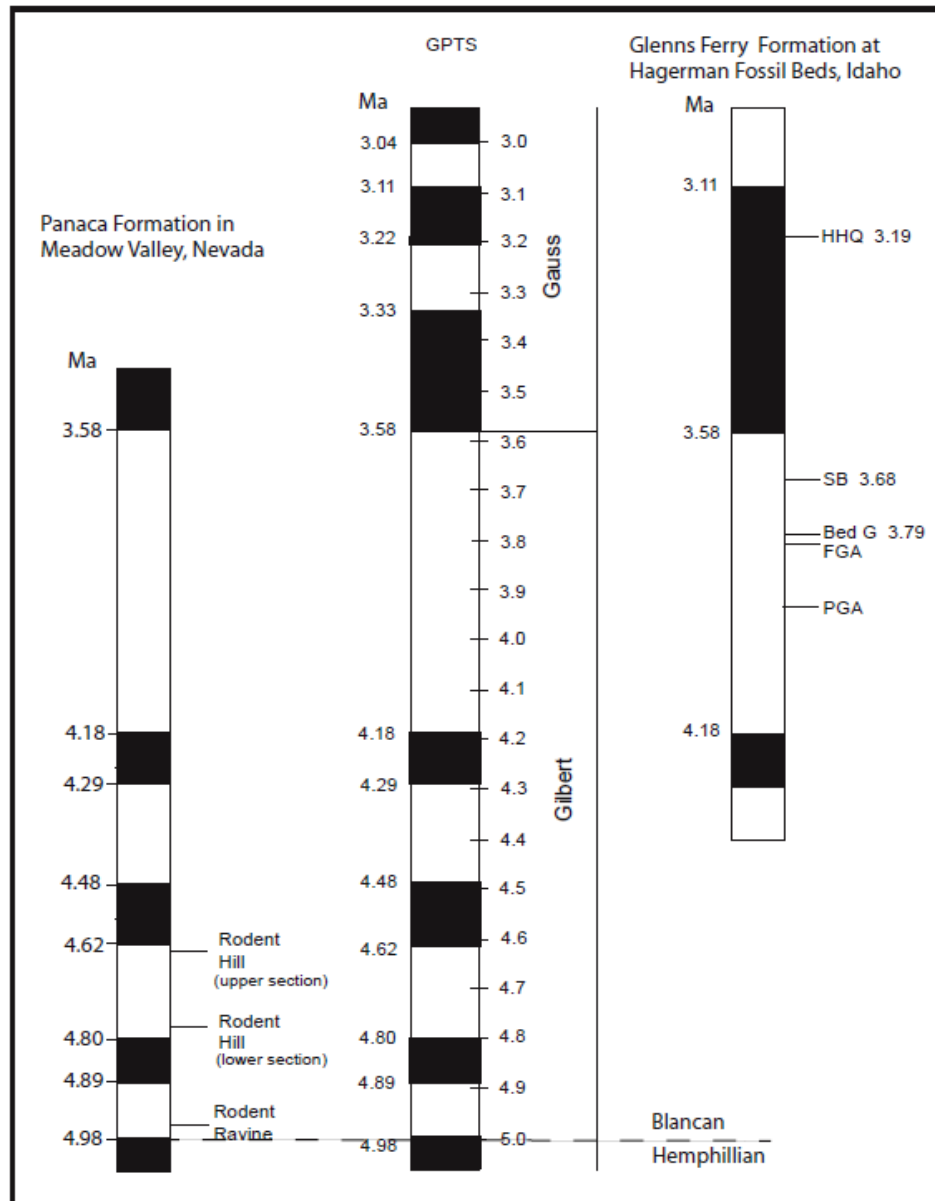


Figure 7. A comparison of the magnetostratigraphy between Panaca Formation in Lincoln County, Nevada and the Glens Ferry Formation at Hagerman Fossil Beds National Monument (HAFO), Idaho. GPTS dates follow Berggren et al. (1995) given in Ma. The Panaca Formation dates are from Mou's three fossil localities; two are from lower and upper sections at the Rodent Hill locality and one from the Rodent Ravine locality. The Glens Ferry column is composed of radioisotopic dates (basalts and ashes) and geomagnetic correlations from Ruez (2009b). The basalt dates for the SB and Bed G are Ar-Ar analyses from Hart and Brueske (1999). The reversal between 3.33 and 3.22 does not appear at HAFO. Abbreviations: *FGA*, Fossil Gulch Ash; *GPTS*, geomagnetic polarity time scale; *HHQ*, Hagerman Horse Quarry, *PGA*, Peters Gulch Ash; and *SB*, Shoestring Basalt. Modified from Mou (1999); Bell et al. (2004); and Ruez (2009a).

1936; Graham, 2009). The USNM collected at Hagerman from 1929 to 1934 (Bjork, 1970; Ruez, 2009a), and subsequently many other museums and research institutions have conducted studies in the Hagerman area. In the 1930s, workers such as Gidley, Gazin, and Gilmore collected and published numerous papers on the newly discovered diverse fauna of Hagerman. Gilmore (1933) described a new species of emydid turtle. Gidley described the horse *Plesippus shoshonensis* (now *Equus simplicidens*) from the site that was later named Gidley's Quarry (Bjork, 1970). Gidley's Quarry, now called the Hagerman Horse Quarry, has yielded more than 150 horse skulls and numerous horse post-cranial bones (Bjork, 1970). Horse skulls and post-cranial material continue to be excavated from these upper Glens Ferry Formation consolidated sands today. The Hagerman Horse Quarry (HHQ) is considered one of the six most important fossil horse sites in the world (NPS website). Gazin described many Hagerman taxa, including peccaries (1938), mustelids (1934), felids (1933), an antilocaprid (1935), and he did extensive work in Gidley's horse quarry (1936).

Malde and Powers (1962) mapped and described the geology of the Western Snake River Plain, including the Hagerman area. Bjork (1970) described the geologic history and sedimentology of the Hagerman area and conducted an extensive systematic study of Hagerman carnivores. Vertebrate studies in the 1960s, led by C. W. Hibbard and his colleagues from the University of Michigan, included such groups as frogs, insectivores, lagomorphs, rodents, birds, and fish (Ruez, 2000b). Neville et al. (1979) studied the paleomagnetism of the Glens Ferry Formation. Neville (1981) used magnetostratigraphy to

constrain the age of the formation and to correlate three Glenns Ferry local faunal assemblages, including the Hagerman fossil assemblage (Figure 7).

Large collections of Hagerman fossils are repositied at the United States National Museum (USNM), the University of Michigan Museum of Paleontology (UMMP), the Idaho Museum of Natural History (IMNH), and Hagerman Fossil Beds National Monument (Ruez and Gensler, 2008). Specimens of the famous Hagerman horse, along with other Hagerman fossils, reside in more than thirty museums in the U.S. and other countries (Bush, 2000; Applegate et al., 2008; P. Gensler, personal communication).

Hagerman Fossil Beds National Monument, comprising 4,352 acres (P. Gensler, personal communication), was established in 1988 as a unit of the National Park Service. The paleontological record is preserved in a continuous stratigraphic section spanning nearly a million years of time (Ruez and Gensler, 2008). The number of specimens and the distribution of localities in the Glenns Ferry Formation mark it as one of the most densely fossiliferous Pliocene sections in the world (Ruez, 2009b). The fossil-rich Glenns Ferry Formation preserves the flora and fauna of a complex ecosystem, including lacustrine, pond and marshland, riparian, and grassland savanna. To date, over 220 species of flora, invertebrates, and vertebrates have been identified from over 550 documented fossil localities within the Monument (P. Gensler, personal communication; Graham, 2009). Hagerman vertebrate remains are found throughout the sandy and muddy facies in the arroyos and ravines, but the channel sands and lags are especially rich in microfossil material. These

channel sands are exposed by wind, forming exposures that are locally called “blowouts.” This results in surface concentrations of isolated teeth and small bones that are recovered by crawling across the sand scanning the surface. These concentrations produce fish vertebrae and spines, frog limb bones, and isolated rodent teeth, along with many small bones (Figure 8). Recovery of small specimens is also conducted through the annual screenwashing of approximately 50 gallons of sediment.



Figure 8. Surface-collected fish vertebrae and pharyngeal arches, frog limb bones, rodent teeth and bone elements, and crayfish gastrolith from locality FS-09-38, collected during 2009 field season at HAFO. Scale in centimeters.

Presently, locality data are assiduously recorded and mapped for every specimen collected on the monument. The use of GPS receivers and ArcGIS

mapping have greatly increased the precision of recorded fossil locations. The diverse fauna provides a good sample of Blancan species diversity in the Snake River Plain region of south-central Idaho.

### 2.2.2 Geographic Setting

Hagerman Fossil Beds National Monument (HAFO) is located near the town of Hagerman on the Western Snake River Plain in Twin Falls County of south-central Idaho (Figure 9). The monument is bounded on the east by the mid-channel of the Snake River. The monument includes arid slopes that extend from the rivers edge to the top of the Bruneau Plateau to the west. The sedimentary bluffs are incised by arroyos and gullies that extend up to a mile, with slope angles that range from 35° to 70° (Farmer and Riedel, 2003). HAFO is located within the U.S.G.S. Hagerman 7.5 minute topographic quadrangle, in two townships. This inland mid-latitude basin is situated at approximately 42°48'44" north latitude and 114°53'55" west longitude; the elevation ranges from 2,800 to 3,400 feet.

### 2.2.3 Geologic Setting

The Glens Ferry Formation is located in south-central Idaho on the Western Snake River Plain (Malde and Powers, 1962; Bjork, 1970; Malde 1972). The Snake River Plain is noted for its extensive middle Miocene volcanic and tectonic activity. The broadly U-shaped Snake River-Yellowstone Plateau is divided into the eastern and western plains. The northwest-to-southeast-trending trough of the Western Snake River Plain (Figure 10) experienced intermittent faulting throughout the Pliocene and Pleistocene (Bjork, 1970). Minor normal



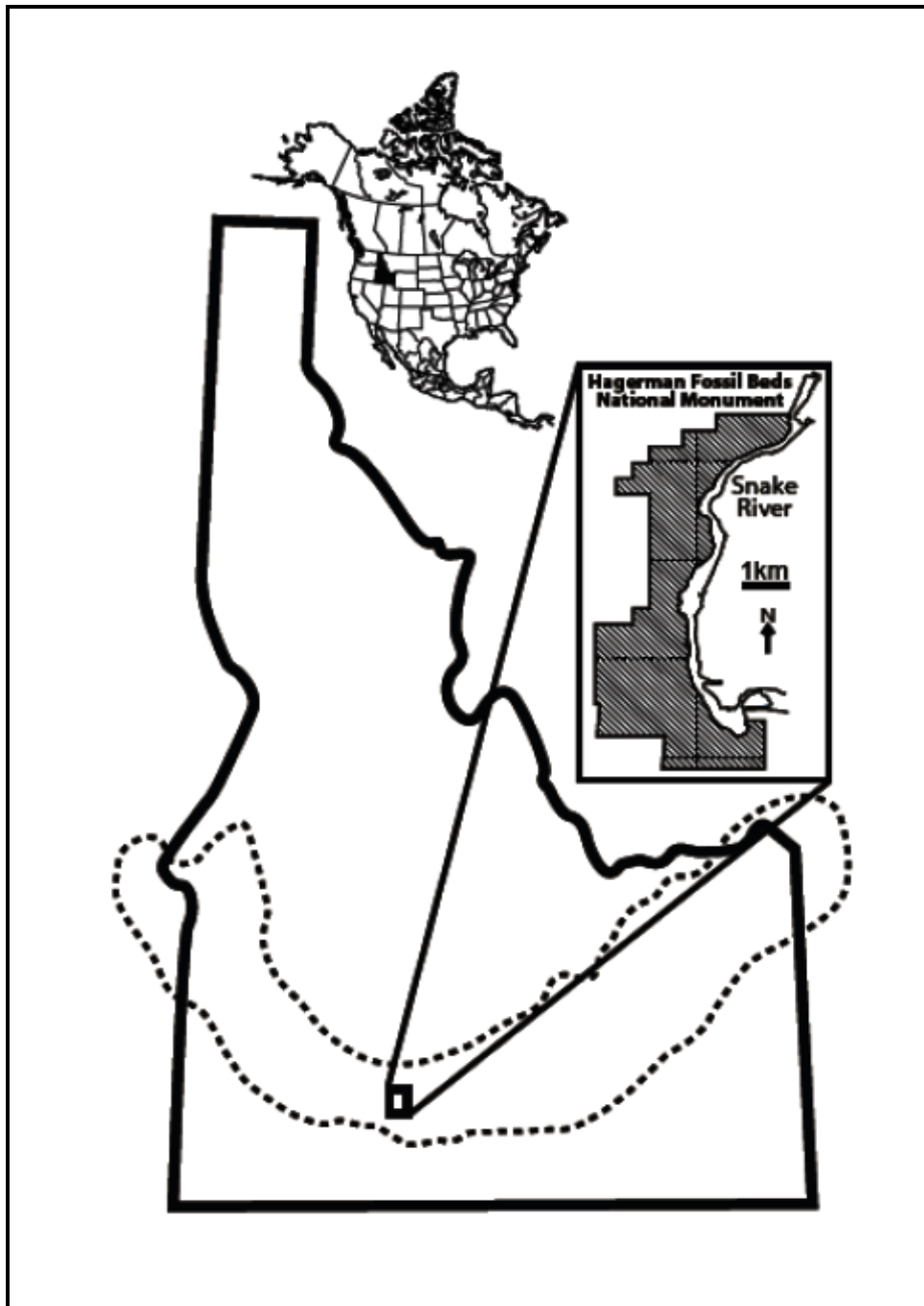


Figure 9. Location of Hagerman Fossil Beds National Monument (HAFO), Idaho. The gray area on the insert map shows the boundaries of HAFO to the west of the Snake River in Twin Falls County. The dotted line outlines the Snake River-Yellowstone Plateau. From Reuz, 2009a.

faults that resulted from this activity can be seen in the Glenns Ferry Formation in the west wall of the Snake River Canyon at Hagerman. The Glenns Ferry overlies basalt flows of the more than 150-meter-thick Banbury Basalt and it is capped by the Pleistocene Tuana Gravel (Malde and Powers, 1962; Bjork, 1970).

The Glenns Ferry Formation, which is approximately 180 meters thick, is part of the Pliocene/Pleistocene Idaho Group of the Western Snake River Plain (Figure 8). The Glenns Ferry Formation consists of intertonguing lacustrine, fluvial, and floodplain facies, extending from the vicinity of Hagerman westward to the Idaho-Oregon border (Malde and Powers, 1962; Bjork, 1970). The lacustrine facies is composed of massive layers of tan silt and fine-grained sands (McDonald et al., 1996). Some thin beds of ripple-marked sandstone and siltstone occur in Peters Gulch in the southern portion of the Monument. The fluvial facies is composed of drab, pale brownish-gray sandstone, with some siltstone, in planar and cross-bedded layers (Malde and Powers, 1962). Ruez (2009b) noted that the 10-cm-thick, mixed claystone-siltstone-sandstone unit beneath the crossbedded channel sandstone are the most fossiliferous. These strata have been interpreted as sediments that were deposited by rivers, lakes, and on floodplains in a subsiding basin from Miocene through early Pleistocene time (Thompson, 1996).

Bjork (1970) characterized the thick floodplain sediments as fine-grained, graded beds of light-olive, silty, light-to-dark claystone with massive siltstone and sandstone. He divided the flood plain sequence in the Glenns Ferry Formation in the Hagerman Valley into three units. His lower unit consists of flood-plain

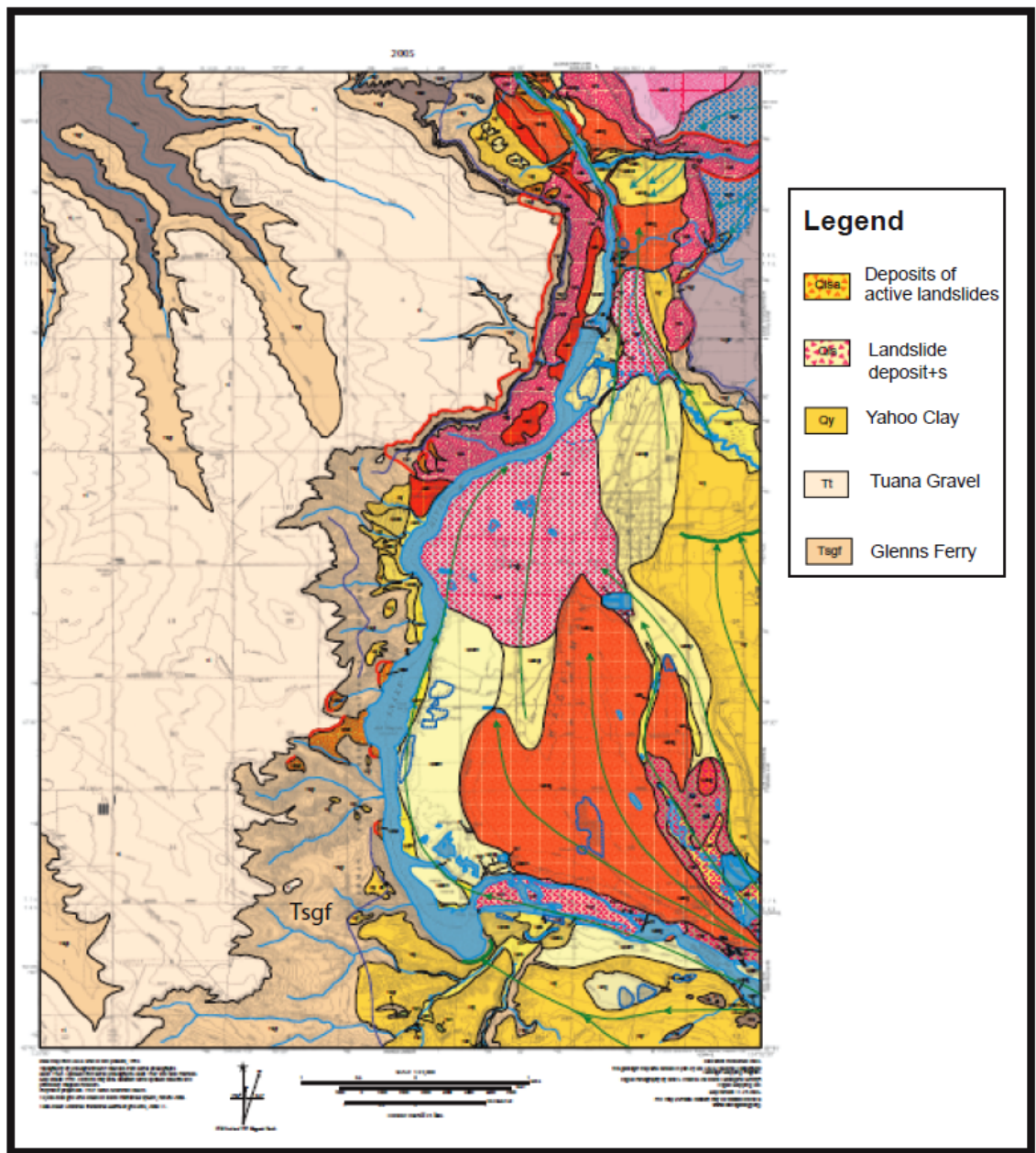


Figure 10. Geologic Map of the Hagerman Quadrangle, Gooding and Twin Falls Counties, Idaho. The Glenns Ferry Formation is labeled as Tsgf and is the salmon-colored area to the west of the Snake River. Modified from [idahogeology.org](http://idahogeology.org) website.

deposits, his middle unit consists of marsh-pond strata deposited during a high-stand period of Lake Idaho, to the west of Hagerman, and his third unit consists of more flood-plain deposits. Bjork's upper flood-plain unit contains carbonate nodules, indicating long dry periods.

Discontinuous volcanic ash units and two basalts are interbedded within the Glenns Ferry Formation flood-plain sediments. These have been used for radiometric dating (Malde and Powers, 1962). Thin beds of paper shales consisting of decomposing plant material are present in the marsh-pond unit. The Hagerman Horse Quarry, near the top of the Glenns Ferry Formation, consists of fluvial deposits; these are well-consolidated coarse sandstone and fine gravel. The Glenns Ferry strata have preserved a diverse assemblage of Blancan age fossils (Ruez and Gensler, 2008).

#### 2.2.4 Age of Glenns Ferry Formation

The age of the Glenns Ferry Formation has been determined by vertebrate biochronology, magnetostratigraphy, and radioisotopic dating of basalts and ash beds. According to a recently revised Blancan chronology (Bell et al., 2004), the Hagerman Fossil Beds fauna is middle Blancan, or stage Blancan III of Repenning's arvicoline divisions (Figure 1), and extends from approximately 4.1 to 3.0 Ma. The geomagnetic polarity patterns from Hagerman Fossil Beds have been interpreted to span the Gilbert-Gauss boundary (Neville et al., 1979), placing the age between 4.18 and 3.33 Ma (Ruez, 2009a). Radiometric dating of the ashes and basalts of the Hagerman area has been problematic. Ruez (2009a) evaluated the previous radiometric dating studies,

and he compiled a composite stratigraphic column that includes radiometric dates and also geomagnetic reversals (Figure 7). He concluded that the Hagerman local fauna ranges in age from approximately 4.0 to 3.2 Ma. The magnetostratigraphy thus places the sediments at Hagerman Fossil Beds about a million years younger than the Panaca sediments (Figure 7).

### 2.3 Summary

The Glens Ferry Formation is a continuous section of lacustrine, floodplain, and fluvial strata spanning one million years, while the fluvial, lacustrine, and eolian Panaca sediments are discontinuous. The Panaca fossils are found in fine-grained fluvial sands on the outer margins of the basin. Many Hagerman Fossil Beds fossils are concentrated in sand channels, but a variety of fossils are found stratigraphically throughout the monument. Previous studies of biostratigraphy, magnetostratigraphy, and radioisotopic dating place the both vertebrate faunal assemblages in the Blancan land mammal age, but the sediments differ slightly in age. The Panaca taxa have been placed in Repenning's Blancan I division (Figure 1), while the Hagerman taxa are assigned to Blancan III, approximately 1 million years younger.

## CHAPTER 3

### METHODOLOGY

#### 3.1 Field and Lab

Initial field work for this project began with mapping of the outer boundaries of the Panaca Formation on USGS Condor Canyon and Panaca 7.5' quadrangle maps in Meadow Valley. Further field work involved surveying for fossiliferous sites and identifying localities for collection on the northeastern margin of Meadow Valley. Field collection began when I received Bureau of Land Management (BLM) collecting permits [surface survey permit N-86852 and excavation permit N87189] for BLM lands in Meadow Valley. The BLM permits allowed for surface collecting in seven sections and five one-meter test plots.

Field methods included fossil surface collection and screenwashing of matrix to collect vertebrate fossil material. I collected fossil material from twenty-four localities and four test plots in Meadow Valley. When fossils were discovered, either as surface float or *in situ*, I recorded the latitude and longitude coordinates in NAD83, along with elevation, with a Garmin GPSMAP 76Cr mapping unit. I plotted these points on a USGS 7.5' quadrangle map. I later downloaded the GPS data onto a Google map and plotted the locality points in ArcGIS on a quadrangle map. All field data were collected according to the Paleontological Locality field data sheet (Form 8270-3) and standards set by BLM.

I collected a 2-gallon bucket of sediment at each prospective site for later screenwashing. Test plot sites were selected based on the amount and diversity

of bone located on the surface and found in the initial screenwash. Horizons containing fossil bone in selected sites were worked along the strike of the horizon with hand tools. Sediment was first sieved through a 17" by 17" wooden box with ¼" hardware cloth to remove gravel, roots, and twigs. I then screenwashed the sediment using a set of three nested sieves according to methods described by Cifelli et al. (1996) and McKenna et al. (2005). Sieve sizes were 1 mm, .7 mm, and .5 mm. I submerged the nested sieves in a large tub of water to collect the microfossils and decrease the amount of sediment; the resulting concentrate was air dried. I screenwashed approximately 300 pounds of sediment. The screenwashing was done in Cathedral Gorge State Park Campground, with the consent of the park staff. This site had the advantages of being close to the field area, having a source of water, and having a place to dispose of waste sediment (in a stream channel near the edge of the campground). The dried concentrate was bagged and taken to the University of Nevada Las Vegas (UNLV) lab for further investigation. Most of the small rodent and bird material came from screenwashing of bone-rich horizons of floodplain and lacustrine very-fine sand. Visually conspicuous bone and teeth fragments were picked in the field and placed in vials and bags.

In the lab, the screenwashed sediment samples were examined for microfossils with the aid of a binocular microscope. I brought the Panaca microfossils to HAFO where I photographed them using a mounted Nikon camera (Figure 11). I identified the fossils to the lowest taxonomic classification possible using literature resources and also using comparative material in the



Figure 11. Surface-collected phalanges, bird bone, horse tooth fragment, and fragmented rabbit bones from the Panaca Formation. Scale in centimeters.

collections at Hagerman Fossil Beds and San Bernardino County Museum (SBCM). Further identification of selected specimens was completed by collaborating with other researchers. Richard White of the International Wildlife Museum in Tucson assisted with the identification of artiodactyl phalanges. James Mead of East Tennessee State University verified the *Sinocapra* phalanges and assisted with Squamata descriptions. Bob Chandler of Georgia College and State University identified the avifauna from Panaca and assisted with bird element descriptions. Chris Sagebiel, collections manager at the SBCM, assisted with camelid, lagomorph, and some rodent identification.

I cleaned larger specimens with a small brush under running water. I placed all microfauna specimens, including post-cranial material and teeth, into glass vials with hand-written curation labels. Each isolated tooth is protected in a gel capsule in glass vials, and the vial is labeled with identification and provenance data. I placed larger specimens in padded archival boxes with



curation labels. Where possible, I glued fragmented or broken specimens with Butvar-98 in alcohol.

I measured all bones with a dial caliper. I measured the dimensions of the rabbit and rodent teeth by using an ocular micrometer calibrated to a millimeter scale in a binocular microscope. Dimensions of teeth are maximum dimensions, read to the nearest 0.01 mm. The transverse width dimensions were measured perpendicular to the anterior-posterior length dimensions. All tooth measurements are maximum dimensions regardless of occlusal wear.

Lagomorph measurements follow the methodology of White (1987, 1991), discussed in Chapter 4. Avian descriptive bone terminology follows Howard (1929). Measurements of larger specimens were obtained using a metric dial caliper and follow bone measurement guidelines of Von den Driesch (1976).

Some of the fossil specimens collected in this study are poorly preserved and have little or no diagnostic value. Many of these specimens are fragmented, post-cranial bones that are not included in the systematic description portion of this thesis (Chapter 4). However, these specimens are listed in Appendix 1, to provide a complete list of all my collected vertebrate material from the Panaca Formation.

My summer internships at Hagerman Fossil Beds National Monument (summers of 2009 and 2010) included monitoring and surface collecting at known fossil localities, surveying for new localities, GPS coordinate collection, locality data collection, plaster jacketing of fragile specimens, screenwashing and picking of material from fossiliferous sites, and maceration. Other duties included

ArcGIS mapping of fossil localities for monitoring and surveying, photographing fossil sites and specimens, identifying specimens, archiving photos and data sheets, and cataloging of fossil specimens. My familiarity with the Hagerman fauna, including specimens I collected, provided an opportunity for this comparative study of two Blancan faunas.

