BIODIVERSITY RESPONSE TO CLIMATE CHANGE IN THE MIDDLE PLEISTOCENE

THE PORCUPINE CAVE FAUNA FROM COLORADO

EDITED BY ANTHONY D. BARNOSKY

Biodiversity Response to Climate Change in the Middle Pleistocene

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To Don Rasmussen, who with his son Larry
found the fossil deposits in Porcupine Cave,
and whose unfailing enthusiasm for
discovery, excavation, and working
with other scientists and volunteers
was essential in moving the project
from concept to reality.

CONTENTS

PART THREE

Effect of Environmental Change on the Porcupine Cave Fauna

PREFACE

Since fossil vertebrates were first discovered at Porcupine Cave on the rim of South Park, Colorado, in 1981, the site has become the world's most important source of information about animals that lived in the high elevations of North America in the middle part of the ice ages, between approximately one million and 600,000 years ago. Beginning in 1985, teams of scientists and volunteers from three major research institutions —the Carnegie Museum of Natural History, the Denver Museum of Nature and Science, and the University of California Museum of Paleontology—spent some 15 field seasons excavating and studying tens of thousands of fossil specimens that have opened a window onto past evolutionary and ecological adjustments. This window into the past allows us to visualize how ongoing global change could affect our living communities. This book reports the results of nearly two decades of research and has been written to appeal to three overlapping audiences.

The first target audience is made up of scholars, students, and others interested in paleontology and in how paleontological data are applied to solving ecological and evolutionary questions. The second audience consists of ecologists and conservationists concerned with understanding and preserving biodiversity and other natural ecological dynamics. To serve these first two audiences, the book strives to illustrate the critical role paleontology plays in understanding ecosystem dynamics, such as the maintenance of biodiversity, and to document carefully the scientific data from Porcupine Cave so that this unique data set can be used now and in the future to illuminate ecological processes.

The third audience is the caving community, which has increasingly used Porcupine Cave and others like it for both scientific and recreational purposes over the past 20 years. The book endeavors to highlight the importance of the fragile but irreplaceable paleontological resources to be found in caves.

The book is divided into three parts. The chapters in part 1 articulate some scientific questions that the data from the cave can help answer; document the location, modern environment, and geological setting of the site as a context in which to interpret the fossil data; and relate the history of the discovery of Porcupine Cave, the spatial distribution and age of the fossil deposits, and the cause of the accumulation of so many fossils. Part 2 documents the identification and occurrence of various taxonomic groups from the many different localities within the cave. Part 3 synthesizes the information presented in the other two parts into a series of analyses designed to explore the implications of the Porcupine Cave fauna for understanding how terrestrial mountain ecosystems react in the face of environmental change, how climate change affects patterns of biodiversity in mammals, and, in light of these processes, how we might expect ecosystems to respond to human-induced global warming.

Given the astounding numbers of fossils that Porcupine Cave has produced—more than 20,000 specimens have been identified, and many times that number are stored in museum drawers awaiting identification—it is impossible to explore all their implications in a single publication. This book should be viewed as a foundation for further research rather than the final word on the matter. We hope that the data and ideas presented herein stimulate debate and provide impetus for a new cohort of scholars to continue the work we have just begun.

ACKNOWLEDGMENTS

Excavating, analyzing, and publishing the Porcupine Cave data has been an arduous task that has taken nearly 20 years and involved more than 30 scientists, more than 100 field hands, and the cooperation of the three major museums where specimens reside: the Carnegie Museum of Natural History (CM), the Denver Museum of Nature and Science (DMNH), and the University of California Museum of Paleontology (UCMP). Thanks are due to all who lent a hand, and especially to the following individuals and institutions.

The kindness of Frank and Connie McMurry (McMurry Land and Livestock Company) in allowing us to excavate in their cave and spend field seasons at their cow camp made the whole project possible. I am deeply indebted to them. The project would also not have been possible without financial support from the U.S. National Science Foundation (grants BSR-9196082 in the early years and EAR-9909353 during the synthesis stage), the UCMP, the CM, and the DMNH.

Don Rasmussen spearheaded the excavation teams for many years and contributed in innumerable ways to the project. He has been a delight to work with. Two colleagues who contributed essential data to this project died before they saw the fruits of their labors: Vic Schmidt (paleomagnetics) and Elaine Anderson (carnivores). Memories of days in the cave and nights at the campfire with them live on. Betty Hill of the CM, Logan Ivy of the DMNH, and Pat Holroyd of the UCMP were extremely helpful in arranging loans of specimens and dealing with sometimes overwhelming curatorial matters. Paul Koch graciously ran isotope samples in his lab at the University of California, Santa Cruz. Karen Klitz of the University of California Museum of Vertebrate Zoology (MVZ) prepared some of the illustrations, and the MVZ was an essential resource for specimen identification.

It is impossible to name here the more than 100 volunteers, students, and employees who helped excavate the deposits and pick matrix, but I am grateful to them all. Many of them were members of the Colorado Grotto of the National Speleological Society or the Western Interior Paleontological Society. Hazel Barton led the cartographic efforts to produce detailed maps of the cave, and I thank her for making her beautiful map available.

As editor, my job was made easier by the contributors to this book, many of whom waited patiently after submission of their manuscripts for the whole package to come together. Special thanks are due to Chris Bell, who has been with the project since the early 1990s and who picked most of the matrix from the Pit. Several scientists gave of their time in providing detailed reviews of various chapters: Elaine Anderson, Jill Baron, Chris Bell, Annalisa Berta, Doug Burbank, Jim Burns, Emmet Evanoff, Bob Feranec, Tom Goodwin, Fred Grady, Elizabeth Hadly, Bill Harbert, Art Harris, R. Lee Lyman, Bruce MacFadden, Bob Martin, David Polly, Don Rasmussen, Bruce Rothschild, Dennis Ruez Jr., Eric Scott, Alan Shabel, David Steadman, Tom Stidham, Tom Van Devender, Blaire Van Valkenburgh, Alisa Winkler, Bill Wyckoff, and Richard Zakrzewski. To them, and to several reviewers who wished to remain anonymous, I give thanks. Gratitude is also extended to Timothy Heaton and Karel Rogers, who read the entire manuscript of the book and provided useful comments.

Discussions with my graduate and postdoctoral students have been intellectually stimulating. Alan Shabel's deep thinking about ecology and willingness to lend a hand as needed were a great benefit, as were discussions with Marc Carrasco, Edward Davis, Bob Feranec, Samantha Hopkins, and Brian Kraatz. Faysal Bibi curated many of the UCMP Pit specimens and helped produce some of the spreadsheets used in the analyses.

Above all, I thank my wife, Liz Hadly, for her help both scientifically and with living life, and my children, Emma and Clara, who make me think about why biodiversity might be important for future generations.

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Palo Alto, California

CHAPTER APPENDIXES

FIGURES

TABLES

ABBREVIATIONS AND DEFINITIONS

AF	Alternating field
HSDk	Highest known stratigraphic datum
Ka	Thousands of years
LSDk	Lowest known stratigraphic datum
Ma	Millions of years
middle Pleistocene	In this volume the Pleistocene is considered to begin at some time slightly younger than 1.77 Ma ago, following the placement of the boundary in the section at Vrica, Italy, by International Geological Correlation Project 41 and International Union of Quaternary Research Subcommission 1d at the 27th International Geological Congress in Moscow in 1984 (Bell et al., in press), and subsequent correlation of the boundary with the magnetostratigraphic and radiometric time scales (Cande and Kent, 1995; Berggren et al., 1995). The use of the term "middle Pleistocene" in this book is informal and refers to the middle third of the Pleistocene, that is, the interval of time from about 600 Ka to 1.2 Ma ago. This is not to be confused with terminology such as "Middle Pleistocene subseries" (note the uppercase *M*), which as of May 1, 2002, was an informal working definition, adopted by the International Commission on Stratigraphy, that encompasses the time interval from circa 126 to 780 Ka ago (http://micropress.org/stratigraphy/gssp.htm).
MNI	Minimum number of individuals
NISP	Number of identified specimens
pcv	Precloacal vertebra
yr BP	Radiocarbon years before 1950

Dental abbreviations

C	Upper canine
I	Upper incisor
M	Upper molar
P	Upper premolar
c	Lower canine
i	Lower incisor
m	Lower molar
p	Lower premolar
1, 2, 3, etc.	Position in the toothrow. Thus M1 stands for the first upper molar and p4 stands for the fourth lower premolar.

Institution abbreviations

AMNH	American Museum of Natural History
CM	Carnegie Museum of Natural History
DMNH	Denver Museum of Nature and Science
FLMNH	Florida Museum of Natural History
GCPM	George C. Page Museum of La Brea Discoveries
GRCA	Grand Canyon National Park
HAFO	Hagerman Fossil Beds National Monument
IMNH	Idaho State Museum of Natural History
KU	University of Kansas, Kansas Museum of Natural History
LACM	Natural History Museum of Los Angeles County
MVZ	University of California Museum of Vertebrate Zoology
SBCM	San Bernardino County Museum

TMM	Texas Memorial Museum
UCMP	University of California Museum of Paleontology
UNSM	University of Nebraska State Museum
USNM	United States National Museum
YPM	Yale Peabody Museum

Measurement abbreviations

AP	Greatest distance from anterior to posterior portion of tooth
BD	Greatest breadth of the distal end
BP	Greatest breadth of the proximal end
DLS	Greatest diagonal length of the ventral surface
GBw	Greatest breadth over the wings
GD	Greatest depth
GL	Greatest length
GLl	Greatest length of lateral edge
GLm	Greatest length of medial edge
Glpe	Greatest length of proximal end
LD	Length of dorsal surface
SD	Smallest breadth of diaphysis
T	Greatest transverse distance (i.e., width) of tooth measured perpendicular to AP

PART ONE

THE DISCOVERY AND DISTRIBUTION OF FOSSILS

ONE

Climate Change, Biodiversity, and Ecosystem Health

The Past as a Key to the Future

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Earth's climate is getting warmer, and it will probably continue to do so over the coming century. The emerging consensus is that human activities are stimulating an increase in global mean temperature that will amount to 1.4–5.8°C by the year 2100 (Houghton et al., 2001), with 90% probability that the change will amount to 1.7–4.9°C in the absence of climate mitigation policies (Wigley and Raper, 2001). Regionally, the changes will be even greater. Average warming for the United States is predicted to be at least 3°C and possibly as much as 6°C (National Assessment Synthesis Team, 2001). The effects of some of these changes are already apparent. For example, a warming of approximately 4°C in Alaska since the 1970s has led to vast expanses of spruce forests being killed by beetles that reproduce faster in warmer temperatures. Roads are buckling and houses are sinking, as what used to be permafrost thaws seasonally.

A growing number of scientists have recognized that global warming can be expected to affect the few remaining intact, naturally operating ecosystems on Earth in unpredictable ways. This issue came to widespread attention just over a decade ago, with the publication of a compendium of papers, edited by Peters and Lovejoy (1992), concerning the effects of global warming on biodiversity. The effects of climate change on biodiversity are a matter of concern because biodiversity is often associated with ecosystem health. Significant losses in biodiversity may be analogous to the death of the canary in the coal mine, which signals that the mine is no longer safe for humans. Though debate continues about whether "more is better" in terms of numbers of species in ecosystems (Norton, 1987; Grime, 1997; Tilman, 1997; McCann, 2000), available information suggests that larger numbers of species help buffer ecosystems in the face of changing environments (Loreau et al., 2001). Thus of key concern is the question of whether climatic warming will reduce biodiversity to the extent that a given ecosystem loses its ability to maintain the baseline functions that define it. Maintaining these baseline functions is, in fact, integral to an operational definition of ecosystem health. In the words of Haskell et al. (1992:9), "An ecological system is healthy . . . if it is stable and sustainable—that is, if it is active and maintains its organization and autonomy over time and is resilient to stress." Put another way, the basic question is: at what point do disruptions to baseline diversity cause ecosystems to cross functional thresholds and catastrophically shift their dynamics (Sheffer et al., 2001)?

Adding to concerns about the effects of climate change on biodiversity is the fragmentation of previously widespread biota by human activities, which itself—probably more so than climate change—often leads to reduction in species richness. As Soulé (1992:xiii) put it, it is simply the wrong time for climate change. "Even if species are able to move quickly enough to track their preferred climate, they will have to do so within a major obstacle course set by society's conversion of the landscape. . . . A species may be impelled to move, but Los Angeles will be in the way" (Peters and Lovejoy, 1992: xviii).

Over the past decade, researchers have continued to study how climate change affects biodiversity, and how biodiversity relates to the health of ecosystems. By necessity, most of these studies have been theoretical (Kerr and Packer, 1998; Ives et al., 1999) and/or focused on experiments at the level of study plots, which track diversity changes in response to environmental changes or treatments that take place over months, years, or at best decades (see, e.g., Brown et al., 1997; Chapin et al., 2000; Tilman, 2000; Reich et al., 2001; Tilman et al., 2001). Difficulties arise in scaling the results from small study plots up to the landscape, ecosystem, and biome levels (Loreau et al., 2001). A further difficulty lies in understanding how results obtained over short time scales compare with the natural baseline of variation inherent over ecologically long time scales: hundreds to thousands to millions of years. To study this question, other researchers have focused on tracking ecosystem changes across major climatic transitions, such as those at the Paleocene-Eocene boundary (Wing, 1998), in the early Oligocene (Prothero and Heaton, 1996; Barnosky and Carrasco, 2002), across the middle Miocene climatic optimum (Barnosky, 2001; Barnosky and Carrasco, 2002), and across the Pleistocene-Holocene transition (Graham and Grimm, 1990; Graham, 1992; Webb, 1992; FAUNMAP Working Group, 1996). To link across temporal scales, some studies have taken a comparative approach, which examines how flora and fauna responded to climate changes over varying time scales from years to decades to centuries to thousands or millions of years (Brown et al., 2001; Barnosky et al., 2003). A missing piece of the puzzle, however, has been data sets that allow scientists to track changes in biodiversity through multiple climatic fluctuations over hundreds of thousands of years in one geographic locality.

This book offers one such data set, in the form of more than 20,000 identified specimens of fossil vertebrates distributed over more than 200,000 years, spanning the time from approximately 1,000,000 to at least 780,000 years ago. The specimens come from more than 26 fossil localities within Porcupine Cave, in the high Rocky Mountains of South Park, Colorado (see chapter 2 for locality details). They span at least two glacial-interglacial transitions as well as smaller-scale climatic fluctuations within glacials and interglacials. The deposits also seem to bracket a major transition in the periodicity of glacial-interglacial cycles, from a 41,000-year rhythm in the early Pleistocene to a 100,000-year rhythm that was firmly in place by 600,000 years ago. Therefore it is possible to track a single ecosystem through climate changes of variable intensity and to assess the biodiversity response, which is one goal of this book. However, an equally important goal has been to make the data available to future researchers in a way that can facilitate additional analyses.

Part 1 provides relevant background information on Porcupine Cave, the fossil deposits themselves, and the modern environment of South Park. Part 2 provides the basis for species identifications (which are critical in assessing the quality of the data and what it can be used for) as well as summaries of actual numbers of specimens representing each species (which are necessary for many ecological analyses). Part 3 focuses on faunal dynamics and how the fossil information applies to understanding the effects of climatic warming on biodiversity. The nature of the data makes it possible to examine how climate change affected biodiversity in terms of trophic and size structure, species richness, species composition, and population change.

An overriding impetus for this effort has been the need to establish a baseline that will allow clear recognition of disruptions to natural biodiversity caused by human-induced global warming. An initial priority is to assess how global warming indicated by the middle Pleistocene glacial-interglacial transitions compares with rates of warming that are currently under way, those that are predicted, and those that have occurred throughout geological time.

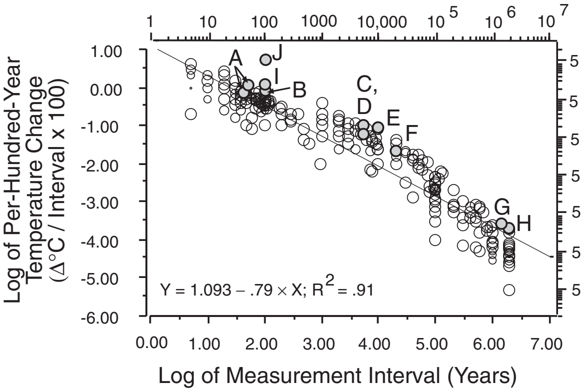

FIGURE 1.1 Per-hundred-year temperature change values for global warming events plotted against the interval of time over which the temperature change was measured. White circles show actual measurements taken from the following sources: 1–130 years from figure 11 in Houghton et al. (1990); 90–900 years from figure 7.1 (bottom) in Houghton et al. (1990); 1000–10,000 years from figure 7.1 (middle) in Houghton et al. (1990); 10,000–130,000 years from figure 6.12 in Bradley (1999); 100,000–900,000 years from figure 7.1 (top) in Houghton et al. (1990); 1,000,000–2,000,000 years from figure 2 in Zachos et al. (2001). Shaded circles mark rates for the following observed, past, or projected global warming episodes: A, global warming measured from 1950 to 1990 (lower dot: Houghton et al., 1990), and using a less conservative estimate of about 0.7°C from 1950 to 2000 (upper dot: Delworth and Knutson, 2000); B, Medieval Warm Period (Hughes and Diaz, 1994; Campbell et al., 1998; Broecker, 2001); C, Pleistocene-Holocene glacial-interglacial transition (upper circle) (Schneider and Root, 1998); D, middle Pleistocene glacial-interglacial transition (lower circle) (Raymo, 1997); E, Paleocene Methane Event, highest estimate (Katz et al., 1999); F, Paleocene Methane Event, lowest estimate (Katz et al., 1999); G, Middle Miocene Climatic Optimum (Barnosky, 2001; Zachos et al., 2001; Barnosky and Carrasco, 2002); H, Late Oligocene Warming Event (Zachos et al., 2001; Barnosky and Carrasco, 2002); I and J, lowest and highest estimates, respectively, for global warming over the next 100 years (Houghton et al., 2001).

Current warming rates have long been recognized to be very fast, and projected rates exceed rates inferred for at least the last 100,000 years (e.g., Schneider et al., 1992; Jackson and Overpeck, 2000). But exactly how anomalous are these fast modern rates in comparison with the many changes in warming rates that ecosystems have experienced and evolved within over the past thousands and millions of years? Determining this is not as straightforward as it sounds, because rates of change typically are computed over differing time intervals. This has been shown to be a problem in studies of evolutionary rates, for example, where there is an inverse relationship between rates of evolutionary change and the length of time over which the change is measured (Gingerich, 2001). Sedimentation rates show the opposite relationship: the thickness of sediments deposited over short time intervals underestimates the total thickness that will accumulate over longer periods (Kirchner et al., 2001). How then do rates of climate change scale with the interval of time over which the climate change is measured?

Figure 1.1 answers this question. The data were compiled from paleotemperature proxies provided mainly by oxygen isotope curves (Barnosky et al., 2003). The shorter the interval of time over which the temperature is measured, the faster the per-hundred-year rate of change appears. Plotting these data in log-log space and highlighting the per-hundred-year temperature change indicated for various past, present, and predicted warming rates place both the middle Pleistocene and the current global warming crisis in perspective. It is clear that some of the major global warming events of the past 65 million years—the Paleocene Methane Event (Katz et al., 1999), the late Oligocene Warming Event (Zachos et al., 2001; Barnosky and Carrasco, 2002), the mid-Miocene Climatic Optimum (Barnosky, 2001; Zachos et al., 2001), middle Pleistocene glacial-interglacial transitions (Raymo, 1997; Schneider and Root, 1998), the Pleistocene-Holocene glacial-interglacial transition (Schneider and Root, 1998), and the Medieval Warm Period (Hughes and Diaz, 1994; Campbell et al., 1998; Broecker, 2001)—define the high end of what is normal for per-hundred-year rates of global warming. Rates of change measured since 1950 do not exceed the bounds of normalcy, although, as in past global warming events, they help define the high end of normal. However, if any but the lowest predictions for the anticipated temperature rise by 2100 come to pass, the rate of change would exceed any rates of change known for the past 65 million years. If the highest projections are borne out, the rate of change would be dramatic.

In view of this fact, the faunal dynamics that characterize Porcupine Cave climatic transitions probably typify how ecosystems respond to climatic warming episodes that are at the high end of "natural" warming rates, but nevertheless do not exceed the range of rates that is normal for Earth. Thus the faunal responses to climate change that are detailed in the following chapters are probably among the most pronounced that might be expected in naturally varying systems. Therefore they may be useful as an ecological baseline against which future changes can be measured. As global warming continues into the coming decades, changes in biodiversity and other faunal dynamics will undoubtedly occur—indeed are probably already occurring (Schneider and Root, 1998; Post et al., 1999; Pounds et al., 1999; Sæther et al., 2000; Both and Visser, 2001; McCarty, 2001). Faunal responses comparable to those defined by the Porcupine Cave data do not necessarily imply that the bounds of ecological health have been exceeded. However, faunal responses that exceed those demonstrated by the Porcupine Cave data may well herald the death of the canary—a shift in the state of ecosystems that is unprecedented.

Acknowledgments

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TWO

The Pleistocene Fossils of Porcupine Cave, Colorado

Spatial Distribution and Taphonomic Overview

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Porcupine Cave, arguably the richest source of information in the world on Irvingtonian-age vertebrates, sits in the Colorado Rocky Mountains at 2900 m (latitude 38°43′45″ N, longitude 105°51′41″ W, USGS Gribbles Park 7.5′ Quad) (figures 2.1, 2.2). Situated on the southwest rim of the highest large intermountain basin in North America, known as South Park, the cave is a three-tiered chamber comprising at least 600 m of passageways (figures 2.3–2.7). South Park itself lies nearly in the center of Colorado (figure 2.1) and hosts diverse biotic communities, some of which are unique in the lower 48 United States for their vegetational affinity to central Asia. Although humans have utilized various resources in South Park for centuries, the basin remains sparsely populated, with a wide variety of non-human-dominated landscapes still intact.

The entrance to Porcupine Cave overlooks a west-facing slope that is near the ecotone between *Festucca-Muhlenbergia* grassland, *Pinus-Pseudotsuga* needleleaf forest, and *Picea-Abies* needleleaf forest (Küchler, 1964). Vegetation outside the entrance consists of sparse stands of *Pinus ponderosa* (Ponderosa pine), *Pinus edulis* (pinyon pine), *Pseudotsuga menziesii* (Douglas-fir), and *Juniperus* (juniper) interspersed with *Artemisia* (sagebrush), *Chrysothamnus* (rabbitbrush), *Cercocarpus* (mountain mahogany), *Yucca* (Spanish bayonet or soapweed), *Coryphantha* (cactus), *Opuntia* (prickly pear), grasses, and other small herbaceous plants (Barnosky and Rasmussen, 1988:269). The existing entrance is through a mine adit. Before emplacement of the adit (most likely in the 1870s), animals would have had to enter the cave through various cracks and fissures that were probably intermittently open and closed.

Since 1985, when the first systematic paleontological excavations took place at the site, crews from the Carnegie Museum of Natural History, the Denver Museum of Nature and Science (previously called the Denver Museum of Natural History), and the University of California Museum of Paleontology have discovered new localities within Porcupine Cave nearly every year. Chapter 4 chronicles the excavation history. Fifteen years of field work at the cave have yielded at least 26 different fossil localities. These localities sample a wide variety of Quaternary and potentially latest Tertiary time periods, and to some extent varying taphonomic situations. This chapter documents the spatial distribution of the many different collecting localities and provides an overview of their suspected geological ages and general taphonomic settings. More details on geological age and correlation are provided in chapters 6 and 7 and in Bell and Barnosky (2000). Older publications on Porcupine Cave (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996) proposed a somewhat younger age for some of the strata than is now believed to be the case (see discussion of the Pit locality below).

Other important Irvingtonian vertebrate paleontological sites from the central Rocky Mountain region include the Hansen Bluff sequence in the San Luis Valley, Colorado (Rogers et al., 1985, 1992) and the SAM Cave deposits in north-central New Mexico (Rogers et al., 2000). These sites are of particular interest in yielding paleomagnetic, radiometric, palynological, and invertebrate paleontological data associated with the fossil vertebrates (Rogers et al., 1985, 1992, 2000; Rogers and Wang, 2002). Specimens of vertebrate fossils and numbers of species are sparse from Hansen Bluff (Rogers et al., 1985, 1992) and moderate in abundance at SAM Cave, with the latter including 2 species of amphibians, 3 of reptiles, approximately 10 of birds, and approximately 30 of mammals, distributed through 14 collecting localities (Rogers et al., 2000).

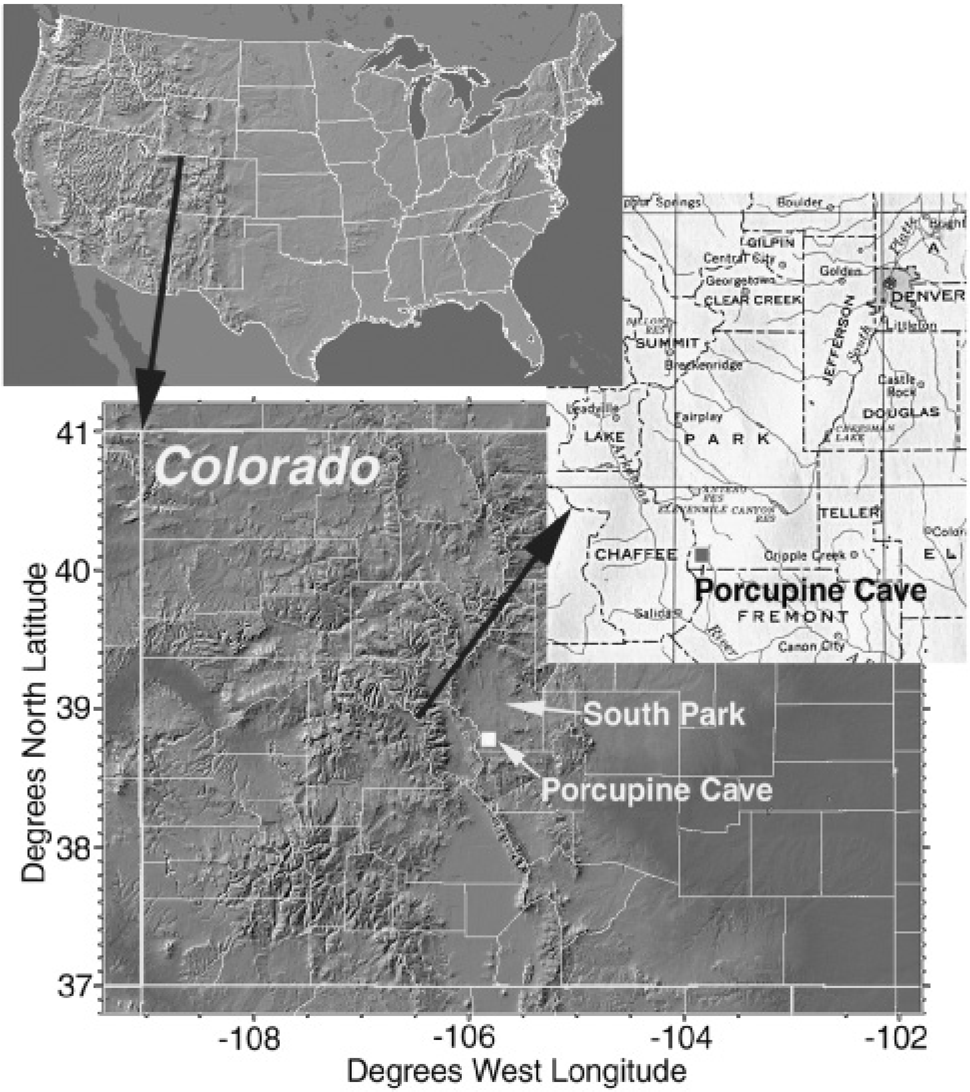


FIGURE 2.1 Location of Porcupine Cave.

Spatial Distribution of Localities

The earliest map of Porcupine Cave was published by Parris (1973). During the course of exploration for fossils, new passageways were discovered in the late 1980s and 1990s, and accordingly renewed mapping efforts were undertaken by members of the Colorado Grotto and Front Range Grotto of the National Speleological Society. The updated map produced for this book (figure 2.3) was surveyed and drafted by teams led by Hazel Barton, Kirk Branson, and Don Rasmussen, and it shows the location of the major fossil localities discovered as of 2000 that are mentioned in this book. In some cases different institutions excavated at the same locality and each institution assigned its own locality number. Table 2.1 presents the resulting synonymies (i.e., the same locality represented by two or more different numbers), keys the names of the various localities to figure 2.3, and summarizes the geological age interpreted for each locality.

General Taphonomic Setting

Hundreds of thousands of vertebrate fossils have been recovered from Porcupine Cave, with identifiable, curated specimens numbering in the thousands from such single localities as the Pit and Velvet Room (DMNH 644). Why were so many bones preserved?

Accumulation of Bones

At least three vectors of bone accumulation seemed to have been active when the cave was open in the early and middle Pleistocene. The most important of these was probably the propensity of wood rats (*Neotoma* spp.) to collect random items to incorporate into their middens (Betancourt et al., 1990). Collected items include carnivoran fecal pellets and raptor regurgitation pellets, which are frequently laden with the bones of small vertebrates (especially mammals) that the

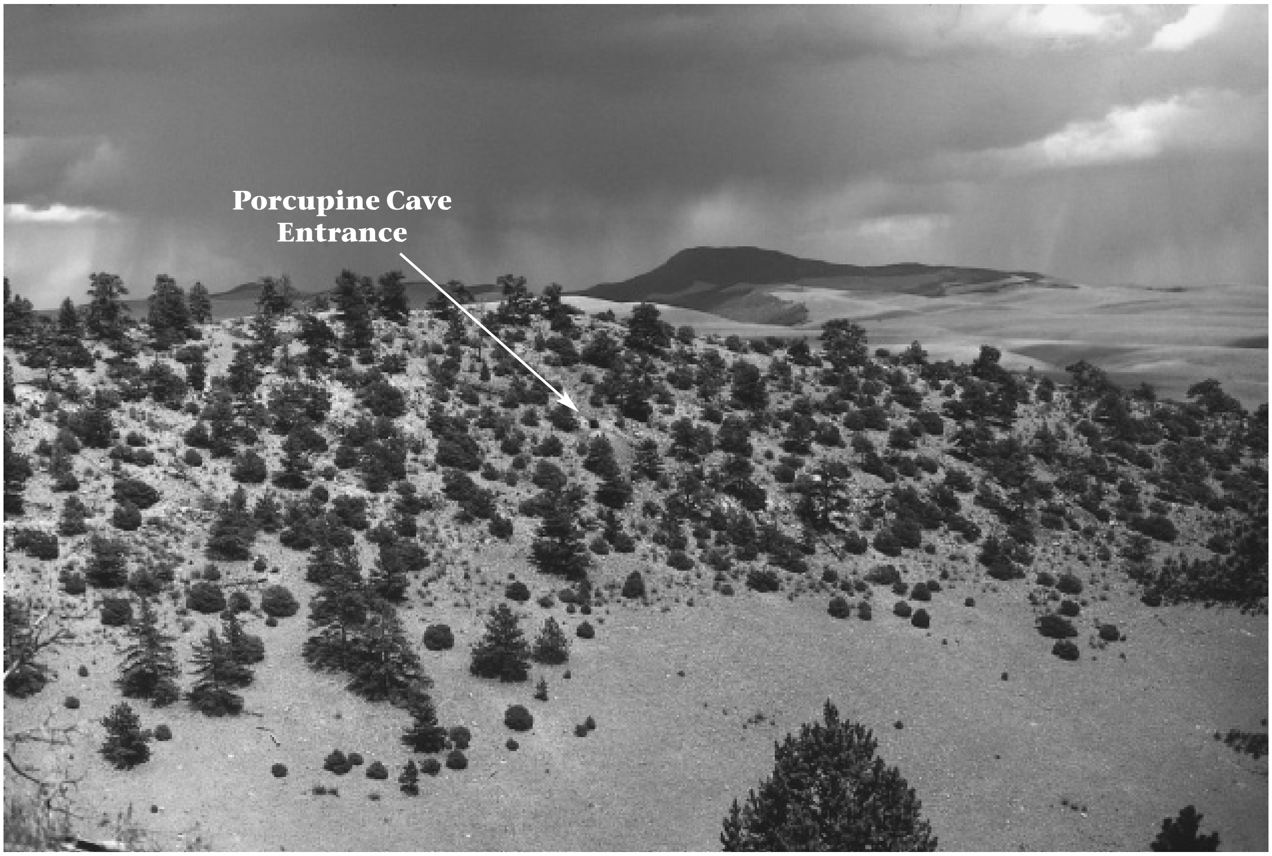


FIGURE 2.2 View of landscape around the cave entrance as of 1986. The view is looking east, with Black Mountain in the distance.

predators ate. Wood rats also dragged isolated bones of large mammals into their midden sites, including bones as large as deer humeri or jaws, horse teeth, and podial elements of horse and elk-sized perissodactyls and artiodactyls. During excavation of Porcupine Cave by CM crews in the 1985–89 field seasons, bushy-tailed wood rats *(Neotoma cinerea)* were observed as far back into the cave as the Pit, and fecal pellets, active nests and middens, and urine deposits (termed "amberat" by some authors) were observed in localities throughout the cave. Active or recently active middens within the cave contained diverse plant remains (e.g., sticks, twigs, seeds), teeth of cows, raptor pellets and carnivoran scat (probably coyote), and in one case a dead wood rat. In fact, all of these items were contained in a single nest approximately 15 m inside the cave.

Direct evidence that this activity went on for decades includes the recovery of a tobacco can with a note dated to 1939 from an active wood rat nest in the Velvet Room when the room was first opened to humans in 1986; the can had been dragged in by wood rats from the cave entrance (see chapter 4). A radiocarbon date of 2180 ± 80 yr BP obtained on a *Neotoma* midden (the Trailside Nest) about 100 m north of the mine adit (at the site known as Trailside Entrance) confirms that wood rats have actively collected in the area for at least millennia (Barnosky and Rasmussen, 1988).

Evidence that wood rat activities contributed to rich accumulations of bone throughout the cave during the early and middle Pleistocene includes the following:

1. Abundant fossils, purportedly of at least five different species of *Neotoma,* including *N. cinerea,* are present in most of the excavated deposits in the cave.
2. Within Velvet Room strata excavated by CM were fossilized middens, characterized by moderately indurated, tannish white layers that feature abundant casts of the shape and size of *Neotoma* fecal pellets (figure 2.8).
3. Many of the larger bones bear paired incisor gnaw marks of a size appropriate to *Neotoma.*
4. The vast majority of the fossil bones are of a size that is appropriate for wood rats to incorporate into their middens.
5. Most of the fossils are of small mammals, with overrepresentation of teeth, skulls with broken crania, mandibles, and other elements resistant to digestion.

These characteristics, coupled with etching by stomach acids in some cases, imply that some bones passed through the digestive tracts of carnivorans and raptors and were contained in fecal or regurgitation pellets before being dragged into the cave. In situations in which rocky outcrops provide roosts for raptors and/or denning areas for mammalian carnivores within the foraging range of wood rats (as at Porcupine Cave), wood rat middens include many bone-laden pellets. Over time, much of the organic matter except bones decays, and the resulting deposits can be exceptionally rich in fossils (Hadly, 1999).

The second most important collection vector may have been the direct activity of mammalian carnivores either taking prey into the cave or dying there. This mode of collection applies especially to some of the few bones that are too large to have been dragged by wood rats. Fossils of bears, badgers and other mustelids, coyotes, and wolves have been found in Porcupine Cave. Pleistocene denning activity is suggested by the presence of dentitions of juvenile coyotes. Extant relatives of all these carnivores use caves as places to bring carcasses of small mammals or parts of large animals that they subsequently gnaw or eat. From 1985 to 1991 it was not uncommon to hear coyotes howling near the cave; signs of black bear activity (e.g., tracks, overturned rocks) were infrequently evident near the cave entrance; and 20 m inside the cave the nearly complete carcass of a recently killed and partially eaten rabbit was found in 1986. Thus extant mammalian carnivores clearly use the cave, and there is no reason to suspect that their extinct relatives did not also use it when adequate entrances were available.

Very rarely in Porcupine Cave are fossil animals much larger than rodents represented by bones of a substantial portion of the skeleton. An exception is a single cranium of the camel *Camelops,* which was recovered by DMNH crews from Tobacco Road (figure 2.3). Because of its size, the skull possibly represents an animal that either fell into the cave through an intermittently open sinkhole, wandered in and could not find its way out, or was dragged in as a partial carcass by a large carnivore such as a bear.

Preservation of Bones

Cave environments protect bones from decay because temperature fluctuations are slight, temperatures are relatively low (thus inhibiting bacterial activity), and caves frequently are formed in limestone, which keeps groundwater at pH values conducive to bone preservation. Porcupine Cave is no exception. The cave appears to have had entrances large enough for wood rats to enter during many periods between about 2 Ma and at least 300 Ka ago. Some openings sufficient for larger animals to pass through probably also existed intermittently. During times of open entrances the bones accumulated. Then all entrances to the cave were apparently sealed between sometime in the Irvingtonian (based on the age of the youngest fossil bones) and the late 1800s, when miners opened an adit that intersected the Gypsum Room. Since that time, bones have once again begun to accumulate in the cave from the processes described previously, but these are easy to differentiate from the fossil bones because they are on the surface of the cave floor and look much fresher.

Implications for Ecological Interpretations

The collection vectors described earlier mean that the sample of Pleistocene bones represents animals that lived mostly within a 5- to 18-km radius of Porcupine Cave. Wood rats generally collect within 50 m of their nest; raptors usually collect their prey within about 5 km of the sites where they regurgitate most of their pellets; and mammalian carnivores such as coyotes and badgers typically hunt within 5 km of their dens (Hadly, 1999). Porder et al. (2003) found that in Yellowstone Park, the bones from two deposits (Lamar Cave and Waterfall Locality) that are taphonomically similar to Porcupine Cave came from within an 8- to 18-km radius of the fossil accumulations.

The derivation of most of the fossil bones from raptor pellets and mammalian carnivore scats means that the sample represents primarily what the predators hunted. Typically the diets of predators such as coyotes, hawks, and owls reflect those small mammals and birds that are abundant on the landscape; that is, they eat what is out there, rather than selectively looking for a certain species. This situation results in a correlation between rank order abundance of small mammal species identified in the pellets and scats and rank order abundance of species in the living community, especially if the predators included a range of both diurnal and nocturnal hunters (Hadly, 1999). The range of mammalian predators that ultimately collected most of the Porcupine Cave specimens potentially included fishers, weasels, ermines, black-footed ferrets, minks, wolverines, badgers, skunks, coyotes, wolves, foxes, bears, bobcats, and cheetahs. Raptors and other avian predators or scavengers potentially included golden eagles, hawks, ravens, falcons, kestrels, great horned owls, and snowy owls. Fidelity between fossil assemblages and the communities they sample has been demonstrated in situations taphonomically similar to Porcupine Cave (Hadly, 1999; Porder et al., 2003). Observations of the modern fauna around the cave confirm that there is gross correspondence in rank order abundance of kinds of species that characterize the region today and those represented in the fossil deposits. For example, the most commonly sighted small mammals are *Spermophilus* spp. (ground squirrels), and individuals of that genus are most common as fossils. Voles likewise occur in high abundance in the modern environment and in the fossil deposits.

Time averaging, or the degree to which a given locality lumps together animals that lived at widely different times (up to thousands of years, for example), is notoriously difficult to assess in cave deposits (Graham, 1993; Gillieson, 1996). In late Holocene deposits that are somewhat analogous to those of the Pit locality in Porcupine Cave, stratigraphic levels averaging 10–30 cm were found to represent time spans from about 200 to 1000 years (Hadly, 1999; Hadly and Maurer, 2001). This degree of time averaging is probably a best-case

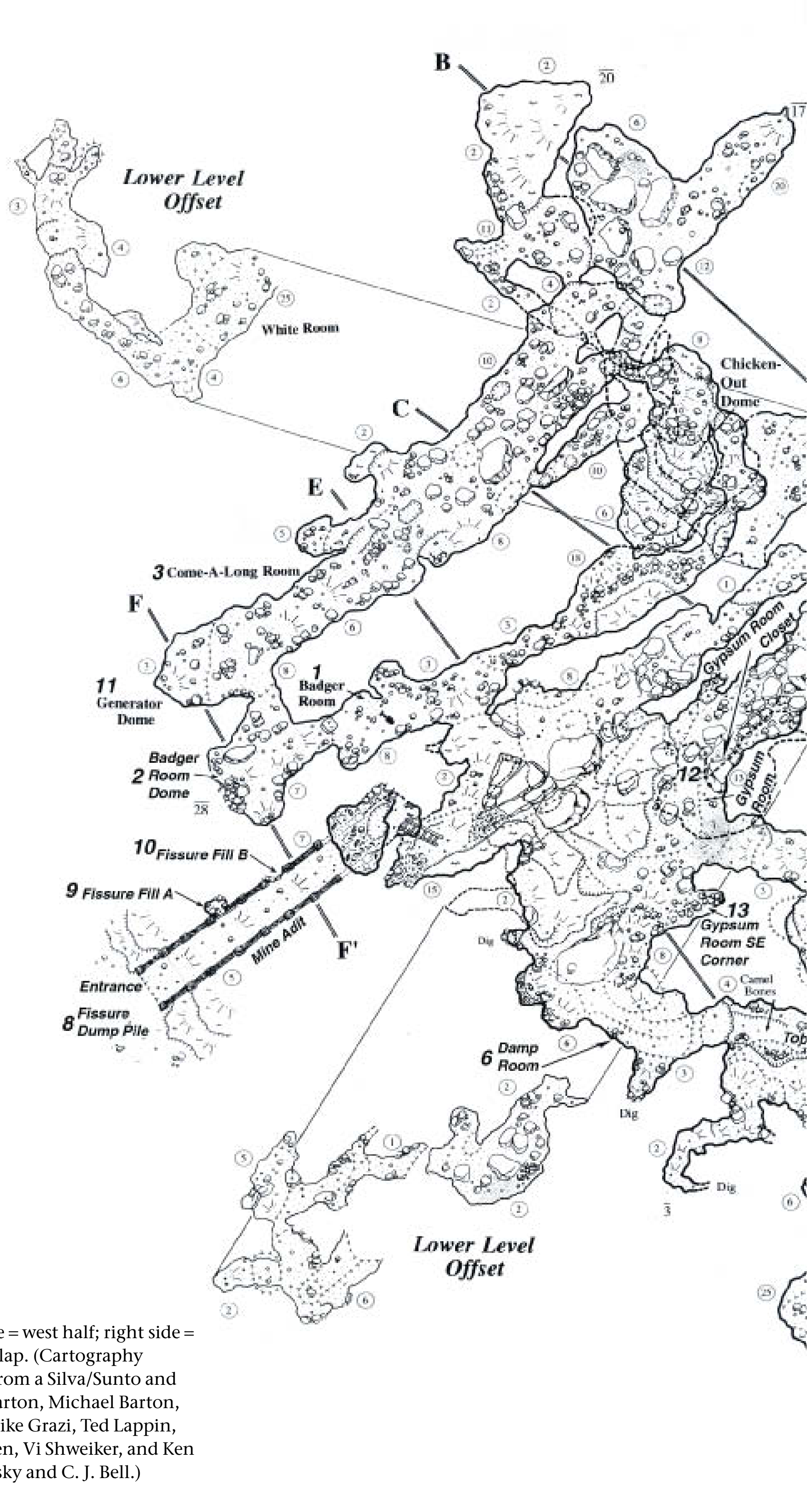
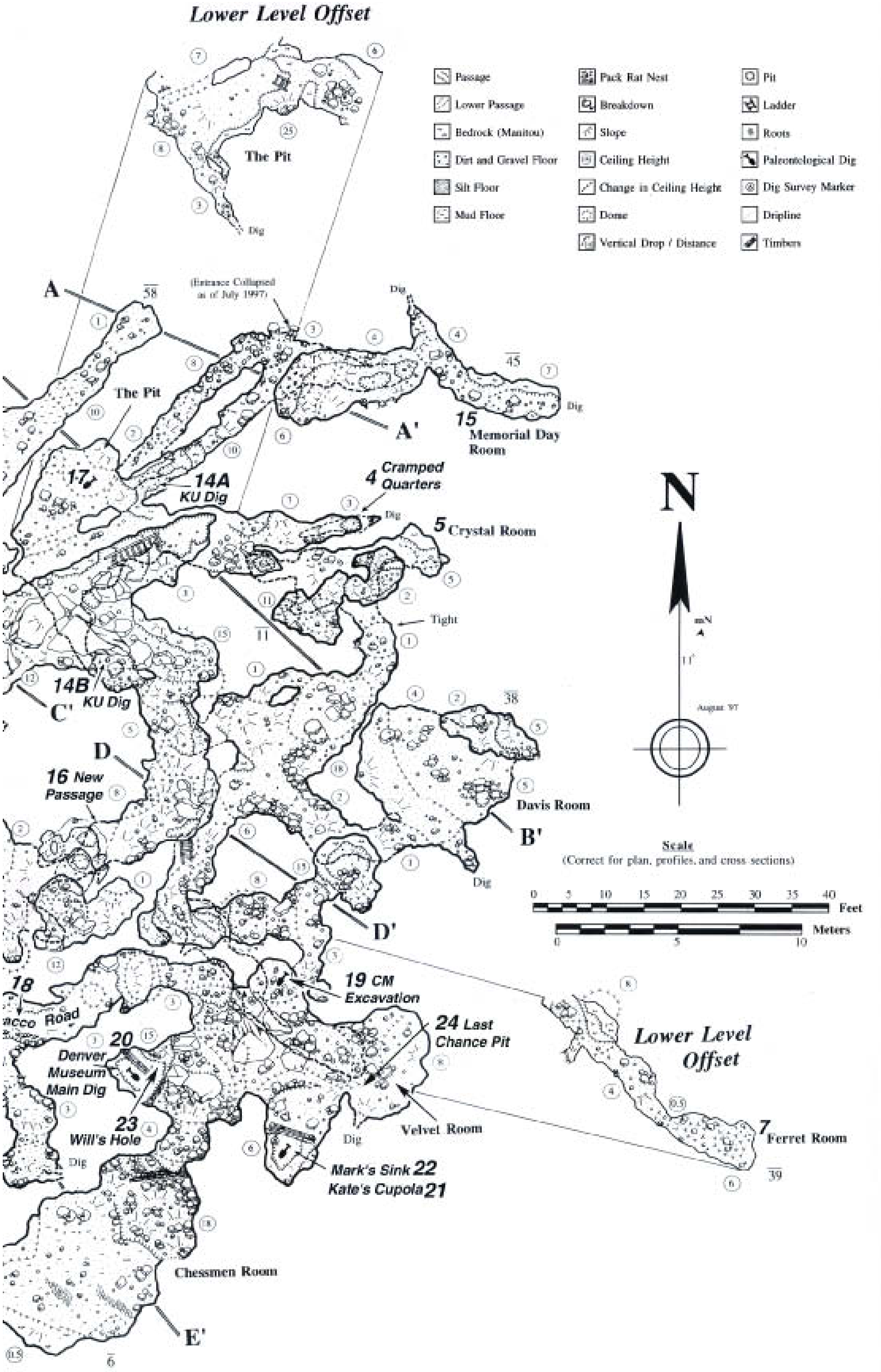


FIGURE 2.3 Map of Porcupine Cave. Left side = west half; right side = east half. Left side and right side slightly overlap. (Cartography [including figures 2.4–2.7] by Hazel Barton, from a Silva/Sunto and tape survey done by Evan Anderson, Hazel Barton, Michael Barton, Beth Branson, Kirk Branson, Greg Glazner, Mike Grazi, Ted Lappin, Fred Luiszer, Emma Rainforth, Don Rasmussen, Vi Shweiker, and Ken Tiner. Collecting sites labeled by A. D. Barnosky and C. J. Bell.)


Lower Level Offset
The Pit
Dig
Passage
Lower Passage
Bedrock (Manitou)
Dirt and Gravel Floor
Silt Floor
Mud Floor
Pack Rat Nest
Breakdown
Slope
Ceiling Height
Change in Ceiling Height
Dome
Vertical Drop / Distance
Pit
Ladder
Roots
Paleontological Dig
Dig Survey Marker
Dripline
Timbers
A
A'
(Entrance Collapsed as of July 1997)
The Pit
15 Memorial Day Room
17
14A KU Dig
4 Cramped Quarters
5 Crystal Room
Tight
14B KU Dig
C'
D
D'
16 New Passage
Davis Room
B'
N
mN
11°
August '97
Scale
(Correct for plan, profiles, and cross sections)
0 5 10 15 20 25 30 35 40 Feet
0 5 10 Meters
18 Tobacco Road
19 CM Excavation
20 Denver Museum Main Dig
24 Last Chance Pit
23 Will's Hole
Velvet Room
Mark's Sink 22
Kate's Cupola 21
Lower Level Offset
7 Ferret Room
Chessmen Room
E'

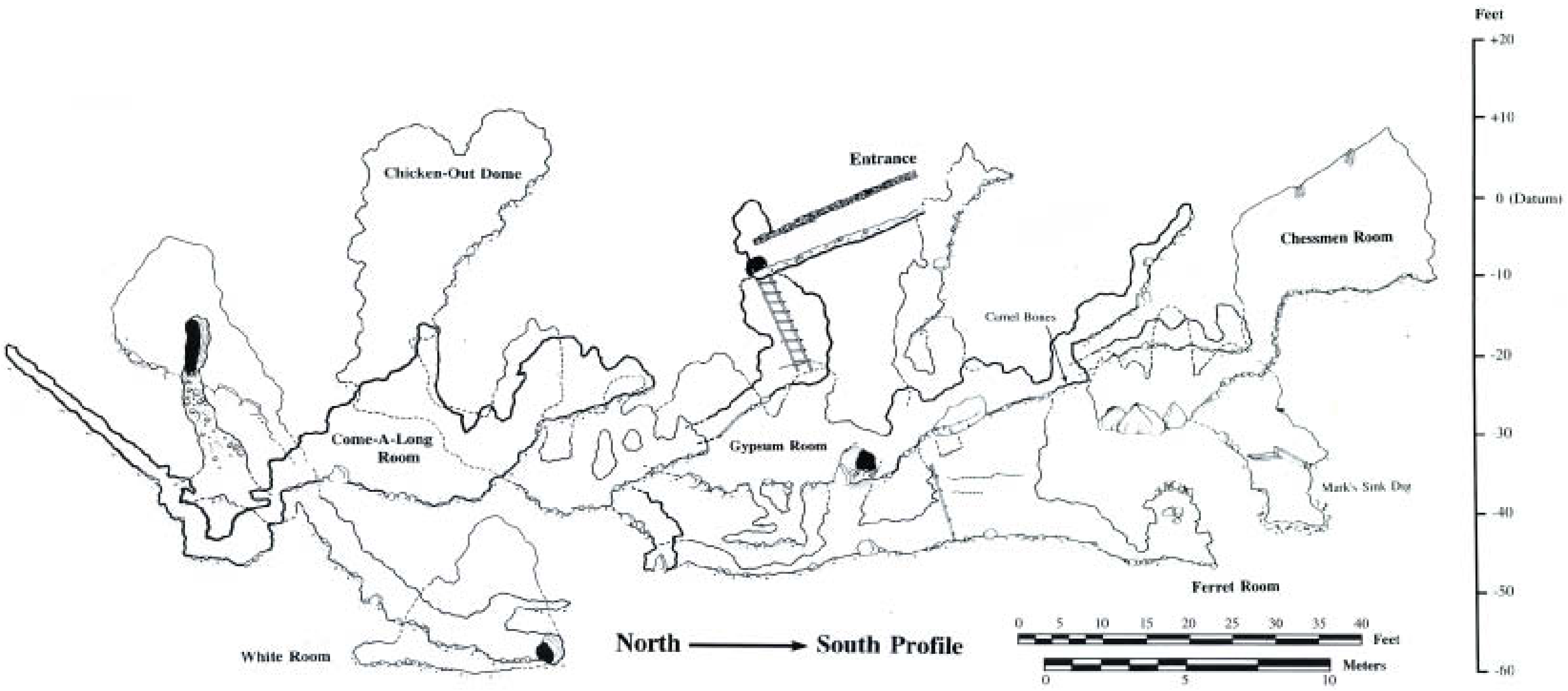


FIGURE 2.4 North to south profile through Porcupine Cave. The profile runs from north of Chicken-Out Dome in the upper portion of the left side of figure 2.3 through the Chessmen Room at the bottom of the right side of figure 2.3.

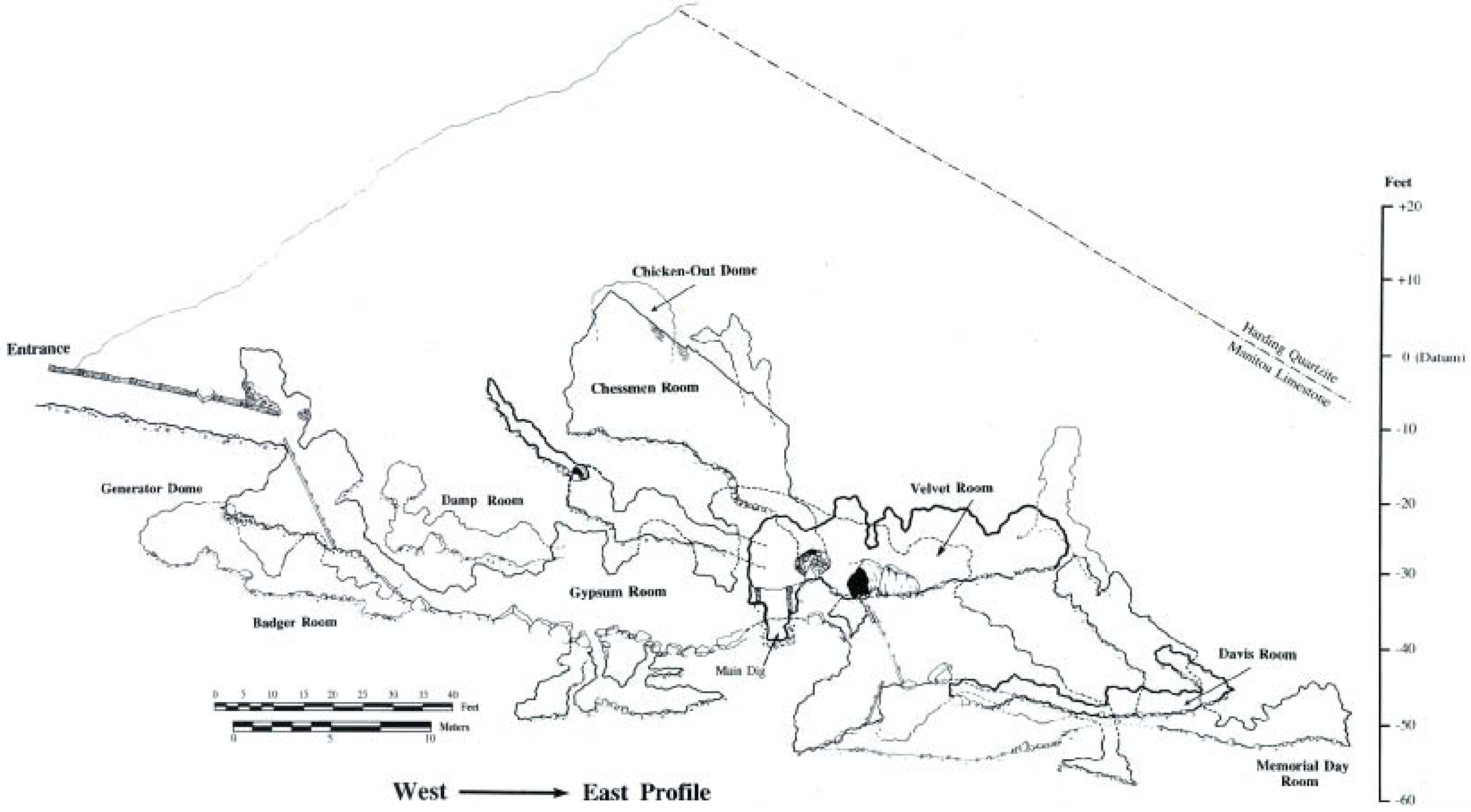


FIGURE 2.5 West to east profile through Porcupine Cave. The profile runs from the entrance adit on the left side of figure 2.3 through the Memorial Day Room on the right side of figure 2.3.