### 3.2 Stratigraphy

The character of the Panaca exposures in Meadow Valley is badland topography in which some areas have overly steep slopes and are inaccessible. I used a Jacob's staff and Brunton pocket transit to construct stratigraphic columns (Plates 1 & 2) of the Panaca Formation, following standard methodology (Compton, 1985). The precise locality of the measured sections is shown on Figure 12. I measured the stratigraphic thickness of the "Limestone Corner" exposure in "Owl Gulch." This exposure is a vertical cliff, 25 meters high (Plate 1). In order to measure the thickness of distinctive lithologic units in this exposure, I tied red flagging at one-meter intervals on a rope, and suspended the flagged rope down the exposure from above. The second section (Plate 2) was measured with a Jacob's staff until steepness of the slope warranted moving laterally to continue up-section. A distinctive marker bed was traced to the closest exposure to continue upward measurement. Lithologies were described in the field by laterally following sediments and the use of a 10x handlens. Fossil localities are placed in proper context on the stratigraphic column. Fossil horizons of previous workers are not shown, as the exact locations of those

Panaca Formation Stratigraphic Column at "Limestone Corner"

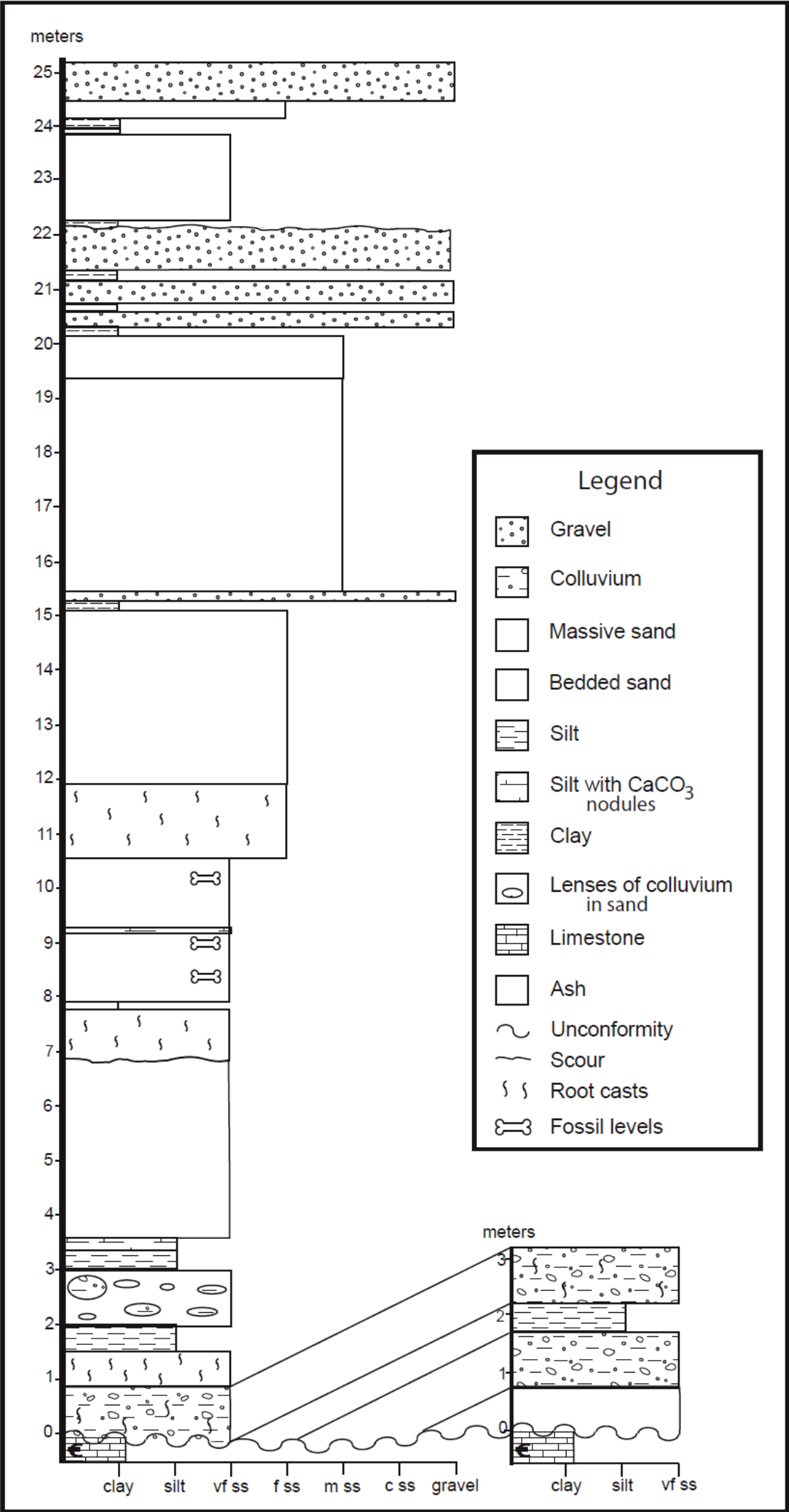


Plate 1. Stratigraphic column of the exposed Panaca Formation lying unconformably on Cambrian limestone near the "Limestone Corner" in Meadow Valley. The two stratigraphic columns are 11 meters apart in the ravine. Fossil levels are indicated.

Upper Portion of the Panaca Formation Stratigraphic Column near  
the "Limestone Corner"

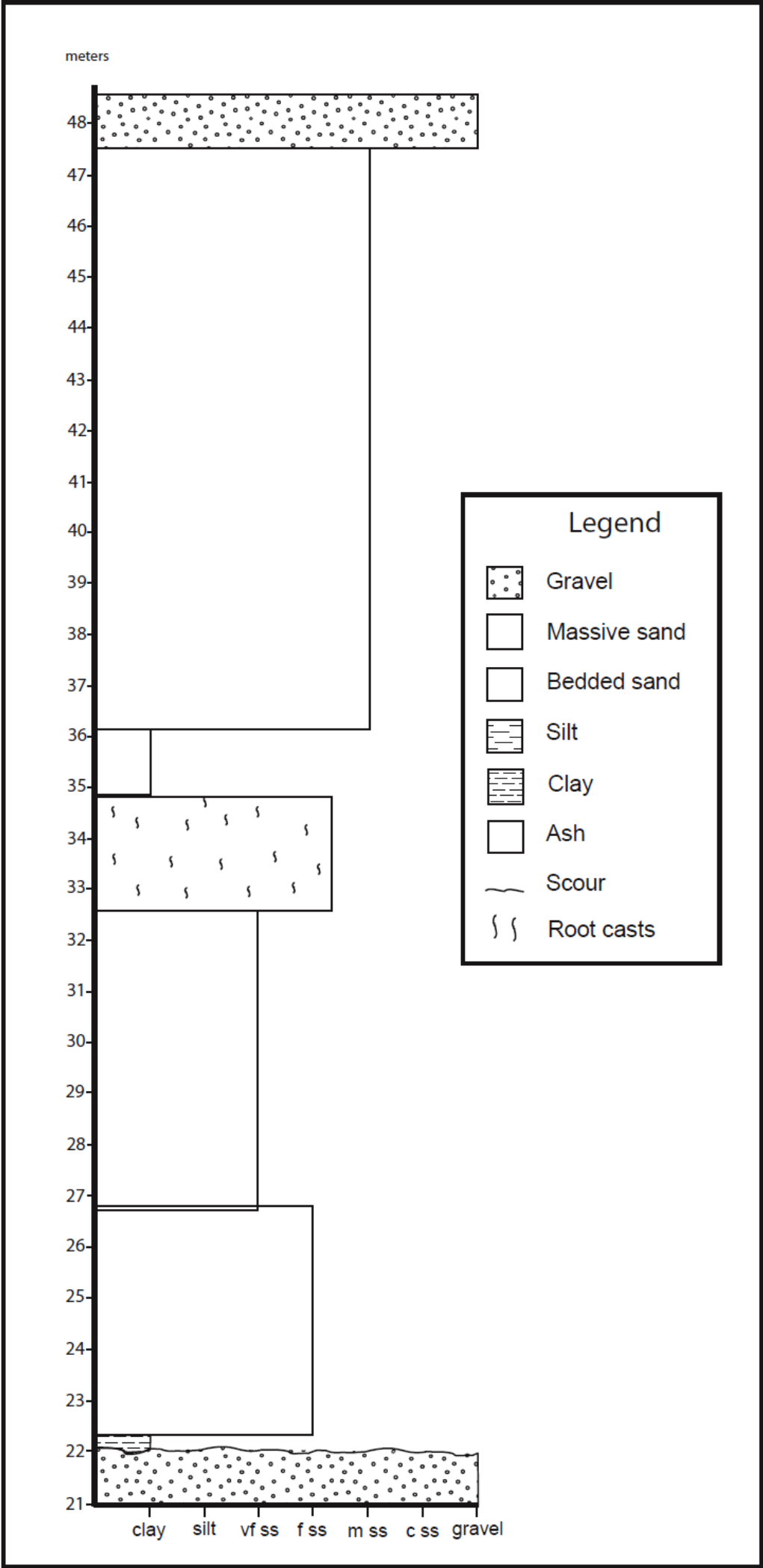


Plate 2. Stratigraphic column of the upper portion of the exposed Panaca Formation. The scour at the 22-meter mark correlates with the 22-meter scour line in Plate 1.

## Location of Measured Sections

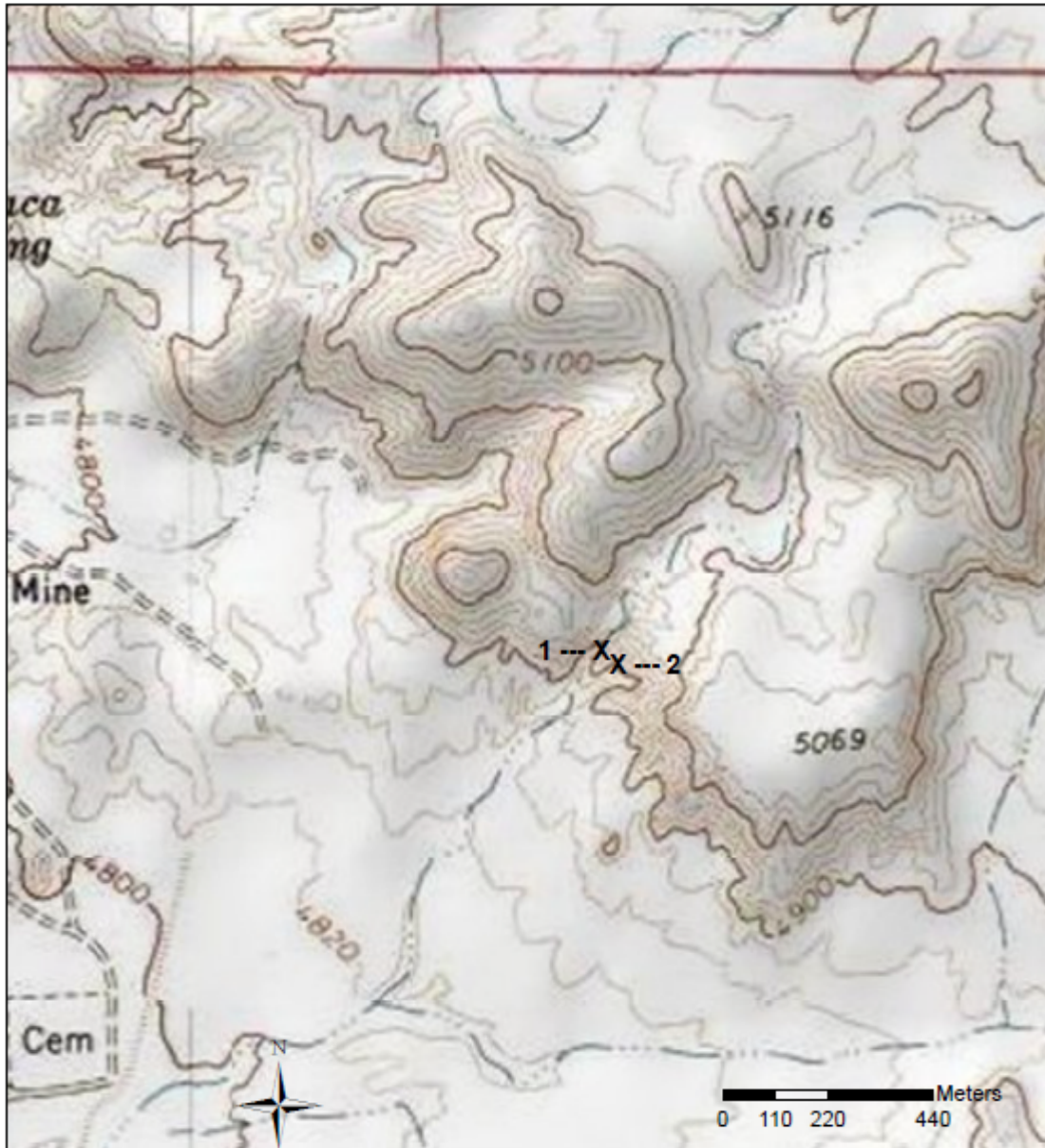


Figure 12. Location of measured sections for Panaca Formation stratigraphic column at the “Limestone Corner” (Plate 1 at x---1) and upper portion of the stratigraphic column near “Limestone Corner” (Plate 2 at x---2). The latitude and longitude of the southwest corner (lower left corner) is 37°47’43.33”N 114°22’45.82”W; elevation is 4787 feet, according to Google Earth.

sites are unknown.

### 3.3 Curation

All the fossil material collected from the Panaca Formation in Meadow Valley is curated according to the standards of the Nevada State Museum and stored in the Nevada State Museum satellite repository at UNLV. Accession numbers, locality coordinates, map of sites, and field notes are filed with the specimens or are available in the accession folder at the Nevada State Museum in Las Vegas.

All collected Hagerman fossil material was photographed, identified, cataloged, and curated at the HAFO laboratory facilities under the stewardship of the National Park Service. My summer internship work at Hagerman Fossil Beds was conducted under the direction of Philip Gensler, NPS Curator/Paleontologist.

### 3.4 Numbers of Identified Specimens (NISP)

Most of the fossils in the Panaca Formation are isolated elements. All of my collection consists of isolated elements, although the SBCM collection includes an 85% articulated *Lepoides* specimen and some articulated bird phalanges in siltstone. I evaluated the relative abundance of the various taxa within my Panaca collection by using NISP assigned to a given taxonomic group, following Marshall and Pilgram (1993) and Klein and Cruz-Urbe (1984). NISP was evaluated for my collection as a whole, as well as for each screenwashed site. NISP was assessed for identifiable complete and fragmented material at

the family level for mammals and the order level for other vertebrate groups, as many elements are not diagnostic to genus or species. Specimens identified with “cf.”, “?” or as “bone fragments” were omitted from the analysis.

Minimum number of individuals (MNI) is the minimum number of individual animals necessary to account for the identified bones (Klein and Cruz-Uribe, 1984). One bone element is chosen to assess the relative abundance. Under some circumstances, this method is considered a stronger method of evaluation than NISP (Marshall and Pilgram, 1993; O'Connor, 2000). However, MNI cannot be assessed for the Panaca collection because complete or mostly complete elements are required. Also, many of the Panaca elements are fragmented, and the treatment of fragments either depresses or raises the count (Klein and Cruz-Uribe, 1984). Complete Panaca specimens are mostly phalanges and metapodials, which are not usually diagnostic to species level.

### 3.5 Abbreviations

The abbreviations used in this thesis are (in alphabetic order):

ACC	anteroconid complex
AER	depth of anteroexternal reentrant
AMNH	American Museum of Natural History
AOU	American Ornithologists Union
AP	anteroposterior length
AR	anterior reentrant
BLM	Bureau of Land Management
DW	distal width
EAR	external anterior reentrant
F:AM	Frick Laboratory, American Museum of Natural History
gen. et. sp. indet.	genus and species indeterminate
GL	greatest length
GLI	greatest length of lateral half
GLm	greatest length of medial half

GW	greatest width
HAFO	Hagerman Fossil Beds National Monument
I	incisor
IAR	interior anterior reentrant
IMNH	Idaho Museum of Natural History
Incertae Sedis	"of uncertain placement"
Ma	million of years
MAR	main anterior reentrant
M1/	upper first molar
M/1	lower first molar
MNI	minimum number of individuals
NALMA	North American Land Mammal Ages
NISP	number of identified specimens
NPS	National Park Service
NSM	Nevada State Museum
PER	depth of the posteroexternal reentrant
PW	proximal width
P2/	upper second premolar
P/3	lower third premolar
SBCM	San Bernardino County Museum
sp. indet.	species indeterminate
TH	thick enamel on anterior edge of PER of P/3
TN	thin enamel on posterior edge of PER of P/3
TR	transverse width
UALP	University of Arizona Laboratory of Paleontology
UCMP	University of California Museum of Paleontology, Berkeley Museum
UMMP	University of Michigan Museum of Paleontology
UNLV	University of Nevada, Las Vegas
USGS	U. S. Geological Survey



## CHAPTER 4

### SYSTEMATIC PALEONTOLOGY OF THE PANACA FAUNA

The Panaca local fauna contains a diverse assemblage of fossil vertebrates including reptiles, birds, and mammals. The Panaca Formation local faunal assemblage is listed below for all known vertebrates in Table 2.

Table 2. A compilation of all vertebrates from the Panaca Formation in Lincoln County, Nevada. The birds are based on this study, the lizards from Hollenhead and Mead (2006), the small mammals from the extensive microtine study by Mou (1999) and the large mammals and carnivores include those recovered in this study as well as Mou's study, and also those in the SBCM and Frick/AMNH collections. The "cf" means "to be compared with", the "?" represents questionable identification; *incertae sedis* is defined as "of uncertain taxonomic position," and \*from communication between Tedford and Mou.

#### Panaca Vertebrate Local Faunal Assemblage List

##### REPTILIA:

- Squamata
  - Iguania
    - Crotaphytidae
      - Crotaphytus* sp. (collared lizard)
      - Gambelia* sp. (leopard lizard)
- Serpentes (snake)
  - Colubridae
    - incertae sedis*

##### AVES:

- Anseriformes
  - Anatidae
    - Cygnus* sp. (swan)
  - Anatinae
    - Anas* sp. (dabbling duck)
- Gruiformes
  - Gruidae
    - Rallus
      - Rallus* sp. (rail)
      - Porzana* sp. (rail)
- Passeriformes
  - Emberizidae
    - Spizella* sp. (chipping sparrow)
    - cf. *Passerina* sp. (sparrow)

Galliformes  
     Odontophoridae  
         *Callipepla* sp. (quail)  
 Accipitriformes  
     Accipitridae  
         *Buteo* sp. (hawk)  
 Charadriiformes  
     cf. Scolopacidae (shorebird)

#### MAMMALIA:

#### INSECTIVORA

    Soricidae (shrew)  
         Soricinae  
             Neomyini  
                 *Paranotiosorex panacaensis*  
                 Neomyini gen. and sp. indet.  
         Soricini  
             *Sorex meltoni*

#### LAGOMORPHA

    Leporidae (rabbits)  
         Archaeolaginae  
             *Hypolagus edensis*  
             ? *Hypolagus edensis*  
             *Hypolagus tedfordi*  
             *Hypolagus* cf. *H. ringoldensis*  
             ? *Hypolagus ringoldensis*  
             *Hypolagus* cf. *H. gidleyi*  
             *Hypolagus* cf. *H. regalis*  
             *Pewelagus dawsonae*  
             *Lepoides lepoides*  
         Leporinae  
             *Nekrolagus progressus*  
             ? *Prontolagus* sp.

#### RODENTIA

    Sciuridae (squirrels)  
         cf. *Spermophilus* sp  
 Geomyidae (pocket gopher)  
     Geomyinae  
         *Pliogeomys parvus*  
         ? *Pliogeomys* sp.  
 Heteromyidae  
     Perognathinae (pocket mouse)  
         *Perognathus mclaughlini*  
         *Oregonomys* sp.  
     Dipodomysinae (kangaroo rat)

	<i>Prodipodomys minor</i>
	? <i>Prodipodomys minor</i>
	<i>Prodipodomys titheni</i>
	? <i>Prodipodomys titheni</i>
Cricetidae	
Sigmodontinae	
Peromyscini	
	<i>Peromyscus hagermanensis</i> (deer mouse)
	<i>Onychomys</i> sp. (grasshopper mouse)
Neotomini	
	<i>Repomys panacaensis</i> (woodrat)
	<i>Repomys minor</i>
Arvicolinae	
Arvicolini	
	<i>Mimomys panacaensis</i> (vole)
Prometheomyinae	
	<i>Nevadomys feifari</i> (arvicoline-like rodent)
	<i>Nevadomys lindsayi</i>
	<i>Nevadomys downsi</i>
CARNIVORA	
Procyonidae	
	<i>Bassariscus casei</i> (ring-tail cat)
Mustelidae	
	<i>Martinogale</i> sp. (skunk)
	<i>Taxidea</i> sp. (badger)
Canidae	
	<i>Canis lepophagus</i> (coyote)
	<i>Canis</i> sp.
	* <i>Borophagus</i> cf. <i>diversidens</i> (hyaenoid dogs)
Felidae	
	* <i>Felis</i> sp. (cat)
	cf. <i>Lynx</i> sp. (bobcat)
*PROBOSCIDA	
	? <i>Cuvieronius</i> (gomphothere)
PERISSODACTYLA	
Equidae	
	<i>Equus (Dolichohippus)</i> cf. <i>simplicidens</i> (horse)
	<i>Equus (Hemionus)</i> sp.
Rhinocerotidae	
	<i>Teleoceras</i> sp. (rhino)
ARTIODACTYLA	
Tayassuidae	
	<i>Platygonus</i> sp. (peccary)
Camelidae	
	<i>Megatylopus</i> sp. (large camel)
	<i>Hemiauchenia</i> sp. (llama)

Bovidae  
    Caprinae  
        Caprini  
            *Sinocapra wiltdownsi* (sheep-like goat)

The systematic classifications and identifications include fossil material collected from surface surveying and screenwashing (see methods section) in this study. Fossil material is disarticulated and commonly fragmented. Teeth are isolated with a few fragmented mandibles and maxillae, and many incisors are broken and unidentifiable to genus. Complete bones are small and predominately metapodials and phalanges from rabbits and rodents.

The Panaca fossil locality is assigned Nevada State Museum (NSM) locality number VM-09-075 (VM = Vegas Museum). Catalogue numbers for each fossil indicate the NSM specimen number, for example, VM-P565 is the specimen number. The field sites are listed as PAN-01, PAN-02, etc. for the twenty-four field collection sites.

Abbreviations for dental terminology are as follows: C, canine; I, incisor; M, molar; and P, premolar; L, left; R, right; /#, lower dentition; #/, upper dentition; /#/ , indeterminate tooth. Phalange terminology is as follows: proximal phalanx is first digit; medial phalanx is second digit, and distal phalanx is third digit, which can be either a claw or a toe bone. All specimens from this study are stored in the Nevada State Museum satellite repository at UNLV.

Class Reptilia Linnaeus, 1758

4.1 Order Squamata Oppel, 1811

Suborder Iguania Laurenti, 1768

Family Crotaphytidae Frost and Etheridge, 1989

*Crotaphytus* Holbrook, 1842

cf. *Crotaphytus* sp.

Collared Lizard

*Referred Material:* Left dentary and maxilla with 15 teeth (VM-P852).

*Age:* early Blancan

*Stratigraphic and geographic range:* Site PAN-24, in the Panaca Formation, southeastern Nevada. The extended range includes the middle Pliocene of California and Idaho (Hollenhead and Mead, 2006).

*Identification:* Specimen mandible (VM-P852) measures 4.16 mm in length. Eight teeth are secured in the anterior section of the mandible, the 9<sup>th</sup> fell out, teeth in the 10-14<sup>th</sup> position are mostly absent, the 15-17<sup>th</sup> are partials and the last 5 teeth are mostly complete. Merkel's canal is not fused. *Crotaphytus* species can be distinguished from *Gambelia* by three traits of the teeth. Tooth shape of *Crotaphytus* is robust at the base and tapers to the tip, whereas *Gambelia* has parallel-sided teeth. *Crotaphytus* has no or slight recurvature of the posterior teeth compared to sharp recurvature in *Gambelia*. *Crotaphytus* has ~25% of unicuspid teeth along the tooth row, while >50% of the teeth are unicuspid in *Gambelia* (Hollenhead and Mead, 2006).

*Discussion:* Pliocene herpetological sites are rare in North America, but two genera of lizards were recently described from the Panaca Formation in southeastern Nevada by Hollenhead and Mead (2006). These Pliocene squamate fossil remains are the earliest described crotaphytid remains and date

to 4.9-4.7 Ma (Hollenhead and Mead, 2006). Other Pliocene fossil specimens come from Anza-Borrego (California) and the Glenns Ferry Formation (Idaho). A skull and mandible of the extinct *Gambelia corona* was recovered from the Palm Springs Formation (California) dating to 4.18-3.58 Ma (Hollenhead and Mead, 2006; Gensler et al., 2006). The Glenns Ferry *Crotaphytus* sp. dentary is from the Hagerman local fauna dated at ~4.0 to 3.1 Ma (Mead et al., 1998). Specimen VM-P852 is a more complete specimen than either of the previously described specimens from the Panaca Formation.

Suborder Serpentes Linnaeus, 1758

Colubridae Oppel, 1811

Genus, Species

*Incertae Sedis*

Snakes

*Referred Material:* Two mid-trunk vertebrae (VM-P548).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-01, in the Panaca Formation, southeastern Nevada. Pliocene snake fossils have been reported from Arizona, Idaho, Kansas, Nebraska, Oklahoma, Texas, and Washington (Holman, 2000).

*Identification:* These two vertebrae can be distinguished as snakes by the presence of the nearly hemispherical condyle and cotyle joint, zygosphenes, and zygantra. The vertebrae have hypapophyses which are thin, short, narrow, and mainly posteriorly directed. The more complete of the two specimens exhibits

small paired zygosphenal articular facets that are oriented ventrally and flattened upward facing prezygapophyseal articular facets. The posterior border of the neural arch is broadly U-shaped. Trunk vertebrae lack the lymphapophyses found on caudal vertebrae and the pleurapophyses located on caudal vertebrae (Holman, 2000).

*Discussion:* Mid-trunk vertebrae are most useful in the identification of snake species (Holman, 2000). Preservation of the two vertebrae from Panaca does not permit identification below the family level.

Class Aves Linnaeus, 1758

4.2 Order Anseriformes Wagler, 1831

Family Anatidae Vigors, 1825

Subfamily Anserinae Vigors, 1825

Tribe Anserini Vigors, 1825

*Cygnus* Bechstein, 1803

Subgenus *Olor*

Swans

(Fig. 13 &14)

*Referred Material:* proximal end of left scapula (VM-P638).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-01, in the Panaca Formation, southeastern Nevada. The extended range includes the late Pliocene near Hagerman, Idaho (Becker, 1987; Bickert, 1990).

*Identification:* Proximal end of left scapula is large with a long and narrow glenoid facet, a raised hemispherical coracoidal articulation, and a robust superiorly flattened acromion. Measurements: Proximal breadth-21.25 mm, proximal depth-7.56 mm, proximal depth of acromion-8.91 mm, width x breadth of coracoidal articulation- 6.32 x 6.25 mm, width x length of glenoid facet-5.51 x 11.73 mm, greatest breadth x depth of shaft- 6.99 x 12.53 mm.

*Discussion:* A large left scapula (VM-P638) was initially compared for size with the following species represented in the HAFO comparative collection: *Chen caerulescens*, *Cygnus (Olor) buccinator*, *Pelecanus erythrorhynchos*, *Ardea herodias*, *Haliaeetus leucocephalus*, and *Aquila chrysaetos* (Figure 13).

*Pelecanus erythrorhynchos* and *P. occidentalis* are smaller and morphologically have quite a distinct scapula with a long, gracile acromion, whereas the fossil scapula (VM-P638) has a robust and flattened acromion. *Ardea herodias* is smaller and the acromion low and rounded superiorly. Both of the eagles, *Haliaeetus* and *Aquila*, have a glenoid facet that is more rounded, and angled more obliquely from the neck of the scapula; in the eagles the coracoidal articulation is low, and the acromion is pneumatic, raised, but not as robust as that of the fossil. *Chen caerulescens* and *Cygnus (Olor) buccinator* are both morphologically similar to the fossil Panaca scapula; however, based on size range for *Cygnus (Olor) buccinator*, the fossil scapula is from a swan.

The Panaca swan (VM-P638) is within the size range of modern North American swans, *Cygnus (Olor) buccinator* and *columbianus* (Figure14). Recently, an associated skeleton (F:AM 20017) has been referred to the late



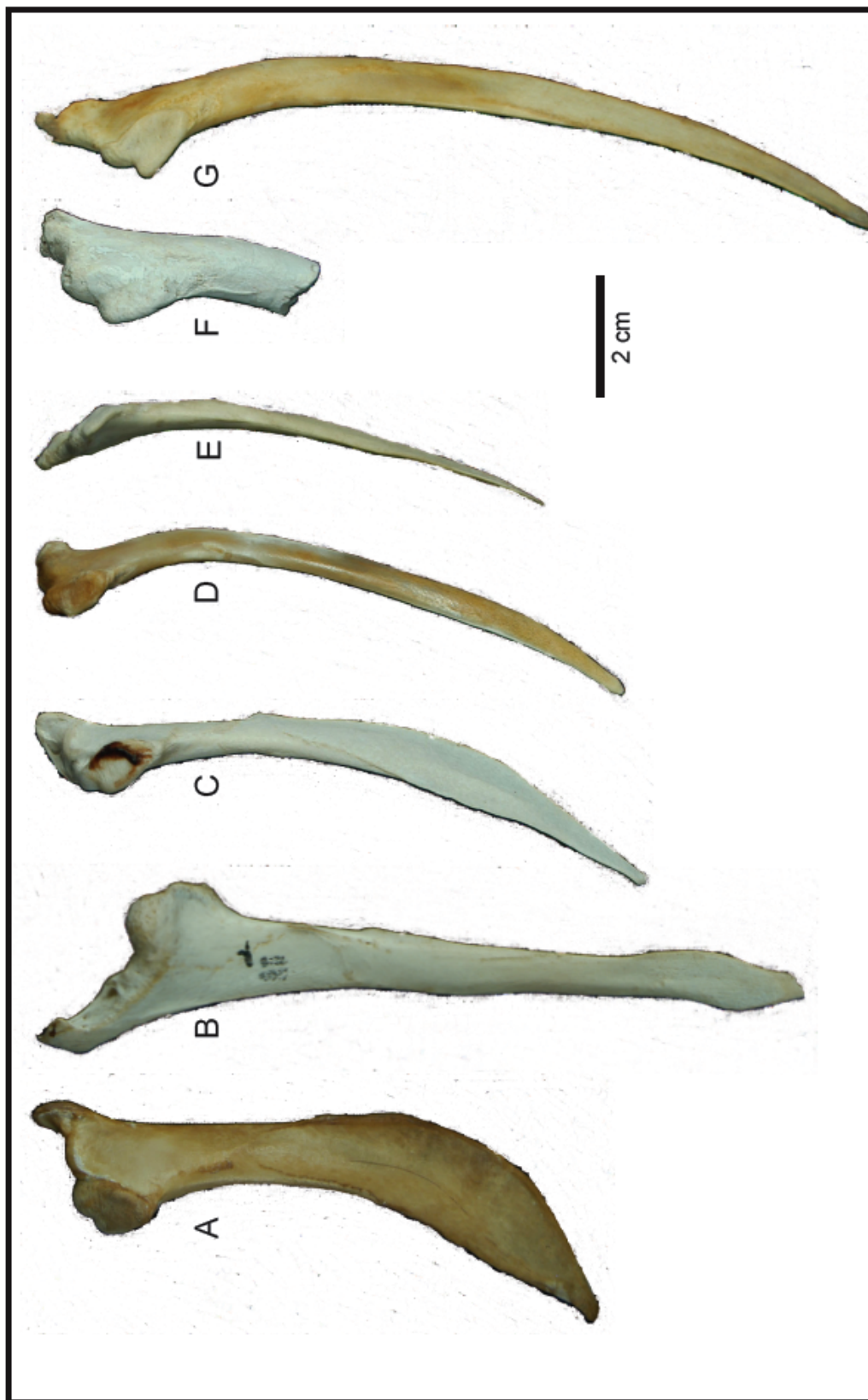


Figure 13. Comparison of scapulas to VM-P638. A. *Aquila chrysaetos*, B. *Haliaeetus leucocephalus*, C. *Pelecanus erythorynchos*, D. *Ardea herodias*, E. *Chen caerulescens*, F. *Cygnus* sp. (VM-P638), G. *Cygnus buccinator*; all are left scapulas except B., the *Haliaeetus leucocephalus*, which is a right.

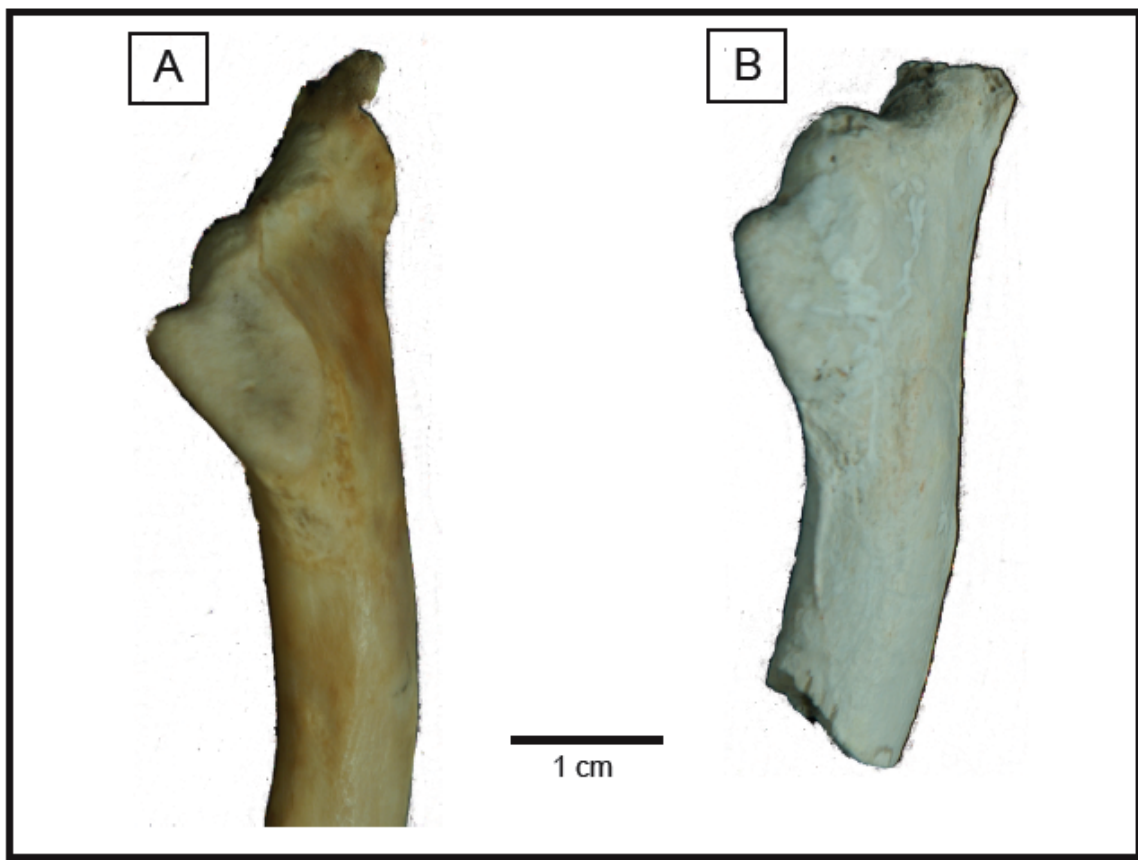


Figure 14. Comparison of left scapulas of *Cygnus buccinators* (A) and the *Panaca Cygnus* sp. (B) in lateral-ventral view.

Hemphillian swan, *Cygnus (Olor) mariae* (Bickart, 1990:13) from the Big Sandy Formation near Wikieup, Arizona. *Cygnus (Olor) mariae* is similar in size and morphology (and therefore for the scapula) to the modern North American *Cygnus (Olor)* swan species. There is a late Pliocene swan from Idaho, *Cygnus (Olor) hibbardi* (Brodkorb, 1958, 1964) from the Hagerman Horse Quarry, Glenns Ferry Formation (Blancan NALMA). Also from Idaho, a swan has been identified (R. Chandler pers. comm.) from the Birch Creek Local Fauna, Owyhee County (Blancan). The scapula is not known for *C. (Olor) hibbardi*, but the size of the holotype left tarsometatarsus (UMMP# 33894) is equal to that of *C. (Olor)*

*columbianus*. A scapula (IMNH 524/12135) from the Birch Creek Local Fauna is identical to that of the Panaca swan (VM-P638). There are no known derived characteristics for the scapula to separate the Old World subgenus *Cygnus* (*Cygnus*) *sp.* from the New World *Cygnus* (*Olor*), and there is a size range overlap for *C. (Olor) buccinator* and *C. (Olor) columbianus* for the scapula. The living swans, *Cygnus (Olor) buccinator* and *C. (Olor) columbianus*, are both first reported from the Pleistocene of North America. Therefore, with confidence the Panaca swan can be identified only to *Cygnus (Olor) sp.* at this time, but with additional material and research it may be shown that the swan specimens from this study and Birch Creek are new records for *C. (Olor) hibbardi*.

Family Anatidae Vigors, 1825

Subfamily Anatinae Vigors, 1825

Tribe Anatini Vigors, 1825

cf. *Anas* Linnaeus, 1758

*sp. indet.*

Dabbling Ducks

*Referred Material:* Left coracoid humeral end (VM-P522), left tibiotarsus distal end (VM-P555), left trochlea of Digit IV (VM-P580).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-01, in the Panaca Formation, southeastern Nevada. The extended range includes middle Pliocene to Lower Pleistocene in Oregon, Texas, Kansas, Arizona and Idaho; Lower Pliocene, South Dakota (Bickart, 1990; Chandler, 1990).

*Identification:* Left coracoid humeral end missing the brachial tuberosity and external side; left tibiotarsus distal end with external condyle heavily abraded and the posterior surface missing, anterior intercondylar fossa relatively wide and deep; left tarsometatarsus trochlea of Digit IV. Measurements: coracoid: length of glenoid facet- 8.20 mm; tibiotarsus: breadth of distal end- 5.74 mm, height of internal condyle- 4.01 mm, width of intercondylar fossa- 3.18 mm; tarsometatarsus: depth of trochlea 4.43 mm, width of trochlea- 1.35 mm.

*Discussion:* The fossils (VM-P522, VM-P555, VM-P580) are from a small duck within the size range of modern teal, *Anas* sp. They agree in size and general appearance with *Anas crecca* (green-winged teal) with which they were compared, however the genus and species cannot be absolutely determined because of the fragmentary condition of the fossils. There are many records of Blancan to early Irvingtonian-aged Anatinae fossils (see Becker, 1987; Brodkorb 1964). Many of these have been referred to Anatinae based on size alone and are in need of a comprehensive review. Several small teal (*Anas*) to bufflehead (*Bucephala*) sized species have been named from western North American deposits of Blancan age and are relevant to this study, e.g., *A. bunkerii* (Wetmore, 1933) and *Bucephala fossilis* (Howard, 1963; Brodkorb, 1964) from the Hagerman Horse Quarry, Idaho; *A. greeni* (Brodkorb, 1964) from the lower part of the Ash Hollow Formation, South Dakota; *A. ogallalae* (Brodkorb, 1962) from the Ogallala Formation, Kansas; *A. pullulans* (Brodkorb, 1961) from the Juntura Formation, Oregon. All are small Anatinae species that may be nonspecific with the *Panaca* fossil.

#### 4.3 Order Gruiformes Bonaparte, 1854

Family Gruidae Vigors, 1825

Subfamily Rallidae Vigors, 1825

*Rallus* Linnaeus, 1758

*Rallus* sp.

sp. indet.

Rails

*Referred Material:* Mandibular symphysis (VM-P536)

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-01, in the Panaca Formation, southeastern Nevada. The extended range includes early Pliocene, Kansas and Pliocene, Idaho (Bickart, 1990; Chandler, 1990).

*Identification:* Mandibular symphysis of a long, pointed, gracile bill missing the very tip of the dentary. Measurements: Length of mandibular symphysis- 10.64 mm, greatest width of symphysis- 2.94 mm, height of left ramus- 2.85 mm.

*Discussion:* The mandibular symphysis (VM-P536) is of a long beaked rail in the genus *Rallus*. The appearance of the fossil is similar to modern *Rallus* spp., slightly smaller than *Rallus limicola*, shorter than *R. longirostris-elegans* group (*fide* Feduccia, 1968), but much longer than *Porzana*, *Coturnicops*, and *Laterallus*. There are three Blancan rails of similar relative size to the Panaca rail that should be compared: *Rallus prenticei* Wetmore (1944) described from the Rexroad local fauna, Kansas and reported from the Hagerman local fauna, Idaho (Feduccia, 1968); *R. lacustris* (Brodkorb, 1958) from the Hagerman local fauna,

Idaho; *R. phillipsi* Wetmore (1957) from Wikieup, Arizona. The premaxilla of *R. prenticei* is known (UMMP V54981) and figured by Feduccia (1968) in comparison to *R. limicola* and is slightly longer than the modern species. Wetmore initially described *R. prenticei* as a larger and more robust species than *R. limicola*. Measurements of *R. lacustris* are larger than *R. prenticei*, *phillipsi*, and *limicola* (Wetmore, 1957; Feduccia, 1968; Bickart, 1990). Therefore, based only on the Panaca mandible (VM-P536), it may be said that it is closest to *R. prenticei* in size, but more fossils of other elements of the skeleton are needed to make a positive identification.

*Porzana* Vieillot, 1816

*Porzana* sp.

sp. indet.

Rail

*Referred Material:* Premaxilla (VM-P581), anterior end of sternum (VM-P554).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-01, in the Panaca Formation, southeastern Nevada. The extended range includes early Pliocene, Kansas and Pliocene, Idaho (Bickart, 1990; Chandler, 1990).

*Identification:* A premaxilla of a short and relatively deep-billed rail; anterior fragment of the sternum at the base of the carina and the medial surfaces of the coracoidal sulci. Measurements: Premaxilla length from the

anterior nasal opening to bill tip- 6.30 mm; greatest width of premaxilla- 2.37 mm; width across coracoidal sulci- 7.00 mm.

*Discussion:* The premaxilla (VM-P581) is from a short-billed rail almost identical to that of the modern Sora, *Porzana carolina*. This rail is much smaller than the *Rallus* sp. described above and with a shorter and relatively deeper bill. The sternal fragment is similar in size, and in the characteristics of the carina and coracoidal sulci, to that of the Sora. Feduccia (1968) reported a Porzana-like rail from the Blacan, Saw Rock Canyon local fauna of Kansas; however the bill fragment is much larger than the modern Sora and therefore, the Panaca *Porzana* rail. The modern Sora first appears in late Pleistocene deposits (Brodkorb, 1967). The lack of other skeletal elements diminishes what can be said about this rail; however Feduccia (1968) speculated that the *Porzana*-like rail from Saw Rock Canyon might be the ancestor to the modern Sora. The Panaca *Porzana*-like rail fossils at hand are virtually identical to the modern Sora and need to be considered when formulating hypotheses of phylogenetic and ancestral relationships of the modern Sora.

#### 4.4 Order Galliformes

##### Order Galliformes

##### Family Odontophoridae Gould, 1844

##### *Callipepla* Wagler, 1832

##### *Callipepla* sp.

sp. indet.

Quail

*Referred Material:* Left coracoid, missing the sterna end (VM-P531).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-01, in the Panaca Formation, southeastern Nevada. The extended range includes San Diego Formation, California (R. Chandler, personal communication).

*Identification:* Left coracoid with a complete humeral end, a long gracile shaft missing only the sternal end. Length of glenoid facet- 6.30 mm, length from scapular facet to brachial tuberosity- 8.41 mm, breadth x depth of mid-shaft- 2.83 x 2.37 mm.

*Discussion:* A quail very similar in size and with characteristics of the coracoid like that of the modern Gambel's quail, *Callipepla gambelii*, California quail, *C. californica*, and scaled quail, *C. squamata*, of western North America today. The fossil (VM-P531) has a well developed attachment for the *m. coracobrachialis* on the internal surface of the shaft, which is also present on *Callipepla*. The brachial tuberosity is slightly more undercut medially than the modern quail coracoids at hand, but this may be a characteristic within the range of variation for *Callipepla*. The California, Gambel's, and scaled quail complex, originally placed in *Lophortyx*, are now in the genus *Callipepla* (American Ornithologists' Union (AOU) Checklist, 1983). The northern bobwhite, *Colinus virginianus*, is found in the central plains and eastern forests of North America. The coracoid of *Callipepla* is distinguishable from *Colinus* by the former being less robust, more gracile and the internal outline of the triosseal canal. In the fossil record, there are two named species of quail from the Blancan *Callipepla*



(*Lophortyx*) *shotwelli* (Brodkorb, 1958) from McKay reservoir beds, eastern Oregon; and *Colinus hibbardi* (Wetmore, 1944) from the Fox Canyon and Rexroad local faunae (Rexroad Formation), western Kansas. There are other records for *Callipepla* (*Lophortyx*) sp. from the San Diego Formation, southern California (R. Chandler, pers. obs.); *Colinus* (*Callipepla*?) sp. from Benson, Arizona (Wetmore, 1924). The Panaca *Callipepla* quail fossil (VM-P531) is not directly comparable to the other named Blancan species or referred material because the coracoid is not known for those species. However, the age and proximity of Panaca to the McKay reservoir beds localities may imply that this is a second record for *C. shotwelli*.

Class Mammalia Linnaeus, 1758

4.5 Order Lagomorpha Brandt, 1855

Family Leporidae Gary, 1821

(Table 3, Fig. 15, 16, 17)

Two subfamilies of leporids have been identified from the Panaca Formation: Archaeolaginae and Leporinae. White (1987, 1991) revised the species within both of these subfamilies and updated the geologic age and geographic distribution. Mou (1999) identified seven species of Archaeolaginae and two species of Leporinae from the Panaca Formation.

Cranial characteristics are the best criteria for identification of leporids, but complete skulls are rare in the fossil record. Leporid cheek teeth are hypsodont and evergrowing. The enamel patterns of P/3s are specific to the various leporid taxa and are most commonly used in identification to species level (White, 1987,

1991; Mou, 1999). The P2/ has some diagnostic value, but Mou (1999) found that the P2/ is valuable for identification only to the species-level in *Lepoides lepoides*. Reentrants contain crenulation patterns that exhibit various degrees of complexity on P/3 and P2/ teeth. See Figure 15 for methods of measurement and nomenclature of tooth structures on the occlusal surface of P/3 and P2/.

Individual leporid teeth are usually difficult to identify to species-level, so mean values of tooth populations are commonly used. Mean values are used for size, penetrance of AER and PER, and angles of deflection of PER (White, 1987; Mou, 1999; Ruez, 2009b). Generally at least five teeth measurements are used for determining a mean value (White, 1987). I did not calculate mean values from the small number of teeth collected in this study, but scatter plots of tooth dimensions suggest that two to three sizes of leporids were collected within this sample (Figures 16 & 17).

Order Lagomorpha Brandt, 1855

Family Leporidae Gary, 1821

Subfamily Archaeolaginae Dice, 1929

*Hypolagus* Dice, 1917

*Hypolagus edensis* Frick, 1921

Small Cottontail

*Referred Material:* Left P/3 (VM-P820, VM-P884, VM-P885, VM-P973), right P/3 (VM-P974).

*Age:* early Blancan

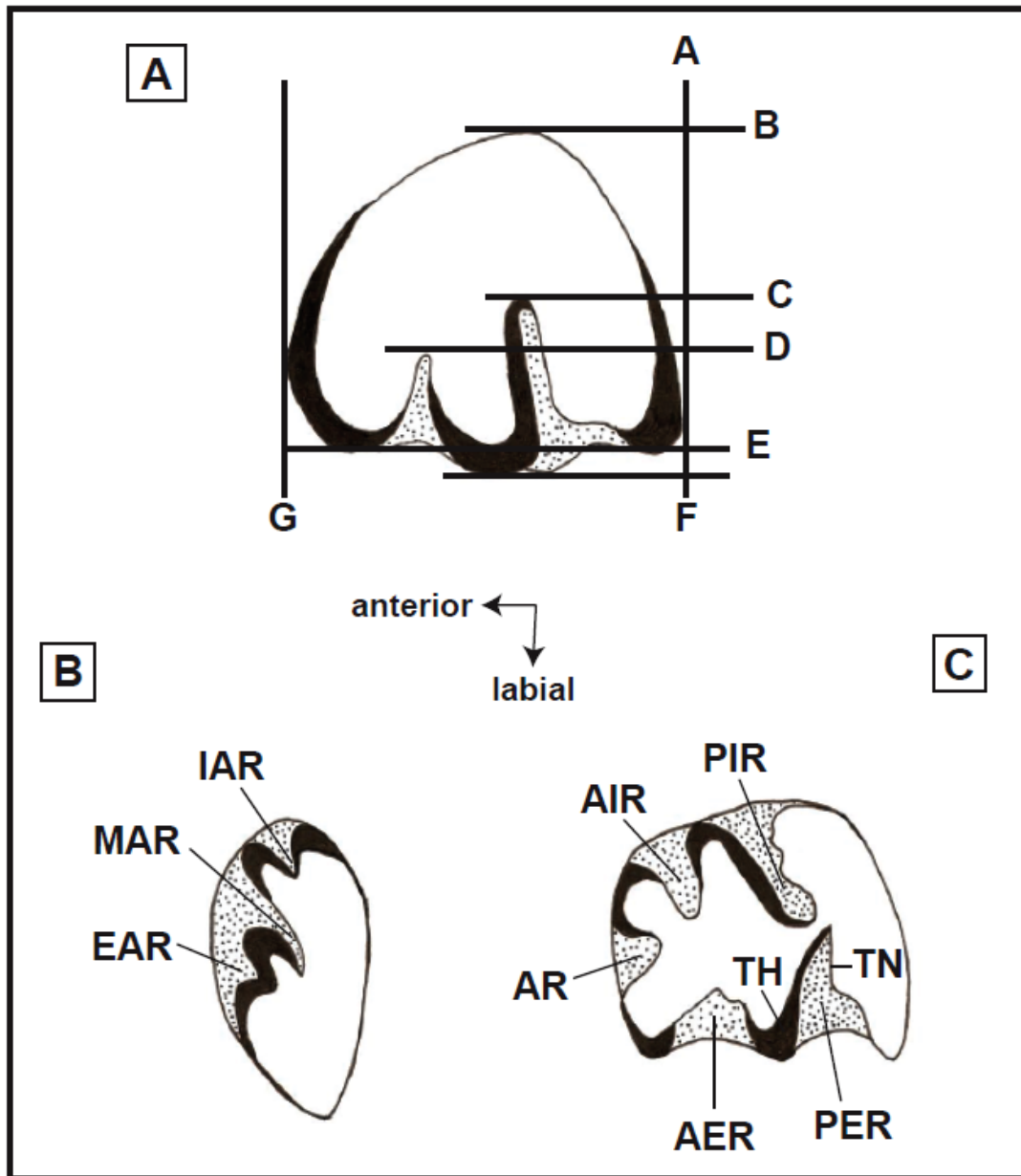


Figure 15. Nomenclature of tooth structures on the occlusal surface of a leporid P/3. A. Diagram of the occlusal surface of an archaeolagine P/3 tooth indicating how measurements were made. Anteroposterior length (AP) F-G, transverse width (TR) A-E, depth of the anteroexternal reentrant (AER) C-E, depth of the posteroexternal reentrant (PER) B-E, line of orientation D. B. Diagram of the occlusal surface of P2/ with labels indicating tooth structures. Abbreviations are as follows: EAR=external anterior reentrant, MAR=main anterior reentrant, IAR=internal anterior reentrant. C. Diagram of occlusal surface of P/3 with labels. Abbreviations: AR= anterior reentrant, AER= anteroexternal reentrant, PER=posteroexternal reentrant, PIR= posterointernal reentrant, AIR=anterointernal reentrant, TH= thick enamel, TN=thin enamel.

*Stratigraphic and geographic ranges:* Sites PAN-19 and PAN-24 in the Panaca Formation, southeastern Nevada. The extended range includes the lower Pliocene of California and Arizona, mid-Pliocene of Idaho, Texas, California, and Washington (White, 1987; Mou, 1999; Ruez, 2009b).

*Identification:* These small P/3s have deeply incised AER without crenulations and lack an AR. The thin enamel in the PER is straight in some teeth (VM-P885 and VM-P974), but is slightly sigmoid in VM-P820 and VM-P973 specimens. The AER and PER are cement-filled in all specimens. Measurements of these specimens are listed in Table 3; and they are the most numerous group plotted on Figure 15.

*Discussion:* *Hypolagus edensis* is a small leporid. The P/3 is distinguishable from other *Hypolagus* species by its deeply penetrated AER, which averages 34 percent across the occlusal surface; there is no AR (White, 1987). The smooth enamel line of the AER distinguishes it from *Pewelagus dawsonae*, another common small species in the Panaca local fauna. Other referred material of *H. edensis* material includes two specimens from the “Limestone Corner” noted by White (1987) and a number of mandibles and isolated teeth described by Mou (1999). *Hypolagus edensis* is well-known from the Blancan Hagerman local fauna, in addition to species *H. gidleyi*. The small size and lack of AR distinguishes these specimens from *Lepoides lepoides*.

*Lepoides* White, 1987

*Lepoides lepoides* White, 1987

Jack Rabbit Ecomorph

*Referred Material:* Left P/3 (VM-P755), right P/3 (VM-P772), left P2/ (VM-P571), right P2/ (VM-P578), left mandible with P/4 and M/1 (VM-P623), right PM/X (VM-P723); left I1/ (VM-P967).

*Age:* Hemphillian to early Blancan

*Stratigraphic and geographic range:* Sites PAN-01: VM-P571, VM-P578; PAN-04: VM-P623; PAN-18: VM-P723; PAN-19: VM-P755, VM-P772; PAN-24: VM-P967 in the Panaca Formation, southeastern Nevada. The extended range includes the lower Pliocene of California and Nebraska (White, 1987; Kelly, 1998; Mou, 1999).

*Identification:* The P/3s are semi-circular in cross section. Both P/3s have an AR present, the PER has strong posterior deflection, and the AR is shallow without crenulation. The P2/s has three reentrants. The left mandible (VM-P623) contains a fragment of I/1, alveoli of P/3, P/4, M/1, and a root fragment of M/2. The jaw is highly fractured, but well-cemented in matrix. The right lower PM/X (VM-P723) is a large, well-preserved typical lower premolar-molar. Specimen (VM-P967) is a large lower incisor. All tooth measurements are listed in Table 3.

*Discussion:* White (1987) characterized *Lepoides lepoides* as near in size to *Lepus arcticus* and considerably larger than other archaeolagines. Other defining characters of this species are a PER that is strongly deflected

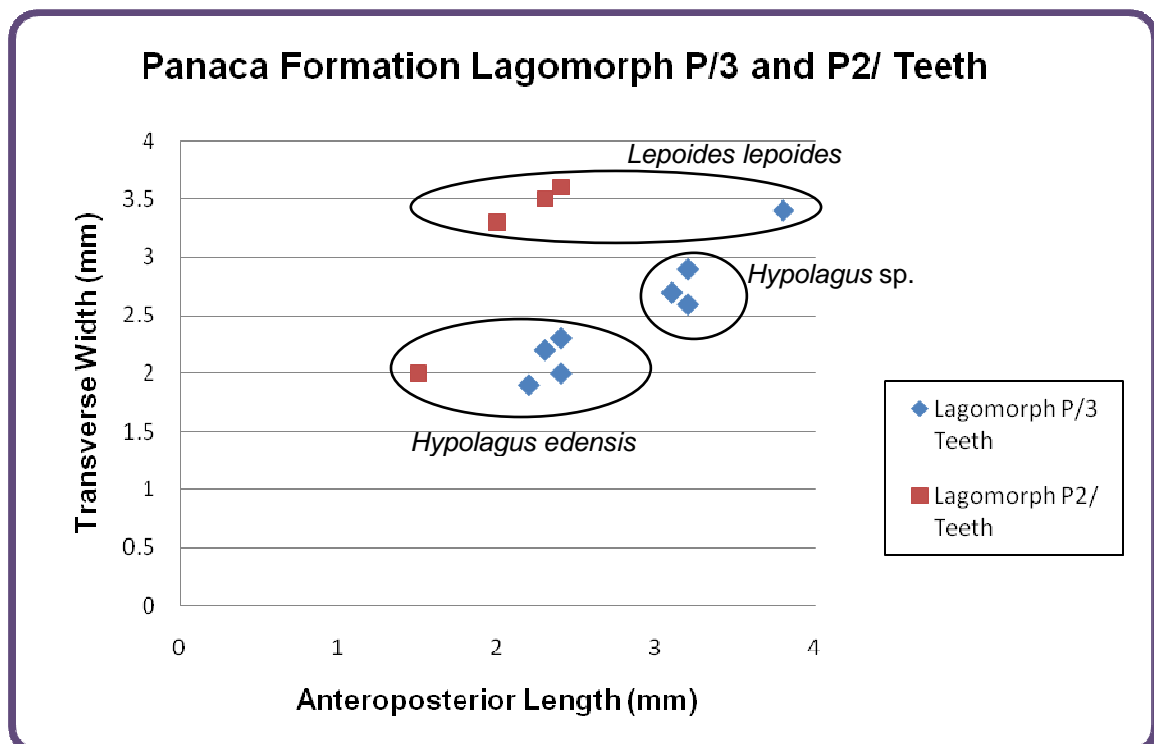


Figure 16. Bivariate plot of lagomorph P/3 and P2/ tooth dimensions as defined in Fig.15A. Circles show lagomorphs grouped by comparable tooth size.

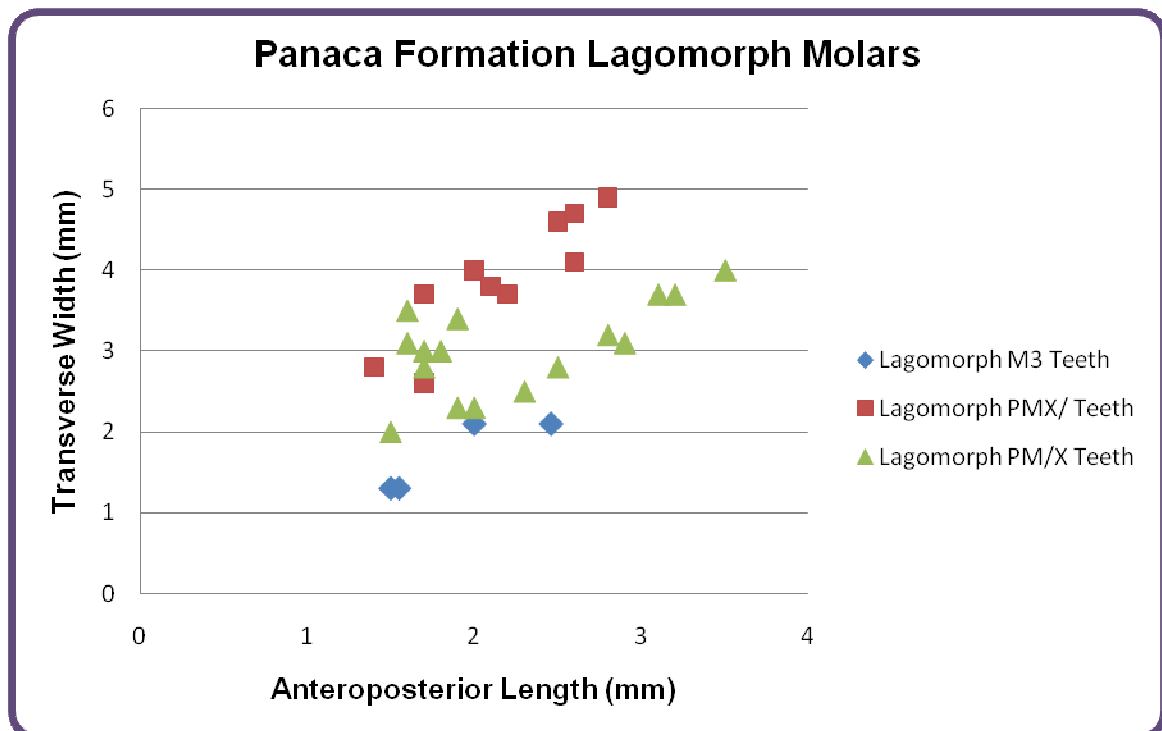


Figure 17. Bivariate plot of lagomorph molar tooth size dimensions as defined in Fig. 15A.