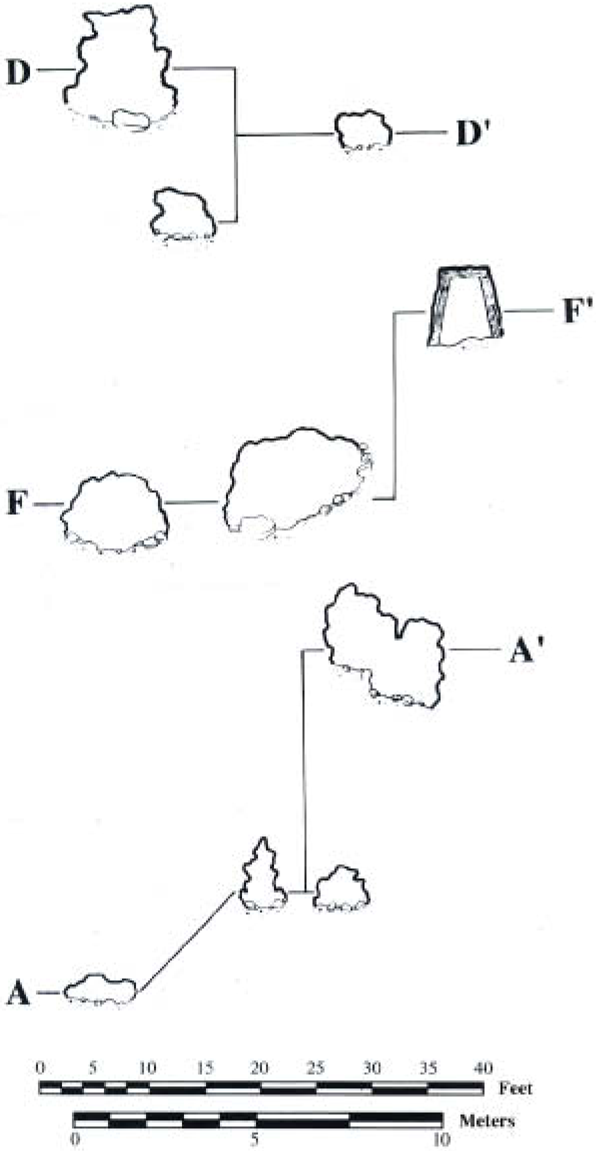


FIGURE 2.6 Detailed profiles through cross sections depicted in figure 2.3: A–A′, D–D′, and F–F′.

scenario for Porcupine Cave. The worst-case scenarios are situations like the Generator Dome locality in the vicinity of a back-dirt pile, in which middle Pleistocene fossils were recovered tens of centimeters below the surface alongside modern debris (e.g., a match), indicating mixing of strata by either animals or humans.

These clearly different amounts of time averaging in different localities, plus some differences in the degree to which the three collection vectors noted previously produced the bones in a given locality, preclude generalized interpretations of the "Porcupine Cave fauna." Instead, the approach taken in this book is to specify from which localities fossils came in the systematic descriptions of the included taxa, and to suggest ecological interpretations only for those localities for which we have adequate sampling, temporal control, and appropriate taphonomic history. We emphasize that subsequent treatments of these fossils must take into account the spatial and temporal provenance of the different localities. In fact, Porcupine Cave is not "a locality" in the Rocky Mountains; it is a cave that contains multiple, closely spaced, but temporally distinct localities.

Description of Localities

Most of the material described in this book was recovered from seven localities: the Badger Room, Fissure Fill A, the Gypsum Room, the Pit, and three spatially distinct excavations in the Velvet Room (Mark's Sink, DMNH 644, CM 1927 / UCMP V93175). Of these, the most closely studied have been the Pit and DMNH 644, because those localities contained stratified sequences composed of multiple stacked layers and yielded thousands of specimens. The Pit locality provides the main basis for interpreting the effects of middle Pleistocene environmental change on ecology and evolution. Material from the Badger Room has also been well studied and synthetically interpreted. Information from DMNH 644 is included inasmuch as is possible, but as of this writing the locality is still undergoing analysis, and complete results are not expected to be available for several more years. Fossils from other localities generally were analyzed only when a contributing author had a particular interest in them. Specimens from incompletely studied localities are reported in the systematic treatments, but they contribute less to the ecological and evolutionary interpretations that form the last third of this book. The sheer volume of material makes it impractical to provide a detailed study of all localities in this book. This fact, and the new discoveries that come to light each field season, inevitably mean that much new information remains to be reported by future generations of investigators.

Relevant information about each locality is presented in the following sections, with localities arranged alphabetically. Unless otherwise noted, specifics of the taphonomic situations are unknown. Most UCMP samples represent subsamples of material that was collected by CM crews.

Badger Room (Figure 2.3, Site 1)

LOCALITY NUMBERS

CM 1928, DMNH 942, UCMP V93176.

COLLECTION PROTOCOLS

Collections housed at the CM and UCMP are split samples of the same test excavations that took place primarily in 1985, 1986, and 1987. Initially fossils were collected from the surface. As the surface was depleted of fossils, trowels and trenching shovels were used to excavate a volume of approximately 0.5 m^3. Fossils were carefully removed as they were uncovered, but no data were recorded about depth below surface, given the nature of the deposits, which made such information meaningless in terms of time relationships. Because screen

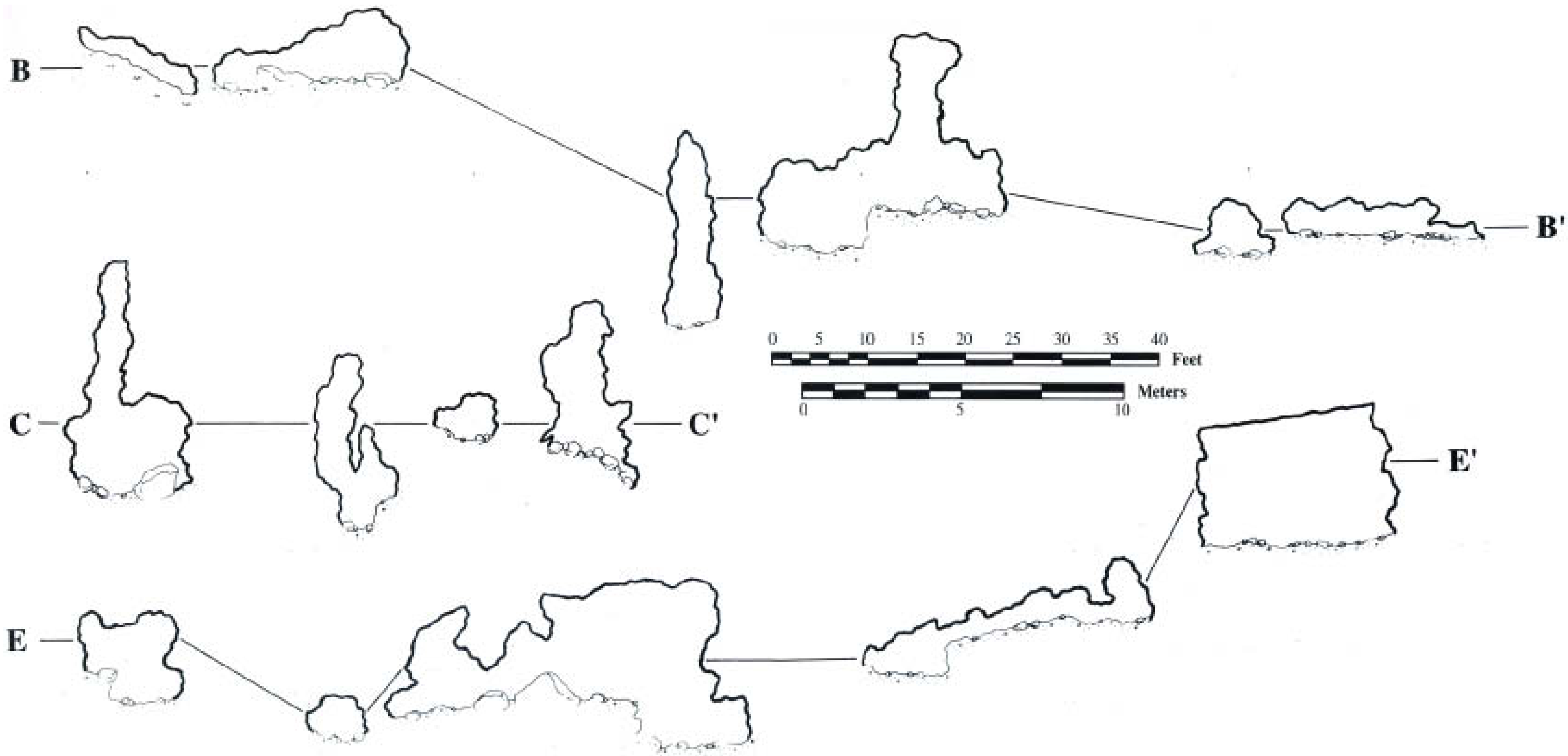


FIGURE 2.7 Detailed profiles through cross sections depicted in figure 2.3: B–B′, C–C′, and E–E′.

TABLE 2.1

Names and Locality Numbers of Major Vertebrate Fossil Sites of Porcupine Cave

Locality	*Designation in Figure 2.3*	*Synonymous Institutional Numbers*	*Comments and Approximate Age*
Badger Room	1	CM 1928 DMNH 942 UCMP V93176	Biostratigraphically correlative with levels 4–8 in the Pit; probably between 780 Ka and 1 Ma old.
Badger Room Dome	2	DMNH 1351	Unknown. Probably Irvingtonian.
Come-A-Long Room	3	DMNH 1353	Unknown. Probably Irvingtonian.
Cramped Quarters	4	CM 2202 DMNH 1346	Unknown. Probably Irvingtonian.
Crystal Room	5	CM 2203 DMNH 1345 UCMP V94014	Unknown. Probably Irvingtonian.
Damp Room	6	CM 1929 UCMP V93178	Unknown. Probably Irvingtonian.
Ferret Room	7	CM 1930 DMNH 1342 UCMP V93179	Unknown. Probably Irvingtonian.
Fissure Dump Pile	8	DMNH 1348	Mixed. Contains specimens of potential Blancan age as well as Irvingtonian.
Fissure Fill A	9	CM 2200 DMNH 1344 UCMP V98022	At least as old as levels 4 and older in the Pit; possibly older.
Fissure Fill B	10	CM 2201	Unknown. Probably Irvingtonian, possibly a Blancan component.
Generator Dome	11	DMNH 1347	Mixed. Contains fossils indicating correlation with older Pit levels alongside a modern match.
Gypsum Room	12	CM 1926 KU CO-121 UCMP V93174	Unknown. Probably Irvingtonian.
Gypsum Room SE Corner	13	DMNH 1343	Unknown. Probably Irvingtonian.
KU Dig 3	14A	KU CO-122	Unknown. Probably Irvingtonian.
KU Dig 1	14B	KU CO-123	Unknown. Probably Irvingtonian.
Memorial Day Room	15	DMNH 1352	Unknown. Probably Irvingtonian.
New Passage	16	CM 1931 UCMP V93177	Unknown. Probably Irvingtonian.
Pit	17	CM 1925 DMNH 2081 UCMP V93173	Fourteen stratigraphic levels are recognizable and dated primarily by biostratigraphy, with accessory information from magnetostratigraphy. Levels 1–3 (1 being the top) are thought to date near 800 Ka, but are potentially as young as 250 Ka. Levels 4–12 probably date to somewhere between 780 and 950 Ka. Level 14 is probably younger than 1 Ma.
Tobacco Road (=DMNH Camel Locality)	18	DMNH 1929	Unknown. Probably Irvingtonian.
Trailside Entrance (=Trailside Cave)	Not shown in figure 2.3. Occurs on trail about 100 m north of adit entrance.	CM 3602	Unknown. An amberat-stained wood rat midden (Trailside Nest) was dated to 2180 ± 80 yr. Reddish sediments from the floor yield a *Camelops* (camel) metapoidal and may be Irvingtonian.

TABLE 2.1 (continued)

Locality	*Designation in Figure 2.3*	*Synonymous Institutional Numbers*	*Comments and Approximate Age*
Velvet Room, CM Excavation	19	CM 1927 UCMP V93175	Seven stratigraphic levels are recognized. Biostratigraphically and sedimentologically, these seem no older than Pit levels 1–4 and may be in part younger than any Pit level. Detailed studies are needed to confirm this.
Velvet Room, DMNH Excavation	20	DMNH 644	Eighteen stratigraphic horizons (A at top, R at bottom). Biostratigraphically and sedimentologically horizons A–C appear younger than 780 Ka. Paleomagnetic data suggest a reversal in level D. Therefore, levels D–M may date to between 780 Ka and 1 Ma.
Velvet Room, Kate's (=Katie's) Cupola	21	DMNH 1349	Mixed. Probably Irvingtonian, possibly a Blancan component.
Velvet Room, Last Chance Pit	24	DMNH 2433	Unknown. Material still under analysis.
Velvet Room, Mark's Sink	22	DMNH 1349	Mixed. Most material probably Irvingtonian; fauna strongly suggests a Blancan component is also present.
Velvet Room, Will's Hole	23	DMNH 1350	Unknown.
Porcupine Cave, undifferentiated	—	CM 1932 DMNH 1354 UCMP V97002	Unknown. Probably Irvingtonian.

NOTE: Supporting evidence for geological ages is presented by the references cited in the text.

washing was not systematically employed, small specimens are probably underrepresented in the CM and UCMP collections. Material housed at the DMNH was collected by DMNH crews using similar techniques, plus screen washing, during field seasons between 1987 and 2000. DMNH extracted less than 1 m^3 of fossiliferous sediment (D. Rasmussen, pers. comm., 2001).

TAPHONOMY

Mammalian carnivores may have used this locality as a den site and dragged in some of the bones, as indicated by gnaw marks on some specimens, fairly abundant representation of badger and coyote specimens (including at least one juvenile coyote), and the abundance of rabbit bones (Anderson, 1996). However, many of the rabbit limb bones are unbroken and show no evidence of gnawing, which led Shabel et al. (chapter 22) to suggest that undevoured carcasses were left in the cave by carnivores. Abundant jaws of rodents (ranging in size from marmots to voles) and other similarly sized specimens indicate that at least some of the fossils derive from carnivore fecal material or raptor pellets, many of which may have been dragged in by wood rats.

Badger Room Dome (Figure 2.3, Site 2)

LOCALITY NUMBER

DMNH 1351.

COLLECTION PROTOCOLS

This material represents a surface collection intermixed with an ancient roof fall that collapsed and sealed a previous entrance to the cave. Some of the large rocks and sediment fell into the Badger Room.

Come-A-Long Room (Figure 2.3, Site 3)

LOCALITY NUMBER

DMNH 1353.

COLLECTION PROTOCOLS

Material was picked up from the surface only; no excavation was conducted.

Cramped Quarters (Figure 2.3, Site 4)

LOCALITY NUMBERS

CM 2202, DMNH 1346.

COLLECTION PROTOCOLS

Material from Cramped Quarters was generated as a bulk sample by cavers seeking a passage to another room. The sediments through which they dug and from which the fossils were derived appeared to have been bioturbated and otherwise mixed prior to excavation of the passage.

Crystal Room (Figure 2.3, Site 5)

LOCALITY NUMBERS

CM 2203, DMNH 1345, UCMP V94014.

COLLECTION PROTOCOLS

Fossils were picked up from the surface with no systematic excavation. The fossils and deposits may be to some extent eroded from other sites. The deposit contains clay nodules resembling those found in the Pit.

Damp Room (Figure 2.3, Site 6)

LOCALITY NUMBERS

CM 1929, UCMP V93178.

COLLECTION PROTOCOLS

Fossils from the Damp Room were recovered when sediments were excavated with shovels to clear a passage into Tobacco Road. No stratigraphic context is available.

Ferret Room (Figure 2.3, Site 7)

LOCALITY NUMBERS

CM 1930, DMNH 1342, UCMP V93179.

COLLECTION PROTOCOLS

Material curated at CM and UCMP was collected only from the surface. The DMNH material came from a test pit near the cave wall and therefore includes fossils from deeper below the surface as well as surface material. Depth below surface was not recorded, but was probably less than 30 cm (D. Rasmussen, pers. comm., 2001).

Fissure Dump Pile (Figure 2.3, Site 8)

LOCALITY NUMBER

DMNH 1348.

COLLECTION PROTOCOLS

The Fissure Dump Pile is the material that was excavated from the adit that miners sank into the hillside in the late 1800s. It occurs just outside and down the slope from the cave entrance. Fossils from here lack any stratigraphic or provenance data other than probably being from the vicinity of the present-day mine adit.

Fissure Fill A (Figure 2.3, Site 9)

LOCALITY NUMBERS

CM 2200, DMNH 1344, UCMP V98022.

COLLECTION PROTOCOLS

This locality was a highly fossiliferous lens located on the north wall of the mine adit approximately 4–6 m from the entrance. CM crews collected with trenching shovels 20 bags of sediment, each with a volume of about 2000 cm^3. Sediments were washed with a hose through stacked screens of 2, 4, 8, 16, 20, and 30 squares/2.54 cm (1 in.). Bones were picked off the coarsest two meshes in the field; the rest was brought back to the lab for picking. The matrix was generally picked without the aid of magnification. Large bones (e.g., horse) were removed from the sample as they were spotted during excavation. A split of the material of which this sample is composed is housed at UCMP and CM. Details of the DMNH collection protocol are available from DMNH.

TAPHONOMY

The taphonomy of the site has not been studied in detail. However, the physical setting is near the top of the current hill, with bones derived from a vertically oriented, unstratified, poorly sorted lens composed of a jumble of sediment and rocks with diameters ranging from less than 1 cm to more than 20 cm in diameter. The preponderance of small bones and fragments coupled with the abundance of bone in the sediment (this is one of the richest localities in the cave) suggests that raptor pellets and carnivore scat played major roles in the accumulation. These features are reminiscent of such fissure fill deposits as New Paris No. 4, Pennsylvania (Guilday et al., 1964) and Strait Canyon Fissure, Virginia (Barnosky, 1993), and they suggest that the bones accumulated in a vertical crack in the dolomite that extended to the surface.

Fissure Fill B (Figure 2.3, Site 10)

LOCALITY NUMBER

CM 2201.

COLLECTION PROTOCOLS

Fissure Fill B occurs at the back of the adit (i.e., farther in than Fissure Fill A). Material was sampled in the same way as described for Fissure Fill A, although much less volume of Fissure Fill B was sampled because it was less rich in bone. Sediments similar to those described for Fissure Fill A are evident at and above Fissure Fill B (i.e., in the roof of the adit heading toward the surface).

Generator Dome (Figure 2.3, Site 11)

LOCALITY NUMBER

DMNH 1347.

COLLECTION PROTOCOLS

Fossils were collected from the surface and from a narrow test trench approximately 30 cm deep. Apparent stratification suggested that the samples from the trench could be broken into an upper layer (upper 15 cm) and a lower layer (lower 15 cm). However, near the base of the deposits a modern match was discovered, suggesting complex bioturbation. Therefore Generator Dome is not considered to be a reliably stratified locality, and it is treated here as a bulk sample from a mixed deposit. It is not clear, however, whether the match was in fact found at the base of a “dump” pile from the main excavation in this room, in which case the two layers may be distinct (D. Rasmussen, pers. comm., 2001).

Gypsum Room (Figure 2.3, Site 12)

LOCALITY NUMBERS

CM 1926, KU CO-121, UCMP V93174. There is no DMNH number assigned other than that noted for Gypsum Room SE Corner.

COLLECTION PROTOCOLS

Most fossils were collected from the surface. In 1988 CM crews established a 1 × 1-m test excavation in the southwest corner of the room, which was approximately 0.9 m deep and consisted of four stratigraphic levels. Sediment from each level was wet screened as described for Fissure Fill A. Level designations appear on the field tags for this test excavation. Other material from the Gypsum Room was collected from the surface up to about 10 cm below the surface by CM crews between 1986 and 1989; these specimens have no indication of level designations on the field tags. Crews from DMNH also collected from the surface, and a KU team collected material from the Gypsum Room at a location they referred to as the “Gypsum Room Closet” (as located on figure 2.3), marked “KU#2” on the KU field map (=KU CO-121).

Gypsum Room SE Corner (Figure 2.3, Site 13)

LOCALITY NUMBER

DMNH 1343.

COLLECTION PROTOCOLS

This collection was made by DMNH crews led by Don Rasmussen in the southeast corner of the Gypsum Room. The deposit appeared to be an ancient wood rat midden against the wall. Approximately 0.8 m^3 of sediment was removed and screened on the spot and only visible bones were saved. The matrix contained abundant rocks and no stratification.

TAPHONOMY

Wood rats may have collected many of the bones, but the taphonomy is not well studied.

KU Dig 3 (Figure 2.3, Site 14A)

LOCALITY NUMBER

KU CO-122.

COLLECTION PROTOCOLS

KU crews made a small collection adjacent to and slightly northeast of the CM Pit dig. More detailed information was not recorded, although it is likely that the material is stratigraphically equivalent to the uppermost three levels of the Carnegie Pit excavation (see subsequent locality description).

KU Dig 1 (Figure 2.3, Site 14B)

LOCALITY NUMBER

KU CO-123.

COLLECTION PROTOCOLS

KU crews made a small collection located about midway between the Pit and New Passage. The depth was less than 50 cm and deposits were not well stratified. More detailed information was not recorded.

Memorial Day Room (Figure 2.3, Site 15)

LOCALITY NUMBER

DMNH 1352.

COLLECTION PROTOCOLS

Bones were collected from the surface only on the day the room was discovered.

New Passage (Figure 2.3, Site 16)

LOCALITY NUMBERS

CM 1931, UCMP V93177.

COLLECTION PROTOCOLS

Specimens were discovered as a new passage was dug east of the Gypsum Room. Stratigraphic context is lacking.

Pit (Figure 2.3, Site 17)

LOCALITY NUMBERS

CM 1925, DMNH 2081, UCMP V93173.

COLLECTION PROTOCOLS

The main Pit excavation (figure 2.3, site 17) was conducted by CM crews from 1985 through 1988. The excavation was approximately 2 × 2 m wide and 2 m deep. Horizontal control was maintained by laying out a grid composed of eight adjacent 0.90-m squares. Six of these squares were excavated and featured 14 stratigraphic levels defined by natural sedimentological breaks, or arbitrary 10-cm thicknesses, whichever was thinner. Stratigraphic levels were traced across excavation squares. Bones were collected as sediment was excavated with a trowel, and all sediment was bagged, hauled out of the cave, and screen washed and picked as described by Barnosky and Rasmussen (1988). Levels 1–3 were dry screened because they were unconsolidated, but lower levels were soaked overnight in a nearby stream and then wet screened. All screening procedures utilized a nested set of screens that successively dropped in mesh size from 4 to 8 to 16 to 20 to 30 squares/2.54 cm. The 30-mesh matrix was not utilized but is stored at UCMP. Bell and Barnosky (2000) provided summary descriptions of lithologic units and other excavation details. The top 10 levels were very fossiliferous, but relatively few fossils occurred below level 10. The CM and UCMP materials represent splits of this CM excavation.

DMNH personnel also collected specimens from the Pit beginning in 1986. For the most part these were not from the CM Pit excavation per se, but from near the surface in the vicinity of the CM excavation, especially beneath and to the south of the wall that separates the Pit into northern and southern compartments. (The Carnegie excavation was in the northern compartment.)

TAPHONOMY

The quantity of bones, dominance of taxa commonly hunted by raptors and small mammalian carnivores, dominance of skeletal elements and breakage patterns characteristic of bones in pellets and scats, small size of most bones, casts of rodent fecal pellets or desiccated rodent fecal pellets similar to wood rat feces, and abundant fossil wood rat specimens all suggest that the deposit represents a wood rat midden that was intermittently active for hundreds of thousands of years.

Tobacco Road (=DMNH Camel Locality) (Figure 2.3, Site 18)

LOCALITY NUMBER

DMNH 1929.

COLLECTION PROTOCOLS

Bones were discovered when dirt was removed with shovels to widen the passageway from the Damp Room into the Velvet Room. Detailed stratigraphic data are lacking.

Trailside Entrance (=Trailside Cave) (Not Shown in Figure 2.3)

LOCALITY NUMBER

CM 3602.

COLLECTION PROTOCOLS

This site is a crevice in the cliff located approximately 100 m north of the mine adit that now forms the entrance to the cave. The geometry of the cliff face relative to the cave suggests that this crevice at some time may have opened into the cave. It contains an amberat-stained wood rat midden, the Trailside Nest, that yielded the radiocarbon date reported in Barnosky and Rasmussen (1988) and noted in table 2.1. In June 1989, Don Rasmussen excavated at the north base of the crevice. Beneath sticks and wood rat scat, a black layer of dirt was found, then a whitish layer, and below that a consolidated reddish layer. From the reddish layer came a camel metapodial (CMNH 75512) and several rodent bones.

Velvet Room: General Comments

As of this writing, at least six distinct collecting localities have been recorded in the Velvet Room. Each of these is listed separately. It is imperative that future investigators clearly differentiate from which excavation the fossils of interest derive, because even within this relatively small room sediments of very different geological ages are represented. In some cases this task requires close attention to the specimen labels and cognizance of which institution collected the specimen in which year. For example, the general identifications on specimen labels for the CM Velvet Room excavation (CM 1927 / UCMP V93175) and the DMNH excavation (DMNH 644) both bear the main notation "Velvet Room"; it is only by looking at the details of the specimen labels that it becomes clear that very different excavations are represented, and that they should not be lumped together.

Velvet Room, CM Excavation (Figure 2.3, Site 19)

LOCALITY NUMBERS

CM 1927, UCMP V93175.

COLLECTION PROTOCOLS

CM crews excavated five adjacent squares, each approximately 0.90 cm on a side and numbered 1–5, abutting the northernmost wall of the Velvet Room (see excavation map in Barnosky and Rasmussen, 1988). Also included was sediment extending from the east wall of the CM squares to beneath the east wall of the alcove in which the excavation was located (this material is labeled “grid 3/4 extension”). Seven stratigraphic levels discernible by natural stratigraphic breaks were removed in 1986 and 1987, before bedrock was encountered approximately 65 cm below the surface. From top to bottom the levels are CM VR levels 1A, 1B, 2A, 2B, 2C, 3 (=3A on field labels), and 4 (=3B on field labels). Details of lithology were reported in Barnosky and Rasmussen (1988). Levels are traceable laterally across the excavated squares. Sediment was scraped with trowels into bags, and fossils were removed as they were uncovered. The bagged sediment was then dry screened (mesh sizes 4, 8, and 16 squares/2.54 cm), and fossils were picked using techniques detailed by Barnosky and Rasmussen (1988).

TAPHONOMY

Abundant dried fecal pellets of rodents; whitish, powdery sediment that bears the casts of rodent fecal pellets (figure 2.8); and all of the features of fossil bones noted for the Pit indicate that the CM excavation samples an ancient wood rat midden.

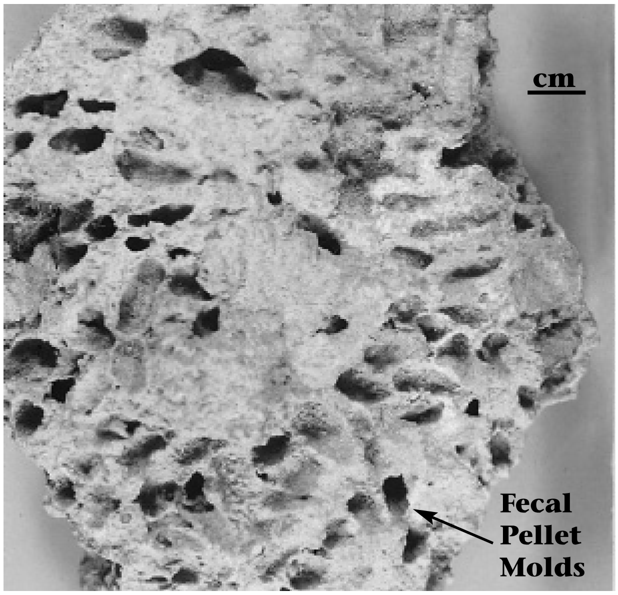


FIGURE 2.8 Portion of a fossilized *Neotoma* midden recovered from middle Pleistocene strata in the CM Velvet Room excavation.

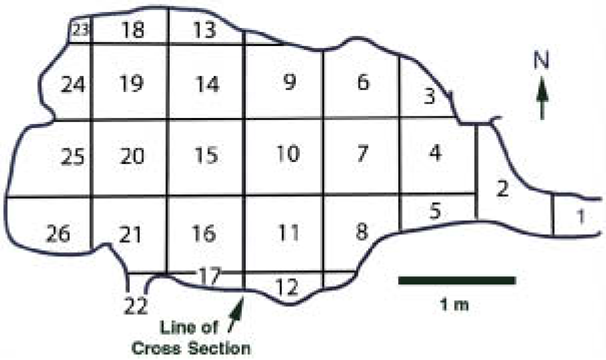


FIGURE 2.9 Plan view of excavation grids for DMNH 644, Velvet Room. The “Line of Cross Section” shows the location of the vertical profile drawn in figure 2.10. (Drawn by D. Rasmussen.)

Velvet Room, DMNH 644 (=Denver Museum Main Dig) (Figure 2.3, Site 20)

LOCALITY NUMBER

DMNH 644.

COLLECTION PROTOCOLS

Beginning in 1992 DMNH crews opened a stratigraphically controlled excavation along the westernmost wall of the Velvet Room. Excavation continued through the 1997 field season, ending when large boulders were encountered at the base of the site. Excavation was carried out by volunteers (most from the Western Interior Paleontological Society) under the direction of Don Rasmussen, Robert Raynolds, and Lou Taylor.

The DMNH excavation was spatially controlled by referencing specimens within 26 grids (grids = squares in this usage), each approximately 0.6 m (2 ft) on a side (figure 2.9). Each grid was excavated in arbitrary stratigraphic levels that were from about 5 to 10 cm (about 2–4 in.) thick. Levels did not always follow natural lithologic breaks, and because of the complex stratigraphy and slope of the deposit, these “microlevels” are not correlative from one grid to the next (for example, level 5 in grid 5 could be a different age than level 5 in grid 17). However, stratigraphic horizons ranging from 5 to 15 cm can be discerned based on lithologic features that are traceable across grids, and on that basis 18 horizons were defined, designated in alphabetical order from A at the top to R at the bottom (figure 2.10; table 2.2). Specimens were collected as the sediment was scraped into bags, and all bagged sediment was run through nested screens of 4, 8, and 16 squares/2.54 cm. The resulting fossiliferous matrix was taken to the DMNH for extraction of specimens by volunteers. Details about the DMNH excavation that will be pertinent to future analyses of the fossils were provided by RGR and LHT (pers. comm. to ADB, 2001):

> Prior to excavation, the surface of the site was delimited by an orthogonal 2-foot by 2-foot (~0.6 × 0.6-m) pattern of 26 grids

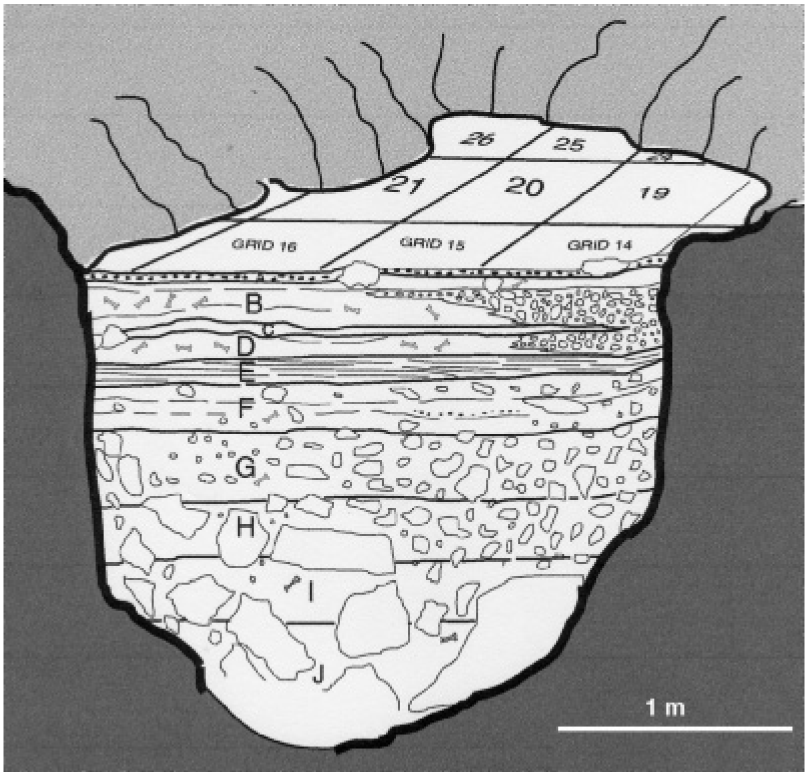


FIGURE 2.10 Profile of the east wall of grids 14, 15, and 16 in DMNH 644, Velvet Room. (Drawn by D. Rasmussen and R. Raynolds.)

[figure 2.9], and a master horizontal datum was established. The ground surface was covered by a veneer of modern wood rat droppings. Below the modern debris lay undisturbed Pleistocene strata, the upper strata of which were more fossiliferous and more clearly bedded than the lower strata. Below ~1 m angular rocks become more common and the strata less fossiliferous.

The grids were excavated from east to west. The earliest excavated grids (1–5) have modest data and were relatively thin [stratigraphically]. Subsequent grids were excavated to depths exceeding 3 m. Grids, or in some cases a pair of adjacent grids, were excavated in a series of numbered levels. Level 1 was at the top and excavation extended down to as far as level 33. While the digging was active, it was not practical to identify natural stratigraphic boundaries in the unconsolidated material; therefore levels were arbitrary, ranged in thickness from 5 to 10 cm, and were maintained with approximately horizontal floors (relative to datum) across grids. Natural stratigraphic divisions became evident as vertical faces were exposed [figure 2.10]. The digging was interrupted by periods of careful section measurement and documentation of stratal patterns visible on the vertical faces. Because the natural stratigraphic divisions slope relative to the horizontal floors of the arbitrary levels, the arbitrary levels are not coeval from grid to grid. Therefore the arbitrary numbered levels should only be used to recognize relative stratigraphic position within any given grid.

After digging ended, it was necessary to correlate the arbitrary levels across grids. Don Rasmussen and Robert Raynolds accomplished this by careful review of field notes, sketches, and figures. The numbered arbitrary levels were correlated into a series of lettered horizons with horizon A being the youngest and extending down to horizon R [table 2.2; figure 2.10]. In general 2 to 4 arbitrary (numbered) levels were grouped into each newly defined horizon [and identified] by a letter designation. In a few cases the horizon boundaries split numbered levels; in these cases the horizon is indicated to contain portions of both levels [table 2.2]. Horizons designated by letters average 14 cm in thickness. Horizon A is characterized by modern *Neotoma* (wood rat) pellets; Horizon C is distinctively gray in color; and Horizon E is particularly well laminated. Other levels are generally rubbly, and all sediments are unconsolidated.

The depositional setting of locality DMNH 644 is unusual in that it appears to define a small alluvial cone that came from the west into the Velvet Room [figure 2.11]. Depositional dips of about 10° are common and exhibit a radial pattern. It is likely that alternation of moist and dry conditions defined variable patterns of filling, resulting in the establishment of bedding patterns. Overall the package of strata becomes finer upward, suggesting [that] the orifice supplying sediments gradually became clogged or cut off.

DMNH 644 was sampled for paleomagnetic analysis in 1993, 1994, and 1995. Analysis of the samples is reported by Friedmann and Raynolds [chapter 6], and compared to biostratigraphic indicators by Barnosky and Bell [chapter 7].

As of the end of 2000, a total of 6090 specimens from this locality were catalogued in the Denver Museum of Nature and Science.

The DMNH excavation is spatially discrete from the CM Velvet Room excavation, and the age relationships of sediments in the two parts of the room are not straightforward. Observations

TABLE 2.2

Conversion from Numbered Arbitrary Levels Applicable Only within Grids
to Correlative Horizons Labeled by Letters Traceable across Grids in DMNH 644, within the Velvet Room

	Horizon		*Level*
Grid 6	A	=	1, 2
	B	=	3, 4, 5, 6
	C	=	7, 8
	D	=	9, 10, 11, 12
	E	=	13, 14
	F	=	15, 16
	G	=	16
Grid 7	A	=	1, 2
	B	=	3, 4, 5
	C	=	6, 7, 8
	D	=	9, 10, 11, 12, 13, 14
	E	=	15, 16
	F	=	17, 18
	G	=	19
	H	=	20, 21
Grid 8, 8A	A	=	1, 2
	B	=	3, 4, 5
	C	=	6, 7, 8
	D	=	9, 10
	E	=	11, 12, 13, 14, 15, 16, 17
	F	=	17, 18
Grid 9, 9A	A	=	1
	B	=	2, 3, 4, 5
	C	=	6
	D	=	7, 8, 9
	E	=	10, 11
	F	=	12, 13
	G	=	13, 14
	H	=	27
	I	=	28
	J	=	29, 30
	K	=	26X
	L	=	27X
	M	=	28X
	N	=	29X
	O	=	30X
	P	=	31X
	Q	=	32X
	R	=	33X
Grid 10	A	=	1
	B	=	2, 3, 4, 5, 6,
	C	=	7, 8, 9, 10
	D	=	11, 12, 13, 14
	E	=	15, 16, 17,18
	F	=	19, 20
	G	=	21, 22, 23
	H	=	23, 24, 25, 26
	I	=	26, 27, 28, 29
	J	=	30
	K	=	26X
	L	=	27X
	M	=	28X
	N	=	29X
	O	=	30X
	P	=	31X
	Q	=	32X
	R	=	33X
Grid 11	A	=	1, 2
	B	=	3, 4
	C	=	4, 5
	D	=	5, 6, 7, 8
	E	=	8, 9, 10
	F	=	10, 11, 12
	G	=	13, 14, 15
	H	=	15, 16, 17
	I	=	17, 18
	J	=	18
	K	=	26
	L	=	27
	M	=	28
	N	=	29
	O	=	30
	P	=	31
	Q	=	32
Grid 12	A	=	1
	B	=	2, 3, 4, 5
	C	=	5, 6
	D	=	7, 8
	E	=	9, 10, 11
	F	=	11, 12, 13
	G	=	13
	H	=	14
	I	=	15
Grid 13	A	=	1
	B	=	2, 3
	C	=	3
Grid 14	A	=	1
	B	=	2, 3
	C	=	3, 6, 7
	D	=	7, 8
	E	=	8, 9, 10A
	F	=	10A, 10B, 10C
	G	=	10D
	H	=	10E, 10F, 10G
	I	=	10H,10J, 11A
Grid 15	A	=	1
	B	=	2, 3, 4, 5
	C	=	6, 7

(continued)

TABLE 2.2 (continued)

	Horizon		Level
	D	=	7
	E	=	8, 9, 10A
	F	=	10A, 10B, 10C
	G	=	10D
	H	=	10E, 10F, 10G
	I	=	10H, 10J, 11A
	J	=	11A
	K	=	26
	L	=	27
Grid 16	A	=	1
	B	=	2, 3, 4
	C	=	5
	D	=	6, 7, 8
	E	=	9, 10
	F	=	11, 12, 13
	G	=	14, 15, 16
	H	=	17, 18
	I	=	19
	J	=	20
	K	=	26
	L	=	27
	M	=	28
	N	=	29
	O	=	30
	P	=	31
	Q	=	32
	R	=	33
Grid 17	A	=	1
	B	=	2, 3, 4
	C	=	5
	D	=	6, 7, 8
	E	=	9, 10
	F	=	11, 12, 13
	G	=	14, 15, 16
	H	=	17, 18
	I	=	19
	J	=	20
Grid 18, 19			Not excavated
Grid 20	A	=	1
	B	=	2
	C	=	3, 4, 5, 6, 7A
	D	=	Eroded?
	E	=	7B, 8, 9, 10
	F	=	11
	G	=	12
	H	=	13, 14, 15
	I	=	15, 16, 17, 18
	J	=	19, 20
	K	=	20
Grid 21	A	=	1
	B	=	2
	C	=	3, 4, 5, 6, 7A
	D	=	Eroded?
	E	=	7B, 8, 9, 10
	F	=	11
	G	=	12
	H	=	13, 14, 15
	I	=	15,16
Grid 22	A	=	1
	B	=	2
	C	=	3, 4, 5, 6, 7
Grid 23, 24	B	=	2
	C	=	3, 4, 5, 6, 7
Grid 25	A	=	1
	B	=	2, 3
	C	=	7A
	D	=	Eroded?
	E	=	7B
Grid 26	A	=	1
	B	=	2, 3
	C	=	7A
	D	=	Eroded?
	E	=	7B

of the DMNH excavation by ADB and CJB in 1994 compared with lithologic descriptions recorded in ADB's field notes at the time of the CM excavation suggest, based on lithologic criteria, that the two excavations may relate in the following way: CM VR level 1 correlating with part of DMNH level A; parts of CM VR levels 2A and 2B correlating with parts of DMNH levels B and C; and parts of CM VR levels 2C, 3, and 4 correlating with parts of DMNH level D. If this is the case, the lower levels of the DMNH excavation are probably older than all of the sediments in the CM excavation. However, these relationships remain speculative at this point. The problems with correlating deposits in different parts of this room are well illustrated in figure 2.11, which shows the relationship of DMNH 644 to Kate's Cupola / Mark's Sink (DMNH 1349).

TAPHONOMY

Characteristics of the fossil bones resemble those described for the CM excavation and the Pit. Sedimentological features of at least levels A–D resemble those noted for the CM exca-

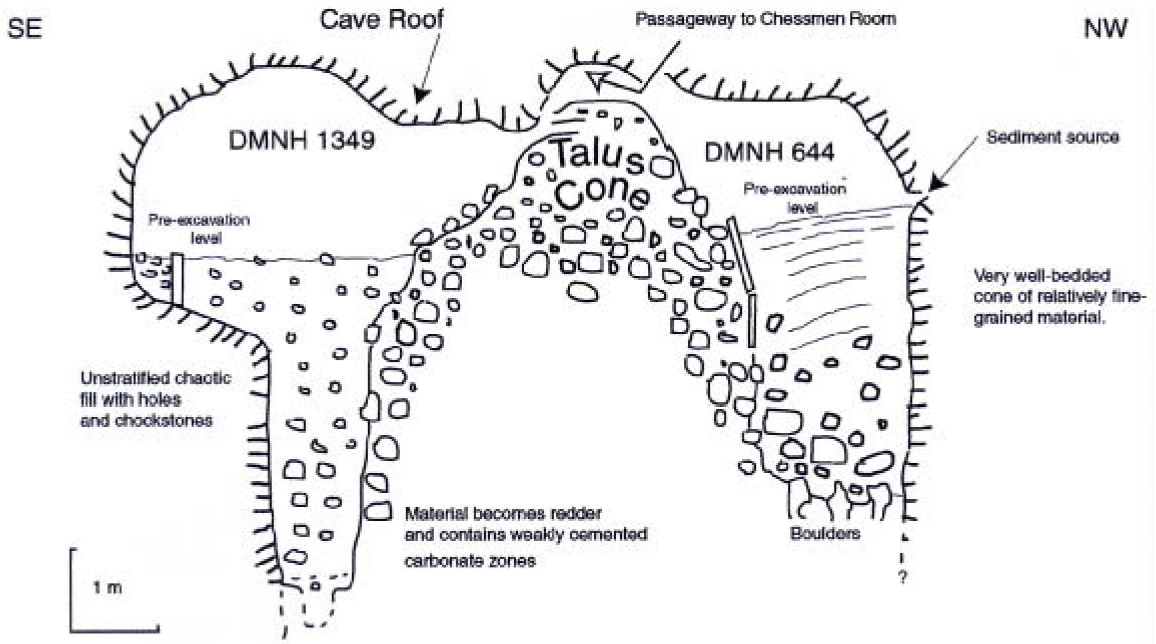


FIGURE 2.11 Southeast to northwest profile through the southern part of the Velvet Room. The view is to the southwest. (Drawn by R. Raynolds.)

vation (Barnosky and Rasmussen, 1988). Therefore it seems likely that wood rats played a prominent role in accumulating many of the fossils.

Velvet Room, Kate's (=Katie's) Cupola (Figure 2.3, Site 21)

LOCALITY NUMBER

DMNH 1349.

COLLECTION PROTOCOLS

This site is actually a continuation of the 1994–95 DMNH excavations of Mark's Sink (see following description). Stratigraphic context is lacking and mixing of materials from the higher portion of Mark's Sink is probable.

Velvet Room, Last Chance Pit (Figure 2.3, Site 24)

LOCALITY NUMBER

DMNH 2433.

COLLECTION PROTOCOLS

This locality, situated in the northeast portion of the Velvet Room, is in the area used to pile the debris from dry screening of DMNH 644. It was discovered in 1999; at that time it was excavated to only a few centimeters, but it was found to be stratified. Because this site appeared to contain a rich fauna, it became a focus for the 2000 field season. Excavation during the 2000 field season reached a depth of less than 1 m. As of this writing, the matrix from DMNH 2433 was being picked and the fauna remains unstudied.

Velvet Room, Mark's Sink (Figure 2.3, Site 22)

LOCALITY NUMBER

DMNH 1349.

COLLECTION PROTOCOLS

The first material recovered from this locality came from a 1993 excavation as cavers dug to find new passages out of the Velvet Room. This by-product of tunneling was bulk sampled and yielded bones that lacked any stratigraphic context. In 1995 a small vertical extension was begun, and in 1996 the excavation was expanded horizontally and especially vertically, with no spatial or vertical provenance supplied for specimens. In 1997 a controlled excavation commenced as a lateral expansion on three sides of the original hole (the fourth side being the cave wall). Excavation levels were 2–15 cm thick, but eventually these were determined to be so bioturbated and otherwise disturbed because of the complex depositional situation that stratigraphic levels were deemed essentially meaningless as indicators of relative time. It is likely that the assemblage time averages up to hundreds of thousands of years. RGR and LHT provided the following description to ADB in 2001:

> This locality started as a test pit to determine if strata similar to [those] found at DMNH 644 existed on the south side of the Velvet Room. In 1993, 1994, and 1995 this test pit was deepened to several meters without encountering well-bedded strata.
>
> A datum was established on the ceiling over the excavation, and 4.2 m of strata were excavated in a series of 55 levels over three field seasons (1997–99). At no time during the excavation process were well-stratified sediments found. Only weakly defined cementation zones and color bands were observed. Deep open holes were common beneath angular boulders. It is apparent that although relatively old faunal elements occur in this locality, the fauna is mixed due to reworking and irregular depositional processes.
>
> As of the end of 2000, the Denver Museum of Nature and Science held 4443 catalogued specimens from this locality.

Velvet Room, Will's Hole (Figure 2.3, Site 23)

LOCALITY NUMBER

DMNH 1350.

COLLECTION PROTOCOLS

A bulk sample of sediments was collected from a small chamber extending off the DMNH Velvet Room excavation. It probably represents strata that are below DMNH level C, but more precise information is unavailable. Stratigraphic mixing is suggested by older-looking black bones found alongside younger-looking tan bones.

Porcupine Cave, Undifferentiated

LOCALITY NUMBERS

CM 1932, DMNH 1354, UCMP V97002.

COLLECTION PROTOCOLS

Specimens with this designation were collected somewhere in Porcupine Cave, but more precise information is not available. Thus it is not possible to place these localities within figure 2.3.

Acknowledgments

Hazel Barton graciously provided the map on which localities were plotted and also provided the detailed cross sections and profiles (figures 2.3–2.7). Don Rasmussen helped in construction of figures 2.9–2.11, pinpointed some of the localities, and commented on a draft of the chapter. Information about various museum locality numbers was provided by Betty Hill (CM), Pat Holroyd (UCMP), Logan Ivy (DMNH), and Desui Maio (KU). Preparation of this chapter was partially supported by NSF grant BSR-9196082. This chapter is University of California Museum of Paleontology contribution 1809.

THREE

The Modern Environment, Flora, and Vegetation of South Park, Colorado

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Colorado State University

South Park is one of the four large intermountain basins that characterize the Rocky Mountains of Colorado (figure 3.1). The basins, typically called "parks," have relatively level to rolling floors and are surrounded by mountain ranges with peaks reaching over 4000 m elevation. The floors of all parks have arid climates with cool summers and very cold winters.

Three characteristics of South Park distinguish it from Colorado's three other major intermountain basins, North Park, Middle Park, and the San Luis Valley:

1. The floor of South Park is much higher in elevation than that of any other intermountain basin in Colorado or in North America.
2. The vegetation on the park floor is a grass-dominated steppe, whereas the other parks are dominated by shrubs.
3. Localized saline groundwater has created saline springs, ponds, and soils in an otherwise nonsaline landscape.

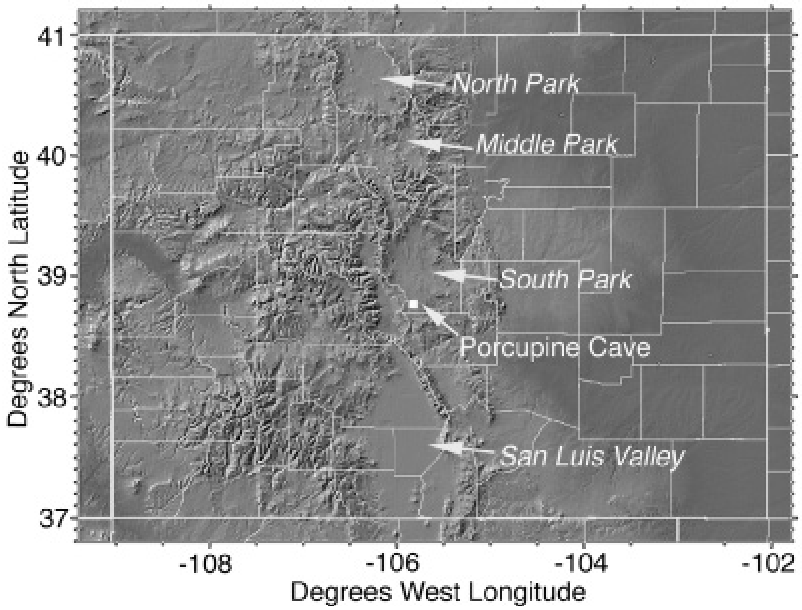
The high elevation of South Park and its surrounding mountains have created persistent habitat and connections for floristic exchange with other high mountain regions in the Northern Hemisphere. Although Colorado has many high mountain ranges, South Park and its surrounding mountains support the highest concentration of plant species that have their main distributions in central Asia (Weber and Wittmann, 2001) and boreal regions of the Holarctic (Hultén, 1968). Although some of the extraordinary plant populations occur in mountaintop alpine tundra environments, most occur on the floor of South Park in steppe, peatland, and salt flat ecosystems.

South Park features large regional variation in elevation and an assortment of bedrock types. Landforms created by geologically recent glaciers and rivers are superimposed on geologically long-lived ridges and bedrock outcrops. The combination of all these factors has created habitat for a wide diversity of species and communities. Well-developed alpine tundra occurs on the highest mountains, and numerous forest types dominated by evergreen and deciduous trees occur on mountain slopes. Mountain-front hills and hogbacks (long ridges formed by tilted resistant rock strata) in South Park support forest and grassland communities that typically are found only much farther south in North America. The grass-dominated steppe shares many species with the northern and western Great Plains, the steppes of central Asia, and the mountains of Chihuahua, Mexico. South Park also contains some of the largest expanses of montane wetlands in the western United States, particularly where groundwater flowing through the glacial outwash of the Mosquito Range mountain front discharges onto the floor of the park. This great ecological variability and geographic position suggest that South Park has acted as a crossroads for many floristic elements and has probably provided important biotic refugia for tens of thousands, if not millions, of years.

Landscape

High mountains of the Front Range form the northern and eastern borders of South Park, with the high point of Mount Evans reaching 4345 m elevation (figure 3.2). On the west the Mosquito Range forms a high and nearly unbroken chain of peaks greater than 4000 m elevation, reaching a high point on Mount Sherman and ending at the Buffalo Peaks (figure 3.3). The Front and Mosquito ranges supported localized ice caps and extensive valley glacier complexes during stades of the Pleistocene, as evidenced by the well-developed cirques and jagged peaks of the skyline. Lateral moraines are prominent on the sides of most large valleys, and in several areas lateral and dead ice moraines have created kettle pond complexes at the mountain front. Glaciers occurred in the Mosquito Range

FIGURE 3.1 Computer image of Colorado terrain, showing the four Colorado parks. The Great Plains are on the right, the Colorado Plateau is on the left, and the Rocky Mountains are in the center.



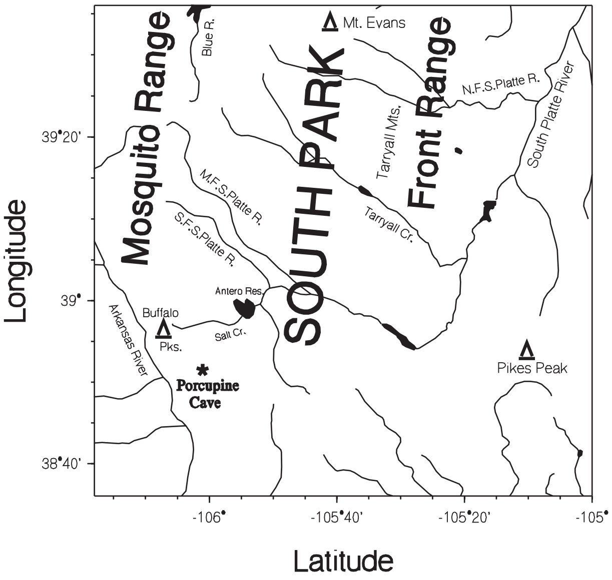


FIGURE 3.2 Sketch map indicating the location of Porcupine Cave and the major features of South Park.

as far south as Buffalo Peaks, but they advanced no closer than 20 km to Porcupine Cave.

The melting of glacier ice created floods capable of moving large amounts of sediment down the mountain fronts, where alluvial fans, outwash plains, and braided rivers formed. Alluvial deposits extend as a blanket from the Mosquito Range east across the floor of South Park. Currently snowmelt from the mountains fills streams and percolates through outwash deposits, causing shallow groundwater to flow down into the interior of South Park.

Limestone and dolomite rocks of the Leadville Limestone formation are prominent in the Mosquito Range and have formed calcareous alluvial deposits. Surface water and groundwater flowing through the alluvium is alkaline, with pHs ranging from 6.5 to more than 8.0 in the region from Kenosha Pass to the South Fork of the South Platte River. The most abundant cations are calcium and magnesium, and the most abundant anion is bicarbonate.

From the South Fork of the South Platte River to the area of Antero Reservoir, the Minturn and Maroon formations outcrop along the western foothills of South Park or are bedded close to the ground surface and buried by outwash gravels. The Minturn Formation contains gypsum beds. Karst topography has formed in several areas, for example in the High Creek drainage, creating ponds (Appel, 1995). Groundwater discharging from these formations is highly saline. Large salt flats occur on the southern, western, and eastern sides of Antero Reservoir, and the reservoir was built atop the greatest concentration of salt springs in Colorado. Salt Creek flows into Antero Reservoir from the southwest, where salt was commercially produced at the Salt Works Ranch in the late 1800s (Simmons, 1992). Surface water, groundwater, and soils contain high concentrations of sodium, sulfate, and chloride ions. A small natural lake located just north of Antero Reservoir is so saline that it never freezes. French fur trappers referred to this portion of South Park as Bayou Salade in the mid-nineteenth century owing to the widespread saline marshes (Frémont, 1887).

A section of the Front Range known as the Tarryall Mountains forms the northeastern side of South Park. The Tarryalls contain granite domes and few peaks higher than 3300 m elevation. Unlike higher-elevation portions of the Front and Mosquito ranges, the Tarryalls do not contain extensive highlands, and valley glaciers did not form there during the Pleistocene. The environment of South Park was certainly very different during glacial stades, but the presence of large

FIGURE 3.3 Looking southwest across the northern portion of South Park toward the Mosquito Range. In the foreground the abundant light-colored low plants are fringed sage, with blue grama grass. The darker areas on the valley floor in the distance are wetlands dominated by arctic rush. Conifer forests dominate the lower portions of the distant mountains, and alpine tundra occurs on the higher mountains.