Table 3. Measurements (in mm) of lagomorph teeth from the Panaca local fauna. Table lists tooth placement with specimen number, AP = anteroposterior, TR = transverse width, PER = posteroexternal reentrant; AER = anteroexternal reentrant measurements.

Lagomorph Tooth Measurements					
Tooth placement	Specimen Number	AP	TR	PER	AER
P/3	VM-P755	3.8	3.4	2	0.9
	VM-P772	3.2	2.6	1.5	0.7
	VM-P820	2.3	2.2	0.9	0.7
	VM-P821	3.1	2.7	1.5	0.8
	VM-P884	3.2	2.9	1.5	1.1
	VM-P885	2.2	1.9	0.9	0.6
	VM-P973	2.4	2.3	1.1	0.8
	VM-P974	2.4	2	1	0.8
P/2	VM-P571	2.3	3.5	—	—
	VM-P578	2.4	3.6	—	—
	VM-P819	1.5	2	—	—
	VM-P819	2	3.3	—	—
M/3	VM-P579	2.46	2.1	—	—
	VM-P773	2	2.1	—	—
	VM-P774	1.5	1.3	—	—
	VM-P822	1.55	1.3	—	—
PMX/	VM-P566	2.5	4.6	—	—
	VM-P617	2.2	3.7	—	—
	VM-P686	2	4	—	—
	VM-P724	2.8	4.9	—	—
	VM-P769	1.4	2.8	—	—
	VM-P770	1.7	2.6	—	—
	VM-P770	1.7	3.7	—	—
	VM-P886	2.1	3.8	—	—
	VM-P976	2.6	4.1	—	—
	VM-P976	2.6	4.7	—	—
PM/X	VM-P556	1.5	2	—	—
	VM-P570	2.8	3.2	—	—
	VM-P676	1.6	3.1	—	—
	VM-P723	1.7	2.8	—	—
	VM-P725	1.9	2.3	—	—
	VM-P726	2.3	2.5	—	—
	VM-P768	2	2.3	—	—
	VM-P790	3.5	4	—	—
	VM-P790	3.2	3.7	—	—
	VM-P823	2.5	2.8	—	—
	VM-P824	3.1	3.7	—	—
	VM-P825	1.8	3	—	—
	VM-P825	1.7	3	—	—
	VM-P825	1.9	3.4	—	—
	VM-P825	2.9	3.1	—	—
	VM-P825	1.6	3.5	—	—
	VM-P887	2	2.2	—	—

posteriorly, an AR on P3/, three anterior reentrants on P2/, and the fact that the diastema between I-P3/ is longer than in other archaeolagines. Neither of the teeth have an anterointernal or posterointernal reentrant, which would classify them as leporine instead of archaeolagine. White (1987) suggested that *L. lepoides* was a jack rabbit ecomorph because the mandible proportions are similar to those of *Lepus*.

Mou (1999) reported that the posterior deflection of PER in *L. lepoides* separates *L. lepoides* from *Hypolagus ringoldensis*, another large leporid species found in the Panaca local fauna. Mou stated that *L. lepoides* is the third most abundant lagomorph species of the Panaca local fauna, following *Pewelagus dawsonae* and *Hypolagus edensis*. She recovered *L. lepoides* specimens throughout the UALP stratigraphic sites. White (1987) described the new species, *Lepoides lepoides* from 12 specimens from the Panaca Formation and over 40 specimens from the Late Hemphillian Santee local fauna of Nebraska. In the SBCM Panaca collection, there are teeth, post-cranial elements, and a mostly complete skeleton identified as *Lepoides*. In addition to the tooth material listed above, 62 post-cranial specimens from 18 sites from the Panaca Formation were confidently assigned to *L. lepoides* based on the large size of the bone elements in this study.



#### 4.6 Order Rodentia Bowditch, 1821

Family Sciuridae Gray, 1821

Spermophilus Cuvier, 1825

cf. *Spermophilus* sp. (small)

sp. indet.

Squirrel

*Referred Material:* Left M/X (VM-P983).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-24, in the Panaca Formation, southeastern Nevada. The extended range includes the Hagerman local fauna from Idaho, Arizona, Kansas, New Mexico, Nevada, Texas, and Washington (Zakrzewski, 1969; Gustafson, 1978; Ruez, 2009b).

*Identification:* A single, lightly worn molar (VM-P983) is well preserved and represents a small squirrel. It has remnants of four broken roots, and is probably a lower M/1 or M/2 molar. A protolophid and metalophid bounds a wide talonid basin. The entoconid is separated from the mesoconid by a shallow v-shaped trigonid. The protoconid is higher than either the mesoconid or entoconid. The anteroposterior length is 2.9 mm; transverse width is 2.9 mm.

*Discussion:* Sciurid teeth are rectangular to subquadrate in outline, and identification is usually based on traits and size of the upper dentition (Black, 1963). Isolated lower teeth are normally not useful for genus-level identification (Gensler, 2002). Ground squirrels have been described from numerous Blancan sites of the Great Plains (Martin et al., 2002). The dental patterns are generally

similar among many species of ground squirrels, but vary in size. Sciuridae is listed in the Panaca local fauna by Mou (1999). In the SBCM Panaca collection there are several isolated teeth identified as *Spermophilus*, but they have not been described or reported. I assign this specimen cautiously to *Spermophilus* as this specimen is similar in size and morphology to sciurids in the Hagerman local fauna (Ruez, 2009b). Further study of sciurids from the Panaca Formation is required for clarification and identification of genera and species.

Family Geomyidae Bonaparte, 1845

Subfamily Geominae Bonaparte, 1845

*Pliogeomys* Hibbard, 1954b

*Pliogeomys* parvus

Pocket Gopher

(Fig. 18)

*Referred Material:* Left P/4 (VM-P891).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-24, in the Panaca Formation, southeastern Nevada. The extended range includes Glens Ferry Formation, Hagerman, Idaho, Oklahoma, and Kansas (Hibbard, 1954; Mou, 1999; Ruez, 2009b).

*Identification:* The collection of a single P/4 tooth, which is the most distinctive for this species, represents the Geomyidae. It was collected by screenwashing. The occlusal outline of the protolophid is subcircular, shorter and wider than the metalophid on this worn specimen (Figure 18A). The two

lophids are joined medially by a narrow loph. Dentine tracts are visible on both sides (Figure 18B). The tooth has two well-developed roots with a fused base. This tooth shows higher dentine tracts (Figure 18B) on the labial side than the lingual side. The tooth has an anteroposterior length of 1.7 mm and a transverse width of 1.4 mm.

*Discussion:* *Pliogeomys*, a more primitive pocket gopher than *Geomys*, is characterized by rooted cheek teeth and a distinctive occlusal pattern. Mou (1999) noted high dentine tracts on the sides of the teeth. She determined that the tracts on the labial sides are higher than on the lingual sides and lower on the protolophid than on the metalophid.

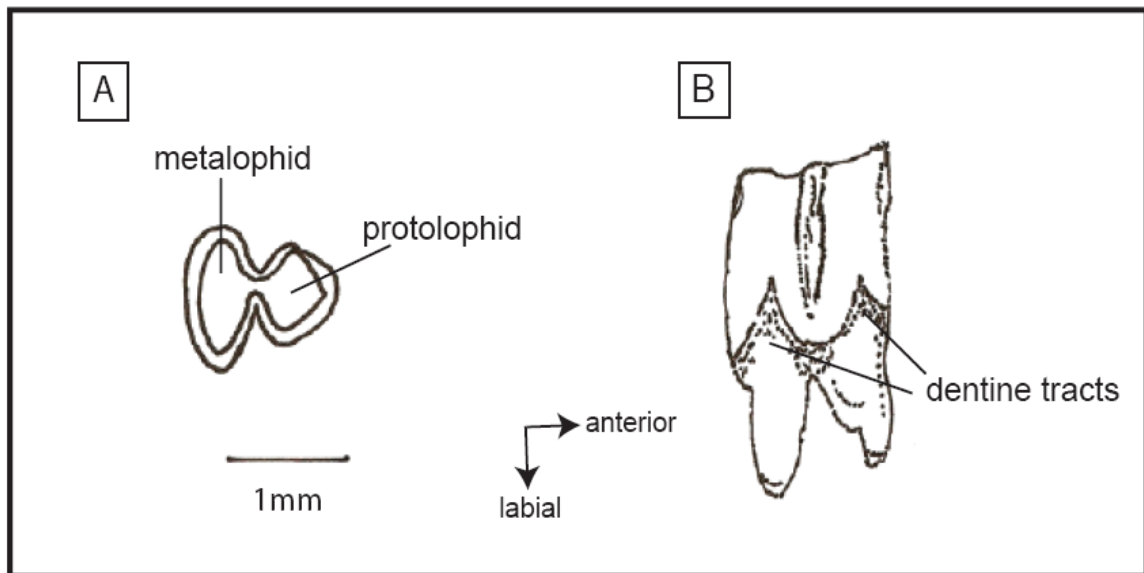


Figure 18. A. Sketch of worn *Pliogeomys* lower left P/4 (VM-P981) occlusal surface from the Panaca Formation. B. Labial view showing the dentine tracts on the P/4 tooth. The tracts are lower on the lingual side than the labial side, and lower on the protolophid than the metalophid.

Only three species of *Pliogeomys* have been described: *Pliogeomys parvus* from the Hagerman and Panaca local faunas, *P. buisi* from the Buis Ranch local fauna, of the Rexroad Formation of Oklahoma, described by Hibbard (1954), and *P. carranzai* from the late Hemphillian Yepomera local fauna of Chihuahua. *Pliogeomys carranzai*, which has a higher crowned tooth with higher dentine tracts than those from the Panaca and Hagerman pocket gopher, is now considered a species of *Geomys* (Martin et al., 2002). This tooth (VM-P891) compares well with Mou's (1999) Panaca description and Zakrzewski's (1969) Hagerman description of *Pliogeomys parvus*, thus I am assigning this specimen to *Pliogeomys parvus*.

Family Heteromyidae Gray, 1868

Dipodomyinae Coues, 1875

Prodipodomys Hibbard, 1939

cf. *Prodipodomys* sp.

sp. indet.

Kangaroo Rat

*Referred Material:* Molar (VM-P593).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-01, in the Panaca Formation, southeastern Nevada. The extended range includes Hagerman local fauna, Idaho, Kansas, Oklahoma, and Arizona (Zakrzewski, 1969; Mou, 1999).

*Identification:* The single tooth is well worn with the individual cusps of each lobe indistinguishable. The two transverse lobes are subequal, one lobe

slightly longer than the other with a single root. The dentine-filled, deep labial groove has a reentrant extending about 50 % across the width of the occlusal surface at the proto-loph. Dentine tracts are low. Roots are small, fused proximally, and curve to the posterior. The anteroposterior length is 0.9 mm and the transverse width measures 1.2 mm. This sole Dipodomyinae tooth from the Panaca Formation is referable as a *Prodipodomys* molar.

*Discussion:* Two Heteromyidae subfamilies are described from the Panaca Formation: Perognathinae (pocket mouse) and Dipodomyinae (kangaroo rat). Perognathinae teeth have two to three roots in both the upper and lower dentition and an asymmetrical occlusal outline of the P4/. As in other rodents, Dipodomyids are distinguished by the geographic position of the cusps, lophs, and the number of roots. Mou (1999) found that the number of roots and the fusion of the roots vary, but in general the lower M2 and M3 have only one root. Lower M/3s do not have dentine and the roots are fused as a single root without a groove. The presence of dentine and a labial groove suggest that this molar is a lower M/1 or M/2. The extreme wear on VM-P593 prevents exact dentary placement and classification beyond a *Prodipodomys*.

Family Cricetidae Rochebrune, 1883

(Table 4, Fig. 19)

The Sigmodontinae, Arvicolinae, and Prometheomyinae are three subfamilies of the Cricetidae with representatives that have been described from the Panaca Formation. Sigmodontinae is represented by *Peromyscus hagermanensis* and the endemic species: *Onychomys*, *Repomys panacaensis*,

and the recently described *Repomys minor*. Only one arvicoline species, the endemic *Mimomys panacaensis*, has been reported (Mou, 1997). Within the Prometheomyinae, three species have been reported, all within the recently erected genus *Nevadaensis*: *N. feifari*, *N. lindsayi*, and *N. downsi*.

Mou (1997, 1999) conducted an extensive study of the Panaca Formation cricetids. She used a large sample size to thoroughly examine the characteristics of the members of this family and calculate mean averages of the several distinguishing features. All cricetid measurements are listed in Table 4.

Subfamily Sigmodontinae Wagner, 1843

Tribe Peromyscini Hershkovitz, 1966

*Peromyscus* Gloger, 1841

*Peromyscus hagermanensis*, Hibbard, 1962

*Referred Material*: M/1 (VM-P893).

*Age*: early Blancan

*Stratigraphic and geographic ranges*: Site PAN-01, in the Panaca Formation, southeastern Nevada. The extended range includes the Hagerman local fauna and faunas of southern Arizona.

*Identification*: This single tooth is well worn, all the cusps, except the anteroconid are worn down. The anteroconid is broad, weakly bilobed; the slightly larger lingual condyle is still visible, but the labial condyle is barely visible. The reentrant valleys are wide and shallow. The anteroposterior length is 1.4 mm and the transverse width is 1 mm. There are two prominent roots. The two roots define this tooth as a lower molar, but the size, shape and remains of the

Table 4. Measurements of cricetid teeth from Panaca local fauna. Table list tooth placement with specimen number, AP = anteroposterior, TR = transverse width, (frag) = fragment and not good measurement. All measurements are in millimeters.

Cricetid Tooth Measurements			
Tooth placement	Specimen Number	AP	TR
M1/	P987	2.4	1.5
	P988	2.2	1.5
	P985	2.3	1.5
	P984	2.1	1.5
	P986 (frag)	–	1.6
	P844	2.3	1.5
	P892	1.8	1.0
	P893	1.4	0.8
	P828 (frag)	–	1.5
	P894	2.1	1.4
M2/	P993	1.0	1.5
	P944	2.0	1.5
	P995	2.0	1.5
	P996	2.0	1.5
	P845 (frag)	1.7	1.4
M/1	P1001	2.5	1.3
	P756	2.5	1.4
	P989	2.5	1.4
	P990	2.0	1.5
	P991	2.0	1.3
	P827	2.6	1.4
	P992	2.5	1.5
	P701	2.8	1.5
	P1003	2.1	1.4
	P1002	2.1	1.5
	P1007	1.7	1.1
M/2	P895	1.8	1.3
	P997	1.8	1.3
	P998	1.6	1.3
	P999	1.9	1.4
	P1000	1.8	1.4
	P8896	1.8	1.2
	P777	1.6	1.3
	P701	1.9	1.3
	P1003	1.7	1.3
	P1002	1.7	1.3
M/3	P701	1.7	1.2
	P897	1.5	1.2
	P754	1.3	0.9

alternating principal cusps in the occlusal outline define it as a *Peromyscus hagermanensis*.

*Discussion:* *Peromyscus* cheek teeth are brachydont and rooted; the upper cheek teeth have three roots, while the lower cheek teeth have only two roots. This tooth is a lower M/1 tooth based on the two roots, the narrow anterior occlusal view, and the visible remains of bilobed anteroconid. These characteristics and the occlusal outline allow for assignment to *Peromyscus*.

*Repomys* May, 1981

*Referred Material:* Left maxilla with M1/, partial M2/ (VM-P1003); left M/2 (VM-P999).

*Age:* early Blacan

*Stratigraphic and geographic ranges:* Site PAN-24, in the Panaca Formation, southeastern Nevada.

*Identification:* The teeth are slender, hypsodont with thick enamel, and do not have an enamel islet on the M1/ or M2/. Teeth appear to be rooted, one root seen on the partial M2/ tooth, but roots can not be observed as teeth rest in mandible fragment.

*Discussion:* The most diagnostic tooth of *Repomys* species are the upper and lower M3 teeth, none of which were collected in this study. The occlusal surface differs with wear, and roots change during stages of wear. Mou emended the diagnosis for *Repomys panacaensis* described by May (1981) after careful review of a large collection of teeth from the Panaca Formation. Mou (1999) found that this species is one of the most abundant small mammals in the



Panaca assemblage. *R. minor* has deeper reentrant valleys on the labial side and lower dentine tracts than *R. panacaensis*. These two moderately worn specimens are cautiously assigned as a species of *Repomys*.

Subfamily Arvicolinae Gray, 1821

*Mimomys* Major, 1902

*Mimomys panacaensis* Mou, 1997

*Referred Material:* PAN-16: right mandible with I/1, M/1, M/2, M/3 (VM-P701), PAN- 19: left M/1 (VM-P756, VM-827); PAN-24: right dentary with M/1 (VM-1001); right dentary with M/1 and M/2 (VM-P1002); left M2/ (VM-P996); right M2/ (VM-P994, VM-P995); right M3/ (VM-897); left M/1 (VM-P989, VM-P992); right M/1 (VM-P990); right M/2 (VM-P895, VM-P896, VM-P997, VM-P998, VM-P1000).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-16 (VM-P701); PAN-19 (VM-P757, VM-P827) and PAN-24 in the Panaca Formation, southeastern Nevada.

*Identification:* Arvicoline teeth are hypsodont and the molars have triangularly prismatic cusps (Mou, 1999; Repenning, 2003). The first lower molar and the last upper molar are the most diagnostic teeth of arvicolines. Mou (1999) stated that the dental morphology has considerable intraspecific variations within the Panaca fauna. Furthermore, the occlusal morphology may change greatly through the wearing stages. Mou (1999) described five stages of wear in

arvicoline tooth patterns. She suggested that a large sample of preferably M/1s and M3/s are required for a reliable identification.

The lower mandible (VM-P701) has a complete dentary (Figure 19) and is from an adult. The complete lower incisor passes beneath the molars. The first lower molar has an anteroconid complex (ACC), three alternating triangles, and a posterior lobe. The lingual triangles are slightly larger than the labial triangles, with uniform thickness of the enamel. The degree of closure is slightly-to-moderately open between the third triangle and the ACC, moderately open between the second and third triangles, moderately open between the first and second triangles, and slightly open between the first triangle and the posterior lobe. Each tooth has two roots. Measurements: mandible length- 20.0 mm, diastema- 2.14 mm, m/1 anteroposterior- 2.8 mm, transverse width- 1.5 mm, M/2 anteroposterior- 1.9 mm, transverse width- 1.3 mm, and M/3 anteroposterior- 1.7 mm, transverse width- 1.3 mm.

The second lower molar has four alternation triangles, a posterior lobe, and two roots. The lingual triangles are slightly larger than the labial triangles. Labially, the dentine tract is absent. The degree of closure between the alternation triangles is moderately open. Figure 19 shows the general structure and features of arvicoline rodents.

The lower third molar has four alternating triangles, a posterior lobe, with lingual triangles slightly larger than the labial ones. Triangle four is reduced and each tooth single tooth shows two roots.

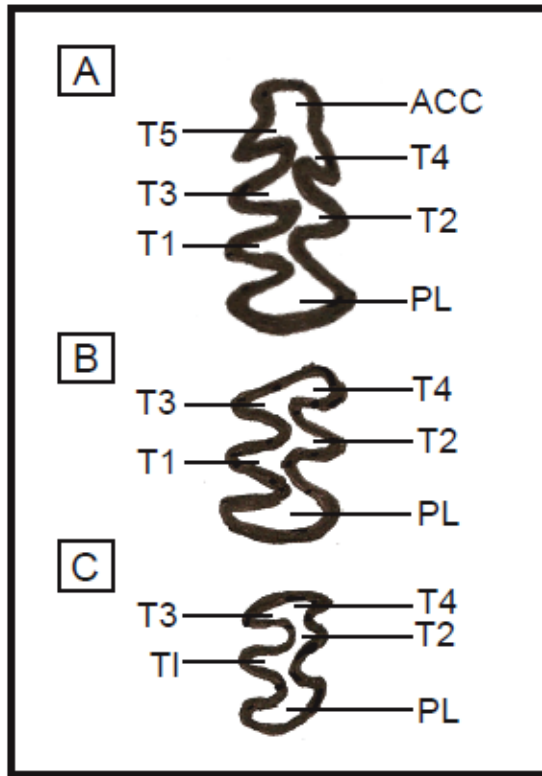


Figure 19. General structure and features of the occlusal surface of the lower left molars of arvicoline rodents. The black is the enamel and the enclosed white is the dentine. A. lower left M/1 showing the posterior lobe (PL), the alternating triangles (T), and the anteroconid complex, also called the anterior cap. Enamel closure between T4 and T5 depicts a closed state. B. lower left M/2 showing the posterior lobe and four alternating triangles. C. lower left M/3 showing the posterior lobe and four open triangles. Abbreviations: PL=posterior lobe, ACC=anteroconid complex, T=numbered triangles, numbered from posterior to anterior of molar.

The upper second molar has an anterior lobe and three alternating triangles. The M2/ has three roots, and the lingual reentrant apex is slightly curved to the posterior.

The upper third molar has a posterior lobe, three alternating triangles and an anterior lobe. The lingual triangles are slightly larger than the labial triangles. The tooth has two roots. These teeth all have deep reentrant valleys on both sides, lingual triangles slightly larger than the labial triangles, various degrees of closure between the triangles and roots, which identifies them as *Mimomys panacaensis*.

*Discussion:* The *Mimomys* population from the Panaca Formation differed from Repenning's (1987) description of *Mimomys (Ophiomys) magilla*, and

prompted Mou (1997) to erect a new species, *Mimomys panacaensis*. She based the new species on several characteristics, including the frequent occurrence of an enamel islet on ACC seen on less worn teeth, the presence of three roots on many of the M2/s, the presence of three roots on approximately 2/3 of the M3/s, the occasional occurrence of an anterior posterior islet on M3/, and on her analysis of schmelzmuster of the enamel band. She found that this species occurs throughout the Panaca Formation. The SBCM workers identified *Peromyscus hagermanensis*, *Mimomys (Ophiomys) magilli*, *Ophiomys*, and *Repomys panacaensis* from the Panaca Formation. It is most likely that the *Mimomys (Ophiomys) magilli* identified by the SBCM workers is the same as *Mimomys panacaensis* described by Mou. Even though I did not see island islets on all the M/1s, they are assigned to *Mimomys panacaensis*.

#### 4.7 Order Carnivora Bowdich, 1821

Family Canidae Fischer de Waldheim, 1817

Subtribe Canina Fisher de Waldheim, 1817

*Canis* Linnaeus, 1758

*Canis* sp.

sp. indet.

*Referred Material:* M/1 fragment (VM-P854), left M/1 fragment (VM-P919).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-24, in the Panaca Formation, southeastern Nevada. The extended range includes Texas, Nebraska, Kansas, Washington, Arizona, New Mexico, Florida, Idaho, and Anza-

Borrego Desert State Park in California (Murray, 2006; Wang and Tedford, 2008; Ruez, 2009b).

*Identification:* Canid carnassial molars are identified by the cuspid pattern on the carnassial pair. Specimen (VM-P854) appears to be a small, smooth fragment of the hypoconid with a portion of the dentine root from labial side of a first lower molar. Specimen (VM-P919) is probably a portion of the carnassial protoconid tooth with a portion of the inner medial section.

*Discussion:* *Canis* was widespread in North America during the Blancan, although a great deal of the *Canis* record is found in the deposits of the Great Plains region of the United States (Wang and Tedford, 2008). Two species of Canidae, *Canis lepophagus* and *Borophagus* cf. *diversidens* were identified from the Panaca Formation. Mou (1999) described a *Canis* maxillary with the upper P3, P4, and partial M1 and the undescribed *Borophagus* material was recovered by the Frick Laboratory collectors. *Canis lepophagus*, the smaller of the two, is coyote-sized, while *Borophagus* is described as a larger-sized, bone-crushing dog. The tooth material described here appears to be from a smaller-sized animal, thus assigned to *Canis* species. These two molar fragments were recovered from the same bag of sediment during screenwashing and probably are parts of the same tooth.

*Canis lepophagus* Johnston 1938

(Table 5, Fig. 20)

*Referred Material:* Left medial phalanx (VM-P604), right medial phalanx (VM-P611), right astragalus (VM-P662).

Age: early Blancan

*Stratigraphic and geographic ranges:* Sites PAN-02 (both phalanges), and PAN-09 in the Panaca Formation, southeastern Nevada. The extended range includes Florida in the east with many western sites in Kansas, Nebraska, Texas, Washington, Arizona, Idaho, and probably Anza-Borrego Desert State Park in California (Munthe, 1998; Murray, 2006; Ruez, 2009b).

*Identification:* The left (VM-P604) and right (VM-P611) medial phalanges have nearly identical measurements and are considered a matching pair. Specimens have a prominent ridge on the medial side of the diaphysis and the lateral condyle is less defined than *Lynx rufus* or *Puma concolor*. The prominent ridge excludes *Taxidea taxus* and the phalanx is shorter than *Procyon lotor*. The specimen is an adult as the epiphyses are fused. The phalange measurements are listed in Table 5. While no measurements could be found for medial phalanges in the literature, their size and morphology match those of a *Canis latrans* comparative specimen.

The right astragalus (VM-P662) measurements are listed in Table 5. The lateral condyle is higher than the medial condyle. In comparison, the ventral facets differ from those of *Lynx rufus* or *Puma concolor*, as well as those of *Taxidea taxus* and *Procyon lotor*. In *Vulpes vulpes* the astragalus is smaller than the Panaca specimen. Although the anterior end is a little weathered, the condyle shape, the dorsal articular surfaces, and size compare well to *Canis latrans*, thus I conclude that the astragalus is similar to a coyote.

Table 5. Measurements of canid elements from the Panaca local fauna. Table lists element with specimen number, GL = greatest length, PW = proximal width, DW = distal width, GW = greatest width, GLm = greatest length of lateral half, GLI = greatest length of medial half. All measurements are in millimeters.

Canid Element Measurements						
Element	GL	PW	DW	GW	GLm	GLI
left medial phalanx	12.95	5.18	4.85	-	-	-
right medial phalanx	12.88	5.32	4.86	-	-	-
right astragalus	26.55	-	-	14.62	24.55	24.55



Figure 20. Comparison of *Canis* medial phalanges. A. left medial phalanx of *Canis latrans*; B. Panaca specimen VM-P604, left medial *Canis lepophagus* phalanx; C. Panaca specimen VM-P611, right medial *Canis lepophagus* phalanx; D. right medial phalanx of *Canis latrans*.

*Discussion:* *Canis lepophagus*, a small canid, is known from primarily Blancan localities (Murray, 2006; Ruez, 2009b). The caninae are distinguished by the accessory cusps on their incisors, their small, simple premolars, the M2/posterior cingulum, an enlarged anterolabial cingulum, and the metaconid being higher than the protoconid (Ruez, 2009b). Large cheek teeth and short canines differentiate *Canis* from *Vulpes* (Ruez, 2009b; personal observation). Teeth are the best elements for identifying canids, but the post-cranial elements have some defining characters as well. Bjork (1970) described an atlas, metacarpals, and the calcaneum of *C. lepophagus*, but not the astragalus or phalanges. Two canid species have been identified from the Panaca Formation: *Canis lepophagus* and *Borophagus* cf. *B. diversidens* (Mou, 1999; Reynolds and Lindsay, 1999). Based on size and morphological similarity to *Canis latrans*, I assign these phalanges and the astragalus to *Canis lepophagus*.

Family Felidae Fischer de Waldeim, 1817

Subfamily Felinae Trouessart, 1885

*Lynx* Kerr, 1792

cf. *Lynx* sp.

sp. indet.

*Referred Material:* Left tarsal navicular (VM-P655), left medial phalanx (VM-P692).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-08 and PAN-11, respectively, in the Panaca Formation, southeastern Nevada. The extended



geographic range includes Nebraska, Kansas, Texas, New Mexico, Arizona, Florida, Washington, Idaho, and California (Martin, 1998; Ruez, 2009b).

*Identification:* Two specimens from the Panaca Formation represent the family Felidae. The triangular shaft of this phalanx (VM-P692) has a prominent concavity on the lateral margin, creating a distinctive curvature characteristic of felid phalanges (Wang and Tedford, 2008). The deep notch on the proximal end, ventral side, is triangular, pointing down the diaphysis. The shallow v-shaped groove on the ventral side of the distal end allows for retraction of the claw (Wang and Tedford, 2008). Measurements as follows: greatest length- 20 mm, greatest breadth of the proximal articular surface- 8.04 mm, breadth of the distal end- 6.45 mm. The navicular (VM-P655) is distinguished by the dorsal articular facets. The greatest length is 17.98 mm and the greatest breadth is 13.15 mm.

Phalanges and tarsals typically do not have diagnostic traits that allow species-level identification, but the distinctive morphology and size of these specimens permit genus-level assignment. These elements are not typically described in great detail, nor are measurements reported in the literature, but these specimens provide evidence of carnivores in addition to the canids in Meadow Valley.

*Discussion:* Element comparisons of size and morphology were made to *Puma concolor* (mountain lion), *Lynx rufus* (bobcat), *Canis latrans* (coyote), *Taxidea taxus* (badger), *Vulpes vulpes* (fox), and *Procyon lotor* (raccoon) for identification from the HAFO comparative collection. The *Vulpes* and *Procyon* specimens were much smaller and morphologically different. Ventral articular

surfaces of the navicular differ from those of *Canis latrans* and *Taxidea taxus*. The ventral articular facets are similar in shape to those of *Puma concolor*, but the *P. concolor* tarsal is approximately twice the size of the Panaca specimen. Based on the similarity in size and morphology between the tarsal and phalanx and those of *Lynx rufus*, I assign these bones to the genus *Lynx*. *Felis* (now *Lynx*) material has been identified but not published by the Frick collectors. I have not seen the Frick material for comparison. Other early Blancan localities with material attributed to *Lynx* are the Rexroad local fauna, Kansas; the Beck Ranch local fauna, Texas; Cosomi Wash in Colorado (Martin, 1998). *Lynx* material also occurs in the Hagerman local fauna, Idaho, and at Anza-Borrego Desert State Park, both of which are considered middle Blancan (Bjork, 1970; Murray, 2006). Additional cranial material is needed for better identification of Panaca felids, but these felid fossils document the occurrence of bobcat-sized cats in the Panaca ecosystem.

#### 4.8 Perissodactyla Owen, 1848

Equidae Gray, 1821

Genus, Species

*Incertae Sedis*

Horse

*Referred Material:* Tooth fragments (VM-P541-(2), VM-P560-(9), VM-P761-(1)).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-01 and PAN-19, respectively, in the Panaca Formation, southeastern Nevada. Equids were widespread on the North American continent during the Pliocene (MacFadden, 1998).

*Identification:* Brownish horse tooth fragments, ranging in length from 10 to 23 mm. Most of the fragments are enamel only, but some have dentine attached. The complex occlusal pattern is distinctively equid, but the fragments do not permit further identification.

*Discussion:* Fragments were collected during screenwashing. Stock (1921) recorded the first evidence of horses in the Panaca Formation with his identification of two phalanges and a tooth. *Equus* was reported to be common in the Panaca Formation in Meadow Valley, according to personal communication between Tedford and Mou (1999). AMNH collected horse material identified as *Equus idahoensis*. Reynolds and Lindsay (1999) list the primitive horse *Dinohippus* sp., as well as *Equus (Dolichohippus)* sp. cf. *E. (D.) simplicidens*, *Equus (Hemionus)* sp. for Meadow Valley. Although the tooth material is too fragmentary for generic identification, it documents additional evidence of equids in the Panaca Formation.

4.9 Artiodactyla Owen, 1848

Family Camelidae Gray, 1821

Subfamily Camelinae Zittel, 1893

Tribe Camelini Webb, 1965

*Megatylopus* Matthew and Cook, 1909

cf. *Megatylopus* sp.

sp. indet.

Camel

*Referred Material:* Left fibula (VM-P624), distal end of metapodial (VM-P653), proximal end of medial phalanx (VM-P663), proximal end of proximal phalanx (VM-P837).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site Pan-04 (VM-P624), PAN-08 (VM-P653), PAN-09 (VM-P663), PAN-21 (VM-P837), in the Panaca Formation, southeastern Nevada. The extended range of *Megatylopus* in the Blancan includes Nebraska, Kansas, Texas, Washington, and Arizona; in the Hemphillian this genus occurred from California to Tennessee and from Texas to Alberta, Canada; it was also widespread in the Miocene (Webb, 1965; Voorhies and Corner, 1986; Honey et al., 1998; Jiménez-Hidalgo and Carrañza-Castaneda, 2010; Paleobiology Database).

*Identification:* The left fibula (VM-P624) was collected off the surface and its anterior surface is moderately weathered and pitted. Hence, the facet for the astragalus on the anterodistal side is not visible. The calcaneum facet is moderately preserved on the posterolateral side. The breadth is 26.6 mm and the greatest length is 26.3 mm from the dorsally, inverted v-shaped tip to the calcaneum articular facet on the posterolateral side. The unique shape, size, and articular facets allow identification to the camel *Megatylopus*.

The distal end of a metapodial (VM-P653) displays well-preserved condyles. One edge of the diaphysis anterior side is deeply weathered, but the shaft is straight and only slightly narrower than the condyles. The lateral condyle is slightly wider, flared and shorter than the medial condyle. The breadth measured 29.3 mm perpendicular to the medial ridge of the condyle and the metapodial fragment length is 46 mm. The condyles are moderately robust and too broad for *Hemiauchenia*, I cautiously assign this specimen to *Megatylopus*.

The greatest breadth of the proximal end of a medial phalanx (VM-P653) is 28 mm. This proximal end fragment is 53 mm long. The articular surface is concave and the edges are preserved, but the diaphysis is weathered and fractured on the ventral side. This specimen is very similar in size to the proximal phalanx and the sites are approximately 8 to 10 meters apart.

The proximal end of a proximal phalanx (VM-837) articular surface is slightly concave and the carinal groove is shallow and narrow whereas *Hemiauchenia* has a narrow deep carinal groove. The proximal and distal extremities are expanded from the triangular diaphysis and the specimen exhibits a proximal dorsal W-shaped suspensory ligament scar characteristic of *Megatylopus* (Voorhies and Corner, 1986). The phalange is moderately proportional, not long and slender as in *Hemiauchenia* or *Lama*. The proximal ends are slightly expanded laterally as in larger camels such as *Camelops* and *Metatylopus*. Specimen measured 32.6 mm from anterior to posterior dissecting the carinal groove and the bone segment measures 66 mm.

*Discussion:* The camelid metapodials and fibula from the Panaca Formation are fragmented and weathered. Within the Panaca fauna two genera of camels have been reported from the Panaca Formation: *Megatylopus* sp. and *Hemiauchenia* sp. (Voorhies and Corner, 1986; Mou, 1999; Reynolds and Lindsay, 1999). *Megatylopus* is larger, long-limbed camel (Webb, 1965; Voorhies and Corner, 1986), while *Hemiauchenia* is more gracile and smaller (Jiménez-Hidalgo and Carrañza-Castaneda, 2010). Voorhies and Corner (1986) described postcranial material of *Megatylopus*, including metapodials and proximal phalanges. The proximal end of VM-P837 is slightly smaller than their listed one measurement, but comparable. Webb (1965) provided detailed sketches and description of many post-cranial elements including tarsals, but no descriptions of metapodials or phalanges. Complete elements with less weathering and comparative material would aid in better genus-level identification. These camelid specimens are referred to *Megatylopus* on the basis of their size, moderate proportions, and morphological characters (Webb, 1965; Voorhies and Corner, 1986; Jiménez-Hidalgo and Carrañza-Castaneda, 2010).

Suborder Ruminantia Scopoli, 1777

Superfamily Bovoidea Gray, 1821

Family Bovidae Gray, 1821

Subfamily Caprinae Gray, 1821

Tribe Caprini Gray, 1821

*Sinocapra* Chen, 1991

*Sinocapra willdownsi* Mead and Taylor, 2005

(Table 5, Fig. 21, 22, 23)

*Referred Material:* medial phalanx (VM-P542),

*Age:* early Blancan

*Stratigraphic and geographic ranges:* Site PAN-01 in the Panaca Formation, southeastern Nevada. Only previously described specimen is in the AMNH collection from the AMNH Limestone Corner locality, in the Panaca Formation, southeastern Nevada (Mead and Taylor, 2005).

*Identification:* The medial (second) phalanx (VM-P542) is short and broad, measuring 30.06 mm long (greatest length on the lateral side) and 12.99 mm breadth at the proximal end. The dorsal extensor protuberance (dexp) is elongate (Figure 21) and a postarticular plateau is lacking (Figure 21.1). The point of attachment of the interdigital ligament is weak to almost absent (Figure 21.2). The medial phalanx is well preserved and compares well with AMNH specimen 52139E, which came from the same locality. Thus, I assign this specimen to *Sinocapra willdownsi*.

*Discussion:* The medial phalanx (VM-P625) was initially compared for size and morphology with *Odocoileus hemionus* and *Antilocapra americana* specimens from the HAFO comparative collection (Figure 22). Phalanges are not commonly used in taxonomic diagnosis; however, Mead and Taylor (2005) described post-cranial bone elements, including three phalanges, associated with the *Sinocapra willdownsi* maxillary tooth row and fragmentary skull material. They assumed these phalanges to be the medial manus phalanges based on

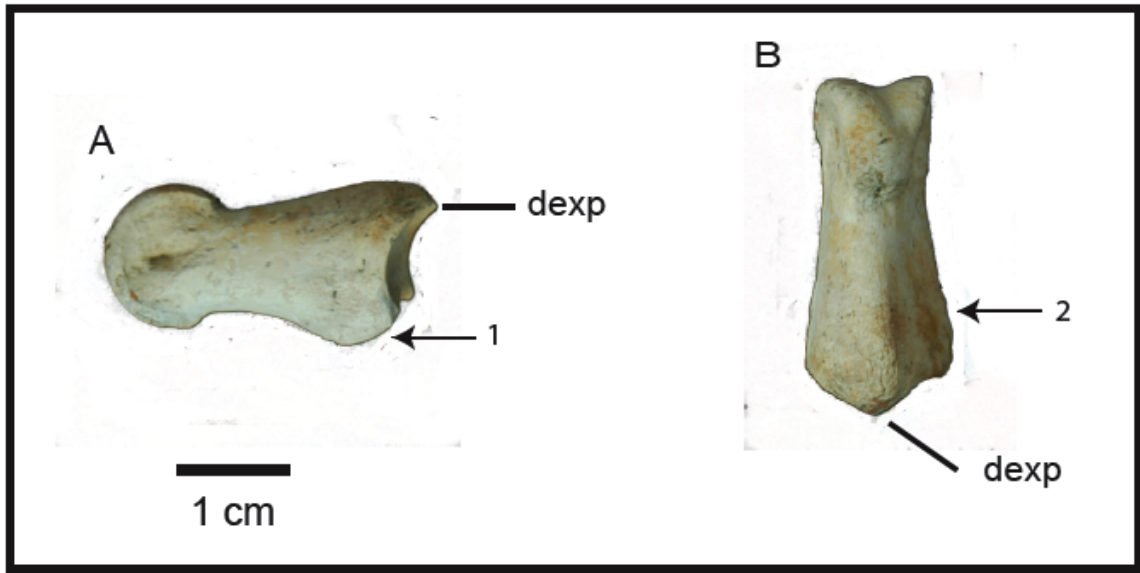


Figure 20. Medial phalanx of *Sinocapra wiltdownsi* (VM-P542). A. medial view. B. dorsal view. Abbreviations: dexp, dorsal extensor protuberance; 1, lack of postarticulate plateau; 2, location area of interdigital ligments; insertion is weak to absent (see text).



Figure 21. Comparison of medial (second) phalanges. A. *Odocoileus hemionus* B. *Sinocapra wiltdownsi* (VM-P625), Blancan C. *Antilocapra americana*.



their precise articulation with the right metacarpal fragment. Specimen VM-P625 matches well in size with the well-preserved AMNH 52138E medial manus phalanx. The phalanx also exhibits the elongate extensor protuberance, lacks the postarticular plateau, and the interdigit ligament insertion is weak.

Mead and Taylor (2005) noted that the phalange joints were designed for tensor and flexor motion, implying that this species was more of mountainous and rocky terrain climber than for running on lowland level landscape. This new specimen adds to the known material representing *Sinocapra willownsi*.

*cf. Sinocapra* Chen, 1991

*Referred Material:* Proximal phalanx (VM-P625).

*Age:* early Blancan

*Stratigraphic and geographic ranges:* PAN-04 in the Panaca Formation, southeastern Nevada. Only previously described specimen is in the AMNH collection from the AMNH Limestone Corner locality, in the Panaca Formation, southeastern Nevada (Mead and Taylor, 2005).

*Identification:* The proximal phalanx (VM-625) measures 43.25 mm (greatest length on the lateral side) and 15.25 mm in breadth at the proximal end. This phalanx is more weathered than is the medial phalanx. The interdigit ligament attachment points are not preserved. Both specimens were collected from the “Limestone Corner,” area approximately six meters apart in the same horizon. The proximal phalanx is assigned to *cf. Sinocapra* based on the morphology of the specimen, comparative measurements (Table 6), and location proximity to the identified medial phalanx and to AMNH specimen 52139E.

Specimen VM-P625 has similar length-to-width ratio and the trend line falls between the two AMNH specimens, both numbered as 52139E (Figure 23). The lack of distinct morphology due to weathering is therefore insufficient for specific identification, so this specimen is assigned to cf. *Sinocapra*.

*Discussion:* Richard White (personal communication) compared the length versus width of specimen VM-P625 to nineteen Early Irvingtonian *Odocoileus* specimens, five Rancholabrean *Oreamnos harringtoni* phalanges, four modern *Oreamnos americana* specimens, and two modern *Ovis canadensis* phalanges (Table 6). In addition, he compared the above named taxa to the two Blancan *Sinocapra* phalanges described by Mead and Taylor (2005) from the AMNH “Limestone Corner” locality in Meadow Valley. These comparative size measurements are listed in Table 6, and plotted in Fig. 23. The *Sinocapra* material plots within the *Odocoileus* cluster and near the two grouped *Ovis canadensis* phalanges, although other characteristics preclude these phalanges from belonging to these taxa. It seems plausible for the *Sinocapra* material to plot near the *Ovis* specimens, as morphological studies show *Sinocapra* is more closely related to sheep than to mountain and true goats (Mead and Taylor, 2005).

The three *Sinocapra* elements plot fairly close to one another and thus have comparable length-to-width ratios. While this phalange is not as diagnostic as the medial phalanx or as cranial material, this specimen adds to the known material representing *Sinocapra*.

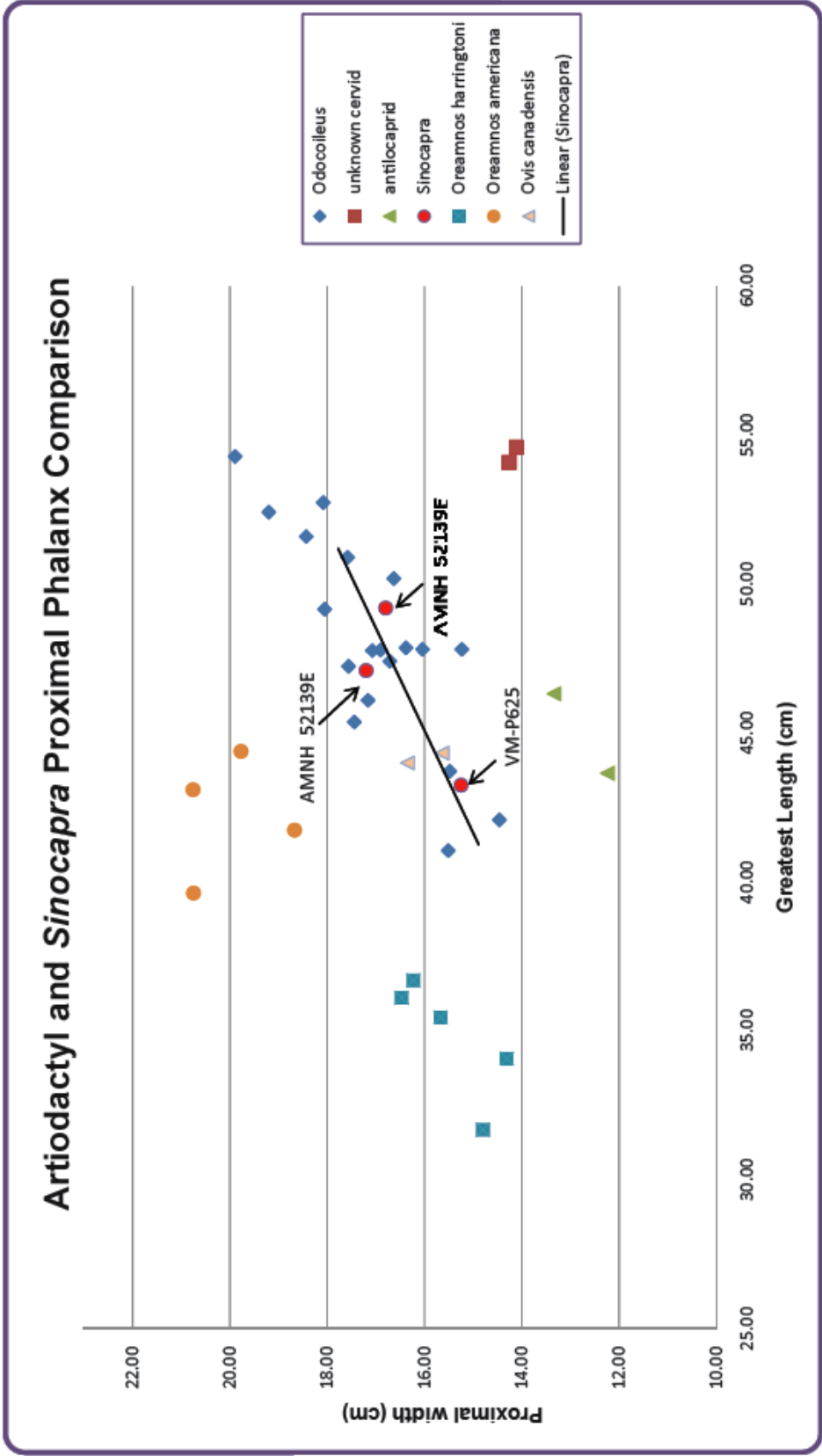


Figure 23. Bivariate plot of Artiodactyls and *Sinocapra* length versus breadth of proximal phalanx measurements. Arrow points to VM-P625 *Sinocapra* proximal phalanx collected in this study. Trend line shows similar ratio in length versus breadth of specimen VM-P625 to known *Sinocapra willowsoni* phalanx. Measurements are in centimeters and were measured by Richard White at the International Wildlife Museum, Tucson.

Table 6. Comparative Artiodactyl proximal phalanx measurements made by Richard White (personal communication). Measurements are in centimeters. Abbreviations are as follows: AWC, Arizona Western College, Yuma; LACM, Los Angeles County Museum; AMNH, American Museum of Natural History; UNLV, University of Nevada, Las Vegas; GRCA, Grand Canyon National Park; NAU, Northern Arizona University; RSW, Richard White, personal collection.

Dimension of the Proximal Phalanx of selected Artiodactyls									
Taxon	Age	Institution	Specimen	Greatest Length Lateral Side	Breadth	Height	Breadth	Height	Breadth at Mid-shaft
					Proximal End	Proximal End	Distal End	Distal End	
Odocoileus	Early Irvingtonian	AWC	10171	51.60	18.43	22.49	15.66	13.06	14.42
Odocoileus	Early Irvingtonian	LACM	118426	50.90	17.58	21.36	15.98	13.40	14.86
Odocoileus	Early Irvingtonian	AWC	14273	47.81	16.04	18.85	13.45	11.76	14.14
Odocoileus	Early Irvingtonian	AWC	14773	47.86	16.38	19.44	14.99	13.29	12.84
Odocoileus	Early Irvingtonian	AWC	10756	41.05	15.51	16.35	12.73	11.40	11.80
Odocoileus	Early Irvingtonian	AWC	10727	47.81	15.23	19.28	13.43		13.16
Odocoileus	Early Irvingtonian	AWC	11631	52.74	18.08	22.75	15.06	14.54	13.75
Odocoileus	Early Irvingtonian	AWC	14011	47.41	16.71	21.86	14.52	12.80	12.78
Odocoileus	Early Irvingtonian	AWC	12387	42.08	14.46	16.01	12.37	11.33	11.60
Odocoileus	Early Irvingtonian	AWC	12848	54.29	19.89	24.32	16.32	15.19	14.80
Odocoileus	Early Irvingtonian	AWC	12648	50.19	16.63	21.05	14.10	12.97	13.22
Odocoileus	Early Irvingtonian	AWC	12073	47.79	16.90	18.97	13.51	12.13	13.43
Odocoileus	Early Irvingtonian	AWC	12210	46.10	17.16	21.32	15.51	12.26	14.51
Odocoileus	Early Irvingtonian	AWC	12374	49.16	18.05	21.33	14.89	13.42	14.50
Odocoileus	Early Irvingtonian	AWC	12343	52.42	19.20	23.40	15.85	14.49	16.24
Odocoileus	Early Irvingtonian	AWC	13582	47.77	17.07	21.19	14.25	13.42	13.69
Odocoileus	Early Irvingtonian	AWC	14946	47.24	17.56	18.86	13.29	12.79	13.23
Odocoileus	Early Irvingtonian	AWC	14963	45.37	17.44	19.09	14.13	12.68	13.49
Odocoileus	Early Irvingtonian	AWC	15016	43.72	15.48	17.51	12.69	11.46	12.22

Dimensions of Proximal Phalanx of selected Artiodactyls cont.										
Taxon	Age	Institution	Specimen	Greatest Length				Height		Breadth at Mid-shaft
				Lateral	Side	Breadth Proximal	End	Proximal	Distal	
Unknown cervid	Early Irvingtonian	AWC	10401	54.60		14.11	13.88	13.67	13.44	12.11
antilocaprid	Early Irvingtonian	AWC	11719	43.65		12.24	14.37	11.12	11.41	10.06
antilocaprid	Early Irvingtonian	AWC	12391	46.32		13.34	16.88	10.39	10.59	9.74
Sinocapra	Early Blancan	UNLV	P625	43.25		15.25	16.44	14.55	11.92	12.72
Sinocapra	Early Blancan	AMNH	52139E	47.10		17.20	-	-	-	-
Sinocapra	Early Blancan	AMNH	52139E	49.20		16.80	-	-	-	-
Oreamnos harringtoni	Rancholabrean	GRCA	509006	35.45		15.67	-	-	-	-
Oreamnos harringtoni	Rancholabrean	GRCA	509055	34.07		14.31	-	-	-	-
Oreamnos harringtoni	Rancholabrean	GRCA	509100	36.69		16.23	-	-	-	-
Oreamnos harringtoni	Rancholabrean	GRCA	509176	36.11		16.47	-	-	-	-
Oreamnos harringtoni	Rancholabrean	GRCA	509275	31.68		14.80	-	-	-	-
Oreamnos americana	Modern	NAU	2797	39.63		20.75	19.88	18.18	14.18	16.77
Oreamnos americana	Modern	NAU	2797	41.74		18.67	20.36	16.08	12.96	15.26
Oreamnos americana	Modern	NAU	2796	43.10		20.76	21.73	19.64	15.21	19.06
Oreamnos americana	Modern	NAU	2796	44.39		19.77	22.15	17.49	13.64	17.57
Ovis canadensis	Modern	RSW	0615	44.00		16.35	17.78	14.69	12.78	13.12
Ovis canadensis	Modern	RSW	0615	44.33		15.64	18.15	13.43	11.62	11.42

\*All measurements in centimeters

## CHAPTER 5

### SPECIES RICHNESS, PALEOECOLOGY, AND PALEOENVIRONMENTS

In this chapter, I use sedimentology, palynology research, and data concerning the presence or absence of recovered fossil taxa, relative abundance analyses, species diversity, and community structure of the paleofaunas to interpret and compare the ecosystems preserved in the Glenns Ferry and Panaca Formations.

#### 5.1 Panaca Study Area

##### 5.1.1 Taxa

I collected fossil material from twenty-four localities and three one-meter-square plots in Meadow Valley, Nevada for a total of 497 cataloged specimens. Mammals, birds, and reptiles are represented in the fossil assemblage. I collected specimens from the surface and from three one-meter-squares, shallow excavations. Sediment from the shallow excavations was screenwashed. Most of the fossil material represents disarticulated microfauna with a few larger specimens; the total volume of fossil material would not fill a ½ gallon bucket. I assigned the recovered fossils to family or genus level, with only a few to the species level. In general, a high percentage of the specimens are fragmented, small-mammal, post-cranial bones. Most of the complete elements I recovered are metapodials, phalanges, and tarsals, along with isolated teeth from several small mammal taxa. A small amount of bird material was discovered, including

two beaks and some post-cranial bones, along with one lizard mandible.

Screenwashing produced some canid, rabbit, and rodent tooth material.

The Panaca local fauna is characterized by fossils that occur mostly as isolated elements, although partial skeletons are also represented. In the mid-1990s, SBCM researchers recovered a mostly complete, articulated *Lepoides* sp. (jack-rabbit) skeleton in Panaca Formation siltstone, along with some bird phalanges. An AMNH field party collected several associated elements that belonged to a caprine bovid that was later described by Mead and Taylor (2005). Most of the material recovered by the SBCM is disarticulated and fragmented. A complete list of the fossil material collected in this study from the Panaca Formation in Meadow Valley is listed in Appendix 1.

#### 5.1.2 Relative Abundance

The relative abundance of various taxa at paleontological and archaeological sites is usually quantified using NISP or MNI analysis. The minimum number of individuals (MNI) quantifies the minimum number of individual animals present by counting the most common specific element from one side of the body. MNI analysis was not attempted in this study because complete elements consisted mostly of phalanges, tarsals, metapodials, and isolated lagomorph teeth, which are not diagnostic enough for determining how many animals may be represented. I counted the number of elements in each taxon to determine the total number of identified specimens (NISP). The relative abundance is expressed as percentages (Table 7) at family and order levels, due to the inability to identify most elements to the genus level or lower. Table 7A,

shows the relative abundance of mammalian families and orders of birds and reptiles, while Table 7B groups all taxa at the level of orders.

I determined NISP and relative abundance for all of the specimens collected, and also for each of the three screenwashed sites. This comparison was made in order to determine whether screenwashing introduced a bias into diversity and relative abundance analyses. These analyses are exhibited in Tables 8A, B, C, and Figure 26, to be compared with the relative abundance within the formation as a whole (Table 7 and Figure 24).

#### 5.1.3 Sedimentary Data

The Panaca basin-fill sediments are flat-lying strata derived from the surrounding highlands. According to Pederson (1999, 2000a), the sedimentology is heterogeneous across the Meadow Valley basin. Local prograding gravel associated with a thin clay unit marks the division between the upper and lower portions of the Panaca Formation (Pederson et al., 2000a), well seen on the northeast side of the valley. This ~37-meter-thick upper section consists of white-to-pale-olive, laminated pond/marsh, calcareous and gypsiferous mudstone with chert nodules (Pederson et al., 2000a). This lithology grades laterally toward the basin margin into pale-yellow, thick, planar-bedded and crossbedded, very-fine-to-fine sands.

Pederson et al. (2000a) described the facies changes of the lower section in detail. He described the most distal strata as laminated, white diatomite, and laminated, pale-yellow, very fine sandstones, with vertebrate fossils, root traces, and calcareous nodules. He further described the medial and proximal facies as



composed of reddish-yellow, medium to thick, planar, very fine sands, or as massive, rippled and cross-stratified, very fine sands. Near the basin margins these sands interfinger with lenses or wedges of colluvium (Pederson et al., 2000a, 2001). The colluvium is composed of clast-supported, angular pebble-to-cobble conglomerate with a pale, reddish-brown matrix with root casts. My observations support the facies change observations and descriptions of Pederson (2001). The proximal facies strata are illustrated in my stratigraphic column (Plate 1). In addition, I noted that other places in the valley contain alternating sequences of localized, fluvial-channel gravels in a fining-upward sequence.

## 5.2 Hagerman Fossil Beds Study Area

### 5.2.1 Taxa

The annual surveying and collection of fossil material at Hagerman typically involves approximately 120 locality sites and the collection of 3,000 to 4,000 specimens. The majority of the specimens are bones and teeth of small mammals collected from ancient flood plain and stream-channel deposits. Specimens are collected largely on the surface, but some are collected from screenwashed sediment; others are collected from excavations in the HHQ quarry. Fossil material consists of small bones, isolated teeth, jaws of disarticulated small animals, isolated large bone and teeth, and a few partially articulated specimens. Mammals, birds, fish, reptiles, and amphibians are represented in the Hagerman local fauna. Specimens are identified to species

level whenever possible. The HHQ, in the upper Glenns Ferry strata, has produced a large number of partially articulated *Equus* specimens. Other partial skeletons include *Platygonus pearcei* (peccary), *Castor californicus* (beaver), *Hemiauchenia* sp. (llama) and *Phalacrocorax idahensis* (cormorant) (McDonald et al., 1996), but much of the material on the Hagerman monument is disarticulated. The number of families present, along with generic richness per family, are listed in Table 9 for both the Hagerman local fauna and the Panaca local fauna.

#### 5.2.2 Relative Abundance

No NISP or MNI analysis has been conducted for the Hagerman fauna, at this time, and such analyses are beyond the scope of this study.

#### 5.2.3 Sedimentology

The 180-meter-thick Glenns Ferry Formation at Hagerman consists of lacustrine, fluvial, and floodplain facies (Bjork, 1970, Ruez, 2009). The lacustrine facies is composed of massive layers of tan siltstone and fine-grained sandstone with thin beds of rippled sandstone and siltstone in some areas. The fluvial facies contains planar and crossbedded layers of pale, brownish-gray channel sandstone with some siltstone (McDonald et al., 1996; Ruez, 2009). The floodplain sediments are fine-grained, graded beds of light-olive, silty, light-to-dark clay with massive siltstone and sandstone. Thin beds of paper shales are present in the middle unit of the flood-plain deposits. The upper flood plain stratum contains pedogenic carbonate nodules (Ruez, 2009).