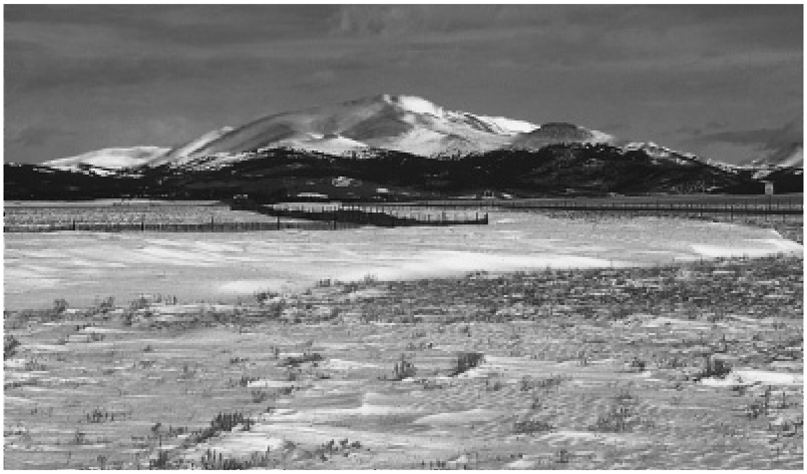


FIGURE 3.4 Winter view looking west to Silverheels Mountain just north of Fairplay. The alpine zone above the treeline has large windblown areas that support fell field vegetation and snowbeds. In the foreground the snowpack is light, with a snow accumulation area on the lee side of the fence in the middle distance and a thin and crusted snow cover in the immediate foreground.

unglaciated mountain regions probably provided important refugia for mountain plants.

The eastern floor of South Park is an arid plain that grades into the foothills of the Tarryall Mountains and the Pikes Peak massif. Pikes Peak is the best-known mountain in the Western Hemisphere and for many nineteenth-century travelers it "had the face of an old friend" (Frémont, 1887:405). In 1806 Zebulon Pike described this granite mountain as "unclimbable," misestimating its elevation at 5651 m—more than 1200 m more than its actual elevation. The first known successful ascent of the peak was accomplished by three members of the Long Expedition to the Rocky Mountains on July 14, 1820, led by the expedition's botanist and historian, Edwin James. It was James who set down the first observations and written impressions of Rocky Mountain alpine tundra plants, animals, and landscapes (James, 1825; Evans, 1997).

South Park's floor attains its highest elevation in the north, and its elevation decreases gradually to the south. From the town of Jefferson, at 2895 m elevation, to the town of Hartsel, at approximately 2700 m elevation, the park floor is a treeless plain, except on sedimentary and intrusive bedrock outcrops, which support forests of aspen, bristlecone pine, and other conifers. South of the Platte River's South Fork, the topography becomes rolling. Hills are forested on their tops, with steppe on slopes and flats. These hills merge into the Arkansas River Hills on the south and west.

Climate

South Park is sheltered from cyclone storms by continuous mountain belts on the north, west, and east. Little precipitation falls on the park floor during the winter, and snow is quickly redistributed by wind into drifts, leaving many areas relatively free of snow and exposed to the action of wind and frost (figure 3.4). In the highest mountain areas, abundant winter snow falls, and as in other high mountain regions in Colorado this snow provides the bulk of the annual precipitation.

South Park's only weather stations are located on the park floor, and the only station with records dating back more than a few years is the one at Antero Reservoir. Mean annual precipitation at Antero is 258 mm, although pan evaporation is 865 mm, 3.35 times precipitation (Spahr, 1981). An average of less than 1 cm of precipitation falls during each of the three

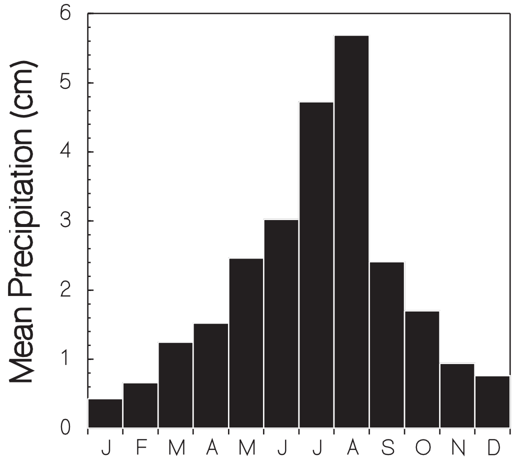


FIGURE 3.5 Mean monthly precipitation for the Antero Reservoir weather station, 1961–97.

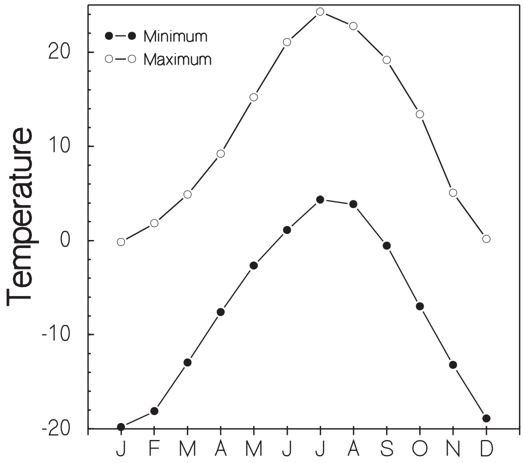


FIGURE 3.7 Monthly maximum and minimum temperatures at the Antero Reservoir weather station.

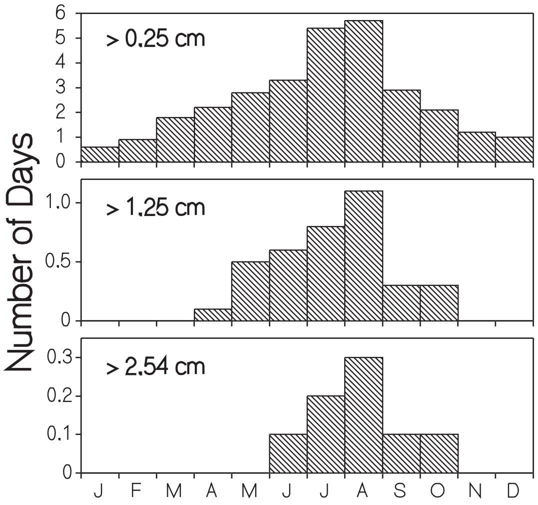


FIGURE 3.6 Mean number of days each month receiving more than 0.25, more than 1.25, and more than 2.54 cm of precipitation at the Antero Reservoir weather station.

winter months, December, January, and February (figure 3.5). More than 20% of the annual precipitation falls during August, and more than 50% of the annual total falls during June, July, and August, driven by monsoonal flow from the southwest. Only July and August average more than a few days with measurable precipitation (>0.25 cm/day), and August is the only month with at least one day when more than 1.25 cm of rain falls (figure 3.6). It is rare for more than 2.54 cm of rain to fall during a single day in South Park, such rainfall occurring only approximately once every three years, and then typically in August.

The mean annual temperature for the Antero station is 2°C. Mean January and July temperatures are –16 and 14°C, respectively (figure 3.7). The highest temperature recorded is 28.6°C, in July. In few years does the temperature exceed 26°C. The coldest measured temperature is –47.8°C, in December. The mean diurnal temperature change is approximately 20°C.

A comparison of South Park's climate with that of boreal sites in Alaska and central Asia, as well as a subalpine forest site in the Colorado Front Range, provides a useful means of understanding the similarity of South Park's climate to that of other mountain areas. Mean January temperatures are lower at the Alaska and Asian sites because they have longer periods of extreme cold weather (table 3.1). South Park does not experience long periods of extreme cold temperatures because polar air masses rarely reach Colorado's interior basins. In addition, the lack of a continuous snow cover allows the ground surface to heat up, preventing the most extreme cold temperatures from developing. Instead cold air masses and cold air drainage onto the floor of South Park combine to produce its extreme cold temperatures. Temperature inversions are dispersed by frequent strong westerly winds. Extreme temperatures rarely persist for more than a few days.

Mean July temperatures are most similar between South Park and Fairbanks, Alaska (table 3.1). Temperatures are warmer at the Asian station and cooler at the Front Range station. Mean annual temperatures are lowest in Fairbanks and warmest in South Park. South Park receives less precipitation than Fairbanks and the Khamar-Daban Mountains of southern Siberia. All sites receive less than 30% of the precipitation that falls at the subalpine site in the Colorado Front Range.

These data indicate that growing-season temperatures are similar between South Park and boreal sites, such as Fairbanks, Alaska, that support continuous conifer forests. The floor of South Park is most likely treeless owing to summer soil drought, much as it is in central Asia, including Mongolia, northern China, and eastern and southern Siberia. Although Fairbanks is in an area of discontinuous permafrost, it is unlikely that permafrost exists in more than a few patches in the highest-elevation cirques and talus slopes surrounding South Park. South Park's semiarid climate is similar to that of both Fairbanks and the Khamar-Daban Mountains.

TABLE 3.1
Weather Data from the Antero Reservoir Station in South Park, Compared with Data from Fairbanks, Alaska, the Colorado Front Range, and the Khamar-Daban Mountains of Southern Siberia

	Antero Reservoir	*Fairbanks*	*Front Range*[a]	*Khamar- Daban*[b]
Elevation (m)	2740	50	3109	730
Mean daily temperature (ºC)				
January	–16	–24	—	–24
July	14	15	12	18
Mean annual temperature (ºC)	2	–3	0	–2
Mean annual precipitation (mm)	258	290	1050	280

[a] Data from the INSTAAR C1 station; Elliott-Fisk (1988).
[b] Data from Epova (1965).

Flora and Vegetation

The richness of South Park's flora and vegetation is due to the diversity of habitats that exist today and that have existed for millennia. Most important is the variety of unglaciated sites, both dryland and wetland. Scientific names for plants discussed in this section are listed in table 3.2. Plant nomenclature throughout follows Weber and Wittmann (2001).

Alpine Tundra

Alpine tundra occurs above treeline, at approximately 3450 m elevation, on all mountains bordering South Park. The flora and vegetation are highly variable because of the diversity of bedrock types in these mountains. Bedrock includes both granite, which forms acid soils, and limestone and dolomite, which form alkaline soils. Tundra plants are highly specific to substrate chemistry, with different plant species and distinctive plant communities occurring on acid and alkaline soils (Bamberg and Major, 1967). Acidic tundra is widespread in Colorado, for example on Pikes Peak and elsewhere in the Front Range, whereas the primary area of alpine tundra on limestone in Colorado is the Mosquito Range.

Strong winter winds redistribute snow, producing the most important alpine tundra environmental gradient (figure 3.4). Windward slopes are blown free of snow, plants are battered by wind, soil freezes deeply, and plant litter blows away, producing a patchy vegetation. Since snow is blown away, a large percentage of the year's precipitation is lost, creating an arid environment. The opposite end of this environmental gradient may be found just a few tens of meters away on the lee side of a ridge, where a snowbed forms. Deep winter snow protects the soil from winter winds and extreme cold. However, because it takes much of the summer to melt the snow, the growing season is significantly shortened. The abundant snowmelt produces water far in excess of the annual precipitation. Below snowbeds meltwater supports wet meadows, marshes, and small streams. Between these two extremes are a variety of meadow ecosystems with well-developed and highly organic soils, moderate moisture conditions, and high species richness.

Acid tundra supports fell field communities on windblown ridges dominated by such cushion plants as dwarf clover and moss campion, snowbeds dominated by tufted hairgrass and Parry's clover, and meadow communities dominated by alpine avens and elk sedge. Tundra with basic soils, as can be seen in Horseshoe Cirque west of Fairplay, supports similar fell fields. However, meadows are dominated by dryad and sedge *(Carex scirpoidea),* calciphiles (calcium-loving plants) that dominate limestone alpine tundra slopes along the cordillera from Colorado to northern Alaska (Cooper, 1986).

A number of very rare and disjunct plants occur in Mosquito Range alpine environments, including *Braya humilis* (alpine braya), *B. glabella* (arctic braya), *Eutrema edwardsii* (Penland alpine fen mustard), *Askellia nana* (dwarf hawksbeard), *Saussurea weberi* (Weber saussurea), *Salix calcicola* (lime-loving willow), and *Eriophorum altaicum* (Altai cottongrass). Many of these species are calciphiles, requiring an abundance of calcium such as occurs on the open habitat maintained on limestone slopes. *Braya* and *Eutrema,* both genera in the mustard family (Brassicaceae), contain species that are widely distributed in boreal mountain ranges of North America (Hultén, 1968). *Braya glabella* has a very closely allied species, *B. rosea,* in the Altai Mountains of central Asia (Weber and Wittmann, 2001). *Eutrema* also occurs in boreal mountain ranges of Asia as far south as the Altai Mountains. *Saussurea weberi* is a Rocky Mountain endemic species representative of a genus with many species in Eastern Asia and Alaska.

Forests

Conifer forests occupy the majority of South Park's mountain slopes from treeline to the floor of South Park (figure 3.3). Upper treeline in the interior of western North America is thought to be controlled by low summer temperatures (Billings, 1988), whereas lower treeline, such as at the foothills of the Mosquito Range, is controlled by summer soil drought

TABLE 3.2

Plant Species Characterizing the Main Vegetation Types in South Park

Ecosystem	*Common Name*	*Scientific Name*
	Alpine tundra	
Fell field	Dwarf clover	*Trifolium nanum*
	Moss campion	*Silene acaulis*
Snowbed	Tufted hairgrass	*Deschampsia cespitosa*
	Parry's clover	*Trifolium parryi*
Meadow	Elk sedge	*Kobresia myosuroides*
	Alpine avens	*Acomastylis rossii*
	Dryad	*Dryas octopetala*
	Sedge	*Carex scirpoidea*
	Forest	
	Engelmann spruce	*Picea engelmannii*
	Subalpine fir	*Abies bifolia*
	Douglas-fir	*Pseudotsuga menzesii*
	Blue spruce	*Picea pungens*
	Limber pine	*Pinus flexilis*
	Aspen	*Populus tremuloides*
	Bristlecone pine	*Pinus aristata*
	Lodgepole pine	*Pinus contorta*
	Ponderosa pine	*Pinus ponderosa*
	Wetland	
Peatland	Spikerush	*Eleocharis quinqueflora*
	Arrowgrass	*Triglochin palustre* *Triglochin maritimum*
	Elk sedge	*Kobresia simpliciuscula* *Kobresia myosuroides*
	Porter's feathergrass	*Ptilagrostis porteri*
Wet meadow	Nebraska sedge	*Carex nebraskensis*
	Arctic rush	*Juncus arcticus*
	Shrubby cinquefoil	*Pentaphylloides floribunda*
Riparian	Plainleaf willow	*Salix planifolia*
	Barrenground willow	*Salix brachycarpa*
	Mountain willow	*Salix monticola*
Salt flat	Alkali grass	*Puccinellia airoides*
	Saltgrass	*Distichlis stricta*
	Glasswort	*Salicornia europea*
	Sea-blight	*Suaeda calceoliformis*
	Mustard	*Thellungiella salsuginosa*
Salt marsh	Three-square	*Schoenoplectus pungens*
	Alkali bulrush	*Bobloschoenus maritimus*
	Arrowgrass	*Triglochin maritimum*
	Sea milkwort	*Glaux maritimum*
	Steppe	
	Blue grama grass	*Chondrosum gracilis*
	Sedge	*Carex stenophylla* ssp. *eleocharis*
	Fringed sage	*Artemisia frigida*
	Lichen	*Xanthoparmelia chlorochroa*
	Arizona fescue	*Festuca arizonica*
	Mountain muhly	*Muhlenbergia montana*

FIGURE 3.8 Wet meadow (foreground) dominated by sedges is important pasture for domestic livestock in South Park. On the hills in the background are large clones of aspen and two strips of conifer forest. The lower strip of bristlecone pine traces a bedrock outcrop, and mixed-conifer forest dominated by Douglas-fir is present on the mountaintop. The hill slopes around the forests are dominated by Arizona fescue grassland.

(Daubenmire, 1974). Six main forest types occur in South Park, dominated by the following:

1. Engelmann spruce and subalpine fir at the highest elevations in mature stands.
2. Lodgepole pine forests in recently burned sites and on drier slopes.
3. Aspen as successional stands on burned slopes and persistent stands on rocky, low-elevation ridges and hogbacks.
4. Bristlecone pine on windblown ridges on the floor of northern South Park, and near treeline in other areas.
5. Mixed-conifer upper montane forests dominated by Douglas-fir and blue spruce in the foothills of the southern portion of South Park.
6. Ponderosa pine forests at low elevations in the southern portion of South Park.

Most notable among the forests are distinctive aspen stands that occur as oval-shaped patches on ridges near lower treeline in the foothills and on hogbacks within South Park (figure 3.8). These patches are most likely clones of genetically identical trunks. The clonal growth of aspen is well known (Barnes, 1966), and clones can be very large, covering many hectares (Grant et al., 1992). Stem suckers emerge from root systems after disturbances such as fire (Mitton and Grant, 1996). Baker (1925) hypothesized that only during the late Pleistocene were conditions suitable for the establishment of aspen seedlings, so it is possible that some clones are 10,000 or more years old. Aspen seedlings are occasionally found after large fires, such as the Yellowstone fires of 1988 (Romme et al., 1995). Many of South Park's stands of aspen occur as isolated clones at the lower treeline separated from continuous forests, so they may be little influenced by forest fires. Long-lived clones may also be limited to rocky outcrops, such as the hogbacks, owing to herbivory of tree roots by pocket gophers in areas with more finely textured soils (Cantor and Whitham, 1989).

Also notable are stands of bristlecone pine on dry ridges and hills on the margins of South Park and on hogbacks throughout the park (figure 3.8). Bristlecone pine is most common in windy environments near upper treeline, for example on the Mount Goliath area of Mount Evans, at the northern end of South Park. However, bristlecone pine is also the most common low-elevation tree in the northern and central portions of South Park. Several bristlecone pine trees on Black Mountain in the southern portion of South Park are more than 2100 years old, and one was 2435 years old at the time of analysis, making them the oldest known trees in the Rocky Mountains (Brunstein and Yamaguchi, 1992). The old bristlecone pines and aspen clones demonstrate the great stability of many South Park habitats. The dry, rocky environment of bedrock hilltops creates substrate stability that limits biological productivity, reduces the potential for fire, and limits herbivory by rodents.

Upper montane forests, occurring between high-elevation spruce and fir forests and low-elevation ponderosa pine forests, are dominated almost completely by Douglas-fir in northern Colorado. However, in southern Colorado, including South Park, this ecosystem is a true mixed-conifer forest containing Douglas-fir with ponderosa pine, subalpine fir, limber pine, Engelmann spruce, aspen, white fir, southwestern white pine, and lodgepole pine. In northern Colorado blue spruce is confined to the riparian zone. However, where monsoon rains occur, as in South Park, blue spruce expands out of the riparian zone and up onto mountain slopes.

The unglaciated eastern portion of South Park, including the Tarryall Mountains, is characterized by spruce and fir forests that in places have an understory of the reindeer lichen *Cladina stellaris* at its only location in the western United States. This is one of the most abundant understory plants, lichen or otherwise, in the boreal forests that stretch from

FIGURE 3.9 The steppe in the foreground is dominated by blue grama grass, with flowering paintbrush *(Castilleja integra)* and other herbaceous dicots. On the valley bottom, the dark areas are wetlands, with shrubby cinquefoil *(Pentaphylloides floribunda)* prominent. In the middle distance, a hogback supports patches of aspen and bristlecone pine forests.

Scandinavia across Russia, Canada, and Alaska. This fruticose lichen can be up to 10 cm tall and forms continuous mats. The unglaciated mountains also provide habitats for large populations of other widely disjunct boreal and mountain plants, such as the sedge *Carex tenuiflora* at its only location south of Minnesota, cottongrass *(Eriophorum gracile),* and bog saxifrage *(Hirculus prorepens)* in quaking peatlands.

The Floor of South Park

The floor of South Park supports four principal natural environments:

1. Grasslands on dry terraces, slopes, and hills with deep water tables.
2. Streams and their floodplains.
3. Wetlands fed by groundwater.
4. Salt flats.

The floor has been highly modified over the past hundred years by agricultural water diversion, flood irrigation, the clearing of riparian vegetation, and the replacement of indigenous bison with cattle. The last wild Colorado bison was killed in the northeastern portion of South Park early in the twentieth century.

Dry terraces, slopes, and hills throughout South Park support vegetation dominated by grass and sedge (figure 3.9). Colorado's other intermountain parks and basins, North Park, Middle Park, and the San Luis Valley, have shrub-dominated vegetation, with big sagebrush *(Seriphidium tridentatum)* and greasewood *(Sarcobatus vermiculatus)* being the most abundant species. However, these species are rare in South Park. The dominance of grasses most likely results from the annual precipitation peak in summer being coincident with the growing season. This coincidence means that plants use the water during the season in which it falls, and soil water reserves fail to accumulate, as they do when the annual precipitation peak occurs in the winter. In regions such as the Great Basin, where precipitation peaks in the winter, melting snow in the spring promotes a short-term abundance of water and deep recharge in the soil. The water therefore is most available to deep-rooting shrubs. The late summer monsoon-driven precipitation peak allows the warm-season grass blue grama to dominate. It is the most abundant grass on the shortgrass prairies of the western Great Plains from Alberta to Texas and is also widespread in the Great Basin. This species provided excellent forage for native and introduced ungulates.

On the level terraces and slopes the sedge *Carex stenophylla* ssp. *eleocharis* and fringed sage dominate rich steppe communities that have an abundance of ground lichens, particularly *Xanthoparmelia chlorochroa.* The two vascular plant species are common not only in montane and northern Great Plains grassland sites in North America, but also on the steppes of central and eastern Asia (Hultén, 1968; Korotkov et al., 1991). The similarity of this South Park steppe community to steppe communities in central Asia is striking. *C. stenophylla* ssp. *eleocharis* is synonymous with *C. duriuscula,* a steppe dominant in eastern Siberia (Yurtsev, 1963).

Steeper hills with gravel soils support a different steppe community dominated by the bunchgrasses Arizona fescue and mountain muhly. The bunchgrasses provide a sharp contrast to the more turf-forming shortgrasses and sedges, like blue grama grass. Arizona fescue is a dominant montane grass in the southwestern United States and Mexico, reaching its northern limit in Colorado in the area of South Park. Its distribution may be closely tied to monsoon rains.

Floodplains through South Park have historically been vegetated by thickets of mountain, plainleaf, and barrenground willow. However, most shrubs have by now been removed from riparian areas to permit cultivation of floodplains for grazing and mowing.

In a few areas the floodplains are too saline for willows and instead are dominated by salt marsh and salt flat plants. Salt

FIGURE 3.10 Salt flats southeast of Antero Reservoir. The dark, low plant is glasswort, and the bunchgrass is alkali grass. An unvegetated salt pan is seen at the middle right, with free salts on the soil surface.

marshes have seasonally standing water, whereas salt flats have high water tables but never standing water. The capillary fringe brings groundwater into the upper soil profile, where it evaporates, causing salts to accumulate. Salt-dominated ecosystems are widespread in the southern portion of South Park, particularly around Antero Reservoir (figure 3.10). This area has provided abundant salt licks for native mammals for millennia. Salt flats are largely barren yet support populations of the salt specialists alkali grass, saltgrass, glasswort, and seablight (Ungar, 1974). These sites also support an eastern Siberian salt flat specialist, the mustard *Thellungiella salsuginosa.*

Wetter saline marshes that periodically or regularly have standing water are strikingly similar to coastal salt marshes, dominated by three-square bulrush, alkali bulrush, arrowgrass, and sea milkwort.

Where groundwater discharges to the ground surface, the soils remain perennially saturated. Wetland plants grow over these springs, forming highly productive clones. The leaves, roots, and stems of these plants decompose only partly in the waterlogged and oxygen-poor soils, and over thousands of years an organic soil forms, called peat or muck. Most peatlands in the northern and central portions of South Park are fed by calcareous water draining from the Mosquito Range and are the only calcareous peatlands, known as extreme rich fens, south of Jackson Hole, Wyoming. (A fen is a peatland supported by groundwater.) South Park's peatlands contain a number of unique plant communities, and probably have more rare and disjunct populations of plants than any other ecosystem type in Colorado (Cooper, 1996; Cooper and Sanderson, 1997). Two main community complexes occur in South Park's peatlands: water tracks and hummock-hollow complexes. Where springs discharge large volumes of groundwater to the surface, sheet flows of water develop, which are termed water tracks. Water tracks support communities dominated by spikerush and arrowgrasses. The other major community complex is created where peat hummocks up to 40 cm tall have developed from the long-term growth of tussock-forming sedges, such as elk sedges and Porter's feathergrass (figure 3.11). *Kobresia simpliciuscula* is a common circumpolar plant species of high-latitude and high-mountain regions. Its abundance in South Park is a striking example of the local abundance of a widely disjunct northern montane species (figure 3.12). *Ptilagrostis porteri* is the only North American species of feathergrass. It is closely allied with a large group of feathergrasses that characterize steppe and peatlands in central Asia (figure 3.13). Its geographic relationships are typical of a group of species that reflect the striking similarity of the floras of South Park and central Asia.

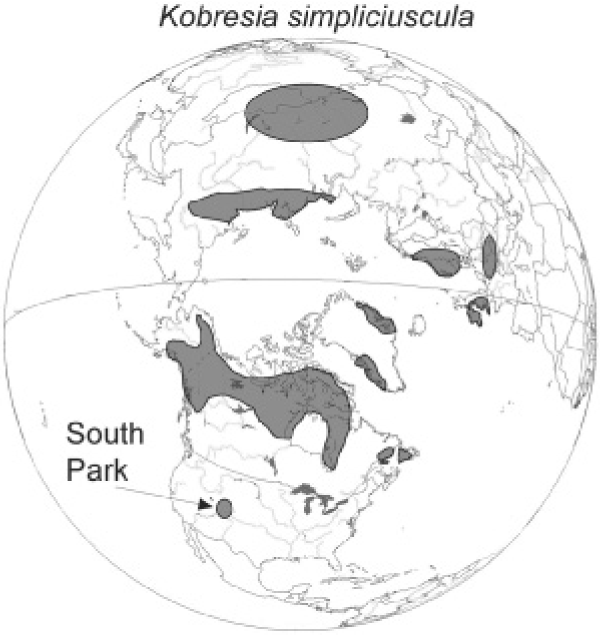
The peat hummocks provide habitat for many of the rare plants occurring in the calcareous fens, including Greenland primrose *(Primula egaliksensis),* small bulrush *(Trichophorum pumilum),* and myrtle leaf willow *(Salix myrtillifolia).* These are all widely disjunct from the main ranges of their species farther north.

Vegetation in the Vicinity of Porcupine Cave

The southern portion of South Park is a rolling landscape of forested hills and grassland slopes with small streams or marshes in the valley bottoms (figure 3.14). The area around Porcupine Cave is undulating, with ponderosa pine, Douglas-fir, and aspen forests on the tops and north-facing slopes of hills. Some of this forest area has clearly developed only during the twentieth century, owing to fire suppression. Thus the forested areas of today are probably larger than those that existed prior to human settlement in the nineteenth century. Few older trees are evident in these forests, and most trees are quite young. However, the presence of stumps indicates the cutting of older trees in many areas.

The steppe communities are similar to those in the northern part of South Park. Blue grama grass, sedge *(Carex stenophylla* ssp. *eleocharis),* and fringed sage dominate with numerous other grasses, herbaceous dicots, and lichens. It is a rich assemblage of plants adapted to mammalian herbivory.

FIGURE 3.11 Tussocks of elk sedge *(Kobresia simpliciuscula)* dominate the calcareous peatland in the foreground. Each plant is approximately 40 cm tall and 30 cm in diameter.



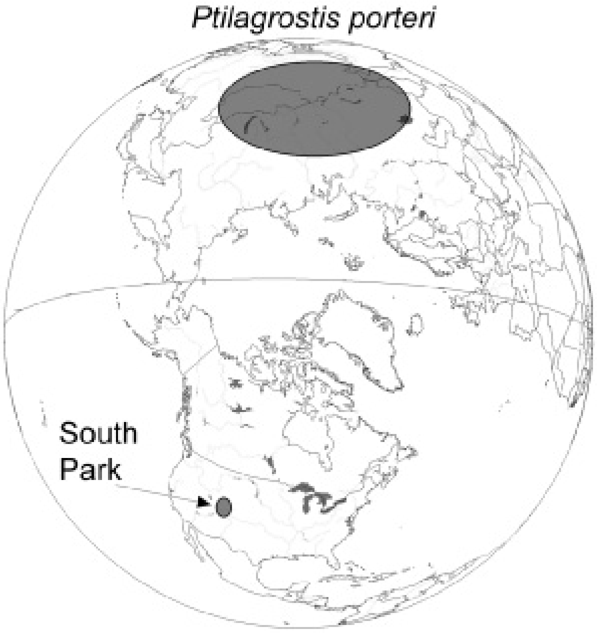


FIGURE 3.12 Map showing the circumpolar distribution of *Kobresia simpliciuscula,* one of the many boreal species abundant in South Park. Shaded areas encircled by dark lines indicate the regions within which the species is currently known. Note the wide distribution of this species in northern North America and Eurasia, and the presence of populations far to the south in the Rocky Mountains of Colorado (South Park) and central Asia.

FIGURE 3.13 Map showing the circumpolar distribution of *Ptilagrostis porteri* in North America and the closely related *P. mongholica* in central Asia. Shaded areas encircled by dark lines indicate the regions within which the species are currently known.

Grasses and sedges have their meristems (growing points) below the ground surface, instead of at the top of each branch, allowing the leaves to be repeatedly eaten without damaging the meristems. The leaves of these plants also have high silica content, which grinds down the teeth of herbivores. Both of these adaptations allow grass and sedge steppe plants to better deal with herbivory by large ungulates, as well as by smaller mammals such as rabbits and mice and by insects such as grasshoppers.

Wet meadows in the valley bottoms are the product of shallow groundwater tables, and sedges such as Nebraska sedge and arctic rush are most abundant, along with a wide range of herbaceous dicots. These wetlands are highly productive, with both abundant forage and perennial water in many areas.

FIGURE 3.14 A wet meadow–steppe–conifer forest complex in the southern portion of South Park. Forests are mixed aspen, ponderosa pine, and Douglas-fir. The steppe is largely dominated by blue grama grass, whereas the meadow is dominated by arctic rush, with flowering Geyer's onion (*Allium geyeri,* the light-colored and most abundant flowering plant) and louseworts (*Pedicularis groenlandica* and *P. crenulata,* the darker flowers in long spikes).

Synthesis

A number of overlapping geological, historical, geographic, climatic, hydrologic, and ecological processes combine to make South Park one of the most ecologically important regions of western North America. The variety of bedrock types that occur in the mountains surrounding South Park produce a diversity of landforms that have created habitats for numerous species. The most striking contrasts are

1. The high and nearly unbroken backbone of the heavily glaciated Mosquito and Front ranges compared with the unglaciated granitic domes of the Tarryall Mountains.
2. Acid and alkaline tundra.
3. Arid steppe adjacent to peatlands.
4. Highly dynamic floodplains adjacent to stable ridges and hills.
5. Flat tablelands adjacent to karst topography with its small ponds.
6. Nearly unvegetated salt flats adjacent to highly productive nonsaline grasslands.

The importance of the high-elevation outcrops of limestone in the Mosquito Range alone is extraordinary. This is the only large area of calcareous alpine tundra in the southern Rocky Mountains. The juxtaposition of calcareous and noncalcareous soils above the treeline provides a wide range of habitats that support a rich tundra flora. Many alpine calciphiles find their primary habitat in the United States in the Mosquito Range.

Glacial erosion has created variation not only in cirque basins and sharp ridges in the high mountains but also at lower elevations. Valley bottoms were widened and flattened, and deposition occurred at the mountain front. Deposition was in the form of dead ice moraines, lateral moraines, and outwash plains from braided rivers, which spread limestone and dolomite eroded from the Mosquito Range eastward across much of South Park. Water flowing down streams and through alluvium and glacial outwash is calcareous, and where groundwater discharges to the surface the best-developed complex of calcareous peatlands in the western United States occurs. The calcareous peatlands support the greatest complex of rare plants in Colorado.

The unglaciated eastern portion of South Park, including the Tarryall Mountains, foothills of the Pikes Peak massif, and the southern portion of South Park, provides stable landscapes that may have changed little over very long time scales. The presence of the boreal forest reindeer lichen *Cladina stellaris* at its only location in the western United States in spruce-fir forests of this region is an excellent example of a plant with poor ability to reproduce and spread. The unglaciated Tarryall Mountains provide a rare stable montane setting where this species has persisted for millennia. Its presence indicates that many species that dominate the boreal forest regions of Canada and Alaska may once have been widespread in Colorado. However, their populations have diminished and have been fragmented by the warm and dry summer climates of the Holocene.

The steppe communities that cover most of South Park's floor extend from Jefferson nearly to Salida and include a mosaic of communities dominated by plant species most common on the northern and western Great Plains, on the central Asian steppe, and in the American Southwest. Most extraordinary is the similarity of the *Carex stenophylla* ssp. *eleocharis–Artemisia frigida* community to a number of steppe communities in central Asia, where high-elevation, cold and dry grasslands are widespread and where many of Colorado's steppe species most likely evolved. South Park is the largest high-elevation steppe in western North America. Nowhere else is there a dry grassland of this extent and diversity. This unique environment highlights the ecological and floristic connections with central Asia that have persisted during suitable climate periods for millions of years. Too little work on these ecological and floristic relationships has occurred for us to know the details of these connections and how the myriad species with distributions almost entirely in eastern Asia or in far northern latitudes have found their way to Colorado and persisted there.

The connection with the central Mexico highlands also adds to the diversity of steppe and forests in South Park. Most likely it is the favorable summer environment created by monsoon rains that allows this element of the regional biodiversity to occur. The southwestern part of North America is the only portion of the continent with a strongly bimodal precipitation regime, with both winter and late summer precipitation. This climate pattern reaches its northern limit in southern and central Colorado, and it influences South Park. It helps to support Arizona fescue–dominated grasslands on dry hillsides, and true mixed-conifer upper-montane forests on midelevation slopes.

The most difficult questions to answer are the following: When did the connections with central Asia, and with the boreal flora now largely confined to Canada and Alaska, occur? Is recolonization possible following local extinction? Hooker and Gray (1880), Darwin (1883), Rydberg (1914), and other early biogeographers knew that many Rocky Mountain species had their main distribution in boreal and arctic regions of the world. They suggested that the colder Pleistocene climates pushed these species south, and when the climate ameliorated at the end of each glacial episode these species migrated back to the north. However, a few species found suitable habitats in the high Rocky Mountains and persisted there, remaining disjunct from the main ranges of their species. It has also been proposed that many species that exist primarily in the north today evolved in the high mountain environments of temperate latitudes and moved north only once arctic environments had developed within the last few millions years (Hultén, 1968). Most likely our present flora is the result of events and connections much older than the Pleistocene (Weber, 1965).

A number of ongoing and increasing threats to the biodiversity of South Park exist. The hydrologic regime of streams and wetlands is threatened by water development—including stream diversions and groundwater pumping—undertaken to supply urban growth along the Colorado Front Range. Disruptions of flow paths can diminish the acreage and diversity of wetlands. Peatlands are most threatened, as their continued existence requires perennially saturated soils. The mining of peat, to produce horticultural potting soil, has decimated many South Park fens. Since these are the only calcareous fens in the region, and support what is probably the region's highest density of rare and disjunct plant species, continued mining could destroy one of the most unusual ecosystem types in Colorado.

The absence of bison and control of fire could affect the long-term future of steppe ecosystems. Efforts should be made to limit further disruptions of the natural hydrologic, fire, and grazing regimes that have been important factors in creating and maintaining South Park's biodiversity.

The plant species and communities of South Park each have their own particular histories and ecological requirements. We know little about how these species arrived in South Park, how they have survived, and how they can respond to future land use and climate change scenarios. Much work remains to be done to unravel the interesting stories of the origin, evolution, migration, and persistence of South Park's unique flora and vegetation.

Acknowledgments

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FOUR

The Historical Context of Porcupine Cave

American Indians, Spaniards, Government Surveyors, Prospectors, Ranchers, Cavers, and Paleontologists in South Park, Colorado

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JOHN O. McKELVY
Buffalo Creek, Colorado

Porcupine Cave is located at the southern end of South Park (figure 4.1), one of four spacious, high-mountain basins in Colorado. Extending approximately 80 km north to south by 56 km east to west, the floor of the South Park basin averages approximately 2700 m in elevation. The area of the floor of the basin is approximately 2300 km^2; the entire area between the surrounding mountain peaks covers over 3600 km^2. South Park's northern boundary, the Park Range, runs from Kenosha Pass west to Hoosier Pass. The Mosquito Range separates the west side of the basin from the Arkansas River Valley. The southern boundary includes the Late Eocene volcanic remnants Black Mountain and Thirtynine Mile Mountain. The Puma Hills and the Tarryall Mountains, which separate the Front Range and Great Plains from the basin, define the eastern edge of South Park. The South Platte River, which originates in the South Park basin, flows northeastward into the Missouri River drainage, then on to the Mississippi River and the Gulf of Mexico. Red Hill, a hogback consisting of Cretaceous Dakota Formation, and Reinecker Ridge, consisting of early Tertiary South Park Formation topped by Eocene welded tuffs, bisect the floor of the basin in the Fairplay area.

Because of the salt springs and marshes prevalent in the basin, Spanish explorers called South Park Valle Salado; the French fur trappers used the Creole name Bayou Salade; and mountain men and trappers later hybridized the name into Bayou Salado. Noting that the basin was a popular feeding area for vast herds of bison, elk, and other game, mountain men, trappers, and early settlers eventually called the area South Park, deriving "Park" from the French word for game preserve, *parc.* The two similar high-elevation basins to the north were called Middle Park and North Park.

South Park encompasses a rich history. Among many who left their mark are the American Indians, Spaniards, trappers, government surveyors, prospectors, miners, ranchers, railroaders, oil and gas explorers, and more recently cavers and paleontologists. This chapter introduces South Park and some highlights of its history, people, activities, and stories—including the discovery, exploration, and unearthing of the Pleistocene treasures of Porcupine Cave.

South Park

Early History

AMERICAN INDIAN HISTORY

American Indians were the first human inhabitants of South Park. The Utes were entrenched in central Colorado when the Spaniards first entered the North American interior in the fifteenth century (Simmons, 1966). Initially they were apparently loosely organized into family groups, but after the acquisition of horses from the Spanish they organized into larger bands (Swift, 1980). Because of the abundant game animals and salt deposits in the basin, Comanches, Kiowas, Cheyennes, and Arapahos also visited South Park during the late 1700s and into the mid-1800s (Simmons, 1966; Nature Conservancy, undated). A series of treaties with the U.S. government between 1863 and 1868 took almost all of the Utes' mountain and park holdings in Colorado, and by the late 1800s most of the Indians had moved from the basin to reservations (Porrata, 1979).

Indian artifacts have been found in South Park during archaeological studies that have been limited primarily to surface work. Folsom points have been found near O'Haver Lake in Chaffee County adjacent to South Park (Shaputis and Kelly, 1982) and on Red Hill in South Park (Simmons, 1966). Rio Grande points have been picked up on the shore of Antero Reservoir, Scottsbluff points were found in the Trout Creek Pass region, and two apparent Alberta points were picked up

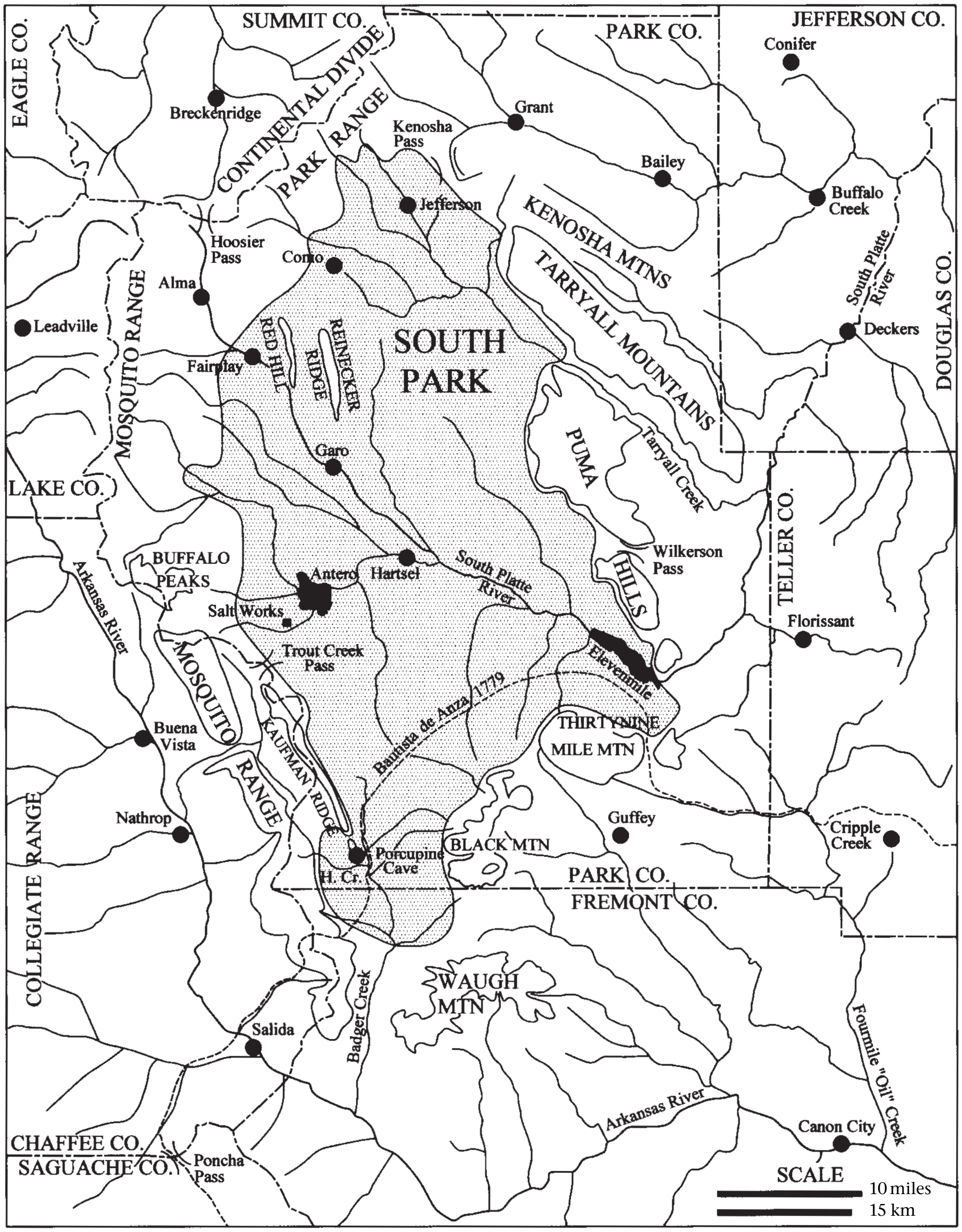

FIGURE 4.1 Generalized map of South Park showing key geographic features, landmarks, Bautista de Anza's trail (from Scott, 1975), and location of Porcupine Cave. (Modified from U.S. Geological Survey 1:500,000 Colorado Base Map, 1969.)

in the northern part of Chaffee County (Shaputis and Kelly, 1982). A buffalo jump with tipi rings is located a short distance from Porcupine Cave on a tributary of Badger Creek.

SPANISH EXPEDITIONS

Although Coronado and his party may have visited eastern Fremont County during his expeditions into the high plains of eastern Colorado in the 1540s (Chamblin, 1978) and members of the Dominguez Escalante expedition of 1776 may have viewed South Park from the southwest rim (Nutt, 1983), it was Juan Bautista de Anza who actually crossed through South Park in 1779 (Scott, 1975). Thomas (1932) translated Bautista de Anza's journals, which tell of his travels in South Park. Having been appointed governor of the province of New Mexico (which included parts of present-day Colorado) in 1777, Bautista de Anza set out from Santa Fe on 15 August 1779, in search of Comanche Chief Cuerno Verde and his formidable band. Bautista de Anza wrote in his diary that the Comanche chief "had exterminated many pueblos, killing hundreds and making as many prisoners whom he afterwards sacrificed in cold blood" (Thomas, 1932:66).

Rather than travel eastward over the Taos Mountains and then north toward the Arkansas River, Bautista de Anza traveled northward along an untried route through the San Luis Valley into Colorado in an attempt to evade discovery by the enemy. He outfitted his force of 573 men with guns, ammunition, provisions, and horses and organized his command into three divisions. On 20 August they were joined by 200 friendly Utes and Apaches just north of the present-day Colorado–New Mexico border near Antonito. From 22 August through 24 August, they moved at night in order to avoid detection. The group crossed Poncha Pass at the northern end of the San Luis Valley on 26 August, then spent the next day traveling 24 km "through a very narrow canyon with almost inaccessible sides, and considerable water," costing them "considerable work to conquer" (Thomas, 1932:128). On 28 August 1779, after crossing the Arkansas River near where Salida is now located, they continued northeastward along the mountainous Ute Trail into South Park. They paused for a day in an arroyo, thought to be in Herring Park (upstream on Herring Creek and within 2 km of Porcupine Cave), to refresh their horses and to dress out and prepare the meat of 50 head of buffalo they had killed within 10 minutes from among a large herd that had interrupted their march. On 30 August Bautista de Anza and his troops left South Park by way of the Cripple Creek area, then traveled over the Front Range just south of Pikes Peak.

Bautista de Anza attacked the Comanches near the Rio de Sacramento (now Fountain Creek) on 31 August 1779, then returned south to Santa Fe via Taos. The number of Comanche dead was estimated at 131 and total leagues traveled during the expedition at 540 (this would equal 2600–3000 km, depending on what kind of "league" was meant) (Lluch, 1962).

A suit of Spanish armor was reportedly found in a rock crevice in the southwestern part of South Park (Simmons, 1966). If the account is true, the suit probably belonged to one of Bautista de Anza's soldiers, for that expedition was the only recorded penetration of South Park by the Spaniards.

EXPLORERS

One of the first American explorers in South Park was Lieutenant Zebulon Montgomery Pike (Simmons, 1966). Following the Louisiana Purchase, Thomas Jefferson sent Pike to explore the area around the headwaters of the Platte River in 1806. Pike followed Oil Creek (Fourmile Creek on present-day maps) into South Park in the Elevenmile Canyon Reservoir area. His expedition camped several nights in South Park during December 1806 and left the park through Trout Creek Pass to the southwest (Scott, 1975).

The party of Lieutenant John C. Frémont of the Army Corps of Topographical Engineers traveled from Pueblo to St. Vrain's Fort via Manitou Springs, Ute Pass, South Park, and North Park in 1842; Frémont came through South Park again in 1844 on his way from California, returning through South Park in 1845. The trapper Kit Carson, who was very familiar with the South Park region, was his guide for at least two of the trips.

The most notable explorations of South Park were the government surveys under the direction of Ferdinand V. Hayden, U.S. Geologist. Hayden's *Report(s) of the . . . Territories* (1873, 1874) incorporated reports from various accompanying specialists, including geologists, mineralogists, paleontologists, zoologists, and geographers. During the first trip of the Hayden Survey into South Park in 1869, the crew entered the basin from the west over Trout Creek Pass, visited the area around the salt springs and Horseshoe Mountain, examined mining and placer operations around Fairplay, and then exited over Kenosha Pass at the north end of the basin. Persifor Frazier Jr., the survey party's mining engineer, described the salt works and the process of salt extraction (Hayden, 1873). Hayden himself (1873) stated that, although very interesting from a geological point of view, the origin of the salt springs remained somewhat obscure to him. Fieldwork during June and the first two weeks of July in 1873 in South Park was much more thorough than that carried out during the 1869 expedition. Survey geologist Dr. Albert C. Peale and other members of Hayden's party reported extensively on the geology of South Park (Hayden, 1874). F. M. Endlich exhaustively examined and reported on the geology in the area surrounding Porcupine Cave, which was known to them as "Ice Cave" (Hayden, 1874; Bloch, 1946).

Captain George M. Wheeler's expedition for the Army Corps of Topographical Engineers, under the direction of Lieutenant W. L. Marshall, also surveyed South Park in 1873 and 1874 (Goetzmann, 1966; Simmons, 1990). Members of both Hayden's and Wheeler's expeditions camped together in the Upper Arkansas Valley near Twin Lakes (Simmons 1990).

TRAPPERS AND TRADERS

Simmons (1966) reported on the fur trappers and traders who journeyed into South Park. James Purcell, a trader, and Ezekial Williams, a mountain man, were two of the earliest Americans of European descent to travel in the basin, arriving between 1800 and 1810. They were followed by Jim Beckwourth, Bill Williams, and one of South Park's more famous visitors, Kit Carson. Carson, along with a group led by Thomas Fitzpatrick, spent the winter of 1830 trapping in the mountains surrounding the basin. Carson then moved on to the salt springs (Salt Works in figure 4.1), where he joined the Gantt party of trappers. Joseph Meek and William Sublette also trapped in the region in the mid-1830s. Many of the trappers during the 1830s were with the Rocky Mountain Fur Company, and furs from South Park were transported down the Arkansas River to Bent's Fort, the first permanent trading post in Colorado. By 1845 the trappers were essentially out of business, silk having replaced fur in hats and beaver skins being no longer in demand for coats. Carson continued trapping in South Park into the 1850s, however, leaving the area in 1852. Beaver were trapped to near-extinction in Colorado during the 1800s, and the last wild bison in the state were killed in Lost Park in Park County in February 1897 (Armstrong, 1972).

Minerals

GOLD AND SILVER PROSPECTING AND MINING

Most of the gold found in South Park came from mineral veins and lodes high in the adjacent mountains and in the thick gravels in the stream valleys. Pleistocene glaciers eroded these mountain deposits, and the streams carried the gold far into the valley, where flakes and nuggets would later attract the attention of prospectors. Gold was reported from South Park as early as 1806, when James Purcell (called Pursley by Pike) told Zebulon Pike of his findings (Simmons, 1966), and nuggets were picked up by trappers during the 1830s and 1840s. Gold mining in South Park did not flourish, however, until the late 1850s, after which it continued into the early 1870s. When hydraulic mining replaced the uneconomical one-man placers, Chinese workers were brought into South Park as cheap labor. In the 1860s the population of the camps began to dwindle, and some were nearly abandoned. Silver gradually brought the area back to life in the early 1870s, and this boom lasted until the Sherman Act of 1893 demonetized silver; subsequently, many of the camps were permanently abandoned. Gold mining was revived briefly as recently as the 1920s, when the South Park Dredging Company began work on the Platte River southeast of Fairplay (Simmons, 1966). Dredging continued until the start of World War II, then began again in 1945 and continued until the early 1950s, when it was discontinued as uneconomical (Simmons, 1966). Placer deposits on Sacramento Creek near Fairplay are still being actively worked today.

MINING CAMPS

Many of the old mining camps and towns existing in the South Park area during the 1800s are shown on the James McConnell School Supplies map of Colorado originally published in 1894 (Pezolt, 1894). That map also shows the geographic names used at the time.

Tarryall, located about 6.4 km northwest of present-day Como on Tarryall Creek (not to be confused with the later settlement of Tarryall located near Tarryall Reservoir in the southeast corner of South Park), boomed in 1859 and saw as many as 13 hydraulics in operation and 300 men working in the area. Hamilton was platted in the spring of 1860 opposite the town of Tarryall on the south bank of Tarryall Creek (Fossett, 1878). By 1868, Tarryall and Hamilton had all but disappeared (Bowles, 1869).

Buckskin Joe's Diggings was a mining district 12.8 km northwest of Fairplay named after Joseph Higganbottom, called Buckskin Joe because of the tanned deerskin clothes he wore. The town of Lauret was established in 1859 in this district, and within three years there were eight steam quartz mills crushing the ore brought into town (*Rocky Mountain News,* 1862). Lauret became the first county seat in Park County.

Fairplay, the current county seat of Park County, and Alma are still active towns in South Park. Fairplay was known first as "Fair Play," then as "Fairplay Diggings," and was called "Platte City" in 1861 (*Miners' Record,* 1861). Its name was changed to "South Park City" in 1869 (Janes, 1869) and remained so until 1874, when it was changed back to Fairplay by the Tenth Territorial Council and House of Representatives (Fossett, 1878). Alma was established at the junction of Buckskin Creek and the South Platte River in 1873, primarily as a supply source for the miners. Fossett (1878) mentions a small smelter in Alma in the late 1870s.

The Trout Creek Mining District, the closest mining district to Kaufman Ridge and Porcupine Cave and one where many claims were staked, extended for about 19 km south of Buffalo Peaks, with a width of 6–10 km (Emerson, 1881). Chubb's Ranch, the settlement at the top of Trout Creek Pass, was within this district. Mining camps near Porcupine Cave included Calumet, noted for rich magnetic ores and large deposits of marble; Turret, near the Independence mine, where copper and gold were produced; and Whitehorn, situated east of Cameron Mountain and one of the larger camps of its time. Wallace and Lawson (1998) and Wallace et al. (1999) describe the geology and mineral potential in the area immediately surrounding Porcupine Cave.

Flynn (1952) mentions other towns, camps, and mining districts that were established in the mid- to late-1800s: Quartzville, located on the east face of Mount Bross in the Independent District; Hillsdale, a lumber camp for the men who furnished the timbers for the mines on North Star Mountain and Mount Bross; Sterling, located in the Mosquito Mining District about 1.6 km south of Lauret; Dudley, whose residents were connected either with the Moose Mine on Mount Bross or with the Dudley smelter; Horseshoe, located about 9.6 km west of Fairplay in the Horseshoe Mining district at the south end of the Mosquito Range; and Leavick, one of the later mining camps in South Park, established in the early 1890s and abandoned in 1921. Balfour was a gold mining site south of Hartsel and southwest of Current Creek Pass where mining continued from 1893 to 1900 (Nutt, 1983). The Montgomery District, which was platted in 1861 about 16 km west of Hamilton and 11.2 km northwest of Lauret (*Rocky Mountain News,* 1861), boomed quickly and declined just as quickly, with only one house still occupied in 1868 (Bowles, 1869).

Prospect pits, adits, and tailings throughout South Park are evidence of the widespread investigation of hundreds of potential sites by prospectors during the 1800s. One of these sites resulted in the discovery of Porcupine Cave, discussed later in this chapter.

COAL MINING

Mining of coal from Late Cretaceous beds flourished near Como in the late 1870s and early 1880s. The South Park Coal Company and the Como Iron, Coal, and Land Company were active in the area and provided coal to the railroads. The Chinese laborers also made their mark in coal mining, having moved into the area from Fairplay to take over the jobs when the other miners went on strike. After an explosion in 1885, many of them left those jobs, and, when the coal mining industry collapsed in the 1890s, most of the remaining Chinese left South Park (Barth, 1997). Coal mining in South Park was limited, never achieving the local impact of gold and silver mining.

SALT WORKS

Salt produced at the Salt Works (figure 4.1), a manufacturing plant located on Salt Creek 4.8 km north of Trout Creek Pass, was used primarily for chloridizing ore, although some was used for domestic and ranching purposes (Simmons, 1966). Lipsey (1959) noted that the Salt Works was established in 1866 by Charles Hall, who homesteaded the ranch where the salt springs were located. The plant was an L-shaped building, approximately 48 m long in the main wing and 21 m in the other; 18 cast iron evaporating kettles brought from Missouri by ox or mule team were used in the extraction of the salt. Legal action over the ownership of the land and the resultant financial problems brought a halt to the operations of the Salt Works after only three years. The source of the salt is undoubtedly from the near-surface Pennsylvanian strata, which contain evaporites, including halite. Dissolution collapse of the evaporites resulted in numerous sinkholes north of this area and south of Fairplay (Shawe et al., 1995).

PEAT MINING

Peat, used in landscaping, has been strip-mined from South Park's wetlands, damaging a number of them. Much of this important habitat for rare plants, plant communities, aquatic and semiaquatic macroinvertebrates, and aquatic beetles has been irreversibly altered or completely destroyed. Sanderson and March (1996) estimated that peat mining has removed nearly 20% of South Park's extreme rich fens. (Cooper describes these fens and the associated ecosystems more fully in chapter 3.)

OIL AND GAS WELL DRILLING

Drilling for oil and gas in South Park has spanned more than a hundred years, beginning in the early 1890s, when the first test well was drilled (Cullen, 1960). Oil Creek (Fourmile Creek on present-day maps), which the explorer Pike followed into South Park, had been named several years earlier from the oil seeps prevalent along its banks. Some of the companies active in South Park have included the McDannald Oil Company, headed by A. T. McDannald (who had acquired the Hartsel Ranch in 1946), which drilled three wells south of Hartsel; the Shell Oil Company, which sank six wells east of Hartsel in 1956 (Cullen, 1960; Simmons, 1966); and the Geary Oil Company, which drilled one well in 1967 and two stratigraphic tests in 1970 (De Voto, 1971). There have been both oil and gas shows in tests, but no wells have been completed as commercial producers in South Park. Active oil and gas exploration continues today.

URANIUM MINING

Subeconomic uranium was found by the Tidewater Oil Company during their drilling of 200 exploration holes in stratified sedimentary deposits in South Park during the late 1950s. Several other companies, including Kerr-McGee Corporation and the Getty Oil Company, drilled exploratory holes in the 1960s, but exploration for uranium had diminished greatly by the 1970s (De Voto, 1971).

Ranching in South Park

The first ranches in South Park were established soon after the first gold mining strikes in the 1850s. Fairplay became as much a ranching center as a mining center. The excellent grazing land in South Park is one of the primary reasons that cattle ranching became the most stable industry in the area. Hay grown in this area has been shipped as far away as Kentucky and even to England as feed for racehorses. The right of landowners having no access to streams to appropriate and divert water to their land also played an important part in the development of this industry. In the 1890s the U.S. government established forest reserves and assessed fees for grazing cattle on these reserves. Following the creation of the Forest Service in 1905, these reserves became national forests (Simmons, 1966). Today fee-grazing continues on Colorado State and Bureau of Land Management acreage as well as on forest service lands. Since the 1950s, water rights have been aggressively pursued by east-slope municipalities.

Some of the more notable ranches in South Park include the Salt Works Ranch, initially homesteaded by the Charles Halls in the early 1860s; the Hartsel Ranch, established in 1862 by Samuel Hartsel, which grew to be the largest ranch in Colorado and one of the largest in the nation by the late 1950s (Bair, 1959); the Guiraud ranch, located on the South Fork of the South Platte in the water gap in Red Hill, established by Adolph Guiraud, who also claimed the first two permanent ditch rights for agricultural purposes in 1861 (Simmons, 1966); and the Stirrup Ranch, homesteaded in 1880 and eventually owned by Wharton H. Pigg (Everett, 1966a).

Other ranches of importance in the park, as noted by Everett (1966a) and Huntley (1976), included the Santa Maria Ranch, the Elkhorn Ranch, the Spinney Ranch, the Switzer Ranch, the IM Ranch on Badger Creek near Black Mountain, the

Badger Springs Ranch northwest of Hartsel, and the VVN Ranch northwest of Black Mountain.

Lon and Badger Gribble were well-known early ranchers; Badger's son Dudley ran horses on Black Mountain (Everett 1966a). The Bassham family first homesteaded in Nathrop in 1870, and Bassam Park was named after George Bassham, who farmed a large area in South Park (Shaputis and Kelly, 1982).

In unpublished personal remembrances, Mary Ann Parrott Locke (1996) told of her father Clarence Parrott homesteading in South Park in March 1917. Clarence had crossed Kansas in 1916 with several wagons of family members, in what they believed was the last organized wagon train to South Park. Clara McDannel ran away from home at the age of 25 and traveled from Illinois to Salida to marry Clarence Parrott in July 1917. Born in 1931, Mary Ann recalled that during her childhood there were wild horses in South Park. Although some of the cattlemen did not approve of the presence of sheepmen in South Park, Clarence and Clara Parrott, accompanied by Rufus Marshall, traveled to New Mexico in 1928, where they purchased sheep that were shipped by train to Salida, then trailed up the Ute Trail to the ranch. When Clarence began selling off his property in South Park, he wanted to keep the peace between the sheepmen and the cattlemen, so he sold part of it to Rufus Marshall, an employee of the Parrotts, and part of it to Tom McQuaid, a cattleman from the Salt Works Ranch.

Everett (1966a) described his ancestors Galatia and Caroline Sprague, who arrived in Colorado in the 1860s by covered wagon pulled by teams of oxen. They homesteaded the ranch now owned by the Everett Land and Cattle Company, the present-day Everetts being fifth- and sixth-generation descendants of the Spragues. The Everett Cow Camp is located several miles up the Ute Trail from Salida toward Hartsel at the site of the Whitehorn mining camp, not far from Porcupine Cave. Glen Everett has been politically active as a Chaffee County commissioner.

Shaputis and Kelly (1982) related the story of Henry Fehling, who came to Chaffee County from Cincinnati in the late 1880s, lived on Cottonwood Creek, and later bought the Rooks Ranch. Drought forced him to move to the valley, where he acquired the Franz Ditch and the Crymble Ranch. Soon he bought another 160 acres and a log house, then went on to purchase several more parcels of land. Henry's son Frank worked for other ranchers as well as his father and eventually bought the Nachtrieb Ranch at Nathrop. Frank Fehling became a Chaffee County commissioner in the mid-1930s and was a member of the Colorado state legislature from 1939 to 1947. Glen McMurry, the son of Frank Fehling's sister Katherine and Elmer McMurry, started working as a cowhand, went on roundups, and rode with other cowboys of the day: Bill Dunlap, the Everetts, the Cogan brothers, Tom McQuaid from the Salt Works Ranch, Bill Hallock, and Frank Christopher. Henry Fehling chose his nephew Glen McMurry to take over the home place. When Frank and Winniebell Fehling moved to the Nachtrieb place, Glen and his wife Margaret moved to the McMurry home south of Nathrop and eventually purchased the McMurry Ranch from his uncle Frank Fehling. When he retired in 1975, Glen sold the ranch to his son Frank. Following in the footsteps of his uncle Frank Fehling, Frank McMurry has also been a Chaffee County commissioner. The Fehling and McMurry holdings are now operated by the McMurry Land and Cattle Company, and Porcupine Cave is located on McMurry land.

Transportation in South Park

EARLY TRAILS AND WAGON ROADS

Several natural passes, including Kenosha, Wilkerson, Trout Creek, and Hoosier, open through the mountains into South Park. Early trappers, traders, explorers, prospectors, and miners reached South Park on foot or horseback following old Indian trails through these passes (see map by Scott, 1975). Wagon roads were eventually built through the passes into South Park in the late 1850s and early 1860s, some of them as tollways. These roads opened up South Park to stage lines and freight companies. Among the companies operating in the park were the Denver-Leadville Stage Line, the Overland Express, the Southern Stage Company, and the Central Overland California and Pikes Peak Express Company. Early stage lines offered overnight accommodations in South Park at Kenosha House and Case Stage Station on the west side of Kenosha Pass and at Michigan House between Kenosha and Hamilton on Michigan Creek, as well as at Eight-Mile House on Tarryall Creek, 3.2 km east of Como.

RAILROADS

Two railroads were constructed through South Park to Buena Vista in an effort to provide a faster and more direct route to the mining camps, and another smaller rail line was constructed near Fairplay. Numerous trees were cut throughout South Park to provide the railroad ties; today many barren hills sport tree stumps. The trains carried supplies to the miners, including groceries, machinery, and feed for the animals, and hauled out ore, bullion, and coal. They also brought tourists to the area from Denver, Colorado Springs, and points east.

The Denver, South Park and Pacific Railroad was incorporated in 1872 as a narrow-gauge line, and grading of the road began in mid-August 1873 (Everett, 1966b). The line was constructed from Denver, over Kenosha Pass to Jefferson and Como, past the Salt Works to Trout Creek Pass (arriving there in December 1879), and then on into Buena Vista (arriving there on 22 February 1880) (Everett, 1966b; Porrata, 1979; Shaputis and Kelly, 1982). Locomotives on the line were given names evocative of the territory through which the trains ran, such as Fairplay and Platte Canyon (Poor, 1976).

Building of the standard-gauge line by the Colorado Midland Railway Company proceeded from Colorado Springs through Manitou Springs and up Ute Pass, then behind Pikes Peak and down Twin Creek to Florissant and Lake George.

From there the route followed the South Platte River up Elevenmile Canyon and across South Park through Hartsel, then over Trout Creek Pass and on to Buena Vista, which the railroad reached by 1885 (Shaputis and Kelly, 1982). At the top of Trout Creek Pass, also known as Hill Top, the Colorado Midland crossed over the top of the Denver, South Park and Pacific line on an 8.7-m iron girder bridge (Shaputis and Kelly, 1982).

The small Denver, South Park and Hilltop Railway Company constructed a line through Horseshoe to the foot of Horseshoe Mountain and a branch line to Leavick in the mountains near Fairplay (Flynn, 1952). Several other railroads were proposed for South Park, but they never materialized. Although not actually in South Park, the Denver and Rio Grande Railroad also ran through Buena Vista, the railroad line having arrived there in 1885 (Shaputis and Kelly, 1982).

The Colorado Midland Railway Company stopped its passenger and freight service in 1918 and dismantled its line in 1921 (Simmons, 1966). The Denver, South Park and Pacific Railroad tried during the 1920s and early 1930s to obtain government approval to abandon its line, but the tracks were not pulled up until 1938 (Simmons, 1966). Although their tracks have been gone for over 60 years, remains of the grades of these two railroads can still be seen in South Park and in the Trout Creek Pass area.

Other Activities in South Park

RELIGION

Notable among South Park's religious leaders was Father John Dyer, an itinerant Methodist minister. He preached his first sermon by a campfire in the Mosquito Mining District on 25 August 1861 (Dyer, 1890). Dyer built a crude shelter of poles and pine boughs at Sterling, where he lived for several weeks. He hired himself out as a miner and mail carrier for additional income. Dyer was known as the "snowshoe itinerant" because of the long Norwegian skis that he used to traverse the park and mountain passes during the winter. Other South Park preachers included Methodists William Howbert and Benjamin Crary, and Catholic circuit preachers Nixon Buckner, Father Joseph Machebeuf, and Father Henry Robinson (Nutt, 1983).

EDUCATION

In 1866 Fairplay had a school in a log cabin, and by the early 1890s several one-room schools existed throughout South Park (Simmons, 1966). South Park's schools today are consolidated into one district centered at Fairplay.

COMMUNICATION

The *Miners' Record,* published weekly from 4 July to 14 September 1861 in Tarryall, was the first newspaper in South Park (Flynn, 1952). Buckskin Joe had a newspaper, the *Western Mountaineer,* as early as 1862 (Nutt, 1983). The first copy of the *Chaffee County Times* was published in 1880; the *Buena Vista Herald* appeared in 1881; and George Newland published the first issue of the *Buena Vista Democrat* in 1883 (Porrata, 1979). The *Fairplay Flume* began in 1879, the *Park County Republican* was first published in 1912, and they merged in 1918 (Nutt, 1983). The *Park County Republican and Fairplay Flume* continues as a weekly publication in Park County today. Telephone lines were extended into Buena Vista in 1893 by the Colorado Telephone Company (Porrata, 1979).

VARIOUS BUSINESSES

Breweries found thirsty clients in the miners; South Park Lager Beer was brewed in Fairplay starting in 1866 (Simmons, 1966). Dairy farming near Jefferson was so successful in the 1890s that a cheese factory was located there (Simmons, 1966). Rancher Samuel Hartsel was also a successful entrepreneur, building a sawmill, trading post, wagon shop, and blacksmith shop; he also developed the hot springs and built a hotel across the river at Hartsel (Simmons, 1966). Although sightseeing expeditions had begun in South Park in the 1830s and 1840s, when bison sightings and Indians were the attraction, it was the Colorado Midland Railway that brought tourists to Hartsel's hotel and hot springs during the late 1880s through the 1910s (Simmons, 1966). The railway also ran weekly and daily Wildflower Excursion trains during the summer in an attempt to increase its passenger traffic (Simmons, 1966). Shaputis and Kelly (1982) reported that the first grist mill west of the Mississippi was built in 1879 by Charles Nachtrieb at Nathrop (the name was derived from Nachtrieb) on what is now Frank McMurry's ranch. Many of the original cupboards in the house on the ranch were made from lumber salvaged when the mill was torn down in the mid-1950s.

CIVILIAN CONSERVATION CORPS

The Civilian Conservation Corps was established in 1933 to employ U.S. male citizens during the Great Depression. One of their camps, located near Trout Creek, was active for several years before closing in 1938 (Shaputis and Kelly, 1982; Simmons, 1990). In an attempt to prevent erosion in the area, the men built check dams and contoured terraces and planted willows along Badger Creek, Herring Creek, and Castle Rock Gulch; thousands of acres were planted with pine trees.

FUN AND GAMES

The baseball game between Alma and Sacramento on 5 July 1880 was termed the "first ever considerable game of baseball" in South Park by the *Fairplay Flume* (Barth, 1997:205). A footrace was held between cowboys and railroaders in 1883, and in 1893 there were pony races, a 0.4-km horse race, and an 0.8-km trotting race (Barth, 1997). Today Fairplay still remembers the partnership of the miners and their burros with its annual World Championship Burro Race over Mosquito Pass (Nutt, 1983).

OUTLAWS

The Espinoza brothers, Jose and Vivian, left a trail of blood through South Park in 1863 (Bair, 1959; Simmons, 1966). The Espinozas were religious fanatics from deep in New Mexico who killed their victims with a shot to the forehead or by driving a pine stick into their foreheads. The brothers entered South Park in 1863 via Ute Pass, leaving dead men in their wake. Two murders on Red Hill Pass, an attempted murder on the road to Fairplay, and then two more victims on Red Hill Pass brought out a posse of seventeen men to track the killers. They found the Espinozas on West Fourmile Creek near Thirtynine Mile Mountain and killed Jose; Vivian managed to escape. (According to another version [Barth, 1997], the brothers were named Vivian, who was killed, and Felipe, who escaped.)

Simmons (1966) told of Jim Reynolds and his gang, who entered the park in 1864. They were more intent on making a fortune than on murder, specializing in robbing stage coaches, ranches, and stage stations. A posse followed them to the Canon City area, where several gang members were captured; however, several more escaped to New Mexico.

Of Burros, Bears, and Dogs

The tales of the burros Prunes and Shorty, the dog Bum, and Old Mose, a notorious grizzly and one of the last grizzlies in the park, are prominent in South Park folklore.

According to Bair (1959), Prunes (1867–1930) was owned by Rupert Sherwood and packed so long for the gold mines in the Alma-Fairplay district that few could remember when he had started. Prospectors would send him down the mountain with a note tied to his saddle; he would return with his packs filled with food and supplies for the miners. His reward was a lump of brown sugar and pancakes. He witnessed Indian raids, lynchings, the coming of the railroads, and the start of the cattle ranching business. After many years of service, Rupert retired Prunes; he grew fat on handouts from the townspeople. After barely surviving a severe blizzard, Prunes was mercifully released from his life in the mining community. When Sherwood died in 1931, his ashes were buried with Prunes' remains. In 1943 a radio broadcast of *Death Valley Days* featured the heroic Prunes.

The story of Shorty and Bum is summarized from Shirley (1994). A granite monument stands on the courthouse lawn in Fairplay, recognizing the relationship between Shorty, a burro with unusually short legs, and Bum, a dog that "bummed" his way around the town and into the hearts of the residents during the late 1940s and early 1950s. Shorty, like Prunes, had worked in the mines near town. When his owner moved on, Shorty was left to fend for himself. As he grew older, his eyesight gave out, and he had trouble searching for food. It was about this time that Bum discovered Shorty in a pasture near the edge of town. Bum became Shorty's seeing-eye dog and led Shorty from house to house begging for food. The duo made many friends in town and never went hungry. They were given shelter on cold nights by the courthouse janitor, usually in his garage, and, on one particularly cold night, in the jail. One spring morning, several years later, Bum was chasing a chipmunk, as dogs sometimes do. Without his dog to guide him, Shorty stepped into the street, was hit by a car, and died. His remains were cremated. Ironically, only a few weeks later, Bum stepped into the path of a semitrailer truck and was also killed. Bum was buried beside Shorty, inseparable in death as they were in life.

Bair (1959) tells about the grizzly bear Old Mose, named for the way he would mosey along when he traveled. The bear was notorious for spreading terror along his 480-km range from the Utah border to his headquarters on Black Mountain. J. W. Hall, who owned a ranch a few miles from the old Stirrup Ranch, was treed by Old Mose and lived to tell about it. Jake Radliff, a famous hunter, was hunting with Henry Seymour and a man by the name of Cory. Each had gone off in his own direction to hunt when Radliff crossed the path of Old Mose near the Park County–Fremont County line. Old Mose circled around and attacked him from behind, severely mauling him. When he cried out for help several minutes after Old Mose had left, the grizzly returned and mauled him again. Cory was the first to reach Radliff, who was still conscious and talking; he told Cory of the attack before losing consciousness. Cory and Seymour carried Radliff to the Mulock Ranch on Badger Creek, where he succumbed to his injuries before medical help could arrive. Pop Rudolph of Canon City was killed by Old Mose on Cameron Mountain. J. W. Asher also lost his life to Old Mose. A skeleton of a cowboy believed to have been killed by Old Mose was found on Thirtynine Mile Mountain. Cattle were killed and fences were torn down on the Stirrup and other nearby ranches.

Wharton H. Pigg, who owned the Stirrup Ranch in 1904, contracted with J. W. Anthony, a noted bear hunter, to hunt down and exterminate Old Mose. Anthony brought his pack of 30 trained bear dogs with him, and for two months they tracked and hunted the grizzly. Death finally came to Old Mose, surrounded by Anthony's dogs, on 26 April 1904, after he took six shots from the hunter's 30-40. Mose was said to weigh 450 kg after hibernation (today's grizzlies in Yellowstone and Glacier parks weigh 90–180 kg) (Bruggers, 1999). His carcass was estimated to weigh 225 kg, he measured 2.7 m from head to tail, and he was reported to have been shot nearly a hundred times before the end came. The bear had lost two toes and a portion of his left hind foot in a trap, and a claw was missing from his right forefoot. Today the pelt and skull of Old Mose reside in a climate-controlled locker at the University of California, Berkeley (Bruggers, 1999) (figure 4.2).

The true age of Old Mose is unknown. Simmons (1966) stated that there was a bounty on his head for 35 years. Bair (1959) reported that he was 40 years old when killed. Copies of correspondence between James Perkins and David Brown, in the appendix to Perkins (1991), indicate that one of Old Mose's teeth was sectioned in the Arizona Game and Fish

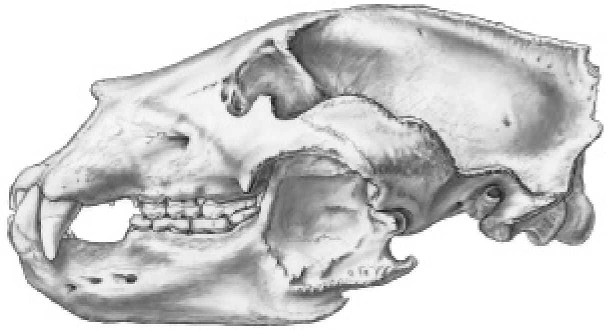

FIGURE 4.2 Old Mose. Skull, University of California, Berkeley, MVZ 113385. (Drawn by Karen Klitz.)

Department's laboratory by Bill Carrell, a specialist in determining age from teeth. He concluded that Old Mose had been 10–12 years old at death.

Porcupine Cave

Discovery and Early Exploration

Porcupine Cave (figure 4.3; see also figure 2.3) is located on Kaufman Ridge, which extends southeast from Trout Creek Pass. It is thought that prospectors first noticed iron oxides on the surface of the hill where the cave is located. Because iron oxides were sometimes surface indicators of gold and silver deposits, they began their diggings, which led to the discovery of the cave. Following an iron-rich fissure into the hill, they shored up their diggings through the loose rubble, and, after building approximately 12 m of adit, accidentally broke through into Porcupine Cave, possibly as early as the mid- to late 1860s.

The date 1890, written in candle smoke, has been found on the ceiling in the Pit and is the oldest known date in the cave. Bloch (1946) wrote that the cave was known to the Hayden Survey party (probably F. M. Endlich in 1873) and to the historian Hubert H. Bancroft as "Ice Cave" because of all the gypsum crystals on the walls, which sparkled like ice under candle and torch illumination. However, after extensive library research, including reading the surviving journals from the Hayden Survey, an exact reference to the cave as "Ice Cave" has not been confirmed.

James M. Eubanks, a homesteader in the area, was the first documented explorer of the cave, as reported in the *Colorado Springs Gazette* in its Annual Edition of 8 March 1925. One article in the *Gazette* stated that the government had set aside 320 acres of land surrounding the cave for a national monument. It planned to open the cavern, believed at the time to be so extensive as to exceed the size of Mammoth Cave in Kentucky. According to another article in the same issue of the *Gazette,* Coloradoans who had been in the cave declared that, once exploration was completed, the cavern would be comparable to the Cave of the Winds near Colorado Springs. Eubanks claimed that the cave had three levels and that the rooms were filled with stalactites and stalagmites, many weirdly shaped. This article is the first record of the name Porcupine Cave being used; the cave was so named because of the porcupines that occupied the adit leading to the cave. In reality Porcupine Cave is nothing like it was presented in 1925. It never became a national monument, and most of the sparse stalactites and stalagmites that were probably in existence over 75 years ago have long since disappeared. Porcupine quills and droppings were found in the adit and on the cave floor near the entrance during the 1980s.

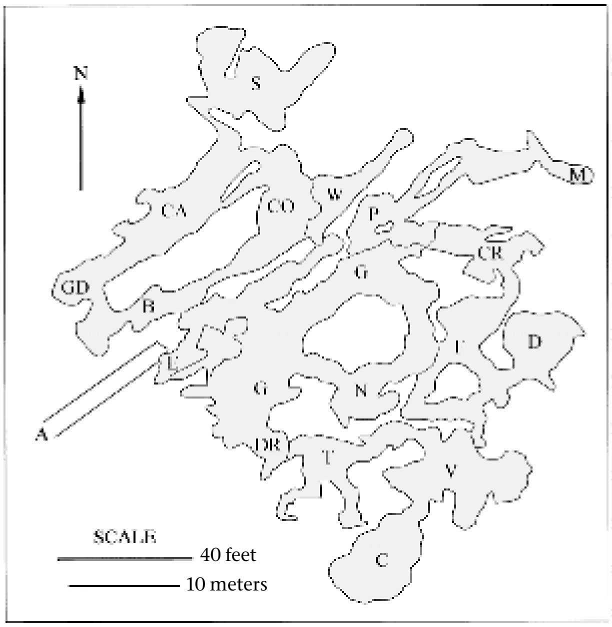

FIGURE 4.3 Generalized map of Porcupine Cave. *Abbreviations:* A, 1800s mine adit; B, Badger Room; C, Chessman Room; CA, Come-A-Long Room; CO, Chicken-Out Dome; CR, Crystal Room; D, Davis Room; DR, Damp Room; E, Discovery Entrance; F, Ferret Room; G, Gypsum Room; GD, Generator Dome; M, Memorial Day Room; N, New Passage; P, the Pit; S, Squat Room; T, Tobacco Road Passage; V, Velvet Room; W, White Room (lowest level of cave). (Modified from Barton, 1997.)

History of the Ownership of the Porcupine Cave Property

Park County records reveal that Jacob G. Decker of Denver applied for the first claim to the property surrounding the cave on 13 May 1922, to use it for cattle ranching under the Homestead Act of 1909. This claim was first contested in 1925 by Lawrence E. Frees of Buena Vista, Colorado, then by Walter A. Filmer, who applied for a claim to the land on 23 October 1928 and patented said claim on 7 February 1931. In March 1931 he sold the land to cattle rancher Frank M. Fehling while keeping easement rights to the cave with an option to purchase it and develop it as a "scenic attraction and a curio." His easement rights ran out in 1941, and the land, including the cave, became the sole property of Fehling, who in 1962 passed it on to Glen McMurry, the father of the present-day owner of the cave. James Eubanks filed a claim on the adjoining section of land on 10 February 1922, before any filings were made on the cave property. It is the authors' belief that Eubanks thought he had filed on the section including the cave and had truly planned to develop it. Shortly after Filmer filed on section 23, Eubanks sold his acreage in section 22 to Frank Fehling.

Mapping and Use by Cavers

By the mid-1940s members of local grottos (regional clubs of cavers within the National Speleological Society) were exploring Porcupine Cave (Bloch, 1946). Since then, cavers from the Colorado Grotto, as well as the Front Range Grotto (Denver) and the Southern Colorado Mountain Grotto (Colorado Springs), have used the cave as a beginner's cave because it is a fairly simple cave to explore, especially after ladders were installed in the more difficult vertical places.

Halliday (1952) reported the first survey of the cave by Warren Pettee, Don Bloch, Jim Hroch, Bill Moore, John Thrailkill, John Streich, and Dick Tagg, members of the Colorado Grotto, the Colorado Mountain Club, and students at the University of Colorado; their map was published in *Caves of Colorado* (Parris, 1973). Because the known area of the cave had nearly doubled in size through the explorations of 1986, the cave was again surveyed in 1987 by members of the Colorado Grotto, and a new map of the cave was drawn by Kirk Branson. In 1997 Hazel Barton, with the assistance of members of the Colorado Grotto and the Front Range Grotto, resurveyed the cave. The resulting map, greatly improved and much more accurate (including two very detailed cross sections through the cave), is reproduced in this volume as figure 2.3.

Recent Excavations

Donald L. (Don) Rasmussen, a geologist, paleontologist, and caver, and his son Dalton (Larry) went into the cave in 1981 in hopes of exploring new parts of the cave and digging out blocked passageways that they had seen in photographs taken by Kirk Branson a few weeks before. It was during this trip that Larry first noticed bones and teeth in the debris being excavated along the wall in the Pit area of the cave. Although the bones and teeth appeared to be from recent animals, Don recognized a horse incisor and realized they were dealing with fossils rather than modern-day animal remains. They also found dirt balls called nodules on the floor of the Pit, some of which contained bones and teeth. Rasmussen made several trips to the cave that year, accompanied at times by friends and family, and he brought home samples of the fossils and nodules for study. Exploration of the cave and the search for new fossil sites continued at a slow pace for several years.

Kirk and Don opened several blocked passageways in Porcupine Cave during the spring and summer of 1986 (Branson and Rasmussen, 1987). They connected the Gypsum Room with another previously known part of the cave with approximately 3 m of new passageway. Two small domed rooms were discovered above this passageway. In late July they dug through 1.2 m of collapsed passageway in a remote part of the cave and entered three new rooms through a very dangerous loose rockslide. One room was completely white with fine gypsum crystals; the second, the highest of the three, was lined with soft, yellow limonite; and the third and smallest room contained cave coral and dogtooth spar. To prevent possible injury to inexperienced cavers, Rasmussen and Branson sealed the entrance to these three rooms after their discovery.

On 3 August 1986, Don Rasmussen, his wife Geraldine (Jerry), Kirk Branson, and Zach McGuire opened a blocked passageway of the cave and found a large unexplored area of the cave that turned out to be highly fossiliferous. To enter this section one had to ascend a 2.4-m chimney (a tubelike vertical passageway) dug through cave fill, then traverse a 7-m-long, 0.5-m-high crawlspace before dropping off a 1.5-m ledge into a small room with a flowstone stalactite hanging at about eye level on the other side of the room. From there, one continued through a short "duck-under" into the largest room in this new cave section. Walking lightly on the floor, which crunched with every step, the explorers found an ancient stalagmite, 2.4 m tall and 1.8 m across, in the middle of the room. A second eroded stalagmite, 1.8 m tall and 2.4 m across, stood approximately 4.5 m to the right of the first one. To the right of the second stalagmite was an old wood rat midden, approximately 4.8 m long and 2.1 m wide in the middle. The large room was named the Velvet Room by Jerry for the Velvet Tobacco tin found on the midden, which, without doubt, had been hauled into the room by wood rats. The smaller room was named the Penny Room for a penny used for scale in photographing the flowstone stalagmite. The 6.9-m crawlspace connecting the new rooms with the previously known cave was named Tobacco Road because it was the route to the tobacco tin.

In the spring of 1987 the Chessman Room was opened by Don Rasmussen and John (Jack) McKelvy through an extremely dangerous blocked passageway from the Velvet Room called the Widow Maker. This room is the nearest room to the surface and one of the largest in the cave. Plant roots hang through cracks in the ceiling, water flows down the walls after a heavy rainstorm or the melting of snow at the surface, stalactites actively form, live insects and bats have been seen, and Ordovician nautiloids protrude from the wall. This room received its name from the small statuettes of limestone on the floor, which have been eroded by dripping water to form a pattern resembling chessmen on a board. Clusters of pebbles on the floor have been polished by the dripping water.

The last room to be opened in Porcupine Cave was the Memorial Day Room, opened over Memorial Day weekend in 1988 by Don and Jerry Rasmussen. They had been exploring leads at the end of a passageway leading out of the Pit when they broke through into the new room. It was completely white with gypsum crystals and had a mud-cracked floor that crunched when stepped on, as had the floor in the Velvet Room. The Memorial Day Room is a narrow, dogleg-shaped room and is the room farthest from the entrance. A small opening in the back wall blows air, indicating additional uncharted cave beyond.

The Tale of the Velvet Tobacco Tin

The Velvet Tobacco tin found in 1986 in the Velvet Room of Porcupine Cave contained a 47-year-old "note in a bottle." The tin had been thrown into the cave in 1939 by two cowboys who were working for Frank Fehling at the time; it was carried from there to the midden by wood rats. The cowboys, Lloyd (Monk) Marshall and Elvis (Happy Jack) Conner, were on their way to a rancher's private rodeo when they passed by the entrance to the cave. On a whim, Marshall wrote a note on a piece of paper that he and Conner signed, put in the tin, and tossed into the cave. The note read: "June 14, 1939, Buena Vista, Colo, The one who finds this Note Please drop us a line Lloyd Marshall Buena Vista Colo Elvis Conner, Nathrop, Colo." After several phone calls to various Marshalls listed in the Buena Vista telephone directory, Kirk Branson first located a cousin of Lloyd Marshall, then his sister, then Lloyd himself, who was living in Oregon. Shortly before Marshall's death in 1988, Branson visited him in Oregon and showed him the tobacco tin with the note he had signed many years ago. Elvis Conner has not been located.

Fossils in Porcupine Cave

Don and Jerry Rasmussen took the fossils collected in 1981 to the University of Kansas the following year for comparison with the mammal collections there. With the help of Larry Martin and Robert (Bob) Hoffmann, professors of vertebrate paleontology and mammalogy, respectively, most of the mammals were tentatively identified. In 1984 Don gave the fossils to Peter Robinson, curator of vertebrate fossils at the University of Colorado Museum of Natural History, for study and possible curation. In May 1985, Don Rasmussen met in Denver with his friend Anthony D. (Tony) Barnosky, then of the Carnegie Museum of Natural History, and told him about the fossil finds in Porcupine Cave. At that time Barnosky, already familiar with cave faunas in the Appalachians, was interested in locating deposits that would similarly elucidate mammal response to climate change in the Rockies. Barnosky went to the cave for the first time with Rasmussen in September 1985, to collect a sample of bones and teeth to take back to the Carnegie Museum for radiocarbon dating and further study, with plans to return the following summer. The bones were found to be older than the 50,000-year limit of the dating process and thus attracted immediate interest.

Rasmussen contacted Frank McMurry, the owner of the cave, explained the possible significance of the cave as an important fossil site, and gained permission for paleontological excavations within the cave. Barnosky returned in July 1986 with his Carnegie field crew, collected specimens from different parts of the cave, and began an excavation site in the Pit. Among the several hundred specimens collected, Barnosky later identified two extinct Irvingtonian (middle Pleistocene) rodents that lived at least half a million years ago (Barnosky and Rasmussen, 1988). This find indicated that the fauna in Porcupine Cave was much older than had been expected and sparked intense interest in the high-elevation Pleistocene fossils of Porcupine Cave—interest that continues today.

Local volunteers led by Don Rasmussen worked side by side in Porcupine Cave with the Carnegie Museum crews in the late 1980s. At the same time, Denver Museum volunteers led by Elaine Anderson were investigating the modern biota in the Porcupine Cave area. Carnegie Museum excavations in the cave ceased in 1990, by which time the work in the Pit, the Velvet Room, and a number of other localities in the cave had produced tens of thousands of specimens. This material was eventually curated into collections at the Carnegie Museum and the University of California Museum of Paleontology, Berkeley. Understanding the significance of the finds by Carnegie and the landowner's interest in keeping the fossils in Colorado, Rasmussen encouraged the Denver Museum of Nature and Science to become a repository for Porcupine Cave fossils in 1992. Led by Don Rasmussen until 1998, crews from the Denver Museum and Western Interior Paleontological Society continued excavations in the cave, especially in the Velvet Room; each field season produced new discoveries, which have been curated at the Denver Museum.

Summary

South Park's history is indeed rich, its activities varied, and its stories fascinating. From the American Indians who inhabited or visited the area hundreds of years ago to the paleontologists of today, each group has left its unique mark. Whether gold or silver, oil or uranium, unknown territory waiting to be explored, a bountiful hunting land, lush ranchland, or Pleistocene fossils, South Park's treasures are in the eye of the beholder. Now South Park has attained fame as the location of Porcupine Cave, the preeminent high-elevation Pleistocene fossil site in North America.

Acknowledgments

The authors acknowledge the assistance of the staffs of the Western History Section of the Denver Public Library (central branch), the Stephen H. Hart Research Library of the Colorado State Historical Society, and the Archives Section of the United States Geological Survey Library in Denver. We thank the members of the Colorado Grotto and Front Range Grotto of the National Speleological Society for mapping Porcupine Cave in 1987 and 1997. Karen Klitz, Museum of Vertebrate Zoology artist at the University of California, Berkeley, graciously provided figure 4.2; Don Rasmussen assisted with figures 4.1 and 4.3. We thank our spouses, Don Rasmussen, Beth Branson, and Sue McKelvy, for their patience and assistance during the time spent researching and writing this chapter. Special thanks are due to the McMurry family for their gracious hospitality and continued support of paleontological excavations in Porcupine Cave. Most of the excavation work was done by volunteers under the supervision of professional leaders from the Carnegie Museum of Natural History, Denver Museum of Nature and Science, and University of California Museum of Paleontology. Primary funding for the excavations and associated research was provided by National Science Foundation grant BSR-9196082 to A. D. Barnosky; other funding came from private donations and institutional budget allocations.

FIVE

The Geology and Speleogenesis of Porcupine Cave

ROBERT G. RAYNOLDS
Denver Museum of Nature and Science

Porcupine Cave is a relatively small, dry cave with approximately 600 m of mapped passageways. The cave entrance is located within the Lower Ordovician Manitou Dolomite on the west face of a north-south-trending ridge in southern South Park, Colorado (figures 5.1, 5.2). This chapter describes our present understanding of the formation and evolution of the cave. Although well known for its Pleistocene fauna, the cave and its environs also preserve a fascinating record of the geological events that created the sepulcher containing the fossil material. The geological story of the cave is first presented from the vantage point of the regional setting, then from the perspective of the cave interior.

Geology of the Porcupine Cave Area

The Manitou Dolomite accumulated on a broad, stable, westward-facing cratonic shelf bathed in shallow, well-oxygenated marine waters teeming with life (Foster, 1972; Gerhard, 1972; Stewart and Poole, 1974). After deposition as fossiliferous limestone, the strata were largely transformed into dolomite in the Porcupine Cave area, a process of recrystallization that obliterated much of the Ordovician fossil record.

At the cave site, the Manitou Dolomite is a 55-m-thick, well-bedded, gray, resistant unit (figure 5.3), which forms substantial cliff faces topped by the extremely resistant Harding Quartzite. The dolomitization process is incomplete, and close examination of the Manitou reveals layers in which crinoid debris occurs. A locally mappable series of algal nodule beds is found 12 m above the base. These nodules are each about 1 cm in diameter and occur in a series of 20- to 80-cm-thick layers over a 2- to 5-m zone that has been traced along the entire ridge face. The same horizon has been found on adjacent ridges in the area, and similar algal nodules have been reported from the Manitou by Chronic (1964:106) and Gerhard (1972:9). The Manitou is rich in chert beds, the chert occurring as isolated concretions, concretion-rich beds, and thin laceworks of chert interwoven with dolomite. Chert colors range from cream to brown and black. In plan view some of the chert concretions appear to be filling in regular networks of cracks or burrow systems.

In the cave area, the Manitou Dolomite was deposited directly on a low-relief, lightly weathered Precambrian granite surface. Basal Cambrian quartzites, which are common elsewhere in Colorado, were either eroded or not deposited in this region. Fluctuations in sea level resulted in the accumulation of a succession of transgressive and regressive deposits (Gerhard, 1972) as well as in episodic subaerial exposure and erosion. Prior to the deposition of the overlying Ordovician Harding Quartzite, the surface of the Manitou Formation was exposed and subjected to intense weathering. A karst surface with orange-red soils formed on the unconformity. In places, cavities and fissures were etched tens of meters down into the carbonate rock (figure 5.4). Burial by the Harding Quartzite and younger strata entombed the weathered surface. By establishing deep zones of weakness and pathways for fluid flow, this Paleozoic weathering set the stage for later cave formation and established a Paleozoic ancestry for Porcupine Cave.

Uplift of the Ancestral Rocky Mountains in the Pennsylvanian caused the Paleozoic shelf sediments to be eroded from the crest of a series of basement-cored uplands (Mallory, 1958, 1972; De Voto, 1972; Kluth and Coney, 1981), the closest being the Hartsel Uplift (the western flank of the ancient Frontrangia uplift), which is exposed 30 km north-northeast of Porcupine Cave (De Voto, 1971). In the cave area, the landscape changed dramatically from a low-relief passive margin to an intermontane basin termed the Eagle Basin. This basin was invaded by an arm of the western sea and hosted accumulations of dark, organic-rich shale. The Early to Mid-Pennsylvanian (Morrowan and Atokan) Belden Shale characterizes the deep and possibly anoxic marine embayment. In places, evaporites also occur (Shawe et al., 1995). The margins of the narrow basin are characterized by thousands of meters of arkosic

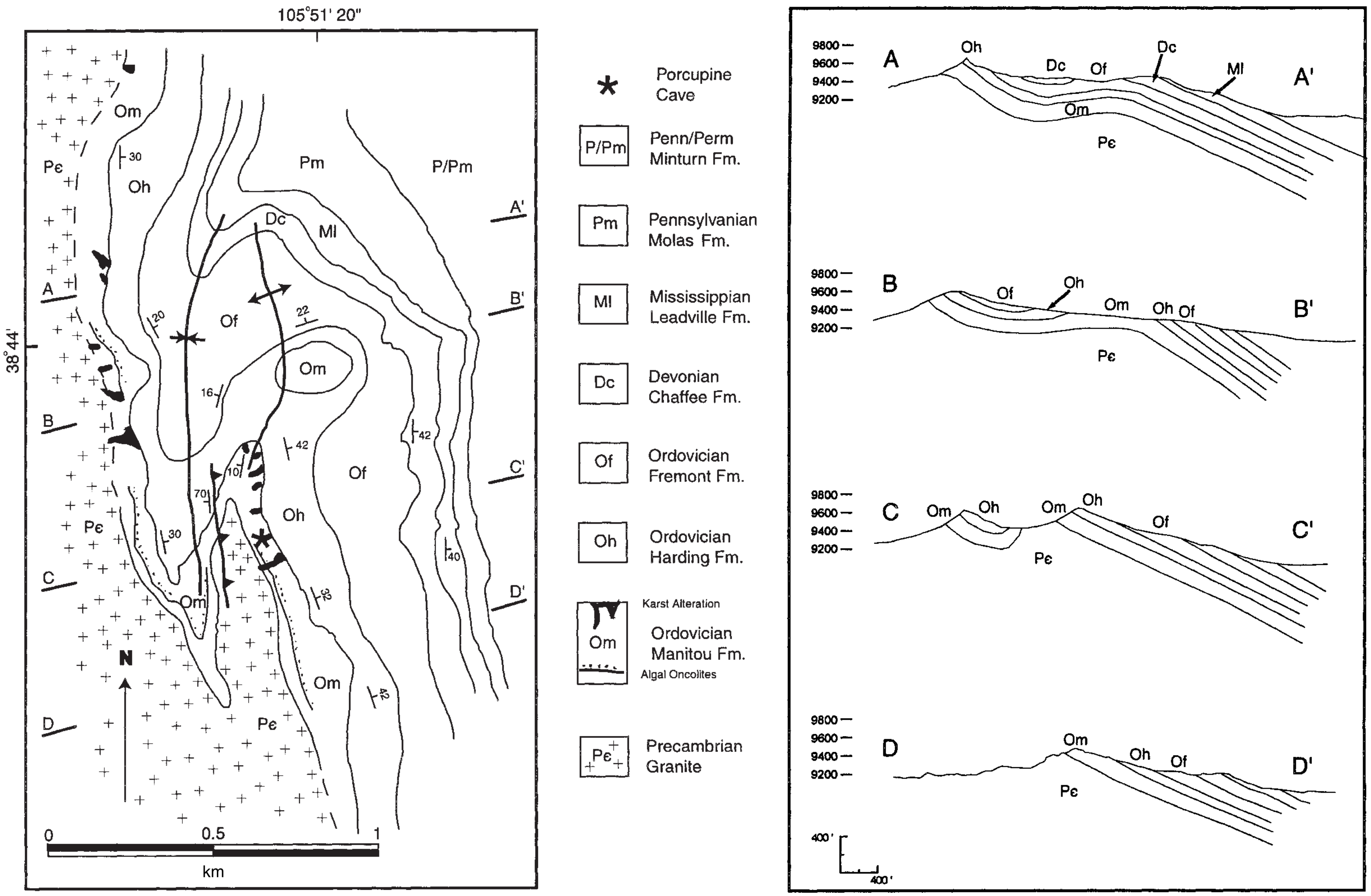

FIGURE 5.1 Geological sketch of the vicinity of Porcupine Cave. The asterisk marks the entrance to Porcupine Cave. (Modified from Quinlivan, 1959.)

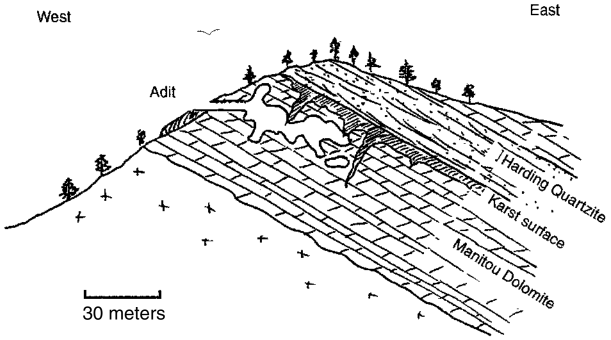

FIGURE 5.2 Cross section showing inclined strata and Porcupine Cave. The resistant Harding Quartzite forms the ridge crest.

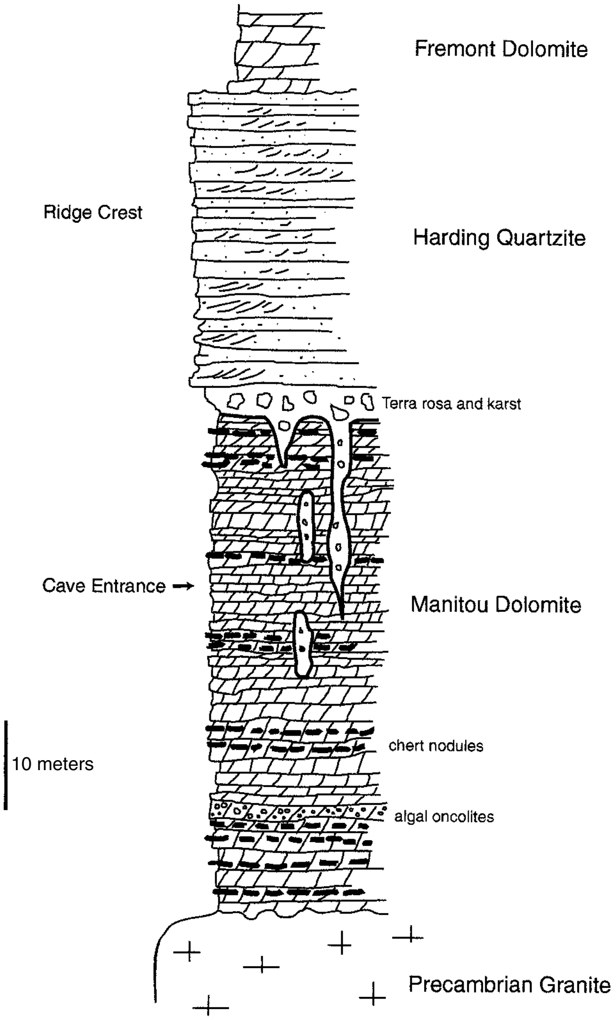

FIGURE 5.3 Stratigraphic section at Porcupine Cave. Black blebs are chert zones; note the layer of algal nodules about 12 m above the base of the Manitou Dolomite.

synorogenic debris belonging to the Mid-Pennsylvanian through Early Permian (Atokan through Wolfcampian) Minturn and Maroon formations. These formations are represented by well-exposed redbeds south-southeast of the cave and by dark shales to the west of the cave site. The site was probably buried by more than 2 km of this strata, requiring subsidence of a comparable amount (c in figure 5.5).

During a period spanning more than 100 million years in the late Paleozoic and early Mesozoic, the Ancestral Rocky Mountains were worn down, and a regional unconformity was mantled by the Jurassic Morrison Formation. The South Park area was for a second time reduced to a low-relief landscape. This gentle Jurassic alluvial plain was inundated by the Cretaceous Interior Seaway about 100 Ma ago. Although Cretaceous strata have since been entirely eroded from the vicinity of the cave, one can develop an estimate of what was once there by examination of regional facies distribution patterns and subsurface drilling data (e.g., Ettinger, 1964). The Manitou Dolomite was buried by an additional cover of more than 1000 m (e in figure 5.5). After regression of the Interior Seaway to the southeast about 70 Ma ago, the area was again a gently undulating coastal plain. The Laramie Formation with its characteristic coal deposits (Washburne, 1910) was deposited across South Park.

Approximately 67 Ma ago the area was uplifted by the Laramide Orogeny, and the Front Range east of the cave site was borne high along the east-dipping Elkhorn thrust (Sawatsky, 1964). At the cave site, strata dip about 35° to the east. The tilting is associated with a series of east-dipping thrusts and gentle north-south basement-involved folds. It is likely that the deformation is Laramide in age, as it reflects the style of widespread Laramide compressive deformation documented in South Park by Ettinger (1964) and Sawatsky (1964). Andesitic volcanoes mantled the deforming land in lava flows (Raynolds, 1997). Large volumes of synorogenic debris making up the South Park Formation were shed to the west of the rising Front Range. It is probable that the compressional deformation resulting in the tightly faulted anticline at the cave site took place during this time and that the cave site was uplifted as overlying strata were breached by erosion (f in figure 5.5). After termination of the Laramide Orogeny the landscape around the cave site was subjected to a long period of weathering, which resulted in the development of yet a third low-relief, gently rolling surface, with the resistant Harding Quartzite holding up ridges (De Voto, 1971).

At the end of the Eocene a series of lava flows and ignimbrites crossed this landscape, flowing along easterly trending valleys located both north and immediately south of the cave site (Epis and Chapin, 1975). The principal ignimbrite, the Wall Mountain Tuff (36.7 Ma), swept as far east as the Denver Basin. The cave ridge stood above these flows, and the ignimbrites are preserved as relict patches, some of which, with their characteristic obsidian cooling rinds, are still present in the paleovalleys surrounding the cave. The erosional surface defined at this time has been termed the Rocky Mountain Surface, and it is a very widespread, low-relief surface covering many thousands of square kilometers (Epis and Chapin, 1975; Epis et al., 1980; Bradley, 1987; Chapin and Kelley, 1997). It is probable that, as the land around the cave was slowly etched

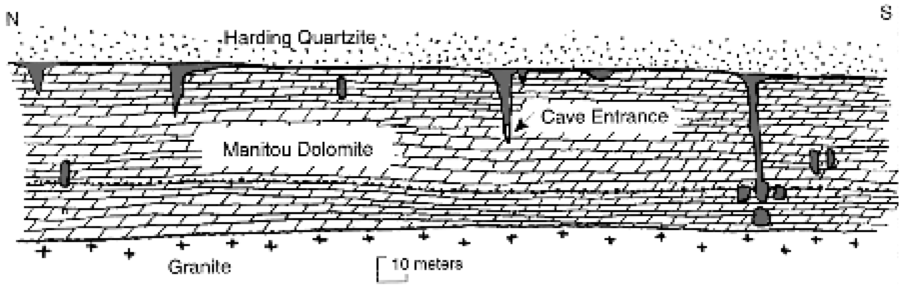

FIGURE 5.4 Panel diagram of the ridge containing Porcupine Cave. Note that, besides Porcupine Cave, there are numerous other karst fissures extending well down into the Manitou Dolomite. There are probably additional undiscovered caves along this ridge.

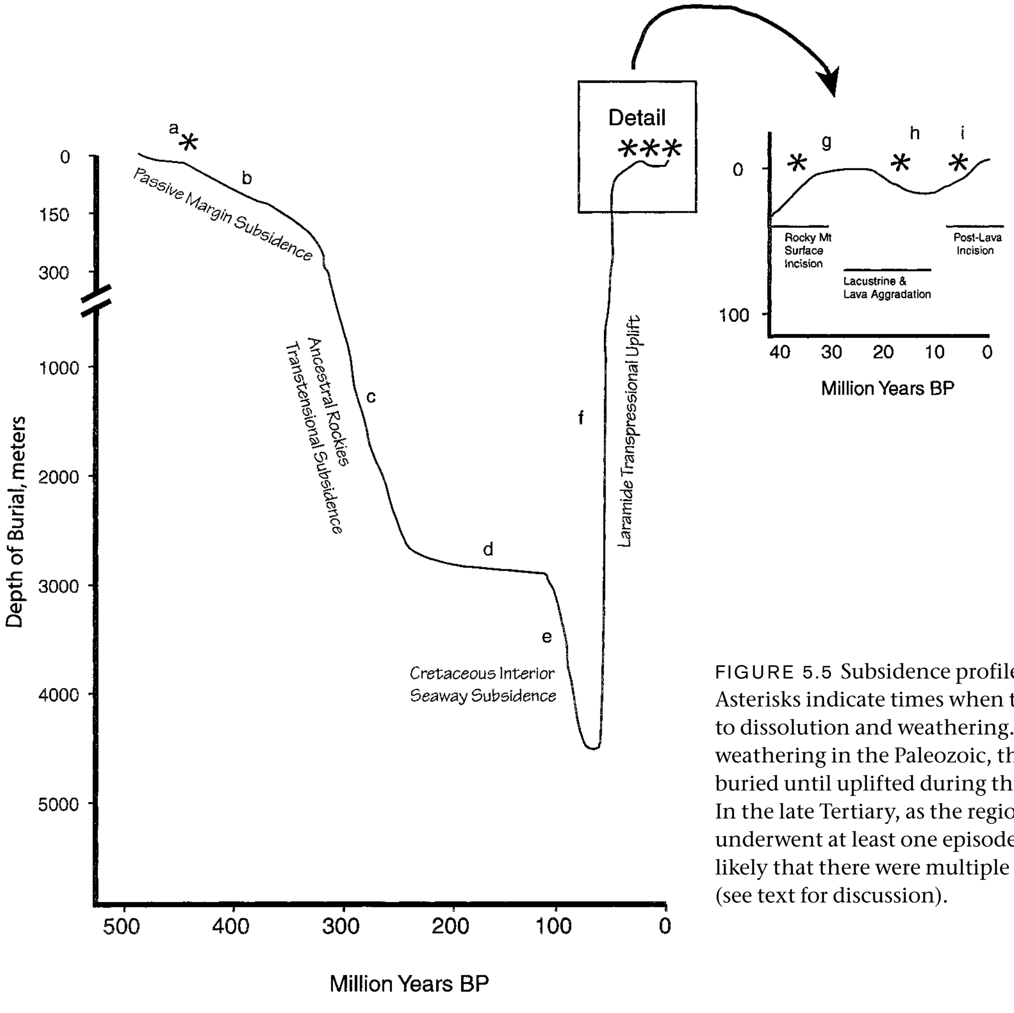

FIGURE 5.5 Subsidence profile at Porcupine Cave. Asterisks indicate times when the cave area was prone to dissolution and weathering. Note that, after initial weathering in the Paleozoic, the cave strata were deeply buried until uplifted during the Laramide Orogeny. In the late Tertiary, as the region was weathered and underwent at least one episode of aggradation, it is likely that there were multiple times of cave formation (see text for discussion).

by this phase of erosion, the groundwater table was fluctuating near the elevation of the cave (g in figure 5.5). Dissolution may have taken place along the old fissures and joints defined by the Paleozoic karsting. This gives the cave the potential for a Mid-Tertiary phase of development.

After the ignimbrites flowed past, the area around the cave ridge aggraded several hundred feet (h in figure 5.5) until about 8.57 ± 0.16 Ma ago (Chapin and McIntosh, pers. comm., 1997), when a small basaltic volcano erupted just 2.5 km southwest of the cave. A hornblende/olivine-rich tongue of scoriaceous mafic lava flowed east from the vent. The morphologies of both the vent and the flow are still evident south of the cave. The lava is resistant to erosion and forms inverted topography where the flow, which once covered the valley floor, now forms a resistant ridge at about the same elevation as the cave (2915 m). Once again the groundwater table may have been at the elevation of the cave site (i in figure 5.5), and the cave may have been further enlarged. This gives the cave a potential Late Tertiary phase of development.

To the east of the cave site, a thick package of Middle to Late Miocene lacustrine strata accumulated on the gently subsiding floor of the South Park basin. The lacustrine facies is termed the Wagon Tongue Formation, and the proximal gravely facies are termed the Trump Formation (De Voto, 1964). Relicts of both facies occur in the Herring Park area south and west of the cave. Wagon Tongue facies sediments can also be found beneath the Late Miocene lava flow south of the cave.

Over the past eight million years the valley has again been down-cut, exhuming the remnants of the Wall Mountain ignimbrite and the Eocene paleovalley, leaving the cave high above the modern water table.

During the Pleistocene, the cave area saw a series of ponded bogs, and fens formed on the valley floor in South Park. Some of these are still present in the area, and some have been dissected by modern erosion. One or more sinkhole-type openings formed over the now dry cave, allowing access for Pleistocene fauna. It is likely that much of the fauna was carried in by wood rats and carnivores, although the presence of disarticulated bones from a large camel suggests that some animals may have fallen into an open chasm. Small rodents and carnivores used the cave for many thousands of years until the openings became choked with sediment, sealing the cave. The cave and its contents awaited discovery by nineteenth-century miners prospecting along the weathered unconformity at the top of the Manitou Dolomite. Ore bodies are concentrated at a similar unconformity on the top of the Mississippian Leadville Limestone.

Porcupine Cave Interior

The record of cave formation inside Porcupine Cave mirrors some of the complexity deduced from the regional geological history. Based on cross-cutting relationships, the earliest features in the cave are elongated veins and fissure fills of strongly altered dolomite with intense limonitic weathering. These features probably derive from the Paleozoic karst surface that developed on the Manitou Dolomite during subaerial exposure prior to accumulation of the Harding Quartzite. Analysis of the ridge adjacent to the cave reveals a series of fissures and weathered zones deep in the Manitou that all emanate from this unconformity (figure 5.4). The modern entrance to the cave is located at the base of an adit cut into one of these mineralized fissures by unsuccessful prospectors.

Much of the cave is composed of rooms cluttered by extensive rock falls in which slabs of roof rock have collapsed to mantle the floor. In areas where the cave has not collapsed, speleothems provide evidence that the cave was once wet. Carbonate dissolution and precipitation actively sculpted the interior of the cave.