## 5.3 Discussion

### 5.3.1 Comparison of Diversity

Species richness or diversity is the number of species in an area or region (Schluter and Ricklefs, 1993; Lomolino et al., 2006). Species diversity varies with the spatial scale on which it is studied. Alpha diversity refers to the species richness of a local ecological community (Schluter and Ricklefs, 1993; Lomolino et al., 2006). Because many of the fossils in the Panaca Formation can not be identified to species, I use generic richness as a metric of diversity. Panaca generic richness is based on vertebrate fossils collected sporadically since 1919, as displayed in Table 9. Hagerman Fossil Beds generic richness is also based on vertebrate fossil material collected since the 1920s (Table 9). Table 9 shows the number of genera within each family for both faunal assemblages.

Beta diversity compares the diversity or species richness of two areas or localities (Schluter and Ricklefs, 1993; Lomolino et al., 2006). One way to look at beta diversity is simply the presence or absence of taxa between the areas of interest. Small mammal families common to both Panaca and Hagerman include Soricidae (shrews), Leporidae (rabbits), Heteromyidae (pocket mice), Geomyidae (pocket gophers), Cricetidae (mice, voles, and wood-like rats), and Mustelidae (weasels, skunks, and badgers). Larger mammals common to both localities include Equidae (horses), Camelidae (camels), Tayassuidae (peccaries), Canidae (dogs), and Felidae (cats). Bird taxa common to both localities include Anatidae (ducks, geese, and swans), Accipitridae (kites, hawks and eagles), Rallidae (rails), and Phasianidae (quail). Other vertebrate taxa found in both

localities include Anura (frogs and toads), Colubridae (snakes), and Crotaphytidae (lizards), although these are more sparsely represented in the Panaca fossil record than in the Hagerman fauna.

Mammal families found only at Hagerman are Castoridae (beavers), Megalonychidae (ground sloths), Ursidae (bears), Mammutidae (mastodons), Antilocapridae (pronghorns), Cervidae (deer) and a Mustelidae (river otter), while families exclusive to the Panaca area are Bovidae (sheep and goats), Procyonidae (ring-tailed cats) and Cricetidae (mice and voles) (*Repomys panacaensis*, *Mimomys panacaensis*, *Nevadaensis feifari*, *N. lindsayi*, *N. downsi*). Passeriformes (perching birds) and Charadriiformes (shorebirds) occur in the Panaca fauna, but they have not been reported from Hagerman.

A comparison of the number of genera present in each of the two faunas (Table 9) shows that the Panaca fauna (43 genera) is less diverse than the Hagerman fauna (91 genera), however the Panaca fauna has a greater diversity of lagomorphs (rabbits). The greatest observed difference is the large number of species of Osteichthyes (fish) in the Hagerman fauna, as well as Emydidae (turtles). Neither fish nor turtles have been reported from the Panaca Formation. Two genera of Crotaphytidae (lizards) have been described from the Panaca fauna (Hollenhead and Mead, 2006) compared to three genera from Hagerman (Mead et al., 1998). Anura (frogs and toads), and Colubridae (snakes) fossil material is very rare in the Panaca Formation, however these two groups are quite common in the Hagerman faunal assemblage. The number of Aves families is three times greater in the Hagerman fauna, but my study represents

the first attempt to identify and synthesize the Panaca Formation avifauna. This is a simplistic view of animal diversity within a locality, which may be attributed to several factors that are discussed later.

Another way to examine the diversity of an assemblage is to look at the relative abundance of the taxa present in a sample from a locality or region. The NISP count includes all identifiable complete and fragmented specimens and is credited with producing higher numbers than MNI analysis (Klein and Cruz-Urbe, 1984). MNI attempts to quantify the number of animals present in the assemblage by using the most common specific element from one side of the body. It is possible to use this method in fossil excavation sites or with screenwashed sites, however small elements obtained by screenwashing tend to be isolated and fragmented bones and teeth, making calculations difficult. For example, in lagomorphs the upper and lower teeth are unique, but only the P/3, P2/, and M/3 teeth are diagnostic, among the usual eleven premolars and molars from each side of the skull. Hence, the number of animals could be underestimated based on the indistinguishable placement of teeth in the dentary using MNI, and the number overestimated using NISP. NISP and MNI reflect different information and cannot be meaningfully compared.

Tables 7A and 7B are similar; the same groups of animals are represented in both analyses, but they are calculated differently. Even though one is calculated by family and orders (Table 7A) and the other by only orders, the differences are small as the number of total specimens varies by a only a few, and the percentages fall within the 1-2% range. The use of only orders,

Table 7. Tables of NISP and calculated relative abundance of vertebrate families collected during this study from the Panaca Formation in Meadow Valley. A. NISP and relative abundance of families of mammals and reptiles and orders of birds. Rodent teeth (which are identifiable to family) are separated into families; however rodent bone (which is usually not identifiable below order level) are grouped together as “Rodentia undifferentiated.” B. NISP and relative abundance of vertebrate orders.

A.

Family/ Order	NISP	Abundance
Camelidae	4	1.00%
Bovidae	2	0.51%
Equidae	3	0.76%
Canidae	5	1.30%
Felidae	2	0.51%
Leporidae	273	69.11%
Cricetidae (teeth)	41	10.37%
Heteromyidae (teeth)	1	0.25%
Sciuridae (teeth)	1	0.25%
Geomyidae	1	0.25%
Rodentia undifferentiated (bone)	47	11.89%
Colubridae	2	0.51%
Crotaphytidae	1	0.25%
Anseriformes	4	1.00%
Gruiformes	5	1.30%
Passeriformes	1	0.25%
Galliformes	1	0.25%

n = 395

[Figure 24 diagram]

B.

Order	NISP	Abundance
Lagomorpha	273	68.60%
Rodentia	90	22.60%
Carnivora	10	2.50%
Perissodactyla	3	0.75%
Artiodactyla	7	1.76%
Serpentes	2	0.50%
Squamata	2	0.50%
Anseriformes	4	1.00%
Gruiformes	5	1.26%
Passeriformes	1	0.25%
Galliformes	1	0.25%

n = 398

[Figure 25 diagram]

## Relative Abundance of Taxa Collected from the Panaca Formation

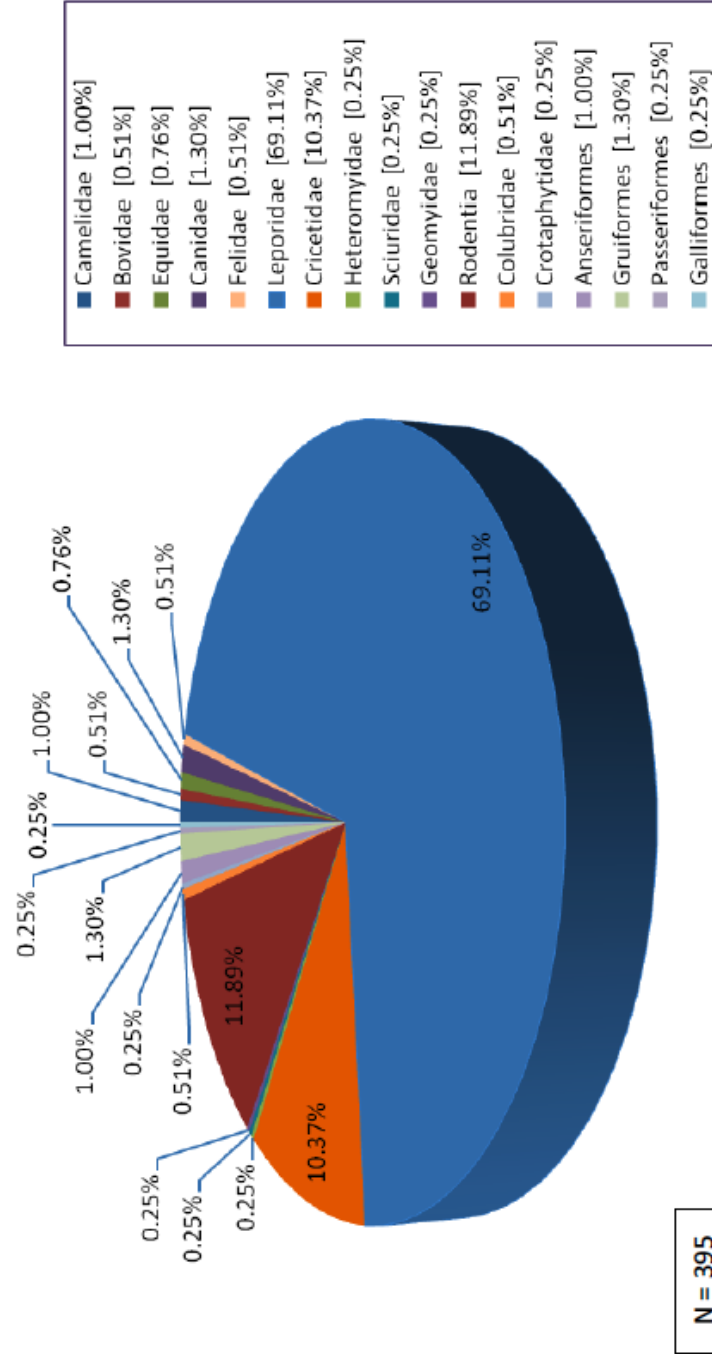


Figure 24. Diagram depicts relative abundance of vertebrate taxa based on NISP values and expressed as percentages. Specimens were collected during this study from the Panaca Formation. The 'n' is the number of identifiable specimens used to calculate the percentage. Reference numbers in Table 7A. Birds are grouped by order, mammals and reptiles are grouped by families.

## Relative Abundance of Vertebrate Orders from the Panaca Formation

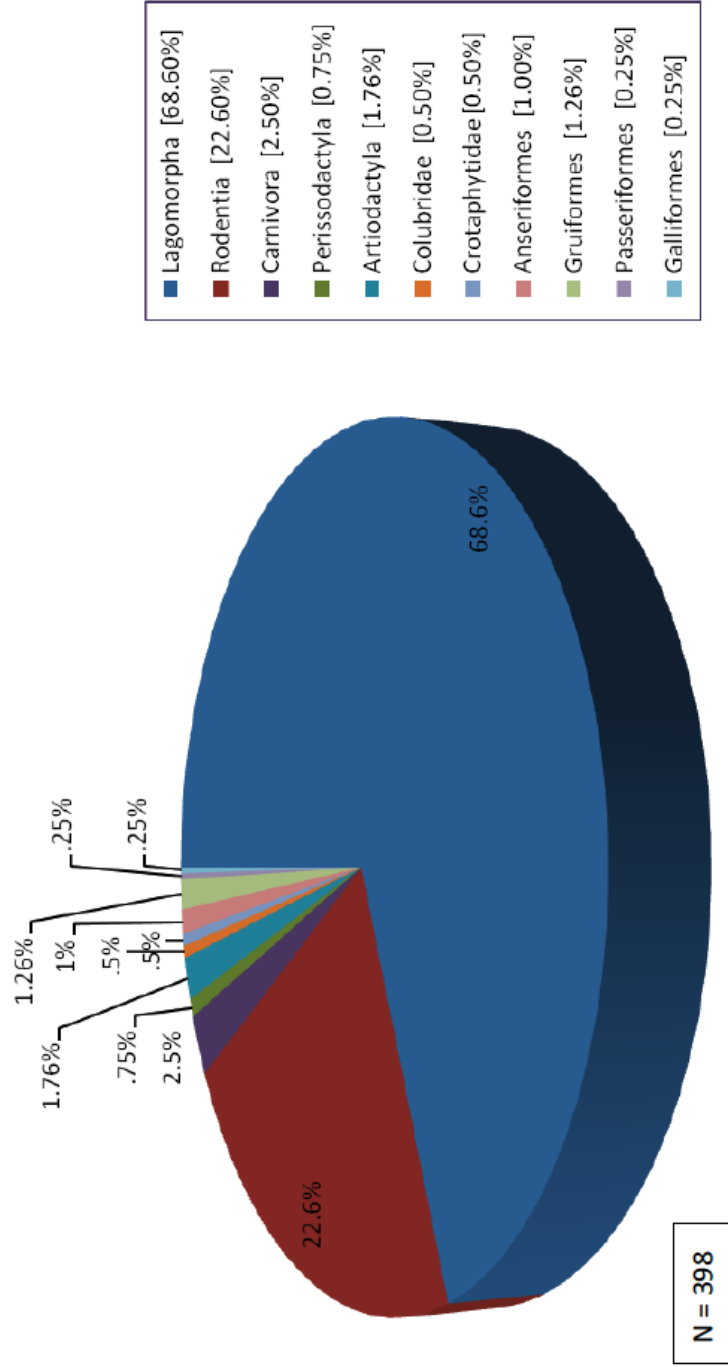


Figure 25. Diagram depicts relative abundance of taxa based on NISP values and expressed as percentages. Specimens were collected during this study from the Panaca Formation. The "n" is the number of identifiable specimens used to calculate the percentages. In contrast to Figure 24, all taxa are grouped by order.



Table 7B, loses representation of family-level groups of animals. For example, in the carnivores, one does not know if the number represents canids, felids, and mustelids, or just one of these families. The number of specimens increases slightly, and the relative abundance of Aves is decreased by 0.55% in the use of orders only. A visual comparative representation of the relative abundance is shown in Figures 24 and 25 pie diagrams. Small mammals comprise more than 90% of the specimens, of which Leporidae accounts for 67%. Large mammals account for less than 3% of the total relative abundance, while birds make up around 3% of the total. Carnivores and reptiles comprise less than 2% of the relative abundance of specimens. The comparison shows that relative abundance is virtually the same, whether displayed by families or orders, but the family-level data (Figure 24) provide more detail about the represented taxa.

Differences are observed when the NISP and relative abundance of the taxa within the Panaca Formation as a whole are compared to each of the three screenwashed sites (PAN-01, PAN-19, and PAN-24). Field site PAN-01 (Table 8A & Figure 26A) includes representatives of mammals, reptiles, carnivores, and birds, with lagomorphs accounting for 55% of the specimens. In comparison, site PAN-19 (Table 8B & Figure 26B) is almost all lagomorphs (87%). Rodents account for ~9%, while one large mammal and 2% carnivore elements make-up the other 3.5%; the site lacks birds and reptiles. The third site, PAN-24 (Table 8C and Figure 26C) lacks birds and large mammals, but is dominated by small mammals (98%), with only 2% representation by canids and reptiles. All three screenwashed sites have a higher percentage of rodents and rabbits than does

Table 8. Tables of NISP and calculated relative abundance of vertebrate families collected during this study from screenwashed sites in the Panaca Formation. Each table and graph lists the material recovered by screenwashing, as well as material collected on the surface. Rodent teeth (which are identifiable to family) are separated into families; however rodent bone (which is usually not identifiable below order level) are grouped together as “Rodentia undifferentiated.” A. Field site PAN-01, B. Field site PAN-19, C. Field site PAN-24.

A. PAN-01

Family/Order	NISP	Abundance
Bovidae	1	1.78%
Equidae	2	3.57%
Leporidae	31	55.37%
Heteromyidae	1	1.78%
Rodentia undifferentiated (bone)	8	14.28%
Colubridae	2	3.57%
Crotaphytidae	1	1.78%
Anseriformes	3	5.36%
Gruiformes	5	8.92%
Passeriformes	1	1.78%
Galliformes	1	1.78%

n = 56

[Figure 26A diagram]

B. PAN-19

Family/Order	NISP	Abundance
Perissodactyla	1	1.18%
Lagomorpha	74	87.05%
Rodentia undifferentiated (bone)	8	9.41%
Carnivora	2	2.35%

n = 85

[Figure 26B diagram]

C. PAN-24

Family/Order	NISP	Abundance
Canidae	2	1.50%
Leporidae	64	48.12%
Cricetidae	33	24.81%
Sciuridae	1	0.75%
Geomyidae	1	0.75%
Rodentia undifferentiated (bone)	31	23.30%
Colubridae	1	0.75%

n = 133

[Figure 26C diagram]

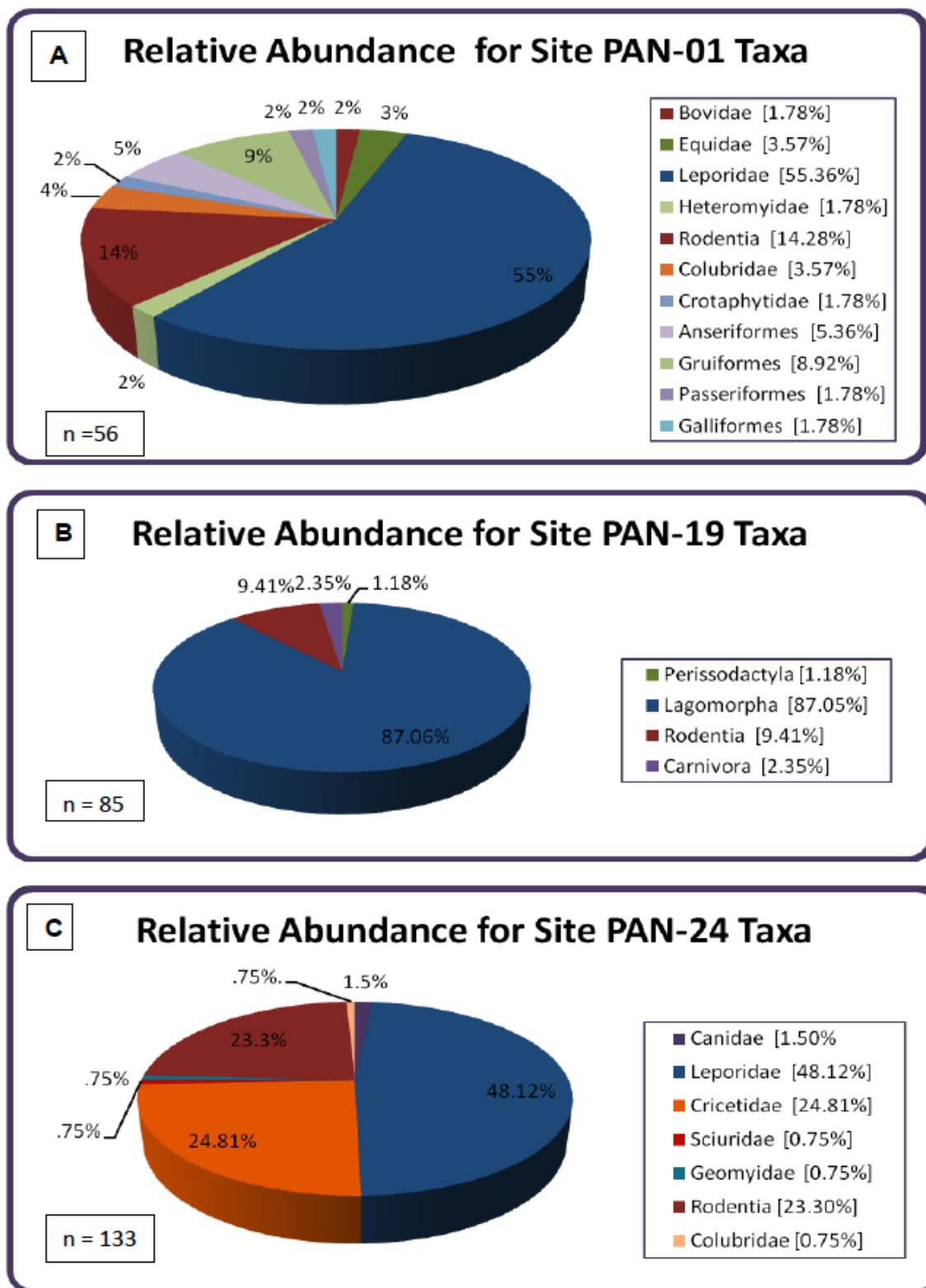


Figure 26. Relative Abundance for screenwashed sites based on NISP values and expressed as percentages. A. PAN-01, B. PAN-19, C. PAN-24.

the fauna as a whole. The relative abundance of small mammals recovered from the screenwashed sites is approximately 15% to 20% higher than in the fauna as a whole (Table 7 and Figure 24). Some families are completely missing from the screenwashed sites and large mammals are underrepresented, relative to their abundance in the total faunal assemblage. Based on the NISP analysis, the Panaca Formation fauna is dominated by lagomorphs. At least two lagomorph species are represented in my collection, *Lepoides lepoides* and *Hypolagus endensis*.

#### 5.3.2 Comparison of Trophic-Level Diversity between Panaca and Hagerman

Table 9 exhibits generic richness per family in the Panaca and Hagerman faunal assemblages. The Hagerman fauna is much more diverse, with 75 genera in 33 families of mammals, birds, and reptiles, compared with 43 genera in 25 families in the Panaca fauna.

Another method of assessment compares mammalian trophic levels within the community structure. Modern mammalian communities vary in terms of their trophic structure. On a continental scale, species of large mammals comprise a much smaller percentage of terrestrial faunas than do small mammals, but the relationship varies based on the spatial scale (Brown and Maurer, 1989; Lomolino et al., 2006). In Figure 27, mammals are divided into large herbivores ( $\geq 44\text{kg}$ ), small herbivores ( $\leq 44\text{ kg}$ ), and carnivores following Martin (1967). The relative abundances of large and small mammals are similar within the Hagerman and Panaca faunas, but carnivores are more conspicuously abundant

Table 9. Comparison of vertebrate faunal assemblages from Panaca and Hagerman Fossil Beds National Monument, showing the numbers of genera within each family. Compiled from AMNH, UCMP, HAFO, SBCM, Mou (1999), Ruez, (2009), Hollenhead & Mead (2006), and McDonald et al. (1996). Hagerman mammals follow Ruez's (2009) reevaluation of HAFO mammalian fauna; the Hagerman Aves, Reptilia and Osteichthyes follow McDonald et al. (1996) and Mead et al. (1998).

<b>Families Present and Generic Richness per Family</b>		
<b>Taxon</b>	<b>Panaca</b>	<b>Hagerman</b>
	number of genera	number of genera
<b>Mammalia</b>		
Xenarthra		
Megalonychidae	—	1
Insectivora		
Soricidae	3	2
Talpidae	—	1
Lagomorpha		
Leporidae	5	2
Rodentia		
Sciuridae	1	2
Geomyidae	1	2
Heteromyidae	3	3
Castoridae	—	2
Cricetidae	5	7
Carnivora		
Mustelidae	2	7
Canidae	2	2
Felidae	1	4
Procyonidae	1	—
Ursidae	—	1
Proboscidea		
Mammutidae	—	1
Gomphotheriidae	1?	—
Perissodactyla		
Equidae	1	1
Rhinocerotidae	1	—
Artiodactyla		
Tayassuidae	1	1
Camelidae	2	2
Bovidae	1	—
Cervidae	—	1
Antilocapridae	—	1

Table 9. continued

<b>Families Present and Generic Richness per Family</b>		
<b>Taxon</b>	<b>Panaca</b>	<b>Hagerman</b>
	number of genera	number of genera
<b>Aves</b>		
Podicipediformes		
Podicipedidae	—	4
Pelicaniformes		
Pelecanidae	—	1
Phalacrocoridae	—	1
Ciconiidae		
Ardeidae	—	2
Threskiornithidae	—	1
Ciconidae	—	1
Anseriformes		
Anatidae	2	6
Accipitridae		
Acciptiridae	1	1
Gruiformes		
Gruidae	—	1
Rallidae	2	4
Strigiformes	—	2
Galliformes		
Phasianidae	1	—
Passeriformes		
Emberizidae	1	—
Cardinalidae	1	—
Charadriiformes		
Scolopacidae	1	—
<b>Reptilia</b>		
Testudines		
Emydidae	—	2
Squamata		
Crotaphytidae	2	2
Colubridae	1	5
<b>Amphibia</b>	1	4
<b>Osteichthyes</b>	—	12

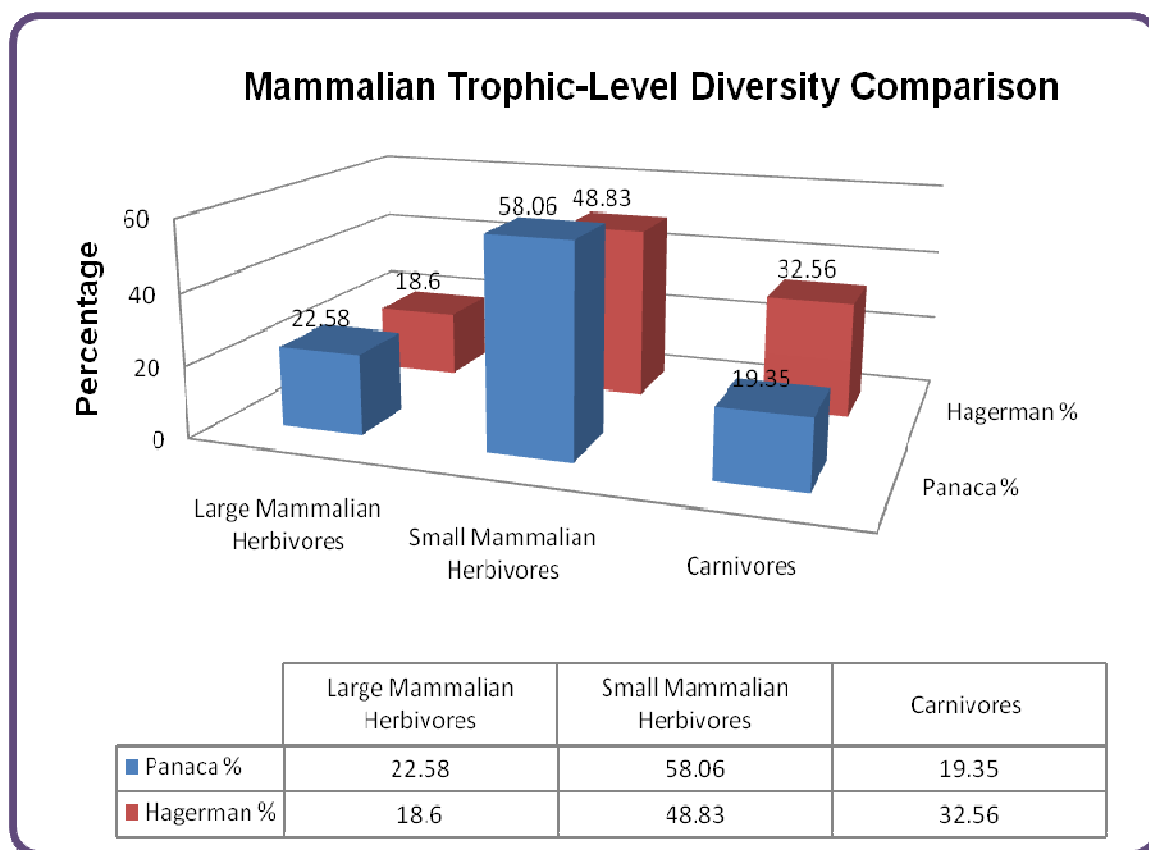
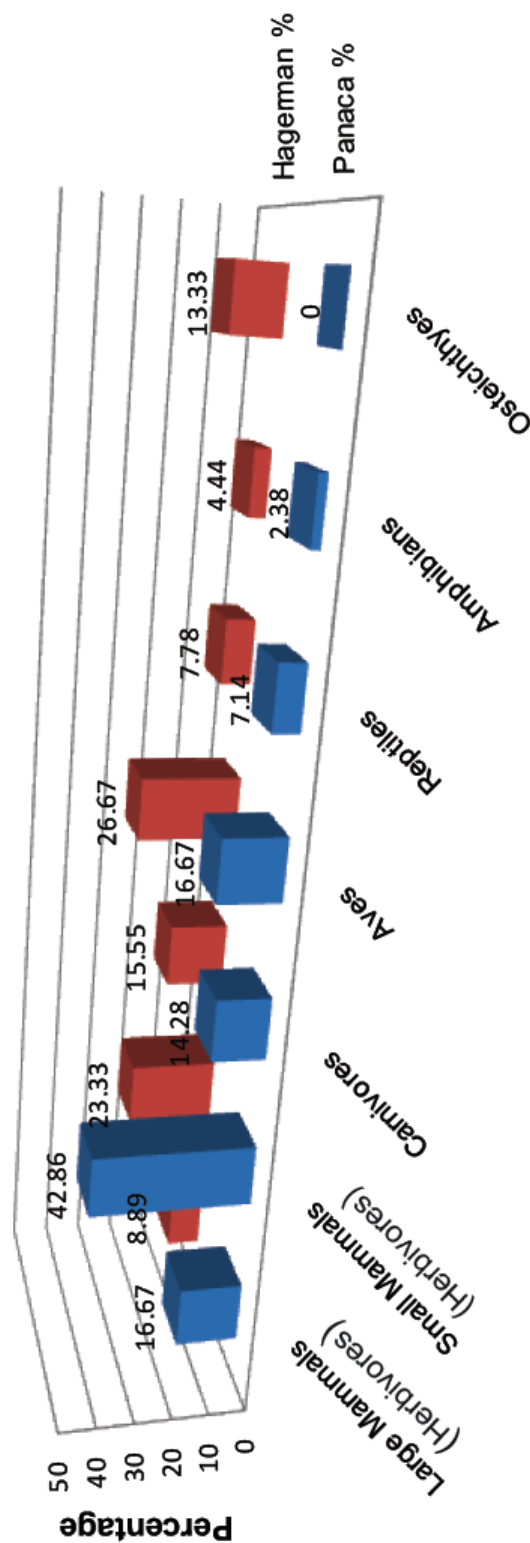


Figure 27. Comparison of mammalian trophic levels between Panaca and Hagerman localities. Trophic levels are divided as large herbivore mammals ( $\geq 44\text{kg}$ ), small herbivore mammals ( $\leq 44\text{kg}$ ), and carnivores. Numbers indicate the percentage of genera in the local fauna occurring in each category.

in the Hagerman fauna. This may be due to a sampling bias, which I discuss later in this chapter.