Two styles of speleothem growth are evident (figure 5.6). An early conformable phase of calcite encrustations, which drape and mantle the cave surfaces, suggests deposition below water. A superimposed deposit of horizontally bedded calcite- and gypsum-rich interlayered material suggests deposition in a cave partially filled by water.

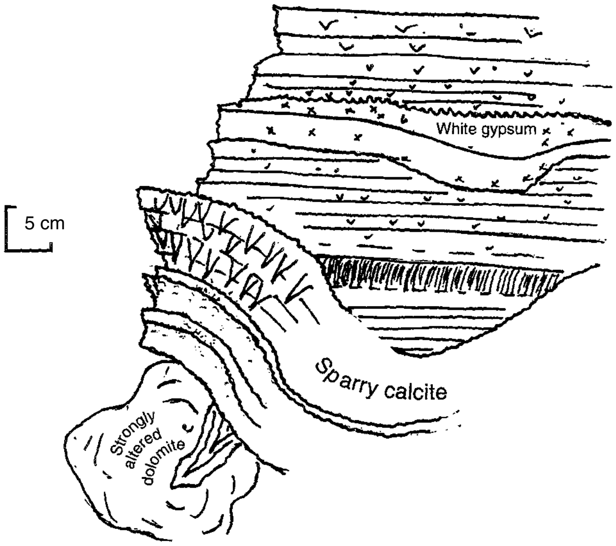

FIGURE 5.6 Speleothems in the Gypsum Room. Note the multiple episodes of speleogenesis, each associated with a characteristic style of carbonate precipitation.

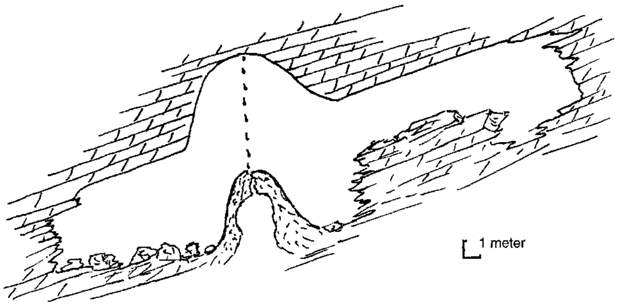

FIGURE 5.7 Hollow stalagmite in the Velvet Room. Note that the stalagmite is positioned directly below a cupola. Although this area of the cave is completely dry today, the evidence indicates past episodes of calcium carbonate precipitation and dissolution.

In many parts of the cave where the ceiling has been stable, a series of cupolas developed. These hemispherical features are often over a meter in diameter and appear to be incised perpendicular to the inclined strata. The cupolas formed from dissolution of carbonate by waters that condensed on the cave ceiling. Directly beneath the cupolas occur a variety of poorly defined and corroded stalagmites (figure 5.7). The stalagmites tell an interesting story. In addition to being generally degraded, they are hollow and dissected. They grew at a time when slowly dripping water focused by the cupolas was supersaturated with calcium carbonate dissolved from the cave roof. At a later time, conditions changed, the falling fluids became corrosive (undersaturated in calcium carbonate), and the stalagmites were eviscerated.

Careful analysis of the strata bearing the Plio-Pleistocene fossils indicates that they were deposited under varying degrees of wetness in the cave. In the Velvet Room, for example, the well-bedded DMNH excavation (DMNH 644) suggests sorting by water of particles on a low-relief debris cone. Although water may not have flowed over the alluvial cone, it is clear that depositional conditions varied sufficiently abruptly to produce stratification. The same is evident in the area where the camel bones were discovered in Tobacco Road. In the Pit (CM 1925), alternating muddy nodules and massive silts have been interpreted to represent alternating wet and dry conditions within the cave (Barnosky and Rasmussen, 1988). Other localities like Mark's Sink (DMNH 1349) are more chaotic and are suggestive of cave fill by slow collapse of roof materials and gradual, random aggradation of dry debris.

The variable style of filling has had a dramatic impact on the nature of the faunal record. Several small excavated sites in the cave have little or no stratigraphic context. Sites excavated in the Gypsum Room and the Badger Room are examples of this. In other cases, such as Mark's Sink (DMNH 1349), significant excavations have been made in materials that are very poorly bedded to nonbedded in character. In this case, the superposition of fossil material is known but the relative ages are still unclear.

In some places in the cave, accumulation of sediment took place in a sufficiently systematic pattern to impose visible stratification and preserve stratified fauna. The DMNH Velvet Room excavation (DMNH 644), the Pit (CM 1925), and the CM Velvet Room excavation (CM 1927) are all examples of this style of deposition.

Acknowledgments

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SIX

Magnetostratigraphic Constraints on the Age of Pleistocene Fossiliferous Strata in Porcupine Cave's DMNH Velvet Room Excavation

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Strata from the Velvet Room in Porcupine Cave contain an abundant and diverse vertebrate fossil record that suggests biostratigraphic ages ranging from as old as 2.0 Ma ago in Mark's Sink (DMNH 1349) to as young as 600 Ka ago in the upper levels of the DMNH Velvet Room excavation (DMNH 644). Unfortunately, few external constraints on stratal age are available. This chapter attempts to improve the confidence of age assignments of the Velvet Room strata through paleomagnetic sampling and analysis.

The aim was to assess whether polarity reversals occur within the section, and if so how they correlate to the Global Magnetic Polarity Time Scale and to the occurrence of taxa within the fossiliferous strata. A combination of normal and reversed magnetic polarity signatures characterizes the sediments, providing the basis for a magnetostratigraphic calibration of fossil age.

Geological Setting of DMNH 644

The sampled strata are from a small alluvial cone (DMNH 644) located on the west side of the Velvet Room in Porcupine Cave (figure 6.1). Systematic excavation identified a succession of well- to weakly bedded gravelly to silty unconsolidated strata approximately 3 m thick. The bedding is best developed within the upper meter of the succession, which is also the most fossiliferous.

DMNH 644, known as the DMNH Velvet Room excavation (and also as the Velvet Room Main Dig), was excavated between 1992 and 1997. A set of 26 grid squares 2 ft (~0.6 m) on a side were established by Donald L. Rasmussen prior to excavation. Over six years the grids were excavated by volunteers from the DMNH under the direction of D. L. Rasmussen, Robert G. Raynolds, and Louis H. Taylor. Each grid was excavated separately in a series of more than 30 levels. The levels were 2–4 cm thick in the upper 1.5 m of excavation and somewhat thicker in the rocky strata extending down to 3 m. The levels were assigned numbers, with level 1 being the youngest. During excavation, careful sketches were made of the vertical faces of unexcavated grids. Examination of the vertical faces revealed gentle depositional dips of up to 20° defining a small cone of alluvial debris. A systematic analysis of the excavated levels based on field notes, sketches, photographs, and measurements permitted the assignment of each level from each grid to one of 18 horizons designated alphabetically, with the youngest being A and the oldest being R. (See chapter 2 for more details about the excavation process.)

The sampled strata present several issues in terms of paleomagnetic interpretation. To begin with, they are very poorly sorted and include grains up to granule and pebble in size. This poor sorting means that the measured vectors may be an artifact of the detrital orientation of large magnetic grains. This problem is probably not important for two reasons. First, most of the detrital grains are from the Paleozoic carbonates that constitute the cave walls, which generally lack a strong magnetic character. Second, the data demonstrate that individual samples, sites, and populations of samples exhibit relatively consistent primary and demagnetization behavior. This finding implies that random physical orientation of large detrital grains with respect to the primary rock magnetic field is a minor factor in the sample.

The strata are completely nonindurated. Although this characteristic facilitates the excavation of fossils, it makes paleomagnetic collection and analysis difficult. We employed a variety of sampling and measurement techniques and a range of demagnetization spectra. The results are locally consistent and match across samples, sites, and methodologies. This finding implies that loose magnetic grains and sampling artifacts play a negligible role in the final results.

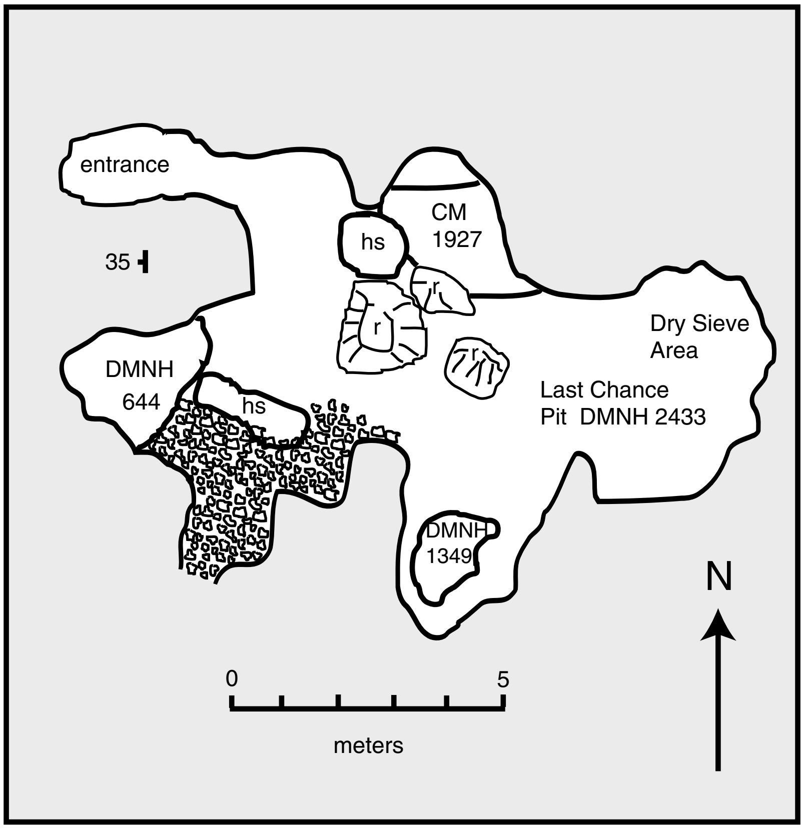


FIGURE 6.1 Map of the Velvet Room. The samples described in this chapter were obtained from DMNH 644. Other excavations in the Velvet Room are shown, as are hollow stalagmites (hs) and large rocks (r). Approximate dip of the roof rock is 35° west in the area indicated by the strike/dip symbol at the upper left of the diagram.

Materials and Methods

Oriented samples were collected from the upper 110 cm of strata (figure 6.2), using a range of tools and techniques, from 1993 to 1995. All samples were analyzed at the University of Southern California's Paleomagnetics Laboratory. Measurements were taken using both spinner and cryogenic magnetometers, with the strongest samples measured on the spinner.

The 1993 samples were collected by R. G. Raynolds by cutting small pedestals in the strata the size of the 2 × 2-cm sample boxes. These samples were exposed to alternating field (AF) demagnetization at steps of 0, 50, 100, 200, 400, 700, and 1000 Oe.

The 1994 samples were collected by workers from the Porcupine Cave project under the direction of R. G. Raynolds. The workers exhumed a small rectangular prism of strata. This oriented pedestal was then covered in plaster and removed from the cave. This specimen, roughly the size and shape of a football, was impregnated with epoxy and dissected for samples. The 30 samples retrieved were subjected to AF demagnetization at steps of 0, 50, 100, 200, 400, and 700 Oe.

The 1995 samples were collected using a hand-held piston coring tool by S. Julio Friedmann. The operator inserted a rectangular metal sheath directly into the strata parallel to bedding. The sheath was removed with a small volume of intact and undisturbed sediments. A plastic box was placed over the end of the sheath, and a plunger extruded the sediments as a plug directly into the sample box. These samples were epoxied in their boxes and were later subjected to AF demagnetization at 0, 50, and 100 Oe; higher demagnetization was not possible owing to sample problems.

Sample groups from the same strata were compiled into sites 1–12 (figure 6.2) and separated into class I and class II sites based on several criteria. The Fisher statistics (Fisher, 1953) of individual demagnetization steps were analyzed on stereonet plots. Zijdervelt plots (Zijdervelt, 1967) were used to recognize multiple magnetic remanence vectors within samples. Class I sites required three samples per site, 2σ values less than 60°, and *k* values of greater than 2 near final demagnetization. Class II sites required a minimum of two samples with 2σ less than 120°. Sites with poorer data were disqualified. The vectors from suitable samples were used to calculate virtual geomagnetic poles (VGPs) for each site. These samples were then arranged into a reversal stratigraphy.

Results

Characteristic Remanences

All samples showed evidence of normal polarity overprinting. Some of this magnetization was viscous and weak, and it was easily removed in the earliest phases of AF demagnetization. However, some samples showed strong vectors indicating normal polarity (figure 6.3A). These vectors plotted directly upon the modern inclination and declination for Porcupine Cave for most of their demagnetization trajectory. Such samples

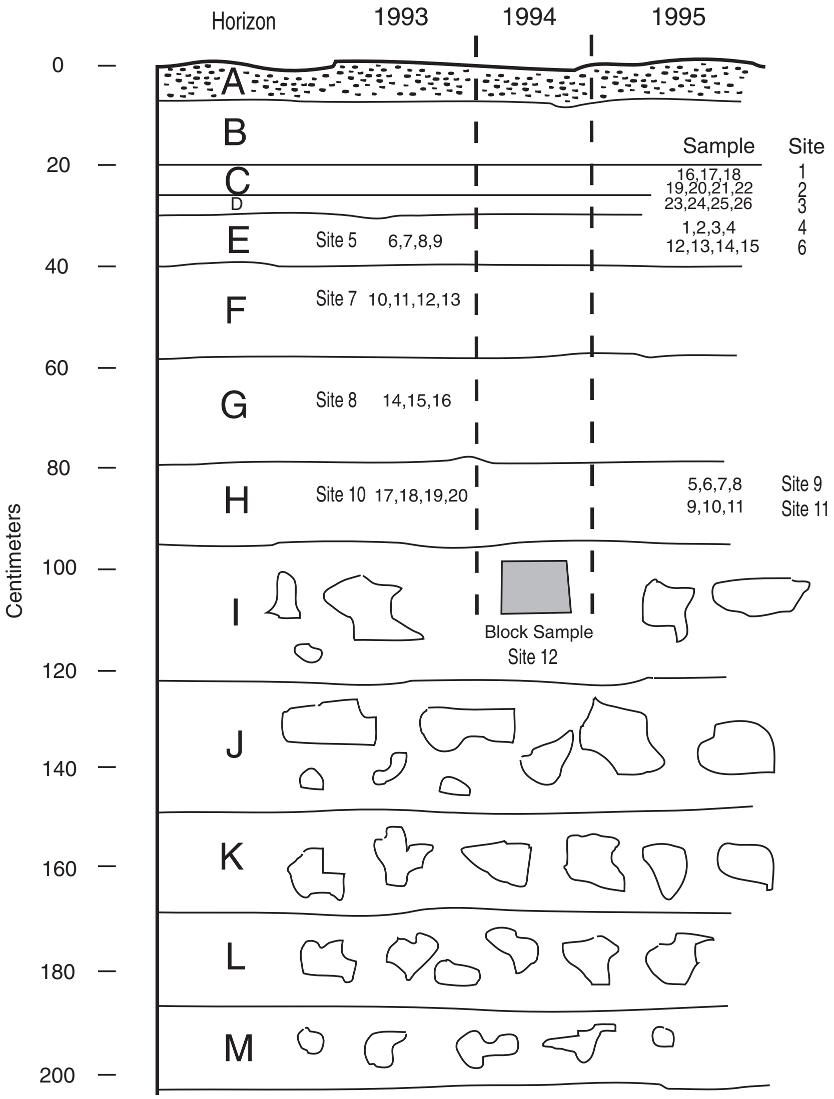


FIGURE 6.2 Stratigraphy and paleomagnetic sampling in DMNH 644. The samples do not extend below unit I at approximately 110 cm.

could be interpreted as either preserved normally magnetized remanence or strong normal overprints. Sites with this kind of magnetic signature carry the designation N? on the reversal stratigraphy (figure 6.4).

A small number of samples showed normal magnetization but with a broad range of vectors. The calculated VGPs for these samples did not overlie the modern pole but were relatively close (figures 6.3B, 6.5A). They also showed a higher standard deviation than the sites interpreted to be strongly magnetized. These sites carry the designation N, although it is possible that they are also overprinted.

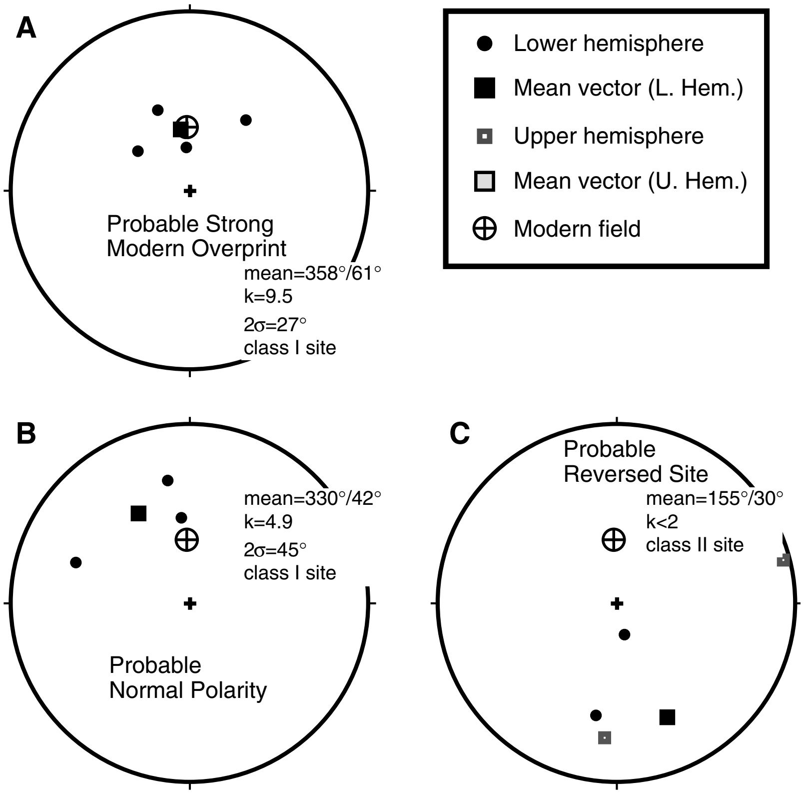
Roughly 25% of all samples showed good evidence of reversed polarity with a weak modern overprint. These samples showed both high declinations (180° ± 50°) and negative inclinations, thus plotting in the upper hemisphere (figures 6.3C, 6.5B). These samples commonly approached the calculated reversed polar attitude during progressive demagnetization. These sites carry the designation R.

The most common magnetic signature for samples was mixed or ambiguous. Typically, the samples yielded a range of inclinations and declinations that did not approach either calculated pole (figure 6.5C). Many samples had negative (upper hemisphere) inclinations with low declinations (0° ± 80°). Since these sites showed significant deviation from modern and ancient calculated normal poles, they probably carry a reversed signature. Because of the ambiguous quality of their remanence, these sites carry the designation R?. Samples that yielded vectors difficult to interpret were marked ??.

Magnetic Stratigraphy

The strata from the DMNH Velvet Room excavation are subdivided into horizons A–R. Only horizons C–I were sampled (figure 6.2). The magnetic stratigraphy from this succession (figure 6.4) shows clear evidence for both normal and reversed magnetization. A few critical sites are discussed in this section.

FIGURE 6.3 Characteristic remanences from Velvet Room strata. (A) Samples interpreted to be strongly overprinted. (B) Samples interpreted to be primary normal magnetization. (C) Samples interpreted to be primary reversed magnetization.



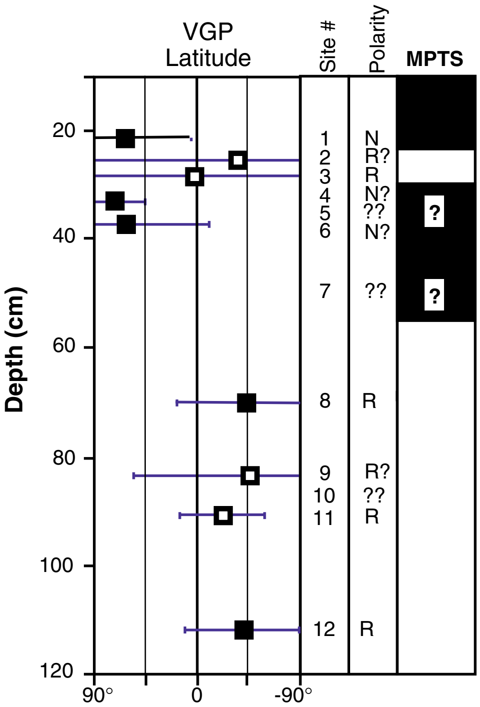


FIGURE 6.4 VGPs and polarity stratigraphy from the Velvet Room. Error bars represent two standard deviations. Solid boxes indicate a class I site; open boxes indicate a class II site. Polarity designations are explained in the text.

SITE 1, HORIZON C

Site 1, horizon C, is a class I site. Unfortunately, only low levels of demagnetization were possible. Nonetheless, the site shows strong normal signatures (low declination, high positive inclinations) that do not overlie the modern field (figure 6.6A). As such, the simplest interpretation is that this is a normally magnetized sample. Since this is the youngest site within the succession, it is most likely that this sample lies within the Brunhes polarity interval.

SITES 2 AND 3, HORIZONS C AND D

Given the high dispersion in the data, site 2 within horizon C is a class II site; site 3 within horizon D is class I site. Both of these sites contain samples with negative inclinations and high to intermediate declinations (figure 6.6B). Both sites migrate away from the modern field with increased demagnetization toward the calculated reversed VGP. Given the class I status of site 3, it is highly likely that this represents true reversed polarity. The simplest interpretation then would be that it lies within the Matuyama polarity interval. It is possible that site 2 lacks a clear signature altogether, or that it straddles the polarity flip between sites 1 and 3.

SITE 8, HORIZON G

This class I site shows the clearest signature of reversed polarity. Each sample begins with a high positive inclination but also a high declination. Through demagnetization up to

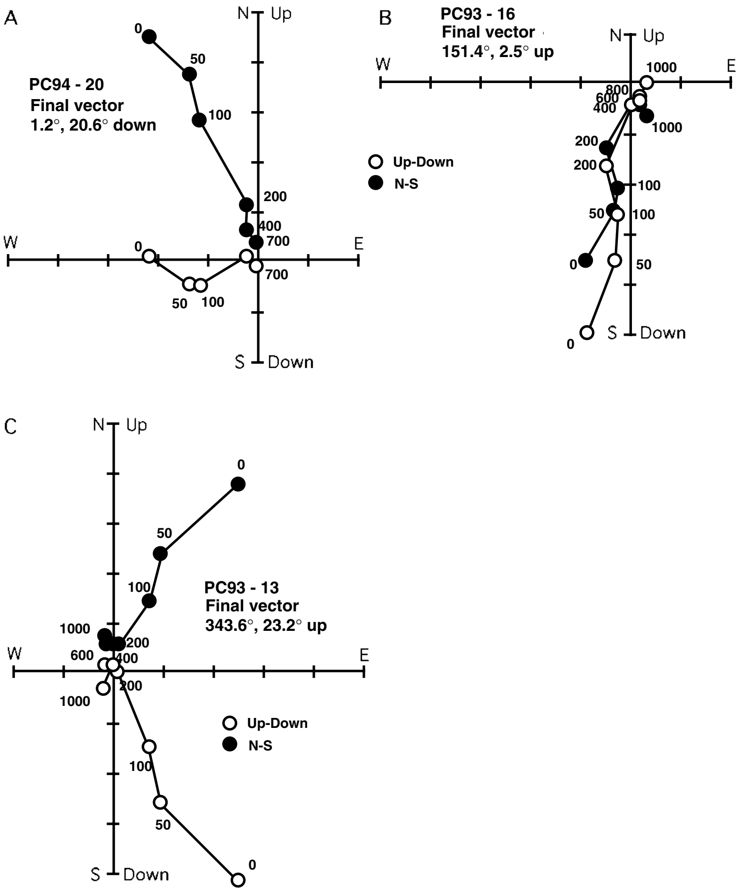


FIGURE 6.5 Zijdervelt diagrams showing the demagnetization trajectories of various samples. (A) PC94-20, from the lower block sample. This sample points north and down throughout its demagnetization, but never overlies the modern field. Although this may reflect normal polarity, it more likely reflects a strong normal overprint. (B) PC93-16, from site 8. This sample points south and up throughout its demagnetization, and approaches the reversed polarity VGP. Its shallow inclinations probably reflect incomplete demagnetization of a normal overprint of a reversed primary polarity. (C) PC93-13, from site 7. This sample points north and up for most of its demagnetization, and ends with a weak ambiguous signal. This site is ambiguous owing to the quality of the samples, but it may reflect incomplete demagnetization of a normally overprinted reversed polarity.

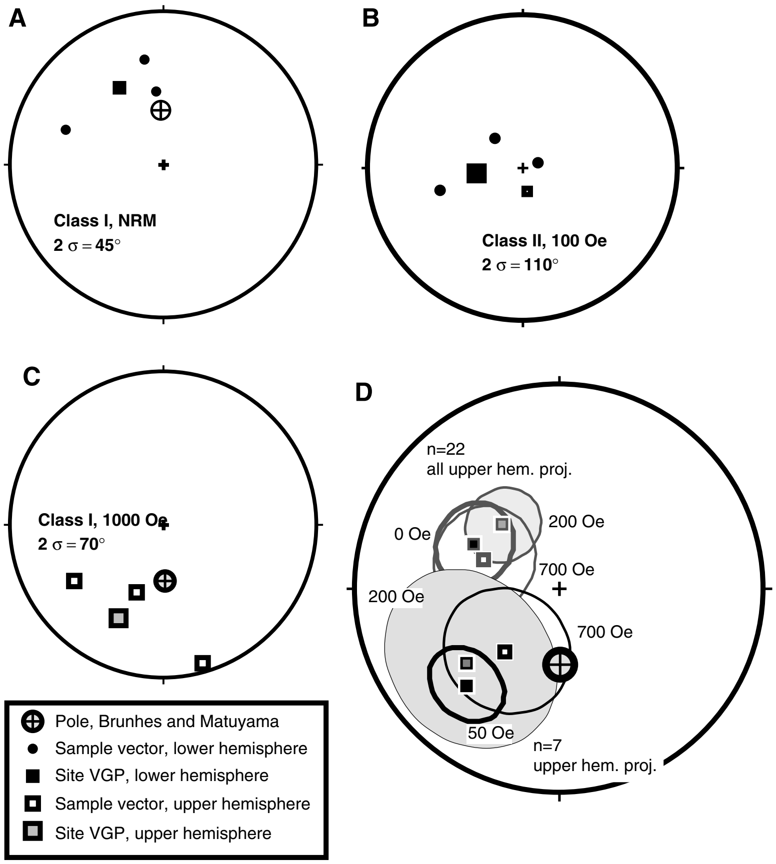


FIGURE 6.6 Detailed stereoplots from sample sites. (A) Site 1 at 100 Oe; (B) site 3 at 100 Oe; (C) site 8 at 1000 Oe; (D) block samples. All samples and means plot upper hemisphere. The data are plotted as two populations, those with strong negative polarity characteristics ($n = 7$) and the remainder ($n = 22$). In D, populations surrounded by the thick line represent low AF demagnetization, and solid squares show mean vectors; 200-Oe populations shown by shaded field, and shaded squares depict means; 700-Oe populations shown by thin line, and open squares show means.

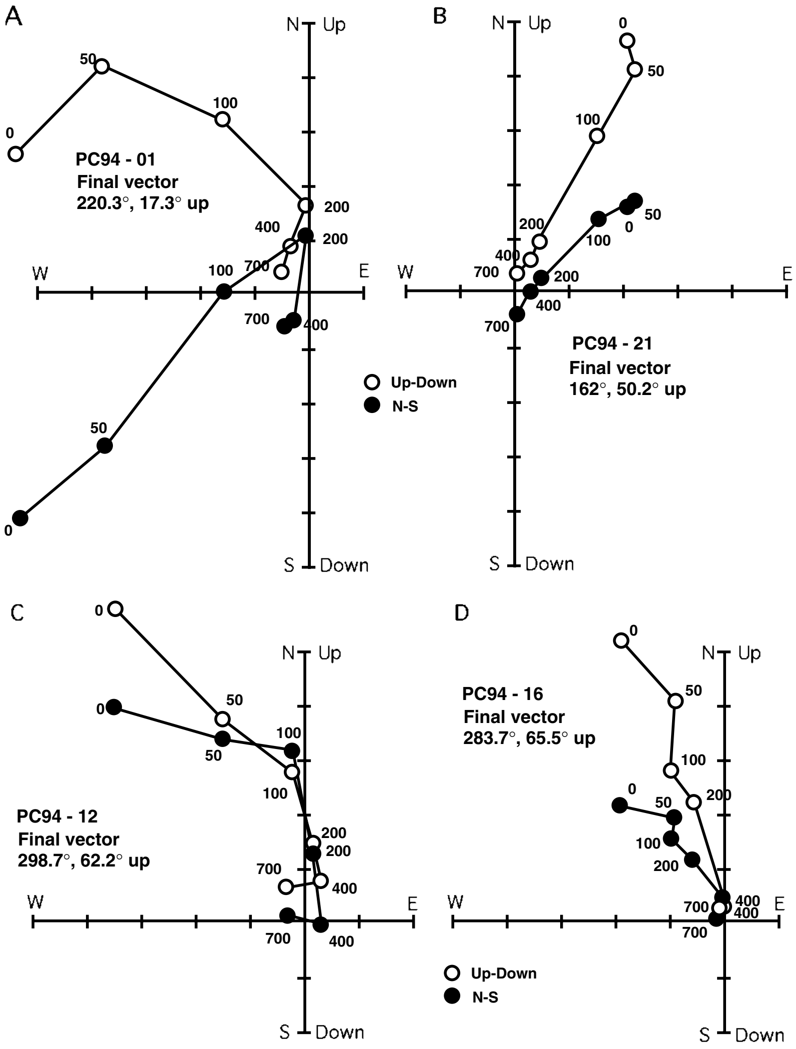


FIGURE 6.7 Zijdervelt diagrams from the 1994 block sample. (A) Stepwise AF demagnetization of sample PC94-01 reveals removal of an overprint (possibly viscous) and a trend toward a stable reversed polarity. The final signal is sufficiently strong and robust to be interpreted confidently as reversed polarity. (B) Sample PC94-21 is similar to sample PC94-01, but shows removal of an overprint with a different vector. (C) Stepwise demagnetization of sample PC94-12 fails to yield a clear polarity. The sample vectors are always either north and up or west and up, an ambiguous result. (D) Sample PC94-16 is similar to sample PC94-12, but is even weaker at final demagnetizations.

1000 Oe, the inclination of each sample flips into the upper hemisphere to end very near the calculated reversed pole (figure 6.6C). These samples must lie within a reversed polarity interval, probably the Matuyama.

SITE 12, HORIZON I

The oriented block is an interesting site owing to both the complete demagnetization spectrum and the large number of samples from one site. In sum, it behaved very much like the entire data set. Of the 30 samples, 7 showed strong reversed polarity signatures, creating a clear class I site (figures 6.6D, 6.7A, 6.7B). One sample (figure 6.5A) showed normal magnetization trending toward the modern field. This could be caused either by primary normal magnetization or by strong normal overprinting. The remaining 22 samples showed a mixture of responses with vectors that plotted in between both calculated poles (figures 6.7C, 6.7D). The simplest interpretation is that the site lies within a reversed polarity interval, with most samples showing some degree of overprinting.

Discussion and Conclusions

The presence of significant numbers of sites and samples carrying a reversed polarity magnetization indicates that these units are older than the Brunhes polarity interval. Given the external constraints on the age of the cave, it is most likely that the long reversed interval sampled in the section is the Matuyama polarity interval (0.781–1.757 Ma; Cande and Kent, 1995). This interpretation suggests the strata represent a duration of no more than a million years and probably less. This estimate results in a minimum average sediment accumulation rate of 0.9 mm per thousand years. If site 1 lies within the Brunhes, then that further delineates the age of the strata.

Sites 4–7 show strong normal overprinting, poor remanence, and high standard deviation, making them difficult to interpret. It is possible that this interval is normally magnetized. Given that the data suggest that sites 2 and 3 are reversed polarity, sites 4–7 could represent Chron 1r.1n from 0.984 to 1.049 Ma ago (Cande and Kent, 1995), commonly called the Jaramillo Event. This conclusion would be consistent with the other paleomagnetic and stratigraphic data and may place further constraints on the age of individual units. This interpretation dates most of the strata above 50 cm to less than 1 Ma ago. Care must be exercised in using this interpretation, owing to the ambiguity of the magnetic signature.

From these observations, we conclude the following:

1. The evidence for reversed polarity for three positions in the sample section is very strong: approximately 30 cm depth in horizon D, approximately 90 cm depth in horizon H, and approximately 110 cm depth in horizon I. This places the sampled interval within the Matuyama reversed polarity interval. It is also possible that a brief normal interval (Chron 1r.1n) occurs within the sampled section.
2. The section sampled between horizons C and I probably represents less than a million years of time.

Acknowledgments

We thank all the members of the Porcupine Cave project who assisted in sample collection. Special thanks are due to Steve Lund, who lent the project his sampling equipment and analysis time, as well as materials in his laboratory at the University of Southern California. The manuscript was greatly improved by the reviews of Doug Burbank, Bill Harbert, and A. D. Barnosky.

SEVEN

Age and Correlation of Key Fossil Sites in Porcupine Cave

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Establishing chronologic control in early and middle Pleistocene deposits is difficult, all the more so in cave deposits. In the absence of a lucky infusion of datable volcanic ash (which Porcupine Cave so far seems to lack), dating methods typically are restricted to magnetostratigraphic associations, biostratigraphic and biochronologic correlations, amino acid racemization, electron spin resonance, and uranium series dating. The latter two techniques have not been applied to samples from Porcupine Cave, although there is still opportunity for future attempts; therefore, all chronologic control comes from the former three. The chronologic information is augmented with sedimentological information that helps sort deposits into glacial and interglacial deposits.

Much of the information on dating the Porcupine Cave deposits, especially that from the Pit excavation, was presented in detail by Bell and Barnosky (2000). Other relevant information was detailed in Barnosky and Rasmussen (1988), Wood and Barnosky (1994), and Barnosky et al. (1996). Friedmann and Raynolds (chapter 6) discuss magnetostratigraphy in the DMNH Velvet Room excavation, and Shabel et al. (chapter 22) discuss age control in the Badger Room. This chapter integrates the earlier interpretations with some new information to hypothesize how key deposits in the cave (Pit, DMNH Velvet Room excavation, CM Velvet Room excavation, Badger Room) relate temporally to each other, to some other localities in the cave, and to the chronologic time scale. The conclusions are basically in accord with those of Bell and Barnosky (2000) but suggest that the age of the top of the Pit sequence is probably closer to circa 780 Ka than previously thought. (See chapter 2 for map locations and excavation information for each of the localities discussed in this chapter.)

The Pit as a Key Reference Section

The least complicated and possibly the temporally longest stratified sequence known in the cave is the CM/UCMP Pit excavation. It was excavated in 14 stratigraphic levels defined either by sedimentological breaks or as being less than 10 cm thick, whichever was thinner. Figure 23.1 illustrates the deposits and provides a schematic of the section. As detailed in Bell and Barnosky (2000), the sedimentological evidence suggests that at least three cool-warm cycles (probably glacial-interglacial cycles) are represented. The oldest stratigraphic levels—14, 13, 12, and 11—have been interpreted as interglacial deposits, although there is no firm basis for understanding levels 14 and 13. Level 10 has been interpreted as glacial; levels 9, 8, 7, and 6, as interglacial; levels 5 and 4, as glacial; and the youngest levels, 3, 2, and 1, as interglacial.

The sediments—dark brown clay and clay nodules for glacials, and less consolidated tan and light brown dust for interglacials—suggest that each glacial was moist and cool relative to its subsequent interglacial. Barnosky and Rasmussen (1988) and subsequent papers (Wood and Barnosky, 1994; Barnosky et al., 1996; Bell and Barnosky, 2000) assumed, based only on the upper glacial-interglacial transition, that all the glacials were moister than all the interglacials. However, the more complete set of information now available from the lower levels suggests that the lower interglacial represented by levels 9–6 was probably moister than the glacial represented by levels 5 and 4, based on the climatic implications of the small mammal remains found there. Palynological, sedimentological, and invertebrate fossil data support this interpretation for Hansen Bluff, Colorado, approximately 200 km south of Porcupine Cave (Rogers et al., 1992). The warmest, most arid of all the interglacials represented at Porcupine Cave appears to have been the youngest one (levels 3–1), as indicated by the character of the sediments (a distinctive loose, dry dust that occurs nowhere else in the sequence), the dominance of xeric taxa such as the ground squirrel *Spermophilus,* and the diversity of herpetofauna (Bell and Barnosky, 2000).

Magnetostratigraphy

Magnetostratigraphic studies in the Pit were undertaken by V. A. Schmidt, University of Pittsburgh Paleomagnetics Laboratory, just prior to his untimely death. Samples from levels

14–8 recorded predominantly reversed polarities, although there is an admixture of intermediate and to a much lesser extent normal components as well. The data suggested to Schmidt (pers. comm., 1993) that levels 14–8 are older than 780 Ka, which marks the Brunhes-Matuyama boundary. They would fall in Chron 1r of Berggren et al. (1995). Samples from the base of level 5 provided equivocal magnetic signatures. Bell and Barnosky (2000) suggested that the presence of predominantly reversed samples with intermediate and normal components in levels 14–8 was consistent with sampling a time near the Brunhes-Matuyama transition from reversed to normal polarity. Viable magnetostratigraphic samples were impossible to obtain above level 8 because of the friable sediments.

Biochronology

Figures 7.1–7.3 show stratigraphic ranges of Pit taxa. Arvicoline rodents currently provide the most feasible link from biostratigraphic to biochronologic time scales (Repenning, 1987; Fejfar and Repenning, 1992; Bell, 2000; Bell et al., in press). At least 10 species of arvicolines range through the Pit (figure 7.2). Biochronologically informative species fall into two groups. One group, including *Phenacomys gryci, Mimomys virginianus,* and *Allophaiomys pliocaenicus,* is known elsewhere, primarily from sites older than 800 Ka. The second group is composed of species that elsewhere first appear 900–800 Ka ago: *Microtus paroperarius, Lemmiscus curtatus* (primitive four-triangle morphotype), and *Microtus meadensis* (see figures 7.1–7.3 and tables 10.1–10.13 for common names). The sympatric occurrence of all these species at Porcupine Cave suggests that levels 8–4 were deposited sometime between 900 and 800 Ka ago. Bell and Barnosky (2000) provided details of the species ranges for the relevant taxa and for species identifications. Bell and Barnosky (2000) believed that levels 8–4 dated to between 850 and 750 Ka. This slightly younger estimate assumed that the Brunhes-Matuyama boundary was captured in the sequence somewhere above level 8. However, based on the absence of viable magnetostratigraphic information above level 8 and the biostratigraphic correlations to the DMNH Velvet Room sequence explained later in this chapter, an estimate of 750 Ka for level 4 could be too young.

Stratigraphically within the Pit, *A. pliocaenicus*, *M. virginianus,* and *P. gryci* disappear at the level 4/3 transition. This probably does not reflect sampling bias because levels 4–1 produce the most specimens of any level. Given that these species disappear by 800 Ka ago elsewhere (by circa 1.5 Ma ago in the case of *P. gryci;* Repenning et al., 1995), it seems probable that levels 4 and below date to at least 800 Ka. The taxa remaining in levels 1 and 2 may have survived elsewhere to about 250 Ka in the case of *M. paroperarius*, *M. meadensis,* and *Mictomys kansasensis/meltoni*, and to the present for *L. curtatus.* However, most localities with *Mictomys kansasensis/meltoni* date to between 2 Ma and 600 Ka, with the most consistently reliable dates on *M. meltoni* being from 600 to 700 Ka. In view of this observation, plus the fact that levels 1–3 probably represent an interglacial that lasted no more than 100,000 years, it seems unlikely that level 1 would be younger than about 600 Ka. These age estimates based on biochronology are consistent with the independent magnetostratigraphic interpretations. Note, however, that the estimate is substantially older than that posited by most earlier papers on Porcupine Cave (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996). Dating the top of the sequence is still problematic. Bell and Barnosky (2000) estimated that Pit levels 1–3 were deposited sometime between 252 and 750 Ka ago. Based on the information presented in this chapter, we revise Bell and Barnosky's (2000) estimate of the upper age of the Pit to be greater than 600 and very probably closer to 800 Ka.

Levels 9 and below contain two additional taxa that, like *P. gryci,* became extinct elsewhere by early Irvingtonian time (circa 1.5 Ma ago). These are the rabbit *Hypolagus* sp. and the ground squirrel *Spermophilus (Otospermophilus)* sp.; the latter was not named as a species but has morphological affinities to early Blancan species in Kansas (Rexroad and Fox Canyon faunas) (Goodwin, chapter 17). Unlike *P. gryci,* both disappear from the Porcupine Cave record by level 9 (figure 7.1). Sampling issues might explain their absence in level 9, where fossils are scarce, but not above that level because specimens become more abundant, and congeners are well represented in higher levels. *Hypolagus* and the Rexroad / Fox Canyon–like morph of *Spermophilus (Otospermophilus)* sp. co-occur with *L. curtatus,* but the other two arvicolines that suggest ages younger than 900 Ka do not appear until higher in the stratigraphic section (figure 7.2). This finding indicates either significant temporal range extensions for *Hypolagus* and the Rexroad / Fox Canyon–like morph of *Spermophilus (Otospermophilus)* sp., as was apparently also the case for *P. gryci* (Bell and Barnosky, 2000), or an even earlier first appearance for *Lemmiscus curtatus* than has previously been recognized. Based on its co-occurrence with *P. gryci*, *M. virginianus,* and *A. pliocaenicus,* Bell and Barnosky (2000) agreed with Repenning (1992) in extending the range of *L. curtatus* from circa 300 to 800 Ka, a decision that has been further substantiated by the association of *L. curtatus* with magnetically reversed sediments in SAM Cave, New Mexico (Rogers et al., 2000). In light of this, it seems more parsimonious to extend the range of one species *(L. curtatus)* downward rather than those of two species (*Hypolagus* and the primitive, unnamed *Spermophilus [Otospermophilus]* sp.) upward. Therefore, it would not be surprising if levels 10 and below in the Pit were substantially older than 800 Ka, even in view of the presence of *L. curtatus.* On these grounds the bottom of the Pit deposit is considered younger than 1 Ma.

Biostratigraphic Zones

Biostratigraphic changes within the stratified Pit sequence may prove useful for correlation of deposits within Porcupine Cave. Two zones based on first or last known stratigraphic appearance data are recognized (figures 7.1–7.3). These zones

HSDk-LSDk Zones	*Marmota* Zone									*Hypolagus* Zone				
Assemblage Zones				*Allophaiomys* Zone										
Relative Abundance Zones	*M.* 5T Z.		?	?	*Mictomys* Zone									
Climatic Interpretation	IG			G		IG					G	IG		
Estimated Age (Ka)	>600 to <850			>780 to <900						>800 to <1000				
Stratigraphic Level	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**8A**	**9**	**10**	**11**	**12**	**13**
Amphibia														
Scaphiopus/Spea (Toad)	■?	■?	■?											
Reptilia														
Natricinae (Snake)	■	■	■	■		■	■		■					
Non-Natricine Colubridae (Snake)		■					■							
Colubroidea (Snake)	■	■	■	■			■		■					
Viperidae (Snake)		■												
Mammalia														
Soricidae														
cf. *Sorex* sp. (Shrew)		■	■	■	■		■		■	■				
Ochotonidae														
Ochotona cf. *O. princeps* (Pika)											■			
Ochotona sp. Trout Cave form (Pika)				■		■								
Ochotona sp. (Pika)	■	■	■	■	■									
Leporidae														
Lepus sp. (Hare or Jackrabbit)	■	■	■	■	■	■								
Sylvilagus sp. (Cottontail Rabbit)	■	■	■		■	■								
Leporid (Rabbit or Hare)	■	■	■	■	■	■	■	■	■	■	■	■		
Aztlanolagus sp. (Aztlan Rabbit)		■	■	■	■	■	■	■	■		■	■		
Brachylagus coloradoensis (Colorado Pygmy Cottontail)	■	■	■	■	■	■	■							
Hypolagus sp. (Rabbit)											■	■		
Sciuridae														
Tamiasciurus hudsonicus (Red Squirrel or Chickaree)	■	■	■	■	■	■	■							
Tamias cf. *T. minimus* (Chipmunk)	■	■	■	■	■									
Marmota sp. (Marmot)	■	■	■	■	■	■	■	■						
Spermophilus (?Otospermophilus) sp. (Ground Squirrel)											■	■		
Spermophilus lateralis (Golden-mantled Ground Squirrel)	■	■	■	■	■	■	■		■		■			
Spermophilus cf. *S. elegans* (Wyoming Ground Squirrel)	■	■	■	■	■	■	■	■?	■	■	■			
Cynomys andersoni new sp. (Prairie Dog)	■			■	■	■	■		■			■		
Cynomys cf. *C. leucurus* (White-tailed Prairie Dog)	■	■	■	■	■									
Geomyidae														
Thomomys sp. (Pocket Gopher)	■	■	■	■	■	■	■	■	■	■	■		■	
Thomomys cf. *T. talpoides* (Northern Pocket Gopher)	■	■	■	■	■	■			■		■			
Thomomys cf. *T. bottae* (Botta's Pocket Gopher)				■		■	■				■			

FIGURE 7.1 Stratigraphic ranges of Amphibia, Reptilia, ochotonids, leporids, sciurids, and geomyids at the Pit. These ranges and those in figures 7.2 and 7.3 are used to define the biostratigraphic zones noted at the top and explained in the text. Levels 13 and 14 lacked fossils; thus the diagram extends back only to level 13. *Abbreviations:* G, glacial; IG, interglacial; LSDk, lowest known stratigraphic datum; HSDk, highest known stratigraphic datum; *M.* 5T Z., *Microtus* 5T Zone.

conceptually resemble the lowest known stratigraphic datum (LSDk) and highest known stratigraphic datum (HSDk), respectively, as described by Walsh (1998). The *Hypolagus* Zone is defined by the HSDk for *Hypolagus.* The overlying *Marmota* Zone is defined by the LSDk for *Marmota.* In practice, the approximate boundary between the zones is placed at the boundary between levels 8A and 9. That placement splits the difference between the last appearance of *Hypolagus* and the first appearance of *Marmota* in the section, and it takes into account the fact that fossils are rare enough in levels 8A and 9 that it is impossible to know if further sampling would produce either taxon. For correlation purposes, other localities

HSDk-LSDk Zones	*Marmota* Zone									*Hypolagus* Zone				
Assemblage Zones				*Allophaiomys* Zone										
Relative Abundance Zones	*M.* 5T Z.		?	?	*Mictomys* Zone									
Climatic Interpretation	IG			G		IG				G	IG			
Estimated Age (Ka)	>600 to <850			>780 to <900						>800 to <1000				
Stratigraphic Level	1	2	3	4	5	6	7	8	8A	9	10	11	12	13
Geomyoidea (not *Thomomys*)							■							
Muridae														
Neotoma cinerea (Bushy-tailed Wood Rat)	■	■	■	■	■	■	■	■	■		■	■		
Neotoma mexicana (Mexican Wood Rat)		■	■											
Neotoma floridana (Eastern Wood Rat)	■	■	■	■	■	■	■		■	■	■			
Neotoma micropus (Southern Plains Wood Rat)			■	■	■	■	■		■	■	■			
Neotoma stephensi (Stephens' Wood Rat)	■	■	■				■							
Neotoma sp. (Wood Rat)	■	■	■	■	■	■	■	■	■	■	■		■	
Peromyscus sp. (Deer Mouse)	■	■	■	■	■	■	■	■	■	■	■			
Arvicolinae														
Allophaiomys pliocaenicus (Vole)				■	■	■	■		■			■		
Mimomys virginianus (Virginia Mimomys)				■	■	■	■		■		■			
Phenacomys gryci (Gryci's Vole)				■							■			
Phenacomys sp. (not *P. gryci* above level 7) (Vole)	■	■	■	■	■	■	■	■	■	■	■	■		
Lemmiscus (4 triangles) (Sagebrush Vole)	■	■	■	■	■	■	■	■			■			
Lemmiscus curtatus (Sagebrush Vole)	■	■	■	■	■	■	■	■		■	■			
Lemmiscus sp. (id to species not possible)	■	■	■	■	■	■	■	■	■	■	■	■		
Microtus meadensis (Meade Vole)	■	■	■	■	■	■	■	■	■					
Microtus paroperarius (Vole)	■	■	■	■	■		■							
Microtus 5T (Vole)	■	■	■	■	■	■								
Microtus sp. (non-diagnostic teeth)						■								
Mictomys spp. (probably Extinct Bog Lemming)	■	■	■	■	■	■	■	■	■	■	■	■	■	
Ondatra sp.	■	■		■	■				■					
Erethizontidae														
Erehizon (Porcupine)	■	■	■	■										

FIGURE 7.2 Stratigraphic ranges of arvicolines and other rodents at the Pit. See figure 7.1 for further explanation.

in the cave that contain *Hypolagus* most likely correlate with Pit levels below 8A; those that contain *Marmota* have a high probability of correlating with levels above 9.

One assemblage zone is recognized: the *Allophaiomys* Zone, which is defined on the co-occurrence of *Allophaiomys pliocaenicus* and *Mimomys virginianus*. A characterizing taxon is *Phenacomys gryci* (figure 7.2). Other localities within the cave that produce these taxa have a high probability of correlating with levels 4–10 if both of the definitive taxa are present.

Two relative abundance zones are also apparent, based on arvicoline rodent percentages detailed in chapter 23 (see figure 23.7). The *Mictomys* Zone (figure 7.2) is defined by *Mictomys* exhibiting a higher percentage of individuals (>25%) within the arvicoline rodent component of the fauna than the combined total of *Microtus* 5T (i.e., *Microtus* characterized by five or more triangles on the first lower molar) and *Microtus meadensis*. The *Microtus* 5T Zone has relatively low numbers of *Mictomys* specimens (<25%), but high percentages of *Microtus* 5T and/or *M. meadensis* specimens (>25% combined). Ambiguity in differentiating the zones arises when the percentages of *Mictomys* versus combined *Microtus* 5T–*M. meadensis* are about equal. This situation occurs in level 3 and to a lesser extent in level 4. However, above and below those levels, the percentages provide a reasonable basis for biostratigraphic differentiation. The boundary between these relative abundance zones is thus recognized to be somewhat fuzzy and to encompass the level 4/3 transition. In general, the *Mictomys* Relative Abundance Zone overlaps broadly with the *Allophaiomys* Assemblage Zone, running from level 12 to level 5, before becoming hard to differentiate in level 4. The *Microtus* 5T Zone spans levels 1 and 2 before becoming hard to differentiate in level 3 (figure 7.4).

Goodwin (chapter 17) also recognized conceptual equivalents to relative abundance zones based on the sciurid

HSDk-LSDk Zones	*Marmota Zone*									*Hypolagus Zone*				
Assemblage Zones				*Allophaiomys Zone*										
Relative Abundance Zones	*M. 5T Z.*		?	?	*Mictomys Zone*									
Climatic Interpretation	IG			G		IG					G	IG		
Estimated Age (Ka)	>600 to <850			>780 to <900						>800 to <1000				
Stratigraphic Level	1	2	3	4	5	6	7	8	8A	9	10	11	12	13
Mustelidae														
Mustela frenata (Long-tailed Weasel)	■				■									
Mustela erminea (Ermine)		■	■			■								
Mustela nigripes (Black-footed Ferret)	■			■										
Mustela species A (Extinct Mustelid)	■	■	■											
Gulo cf. *G. schlosseri* (Schlosser's Wolverine)														
Lutra canadensis (American River Otter)				■										
Taxidea taxus (Badger)	■	■	■	■										
Spilogale putorius (Spotted Skunk)	■		■	■	■		■				■	■		
Brachyprotoma obtusata (Short-faced skunk)			■											
Canidae														
Canis latrans (Coyote)	■													
Canis edwardsi (Edward's Wolf)		■												
Vulpes velox (Swift or Kit Fox)	■		■											
Urocyon cinereoargenteus (Gray Fox)	■													
Tayassuidae														
Platygonus sp. (Peccary)		■												
Cervidae														
cf. *Odocoileus* sp. (Deer)		■	■											
Antilocapridae														
Antilocapra (Pronghorn) or *Tetrameryx* (Antelope)		■												
Antilocapridae, genus and species indeterminate	■	■	■											
Bovidae														
Ovis sp. (Bighorn Sheep)	■													
Oreamnos harringtoni (Extinct Mountain Goat)		■												
Equidae														
Equus (Hemionus) sp. (Horse)	■													
Equus sp. (large) (Horse)	■	■				■								
Equus sp. (small) (Horse)	■													

FIGURE 7.3 Stratigraphic ranges of carnivores, artiodactyls, and equids at the Pit. See figure 7.1 for further explanation.

component of the fauna. Levels 6 and deeper contain ?*Cynomys andersoni* as the only prairie dog species; levels 4 and 5 yield ?*C. andersoni* and *C.* cf. *C. leucurus* in about equal abundances; and levels 1–3 produce *C.* cf. *leucurus* almost exclusively. Wood and Barnosky (1994), Barnosky et al. (1996), and Bell and Barnosky (2000) noted dramatic increases in the relative abundance of *Cynomys* and *Spermophilus* relative to *Marmota* at the level 3/4 transition.

Lemmiscus exhibits a population-level change that may be useful in correlation. Lower first molars with only four closed triangles are equal or greater in abundance than those with five closed triangles in levels 3–10 (see figure 23.8). The first six-triangle forms appear in level 1. Thus other Porcupine Cave localities in which *Lemmiscus* populations are characterized by a predominance of five-triangle forms correlate more likely with levels 1 and 2 than with lower levels of the Pit, and populations with six triangles probably are coeval with or younger than the uppermost Pit level.

The CM Velvet Room Excavation

Biostratigraphy

As noted in chapter 2, this excavation included five stratigraphic levels, the sediments of which very closely resembled the distinctive loose, dry dust of levels 1–3 of the Pit. Paleomagnetic samples taken from beneath the lowest level were interpreted as questionably normal by Fred Luiszer and V. A.

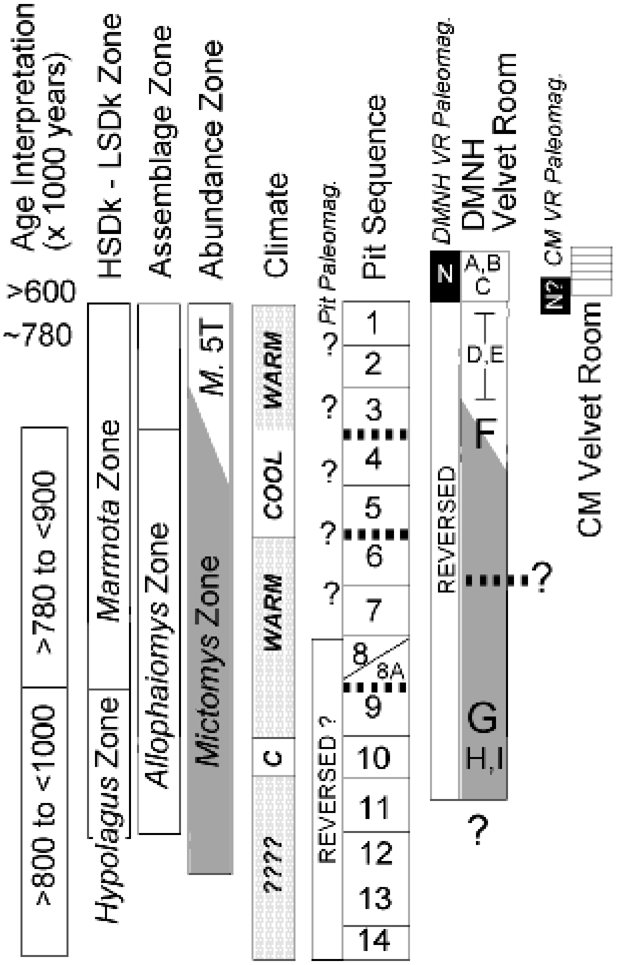

FIGURE 7.4 Correlation of the Pit sequence with the CM and DMNH Velvet Room excavations. Correlation of the sections is based on the biostratigraphic zones defined in the Pit and the local magnetostratigraphic evidence in each section. Correlation to the time scale is by biochronology and assumption that the reversed (white) magnetic interval indicates the Matuyama magnetic epoch. Dark gray shading denotes parts of the respective sections that fall in the *Mictomys* Zone. Climatic intervals are defined by sediment type. Numbers in the Pit Sequence column schematically represent the stratigraphic levels. Heavy dotted lines denote suspected unconformities. N in the Velvet Room columns indicates normally magnetized (black) parts of the section. Question marks in the Pit Paleomag. column indicate lack of data. The question mark at the base of the DMNH Velvet Room column expresses uncertainty about the age of the basal part of the section.

Schmidt (pers. comm., 1993). Most of the fossils have not yet been processed, but based on the small sample of arvicolines so far identified (see table 10.11), the deposits seem to fall within the *Microtus* 5T Relative Abundance Zone. The lowest fossiliferous level in the excavation, level 3, is the only one from which a reasonably large sample of arvicolines has been identified, and it shows the following percentages for minimum number of individuals: *Mictomys,* 19%; *M. meadensis,* 19%; and *Microtus* 5T, 23%.

Of interest is one specimen of *Allophaiomys pliocaenicus* present in level 3. This finding hints that level 3 of the CM Velvet Room could fall within the *Allophaiomys* Assemblage Zone of the Pit, although the other requisite taxon, *Mimomys virginanus,* has not been recovered from the CM Velvet Room. The presence of *A. pliocaenicus* suggests that level 3 in the CM Velvet Room could be as old as level 4 in the Pit.

However, all other lines of evidence suggest that the CM Velvet Room deposits are younger than the *Allophaiomys* Assemblage Zone sensu stricto (i.e., also containing *Mimomys virginianus*) in the Pit. In the *Lemmiscus* sample from level 3 in the CM Velvet Room, approximately 31% of the specimens are four-triangle morphs; the rest are five-triangle forms. In the highest level of the CM Velvet Room, 100% of the *Lemmiscus* specimens exhibit either five or six triangles; six-triangle forms also occur in level 2A. This finding would suggest that levels 1 and 2 in the Velvet Room are younger than any levels in the Pit, possibly excepting Pit level 1 (see figure 23.8).

These lines of evidence suggest that the CM Velvet Room excavation is at least as young as levels 1–4 in the Pit. The presence of six-triangle forms of *Lemmiscus* in CM Velvet Room level 2A implies correlation with level 1 (or younger) in the Pit. The high percentage of five-triangle morphs of *Lemmiscus* in CM Velvet Room level 3, combined with the clear dominance of *Microtus* 5T and *M. meadensis* over *Mictomys,* suggests that even that level is younger than Pit level 4, despite the occurrence of *Allophaiomys pliocaenicus.* The equivocally normal paleomagnetic signature at the base of the excavation hints that the sediments in the CM Velvet Room excavation are younger than 780 Ka, but the paleomagnetic data are far from firm.

DMNH Velvet Room Excavation

The DMNH Velvet Room excavation is a stratified sequence excavated as described in chapter 2. Horizons are designated by letter, with A the highest and deeper horizons progressing through the alphabet. The sediments of horizons A–C are very similar to those of levels 1–3 of the CM Velvet Room excavation (chapter 2). All sediments are unconsolidated. The brown clays that intermittently characterize Pit levels below level 3 were not observed in the Velvet Room. However, DMNH Velvet Room horizons below C generally contain more clasts than horizons A–C (see figure 2.11).

The magnetostratigraphy of the site is described in chapter 6. The uppermost horizons are normally magnetized down to horizon C. Horizons D–I demonstrate reversed polarity. The Brunhes-Matuyama boundary at 780 Ka therefore appears to be located near the transition from horizon C to horizon D.

Biostratigraphy

The arvicoline and sciurid rodents are the only components of the fauna that have been studied sufficiently to allow

TABLE 7.1

Percentages of Arvicoline Rodents Identified from the DMNH Velvet Room Excavation

	Horizon								
Taxon	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*
Phenacomys sp. (not *P. gryci*)	—	4	—	—	—	—	33	—	—
Microtus meadensis	—	—	54	33	40	32	—	—	—
Lemmiscus (4 triangles)	8	—	—	—	7	4	—	23	33
Lemmiscus curtatus (sagebrush vole)	83	85	23	13	20	12	33	9	—
Microtus paroperarius	—	2	8	7	7	4	33	41	33
Microtus sp. (5+ triangles)	8	20	15	33	7	4	—	—	—
Mictomys kansasensi/meltoni	—	—	—	13	7	16	—	23	17
Mictomys sp.	—	—	—	—	7	28	—	9	17
Total minimum number of individuals	12	51	13	15	14	25	3	23	7

biostratigraphic conclusions to be reached. Relative abundance calculations (table 7.1; see also tables 10.11, 10.12) place horizons C–F in the *Microtus* 5T Zone. The sample in horizon G is too small to record the pertinent taxa. Horizons H and I clearly fall within the *Mictomys* Zone, with *Mictomys* specimens composing 32% and 34% of the samples, respectively, and *Microtus meadensis* and *Microtus* 5T composing 0%.

Horizons A–G are characterized by a majority of *Lemmiscus* specimens with at least five triangles, resembling levels 1 and 2 in the Pit. In fact, the proportion of five-triangle specimens in Velvet Room horizons A–C (treated as a lumped sample) is significantly greater than that in Pit levels 1 and 2 ($p < 0.0001$ for χ^2 and Fisher's exact test). Given the trend for populations of *Lemmiscus* to exhibit more five-triangle forms through time, horizons A–C in the Velvet Room probably are younger than levels 1 and 2 in the Pit. Horizons H and I yield more four-triangle forms, resembling Pit levels 3 and below. More four- than five-triangle forms characterize horizons H and I ($p < 0.0001$ for both χ^2 and Fisher's exact test) in comparison with levels A, B, and C in the DMNH excavation and levels 1 and 2 in the Pit, but not in comparison with levels below 2 in the Pit ($p = 0.15$ for Fisher's exact test; $p = 0.08$ for χ^2). This would be consistent with correlating horizons H and I somewhere below Pit level 2.

DMNH Velvet Room horizons D–G contain more five-triangle than four-triangle *Lemmiscus*. They show statistically more four-triangle forms than horizons A–C, but fewer four-triangle forms than horizons H and I ($p < 0.005$ for χ^2 and Fisher's exact test). Individually each of horizons D–G produced a very small sample of *Lemmiscus* (see tables 10.11, 10.12), but even so most horizons exhibit (horizons E and F) or approach (horizon D) statistically significant differences with the horizon H and I sample, but not with the horizon A–C sample (horizon E, with statistically more four-triangle forms, being the exception). Horizon G, with a single specimen, could not be statistically differentiated from either the A–C or H and I samples. Horizons D–F as a lumped sample could not be statistically distinguished from Pit levels 1–3 ($p = 0.77$ for χ^2; $p > 0.9999$ for Fisher's exact test). The *Lemmiscus* morphotype percentages thus are consistent with correlating DMNH Velvet Room horizons D–F near Pit levels 1–3. However, consideration of the *Mictomys/Microtus* (44%/36%) abundances constrains placement of Velvet Room horizon F nearer to Pit levels 3 or 4—the transitional zone between the two relative abundance zones—than to Pit level 1.

Based on the derived condition of *Cynomys* cf. *C. leucurus* and *Spermophilus* cf. *S. elegans,* Goodwin interpreted horizons A and B as younger than the entire Pit sequence (chapter 17).

These considerations suggest that horizons A–C are younger than levels 1–3 in the Pit (figure 7.4). Horizons F–I probably correlate with Pit levels 4 and below. Interestingly, Baxter (chapter 15) reported one *Hypolagus* specimen from horizon G in the DMNH Velvet Room excavation, which would imply that horizons G and below extend into the *Hypolagus* zone, i.e., are at least as old as levels 9 or 10 in the Pit. If so, an unconformity or extremely low depositional rates between horizons F and G would be implied.

However, considerably more study of the complete DMNH Velvet Room fauna is needed before these conclusions should be regarded as firm. For example, the absence of taxa such as *Allophaiomys pliocaenicus* and *Mimomys virginianus* presents an inconsistency if DMNH Velvet Room horizons F–I correlate with levels 4 to as old as 10 in the Pit. However, these taxa are always found in low abundance in the Pit, which yielded only 23 specimens of *A. pliocaenicus* and 17 of *M. virginianus* in the sample of 1004 arvicolines. The DMNH Velvet Room sample comprises 254 arvicoline specimens, only 118 of which are from horizons where the two "missing" taxa would be expected. Therefore it is possible that the absence of these taxa simply reflects the relatively lower sample size. Both taxa, as well as *Phenacomys gryci,* are present in DMNH Velvet Room excavation samples that could not be reliably assigned to a stratigraphic horizon (see table 10.13).

The Badger Room

Arvicoline rodents from the Badger Room clearly place it within the *Allophaiomys* Assemblage Zone and *Mictomys* Relative Abundance Zone (see table 10.1). The only arvicolines identified from the sample of 50 teeth are *A. pliocaenicus, Mimomys virginianus, Phenacomys gryci, Mictomys kansasensis/meltoni,* and a single specimen of *Microtus* 5T. Also present in the fauna is *Marmota,* a finding that places the locality securely within time encompassed by the *Marmota* LSDk Zone in the Pit. These data indicate that the Badger Room sediments analyzed by Shabel et al. (chapter 22) are coeval with some part of the interval represented by levels 8–4 in the Pit. The absence of *Lemmiscus curtatus* in this assemblage is puzzling, given that *Lemmiscus* is represented in most Pit levels. Small sample size may explain this, as may the different taphonomic vector that apparently characterizes the Badger Room relative to the Pit (Shabel et al., chapter 22).

Amino Acid Racemization

Relative age placements of Porcupine Cave localities derived from amino acid racemization are consistent with the biostratigraphic and paleomagnetic conclusions noted previously. Bell and Barnosky (2000) described the relative age results obtained from the Badger Room, Pit level 2, Pit level 6, and CM Velvet Room level 1. The technique suggested that Pit levels 2 and 6 and the Badger Room samples were approximately similar in age, but that CM Velvet Room level 1 was substantially younger. A sample from the Gypsum Room was intermediate in age between the Pit and CM Velvet Room samples. Absolute age derivations from amino acid racemization were inconsistent with other age data from Porcupine Cave and were deemed unreliable because assumptions for applying the technique to absolute age determinations, such as constant temperature through time, clearly did not hold.

Additional Paleomagnetic Data

To assess the feasibility of magnetostratigraphic analyses in the cave, a series of samples collected in 1988 was analyzed by Fred Luiszer in the University of Colorado Paleomagnetism Laboratory; the results were interpreted by Luiszer and subsequently by V. A. Schmidt (pers. comm., 1993). The results suggested that sediments about 10 cm below the surface of the Gypsum Room were potentially normally magnetized. Additional samples were taken and interpreted by Schmidt in 1990. Those from Tobacco Road taken near the surface from sediments about 1 m below the ceiling showed some signs of reversal; this location was about two-thirds of the way toward the Velvet Room. Farther toward the Velvet Room, samples from near the surface exhibited normal polarity. None of these samples provided conclusive results, but the observations indicated that future work could prove fruitful.

Climatic Correlations

In the Pit, the contacts between glacial and interglacial stratigraphic levels are abrupt, with dramatically differing sediments on each side of the contact. Within each climatic interval, the sedimentary transitions across stratigraphic levels are much more subtle, or, in the case of arbitrary levels, lacking entirely (Barnosky and Rasmussen, 1988; Bell and Barnosky, 2000). This pattern suggests episodic deposition, with periods of nondeposition (unconformities or disconformities between climatic intervals) separating a sequence of discrete sediment packages, each of which samples some unknown slice of time within its respective climate interval. Which of the several middle Pleistocene glacial and interglacial stages are represented is unknown, although the dating considerations discussed earlier provide some constraints.

If the correlation expressed in figure 7.4 is correct, Pit levels 1–3 probably accumulated during interglacial stage 19 or 21, using the oxygen isotope chronology of Raymo et al. (1997) and Raymo (1998) (figure 7.5). Because the correlation of Pit to Velvet Room sediments suggests that levels 1–3 are older than 780 Ka, stage 21 is the most likely candidate. In that case, the climatic intervals that precede levels 1–3 may match sequentially with the glacial-interglacial cycles interpreted from the oxygen isotope curve (Raymo et al., 1997; Raymo, 1998), as indicated in figure 7.5 (climatic intervals 22, A, B, C). This would be consistent with the sedimentological and faunal evidence (chapter 23), which suggests that levels 1–3 represent the warmest and most arid of the warm periods, because the oxygen isotope excursion that precedes stage 22 (A in figure 7.5) was considerably less pronounced than that for stage 21. Alternatively, some other sequential combination of the glacials and interglacials noted earlier and those labeled D, F (glacials) and E (interglacial) in figure 7.5 could be represented. It does not seem likely that glacials or interglacials older or younger than these are represented, in view of the suspected age of the Pit and Velvet Room sequences.

This interval of time is of interest from a climatic point of view in that it spans at least part of the transition from a 41,000-year rhythm for glacial-interglacial cycles to a 100,000-year rhythm. Transition to the 100,000-year cycle began about 1 Ma ago. By about 800 Ka ago the 100,000-year cycle started to become dominant (Raymo, 1998), and it was firmly established by circa 640 Ka ago (Schmieder et al., 2000). Thus the upper cycle at Porcupine Cave (levels 1–5) very probably accumulated during the time of the 100,000-year periodicity, whereas the lower Porcupine Cave levels may sample the transitional climatic intervals as the 41,000-year rhythm switched over to 100,000-year periodicity.

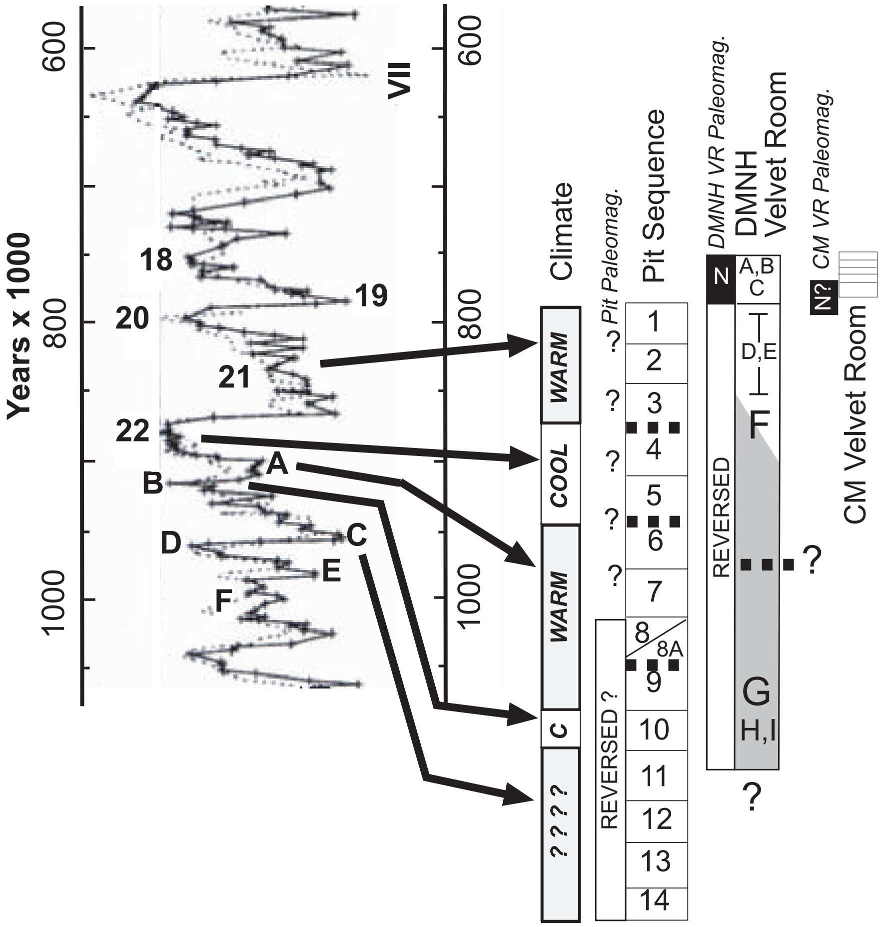

FIGURE 7.5 Potential correlation of the Porcupine Cave stratigraphic sequences with global climate changes indicated by the oxygen isotope curve. The oxygen isotope data are adapted from Raymo et al. (1997).

Conclusions

The combination of magnetostratigraphic, biochronologic, biostratigraphic, and amino acid racemization techniques that has been applied to Porcupine Cave sediments suggests that the Pit sequence has an age near 780 Ka at its top and is as old as 900 Ka or 1 Ma at its bottom. The DMNH Velvet Room appears younger than the uppermost Pit sediments at its top (levels A–C), with levels D and E potentially coeval with Pit levels 1–3, level F in the vicinity of Pit levels 3 or 4, and levels G–I potentially as old as Pit levels 9 or 10. The CM Velvet Room sediments appear at least as young, and probably younger, than level 1 in the Pit. The Badger Room seems coeval with the interval represented by levels 8–4 in the Pit. The correlations between the Pit, Velvet Room, and Badger Room localities are based primarily on a combination of LSDk-HSDk zones, relative abundance zones, and assemblage zones defined for arvicoline rodents in the Pit, which are the only component of the fauna that has been well enough identified from all the pertinent localities and levels for meaningful biostratigraphic application. These zones presently are applicable only within Porcupine Cave and possibly in the immediate vicinity; they should not be assumed to apply over broader geographic regions. The correlations are supported by biostratigraphic evidence from squirrels and rabbits, internally consistent paleomagnetic data, and the amino acid racemization results.

Nevertheless, important caveats should be kept in mind. The stratigraphy in the cave is complex and unconformities probably abound, as illustrated in the Pit and probably in the DMNH Velvet Room. Especially in the DMNH Velvet Room, the assignment of specimens from a particular excavation bag to a definite stratigraphic interval is sometimes difficult. Moreover, the arvicoline biochronology is correlated to an independent time scale primarily from sites at much lower elevations than Porcupine Cave. Thus the role of biogeographic differences in influencing interpretations of temporal distributions has been little studied; in fact, the Porcupine Cave data are among the most applicable in this regard. Finally, many additional specimens remain to be identified from both of the Velvet Room excavations, as well as from most of the other localities in the cave. Much of the material has not even been processed out of the matrix.

As the sample size from the Velvet Room and other localities in Porcupine Cave grows in the coming years, additional analyses and comparisons to other important sites—such as those at nearby Hansen Bluff and SAM Cave (Rogers et al., 1985, 1992, 2000; Rogers and Wang, 2002)—should provide valuable tests of the chronology proposed here. These further tests are particularly crucial because, as the most diverse sample of high-elevation Irvingtonian fauna located in the heart of the Rocky Mountains, Porcupine Cave provides a unique perspective on faunal dynamics, faunal provinciality in the West, and attendant biochronologic questions.

Acknowledgments

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EIGHT

Biology of Wood Rats as Cave Dwellers and Collectors

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Wood rats, genus *Neotoma,* also widely known to speleologists as packrats, are commonly found in caves within their range, but they are primarily adapted for life outside caves. They are terrestrial rodents of the family Muridae, subfamily Sigmodontinae. The center of abundance and diversity of *Neotoma* is in the arid southwestern United States and Mexico. Since the diet of *Neotoma* consists mainly of foliage and fruits, they must forage outside caves for food, much of which is carried inside for use or storage. The abundant fragments of plant materials, predator scats, and owl pellets dropped on the middens and rock shelves provide a good record of ecological communities and of the climate changes that have occurred outside the dens or caves over thousands of years. Indeed a major account of biotic changes in the Southwest is based entirely on remains of plants and animals recovered from middens of species of *Neotoma* (Betancourt et al., 1990).

Porcupine Cave exhibits signs of current wood rat activity in the entrance adit, Badger Room, Gypsum Room, Pit, Velvet Room, and Damp Room. In fact, fecal pellets, urine deposits, or nests attest to wood rats' use of most of the several hundred meters of mapped passageway. Fecal pellets were found mixed with small bones in many of the matrix samples from various levels in Porcupine Cave. Cave explorers commonly report seeing wood rats in caves, sometimes far from any entrance (chapter 2; D. L. Rasmussen, pers. comm.).

Colorado's pioneer mammalogist, E. R. Warren (1910:117), wrote as follows: "I have found them in abandoned mine tunnels, about the timbers, and in drifts. I took one in an abandoned tunnel near Querida, Custer County, at a point about 225 feet in from the entrance; it had a nest there, and there was another nest in a drift close by." According to Cary (1911:113), "Miners at the Stevens Mill, at timberline on Mt. McClellan, reported a few rats living in the mine several hundred feet from the entrance, and stated that the animals often passed them on the ladders." The greatest distance from the surface I have seen reported for *N. cinerea* within a cave is that cited by Turner (1974:103): "I have observed *N. cinerea* in Wind Cave [South Dakota] at depths of 325 feet below ground surface, and 2300 feet from any known entrance of the cave."

Bailey (1928) reported that both *N. albigula* and *N. micropus* were present at Carlsbad Cavern, *N. albigula* being abundant in caves and canyon walls and in the great western entrance but not below the brink of the shaft that drops 30 m into the deep interior. *N. micropus* occupies stick and cactus houses in the open valley for shelter. Bailey (1933) reported that *Neotoma pennsylvanica* (now known as *N. floridana magister*) was common in the limestone cliffs and in most of the caves of the Mammoth Cave region of Kentucky, where individuals followed the whole length of extensive passages.

The only species of wood rat living today in Porcupine Cave and vicinity is the bushy-tailed wood rat, *Neotoma cinerea* (figure 8.1). Within the genus, it is the species most highly specialized for living in cliffs and caves. It is found only at higher elevations in western North America and is superbly adapted to climbing vertical cliffs. The deep rock fissures and caves it occupies serve as heat sinks that stabilize air temperatures within its dens in both winter and summer. In Porcupine Cave some floors are carpeted with pellets and plant litter, including in many places great quantities of small bones mixed with sediment. The wood rats have also left on walls and rock ledges solid dark deposits and urine stains widely known as amberat.

During the Irvingtonian, at least five extant species of wood rats lived around Porcupine Cave at various times: *N. cinerea, N. mexicana, N. floridana, N. micropus,* and *N. stephensi* (chapter 18). This chapter describes the basic ecology of bushy-tailed wood rats, *N. cinerea,* how they differ in ecology from their congeners, and how they leave evidence of their activities in caves.

Definitions

The literature on wood rat dens and middens is often sketchy and ambiguous. For example, words used by hunters, naturalists, and cavers to describe the "sign" at a den or cave en-

FIGURE 8.1 Bushy-tailed wood rat, *Neotoma cinerea,* the species of wood rat living in Porcupine Cave today.

trance have different meanings to different people. I defined my use of such terms, as widely understood by mammalogists, in Finley (1990:28), and I repeat and augment the definitions here.

In this chapter, I follow the convention of using "wood rat" as the common name for *Neotoma,* in keeping with standardized use in the mammalogy literature. "Wood rat" as used here is synonymous with the more vernacular "packrat."

CACHE A quantity of food materials piled or stuffed into a sheltered space, such as a crevice, log, or burrow, for later use.

DEN Any natural or constructed shelter used regularly for protected living space, rest, or the rearing of young, such as a rock crevice.

FECAL DEPOSIT A layer consisting mainly of fecal droppings that may or may not be indurated by dried urine.

FOOD LITTER Food materials brought to a place for feeding and dropped as unconsumed debris.

HOUSE A den constructed of a pile of various materials and containing one or more passages or chambers. It may be located in the open or at a site under some natural shelter, such as a tree.

MIDDEN A layer or accumulation of materials brought to or dropped at any location by an animal, usually but not necessarily the den occupant and including any other materials, such as leaves, pollen, and silt, deposited there by other means.

NEST A cup or ball of soft material, such a shredded juniper bark, within a house or other den, used as a bed.

PALEOMIDDEN A "fossil" midden, which has persisted long enough to survive environmental changes but has not necessarily been altered over time.

POST A site used by an animal repeatedly for some function, such as feeding, urination, or scent deposition. Posts may give rise to deposits, such as food litter found either within or away from dens. Urination posts on rock ledges or cave walls often give rise to conspicuous dry stains (amberat) on walls or under ledges sheltered from the weather.

SIGN Any direct physical evidence of the animal activity that produced it.

URINARY DEPOSIT A layer of dried urine, usually including some fecal pellets or other materials.

The term "amberat" has been used in many different ways. I have not customarily used the term because of its ambiguity. The oldest reference I have found for "amberat" is by Orr (in litt., 1957, cited in Jackson, 1965). He called it "amberat" because "It has no proper name, but smells of rats" but he was uncertain of its origin. Jackson (1965) showed a photograph of two chunks of material from Defense Cave. One was a rough chunk of indurated rat pellets and plant litter that he called "ancient cave rat guano." The other was a glossy black, solid deposit that he called "amberat."

Paleoecologists Spaulding et al. (1990:60–63) called amberat the "crystallized packrat urine" that saturates and preserves solid plant and other materials. In their lengthy discussion of the "Physical Properties of Middens" they seem to regard the term as synonymous with urine. "Amberat" is also sometimes used to refer to the glossy urine deposits that resemble a shiny black curtain on a cliff face.

Ecological Attributes of *Neotoma* Species

Six species of *Neotoma* are extant in Colorado: *N. cinerea, N. mexicana, N. floridana, N. albigula, N. micropus,* and *N. lepida* (Finley, 1958). They live in different parts of the state such that rarely more than three species are sympatric. The most widespread is *N. cinerea,* which lives throughout the higher mountains. *N. mexicana* is found in the foothill zone on both the east and west slopes and occurs only about 700 m lower in elevation than Porcupine Cave. *N. floridana* lives on the Great Plains north of the Arkansas River, and *N. micropus* lives on the plains primarily south of the river. *N. albigula* lives at low elevations in southwestern and southeastern Colorado. *N. lepida,* having a range west of the Colorado River throughout the Southwest, extends into Colorado only in the lower drainages of northwest Colorado (Finley, 1958). Here I accept the analysis of Hoffmeister (1986), who showed that *devia* is a subspecies of *N. lepida,* not a separate species of *Neotoma.* Of the species currently known from Colorado, only *N. albigula* and *N. lepida* have not been found in Porcupine Cave (chapter 18).

Houses, rock dens, and caves provide protection for wood rats against adverse weather (Brown, 1968) as well as most predators. Nevertheless, wood rats do fall prey to their enemies when they emerge from their dens to forage for food or gather den materials. No doubt this danger accounts for the caution and speed with which wood rats usually move from one bit of outdoor cover to another (Finley, pers. obs.). Wood rats generally forage within 30 m of the den entrance (Finley, 1990), probably to minimize danger from predation.

Wood rats of different species live in various kinds of dens. Some use rock crevices and fissures, in which varying amounts of materials may be piled. Others build houses of sticks or other materials in or over a base of shrubs or cactus. Tunnels and chambers within the house usually extend below ground and may be more extensive than those within the house. Rock-dwelling species, such as *N. cinerea* (Smith, 1997) and *N. mexicana* (Cornely and Baker, 1986), may pile few or many sticks and other materials at the entrance to a rock fissure, but the stick pile rarely forms a house with passages and chambers (Finley, 1958). The species that form large houses, such as *N. fuscipes* in California, are indefatigable collectors and continue to add sticks to their houses, sometimes to a height of 2 m (Linsdale and Tevis, 1951; Carraway and Verts, 1991). At the other extreme, *N. mexicana* has a weak collecting habit, and its small dens under rock ledges may be easily overlooked because of the few collected materials other than long twigs and food litter. *N. floridana* and *N. albigula* may live in either kind of den, depending on available cover and the presence of other species (Rainey, 1956; Finley, 1958; Wiley, 1980).

In the recent past some rock shelters have been occupied by a different species of wood rat than the one found in them today (Finley, pers. obs.). In the case of fossil deposits, extinct species of *Neotoma* may have been present. Nine extinct species have been proposed for *Neotoma* from the Blancan or Irvingtonian: *N. quadriplicata, N. taylori, N. spelaea,* and *N. fossilis* (Kurtén and Anderson, 1980), and *N. amblidonta, N. ozarkensis, N. findleyi, N. pygmaea,* and *N. magnodonta* (Repenning, in litt.).

Climbing ability varies with the habitat and kind of den. *N. cinerea* is an agile cliff climber and readily scrambles up cliffs (Finley, pers. obs.) and over the walls of caves. *N. fuscipes* is an excellent tree climber and sometimes builds its bulky houses among tree limbs several feet above the ground (Carraway and Verts, 1991). *N. albigula* uses rock dens in some areas and can also build well-fortified houses of cactus joints (Voorhies and Taylor, 1940). It readily climbs for escape to the top of cholla cactus. Both *N. floridana* and *N. micropus* may use rock dens, build stick houses, or live in burrows under a thicket (Finley, 1958; Braun and Mares, 1989).

Species of wood rats have diversified in food preferences as well as kinds of dens. In general, the species that occur in more boreal or mesic life zones, such as *N. cinerea, N. mexicana,* and *N. floridana,* depend primarily on the leaves of woody plants and forbs. *N. cinerea* eats conifer needles as a substantial part of its diet, whereas *N. floridana* makes little use of conifers, eating mainly a wide variety of broad-leaved plants, cacti, and spiny shrubs (Rainey, 1956; Finley, 1958). *Neotoma stephensi* is a dietary specialist depending mostly on juniper *(Juniperus monosperma)* for food (Vaughn, 1982; Jones and Hildreth, 1989; Dial and Czaplewski, 1990). The wood rats of more austral life zones or xeric habitats, such as *N. micropus, N. albigula,* and *N. lepida,* depend more on the pulp of many kind of cactus and succulent shrubs, which they consume in large quantities for water as well as food. Some species of cholla and prickly pear (*Opuntia* spp.) are also heavily used for house building and defense against intruders.

In Colorado three species, *Neotoma cinerea, N. mexicana,* and *N. albigula,* display ecological as well as morphological divergence within each species on the east and west sides of the state. All three live in divergent habitats and in some areas sympatrically with the other two species (Finley, 1958). In the Southwest two or three species of *Neotoma* often occur at the same locality in the same or different habitats. In Grand Canyon National Park there are five species: three are confined to the South Rim *(N. mexicana, N. stephensi,* and *N. albigula),* one is confined to the North Rim *(N. cinerea),* and one is found in the canyon on both sides of the Colorado River *(N. lepida)* (Hoffmeister, 1971). These conditions illustrate the difficulty of trying to ascribe environmental conditions or communities to types of wood rats. Where more than one species of *Neotoma* occurs at the same locality, the species are usually separated by different shelter types or narrow vegetative types, not by broad community types such as grassland or sagebrush. However, some species are confined to different climatic limits of temperature and aridity, irrespective of vegetative communities. A brief summary of the ecological diversity of wood rat species in the United States was given by Finley (1990:32).

Taphonomy and Interpretation of Packrat Sign

Wood rats collect and accumulate at their dens great quantities of sticks, bones, owl pellets, carnivore scats, and almost anything they can carry. In caves and rock shelters these are protected for hundreds or thousands of years. *Neotoma* can thus be a valuable taphonomic agent for preservation of cave deposits and their bone remains.

Donald L. Rasmussen recognized the richness and nature of the fossil deposits at Porcupine Cave and the unique taphonomy that depended so much on wood rats (Barnosky and Rasmussen, 1988; Rasmussen and Anderson, 1996). In searching for other cave entrances along the dolomite ridges of southern Park County, he scanned the rock overhangs and fissures, which were sometimes located where the wood rats had access into the karst fissures of cave systems. The Trailside Nest (a misnomer—it is not a true nest) near the adit entrance to Porcupine Cave is one such den; it was active as far back as 2000 years ago (Barnosky and Rasmussen, 1988). Another such den was found near the base of the next ridge, 1 km to the west.

Owls have long been recognized by mammalogists as among the best sources of information on the kinds of small mammals at any locality (Finley, 1954), and packrat middens may be almost as useful because they commonly contain both raptor pellets and carnivore scats that the wood rats collected. Owl pellets contain the undigested fur, bones, and teeth of their prey as regurgitated by the owls, and thus provide a widely used record of owl food habits (Craighead and Craighead, 1969 [1956]). Faunal data from unconsolidated wood rat middens are comparable to those from owl pellets and may reveal the presence of rare or extralocal species. For example, in July 1990 I found the skull of a black-footed ferret *(Mustela nigripes)* at a den of *N. cinerea* in Saguache County, Colorado, where no ferrets had been recorded in decades. The skull was partially buried in a crevice of a rock den with loose soil and midden materials. The upland above the lava rimrock had soil too shallow to support the burrows of prairie dogs *(Cynomys),* the prey of ferrets. The ferret had probably been captured by a raptor at the nearest prairie dog town in the valley, about 3 km distant, and carried to a nest or roost in a pine tree below the rimrock near the wood rat den, probably a few decades ago.

The middens at modern dens of *N. cinerea* sometimes include larger bones, up to the size of the cannon bone of a deer, collected and piled with sticks at the entrance to a rock den. Coyotes, bobcats, and other carnivores that have their dens in cave openings also carry in the carcasses of their kills to be eaten. The smaller bones may then be carried farther into the cave by wood rats. Wood rats also collect scats from along the ridge on which they live, as well as regurgitated owl pellets from beneath nests on ledges and trees. The owl pellets and scats of predators in old cave deposits disintegrate, leaving the bones mixed with the sediment. In some cases the bones, or the pellets and scats themselves, may be fluvially redeposited within the cave and left in stratified deposits. However, no such stratified deposits that would indicate substantial reworking have been found thus far in Porcupine Cave.

This complex taphonomic history means that the radius of possible occurrence of a fossil animal may be as much as several kilometers and a few hundred meters of elevation from the cave entrance, depending on local topography. Hadly (1999) estimated that most remains in the deposits of Lamar Cave, Wyoming, came from within a radius of about 5 km. The seasonal hunting ranges of many species of hawks and owls are within 5 km (Craighead and Craighead, 1969 [1956]), and the ranges of golden eagles are somewhat larger (McGahan, 1967). Communities currently within a few kilometers of Porcupine Cave include montane coniferous forest, montane grassland, rock outcrops and ridges with bristlecone and limber pines, shortgrass prairie (grazed), riparian shrubs and forbs, small streams, peat bog, and stock ponds (see Cooper, chapter 3, for more details). Many mammals and birds are restricted more by fidelity to topographic type than by fidelity to vegetative type. Such considerations restrict the possible ecological implications of the presence of any species found in the bone deposits. Species from diverse habitats found within a radius of a few kilometers are represented in the cave samples because of varied terrain and vegetation. Species that are not topographically limited no doubt moved higher or lower with climate changes, and others may have moved within range. These considerations must be kept in mind when using faunal remains from caves as indicators of climate or community dynamics.

Time averaging, that is, the stratigraphic mixing that associates as fossils animals that actually lived at different times, can further obscure the fine details of community composition as communities change with time. In deposits in Lamar Cave similar in taphonomy and thickness to those of the Pit in Porcupine Cave, time averaging per level ranged from 300 to 1400 years (Hadly, 1999). However, the comparability of the fossil "community" with that of the neoecologist must be taken into account. The community of the latter is often of such small dimension or so patchy as to contain a few characteristic vertebrates and many that range over several wider communities. Many carnivores and raptors are highly opportunistic in hunting and frequently move from one locality and prey species to another (Craighead and Craighead, 1969 [1956]). Better communication among neoecologists and paleontologists would result if unambiguous terms were used to specify the time-averaged fauna of fossil assemblages versus the neoecologists' concept of a community.

In order to discern how faunal data from modern middens compare with records of the local fauna obtained by trapping and observation at each den at the time the den was studied, I compiled my records of associated vertebrates from 159 dens of four species of *Neotoma* in Colorado. Data were collected during the years 1948–51. The results are shown in tables 8.1–8.4 for 57 dens of *N. cinerea,* 51 dens of *N. mexicana,* 39 dens of *N. albigula,* and 12 dens of *N. floridana.* Traces of associated vertebrates include bones of mammals and reptiles in the unconsolidated midden, small mammals trapped at the den, and small mammals and reptiles seen or captured at the den. Observations of birds were not included, although bones of some larger birds were recorded. All remains appeared to be from recent years.

The data show not only the great variety of vertebrates represented, but also that the wood rats effectively sample a diversity of carnivores and ungulates not easily recorded by brief survey. In wood rat houses, particularly, many bones of small commensal mammals and reptiles were found, that is, bones from animals that were attracted to the houses for shelter and that died there. In California and Oregon, the large houses of *N. fuscipes* are especially rich in vertebrate and invertebrate commensals (Carraway and Verts, 1991). Bones of such cohabitants are less likely to be found in rock dens, which cannot be dismantled for study, but they may account for many of the small bones found in caves. The bone samples, however, cannot be considered to represent precise numbers of individuals. Plant remains, either as food litter or as den materials from dens of different species, may reveal differences in the life zones and communities where the wood rats lived. Plant parts are usually gathered within 30 m of the den (Finley, 1990:35).

Conclusions

The location and geological conditions at Porcupine Cave have combined to provide a unique, rich fossil record of early and middle Pleistocene faunas that have been preserved and sampled largely thanks to the ecological habits of the bushy-tailed wood rat. The efforts of a great many dedicated people

TABLE 8.1
Vertebrate Associates of *Neotoma cinerea* in Colorado

Species	*Caught at or near Den*	*Seen at or near Den*	*Remains in Den*
Plecotus townsendii	•	—	—
Homo sapiens	—	—	•
Sylvilagus sp.	—	—	•
Lepus americanus	—	—	•
L. townsendii	—	—	•
Tamias minimus	•	•	—
T. quadrivittatus	—	—	•
Marmota flaviventris	—	—	•
Ammospermophilus leucurus	•	—	—
Spermophilus lateralis	•	—	•
S. richardsoni	—	—	•
Cynomys gunnisoni	—	—	•
C. leucurus	—	—	•
Tamiasciurus hudsonicus	—	—	•
Thomomys talpoides	—	—	•
Castor canadensis	—	—	•
Peromyscus boylii	•	—	—
P. crinitus	•	—	—
P. maniculatus	•	•	•
P. truei	•	—	—
Neotoma cinerea	—	—	•
N. mexicana	—	—	•
Microtus sp.	—	—	•
Erethizon dorsatum	—	—	•
Canis latrans	—	—	•
Ursus americanus	—	—	•
Martes americana	—	—	•
Mustela frenata	—	—	•
Mephitis mephitis	—	—	•
Taxidea taxus	—	—	•
Felis catus	—	—	•
Lynx rufus	—	—	•
Equus caballus	—	—	•
Sus scrofa	—	—	•
Cervus elaphus	—	—	•
Odocoileus hemionus	—	•	•
Ovis aries	—	—	•
Bos taurus	—	—	•
Branta sp.	—	—	•
Falco mexicanus	—	—	•
Dendragapus obscurus	—	—	•
Centrocercus urophasianus	—	—	•
Gallus gallus	—	—	•
Bubo virginianus	—	—	•
Pica pica	—	—	•
Corvus corax	—	—	•
Urosaurus ornatus	•	—	—
Uta stansburiana	—	•	—
Crotalus viridis	•	•	•

NOTE: •, present.

TABLE 8.2

Vertebrate Associates of *Neotoma mexicana* in Colorado

Species	*Caught at or near Den*	*Seen at or near Den*	*Remains in Den*
Notiosorex crawfordi	—	—	•
Antrozous pallidus	—	—	•
Homo sapiens	—	—	•
Sylvilagus sp.	—	—	•
Lepus sp.	—	—	•
Tamias minimus	•	•	—
T. quadrivittatus	•	—	—
Ammospermophilus leucurus	•	—	—
Spermophilus variegatus	—	—	•
Cynomys gunnisoni	—	—	•
C. cf. *leucurus*	—	—	•
C. ludovicianus	—	—	•
Thomomys cf. *bottae*	—	—	•
Pappogeomys castanops	—	—	•
Perognathus flavus	—	—	•
P. hispidus	—	—	•
Dipodomys ordii	—	—	•
Castor canadensis	—	—	•
Onychomys leucogaster	—	—	•
Peromyscus boylii	•	—	—
P. difficilis	•	—	—
P. leucopus	•	—	—
P. maniculatus	•	—	•
P. truei	•	—	—
Reithrodontomys sp.	—	—	•
Neotoma albigula	—	—	•
Ondatra zibethicus	—	—	•
Rattus norvegicus	—	—	•
Erethizon dorsatum	—	—	•
Canis latrans	—	—	•
Spilogale gracilis	—	—	•
Mephitis mephitis	—	—	•
Lynx rufus	—	—	•
Odocoileus hemionus	—	—	•
Bubo virginianus	—	•	—
Asio flammeus	—	—	•
Sceloporus graciosus	•	•	—
S. undulatus	•	—	—
Uta stansburiana	•	•	—
Cnemidophorus tigris	•	•	—
Crotalus viridis	•	—	—
Unidentified snake	—	—	•
Unidentified fish	—	—	•

NOTE: •, present.

TABLE 8.3
Vertebrate Associates of *Neotoma albigula* in Colorado

Species	*Caught at or near Den*	*Seen at or near Den*	*Remains in Den*
Sylvilagus sp.	—	•	•
Tamias quadrivittatus	•	—	—
Spermophilus tridecemlineatus	•	—	—
S. variegatus	•	•	•
Cynomys sp.	—	—	•
Thomomys cf. *bottae*	—	—	•
Dipodomys ordii	•	—	•
Castor canadensis	—	—	•
Peromyscus boylii	•	—	—
P. crinitus	•	—	—
P. leucopus	•	—	—
P. maniculatus	•	—	—
P. truei	•	—	—
Neotoma mexicana	•	—	•
Ondatra zibethica	—	—	•
Erethizon dorsatum	—	—	•
Spilogale gracilis	—	—	•
Odocoileus hemionus	—	—	•
Ovis aries	—	—	•
Bos taurus	—	—	•
Buteo sp.	—	—	•
Phasianus colchicus	—	—	•
Cnemidophorus tigris	•	•	—
Crotaphytus collaris	•	•	—
Phrynosoma cf. *cornutum*	—	—	•
Sceloporus undulatus	•	•	•
Uta stansburiana	•	•	—
Elaphe guttata	•	—	—
Masticophis flagellum	—	•	—
Unidentified lizard	—	—	•
Unidentified snake	—	—	•
Scaphiopus multiplicatus	—	—	•

NOTE: •, present.

TABLE 8.4
Vertebrate Associates of *Neotoma floridana* in Colorado

Species	*Caught at or near Den*	*Seen at or near Den*	*Remains in Den*
Sylvilagus sp.	—	•	—
Geomys bursarius	—	—	•
Dipodomys ordii	•	—	—
Peromyscus maniculatus	•	—	—
Unidentified carnivore	—	—	•
Bos taurus	—	—	•
Equus caballos	—	—	•
Melagrus gallopavo	—	—	•
Sceloporus undulatus	—	•	—
Cnemidophorus sexlineatus	—	•	—
Masticophis flagellum	•	—	—
Crotalus viridis	—	•	—

NOTE: •, present.

have made possible the recovery and study of the wealth of information contained in the cave deposits. Correct interpretation of the data has depended on understanding the complex biology and history of these deposits, as well as the geology of the cave itself. This review of the major role of wood rats in cave taphonomy puts into perspective the favorable factors, as well as the limitations of interpretation, inherent in the biology of wood rats. The most important among the favorable factors are the collecting and cave-dwelling behaviors of *Neotoma.* Major limitations are the ecological diversity of wood rat populations, the wide range of environmental conditions in the vicinity of the cave, and the many known changes of climatic conditions in the Pleistocene.

Acknowledgments

I thank Don Rasmussen and A. D. Barnosky for the invitation to participate in the Porcupine Cave project. I am grateful to Don and Jerry Rasmussen for the benefit of many conversations about wood rats and the history of caves in South Park, and for their guidance both inside the cave and in the surrounding hills. I thank Donna Shay for help in collecting and preparing mammal specimens, and for improvements made to a draft of this chapter. Reviews of this chapter by A. D. Barnosky, Don Rasmussen, Tom Van Devender, and an anonymous reviewer did much to improve it. E. A. Hadly provided a reprint of her 1999 paper on Lamar Cave.

NINE

Paleopathology and Taphonomic Modification of Mammalian Bones from Porcupine Cave

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> Disease is as old as life, for disease is a part of life, life in changing conditions.
>
> RUDOLF VIRCHOW *(1858)*

The story of Porcupine Cave would be incomplete without an understanding of health, disease, trauma, and the calamities that befell the animals whose remains were fossilized, as well as the conditions that led to the accumulation of the many bones in the cave.

Paleopathology was first defined in *Funk and Wagnall's Standard Dictionary* in 1895 and was first referred to by physician R. W. Shufeldt in 1892 (Jarcho, 1966; Ubelaker, 1982). All of the early works defined paleopathology as the study of ancient disease. Yet it was not until widespread interest in ancient Egypt took hold, and the British anatomists Grafton Elliot Smith and Warren Dawson published their work on human mummies in 1924, that the word entered mainstream jargon. Sir Marc Armand Ruffer brought paleopathology into the general scientific realm through his work on human Egyptian mummies in 1891. He defined paleopathology as the study of disease in ancient human populations (Ruffer, 1921). After Ruffer's untimely death in 1917, Roy L. Moodie compiled and published Ruffer's manuscripts, which showed that fossilized vertebrates exhibited signs of disease and trauma. Moodie (1924:21) expanded the definition of paleopathology to include the study of "not only . . . diseases found in the mummified animal and human remains of Egypt, but [also] those of prehistoric man and fossil vertebrates as well." This definition of paleopathology is widely accepted today, and new techniques have led to innovative discoveries that have enabled scientists to document the demography of disease and its effects through time (Rothschild and Martin, 1993).

Taphonomy is the study of all the processes that interact to produce a recovered fossil from a once-living organism (Lyman, 1994). A clear understanding of taphonomy is essential to using fossils to interpret once-living biota, including paleoecological reconstructions, among other endeavors.

This chapter reports the paleopathology and taphonomic alterations evident in several specimens recovered from the Porcupine Cave deposits, and also provides background information about the accumulation of bones in a cave setting.

Materials and Methods

The specimens that were examined are listed in appendix 9.1. All measurements are in millimeters unless otherwise noted, and dimensions are illustrated in figures 9.1–9.3. A dial caliper and osteometric board were used to obtain measurements.

Abbreviations specific to this chapter are as follows:

CB	Canine breadth
CC	Width across canines
CL	Canine length
DB	Distal breadth
FH	Femur head measurement
FMH	Foramen magnum height
FMW	Foramen magnum breadth
GB	Greatest breadth across zygomas
GL	Greatest length
HS	Height of skull
ID	Inner diameter
L	Left
L/WM1	Length/width of M1
L/WM2	Length/width of M2
L/WP1	Length/width of P1
L/WP2	Length/width of P2
L/WP3	Length/width of P3
LP4	Length of P4 blade
LPC	Length of P4 across protocone
LSW	Least shaft width
LTR	Length of tooth row, C-M2

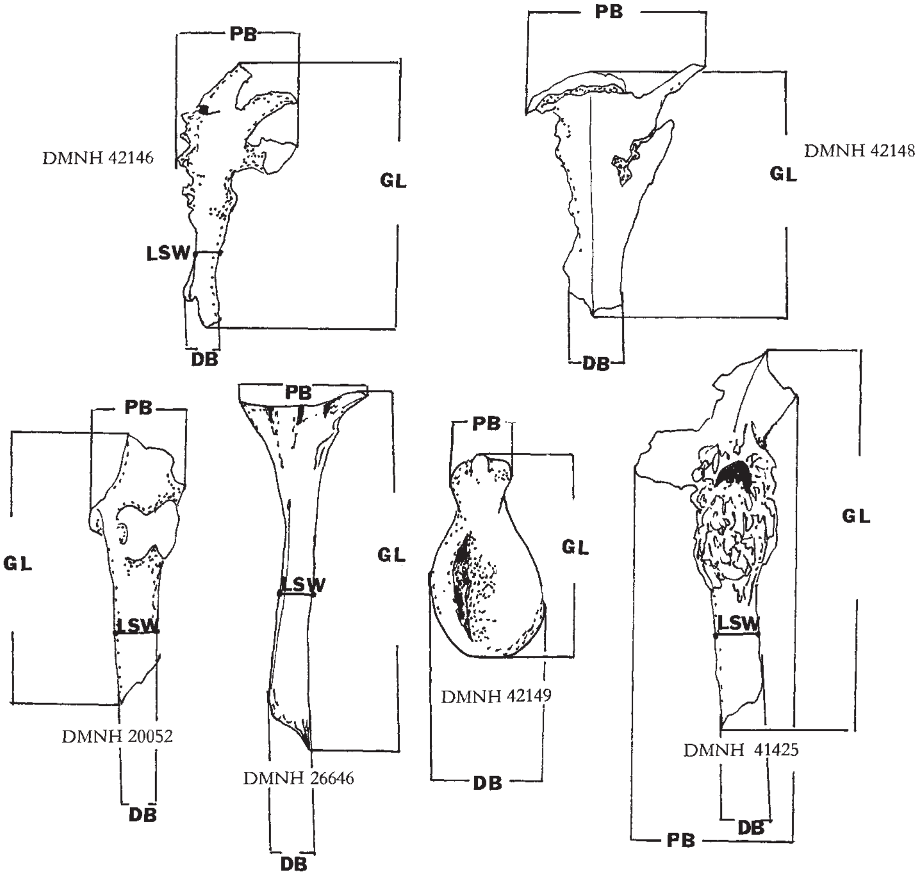


FIGURE 9.1 Dimensions of measurements for rodent and lagomorph specimens discussed in the text. (Drawing by C. Suzane Ware.)

PB	Proximal breadth
PL	Palatine length
POC	Postorbital constriction
POP	Postorbital process
R	Right
W I3-I3	Width across incisor row
W P4-P4	Width across premolars
WOC	Width across occipital condyles
WP4BL	Width of P4 blade
WP4PC	Width across P4 protocone

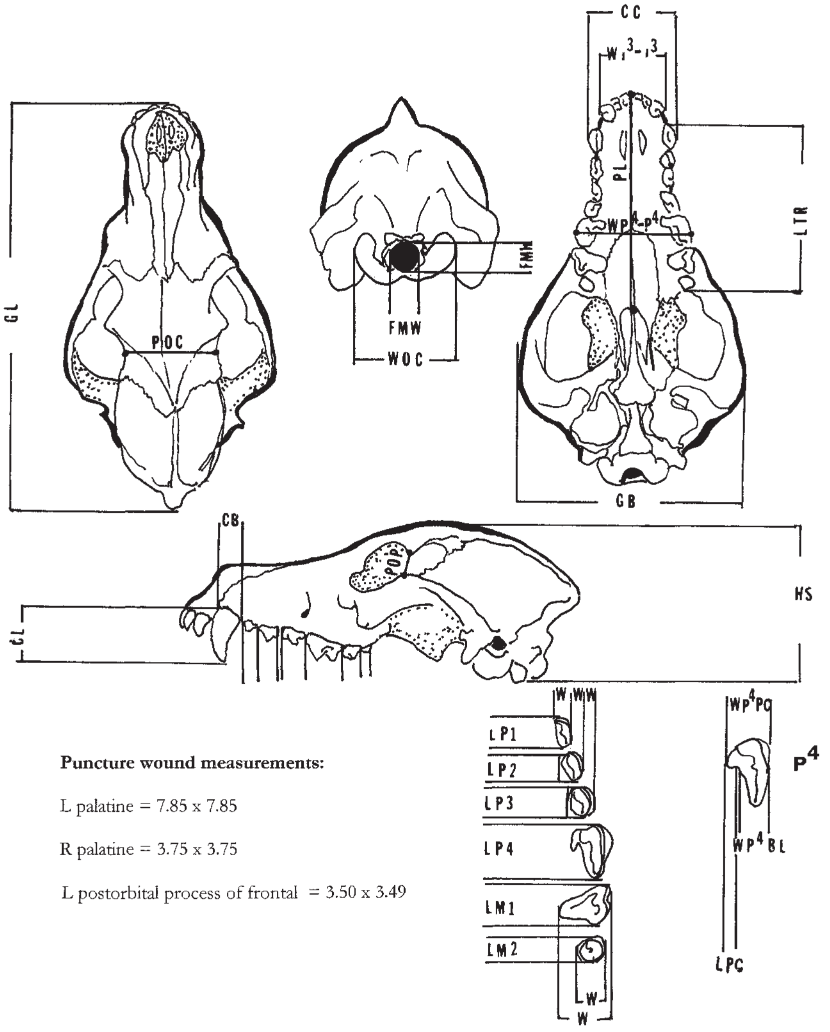
Bone Accumulation in Caves

Bones are deposited at sites such as Porcupine Cave by four major processes (Andrews, 1990):

1. Animals die in the cave, particularly during hibernation, denning, or both.
2. Animals fall into the cave through a sinkhole at the surface.
3. Animals are taken into the cave by predators.
4. Bones are transported into the cave by wood rats *(Neotoma)* after having passed through the digestive tracts of carnivores or raptors or having become disarticulated from carcasses decomposing outside the cave entrance.

The latter two taphonomic scenarios in particular seem to have been important at Porcupine Cave, although the possibility of some animals falling into the cave through intermittently open crevices cannot be discounted. Such sinkhole accumulations have been documented many times at other cave sites (Buckland, 1823; Brain, 1958; Morris, 1974), although as yet no characteristic sinkhole accumulations have been recognized at Porcupine Cave. For example, White et al. (1984) pointed out that natural trap sites have a high concentration of carnivore skeletal material. Morris (1974) noted that natural trap sites are characterized by relatively complete skeletons in caves, deposited largely intact, unless subsequent damage has occurred by trampling, gnawing, or weathering. Neither a particularly high concentration of carnivores nor complete skeletons are found in Porcupine Cave.

As with other cave sites, predation was a major factor in creating the skeletal deposits at Porcupine Cave. Owls and raptors may contribute large amounts of small mammal bones to cave deposits. The regurgitated pellets of predatory birds contain bones with a suite of distinctive physical characteristics that distinguish them from the bones found in carnivore scat. Because some of these birds (the Snowy Owl, *Nyctea*



Puncture wound measurements:

L palatine = 7.85 x 7.85

R palatine = 3.75 x 3.75

L postorbital process of frontal = 3.50 x 3.49

FIGURE 9.2 Dimensions of measurements for DMNH 30076, *Canis latrans* skull, discussed in the text and illustrated in figure 9.7. (Drawing by C. Suzane Ware.)

scandiaca; the Barn Owl, *Tyto alba;* and the Great Horned Owl, *Bubo virginianus*) swallow their prey whole and have a shorter digestive tract than mammalian carnivores, these characteristics include minimal corrosive damage to the bones; skulls often nipped off behind the orbits; minimal damage to maxilla and mandible, with teeth often intact and still in the alveoli; and minimally affected articulation surfaces of the long bones.

Bones that have passed through the digestive tracts of mammalian carnivores, such as the coyote, *Canis latrans,* or the red fox, *Vulpes vulpes,* tend to exhibit severe damage from initial dismemberment and chewing, as well as from highly corrosive stomach acids acting upon them after ingestion. The characteristics of bones from carnivore scat in comparison with those from raptor pellets include extreme damage to maxillae and mandibles, including loss or partial digestion of teeth. Teeth and bones in the carnivore digestive system are subject to the effects of passage through a long digestive tract, where they spend much more time exposed to highly corrosive stomach acids. Since carnivores are known to chew the ends of bones to extract the nutrients, the ends of long bones are usually absent. The ends of long bones may also be absent owing to their vulnerability to the digestive process: the bone diaphysis erodes and the bones become rounded in appearance (Andrews, 1990:figures 1, 3).

The specimens described in the remainder of this chapter and others discussed in chapter 22 document many of these characteristics of predation. In addition, wood rats (and potentially other rodents) are implicated through such features as the presence of gnaw marks on the bones, and by the sheer numbers of fossil specimens. Mead and Murray (1991:124) note that "middens containing large numbers of bones [as do those in Porcupine Cave] are indicative of raptor pellet introduction." Dial and Czaplewksi (1990) have observed ground squirrels *(Spermophilus),* white-footed mice *(Peromyscus),* lizards, and snakes using wood rat middens; owls regurgitating pellets over and near the middens; and porcupines *(Erethizon)* bringing bones into the area of wood rat dens. All of these taxa have been found as fossils in the deposits of Porcupine Cave.