The histogram displayed in Figure 28 compares relative abundance of all vertebrate taxa in both the fossil assemblages collected over time, with the mammals divided into large herbivores, small herbivores, and carnivores. The percentages were calculated using the number of genera per family and grouped by various categories from Panaca and Hagerman. This provided one method of

### Relative Abundance of Represented Genera in Various Categories in the Panaca and Hagerman



	Mammals					
	Large Mammals	Small Mammals	Carnivores	Aves	Reptiles	Osteichthyes
Panaca %	16.67	42.86	14.28	16.67	7.14	0
Hagerman %	8.89	23.33	15.55	26.67	7.78	13.33

Figure 28. Comparison of the relative abundance of various genera of vertebrates collected at Panaca and hagerman localities. Numbers indicate the percentage of genera in the local faunal assemblage in each category.



comparing relative abundance between both Panaca and Hagerman. These percentages do not mimic relative abundances calculated from NISP data shown in Table 7, nor can they be compared. Several differences are revealed. The relative abundance of mammalian carnivores and reptiles is nearly identical at the two localities. Large and small mammals have twice the relative abundance at Panaca than in the Hagerman fauna. In this analysis, birds and amphibians account for roughly twice the relative abundance at Hagerman than at Panaca. The high diversity of fish at Hagerman represents ~13% of the total, while no fish are known from the Panaca Formation.

### 5.3.3 Paleoenvironment Reconstruction

Paleoenvironment reconstructions of paleofaunal assemblages are generally based on 1) sedimentological data, and 2) the assumption that extant analog taxa have similar environmental preferences as taxa present in the fossil assemblage (Gensler, 2002). Analysis of the morphology and isotopic composition of teeth often helps to determine dietary preference, which in turn aids in identifying the paleoenvironment (Feranec, 2003). Some animals live in specific habitats, while others are generalists. Many of the rodents, mustelids, canids, and felids present in the Hagerman and Panaca fossil assemblages can live in diverse habitats and therefore provide few clues to the paleoenvironment.

Hagerman and Panaca large mammal faunas contain both browsers and grazers. The Hagerman antilocaprids (pronghorns) browsed and grazed on forbs, grasses, and shrubs, with grass being a small part of their diet (Janis and Manning, 1998). Other Hagerman browsers include *Mammut americanum*

(mastodon), *Odocoileus* (deer), and *Camelops* (camel) (Gensler, 2002). *Platygonus pearcei* (peccary), which is found in both faunas, was an herbivore feeding mainly on roots, nuts, and cacti (Wright, 1998). The Panaca and Hagerman camelids, *Camelops*, *Megatylopus*, and *Hemiauchenia* (llama), are interpreted to be intermediate (mixed) feeders with a preference for browsing (Dompiere, 1995; Feranec, 2003). Grazers include equids (horse), which occur in both faunas. Smaller mammals, such as *Thomomys* (pocket gophers) at Hagerman and some voles in both faunas inhabit more mesic or moderate conditions (Springer et al., 2009).

Aquatic taxa in the Hagerman fauna document the unequivocal presence of aquatic habitats (Table 8). *Castor californicus* (beaver) is a common member of the fauna, as well as *Satherium piscinaria* (river otter). *Pliopotamys minor*, an ancestral pygmy muskrat, is fairly abundant in the sandy channel facies at Hagerman. The abundance of fish, frogs, and pond turtles further supports the interpretation of aquatic habitats for the Hagerman fauna. Abundant water supported a diverse avifauna of Anatidae (geese, ducks, and swans), Pelicaniformes (pelicans and cormorants), Gruiformes (rails and cranes), and Ciconiidae (storks, herons, and spoonbills). Many species within these orders survive well in a riparian habitat, but pelicans and swans, both of which are present in the Hagerman fauna, are indicators of large bodies of open water such as lakes or wide rivers (R. Chandler, personal communication). The flood plain sediments of the Glens Ferry Formation suggest a large, meandering river system flowing into Pliocene Lake Idaho, which extended into eastern Oregon

(McDonald et al., 1996). Lake shores and meandering river systems today support diverse riparian habitats (Lomolino et al., 2006).

Fluvial and lacustrine sediments in the Panaca Formation, in addition to the Panaca avian fauna, indicate standing water and marshy-pond habitats. But the Panaca faunal assemblage lacks *Castor californicus* (beaver), *Satherium piscinaria* (river otter), *Pliopotamys minor* (pigmy muskrat), and the fish, frogs, and turtles that are so abundant at Hagerman. The presence of *Anas* (duck), two species of *Rallus* (rails), Charadriiformes (shorebird), and *Cygnus* (swan) shows that the Panaca avifauna included several water birds. Their presence likely indicates a riparian system and possibly a moderately large body of water. Swans in particular need open expanses of water for take-off and landing (R. Chandler, personal communication). Pluvial lake levels in Meadow Valley may have fluctuated during seasonal changes in precipitation or even during extended wet and dry periods as some lakes in the region do today. Both the avian fauna and the sediments show that aquatic habitats existed in the lower Panaca sediments, but the lake apparently disappeared later, during a drier period, as is recorded in the eolian sediments of the upper portion of the Panaca Formation. The presence of arid-dwelling inhabitants such as *Bassariscus casei* (ring-tail cat), *Lepoides lepoides* (jackrabbit ecomorph), *Repomys* (woodrat-like rat), and *Prodipodomys* (kangaroo rat) suggest a more xeric environment, which probably existed adjacent to the riparian and open-water habitats.

The presence of other birds, including buntings, quail, and hawks, provide a wider picture of the Blacan paleoenvironment in Meadow Valley. Rabbits are

a staple for buteos (buzzard hawk). *Callipepla* (quail) inhabits shrubby areas and open woodlands, while the Passeriform species (sparrows and buntings) feed on seeds in semi-open areas. Likewise, the Hagerman avifauna contains predatory birds of the family Stigidae (owls) and the genus *Neophrontops* (old world vultures), but the Hagerman Passeriforms have yet to be studied (McDonald et al., 1996).

Plant fossil and pollen analysis also provide valuable indicators of paleoenvironments. Pollen and plant fossils in the Hagerman biota include pines, willows, birches, elms, and many types of flowering plants. McDonald et al. (1996) suggested that the Hagerman environment was savanna-like with patches of pine woodland in the valley, while willow, alder, birch, and elms flourished along the streams. No plant fossils have been recovered from the Panaca Formation, nor has pollen analysis been attempted.

#### 5.3.4 Potential Paleoecological Bias

Several potential problems arise in paleoecological analyses due to methods of collection, methods of assessment, and the affects of taphonomic processes. A comparison of the presence or absence of taxa not may be adequate to assess the real differences and similarities between sites (Klein and Cruz-Urbe, 1984). Many factors operate between the death and burial of a vertebrate animal and its recovery as a fossil (Voorhies, 1969; Wolfe, 1973). Wolfe (1973) listed fifteen biological, geographical, and geological factors that may alter the represented fossil vertebrate fauna, but he considered size, element shape, and the depositional environment to be the most important.

Fossils recovered from a locality may include remains of those organisms that lived within the area of deposition (proximal), as well as those washed in by inflowing rivers (distal) (Wolfe, 1973; Rogers and Brady, 2010). Such a mixture of proximal and distal elements is probable for the faunal assemblages from both Panaca and Hagerman.

Another assumption in microvertebrate sites is that hydrodynamic fossil size and shape sorting are the same in similar depositional sediments. The actual differences in the faunal assemblage collected from these localities may be related to taphonomy, rather than ecology, thus affecting species richness and relative abundance assessments (Blob and Fiorillo, 1996; Dodson, 1973; Wolfe, 1973). Other factors related to hydrodynamic sorting is sorting modified by mechanical breakage and the reworking of sediments (Wolfe, 1973; Aslan and Behrensmeyer, 1996; Rogers and Brady, 2010).

The NISP and relative abundance data suggest that biases are present within the individual screenwashed sites (Figure 26) and possibly for the total taxa collected in this study, as seen in Figure 24. First, the screenwashed sites yielded predominantly rabbits and rodents. In a study of small bones in paleoecological interpretations, Dodson (1973) concluded that small bone accumulations may be poor indicators of the ecosystem. Dodson's (1973) study is described in more detail below. Shotwell's (1955) analysis of microvertebrate sites assumed that the mammals from proximal communities are represented by more specimens per individual than those from distal communities. The individuals from distal communities are represented by a fewer number of

elements. Thus, he notes that these mammals are present within the region and are a part of the assemblage. Second, the locations of the three screenwashed sites are in various places in Meadow Valley; two are on the north side near the “Limestone Corner,” and site PAN-24 is on the valley’s southeast side.

Specimens probably represent different habitats within the ecosystem. Each screenwashed site may be faithfully recording the fauna that lived in proximity to that site, and the differences are due to the heterogeneity of the original ecosystems. In addition, those three sites occur within different stratigraphic horizons and thus represent slightly different ages. Larger mammal specimens seem to occur on or near the surface, but not in the screenwashed sediment. So each sampling method preferentially samples different components of the fauna.

Previous collections from the Panaca Formation show that mammalian taxa are missing in my study. Mou (1999) recovered a greater number of rodents and lagomorph genera than large mammals, probably due to the enormous amount of screenwashing she conducted. Previous surface collection by Stock and the AMNH collectors produced a greater diversity of large mammals. The SBCM researcher’s screenwashed ~2500 lbs of sediment to recover a large number of small mammal bones and teeth, and they surface-collected fragmented camel and peccary material from Meadow Valley. Voorhies (1973) study of how concentrations of fossil bones originate, noted collecting bias between collections from the surface versus sieving. He suggested that collecting over a period of time and using both methods of collection provided a better sample of the faunal assemblage. Table 9 lists the genera collected in all

taxa from the Panaca Formation in Meadow Valley from the 1920s to the present. This list represents the species richness of the Panaca local faunal assemblage, while the screenwashed sites (Figure 26) likely reflect the fauna in proximity to that site.

Jamniczky et al. (2008) explored the question of the sample size required for studying relative abundance and diversity in vertebrate microfossil assemblages. They developed a standardized protocol for the minimum required sample size, using rarefaction as a statistical technique. Their method requires extensive microfossil collection through screenwashing of matrix and the statistical analysis of the recovered data. That technique was not possible in this study due to the limitation of excavation permitted by the Bureau of Land Management; a greater sample size will always improve the statistical reliability of the data set, but the combined data from the past and this study provide a good characterization of the Panaca fauna.

The total collection of fossils over time (Table 9) is obviously a better representation of species diversity in the Panaca Formation than is the fossil assemblage collected in this study. Differing stream velocities, current dispersal, and other taphonomic processes affect the assemblage of animal material that can be potentially collected as fossils. The NISP count and calculation of relative abundance is dependent on the fossil collection, thus analysis is affected by these factors (Voorhies, 1969; Dodson, 1973). While, in general, more volume and greater velocity of water are required to move or bury larger bones compared to smaller bones, bone mass and density are also factors in their

transportation and burial (Dodson, 1973; Voorhies, 1973). Dodson (1973) experimented with the decomposition and current dispersal of a toad, a frog, and a mouse to determine rates of disarticulation and bone movement, and also water velocities required for movement of skeletal material of comparable size. He concluded that microvertebrate assemblages more faithfully record the velocity of stream currents than they do the paleoecology of an area.

Thus, one needs to realize the possible biases present when analyzing a microvertebrate site or local assemblage. The differences and similarities in diversity between paleofaunal sites may be due to taphonomic factors rather than ecological ones. These taphonomic factors may also influence the reliability of relative abundance data. Greater sample size and varied collection methods improve the reliability of species richness and relative abundance analyses.

#### 5.3.5 Preservation and Collection Biases

In this section, I review additional biases affecting the interpretation of the Panaca and Hagerman paleofaunas. In earlier sections, I have used sedimentological and diversity data to interpret the Panaca and Hagerman ecosystems, and I have considered paleoecological biases resulting from assessment methods and taphonomic processes. Here I investigate preservation and collection biases found within both localities.

Based on my own experience, distinguishing fossil bone from modern bone is easier with Hagerman specimens than with Panaca specimens. At Hagerman, tooth enamel is preserved as dark brown or black, and it is easily recognizable. Color in other elements varies from dark gray to black, brown to



tan, or off-white, depending on the sediment type. Fossils are not usually bleached white. Occasionally gnaw marks or groves are seen on the fossil bones. The fossil bone condition makes it readily distinguishable from modern material, which is also found on the surface or partially buried in the soft strata. Most Hagerman modern elements show signs of decay and weathering, such as flaking and cracking, and there are texture and hardness differences as well. I have observed all five stages of weathering in modern bone described by Behrensmeyer (1978) during surveying at Hagerman Fossil Beds National Monument.

Most of the Hagerman material is well-preserved, and some of it is pristine, but it is usually fragmented. Much of the bone fragmentation occurred before or during burial. This breakage is related to factors such as decomposition, predation, and sedimentary transport acting on the remains prior to their final deposition. Also, extended post-burial surface exposure and weathering results in the breakage of the fossil bones. Concentrations of fragmented bone are occasionally found where the exposed bone has weathered beyond identification, before being discovered by a paleontologist.

In contrast, a lot of bleached bone occurs on the surface in the Panaca Formation as both fossil bone and modern bone. The bleached color is not a distinguishing characteristic of the modern bone; some of the fossil bones, such as the *Sinocapra* phalanges, are also bleached white. I used bone flaking, characteristics of the broken edges, and hardness of the bone to aid in distinguishing fossil bone from modern bone. Some modern bones appear

polished, and they retain a surface sheen, probably due to digestion and regurgitation by predatory birds, making them initially indistinguishable from the fossil material. I used observations of the collection area, such as the location of nearby owl pellets, bird droppings, and perches, to aid in distinguishing fossil and modern bone. I examined some specimens under the microscope to look for surface modification. In order to differentiate modern bone from fossilized material some researchers have studied altered organic and mineral structure, which causes slight differences to bone hardness and the surface (Chandler, 1982; Hoffman, 1988). However, I did not observe such differences in the bones from the Panaca Formation.

One colleague told me that modern bone burns, while fossil bone does not. Due to the difficulty I experienced distinguishing modern from fossil bone, I conducted an experiment with modern bone and a scrap of known fossil bone, to test this putative difference. The fossil bone changed color on the surface, but did not burn, while the modern bone did indeed burn and was chemically altered. However, I did not use this test to routinely identify fossil bone because it caused a discoloration to the surface of the fossilized bone. Bone collection from the screenwashed Panaca sediments were considered fossilized.

Most of the skeletal material is well-preserved, showing stage 0 to 1 weathering before burial (Behrensmeyer, 1978). Many of the rabbit bones exhibit fresh or “green” breaks with pristine preservation, indicating breakage prior to relatively quick burial. The presence of *Buteo* hawks in the assemblage supports

the interpretation that the large number of rabbit-bone breakage is due to predation by hawks (Holman, 1988; Lyman, 1994).

The condition of the bone affects its collection; hence, fossilization characteristics introduce a bias in both preservation and collection. Difficulty in differentiating fossilized and modern material affects its collection in the field. Museums have limited storage space, so the collection of bone shards, fragmented bone, or unidentifiable material may be discouraged.

As previously mentioned, the intensity of collection and method of collection, surface or screenwashing, from a locality potentially influences the taxa recovered, as has been seen in the Panaca collection. Intensive screenwashing by Mou (1999) yielded numerous specimens and a diverse rodent population, while surface-collecting preferentially yields the remains of larger animals. Both techniques are required to adequately sample the fauna.

Both Hagerman and Panaca localities contain well-preserved fossils, although at both localities much is fragmented and disarticulated. The somewhat better preservation, together with the higher intensity of research, in the Hagerman deposits, probably has resulted in the Hagerman local fossil assemblage being a more complete and representative sample of the original mid-Blancan ecosystem than is the case with the Panaca assemblage. However, both the Hagerman and Panaca fossil biotas are preserved well enough and have been studied enough to permit meaningful conclusions to be drawn concerning the main differences and similarities between these Blancan ecosystems.

## 5.4 Climatic Proxies

The Pliocene climate is currently being analyzed through studies of fossil floras, pollen, and climate modeling. Climate modeling uses estimates of sea-surface temperatures based on microfossils from deep ocean cores, along with land-based pollen and paleobotanical flora records for global climate model simulations (Smith and Patterson, 1994; Chandler, 1997; Jiang et al., 2005; Salzmann et al., 2008). These studies infer that the mid-Pliocene was generally warmer and moister than present, especially at higher latitudes. Pliocene temperatures have been estimated to be warmer with less of a mean temperature range than at present (Chandler, 1997; Ruez and Gensler, 2006; Salzmann et al., 2008), however the overall climate was in a cooling trend from the earlier Miocene climatic optimum (Zachos et al., 2001).

Jiang et al. (2005) suggested that the global mid-Pliocene precipitation was as much as 4% higher than today. Pliocene rainfall for Hagerman has been estimated to have been about twice the annual rainfall of today (McDonald et al., 1996; Ruez, 2006). In a study of sediments and pollen from the Glens Ferry Formation lacustrine sediments near Bruneau, Idaho, Thompson (1996) concluded that the southern Idaho Pliocene climate was warmer and wetter than at present, however he also discovered that the mid-Pliocene summers were cooler than Idaho summers are today.

Research on the Pliocene flora of North America has revealed generally warmer and moister conditions than today, with a trend of increasing aridity from the Miocene into the early Pliocene Epoch (Webb and Opdyke, 1995). Based on

the terrestrial flora and fauna, Webb and Opdyke (1995) suggested that western North America experienced a biome progression from Miocene tropical forest to savanna to steppe by the early Pliocene. This steppe expansion recognized in the early Pliocene did not occur uniformly or encompass all of North America (Webb and Opdyke, 1995). Pliocene floras record regional differences in western, mid-latitude, inland basins of North America, as would be expected due to differences in latitude, local relief, and basin positions with respect to mountain barriers and the ocean (Axelrod, 1948; Webb and Opdyke, 1995). The Pacific Northwest Pliocene flora indicates mesic forest biomes represented by the Hagerman flora of broad-leaf deciduous forests in riparian habitats, with equids grazing on the nearby savanna (Webb and Opdyke, 1995). Thompson (1996) described the Glenns Ferry Formation pollen record from southwestern Idaho, deposited during the lowest part of the Gauss normal chron, as a mosaic of islands of forest surrounded by lower elevation steppe. The Hagerman fossil assemblage represents the oldest fauna in the Glenns Ferry strata and corresponds to the upper part of the reversed Gilbert chron and the lower part of the normal Gauss chron (Bell et al., 2004). Axelrod's (1948) analysis of the early Pliocene Ricardo flora inferred that the Mojave region had experienced a semiarid climate with yearly rainfall of about 38 cm, distributed as summer showers and winter rains. Furthermore, he inferred that summers had been hot and winters temperate in the Mojave region.

Carbonate nodules seen in both localities have long been recognized as indicators of seasonal aridity (Webb and Opdyke, 1995). These deposits are

seen only in the upper Glenns Ferry Formation, but occur throughout much of the strata in the Panaca Formation. In the Pliocene, the Great Basin is inferred to have had a steppe biome at lower elevations, with pinyon forest on the higher slopes (Axelrod, 1948). Based on the fauna and flora, together with sedimentology, seasonal changes occurred in both localities, but the Panaca area likely sustained longer periods of aridity than the Hagerman area.

### 5.5 The Amboseli Basin as a Modern Analog for Pliocene Basins of Western North America

In this section I briefly compare the Blancan Panaca and Hagerman faunas with the modern fauna of the Amboseli Basin of Kenya. East Africa has the advantage of having a diverse assemblage of large mammals that are ecological proxies for the many species of large mammals that were eliminated from North America at the end of the Pleistocene.

The Amboseli Basin is an inland basin in the rain shadow of Mount Kilimanjaro. The low point is occupied by Amboseli Lake, a shallow, seasonal playa. The lake and surrounding wetlands are fed by springs and small streams from Mount Kilimanjaro (Western and Behrensmeyer, 2009). Rainfall averages about 30 cm (11.8 inches) per year, with bi-seasonal flooding alternating with dry periods (Behrensmeyer and Boaz, 1980). The basin supports several habitats, including lake, swamps, dense woodland, open woodland, open grassland or savanna, and shrubby areas (Behrensmeyer and Boaz, 1980). Sedimentologically, the area is dominated by fluvial, swamp, and lacustrine

deposits.

Modern bone assemblages have been studied in the Amboseli Basin for forty years (Behrensmeyer, 1978; Behrensmeyer et al., 2000). Researchers have used this basin to address the question of whether accumulations of bones accurately represent the living populations from which the bones were derived (Western and Behrensmeyer, 2009). Western and Behrensmeyer (2009) concluded that bone assemblages accurately reflect the diversity and relative abundance of fifteen large herbivore species weighing 20 to 4,000 kg. Thus, the Amboseli Basin serves to validate the methodology of this study, as well as to provide a modern analog for comparison with the Hagerman and Panaca basins.

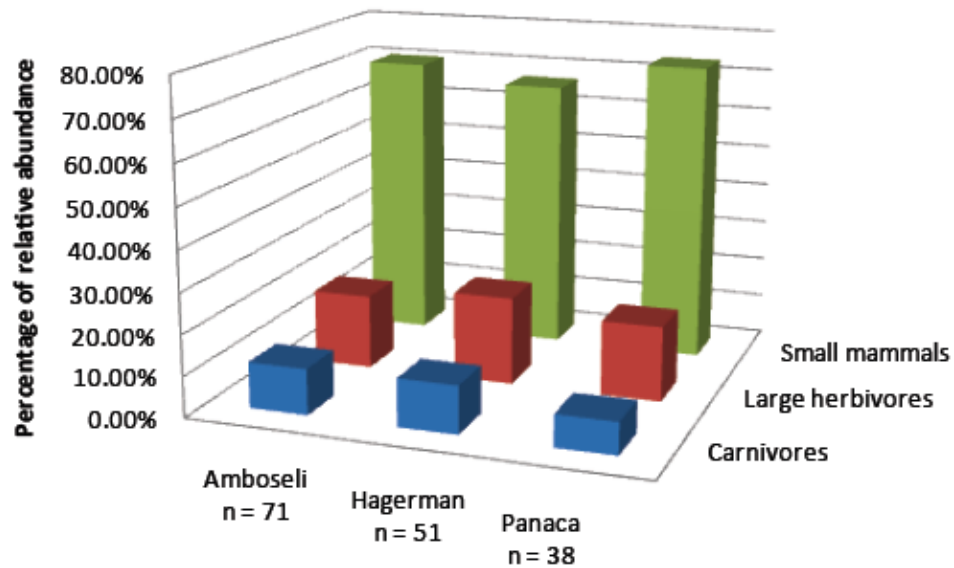
Like the Amboseli Basin, the Pliocene basins examined in this study were inland basins influenced by seasonality and dominated by fluvial and lacustrine sediments. The Hagerman basin experienced wet-and-dry seasonality (Ruez, 2006) with an estimated rainfall of 30 cm (~12 inches) per year (Smith and Patterson, 1994), the same amount of rainfall as Amboseli. No rainfall estimates are available for the Panaca Basin in the Pliocene, but studies of the Mojave Desert (Axelrod, 1948) suggest that the bi-seasonal rainfall was approximately 38 cm (15 inches), but still comparable to Amboseli. The Pliocene Hagerman area supported a suite of habitats similar to those of Amboseli. The Pliocene Panaca Basin was smaller and less ecologically diverse, but also with a mixture of lake, riparian, and nearby arid habitats.

Figure 29 shows a comparison of the mammalian fauna of the Amboseli Basin with the Blancan faunas of Panaca and Hagerman. Species diversity is

high in the Amboseli Basin (71 species), compared to fifty-one mammalian species recorded from Hagerman and thirty-eight from the Panaca. Very similar percentages of large herbivores and small herbivores occur in the three faunas, however carnivores, at about 8% of the taxa, are conspicuously less diverse at Panaca than at Hagerman (12%) and Amboseli (11%). Two factors are probably responsible for the lower diversity of carnivores in the Panaca fauna: (1) collection bias, and (2) island biogeographic effects. As discussed in Chapter 2, the Hagerman fauna has been more intensively studied than has the Panaca fauna, and carnivores are always more rare than herbivores; so some species of rare carnivores may have been present in the Panaca Basin that have not yet been documented in the fossil record. The second factor—*island biogeographic effects* (Lomolino et al., 2006)—may be playing a larger role in the low diversity of carnivores in the Panaca fauna. Like a small, remote island far from the mainland, the Panaca Basin was a relatively small, isolated basin, subject to occasional severe environmental changes. Rare species of carnivores would have been vulnerable to local extirpation, and the “mainland” of rich species diversity from which immigrant species could immigrate, was far away. This island biogeographic effect also may account for the overall lower species diversity of the Panaca fauna, compared to Hagerman and Amboseli.



## Mammal Trophic-Level Diversity Comparison



	Amboseli n = 71	Hagerman n = 51	Panaca n = 38
Carnivores	11.30%	11.76%	7.89%
Large herbivores	18.30%	21.60%	18.40%
Small mammals	70.40%	66.60%	73.60%

Figure 29. Comparison of mammalian trophic-levels between the modern Amboseli Basin and the Blancan Hagerman and Panaca basins. Trophic levels are divided as large herbivore mammals ( $\geq 44\text{kg}$ ), small herbivore mammals ( $\leq 44\text{kg}$ ), and carnivores. Amboseli mammal genera determined from Grimshaw et al. (1995). Numbers indicate the percentage of genera in the local fauna occurring in each category. [n = total number of taxa]

## CHAPTER 6

### SUMMARY AND FUTURE WORK

This study of the early Blancan Panaca vertebrate fauna of southeastern Nevada reveals the paleoecological and paleoenvironmental characteristics of Pliocene mid-latitude basins of western North America. The Panaca vertebrate faunal assemblage contains 44 species in 25 families. In my study, I updated the Panaca local faunal assemblage list to include birds and reptiles, which had previously not been documented, in addition to the mammals. I have identified nine genera of birds in seven families. The sedimentology of the Panaca Formation, the presence of environment-sensitive taxa, taxonomic diversity, and relative abundance data all contribute to a paleoenvironmental reconstruction and interpretation of the paleoecology.

Five of the nine genera of birds recognized from the Panaca Formation inhabit aquatic environments. The duck (*Anas*), two types of rails (*Rallus*), and the shorebird (cf. *Scolopacidae*) can occupy marsh or riparian habitats, but *Cygnus* (swan) requires a large body of open water, in this case a pluvial lake. The sediments also support the interpretation of a lake. Many of these bird taxa are migratory, and the Panaca Basin doubtless provided suitable winter habitat for some migratory species. Others probably used this basin as a rest stop in their migratory travels. The other birds, the bunting (*Passerina*), quail (*Callipepla*), and hawk (*Buteo*) provide a different picture of the Blancan paleoenvironment away from the water. Quail (*Callipepla*) inhabit shrubby areas and open woodlands, commonly located near streams and water in more arid

environments. The *buteos* may have a wider range than some birds, but this predator would stay near its food source, the abundant rabbit population in Meadow Valley. The abundance of 'green breaks' on rabbit bones supports this interpretation.

The mammalian environment-sensitive species such as *Bassaricus casei* (ring-tail cat), *Repomys* (woodrat-like rat), *Prodipodomys* (kangaroo rat), and *Lepoides lepoides* (jackrabbit) are indicators of more xeric conditions. These mammals, as well as the lizard species, prefer rocky open areas in sagebrush, desert scrub, or pinyon-juniper habitats, usually not too far from water. These drier habitats probably existed in the valley and on adjacent slopes away from the riparian and open-water areas. Furthermore, kangaroo rats, woodrats, black-tailed jackrabbits, hawks, and coyotes are common in Nevada's arid environments today.

Two of the endemic species from the Panaca fauna have immigrant ancestors who crossed the Bering land bridge, namely *Mimomys panacaensis* (vole) and *Sinocapra wiltdownsi* (bighorn sheep-like bovid). *M. panacaensis* was an immigrant from Eurasia that does not show the derived schmelzmuster conditions of other American cricetid lineages (Mou, 1998). The beginning of the Blancan has been defined by the immigration of *Mimomys* into North America (Mou, 1998; Repenning, 2003). *Sinocapra* is believed to have evolved from an ancestor that migrated from China (Mead and Taylor, 2005).

The basin-fill sediments of the Panaca Formation are heterogeneous and display facies changes over relatively short distances. The fluvial and lacustrine

sediments of the lower portion of the Panaca Formation indicate a fluvial system; a stream flowed into an unnamed inland lake that was much smaller and more ephemeral than Lake Idaho. The sediments change stratigraphically from the lower laminated muds and silts to eolian cross-bedded sands in the upper portion. The eolian sediments record the disappearance of the lake during a later drier period in the late Gilbert chron. The fossils are recovered from the silts and fine sands and tend to be associated with calcareous nodules. These sediments suggest floodplain and lacustrine environments that commonly contain vertebrate remains.