Additional potential modifications of bones in fossil sites are those that occur after the bones have been deposited at the site (Andrews, 1990; Lyman, 1994). Although trampling is

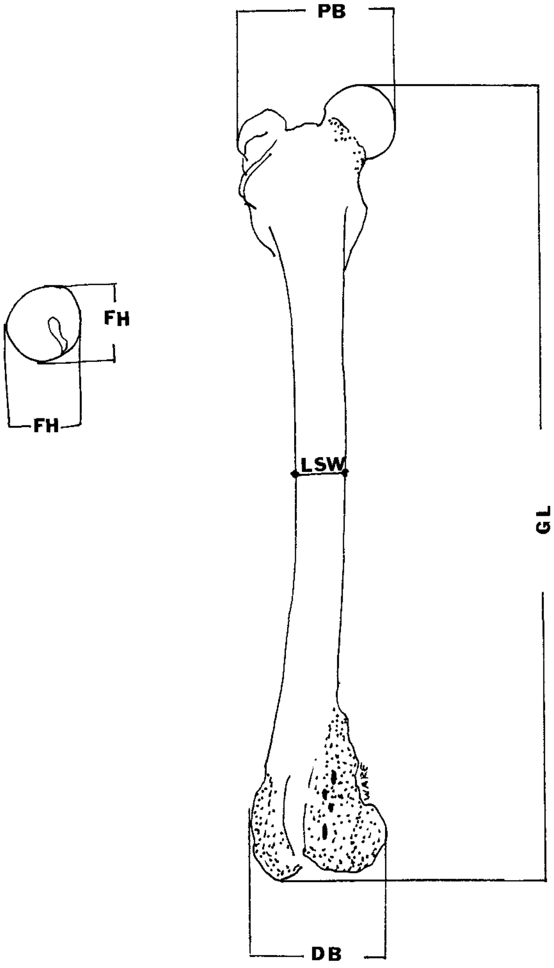


FIGURE 9.3 Dimensions of measurements for DMNH 26646, *Canis latrans* femur, discussed in text and illustrated in figure 9.9. (Drawing by C. Suzane Ware.)

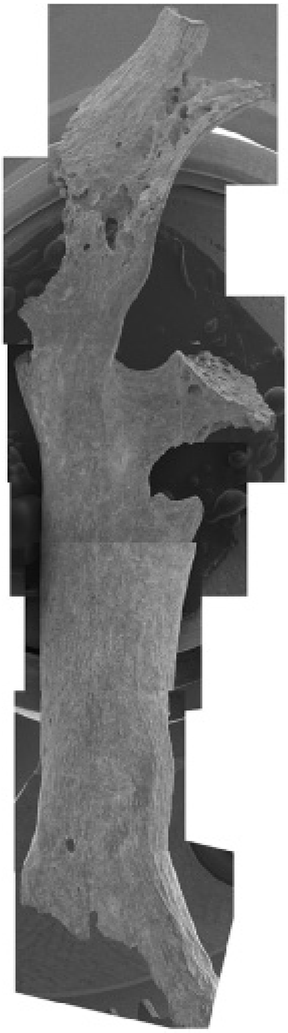


FIGURE 9.4 *Lepus* sp. (hare or jackrabbit), DMNH 42146, innominate fragment from Mark's Sink. (SEM photograph by Louis H. Taylor.)

not evident for bones at Porcupine Cave, crushing and/or fracturing of bones by falling rocks and the weight of accumulating deposits, as well as by human foot traffic, was probably not uncommon.

Sometimes the damage seen on a bone is not the work of disease or trauma, or of postmortem processes related to predation or scavenging, but instead was sustained during the excavation or handling of the fossil. By the time a bone that has been collected in Porcupine Cave moves through the process of collection, screen washing, picking, accessioning, and cataloging in a museum collection, there have been many opportunities to damage it. Such excavation-induced damage of bone was not characteristic of the specimens discussed in this chapter.

Paleopathology and Taphonomic Alteration

More than a hundred specimens from Porcupine Cave show signs of disease and trauma, and many more have been gnawed by rodents. In this preliminary study only a few specimens are described and figured as a representative sample. Appendix 9.1 lists additional specimens that were examined and ascribed to the following categories of bone modification: carnivore digestion; raptor digestion; disease, injury, or trauma; and rodent gnawing.

Carnivore Digestion

LEPUS *SP. (HARE OR JACKRABBIT)*

DMNH 42146 from Mark's Sink (8/96); innominate fragment (figure 9.4). Measurements: GL, 32.95; GB, 7.50; LSW, 3.85; PB, 11.50. This specimen exhibits extreme acid etching and severe corrosion over its entire surface. Articular surfaces are missing and the bone itself is severely compromised in density and completeness. The bone has passed through the digestive system of a carnivore, as evidenced by its overall eroded appearance and fragility.

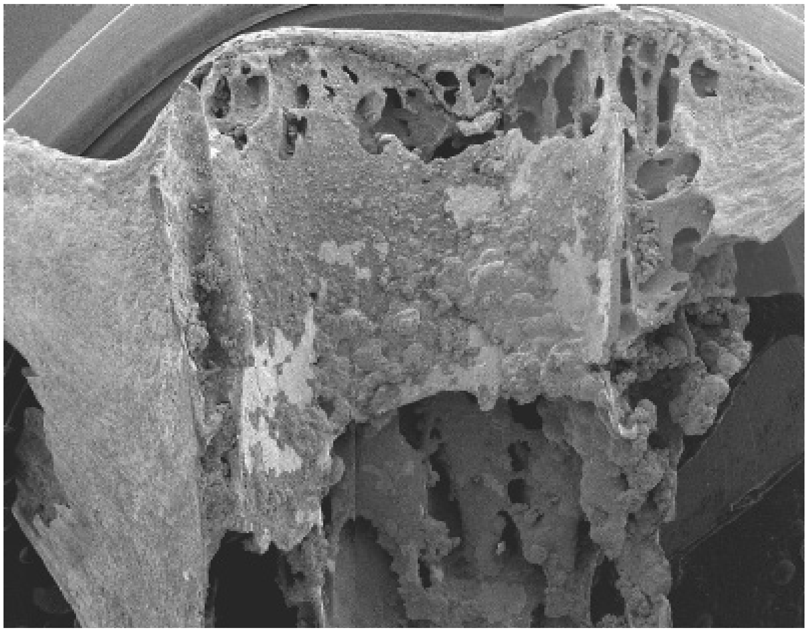


FIGURE 9.5 *Lepus* sp. (hare or jackrabbit), DMNH 42148, fragmentary thoracic vertebra from Mark's Sink. (SEM photograph by Louis H. Taylor.)

LEPUS *SP. (HARE OR JACKRABBIT)*

DMNH 42148 from Mark's Sink (8/96); fragmentary vertebra (figure 9.5). Measurements: GL, 17.95; GB, 14.0. This vertebral fragment exhibits extreme acid etching and severe corrosion over its entire surface, which suggest digestion by a carnivore. The proximal centrum is intact. The dorsal side shows breakage and erosion. The ventral side exhibits extreme damage by digestive acids. The transverse processes are eroded to the point of being sharp fragments.

LEPUS *SP. (HARE OR JACKRABBIT)*

DMNH 20052 from the Badger Room (7/94); right calcaneum (figure 9.6). Measurements: GL, 19.80; GB, 10.50; LSW, 5.50. This calcaneum exhibits the wear typical of passage through the intestinal tract of a carnivore. Since this bone is one of the denser ones in the body, much of the bone remains intact even after digestion. The wear is most severe on the dorsal side opposite the articular facets for the talus muscle. The proximal end of the calcaneal tuber and the distal end of the calcaneus are missing. On the dorsal side the surface of the bone is extremely damaged and exhibits severe bone loss. The remaining bone has a honeycomb appearance.

Puncture Wounds

CANIS LATRANS *(COYOTE)*

DMNH 30076 from the Badger Room (7/94); skull (figure 9.7). Measurements (values marked [a] are for alveoli only): GL, 186.0; POC, 37.50; GB, 90.0; HS, 55.35; CC, 28.65; L/WP2, R L 12.60, W 3.90; W I3-I3, R 12.40[a]; L/WP3, L 12.65, R 12.65 / L 4.80, R 4.75; W P4-P4, 53.50; LPC, R 6.30; FMB, 11.05 (ID); WP4PC, R 9.50; FMH, 12.50 (ID); WP4BL, R 2.35; POP, L 22.25, R 19.05; L/WM1, L 13.10 R 13.10 / L 14.90, R 14.55; WOC, 30.0; L/WM2, L 7.80, R 7.80 / L 10.90, R 10.90; HS, 55.35; PL, 93.45 (from R side); CL, L 10.25[a], R 10.25[a]; LTR, R C-M2, 99.80; CB, L 6.50[a]. This skull is extremely fragile. The dentition is partially complete and is typical in size and morphology of that of a modern coyote. The dentition, which includes the L P3-M2 and R P1-M1, is heavily worn. The right parietal area of the skull is severely damaged from the frontoparietal suture posteriorly to the occiput (including the sagittal crest). The left parietal area is cracked and extremely fragile from weathering and postmortem breakage. The left nasal area (including both ventral and dorsal locations) is missing. The bullae are badly damaged bilaterally. There is severe damage to the nasal, maxilla, and lacrimal areas on the dorsal side.

The skull shows two puncture wounds and one area where the puncture is visible but has not broken through. One puncture wound is slightly anterior to the left postorbital process of the frontal on the dorsal side. Another is directly between the right P4 and M1 on the palate. A third puncture wound, which did not perforate the left palatine, shows as a slight depression adjacent to P3. These puncture wounds are consistent with the bite pattern and canine tooth size of *Canis latrans.* As Grooms (1993:71, 73, 158) shows, it is possible for coyotes to inflict such puncture wounds during a myriad of behavior patterns. The puncture marks measure 7.85 × 7.85 mm (left palatine), 3.75 × 3.75 mm (right palatine), and 3.50 × 3.49 mm (frontal).

FIGURE 9.6 *Lepus* sp. (hare or jackrabbit), DMNH 20052, right calcaneum from the Badger Room. (SEM photograph by Louis H. Taylor.)

Trauma or Disease

RODENTIA CF. NEOTOMA *OR* SPERMOPHILUS *(WOOD RAT OR GROUND SQUIRREL)*

DMNH 41425 from DMNH Velvet Room excavation (G8/8A) (7/93); right innominate (figure 9.8). Measurements: GL, 32.50; GB, 11.60; LSW, 4.95. This specimen, a right innominate, shows wear patterns consistent with bone from a regurgitated owl or raptor pellet. The ends are missing, but the bone is not highly corroded and the acetabulum morphology is distinct. This specimen shows acute osteomyelitis (an opportunistic staphylococcal infection that causes an inflammation of the bone marrow) resulting from infection incurred after a break. The disease is severe and involves the entire acetabulum area.

CANIS LATRANS *(COYOTE)*

DMNH 26646 from the Badger Room (7/94); right femur (figure 9.9). Measurements: GL, 168.5; PB, 33.4; DB, 27.3; LSW, 11.3; FH, 16.3 × 16.2. This femur shows extensive pathology involving the entire distal end, both posteriorly and anteriorly. The patellar groove (trochlea) is slightly eroded dorsally. Both the lateral and medial epicondyles are heavily encrusted with extra bone callus, giving the entire distal surface a heavily porous appearance. The caudal aspect of the lateral and medial epicondyles shows extensive corrosion, lipping, and callus buildup. The popliteal surface is relatively smooth, but in the area of the medial supracondylar tuberosity there is extensive callus. Both the lateral and medial condyles are lipped, with the lateral condyle showing two small holes on the surface. The overall portrait of this femur suggests typical degenerative joint disease in the form of arthritis, which has contributed to the loss of the medullary architecture. In addition to the presence of degenerative joint disease, osteomyelitis brought on by a staphylococcal infection, probably as a result of a fracture, is shown on the bone. Since there is no visible injury in this area and no signs of a badly healed fracture, we conclude that the break that originally caused this trauma may have been in the proximal area of either the tibia or the fibula and would have traveled upward to the distal end of the femur. The head of the femur is relatively untouched, with the exception of some erosion at the junction of the epiphysis and the neck of the bone. This weathering could be the result of the femur's exposure in the cave over time. The proximal end of the femur (greater trochanter, trochanteric fossa, lesser trochanter, intertrochanteric crest) exhibits no anomalies, and the fovea is clearly delineated and undamaged. The diaphysis is smooth with no anomalies.

RODENTIA

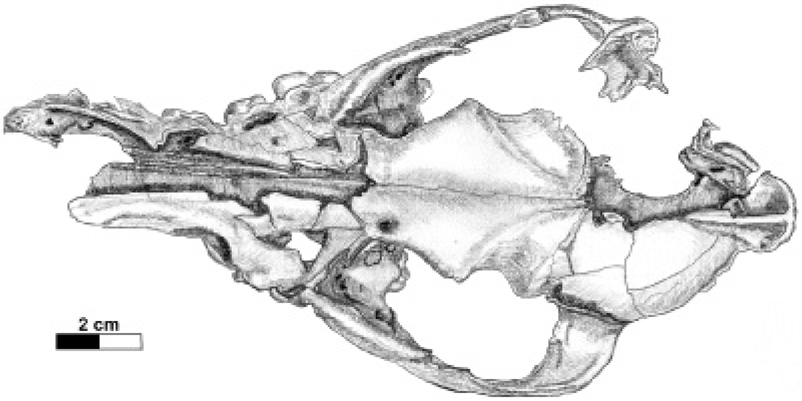
DMNH 42149 from Mark's Sink (L23) (7/97); metapodial (figure 9.10). Measurements: GL, 13.50; GB, 7.15; PB, 3.49; DB, 7.15. This metapodial shows a swollen proximal area with a draining sinus, which is the bone's response to an earlier break. The distal articular surface is undamaged. This specimen is consistent with others that have shown the bone's response to injury and resulting infection. The draining sinus has no rounded edges or other indications that the animal lived with this affliction; the edges are sharp and well defined, suggesting that this was the cause of death.

Rodent Gnawing

LEPUS *SP. (HARE OR JACKRABBIT)*

DMNH 42147 from Mark's Sink (8/96); long bone fragment (figure 9.11). Measurements: GL, 45.05; GW, 13.40; LSW, 3.50. This long bone fragment has been severely altered through the process of postmortem gnawing, possibly by wood rats.

FIGURE 9.7 *Canis latrans* (coyote), DMNH 30076, skull from the Badger Room. (Drawing by PJ Kremer.)



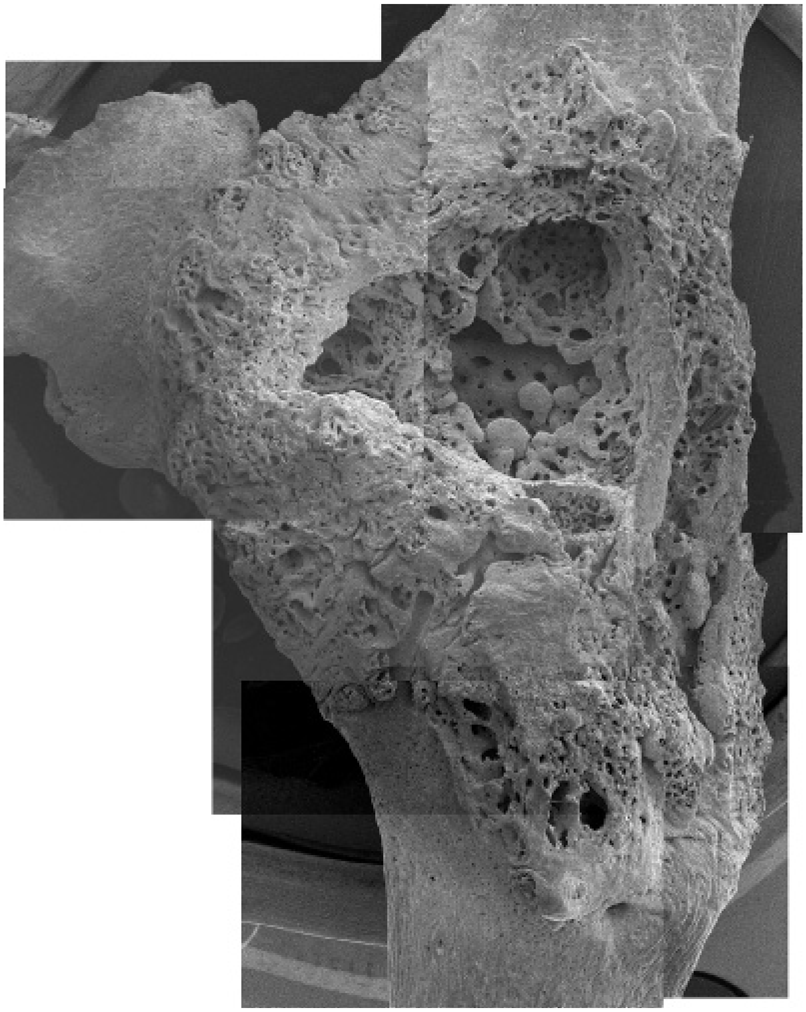


FIGURE 9.8 Rodentia cf. *Neotoma* (wood rat) or *Spermophilus* (ground squirrel), DMNH 41425, right innominate from the DMNH Velvet Room excavation. (SEM photograph by Louis H. Taylor.)

Splitting on the articular ends, the wedge-shaped bone loss areas, and the linear markings on the diaphysis are all consistent with this type of bone modification.

Discussion and Conclusions

Taphonomic features of Porcupine Cave bones include those characteristic of predation and wood rat accumulations of raptor pellets and carnivore scat, including acid etching and digestion of some specimens (figures 9.4, 9.5, 9.6), broken parts of bones, and abundance of small mammal taxa. There is also postmortem modification from breakage, gnawing, weathering, and excavation (DMNH 42147, figure 9.11).

From a paleopathology standpoint, the disease, trauma, and calamity evident from the fossils of Porcupine Cave fall into four categories:

1. Injury and puncture wounds, such as those exhibited in the skull of *Canis latrans* (DMNH 30076, figure 9.7).
2. Fractures, such as that of the metapodial (DMNH 42149, figure 9.10).
3. Infectious disease, such as the osteomyelitis exhibited in the *Lepus* sp. innominate (DMNH 42146, figure 9.4) and the *Canis latrans* femur (DMNH 26646, figure 9.9).
4. Trauma, such as that seen in the original break of the rodent (*Spermophilus* or *Neotoma* sp.) innominate (DMNH 41425, figure 9.8).

Additional examples are listed in appendix 9.1. Some specimens fit one of the criteria, while others exhibit most or all of them.

The examples discussed in this chapter add to the overall understanding of the bone material in Porcupine Cave. This first survey of the data suggests that further study of the paleopathology of fossils from the cave would be fruitful in determining the extent to which disease was present, how bone has responded to stress and trauma, and how animals have used the bone material as a source of calcium and nutrients. In this way, the bones of the dead become the key to understanding the living.

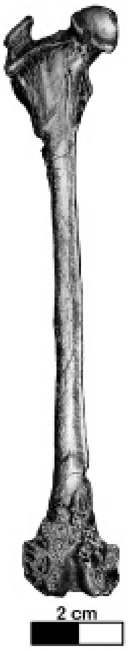


FIGURE 9.9 *Canis latrans* (coyote), DMNH 26646, right femur from the Badger Room. (SEM photograph by Louis H. Taylor.)

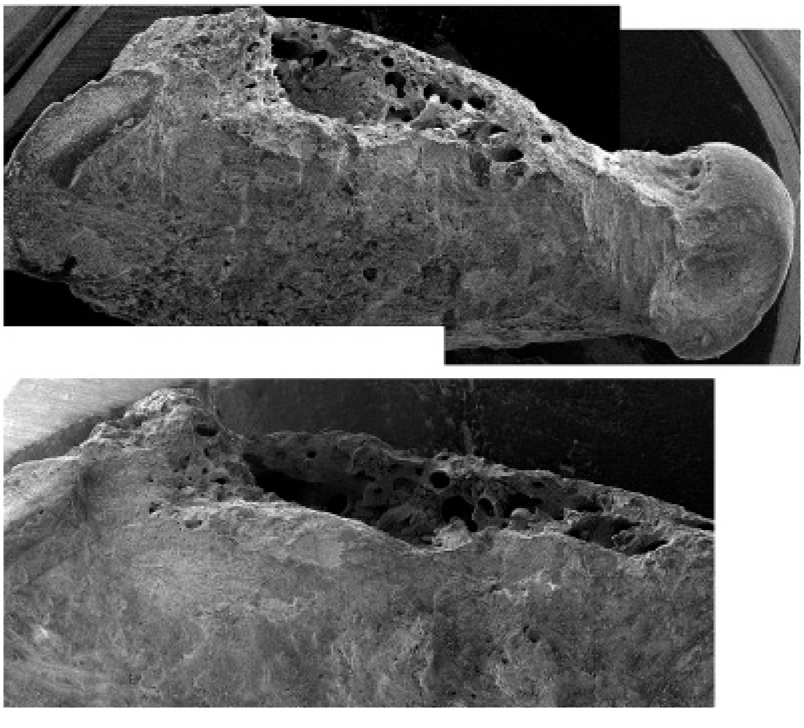
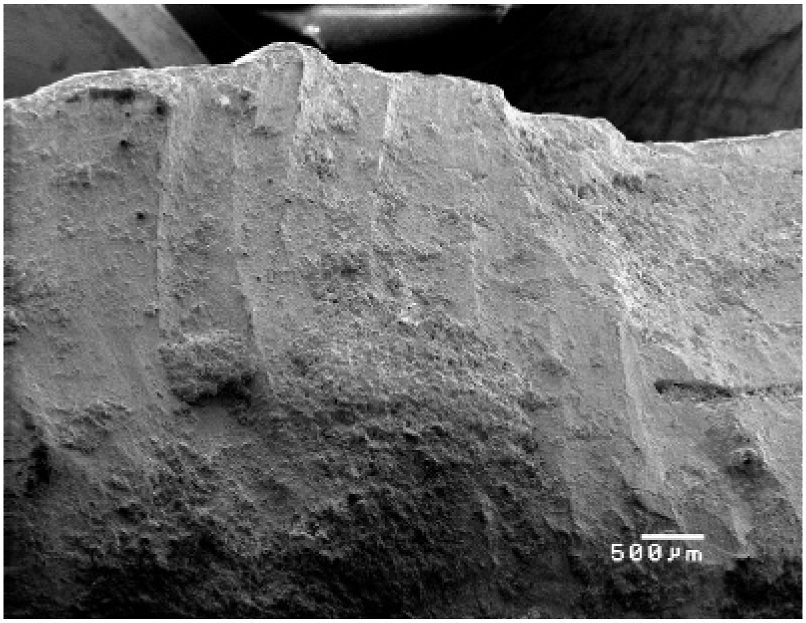


FIGURE 9.10 Rodentia cf. *Neotoma* (wood rat), DMNH 42149, metapodial from Mark's Sink. (SEM photograph by Louis H. Taylor.)

FIGURE 9.11 *Lepus* sp. (hare or jackrabbit), DMNH 42147, gnawed long bone fragment from Mark's Sink. (SEM photograph by Louis H. Taylor.)



Appendix 9.1. Specimens from Porcupine Cave Showing Taphonomic or Paleopathological Modification

Carnivore Digestion

BADGER ROOM

DMNH 42661, Artiodactyla femur head fragment (1994); DMNH 42721, *Lepus* sp. metapodial (7/94).

CRYSTAL ROOM

DMNH 42660, Artiodactyla, long bone fragment (7/94).

MARK'S SINK

DMNH 42650, *Lepus* sp. long bone fragment; DMNH 42651, *Lepus* sp. metapodial; DMNH 42654, *Lepus* sp. metapodial; DMNH 42656, *Lepus* sp. femur fragment; DMNH 42658, Artiodactyla long bone fragment (7/94); DMNH 42668, Rodentia skull fragment; DMNH 42673, *Lepus* sp. long bone fragment; DMNH 42685, Rodentia calcaneum; DMNH 42689, Rodentia rib fragment; DMNH 42691, Rodentia long bone fragment; DMNH 42692, *Lepus* sp. ulna fragment (1994); DMNH 42711 Rodentia femur fragment (L18); DMNH 42715, *Lepus* sp. metapodial (8/8A) (7/93); DMNH 42716 *Lepus* sp. metapodial (18); DMNH 42717 *Lepus* sp. metapodial (L18).

Raptor Digestion

BADGER ROOM

DMNH 42659, Artiodactyla long bone fragment (7/94); DMNH 42665, *Lepus* sp. L innominate fragment (7/94); DMNH 42690, *Lepus* sp. R innominate fragment (L6).

DMNH VELVET ROOM

DMNH 42706, Rodentia tibia fragment (8/8A) mixed (7/93).

FISSURE FILL A

DMNH 42720, *Lepus* sp. calcanea (7/94).

MARK'S SINK

DMNH 42662, *Lepus* sp. innominate; DMNH 42664, *Lepus* sp. femur fragment; DMNH 42669 *Lepus* sp. R innominate fragment (G9-Lb) (1994); DMNH 42671, Rodentia ulna fragment; DMNH 42675, *Lepus* sp. calcanea (32 specimens); DMNH 42708, Rodentia calcaneum (L 33); DMNH 42710 Rodentia tibia fragment (1994); DMNH 42714, *Lepus* sp. long bone fragment (L23) (7/97); DMNH 42716, *Lepus* sp. tibia fragment (L23) (1994); DMNH 42718, *Lepus* sp. metapodial; DMNH 42722, *Lepus* sp. femur head fragment (MS50-KS52).

Disease, Injury, or Trauma

BADGER ROOM

DMNH 42653, *Lepus* sp. long bone fragment (swelling) (7/94); DMNH 42655, Rodentia L innominate fragment (periostosis) (7/94); DMNH 42678, Rodentia metapodial (break) (7/94); DMNH 42687, *Lepus* sp. metapodial (puncture) (mixed) (7/94); DMNH 42701, Rodentia rib (bony exostoses) (1993); DMNH 42725, *Lepus* sp. metapodial (bony exostoses) (1993).

GENERATOR DOME

DMNH 42675, Rodentia metapodial (puncture); DMNH 42686, Rodentia metapodial (puncture); DMNH 42694, Rodentia claw (puncture); DMNH 42700, *Lepus* sp. metapodial fragment (puncture); DMNH 42726, *Lepus* sp. metapodial (puncture) (L1).

FISSURE FILL A

DMNH 42676, Rodentia metapodial (bony exostoses) (7/94); DMNH 42693, Rodentia rib fragment (infection) (7/94).

MARK'S SINK

DMNH 42663, *Lepus* sp. distal femur fragment (periostosis) (L2~) (1997); DMNH 42670, Rodentia calcaneum (periostitis) (L23) (7/97); DMNH 42679, Rodentia tibia/fibula fragment (fused/periostosis) (G10-L3); DMNH 42681, Rodentia tibia fragment (puncture) (L2~); DMNH 42682, Rodentia rib (bony exostoses) (L1~); DMNH 42683, *Lepus* sp. metapodial (puncture); DMNH 42684, Rodentia metapodial (swelling) (L1~) (1994); DMNH 42688, *Lepus* metapodial (swelling) (G4, L6); DMNH 42696, *Lepus* sp. proximal femur fragment (puncture); DMNH 42698, *Lepus* sp. metapodial (osteomyelitis from puncture) (L24) (7/97); DMNH 42699, *Lepus* sp. long bone fragment; DMNH 42702, Rodentia patella (arthritis) (L23) (7/97); DMNH 42704, Rodentia metapodial (L31) (7/97); DMNH 42707, Rodentia metapodial (bony exostoses) (L23) (7/97); DMNH 42709, Rodentia metapodial (periostitis) (G7) (1994); DMNH 42713, *Lepus* sp. metapodial (osteomyelitis + periostitis) (L23) (7/97); DMNH 42719, *Lepus* sp. scapula fragment (L29) (7/97); DMNH 42724, *Spermophilus* metacarpal (swelling) (L26) (7/97).

DMNH VELVET ROOM

DMNH 42666, *Spermophilus* sp. tibia/fibula (fused) (G4-LI) (7/92); DMNH 42677, Rodentia radius (break + bony exostoses) (G7) (1994); DMNH 42697, Rodentia metapodials (fused from badly healed break) (main dig B) (G21-L11); DMNH 42703, Rodentia R edentulous jaw fragment (dental abscess) (8/8A) (7/93); DMNH 42727, Rodentia clavicle (healed break) (G1, Lb) (7/92).

Rodent Gnawing

FISSURE FILL A

DMNH 42667, *Taxidea taxus* jaw fragment (7/94).

MARK'S SINK

DMNH 42657, *Lepus* sp. rib fragment; DMNH 42672, *Lepus* sp. calcaneum; DMNH 42680, Artiodactyla metapodial (L30) (7/94); DMNH 42705, Rodentia metapodial (L18) (7/97); DMNH 42723, *Silvilagus* sp. calcaneum.

WILL'S HOLE

DMNH 42652, *Lepus* sp. distal femur fragment (G7-L26) (7/97).

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PART TWO

SYSTEMATIC ACCOUNTS OF TAXA

TEN

A Summary of Fossilized Species in Porcupine Cave

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This chapter has been compiled from information provided by the authors of chapters in part 2.

At least 127 species are known as fossils from the 26 localities in Porcupine Cave (2 amphibians, 4 reptiles, 48 birds, and 73 mammals). More than 20,000 specimens have been studied in detail. The fauna includes two species that are newly recognized and extinct, *Brachylagus coloradoensis* (Colorado pygmy cottontail) and ?*Cynomys andersoni* (prairie dog), and two more that suggest that new species should be formally recognized when more material becomes available, *Mustela* sp. A (extinct marten) and *Martes* sp. A (extinct mustelid). Twenty-eight extant species (20 birds and 8 mammals) make their earliest North American appearance in Porcupine Cave deposits: *Falcipennis canadensis* (Spruce Grouse), *Centrocercus urophasianus* (Greater Sage Grouse), *Dendrograpus* cf. *D. obscurus* (Blue Grouse), *Numenius madagascariensis* or *N. arquata* (Far Eastern or Eurasian Curlew), *Phalaropus* cf. *P. lobatus* (Red-necked Phalarope), *Nyctea scandiaca* (Snowy Owl), *Pica hudsonia* (Black-billed Magpie), *Gymnorhinus cyanocephalis* (Pinyon Jay), *Corvus corax* (Common Raven), *Eremophila alpestris* (Horned Lark), *Tachycineta* cf. *T. bicolor* (Tree Swallow), *Sitta carolinensis* (White-breasted Nuthatch), *Spizella breweri* (Brewer's Sparrow), *Spizella* cf. *S. passerina* (Chipping Sparrow), *Zonotrichea leucophrys* (White-crowned Sparrow), *Chondestes grammacus* (Lark Sparrow), *Junco hyemalis* (Dark-Eyed Junco), *Leucosticte tephrocotis* (Gray-crowned Rosy-finch), *Leucosticte artrata* (Black Rosy-finch), *Carpodacus cassinii* (Cassin's Finch), *Mustela nigripes* (black-footed ferret), *Spermophilus* cf. *S. elegans* (Wyoming ground squirrel), *Lemmiscus curtatus* (sagebrush vole), *Neotoma cinerea* (bushy-tailed wood rat), *Neotoma mexicana* (Mexican wood rat), *Neotoma floridana* (eastern wood rat), *Neotoma micropus* (southern plains wood rat), and *Neotoma stephensi* (Stephens' wood rat). *Sylvilagus audubonii* (desert cottontail) and *Sylvilagus nuttalli* (Nuttall's cottontail) may also have their earliest records in Porcupine Cave, a possibility regarded as tentative given the difficulty in distinguishing the dental remains of these species (chapter 15).

Most genera represented by the fossils are still extant, but at the species level an admixture of many extinct with extant species predominates. The large number of extinct species is no surprise, given the antiquity of the deposits. Among extinct species, the cave yields the earliest North American record for *Oreamnos harringtoni* (extinct mountain goat), as well as the earliest records in mountainous western America for *Brachyprotoma obtusata* (short-faced skunk), *Gulo* cf. *G. schlosseri* (Schlosser's wolverine), *Martes diluviana* (extinct fisher), and *Miracinonyx* cf. *M. inexpectatus* (Irvingtonian cheetah). Two taxa exhibit their youngest geological record in Porcupine Cave: *Hypolagus* (rabbit) and *Phenacomys gryci* (Gryci's vole).

Most of the fossils date from the Irvingtonian North American Land Mammal Age (NALMA), especially in the range of about 600 Ka to perhaps as old as 1 Ma (chapters 2, 7). However, at least two localities in the cave, Mark's Sink and Fissure Fill A, may be considerably older, potentially reaching into the Blancan NALMA, as suggested by arvicoline rodents (chapter 19) and horses (chapter 20), respectively. The Blancan-Irvingtonian boundary dates to somewhere between 1.3 and 1.5 Ma (Bell et al., in press).

This chapter presents summary species lists for each locality, and when possible provides estimates of number of identifiable specimens (NISP) and minimum numbers of individuals (MNI) for each species at each locality. These lists make clear that the most abundant fossils are those of small mammals, particularly rodents such as ground squirrels, wood rats, and voles, which are represented by thousands of specimens each. Other rodents and rabbits are commonly represented by hundreds of specimens per species. Insectivores, carnivores, and ungulates are much less common and typically are known by tens of specimens. Each amphibian, reptile, and bird species generally is represented by fewer than 10 specimens.

TABLE 10.1

Faunal List for the Badger Room

	MNI	*NISP*
Amphibia		
Anura (frog or toad)	1	4
Aves		
Anatidae, indeterminate	1	1
Buteo sp. (Hawk)	1	1
Corvus brachyrhynchos (American Crow)	1	1
Corvus corax (Common Raven)	1	1
Mammalia		
† Mylodontidae (ground sloth)	1	1
Soricidae cf. *Sorex* sp. (shrew)	1	3
Ochotonidae		
Ochotona cf. *O. princeps* (pika)	3	18
Leporidae		
Lepus sp. (hare or jackrabbit)	≥47	≥632
Sylvilagus sp. (cottontail rabbit)	≥9	≥58
Leporid (rabbit or hare)	≥86	≥1071
† *Aztlanolagus* sp. (Aztlan rabbit)	1	1
Brachylagus coloradoensis (Colorado pygmy cottontail)	x	x
cf. *Brachylagus* (pygmy cottontail)	2	6
Sciuridae		
Marmota sp. (marmot)	9	74
Spermophilus sp. (species indeterminate) (ground squirrel)	≥10	≥150
Spermophilus lateralis (golden-mantled ground squirrel)	2	5
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	4	15
† *Cynomys andersoni* new sp. (prairie dog)	5	26
Cynomys sp. (prairie dog)	1	4
Geomyidae		
Thomomys sp. (pocket gopher)	≥3	≥16
Muridae		
Neotoma sp. (wood rat)	4	8
Peromyscus sp. (deer mouse)	≥2	≥16
Arvicolinae		
† *Allophaiomys pliocaenicus* (vole)	4	7
† *Mimomys virginianus* (Virginia mimomys)	9	14
† *Phenacomys gryci* (Gryci's vole)	6	8
Microtus 5T (vole)	1	1
† *Mictomys kansasensis/meltoni* (extinct bog lemming)	9	15
Ondatra sp. (muskrat)	1	1
Erethizontidae		
Erethizon sp. (porcupine)	1	1
Mustelidae		
† *Martes diluviana* (extinct fisher)	2	4
Mustela frenata (long-tailed weasel)	1	4
Mustela nigripes (black-footed ferret)	1	2
† *Mustela* species A (extinct mustelid)	1	1
cf. *Lutra* (river otter)	1	1
Taxidea taxus (badger)	8	122
Spilogale putorius (spotted skunk)	11	45
† *Brachyprotoma obtusata* (short-faced skunk)	1	1
Mephitis mephitis (striped skunk)	1	1
Canidae		
Canis latrans (coyote)	3	73
† *Canis edwardii* (Edward's wolf)	2	15
Canis sp. (small canid)	1	1
Vulpes vulpes (red fox)	1	1
Felidae		
Lynx rufus (bobcat)	1	4
† *Miracinonyx* cf. *M. inexpectatus* (Irvingtonian cheetah)	1	1
Tayassuidae		
† *Platygonus* sp. (peccary)	1	1
Cervidae		
Odocoileus sp. (deer)	1	4
Antilocapridae		
Antilocapridae, genus and species indeterminate	2	7
Bovidae		
Ovis sp. (bighorn sheep)	1	5
Ovibovini, genus and species indeterminate	1	1
Equidae		
† *Equus* sp. (large) (horse)	1	3
† *Equus* sp. (small) (horse)	1	7

NOTES: x, taxa present, but estimates for MNI and NISP are unavailable; †, extinct species.

Only the Pit (CM 1925 / UCMP V93173) and Badger Room (CM 1928 / DMNH 942 / UCMP V93176) are considered completed excavations and have had nearly all specimens identified. For this reason, the paleoecological, evolutionary, and paleoenvironmental conclusions presented in part 3 focus primarily on those two localities.

All of the other localities should be regarded as incompletely sampled, or, as in the case of the DMNH Velvet Room localities, well sampled but with many of the specimens remaining to be identified. Absence of a species in the faunal lists for these localities does not necessarily imply that the species is not there; much unidentified material awaits analy-

TABLE 10.2

Faunal Lists for Badger Dome, Come-A-Long Room, Cramped Quarters, Crystal Room, and Damp Room

	MNI	*NISP*
Badger Dome		
Mammalia		
Mustelidae		
Taxidea taxus (badger)	1	4
Come-A-Long Room		
Mammalia		
Sciuridae		
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	1	1
Antilocapridae		
Antilocapridae, genus and species indeterminate	1	1
Cramped Quarters		
Mammalia		
Felidae		
Lynx rufus (bobcat)	1	1
Crystal Room		
Mammalia		
Arvicolinae		
† *Microtus paroperarius* (vole)	1	1
Microtus 5T (vole)	1	1
Mustelidae		
Taxidea taxus (badger)	1	1
Canidae		
† *Canis edwardii* (Edward's wolf)	1	2
Felidae		
Lynx rufus (bobcat)	1	3
Camelidae		
† *Camelops* sp. (camel)	1	1
Antilocapridae		
Antilocapridae, genus and species indeterminate	1	1
Bovidae		
† *Oreamnos harringtoni* (extinct mountain goat)	1	1
Equidae		
† *Equus* sp. (large) (horse)	1	1
Damp Room		
Unidentified specimens	x	x

NOTES: x, estimates for MNI and NISP are unavailable; †, extinct species.

sis. For these cursorily or unanalyzed localities, the species lists, as well as the NISP and MNI estimates, are subject to change as future workers examine the specimens. They should be interpreted in light of the excavation information provided in chapter 2 and used primarily as a guide for where future efforts might most profitably be focused. The NISP and MNI of lagomorphs in the Badger Room are inflated relative to those of lagomorphs at other localities because postcranial bones, cranial material, and teeth were all identified in the Badger Room, whereas only cranial and dental fossils were identified from other localities. Comparisons between the Badger Room and Pit localities (chapters 7, 22, 23) take this into account.

Convention for Dental Terminology and Higher Taxonomy

The systematic accounts of identified taxa appear in the following chapters of part 2. All authors except Bell et al. (chapters 11, 19) follow Linnaean taxonomy above the genus level; Bell et al. conceptualize the higher taxa as monophyletic units and leave Linnaean ranks out of their treatment. In general, one author or group of collaborating authors analyzed all of the specimens of a given higher taxon. An exception is the leporids, in which specimens of the DMNH Velvet Room are identified and reported by Baxter (chapter 15) as part of her interest in DMNH materials, and those of the Pit are treated by Barnosky and Hopkins (chapter 16) in the context of their work on UCMP and CM localities.

Species Lists

Tables 10.1–10.13 list the species that are documented in this book from each of the Porcupine Cave localities. NISP is derived by counting each specimen that was identified as belonging to a particular taxon. MNI, in contrast, attempts to recognize the minimum number of individuals that would account for all of the specimens assigned to a given taxon. NISP overestimates the actual number of individuals, whereas MNI typically underestimates the actual number of individuals (Lyman, 1994). Which elements of the skeleton can be identified to species varies among taxa. However, these biases

TABLE 10.3

Faunal Lists for Ferret Room, Fissure Dump, Fissure Fill A, and Fissure Fill B

	MNI	*NISP*
Ferret Room		
Aves		
Anas sp. (Duck)	1	1
Pica hudsonia (Black-billed Magpie)	1	1
Spizella cf. *S. passerina* (Chipping Sparrow)	1	1
Mammalia		
Arvicolinae		
† *Phenacomys gryci* (Gryci's vole)	1	1
* *Lemmiscus* (four triangles) (sagebrush vole)	1	1
† *Mictomys vetus/landesi* (extinct bog lemming)	1	1
Mustelidae		
† *Martes* species A (extinct marten)	1	1
Mustela erminea (ermine)	1	1
Mustela vison (American mink)	1	1
† *Mustela* species A (extinct mustelid)	1	1
Spilogale putorius (spotted skunk)	1	3
Canidae		
Canis latrans (coyote)	1	2
Tayassuidae		
† *Platygonus* sp. (peccary)	1	1
Antilocapridae		
Antilocapridae, genus and species indeterminate	1	2
Fissure Dump		
Mammalia		
Mustelidae		
Mustela frenata (long-tailed weasel)	1	1
Equidae		
† *Equus (Asinus)* cf. *E. (A.) cumminsi* (horse)	1	3
Fissure Fill A		
Mammalia		
Soricidae		
cf. *Sorex* sp. (shrew)	1	1
Sciuridae		
† *Cynomys andersoni* new sp. (prairie dog)	2	3
Arvicolinae		
† *Allophaiomys pliocaenicus* (vole)	3	5
† *Mimomys virginianus* (Virginia mimomys)	3	12
† *Phenacomys gryci* (Gryci's vole)	1	1
Phenacomys sp. (not *P. gryci*) (vole)	1	5
† *Microtus paroperarius* (vole)	1	1
† *Mictomys kansasensis/meltoni* (extinct bog lemming)	7	13
† *Mictomys* sp. (probably extinct bog lemming)	8	28
Ondatra sp. (muskrat)	1	1
Mustelidae		
Taxidea taxus (badger)	2	10
Spilogale putorius (spotted skunk)	1	1
Mephitis mephitis (striped skunk)	1	1
Canidae		
Canis latrans (coyote)	2	24
† *Canis edwardii* (Edward's wolf)	1	2
Vulpes velox (swift or kit fox)	1	1
Equidae		
† *Equus (Asinus)* cf. *(E.) (A.) cumminsi* (horse)	1	1
Fissure Fill B		
Unidentified specimens	x	x

NOTES: x, estimates for MNI and NISP are unavailable; †, extinct species; *, extinct morphotype.

generally remain constant in comparing relative abundances between stratigraphic levels and localities, making it possible to use NISP and MNI to understand various aspects of faunal dynamics through time. These dynamics are discussed in part 3.

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TABLE 10.4

Faunal Lists for Generator Dome, Gypsum Room, Gypsum Room SE Corner, KU Digs 1 and 3, and Memorial Day Room

	MNI	*NISP*
Generator Dome		
Amphibia		
Anura	1	1
Aves		
Rallus cf. *R. limicola* (Virginia Rail)	1	1
Melospiza melodia (Song Sparrow)	1	1
Accipitridae, indeterminate	1	1
Emberizidae, indeterminate	1	1
Mammalia		
Ochotonidae		
Ochotona cf. *O. princeps* (pika)	2	2
Sciuridae		
† *Spermophilus* cf. *S. meadensis* (Meade ground squirrel)	1	1
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	1	2
† *Cynomys andersoni* new sp. (prairie dog)	6	22
Arvicolinae		
† *Allophaiomys pliocaenicus* (vole)	2	3
† *Mimomys virginianus* (Virginia mimomys)	3	3
† *Phenacomys gryci* (Gryci's vole)	1	1
† *Mictomys* sp. (probably extinct bog lemming)	1	1
Mustelidae		
† *Martes diluviana* (extinct fisher)	1	1
† *Martes* species A (extinct marten)	1	1
Mustela erminea (ermine)	1	1
† *Mustela* species A (extinct mustelid)	1	1
Taxidea taxus (badger)	2	37
Spilogale putorius (spotted skunk)	1	8
† *Brachyprotoma obtusata* (short-faced skunk)	1	2
Mephitis mephitis (striped skunk)	1	1
Canidae		
Canis latrans (coyote)	3	26
† *Canis edwardii* (Edward's wolf)	1	8
Vulpes vulpes (red fox)	1	1
Ursidae		
Ursus americanus (black bear)	1	1
Antilocapridae		
Antilocapridae, genus and species indeterminate	1	1
Equidae		
† *Equus* sp. (small) (horse)	1	2
Gypsum Room		
Reptilia		
Natricinae (snake)	1	14
Non-Natricine Colubridae (snake)	1	2
Colubroidea (snake)	1	5
Mammalia		
Soricidae		
cf. *Sorex* sp. (shrew)	1	1
Sciuridae		
Marmota sp. (marmot)	1	1
Arvicolinae		
† *Allophaiomys pliocaenicus* (vole)	4	5
† *Mimomys virginianus* (Virginia mimomys)	2	2
† *Microtus meadensis* (Meade vole)	8	12
* *Lemmiscus* (four triangles) (sagebrush vole)	3	5
Lemmiscus curtatus (sagebrush vole)	2	4
Lemmiscus sp. (cannot identify to species)	3	10
Microtus 5T (vole)	7	9
† *Mictomys kansasensis/meltoni* (extinct bog lemming)	3	5
Mictomys sp. (probably extinct bog lemming)	5	24
† *Phenacomys gryci* (Gryci's vole)	1	1
Mustelidae		
† *Martes* new species (extinct marten)	1	1
Taxidea taxus (badger)	1	1
Spilogale putorius (spotted skunk)	1	1
Equidae		
† *Equus* sp. (small) (horse)	1	1
Gypsum Room SE Corner		
Unidentified specimens	x	x
KU Dig 1		
Unidentified specimens	x	x
KU Dig 3		
Unidentified specimens	x	x
Memorial Day Room		
Unidentified specimens	x	x

NOTES: x, estimates for MNI and NISP are unavailable; †, extinct species; *, extinct morphotype.

TABLE 10.5

Faunal Lists for New Passage, Tobacco Road, Trailside Entrance, Velvet Room Last Chance Pit, Velvet Room Kate's Cupola, and Velvet Room Will's Hole

	MNI	*NISP*
New Passage		
Mammalia		
Arvicolinae		
† *Microtus meadensis* (Meade vole)	1	1
Tobacco Road		
Mammalia		
† *Camelops* sp. (camel)	1	1
Trailside Entrance		
Mammalia		
† *Camelops* sp. (camel)	1	1
Velvet Room Last Chance Pit		
Aves		
Calcarius cf. *C. pictus* (Smith's Longspur)	1	1
Velvet Room Kate's Cupola		
Mammalia		
Arvicolinae		
† *Mimomys virginianus* (Virginia mimomys)	1	1
† *Lemmiscus* (four triangles) (sagebrush vole)	1	1
Microtus 5T (vole)	1	1
† *Mictomys kansasensis/meltoni* (extinct bog lemming)	1	2
† *Mictomys vetus/landesi* (extinct bog lemming)	2	2
† *Mictomys* sp. (extinct bog lemming)	1	1
† *Ophiomys parvus* (Snake river vole)	1	1
Phenacomys sp. (not *P. gryci*)	1	2
Equidae		
† *Equus* sp. (large) (horse)	1	4
† *Equus* sp. (small) (horse)	1	2
Velvet Room Will's Hole		
Aves		
Buteo sp. (Hawk)	1	2
Dendragapus cf. *D. obscurus* (Blue Grouse)	2	4
Lagopus cf. *L. leucurus* (White-tailed Ptarmigan)	1	1
Sitta carolinensis (White-breasted Nuthatch)	1	1
Passeriformes, indeterminate	6	50
Mammalia		
Spermophilus lateralis (golden-mantled ground squirrel)	6	17
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	20	61
Cynomys cf. *C. leucurus* (white-tailed prairie dog)	1	2
Arvicolinae		
† *Microtus meadensis* (Meade vole)	2	3
* *Lemmiscus* (four triangles) (sagebrush vole)	1	1
Mustelidae		
† *Martes diluviana* (extinct fisher)	1	1
Mustela erminea (ermine)	1	1
Mustela nigripes (black-footed ferret)	1	2
Mustela vison (American mink)	1	2
† *Mustela* species A (extinct mustelid)	1	2
† *Gulo* cf. *G. schlosseri* (Schlosser's wolverine)	1	1
Taxidea taxus (badger)	1	1
Spilogale putorius (spotted skunk)	1	4
† *Brachyprotoma obtusata* (short-faced skunk)	1	1
Mephitis mephitis (striped skunk)	1	1
Canidae		
Canis latrans (coyote)	1	5
† *Canis edwardii* (Edward's wolf)	1	1
Vulpes vulpes (red fox)	1	1
Urocyon cinereoargenteus (gray fox)		
Felidae		
Lynx rufus (bobcat)	1	1
Cervidae		
cf. *Odocoileus* sp. (deer)	1	1

NOTES: †, extinct species; *, extinct morphotype.

TABLE 10.6

Amphibians, Reptiles, and Birds from Velvet Room Mark's Sink

	MNI	*NISP*
Amphibia		
Anura (frog or toad)	1	9
Ambystomatidae (salamander)	1	1
Reptilia		
Natricinae (snake)	1	22
Non-Natricine Colubridae	1	4
Colubroidea (snake)	1	13
Viperidae (snake)	1	4
Phrynosoma (horned lizard)	1	2
Phrynosomatidae (lizard)	1	3
Lizard	1	2
Aves		
Anas crecca or *A. discors* (Green-winged or Blue-winged Teal)	1	1
Anas sp. (Duck)	1	1
Podilymbus podiceps (Pied-billed Grebe)	1	2
cf. *Podiceps* sp. (Grebe)	1	1
Anatidae, indeterminate	1	3
Buteo sp. (Hawk)	1	4
Accipitridae, indeterminate	1	1
Falco sparverius (American Kestrel)	1	1
Falco sp. (Falcon)	1	1
Centrocercus urophasianus (Sage Grouse)	2	14
Falcipennis canadensis (Spruce Grouse)	1	1
Phasianidae, indeterminate	1	2
cf. *Porzana carolina* (Sora)	1	1
Numenius cf. *N. madagascariensis* (Far Eastern or Eurasian Curlew)	1	1
Phalaropus cf. *P. lobatus* (Red-necked Phalarope)	1	1
Scolopacidae, indeterminate	1	1
Larus sp. (Gull)	1	1
Bubo virginianus (Great Horned Owl)	1	1
Nyctea scandiaca (Snowy Owl)	1	2
Asio sp. (Owl)	1	1
Strigidae, indeterminate	1	1
Picoides villosus (Hairy Woodpecker)	1	1
Colaptes auratus (Northern Flicker)	2	7
Corvus brachyrhynchos (American Crow)	1	2
Melospiza cf. M. *lincolnii* (Lincoln's Sparrow)	2	2
Zonotrichia leucophrys (White-crowned Sparrow)	2	2
Zonotrichea sp.	1	1
Hirundinidae, indeterminate	1	1
Chondestes grammacus (Lark Sparrow)	1	1
Junco hyemalis (Dark-eyed Junco)	1	1
Calcarius lapponicus (Lapland Longspur)	3	3
Calcarius cf. *C. lapponicus* (Lapland Longspur)	1	1
Calcarius ornatus (Chestnut-collared Longspur)	2	2
Emberizidae, indeterminate	3	3
Leucosticte tephrocotis (Gray-crowned Rosy-finch)	13	20
Leucosticte atrata (Black Rosy-finch)	3	3
Leucosticte sp. (Rosy-finch)	1	1
Carpodacus cassinii (Cassin's Finch)	1	1

TABLE 10.7

Mammals from Velvet Room Mark's Sink

	MNI	*NISP*
Mammalia		
Ochotonidae		
Ochotona cf. *O. princeps* (pika)	14	35
Leporidae		
Lepus sp. (hare or jackrabbit)	x	x
Sylvilagus sp. (cottontail rabbit)	x	x
† *Aztlanolagus* sp. (Aztlan rabbit)	x	x
† *Brachylagus coloradoensis* new sp. (Colorado pygmy cottontail)	x	x
† *Hypolagus* sp. (rabbit)	x	x
Sciuridae		
Marmota sp. (marmot)	1	1
Spermophilus lateralis (golden-mantled ground squirrel)	15	47
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	123	356
Spermophilus (Spermophilus) sp. (ground squirrel)	1	1
† ?*Cynomys andersoni* new sp. (prairie dog)	2	9
Cynomys sp. (prairie dog)	1	1
Cynomys cf. *C. leucurus* (white-tailed prairie dog)	5	10
Arvicolinae		
† *Allophaiomys pliocaenicus* (vole)	24	43
† *Mimomys virginianus* (Virginia mimomys)	64	114
† *Ophiomys parvus* (vole)	7	14
† *Phenacomys gryci* (Gryci's vole)	11	17
Phenacomys sp. (not *P. gryci*) (vole)	13	19
* *Lemmiscus* (four triangles) (sagebrush vole)	23	40
Lemmiscus curtatus (sagebrush vole)	29	56
† *Microtus meadensis* (Meade vole)	54	83
† *Microtus paroperarius* (vole)	14	26
Microtus 5T	41	71
† *Mictomys kansasensis/meltoni* (extinct bog lemming)	68	133
† *Mictomys vetus/landesi* (extinct bog lemming)	15	23
† *Pliolemmus antiquus* (extinct lemming)	2	3
Mustelidae		
† *Martes diluviana* (extinct fisher)	1	6
† *Martes* species A (extinct marten)	1	5
Mustela frenata (long-tailed weasel)	7	36
Mustela erminea (ermine)	4	11
Mustela nigripes (black-footed ferret)	1	5
Mustela vison (American mink)	3	10
† *Mustela* species A (extinct mustelid)	3	5
Taxidea taxus (badger)	1	10
Spilogale putorius (spotted skunk)	15	85
† *Brachyprotoma obtusata* (short-faced skunk)	1	2
Canidae		
Canis latrans (coyote)	2	38
† *Canis edwardii* (Edward's wolf)	1	5
Vulpes velox (swift or kit fox)	3	28
Vulpes vulpes (red fox)	2	3
Felidae		
Lynx rufus (bobcat)	1	2
Tayassuidae		
† *Platygonus* sp. (peccary)	1	1
Antilocapridae		
Antilocapridae, genus and species indeterminate	1	2
Bovidae		
Ovis sp. (bighorn sheep)	1	1

NOTES: x, estimates for MNI and NISP are unavailable; †, extinct species; *, extinct morphotype.

TABLE 10.8
Faunal List for Specimens Found in Porcupine Cave That Lack More Detailed Provenance Data

	MNI	*NISP*
Aves		
Centrocercus urophasianus (Sage Grouse)	1	1
Dendragopus cf. *D. obscurus* (Blue Grouse)	1	1
Mammalia		
Arvicolinae		
† *Microtus meadensis* (Meade vole)	4	7
Lemmiscus curtatus (sagebrush vole)	1	1
Lemmiscus sp. (cannot identify to species)	2	2
Mustelidae		
Mustela frenata (long-tailed weasel)	1	1
† *Gulo* cf. *G. schlosseri* (Schlosser's wolverine)	1	1
Taxidea taxus (badger)	1	1
Spilogale putorius (spotted skunk)	3	5
Canis latrans (coyote)	1	1
Ursidae		
Ursus americanus (black bear)	1	1
Felidae		
Lynx rufus (bobcat)	1	1
† *Miracinonyx* cf. *M. inexpectatus* (Irvingtonian cheetah)	1	1
Tayassuidae		
† *Platygonus* sp. (peccary)	1	1
Camelidae		
† *Hemiauchenia* sp. (camel)	1	1
Antilocapridae		
Antilocapridae, genus and species indeterminate	1	8
Equidae		
† *Equus* sp. (large) (horse)	1	1
† *Equus* sp. (small) (horse)	1	1

NOTE: †, extinct species.