The taxa and strata suggest a paleoenvironment comparable to the present-day Pahrnagat Valley in southeastern Nevada, with broad-leaf tree and shrub growth along the riparian areas, some marshes, wet meadows, and steppe on the slopes. The climate is seasonal, with wet and dry periods and the lake levels fluctuated in response to multi-year droughts and wetter intervals. The present-day climate of Pahrnagat Valley is drier and has a greater temperature fluctuation than the early Blancan Panaca area.

### 6.1 Comparison to the Hagerman Local Fauna

The middle Blancan Hagerman Fossil Bed faunal assemblage provides a useful comparison for the Panaca local faunal. A number of factors contributed to the decision to use Hagerman Fossil Beds as a comparison. The geology of southern Idaho area is well studied, and the rich vertebrate fossil fauna of the Hagerman area was recognized early. This prompted the continued collection,

identification, and description of Hagerman fossils by a variety of institutions and researchers. Paleontologists studied the pollen record, the fish, and amphibian fossils from the persistent Lake Idaho, in addition to the mammals, to interpret paleoclimate and paleoenvironments during the Pliocene and Pleistocene epochs. Finally, I had the opportunity to learn about the Hagerman Fossil Beds geology and vertebrate fauna first hand, during two summer internships.

The fluvial and floodplain sediments of the Hagerman Fossil Beds along with the taxa provide a characterization of the paleoecology and a paleoenvironment interpretation. The meandering streams flowed into a persistent large lake, (Pliocene Lake Idaho), which rose and fell in response to climate change. The water habitats supported a wide variety of aquatic taxa, as well as terrestrial forms feeding in the broad-leaf deciduous woodlands, marsh-meadow, and savanna-like floodplain habitats. The fossil record and sediments support this interpretation of the paleoenvironment. Pollen records of pine woodland, the presence of grazers, such as horses, and woodrats reflect drier areas of the ecosystem away from the water. The wetter environment supported a wide variety of vertebrate taxa, as well as providing the conditions for sediments to preserve an extensive assemblage of fossils.

## 6.2 Future Work

Confidence in the validity of the species diversity data could be strengthened with an increase in sample size. This could be done in several ways: 1) continue monitoring the present sites for newly exposed material, 2)

expand survey and surface collection of the Panaca Formation, 3) examine and identify previously collected material from AMNH and SBCM. Also, additional screenwashing of productive sites could potentially yield new species of birds, reptiles, and small mammals. It is critical to monitor known fossil sites. I have personal knowledge of a felid skull that was previously located in the foothills near the town of Panaca, but it was not collected due to the lack of a permit. I have not been able to locate any part of the skull, and it appears to be lost. Expansion of surveying and collection, not only in Meadow Valley, but also in other Panaca outcrops would increase the sample size and potential for greater diversity.

Previously collected material stored in museum basements needs to be identified, described, and published. Entire projects can be centered on these collections. Again, the increased sample size could verify suspected species and add additional taxa, thereby increasing species diversity and contributing to relative abundance calculations.

As no fossil plants have been recovered from the Panaca Formation, pollen analysis would provide data about the plant communities of the area. A study of the pollen would support or falsify my interpretation of brushy riparian habitats along the streams and pluvial lake, with steppe on the slopes.

The identification of the bivalves reported in the literature (Mou, 1999; Pederson 1999; Reynolds and Lindsay, 1999), but not seen by me, may also provide new information about climate and indicate specific environmental conditions. Furthermore, a diatom study of the lacustrine sediments could

potentially be used to estimate what the lake conditions were like at the time the diatoms lived there. Such a limnological study would help explain why fish and other freshwater inhabitants have not been recovered from the Panaca Formation lacustrine sediments. Was the chemistry of the lake unsuitable for fish, or were fish simply unable to find their way into this isolated basin?

This study also allows for a comparison of other Blancan faunas besides the Hagerman Fossil Beds assemblage. Other Blancan faunas that could be compared with the Panaca fauna include the Palm Springs Group of Anza-Borrego State Park in California, the faunas of San Pedro and San Simon valleys of Arizona, and the Rexroad and Fox Canyon local faunas in the Rexroad Formation of Kansas. Some of these sites are better temporal matches than the slightly younger Hagerman local fauna. This study can be used to compare species diversity and relative abundance at other localities, as well as track the dispersal of immigrating species from Asia, examine endemism among Blancan vertebrates, site-specific differences of species, along with interpretations of the paleoecology and paleoenvironment of each locality.

Additional work could be done on the structure of terrestrial communities, and comparisons with modern ecosystems such as the Amboseli Basin of East Africa.

APPENDIX 1. List of fossil material collected from Panaca Formation in Meadow Valley, Lincoln County, Nevada. ["cf." = to be compared with, "?" = best guess, "sp." = species, "(x)" = represents the number of elements]

**VM-2009-075 locality PAN-01**

<u>Specimen Number</u>	<u>Taxon</u>	<u>Element</u>
P517	unknown	unidentified
P518	Aves	cervical vertebra
P519	<i>Hypolagus</i> sp.	distal end of right calcaneum
P520	Rodentia	distal end of radius
P521	Mammalia	medial phalanx
P522	Anatidae	coracoid, femoral end
P523	Rodentia?	proximal phalanx
P524	Mammalia	calcaneum fragment
P525	Leporidae	distal end of metapodial
P526	Rodentia?	proximal end of right ulna
P527	Rallidae	synsacrum
P528	<i>Hypolagus</i> sp.	right fifth metacarpal
P529	Leporidae	proximal phalanx
P530	<i>Lepoides lepoides</i>	proximal end of left ulna
P531	cf. <i>Callitepla</i> sp.	left coracoid, femoral end
P532	cf. Aves	unidentified
P533	Squamata	bottom centrum of vertebra
P534	cf. <i>Rallus</i> sp.	carpometacarpus, second metacarpal
P535	Leporidae	distal end of right humerus
P536	cf. <i>Rallus</i> sp.	mandibular symphysis, beak
P537	<i>Lepoides lepoides</i>	proximal end of left radius
P538	Mammalia	l/1, (2)
P539	Mammalia	femur ball
P540	Aves	midshaft of radius
P541	Equidae	tooth fragments
P542	<i>Sinocapra wiltdownsi</i>	medial phalanx
P543	Mammalia	bone fragments
P544	Leporidae	distal end of metapodial
P545	<i>Hypolagus</i> sp.	distal end of left tibia
P546	Mammalia	incisor fragments
P547	Rodentia	proximal end of left femur
P548	Colubridae	midtrunk of vertebra, (2)
P549	cf. Rodentia	proximal end of right femur
P550	Leporidae	tarsal navicular fragment
P551	<i>Hypolagus</i> sp.	right calcaneum fragment
P552	<i>Hypolagus</i> sp.	proximal phalanx
P553	Mammalia	caudal vertebra



P554	cf. <i>Porzana</i> sp.	anterior end of sternum
P555	cf. <i>Anas</i> sp.	left tibiotarsus
P556	Leporidae	PM/X
P557	Leporidae	I1/
P558	Leporidae	I2/
P559	Mammalia	bone fragments
P560	Equidae	tooth fragments
P561	Leporidae	incisor fragments
P562	Mammalia	bone fragments
P563	<i>Hypolagus</i> sp.	proximal end of left second metacarpal
P564	Mammalia	bone fragments
P565	Leporidae	I/1, right
P566	Leporidae	PMX/, left, (2)
P567	Leporidae	premaxilla with partial I/1
P568	Mammalia	tooth fragments
P569	Leporidae	PMX/ fragments
P570	Leporidae	PM/X, left
P571	<i>Lepoides lepoides</i>	P2/, left
P572	Mammalia/Aves	bone fragments
P573	Leporidae	incisor fragment
P574	Leporidae	P/3, left fragment
P575	<i>Lepoides lepoides</i>	right astragalus
P576	Leporidae	distal end of proximal phalanx
P577	Leporidae	proximal end of left third metatarsal
P578	<i>Lepoides lepoides</i>	P2/, right
P579	Leporidae	M/3, left
P580	Anatidae	condyle, distal to tarsometatarsus trochlea of fourth digit
P581	<i>Porzana</i> sp.	premaxilla, beak tip
P582	Aves	phalanx
P583	cf. <i>Rallus</i> sp.	synsacrum fragment
P584	Rodentia	proximal phalanx
P585	Rodentia	caudal vertebra
P586	Mammalia	bone fragments
P587	Rodentia	patella fragment
P588	Rodentia	proximal phalanx
P589	Rodentia	distal phalanx
P590	Rodentia	caudal vertebra
P591	Mammalia	unidentified bone
P592	Mammalia	tooth fragments
P593	cf. <i>Prodipodomys</i> sp.	molar
P594	Mammalia	left scapula
P595	Leporidae	right carpal
P596	Mammalia	maxillary with (cf.) P4/

P597	Mammalia	bone fragments
P598	Mammalia	bone fragments

**VM-2009-075 locality PAN-02**

P599	<i>Lepoides lepoides</i>	left tarsal navicular
P600	<i>Lepoides lepoides</i>	left second metatarsal
P601	Leporidae	distal end of right humerus
P602	<i>Lepoides lepoides</i>	left tarsal
P603	<i>Lepoides lepoides</i>	pubis fragment
P604	<i>Canis lepophagus</i>	left medial phalanx
P605	Mammalia	bone fragments
P606	Leporidae	lower incisor
P607	<i>Hypolagus</i> sp.	left fourth metacarpal
P608	Mammalia	distal end of metapodial
P609	<i>Lepoides lepoides</i>	distal end of metatarsal
P610	<i>Lepoides lepoides</i>	distal end of metatarsal
P611	<i>Canis lepophagus</i>	right medial phalanx
P612	Mammalia	bone fragment
P613	cf. Leporidae	tarsal fragment
P614	Leporidae	PM/X, left fragment
P615	Leporidae	PMX/, right
P616	Leporidae	PM/X fragment
P617	Leporidae	PMX/, right
P618	Leporidae	distal end phalanx
P619	Mammalia	unidentified
P620	Mammalia	bone fragments

**VM-2009-075 locality PAN-03**

P621	<i>Lepoides lepoides</i>	proximal end of left third metatarsal
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**VM-2009-075 locality PAN-04**

P622	Artiodactyla, cf. Cervidae	cf. condyle fragment
P623	<i>Lepoides lepoides</i>	left mandible with P/4 and M/1
P624	cf. <i>Megatylopus</i> sp.	left fibula
P625	cf. <i>Sinocapra</i> sp.	proximal phalanx
P626	Mammalia and Aves	bone fragments
P627	<i>Lepoides lepoides</i>	midshaft of humerus
P628	<i>Hypolagus</i> sp.	left pubis fragment
P629	<i>Lepoides lepoides</i>	proximal end of right third metatarsal
P630	Leporidae	distal end of proximal phalanx
P631	<i>Lepoides lepoides</i>	proximal end of right ilium

P632	<i>Lepoides lepoides</i>	right astragalus
P633	<i>Lepoides lepoides</i>	medial phalanx

#### **VM-2009-075 locality PAN-05**

P634	<i>Lepoides lepoides</i>	left astragalus
P635	Mammalia	post zygopophysis fragment
P636	Mammalia	bone fragments

#### **VM-2009-075 locality PAN-06**

P637	Leporidae	midshaft of metapodial
P638	<i>Cygnus</i> sp.	proximal end of left scapula
P639	Mammalia	bone fragments

#### **VM-2009-075 locality PAN-07**

P640	Leporidae	distal end of phalanx
P641	<i>Lepoides lepoides</i>	proximal phalanx
P642	<i>Lepoides lepoides</i>	left tarsal navicular
P643	<i>Lepoides lepoides</i>	distal end of metapodial
P644	Leporidae	proximal phalanx
P645	<i>Lepoides lepoides</i>	left astragalus
P646	Leporidae	medial phalanx
P647	Leporidae	proximal end of proximal phalanx
P648	Leporidae	distal phalanx
P649	Leporidae	proximal end of left fourth metatarsal
P650	Leporidae	distal phalanx
P651	Mammalia	bone fragments
P652	Leporidae	proximal end of left second metatarsal

#### **VM-2009-075 locality PAN-08**

P653	cf. <i>Megatylopus</i> sp.	distal end of metapodial
P654	<i>Lepoides lepoides</i>	proximal end of right humerus
P655	cf. <i>Lynx</i> sp.	left tarsal navicular

#### **VM-2009-075 locality PAN-09**

P656	<i>Lepoides lepoides</i>	left calcaneum
P657	<i>Lepoides lepoides</i>	distal end of right tibia
P658	<i>Lepoides lepoides</i>	left pelvis fragment

P659	<i>Lepoides lepoides</i>	proximal end of right radius
P660	<i>Lepoides lepoides</i>	proximal end of left ulna
P661	<i>Lepoides lepoides</i>	distal end of right radius
P662	<i>Canis lepophagus</i>	right astragalus
P663	cf. <i>Megatylopus</i> sp.	proximal end of medial phalanx
P664	Leporidae	midsection of radius
P665	Leporidae	proximal end of left second metatarsal
P666	Leporidae	proximal phalanx
P667	Leporidae	medial phalanx
P668	<i>Lepoides lepoides</i>	distal phalanx
P669	Leporidae	distal end of metapodial
P670	Leporidae	proximal end of left ulna
P671	<i>Hypolagus</i> sp.	proximal end of left tibia
P672	Leporidae	medial phalanx
P673	<i>Hypolagus</i> sp.	proximal end of right humerus
P674	Leporidae	I1/, right
P675	Leporidae	PMX fragments
P676	Leporidae	PM/X, right
P677	Leporidae	left mandible dentary fragment with P/3 alveolus and incisor fragment
P678	Mammalia	medial phalanx
P679	Rodentia	proximal end of right femur

#### **VM-2009-075 locality PAN-10**

P680	<i>Lepoides lepoides</i>	medial phalanx
P681	Leporidae	proximal phalanx
P682	<i>Lepoides lepoides</i>	proximal phalanx
P683	<i>Lepoides lepoides</i>	proximal end of right fourth metatarsal
P684	<i>Hypolagus</i> sp.	distal end of right humerus
P685	<i>Hypolagus</i> sp.	right fourth metacarpal
P686	Leporidae	PMX/, right, (2)
P687	Rodentia	distal end of metapodial
P688	Leporidae?	left femur ball

#### **VM-2009-075 locality PAN-11**

P689	<i>Hypolagus</i> sp.	second right metatarsal
P690	<i>Lepoides lepoides</i>	left ischium fragment
P691	<i>Lepoides lepoides</i>	distal end of right humerus
P692	cf. <i>Lynx</i> sp.	left medial phalanx

**VM-2009-075 locality PAN-13**

**VM-2009-075 locality PAN-14**

## VM-2009-075 locality PAN-15

**VM-2009-075 locality PAN-16**

**VM-2009-075 locality PAN-17**

**VM-2009-075 locality PAN-18**

P717	Leporidae	proximal end of left second metatarsal
P718	Leporidae	right ischium fragment
P719	Leporidae	midshaft of radius
P720	cf. Leporidae	femur ball fragments
P721	Leporidae	I1/
P722	Leporidae	I/1
P723	<i>Lepoides lepoides</i>	PM/X, right
P724	Leporidae	PMX/, right
P725	Leporidae	PM/X, left fragment
P726	Leporidae	PM/X, right
P727	Leporidae	I2/, fragment
P728	Mammalia	medial phalanx, (2)
P729	Mammalia	bone fragments
P730	Mammalia	medial phalanx

**VM-2009-075 locality PAN-19**

P731	<i>Lepoides lepoides</i>	distal end of right humerus
P732	Leporidae	proximal midshaft of right ulna
P733	<i>Lepoides lepoides</i>	proximal end of left ulna
P734	<i>Hypolagus</i> sp.	distal end of right tibia
P735	<i>Lepoides lepoides</i>	right tarsal
P736	Leporidae	left astragalus fragment
P737	<i>Lepoides lepoides</i>	right astragalus, (2)
P738	<i>Lepoides lepoides</i>	right calcaneum
P739	<i>Lepoides lepoides</i>	right calcaneum
P740	<i>Hypolagus</i> sp.	right calcaneum
P741	<i>Hypolagus</i> sp.	right calcaneum fragment
P742	<i>Hypolagus</i> sp.	left calcaneum fragment
P743	<i>Hypolagus</i> sp.	proximal end of proximal phalanx
P744	Leporidae	distal phalanx
P745	<i>Hypolagus</i> sp.	distal phalanx
P746	Leporidae	distal end of phalanx
P747	<i>Hypolagus</i> sp.	proximal end of right fourth metatarsal
P748	Leporidae	distal end of metatarsal
P749	Leporidae	proximal end of left second metatarsal
P750	Leporidae	PMX/, right
P751	Leporidae	PM/X, right
P752	Leporidae	P2/ fragment
P753	Leporidae	dentary fragment with PMX/
P754	Cricetidae	M/3, left
P755	<i>Lepoides lepoides</i>	P/3
P756	<i>Mimomys panacaensis</i>	M/1, left

P757	cf. Carnivora	cf. metacarpal
P758	Mammalia	axis fragment
P759	Mammalia	right tarsal
P760	Mammalia	PMX/X fragments
P761	Equidae	tooth fragments
P762	Leporidae	proximal phalanx
P763	Leporidae	left ulna fragment
P764	<i>Lepoides lepoides</i>	distal end of left tibia
P765	Leporidae	I2/
P766	Leporidae	I1/
P767	Leporidae	I/1
P768	Leporidae	PM/X, right
P769	Leporidae	PMX/, right
P770	Leporidae	PMX/, right, (2)
P771	Leporidae	PM/X fragments
P772	<i>Lepoides lepoides</i>	P/3, right
P773	Leporidae	M/3
P774	Leporidae	M/3
P775	Leporidae	PM/X fragments
P776	Leporidae	bone fragments
P777	Cricetidae	dentary with M/2, M/1 alveolus and incisor fragment
P778	Mammalia	lower incisor
P779	Mammalia	bone fragments
P780	Mammalia	small bone fragments
P781	Mammalia	bone fragments
P782	Mammalia	tooth fragment
P783	Mammalia	bone fragments
P784	Rodentia	incisor
P785	Rodentia	metapodial
P786	Leporidae	distal end of phalanx
P787	<i>Lepoides lepoides</i>	right femur ball
P788	Leporidae	I1/, left
P789	Leporidae	I/1, (2)
P790	Leporidae	PM/X, right
P791	Leporidae	P2/, left
P792	cf. Mammalia	cf. vertebra
P793	Mammalia	distal phalanx
P794	Mammalia	cf. tarsal fragment
P795	Mammalia	tarsal or carpal
P796	Mammalia	incisor, (4)
P797	Carnivora	distal sesamoid
P798	Rodentia	distal end of right humerus
P799	Leporidae	left femur ball
P800	Rodentia	proximal end of right femur
P801	Leporidae	distal end of humerus, (3)

P802	Leporidae	distal epiphysis of right tibia
P803	Leporidae	distal end of phalanx, (3)
P804	Leporidae	distal epiphysis of right tibia
P805	Leporidae	distal end of tibia
P806	Leporidae	distal condyle of metapodial, (3)
P807	Leporidae	proximal end of right second metatarsal
P808	Leporidae	proximal end of right third metatarsal
P809	<i>Lepoides lepoides</i>	proximal end of right fourth metatarsal
P810	Leporidae	proximal end of right fourth metatarsal
P811	Leporidae	proximal end of fourth metacarpal
P813	<i>Lepoides lepoides</i>	proximal end of right calcaneum
P814	<i>Lepoides lepoides</i>	right tarsal navicular
P815	Leporidae	right tarsal
P816	Leporidae	carpal
P817	Leporidae	I/1
P818	Leporidae	I1/
P819	Leporidae	P2/
P820	<i>Hypolagus edensis</i>	P/3, left
P821	<i>Hypolagus</i> sp.	P/3, left
P822	Leporidae	M/3, right
P823	Leporidae	PM/X, left
P824	Leporidae	PM/X
P825	Leporidae	PMX/, (5)
P826	Leporidae	PMX/X, (14)
P827	<i>Mimomys panacaensis</i>	M/1, left
P828	Cricetidae	M1/ fragment
P829	Mammalia	bone fragments
P830	Leporidae	tarsal cuneiform
P831	Leporidae	I/1
P843	Leporidae	right calcaneum fragment
P844	Cricetidae	M/1, left
P845	Cricetidae	M2/, left fragment

**VM-2009-075 locality PAN-20**

P832	<i>Lepoides lepoides</i>	proximal end of right femur (juvenile)
P833	<i>Lepoides lepoides</i>	right acetabulum

**VM-2009-075 locality PAN-21**

P834	<i>Hypolagus</i> sp.	proximal end of right ulna
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P835	Leporidae	right calcaneum
P836	Leporidae	left calcaneum
P837	cf. <i>Megatylopus</i> sp.	proximal end of proximal phalanx

**VM-2009-075 locality PAN-22**

P838	<i>Lepoides lepoides</i>	left tarsal cuneiform
P839	Mammalia	bone fragments

**VM-2009-075 locality PAN-23**

P840	<i>Hypolagus</i> sp.	left tarsal navicular
P841	<i>Hypolagus</i> sp.	right astragalus
P842	<i>Hypolagus</i> sp.	left calcaneum

**VM-2009-075 locality PAN-24**

P846	Mammalia	glenoid fossa of scapula
P847	Mammalia	metapodial
P848	Mammalia	unidentified bone fragments
P849	Mammalia	I/1
P850	Mammalia	maxilla fragment with two alveolus
P851	Mammalia	tooth root
P852	cf. <i>Crotaphytus</i> sp.	dentary mandible with teeth
P853	cf. Galliformes	second phalanx
P854	<i>Canis</i> sp.	M/1 fragment
P855	cf. Rodentia	caudal vertebrae
P856	Rodentia	proximal end of scapula
P857	Rodentia	medial phalanx
P858	Rodentia	proximal phalanx
P859	Rodentia	I1/
P860	Rodentia	I/1
P861	Mammalia	coracoid process of scapula
P862	Leporidae	proximal end of left radius
P863	Leporidae	glenoid fossa of right scapula
P864	Leporidae	epiphysis of right humerus
P865	<i>Hypolagus</i> sp.	distal end of right tibia
P866	<i>Hypolagus</i> sp.	distal end of right tibia
P867	<i>Lepoides lepoides</i>	distal epiphysis of right tibia
P868	Leporidae	patella
P869	cf. <i>Lepoides lepoides</i>	left femur ball
P870	<i>Lepoides lepoides</i>	distal end of right calcaneum
P871	<i>Hypolagus</i> sp.	right calcaneum, (2)
P872	Leporidae	proximal end of right calcaneum
P873	<i>Hypolagus</i> sp.	proximal end of left calcaneum

P874	<i>Hypolagus</i> sp.	proximal end of left astragalus
P875	<i>Lepoides lepoides</i>	right astragalus
P876	Leporidae	proximal end of right metatarsal, (2)
P877	Leporidae	proximal end of left fourth metacarpal
P878	Leporidae	proximal end of right second metacarpal
P879	Leporidae	medial phalanx
P880	Leporidae	proximal end of proximal phalanx
P881	<i>Hypolagus</i> sp.	proximal phalanx
P882	<i>Hypolagus</i> sp.	distal phalanx
P883	Leporidae	I/1
P884	<i>Hypolagus edensis</i>	P/3, right
P885	<i>Hypolagus edensis</i>	P/3, left
P886	Leporidae	PMX/, right
P887	Leporidae	PM/X, left fragment
P888	Leporidae	PM/X fragment
P889	Leporidae	PMX/X fragments
P890	Leporidae	PM/X, (3)
P891	<i>Pliogeomys parvus</i>	P/4
P892	Cricetidae	left M1/ with mandible fragment
P893	<i>Peromyscus hagermanensis</i>	M1/
P894	Cricetidae	M1/, right
P895	<i>Mimomys panacaensis</i>	M/2, right
P896	<i>Mimomys panacaensis</i>	M/2, right
P897	<i>Mimomys panacaensis</i>	M/3, right
P898	Mammalia	large bone fragments
P899	Mammalia	small bone fragments
P900	Mammalia	caudal vertebrae, (3)
P901	Mammalia	pelvis fragment
P902	Mammalia	femur ball fragment
P903	cf. Rodentia	femur ball, (5)
P904	Mammalia	right astragalus
P905	Mammalia	tarsal or carpal
P906	Mammalia	carpal
P907	Mammalia	carpal
P908	Mammalia	proximal end of third phalanx
P909	Mammalia	epiphysis of medial phalanx
P910	Mammalia	proximal end of medial phalanx
P911	Mammalia	I/1
P912	Mammalia	tooth fragment
P913	Mammalia	tooth fragments
P914	Mammalia & Leporidae	tooth fragments
P915	cf. Leporidae	proximal end of phalanx, (4)
P916	Mammalia	unidentified bone fragment

P917	Carnivora	carnassial hypoconid molar fragment
P918	Carnivora	P4/, left fragment
P919	<i>Canis</i> sp.	M/1, left fragment
P920	Rodentia	caudal vertebrae fragments
P921	Rodentia	caudal vertebrae, (2)
P922	cf. Rodentia	proximal end of scapula
P923	Rodentia	humerus ball fragment
P924	Rodentia	distal end of left humerus
P925	Rodentia	distal end of right humerus
P926	Rodentia	proximal end of right ulna
P927	Rodentia	proximal end of left ulna
P928	Rodentia	distal end of left tibia
P929	Rodentia	distal end of femur
P930	Rodentia	left calcaneum
P931	Rodentia	left calcaneum
P932	Rodentia	proximal end of metatarsal, (2)
P933	Rodentia	proximal end of metacarpal
P934	Rodentia	right astragalus
P935	Rodentia	proximal phalanx
P936	Rodentia	medial phalanx
P937	Rodentia	medial phalanx
P938	Rodentia	proximal end of medial phalanx
P939	Rodentia	distal phalanx
P940	Rodentia	distal end of phalanx
P941	Rodentia	I/1
P942	Rodentia	I/1, (3)
P943	Rodentia	I/1, (7)
P944	Rodentia	I1/, (2)
P945	Rodentia	maxilla fragment
P946	Rodentia	midshaft of humerus, (5)
P947	Leporidae	distal end of humerus
P948	<i>Lepoides lepoides</i>	right calcaneum
P949	Leporidae	distal end of left calcaneum
P950	Leporidae	proximal end of right calcaneum
P951	Leporidae	right astragalus, (2)
P952	Leporidae	left tarsal navicular
P953	Leporidae	right tarsal cuboid
P954	Leporidae	left fourth metacarpal
P955	Leporidae	proximal end of right fifth metacarpal
P956	Leporidae	distal end of metapodial
P957	<i>Lepoides lepoides</i>	distal end of metapodial, (2)
P958	Leporidae	distal end of metapodial
P959	Leporidae	proximal phalanx, (2)
P960	Leporidae	proximal end of proximal phalanx

P961	Leporidae	proximal end of proximal phalanx
P962	Leporidae	medial phalanx
P963	Leporidae	proximal end of medial phalanx
P964	Leporidae	distal phalanx, (2)
P965	Leporidae	distal phalanx, (9)
P966	Leporidae	distal end of phalanx, (12)
P967	<i>Lepoides lepoides</i>	I1/, left
P968	Leporidae	I1/, (2)
P969	Leporidae	I/1
P970	Leporidae	I/1, (2)
P971	Leporidae	I2/
P972	Leporidae	P2/, left
P973	<i>Hypolagus edensis</i>	P/3, left
P974	<i>Hypolagus edensis</i>	P/3, right
P975	Leporidae	M/3 fragment
P976	Leporidae	PMX/, (2)
P977	Leporidae	PM/X, (4)
P978	Leporidae	PMX/, (8)
P979	Leporidae	PMX/X fragments
P980	Leporidae	right premaxilla fragment
P981	Leporidae	maxilla fragment, (2)
P982	Leporidae	dentary fragment
P983	cf. <i>Spermophilus</i> sp.	M/X
P984	Cricetidae	M1/, right
P985	Cricetidae	M1/, left
P986	Cricetidae	M1/, left fragment
P987	Cricetidae	M1/, left
P988	Cricetidae	M1/, left
P989	<i>Mimomys panacaensis</i>	M/1, left, (2)
P990	<i>Mimomys panacaensis</i>	M/1, right
P991	Cricetidae	M/1, left fragment
P992	<i>Mimomys panacaensis</i>	M/1, left
P993	Cricetidae	M2/, left fragment
P994	<i>Mimomys panacaensis</i>	M2/, right
P995	<i>Mimomys panacaensis</i>	M2/, right
P996	<i>Mimomys panacaensis</i>	M2/, left
P997	<i>Mimomys panacaensis</i>	M/2, right
P998	<i>Mimomys panacaensis</i>	M/2, left
P999	<i>Repomys</i> sp	M/2, left
P1000	<i>Mimomys panacaensis</i>	M/2, left
P1001	<i>Mimomys panacaensis</i>	right dentary with M/1
P1002	<i>Mimomys panacaensis</i>	right dentary with M1 & M2
P1003	<i>Repomys</i> sp.	left maxilla with M1/ & M2/
P1004	Cricetidae	right mandible with I/1, M/1, M/3
P1005	Cricetidae	left maxilla with M1/ & partial M2/

P1006	Cricetidae	Tooth
P1007	Cricetidae	cf. M/1
P1008	Cricetidae	cf. M2/
P1009	Cricetidae	cf. PM/X fragment
P1010	Cricetidae	root fragment
P1011	Mammalia	bone fragments

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