TABLE 10.9

Faunal List for Upper Six Levels of the Pit

	Level											
	1		*2*		*3*		*4*		*5*		*6*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Amphibia												
Pelobatidae (toad)	?	?	?	?	?	?	—	—	—	—	—	—
Reptilia												
Natricinae (snake)	1	1	1	2	1	1	1	3	—	—	1	1
Non-Natricine Colubridae (snake)	—	—	1	1	—	—	—	—	—	—	—	—
Colubroidea (snake)	1	1	1	2	1	2	1	2	—	—	—	—
Viperidae (snake)	—	—	1	1	—	—	—	—	—	—	—	—
Phrynosomatidae (lizard)	?	?	?	?	?	?	—	—	—	—	—	—
Aves												
cf. *Aquila chrysaetos* (Golden Eagle)	1	1	—	—	—	—	—	—	—	—	—	—
Mammalia												
Soricidae												
cf. *Sorex* sp. (shrew)	—	—	2	3	1	1	1	1	1	1	—	—
Ochotonidae												
Ochotona sp. Trout Cave form (pika)	—	—	—	—	—	—	1	1	—	—	1	2
Ochotona sp. (pika)	4	26	1	3	1	1	2	11	1	3	—	—
Leporidae												
Lepus sp. (hare or jackrabbit)	7	19	2	3	5	10	2	2	1	1	1	1
Sylvilagus sp. (cottontail rabbit)	4	4	5	9	1	2	—	—	1	1	1	1
Leporid (rabbit or hare)	9	124	13	161	13	142	6	45	5	37	4	28
† *Aztlanolagus* sp. (Aztlan rabbit)	—	—	1	1	5	6	3	7	4	8	1	4
† *Brachylagus coloradoensis* new sp. (Colorado pygmy cottontail)	3	23	3	15	2	8	1	1	1	3	1	1
Sciuridae												
Tamiasciurus hudsonicus (red squirrel or chickaree)	1	1	1	4	1	3	1	7	1	3	1	2
Tamias cf. *T. minimus* (chipmunk)	1	2	1	5	1	2	1	5	1	1	—	—
Marmota sp. (marmot)	9	109	13	127	9	131	37	441	16	226	15	154
Spermophilus lateralis (golden-mantled ground squirrel)	9	54	7	43	5	63	7	31	3	23	3	14

TABLE 10.9 (continued)

	Level											
	1		*2*		*3*		*4*		*5*		*6*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	59	497	36	181	18	115	12	71	13	95	5	70
† ?*Cynomys andersoni* new sp. (prairie dog)	1	1	—	—	—	—	1	4	1	1	2	3
Cynomys cf. *C. leucurus* (white-tailed prairie dog)	10	71	25	216	7	48	1	1	1	1	—	—
Geomyidae												
Thomomys sp. (pocket gopher)	8	53	3	9	3	37	4	33	4	21	6	19
Thomomys cf. *T. talpoides* (northern pocket gopher)	2	3	2	2	1	1	2	4	3	5	2	4
Thomomys cf. *T. bottae* (Botta's pocket gopher)	—	—	—	—	—	—	1	1	—	—	2	3
Muridae												
Neotoma cinerea (bushy-tailed wood rat)	44	278	64	432	3	17	4	9	7	30	3	10
Neotoma mexicana (Mexican wood rat)	—	—	2	5	2	6	—	—	—	—	—	—
Neotoma floridana (eastern wood rat)	1	1	4	15	20	81	4	15	1	2	1	2
Neotoma micropus (southern plains wood rat)	—	—	—	—	1	2	—	—	1	3	1	4
Neotoma stephensi (Stephens' wood rat)	3	11	1	4	1	4	—	—	—	—	—	—
Neotoma sp. (wood rat)	11	65	8	44	30	221	18	154	9	63	3	43
Peromyscus sp. (deer mouse)	4	20	14	26	5	27	10	34	5	19	2	2
Arvicolinae												
† *Allophaiomys pliocaenicus* (vole)	—	—	—	—	—	—	3	6	2	3	3	3
† *Mimomys virginianus* (Virginia mimomys)	—	—	—	—	—	—	1	1	2	4	1	1
† *Phenacomys gryci* (Gryci's vole)	—	—	—	—	—	—	1	1	—	—	—	—
Phenacomys sp. (not *P. gryci*) (vole)	1	1	1	1	1	1	2	7	1	3	2	4
* *Lemmiscus* (four triangles) (sagebrush vole)	8	13	6	9	7	12	15	27	4	4	1	2
Lemmiscus curtatus (sagebrush vole)	29	55	6	10	4	7	7	12	2	3	1	2
Lemmiscus sp. (cannot identify to species)	13	44	3	7	3	10	17	57	8	26	4	13
† *Microtus meadensis* (Meade vole)	15	22	27	38	8	12	8	13	2	4	1	1
† *Microtus paroperarius* (vole)	3	5	2	4	4	6	4	7	1	1	—	—

(continued)

TABLE 10.9 (continued)

	Level											
	1		*2*		*3*		*4*		*5*		*6*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Microtus 5T (vole)	16	29	23	36	4	7	3	5	1	2	1	1
Microtus sp. (teeth nondiagnostic)	—	—	—	—	—	—	—	—	—	—	1	1
† *Mictomys kansasensis/meltoni* (extinct bog lemming)	2	4	3	4	7	11	18	31	7	11	4	6
† *Mictomys* sp. (probably extinct bog lemming)	1	3	2	8	3	13	15	99	7	44	5	31
Ondatra sp. (muskrat)	1	1	1	3	—	—	1	5	1	1	—	—
Erethizontidae												
Erethizon sp. (porcupine)	1	1	1	1	1	1	1	1	—	—	—	—
Mustelidae												
Mustela frenata (long-tailed weasel)	3	11	—	—	—	—	—	—	1	1	—	—
Mustela erminea (ermine)	—	—	1	1	1	1	—	—	—	—	1	1
Mustela nigripes (black-footed ferret)	1	1	—	—	—	—	1	1	—	—	—	—
† *Mustela* species A (extinct mustelid)	1	1	1	2	1	1	—	—	—	—	—	—
canadensis (American river otter)	—	—	—	—	—	—	1	1	—	—	—	—
Taxidea taxus (badger)	3	7	3	3	1	1	1	1	—	—	—	—
Spilogale putorius (spotted skunk)	3	5	—	—	1	2	1	1	1	1	—	—
† *Brachyprotoma obtusata* (short-faced skunk)	—	—	—	—	1	1	—	—	—	—	—	—
Canidae												
Canis latrans (coyote)	1	3	—	—	—	—	—	—	—	—	—	—
† *Canis edwardii* (Edward's wolf)	—	—	1	1	—	—	—	—	—	—	—	—
Vulpes velox (swift or kit fox)	1	1	—	—	1	3	—	—	—	—	—	—
Urocyon cinereoargenteus (gray fox)	1	1	—	—	—	—	—	—	—	—	—	—
Tayassuidae												
† *Platygonus* sp. (peccary)	—	—	1	1	—	—	—	—	—	—	—	—
Cervidae												
cf. *Odocoileus* sp. (deer)	—	—	1	1	1	1	—	—	—	—	—	—
Antilocapridae												
Antilocapra (pronghorn) or † *Tetrameryx* (antelope)	—	—	1	1	—	—	—	—	—	—	—	—
Antilocapridae, genus and species indeterminate	1	4	1	1	1	2	—	—	—	—	—	—
Bovidae												
Ovis sp. (bighorn sheep)	1	1	—	—	—	—	—	—	—	—	—	—
† *Oreamnos harringtoni* (extinct mountain goat)	—	—	1	1	—	—	—	—	—	—	—	—

TABLE 10.9 (continued)

	Level											
	1		*2*		*3*		*4*		*5*		*6*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Equidae												
† *Equus (Hemionus)* sp. (horse)	1	2	—	—	—	—	—	—	—	—	—	—
† *Equus* sp. (large) (horse)	1	1	1	1	—	—	—	—	—	—	1	1
† *Equus* sp. (small) (horse)	1	2	—	—	—	—	—	—	—	—	—	—

NOTES: †, extinct species; *, extinct morphotype; ?, stratigraphic placement uncertain but probably from one of the indicated levels.

TABLE 10.10

Faunal List for Lower Seven Levels of the Pit

	Level													
	7		*8*		*8A*		*9*		*10*		*11*		*12*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Reptilia														
Natricinae (snake)	1	1	—	—	1	4	—	—	—	—	—	—	—	—
Non-Natricine Colubridae (snake)	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Colubroidea (snake)	1	1	—	—	1	3	—	—	—	—	—	—	—	—
Mammalia														
Soricidae														
cf. *Sorex* sp. (shrew)	1	1	—	—	1	1	1	2	—	—	—	—	—	—
Ochotonidae														
Ochotona cf. *O. princeps* (pika)	—	—	—	—	—	—	—	—	1	1	—	—	—	—
Leporidae														
Leporid (rabbit or hare)	2	23	1	7	1	8	1	2	2	17	1	4	—	—
† *Aztlanolagus* sp. (Aztlan rabbit)	1	3	2	2	1	1	—	—	1	2	1	4	—	—
† *Brachylagus coloradoensis* (Colorado pygmy cottontail)	1	1	—	—	—	—	—	—	—	—	—	—	—	—
† *Hypolagus* sp. (rabbit)	—	—	—	—	—	—	—	—	1	1	1	1	—	—
Sciuridae														
Tamiasciurus hudsonicus (red squirrel or chickaree)	1	3	—	—	—	—	—	—	—	—	—	—	—	—
Marmota sp. (marmot)	7	84	4	19	—	—	—	—	—	—	—	—	—	—
Spermophilus (?Otospermophilus) sp. (ground squirrel)	—	—	—	—	—	—	—	—	1	1	1	1	—	—
Spermophilus lateralis (golden-mantled ground squirrel)	1	4	—	—	1	3	—	—	1	8	—	—	—	—
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	5	35	3[a]	24[a]	4	35	1	5	2	19	—	—	—	—
† ?*Cynomys andersoni* new sp. (prairie dog)	1	3	—	—	1	8	—	—	—	—	1	2	—	—
Geomyidae														
Thomomys sp. (pocket gopher)	2	16	2	4	1	3	1	3	1	4	—	—	1	1
Thomomys cf. *T. talpoides* (northern pocket gopher)	—	—	—	—	1	1	—	—	1	1	—	—	—	—
Thomomys cf. *T. bottae* (Botta's pocket gopher)	1	1	—	—	—	—	—	—	1	1	—	—	—	—
Geomyoid, indeterminate (not *Thomomys*)	1	2	—	—	—	—	—	—	—	—	—	—	—	—

Muridae														
Neotoma cinerea (bushy-tailed wood rat)	2	8	—	—	2	3	—	—	1	4	1	2	—	—
Neotoma mexicana (Mexican wood rat)														
Neotoma floridana (eastern wood rat)	2	6	—	—	1	1	1	1	1	1	—	—	—	—
Neotoma micropus (southern plains wood rat)	1	1	—	—	1	1	2	3	2	9	1	2	—	—
Neotoma stephensi (Stephens' wood rat)	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Neotoma sp. (wood rat)	3	22	2	15	2	13	2	4	2	18	—	—	1	1
Peromyscus sp. (deer mouse)	2	6	—	—	3	9	1	1	1	1	—	—	—	—
Arvicolinae														
† *Allophaiomys pliocaenicus* (vole)	2	4	—	—	3	5	—	—	—	—	2	2	—	—
† *Mimomys virginianus* (Virginia mimomys)	1	4	—	—	1	5	—	—	1	2	—	—	—	—
† *Phenacomys gryci* (Gryci's vole)	—	—	—	—	—	—	—	—	1	1	—	—	—	—
Phenacomys sp. (teeth nondiagnostic) (vole)	1	3	1	1	1	1	1	1	1	1	1	1	—	—
* *Lemmiscus* (four triangles) (sagebrush vole)	1	1	2	2	—	—	—	—	1	2	—	—	—	—
Lemmiscus curtatus (sagebrush vole)	1	1	2	2	—	—	1	1	1	1	—	—	—	—
Lemmiscus sp. (cannot identify to species)	2	4	1	2	4	4	1	1	3	6	1	1	—	—
† *Microtus meadensis* (Meade vole)	1	1	1	1	1	1	—	—	—	—	—	—	—	—
† *Microtus paroperarius* (vole)	2	3	—	—	—	—	—	—	—	—	—	—	—	—
† *Mictomys kansasensis/meltoni* (extinct bog lemming)	7	9	5	6	4	6	—	—	3	5	3	3	—	—
† *Mictomys* sp. (probably extinct bog lemming)	6	32	4	19	6	15	1	1	4	12	3	11	1	1
Ondatra sp. (muskrat)	—	—	—	—	1	1	—	—	—	—	—	—	—	—
Mustelidae														
Spilogale putorius (spotted skunk)	1	1	—	—	—	—	—	—	1	1	2	2	—	—

NOTES: †, extinct species; *, extinct morphotype; [a], specimens were not available for detailed study.

TABLE 10.11

Faunal List for the Velvet Room CM Excavation

	Level															
	1		*1B*		*2A*		*2B*		*2C*		*3*		*4*		*Undifferentiated*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Reptilia																
Natricinae (snake)	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Non-Natricine Colubridae (snake)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Colubroidea (snake)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Viperidae (snake)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Mammalia																
Ochotonidae																
Ochotona sp. (pika)	—	—	1	2	—	—	1	1	—	—	1	2	—	—	—	—
Sciuridae																
Tamias cf. *T. minimus* (chipmunk)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Marmota sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Spermophilus lateralis (golden-mantled ground squirrel)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	6
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32	72
Cynomys cf. *C. leucurus* (white-tailed prairie dog)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	6
Neotoma sp. (wood rat)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	>1
Arvicolinae																
† *Allophaiomys pliocaenicus* (vole)	—	—	—	—	—	—	—	—	—	—	1	1	—	—	3	4
* *Lemmiscus* (four triangles) (sagebrush vole)	—	—	—	—	—	—	1	1	—	—	4	5	—	—	7	12
Lemmiscus curtatus (sagebrush vole)	—	—	3	5	—	—	3	4	—	—	6	11	—	—	5	8
Lemmiscus sp. (cannot identify to species)	—	—	2	4	—	—	1	2	—	—	2	4	—	—	13	40
† *Microtus meadensis* (vole)	—	—	—	—	—	—	—	—	—	—	7	11	—	—	19	29
† *Microtus paroperarius* (vole)	—	—	—	—	—	—	—	—	—	—	1	1	—	—	3	4
Microtus 5T (vole)	—	—	1	1	—	—	1	1	—	—	7	9	—	—	13	23
† *Mictomys kansasensis/meltoni* (extinct bog lemming)	—	—	—	—	1	1	—	—	—	—	4	6	—	—	17	33
† *Mictomys* sp. (probably extinct bog lemming)	—	—	1	2	—	—	—	—	—	—	2	8	—	—	17	70
† *Mimomys virginianus* (Virginia mimomys)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Phenacomys sp. (teeth nondiagnostic) (vole)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	4
Mustelidae																
Mustela frenata (long-tailed weasel)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Spilogale putorius (spotted skunk)	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—

NOTES: x, estimates for MNI and NISP are unavailable; †, extinct species; *, extinct morphotype. Undifferentiated = present in Velvet Room CMNH excavation, but exact provenance unknown.

TABLE 10.12

Faunal List for Upper Six Horizons of the DMNH Velvet Room Excavation

	Horizon											
	A		*B*		*C*		*D*		*E*		*F*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Reptilia												
Natricinae (snake)	—	—	—	—	1	1	1	4	1	2	1	4
Colubroidea (snake)	—	—	—	—	—	—	—	—	1	1	—	—
Viperidae (snake)	—	—	—	—	—	—	—	—	1	1	—	—
Aves												
Anas sp. (Duck)	—	—	1	2	—	—	—	—	—	—	—	—
Aythya cf. *A. americana* (Redhead)	1	1	—	—	—	—	—	—	—	—	—	—
Anatidae, indeterminate	—	—	2	2	—	—	—	—	—	—	—	—
cf. *Aquila chrysaetos* (Golden Eagle)	—	—	—	—	1	1	—	—	—	—	—	—
Buteo sp. (Hawk)	—	—	1	1	—	—	—	—	—	—	—	—
Accipitridae, indeterminate	—	—	—	—	—	—	—	—	1	1	—	—
Falco sp. (Falcon)	—	—	1	3	—	—	—	—	—	—	—	—
Centrocercus urophasianus (Sage Grouse)	1	1	—	—	1	1	—	—	—	—	—	—
Pica hudsonia (Black-billed Magpie)	—	—	—	—	1	1	—	—	—	—	—	—
Gymnorhinus cyanocephalus (Pinyon Jay)	—	—	1	1	—	—	—	—	—	—	—	—
Corvus brachyrhynchos (American Crow)	—	—	—	—	—	—	—	—	1	1	—	—
Eremophila alpestris (Horned Lark)	—	—	2	3	—	—	—	—	—	—	—	—
Tachycineta cf. *T. bicolor* (Tree Swallow)	—	—	1	1	—	—	—	—	—	—	—	—
Sitta sp. (Nuthatch)	—	—	—	—	1	1	—	—	—	—	—	—
Spizella breweri (Brewer's Sparrow)	1	1	—	—	—	—	—	—	—	—	—	—
Zonotrichia leucophrys (White-crowned Sparrow)	—	—	—	—	—	—	—	—	1	1	—	—
Junco hyemalis (Dark-eyed Junco)	1	1	—	—	—	—	—	—	—	—	—	—
Calcarius sp. (Longspur)	—	—	2	2	—	—	—	—	—	—	—	—
Agelaius phoeniceus (Red-winged Blackbird)	—	—	—	—	1	1	—	—	—	—	—	—
Leucosticte tephrocotis (Gray-crowned Rosy-finch)	—	—	1	1	1	1	1	1	—	—	—	—
Leucosticte atrata (Black Rosy-finch)	—	—	1	1	—	—	—	—	—	—	—	—

(continued)

TABLE 10.12 (continued)

	Horizon											
	A		*B*		*C*		*D*		*E*		*F*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Mammalia												
Ochotonidae												
Ochotona cf. *O. princeps* (pika)	—	—	—	—	—	—	—	—	1	1	—	—
Ochotona sp. Small morph "A" (pika)	1	1	—	—	—	—	—	—	—	—	—	—
Ochotona sp. (pika)	1	1	2	7	1	1	1	1	—	—	1	5
Leporidae												
Lepus sp. (hare or jackrabbit)	x	x	x	x	x	x	x	x	x	x	x	x
Sylvilagus sp. (cottontail rabbit)	x	x	x	x	x	x	x	x	—	—	—	—
Leporid (rabbit or hare)	—	—	—	—	—	—	—	—	—	—	—	—
† *Aztlanolagus* sp. (Aztlan rabbit)	—	—	—	—	—	—	x	x	x	x	x	x
Sciuridae												
Tamias cf. *T. minimus* (chipmunk)	—	—	—	—	1	1	1	1	—	—	1	1
Spermophilus lateralis (golden-mantled ground squirrel)	1	1	—	—	1	1	1	2	—	—	1	1
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	6	10	38	125	12	30	3	7	2	2	—	—
Cynomys cf. *C. leucurus* (white-tailed prairie dog)	1	1	12	33	1	2	3	4	—	—	—	—
Arvicolinae												
Phenacomys sp. (teeth nondiagnostic) (vole)	—	—	2[a]	2[a]	—	—	—	—	—	—	—	—
* *Lemmiscus* (four triangles) (sagebrush vole)	1	1	—	—	—	—	—	—	1	2	1	1
Lemmiscus curtatus (sagebrush vole)	10	16	39[a]	69[a]	3	5	2[b]	2[b]	3[c]	4[c]	3	4
† *Microtus meadensis* (Meade vole)	—	—	—	—	7[d]	12[d]	5[b]	9[b]	6[c]	11[c]	8	11
† *Microtus paroperarius* (vole)	—	—	1	2	1	1	1	1	1	1	1	1
Microtus 5T	1	2	9[a]	12[a]	2	3	5	5	1	1	1	2
† *Mictomys kansasensis / meltoni* (extinct bog lemming)	—	—	—	—	—	—	2[b]	2[b]	1[c]	1[c]	4	8
† *Mictomys* sp. (probably extinct bog lemming)	—	—	—	—	—	—	—	—	1	3	3	10
Mustelidae												
† *Martes diluviana* (extinct fisher)	—	—	—	—	—	—	—	—	—	—	1	1
Mustela frenata (long-tailed weasel)	1	1	3	11	1	1	1	1	—	—	1	2

TABLE 10.12 (continued)

	Horizon											
	A		*B*		*C*		*D*		*E*		*F*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Mustela erminea (ermine)	2	3	2	5	—	—	—	—	—	—	—	—
Mustela nigripes (black-footed ferret)	—	—	—	—	1	2	—	—	—	—	—	—
Mustela vison (American mink)	—	—	—	—	1	1	—	—	—	—	—	—
Taxidea taxus (badger)	1	1	—	—	1	1	—	—	1	1	—	—
Spilogale putorius (spotted skunk)	—	—	1	1	—	—	1	1	—	—	—	—
Canidae												
Canis latrans (coyote)	—	—	—	—	—	—	—	—	1	1	—	—
Vulpes velox (swift or kit fox)	1	2	1	1	—	—	—	—	—	—		
Tayassuidae												
† *Platygonus* sp. (peccary)	—	—	1	1	—	—	—	—	—	—	—	—
Cervidae												
cf. † *Navahoceros* sp. (deer)	1	2	—	—	—	—	—	—	—	—	—	—
Antilocapridae												
† *Stockoceros* (antelope)	—	—	—	—	1	1	—	—	—	—	—	—
Antilocapridae, genus and species indeterminate	1	3	—	—	—	—	—	—	—	—	—	—

NOTES: x, estimates for MNI and NISP are unavailable; †, extinct species; *, extinct morphotype. [a], Includes specimens from B or C; [b], includes specimens from D or E; [c], includes specimens from E or F; [d], includes specimens from C or D.

TABLE 10.13

Faunal List for Lower Six Horizons and Undifferentiated Material from the DMNH Velvet Room Excavation

	Horizon													
	G		*H*		*I*		*J*		*K*		*L*		*Undifferentiated*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
							Reptilia							
Natricinae (snake)	1	2	—	—	—	—	—	—	—	—	—	—	1	1
Non-Natricine Colubridae (snake)	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Colubroidea (snake)	1	1	1	1	—	—	—	—	—	—	—	—	—	—
							Aves							
Anser sp. or *Chen* sp. (Goose)	—	—	—	—	1	1	—	—	—	—	—	—	—	—
Anas sp. (Duck)	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Anatidae, indeterminate	—	—	—	—	—	—	—	—	—	—	—	—	1	2
cf. *Aquila chrysaetos* (Golden Eagle)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Buteo sp. (Hawk)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Accipitridae, indeterminate	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Falco sp. (Falcon)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Centrocercus urophasianus (Sage Grouse)	—	—	—	—	—	—	—	—	—	—	—	—	2	3
Falcipennis canadensis (Spruce Grouse)	—	—	—	—	—	—	—	—	—	—	—	—	1	4
Dendragopus cf. *D. obscurus* (Blue Grouse)	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Phasianidae, indeterminate	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Nyctea scandiaca (Snowy Owl)	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Asio otus (Long-eared Owl)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Troglodytidae, indeterminate (cf. *Thryothorus*)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
							Mammalia							
Ochotonidae														
Ochotona cf. *O. princeps* (pika)	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Ochotona sp. Trout Cave form (pika)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Ochotona sp. Small morph “A” (pika)	—	—	—	—	—	—	1	2	—	—	—	—	—	—
Ochotona sp. (pika)	—	—	1	2	2	4	1	1	—	—	—	—	6	15
Leporidae														
Lepus sp. (hare or jackrabbit)	—	—	x	x	—	—	—	—	—	—	—	—	—	—

Sylvilagus sp. (cottontail rabbit)	—	—	x	x	—	—	—	—	—	—	—	—	—	—
Hypolagus sp. (rabbit)	x	x	—	—	—	—	—	—	—	—	—	—	—	—
Sciuridae														
Tamias cf. *T. minimus* (chipmunk)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Marmota sp. (marmot)	—	—	—	—	—	—	—	—	—	—	—	—	x	x
Spermophilus lateralis (golden-mantled ground squirrel)	—	—	—	—	—	—	—	—	—	—	—	—	1[a]	7
Spermophilus cf. *S. elegans* (Wyoming ground squirrel)	—	—	—	—	—	—	—	—	—	—	—	—	1[a]	143
Cynomys cf. *C. leucurus* (white-tailed prairie dog)	—	—	—	—	—	—	—	—	—	—	—	—	1[a]	32
Muridae														
Neotoma cinerea (bushy-tailed wood rat)	—	—	—	—	—	—	—	—	—	—	—	—	x	>500?
Neotoma mexicana (Mexican wood rat)	—	—	—	—	—	—	—	—	—	—	—	—	x	1
Neotoma floridana (Florida wood rat)	—	—	—	—	—	—	—	—	—	—	—	—	x	2
Neotoma micropus (southern plains wood rat)	—	—	—	—	—	—	—	—	—	—	—	—	x	5
Neotoma stephensi (Stephens' wood rat)	—	—	—	—	—	—	—	—	—	—	—	—	x	5
Arvicolinae														
† *Allophaiomys pliocaenicus* (vole)	—	—	—	—	—	—	—	—	—	—	—	—	3	5
† *Mimomys virginianus* (Virginia mimomys)	—	—	—	—	—	—	—	—	—	—	—	—	4	6
† *Phenacomys gryci* (Gryci's vole)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Phenacomys sp. (nondiagnostic teeth) (vole)	1	1	—	—	—	—	—	—	—	—	—	—	3	5
**Lemmiscus* (four triangles) (sagebrush vole)	—	—	5[b]	7[b]	2[c]	2[c]	1[d]	1[d]	—	—	—	—	5	7
Lemmiscus curtatus (sagebrush vole)	1	1	2	3	—	—	—	—	—	—	—	—	26	51
Lemmiscus sp. (cannot identify to species)	—	—	—	—	—	—	—	—	—	—	—	—	3	10
† *Microtus meadensis* (Meade vole)	—	—	—	—	1[e]	1[e]	—	—	—	—	—	—	5	8
† *Microtus paroperarius* (vole)	1	2	9	12	2	2	2[d]	2[d]	—	—	—	—	2	5
Microtus 5T	—	—	—	—	—	—	—	—	—	—	—	—	16	32
† *Mictomys kansasensis/meltoni* (extinct bog lemming)	—	—	5[b]	7[b]	1	1	2[d]	3[d]	—	—	—	—	3	5
† *Mictomys* sp. (probably extinct bog lemming)	—	—	2[b]	3[b]	1[c]	1[c]	—	—	—	—	—	—	2	3
Ondatra sp. (muskrat)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Mustelidae														
† *Martes* new species (extinct marten)	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Mustela frenata (long-tailed weasel)	—	—	—	—	—	—	1[d]	1[d]	—	—	—	—	4	15
Mustela erminea (ermine)	1	1	1	2	1[e]	4[e]	—	—	—	—	—	—	—	—
Mustela nigripes (black-footed ferret)	—	—	—	—	—	—	—	—	—	—	—	—	1	3
Mustela vison (American mink)	—	—	—	—	—	—	—	—	—	—	—	—	1	2
† *Mustela* species A (extinct mustelid)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Taxidea taxus (badger)	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Spilogale putorius (spotted skunk)	—	—	—	—	1	1	1[f]	2[f]	—	—	1[g]	1[g]	1	3
† *Brachyprotoma obtusata* (short-faced skunk)	—	—	—	—	1	1	—	—	—	—	—	—	1	3

(continued)

TABLE 10.13 (continued)

	Horizon													
	G		*H*		*I*		*J*		*K*		*L*		*Undifferentiated*	
	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP
Canidae														
Canis latrans (coyote)	—	—	—	—	—	—	—	—	—	—	—	—	1	3
† *Canis edwardii* (Edward's wolf)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Vulpes velox (swift or kit fox)	—	—	—	—	1	1	1[f]	1[f]	—	—	—	—	1	4
Vulpes vulpes (red fox)	—	—	—	—	—	—	—	—	—	—	—	—	1	3
Urocyon cinereoargenteus (gray fox)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Felidae	—	—	—	—	—	—	—	—	—	—	—	—		
Lynx rufus (bobcat)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Tayassuidae														
† *Platygonus* sp. (peccary)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Cervidae														
Cervus canadensis (wapiti elk)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Odocoileus sp. (deer)	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Antilocapridae														
Antilocapridae, genus and species indeterminate	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Equidae														
† *Equus (Hemionus)* sp. (horse)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
† *Equus* sp. (large) (horse)	—	—	—	—	—	—	—	—	—	—	—	—	1	1
† *Equus* sp. (small) (horse)	—	—	—	—	—	—	—	—	—	—	—	—	1	5

NOTES: x, estimate for MNI and NISP is unavailable; †, extinct species; *, extinct morphotype. [a], Specimens are uncounted and thus both MNI and NISP may be more than 1; [b], includes specimens from H or I; [c], includes specimens from I or J; [d], includes specimens from below I; [e], includes specimens from below H; [f], includes specimens from below J; [g], includes specimens from below L. Undifferentiated = present in the DMNH Velvet Room excavation, but exact provenance unknown.

ELEVEN

Synopsis of the Herpetofauna from Porcupine Cave

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Although the fossil herpetofauna of Porcupine Cave is depauperate relative to the avian and mammalian faunas (both taxonomically and in total numbers of specimens and number of individuals represented), even the limited record available yields important information that complements and augments the data derived from studies of the other, more extensive vertebrate groups. The combined sample of amphibians and reptiles from all localities within the cave includes only 141 specimens representing a minimum of seven taxa. The nature of the preserved material in most cases prohibits reliable identification to species or even to genus, but given the high elevation of the site (2900 m), the presence of any amphibian and reptile taxa in the middle Pleistocene is significant. In this chapter we document the presence and taxonomic diversity of amphibians and reptiles recovered from the cave and explore the paleoclimatic information that can be derived from the study of these remains when they occur in controlled stratigraphic contexts.

Methodological Approach

There are difficulties, often unacknowledged, in seeking fine-scale taxonomic resolution of isolated skeletal elements of amphibians and reptiles. Our identifications are based on the reliable diagnostic features of the fossil material available. Whenever possible we minimized the use of geographic parsimony to refine our identifications, in part because of the antiquity of the material and our uncertainty regarding the distribution (or taxonomic evolution) of amphibian and reptile lineages in the middle Pleistocene. More importantly, the use of geography to refine taxonomic identifications prohibits or limits the use of the identified taxa in any kind of environmental or zoogeographic reconstructions. Failure to recognize this fact can result in circularity in construction of hypotheses of the impacts of climatic or environmental change on faunal dynamics. The only taxonomic assumptions we make that employ geography are those on the continental scale. Where these assumptions are made, they are explicitly stated.

Snakes are represented by a greater number of fossil specimens (117) than any other herpetofaunal group from Porcupine Cave. We recognize three major groups of snakes in the Porcupine Cave collection; all are colubroids, and some specimens cannot be identified beyond Colubroidea. To determine regional position within the vertebral column, we used vertebral characters discussed by LaDuke (1991a). Only precloacal vertebrae were identified beyond Colubroidea. Vertebrae preserving diagnostic features of Natricinae and Viperidae were identified to those taxa. Other non-Natricine colubrids were also recovered from Porcupine Cave, but it is difficult even to identify definitively from which major colubrid clade these specimens were derived. For example, it can be difficult in some cases to differentiate isolated vertebrae of Xenodontinae from those of some species of Colubrinae (Cadle, 1987; Holman, 2000). These specimens are referred to throughout this chapter as "non-Natricine Colubridae." Specimens are not identified to genus or species. We impose this limitation primarily because we are unable to replicate the work of others who allocated isolated vertebrae to genus or species. As a result, the incomplete nature of many specimens, combined with our methodological approach, potentially leads to an underrepresentation of the snake diversity in Porcupine Cave.

The discovery of discrete vertebral characters to separate major clades of snakes remains a significant challenge for paleoherpetologists. A necessary prerequisite to such a discovery is a more thorough understanding of the morphological and serial variation within extant snake lineages. The few completed studies on vertebral variation in snakes (Hoffstetter and Gayrard, 1965; Thireau, 1967; Gasc, 1974; Smith, 1975;

LaDuke, 1991b; Moon, 1999) lay an important foundation for such research, but more work must be done.

Results

Specimens are housed in the Carnegie Museum of Natural History (CM), the Denver Museum of Nature and Science (DMNH), and the University of California Museum of Paleontology (UCMP). A detailed listing of the specimen numbers and identified remains is provided in appendix 11.1. Diagnostic features used to identify fossil remains are discussed for each taxon. The review presented here supersedes the preliminary discussion presented by Bell and Barnosky (2000).

Identified Taxa

Amphibia

Caudata

Ambystomatidae

DIAGNOSIS A single salamander vertebra (DMNH 44765) was recovered from the cave. The specimen is amphicoelous, with the centrum and most of the neural arch preserved. The diapophyses and parapophyses are broken distally, but there is some indication that they supported bicipital ribs. On the ventral side of the vertebra a single spinal nerve foramen pierces each side of the centrum immediately posterior to the transverse processes where they meet the centrum. Single intravertebral spinal nerve foramina appear in this position in the trunk vertebrae of Ambystomatidae, Plethodontidae, Salamandridae, and Sirenidae (Edwards, 1976). The larger size, reduced transverse processes, and distinct vertebral morphology of sirenids exclude them from further consideration. The amphicoelous condition of the Porcupine Cave fossil argues against assignment to the Salamandridae, a group in which the vertebrae are usually opisthocoelous (Estes, 1981). Discrete characters permitting separation of ambystomatids from the diverse plethodontids are often lacking. In general, the vertebrae of North American plethodontids are relatively slender, with long, narrow centra and a very low neural arch supporting a weak neural spine (Tihen and Wake, 1981). In *Ambystoma* and the Porcupine Cave fossil the vertebrae are more robust, and there is an extremely reduced neural spine (= neural ridge) with a posteriorly vaulted neural arch terminating at its posterodorsal end in a small dimple or depression (Hilton, 1948). This feature and the overall morphology of the fossil permit identification to the Ambystomatidae.

REMARKS The specimen is likely from a species of *Ambystoma,* the only currently recognized extant genus of the family and the only one to which Pleistocene fossils have been allocated. The *Ambystoma* lineage has a fossil record purportedly extending back to the Oligocene (Holman, 1968). *Ambystoma tigrinum* is present in Park County today (Hammerson, 1999) and is known to occur within a short distance of Porcupine Cave (see the section “Comparison with Local Modern Fauna”).

FIGURE 11.1 UCMP 399996; sacrococcyx referred to Pelobatidae shown in ventral (top) and dorsal (bottom) views. Scale bar = 2 mm.

Anura

Pelobatidae

DIAGNOSIS AND REMARKS Among the 15 anuran bones recovered from the cave, one is identified as a pelobatid. The specimen (UCMP 399996) is a sacrococcyx (fused sacral vertebra and urostyle; figure 11.1) with moderately developed webbing between the transverse processes of the sacral vertebra and the shaft of the urostyle (a feature that varies too widely to be of systematic value; Zweifel, 1956; Kluge, 1966). We can find no features that permit finer taxonomic allocation of this fossil. Sacrococcygeal fusion is a regular feature in the Pelobatidae (Cope, 1889; Noble, 1922) and appears to be a synapomorphy for the group, but it is incompletely developed in *Pelobates cultripes* (Kluge, 1966). Fusion is often cited in the North American Quaternary paleoherpetological literature as a definitive character of the Pelobatidae, the only anuran group native to the United States in which such fusion regularly occurs. We acknowledge, however, that fusion is known to occur in no fewer than six other anuran groups; it is a regular feature in the Pipidae (Noble, 1922; Cannatella,

1985) and is also known to take place in the Bombinatoridae (in a possibly teratological specimen of *Bombina;* Holman, 1963:161; but see also Beddard, 1907), Bufonidae (in *Frostius,* and within *Dendrophryniscus* and *Melanophryniscus;* Izecksohn, 1968, 1971; McDiarmid, 1971; Cannatella, 1986), Hylidae (in *Phyllomedusa psilopygion;* Cannatella, 1980), Megophryidae (in *Megophrys aceras,* and within *M. nasuta* [= *M. montana*] and *M. major;* Beddard, 1907; Boulenger, 1908; Cannatella, 1985: 127), and Microhylidae (in *Breviceps* and *Probreviceps;* Beddard, 1908; Parker, 1934). A teratological fusion of the urostyle with an incompletely developed vertebral element in *Rana pipiens* (Ranidae) was reported by Holman (1963:164), but we are aware of no other fusions in the Ranidae. The overall morphology of the Porcupine Cave specimen strongly supports referral to Pelobatidae and not to the other taxa listed. Four species of Pelobatidae inhabit Colorado today, but no historical records are known from Park County (Hammerson, 1999).

Other anuran bones recovered from Porcupine Cave include limb bones, vertebral elements, and a single angulosplenial (see appendix 11.1). In our opinion, these specimens are not sufficiently diagnostic to permit informative identifications more specific than Anura.

Reptilia

Squamata

"Lizards"

Squamates constitute the bulk of the herpetological remains recovered from Porcupine Cave. The squamate remains are dominated by isolated snake vertebrae, but eight lizard specimens also were recovered. Two of these lizard remains (vertebrae) are not identifiable. Three others are from relatively small-bodied species and have slender conical teeth with weakly tricuspid crowns; this morphology is consistent with identification as non-acrodont Iguania, but because of the fragmentary nature of the material more precise taxonomic allocations are not possible for these specimens. The three remaining specimens are referred to Phrynosomatidae (sensu Frost and Etheridge, 1989).

Phrynosomatidae

PHRYNOSOMA

DIAGNOSIS We refer two specimens to the genus *Phrynosoma.* The fossil maxilla (DMNH 44766; figure 11.2) shows an anteroposteriorly restricted, triangular ascending process that terminates in a sharp dorsal tip; this morphology is a synapomorphy of *Phrynosoma* and is not known for any other lizards native to North America. The dentary (DMNH 44767) is referred to *Phrynosoma* based on the distinctive, pronounced mediolateral curvature with a flattened ventral portion at the posterior end; this morphology is widespread in *Phrynosoma* (Montanucci, 1987; Mead et al., 1999), and we consider it to be a synapomorphy of the group.

FIGURE 11.2. DMNH 44766; right maxilla referred to *Phrynosoma* shown in lateral (top), occlusal (middle), and medial (bottom) views. Scale bar = 3 mm.

REMARKS *Phrynosoma cornutum, P. hernandesi,* and *P. modestum* inhabit Colorado today (Hammerson, 1999), but none of the species is reported from Park County. Of the three, *P. hernandesi* has the widest geographic distribution and the widest elevational occurrence in Colorado; it is reported to occur as high as 3355 m (Hammerson, 1999) in La Plata County. The Porcupine Cave specimens thus document a wider geographic distribution for *Phrynosoma* in the past, but one that is within the known elevational tolerance of extant members of the genus.

GENUS INDETERMINATE

A single specimen (UCMP 399995) of an isolated, broken dentary has relatively slender, weakly tricuspid teeth and a shallow dental gutter with an open Meckelian groove (figure 11.3).

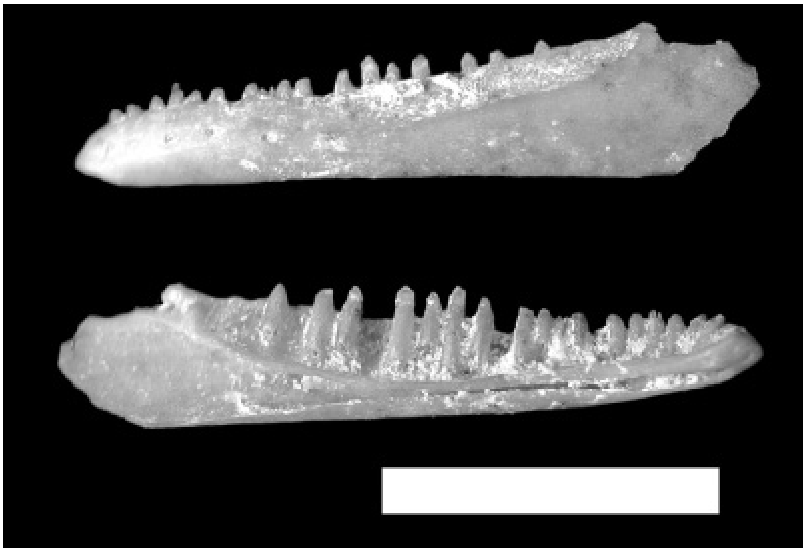


FIGURE 11.3. UCMP 399995; left dentary referred to Phrynosomatidae shown in lateral (top) and medial (bottom) views. Scale bar = 4 mm.

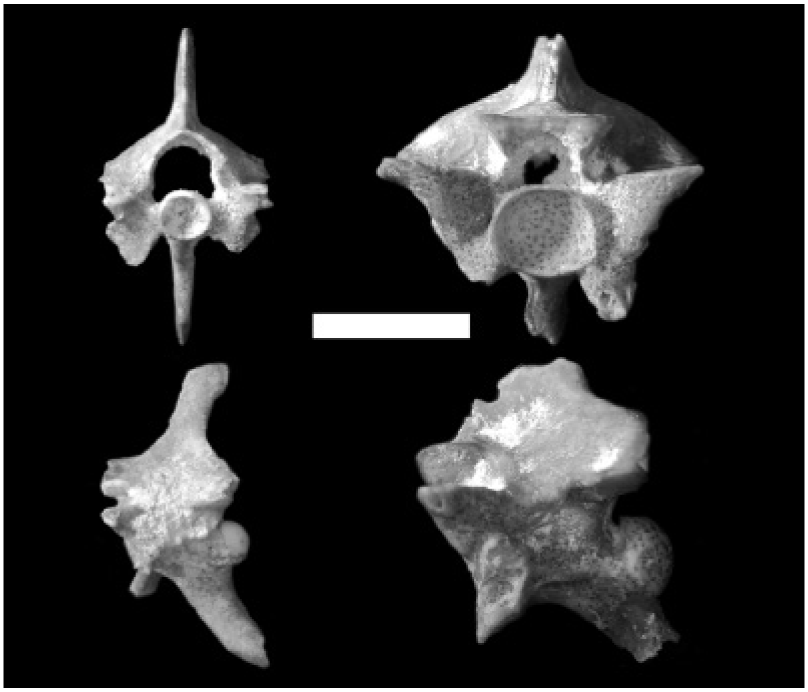


FIGURE 11.4. Porcupine Cave specimens referred to Viperidae. Left pair (CMNH 65500; anterior precloacal vertebra) and right pair (DMNH 27893; precloacal vertebra) shown in anterior (top) and left lateral (bottom) views. Scale bar = 5 mm.

It lacks the diagnostic morphology of *Phrynosoma,* and so it constitutes a second phrynosomatid taxon from the cave. The specimen resembles *Sceloporus undulatus* (which is currently found in Park County and is known to range as high as 2805 m elevation; Hammerson, 1999), but there are no diagnostic features of this element that permit definitive identification even to genus.

Serpentes

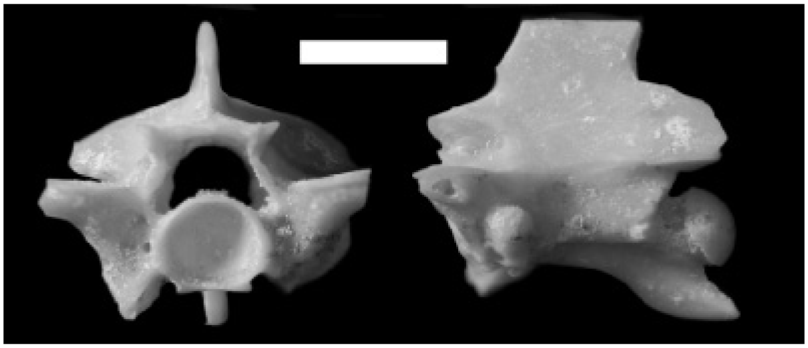
Viperidae

DIAGNOSIS AND REMARKS Seven vertebrae are assigned to Viperidae (see appendix 11.1). These specimens have an extremely elongate hypapophysis that is predominantly posteroventrally oriented (more ventrally directed than posteriorly directed; figure 11.4). Several North American viperid taxa *(Agkistrodon, Crotalus,* and *Sistrurus)* share this general characteristic. In our experience, the vertebral characters purported to separate these taxa (e.g., Holman, 1979) are subject to such variation that we question their utility in identifying fossil snakes. Both *Crotalus* and *Sistrurus* inhabit Colorado today but are not reported from Park County (Hammerson, 1999).

Natricinae

DIAGNOSIS AND REMARKS A total of 67 vertebrae are assigned to Natricinae and have the following characteristics

FIGURE 11.5. DMNH 27888; precloacal vertebra referred to Natricinae shown in anterior (left) and left lateral (right) views. Scale bar = 2 mm.



(figure 11.5): a well-developed hypapophysis that is predominantly posteriorly angled (not distinctly directed ventrally); prezygapophysial accessory processes that are elongate spines; and very well-developed osseous paralymphatic channels that are present in all specimens. Recognition of Natricinae solely on the basis of vertebral morphology is difficult because vertebral morphology in natricines appears to reflect a more generalized morphology shared with other colubroid lineages, notably the Elapidae. Qualitative vertebral characteristics are widely used in an effort to distinguish these lineages (e.g., Hoffstetter, 1939; Holman, 1979; Rage, 1984), but such characters are not demonstrated to be uniform with respect to individual, ontogenetic, intracolumnar, and intraspecific variation for a wide range of snake taxa (see also comments by Cadle, 1987, 1988; Kluge, 1993; Czaplewski et al., 1999a). Studies on the variability of similar characters applied to differentiate other snake taxa on the basis of vertebrae demonstrated considerable individual and intracolumnar variation (Kluge, 1988; Bell and Mead, 1996).

The issue here is really one of higher-order ambiguity; thus there do not appear to be any discrete vertebral characters that can be used to separate *all* natricines from *all* elapids, and we are not confident in the use of characteristics previously applied by others to recognize natricines, especially with respect to elapids. As a result, we employed continental-scale geographic data in our analysis and compared the Porcupine Cave sample to the only North American elapids, *Micrurus* and *Micruroides*. Many extant species of *Micrurus* are known from throughout the Americas (Campbell and Lamar, 1989), but we were unable to examine vertebral morphology for any species other than *M. tener* (species taxonomy follows that adopted by Crother et al., 2001), the only species now inhabiting the United States (where it is found along the Gulf coast from Texas to Florida, and north along the east coast into North Carolina). *Micruroides* is monotypic; the single species *M. euryxanthus* inhabits the Sonoran Desert region of the southern United States and northwestern Mexico (Campbell and Lamar, 1989). The highest elevation recorded for *M. tener* is close to 2000 m (Roze and Tilger, 1983; Campbell and Lamar, 1989), and that for *M. euryxanthus* is 1800 m (Roze, 1974).

Both *M. tener* and *M. euryxanthus* have a relatively short neural spine, a distinctive vertebral morphology that is not found in the Porcupine Cave specimens we refer to Natricinae. Although this character is not universally diagnostic within either Elapidae or Natricinae, its absence in the Porcupine Cave sample, combined with the geographic and elevational range in North American natricines and elapids, indicates that the most parsimonious assignment of the Porcupine Cave specimens is to Natricinae.

There are currently six species of natricine snakes inhabiting Colorado *(Nerodia sipedon, Thamnophis cyrtopsis, T. elegans, T. proximus, T. radix,* and *Tropidoclonion lineatum). Thamnophis elegans* inhabits the immediate vicinity of the cave today and is known from elevations as high as 3992 m in Colorado (Hammerson, 1999). The past distribution, thermal tolerance, and elevational extent of these taxa remain unknown and cannot be clarified by study of the material from Porcupine Cave.

NON-NATRICINE COLUBRIDAE

DIAGNOSIS AND REMARKS The 10 vertebrae assigned to non-Natricine Colubridae (figure 11.6) are trunk vertebrae that lack a hypapophysis; instead they possess a prominent hemal keel, which terminates as a blunt process ventral to the anterior margin of the condyle. Paralymphatic channels in non-Natricine Colubridae are weakly developed relative to those of natricines. It is likely that at least two species of non-Natricine colubrids are present in the Porcupine Cave sample. UCMP 399993 is a large, relatively robust vertebra, resembling in its general appearance a vertebra of an adult stout-bodied snake such as *Pituophis*. UCMP 399972 is a smaller, more gracile element, more dorsoventrally compressed and similar in general appearance to *Lampropeltis*. In the absence of diagnostic characters for these specimens, generic allocations are not made for either.

Discussion

Regional Comparisons

Previous studies of late Pleistocene North American herpetofaunas appear to indicate both taxonomic and geographic stability of reptile and amphibian taxa throughout the Rancholabrean mammal age and into the Holocene (Fay, 1984, 1988; Brewer, 1985; Holman, 1991, 1992, 1995, 1999). The question

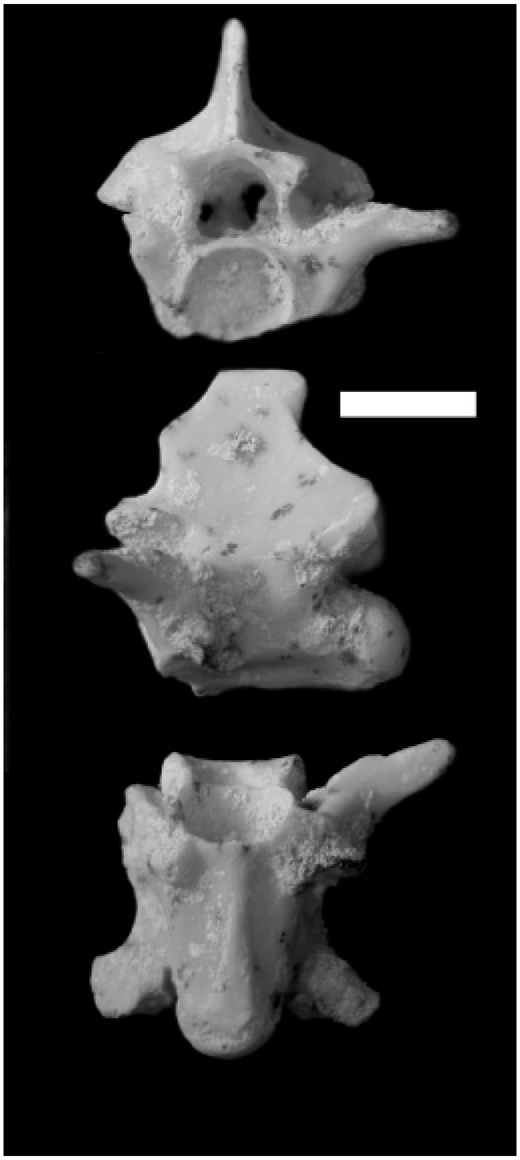


FIGURE 11.6. UCMP 399993; precloacal vertebra referred to non-Natricine Colubridae shown in anterior (top), left lateral (middle), and ventral (bottom) views. Scale bar = 4 mm.

of stability in early and middle Pleistocene faunas is not as well explored (see, e.g., Holman, 1995). Unfortunately, the material preserved in Porcupine Cave does not permit species-level identifications, and consequently we are limited in our ability to make definitive statements about fine-scale taxonomic and geographic stability. Nor is it possible for us to indicate in any specific way that climate changes might have affected amphibian and reptile species in central Colorado in the middle Pleistocene.

Comparisons of a more regional nature also are difficult. There are relatively few herpetofaunal assemblages from roughly contemporaneous deposits in the Rocky Mountain region (late Pleistocene and Holocene faunas far outnumber those of early and middle Pleistocene age in the western United States generally). In addition, our somewhat more conservative approach to taxonomic identifications limits the kinds of informative comparisons that can be made. Nonetheless, some meaningful comparisons are possible with faunas from two localities south of Porcupine Cave: the Hansen Bluff faunal sequence in Colorado and the SAM Cave fauna in northern New Mexico.

The Hansen Bluff faunal sequence includes a diverse herpetofauna that was recovered from the Alamosa Formation in the San Luis Valley of south-central Colorado (16 km southeast of Alamosa, 2300 m elevation; Rogers et al., 1985, 1992). External chronological control was established by means of a paleomagnetic profile and the presence in the section of the Bishop Ash (the average age of which is now calculated at 758.9 ± 1.8 Ka; Sarna-Wojcicki et al., 2000). This lower-elevation fauna was reported to include *Ambystoma,* the hylid frog *Pseudacris,* the pelobatid *Scaphiopus,* two species of the frog *Rana,* two species of the toad *Bufo,* the xenodontine snake *Heterodon,* the colubrine *Pituophis,* two species of the natricine *Thamnophis,* the viperid *Crotalus,* and three phrynosomatid lizards *(Holbrookia, Phrynosoma,* and *Sceloporus).*

The SAM Cave fauna was recovered from a lava tube deposit located at 2737 m in Rio Arriba County, New Mexico (just north of San Antonio Mountain; Rogers et al., 2000). Six discrete faunas were recovered from the cave, the oldest of which have no external age control but contain the arvicoline rodents *Allophaiomys, Mictomys kansasensis, Microtus, Clethrionomys,* and *Lemmiscus* (with both four- and five-closed triangles). These rodents suggest an age roughly contemporaneous with at least some of the deposits in Porcupine Cave (e.g., the Pit locality; Bell and Barnosky, 2000). The preserved herpetofauna associated with these mammals was relatively depauperate, similar to that of Porcupine Cave, which is at a slightly higher elevation (2900 m). Reported taxa at SAM Cave include the salamander *Ambystoma,* the hylid frog *Pseudacris,* and the viperid *Crotalus*. Somewhat younger deposits in SAM Cave include the lizard *Phrynosoma* and the natricine *Thamnophis* as well.

These faunas suggest that the restricted taxonomic diversity of modern amphibians and reptiles at higher elevations in Colorado (Hammerson, 1986, 1999) is not unique to recent times. In overall herpetofaunal diversity, SAM Cave and Porcupine Cave are roughly comparable, and the relatively high elevations of these sites may be responsible for the low diversity and small sample sizes of amphibians and reptiles in the respective faunas. The Hansen Bluff fauna is approximately 600 m lower in elevation than that from Porcupine Cave, and Hansen Bluff contains a much more diverse anuran fauna, and possibly a slightly greater diversity of phrynosomatid lizards.

Comparison with Local Modern Fauna

To our knowledge, intensive surveys of the extant herpetofauna in the immediate vicinity of Porcupine Cave have not been conducted. Limited efforts to document extant herpetofaunal diversity in the immediate vicinity of the cave were conducted by Robert Finley Jr. and resulted in multiple observations of the tiger salamander *Ambystoma tigrinum* (including 10 vouchered specimens) and the garter snake *Thamnophis elegans* (including four vouchered specimens) within a few miles of the cave (all vouchered specimens are deposited in the Biological Survey Collection in the Museum of Southwestern Biology, University of New Mexico; C. Ramotnik, pers. comm., January 2002). Anecdotal observations of "racers" and of small lizards and anurans cannot be confirmed at this time and do not appear to be supported by voucher specimens in collections. Four amphibian species *(Ambystoma tigrinum, Bufo boreas, Pseudacris triseriata,* and *Rana pipiens)* are recorded from Park County, and all four are known to occur above 3300 m elevation within the state (Hammerson, 1986, 1999). One other anuran species *(Rana sylvatica)* lives today in the north-central portion of the state and is known in Colorado from elevations as high as about 2987 m (Hammerson, 1986). The only definitively identified anuran specimen from Porcupine Cave is referred to Pelobatidae, a group represented by four species in the extant Colorado fauna (Hammerson, 1999). None of the four species is reported from Park County, and all occur today at lower elevations than Porcupine Cave (*Spea bombifrons* has the highest elevational record of the modern species; it reaches elevations up to 2440 m in the San Luis Valley; Hammerson, 1999).

Three extant reptile species also are reported from Park County—*Sceloporus undulatus, Thamnophis elegans,* and *Opheodrys* (=*Liochlorophis*) *vernalis*—and all are reported from elevations above 2700 m. There are no historical records of *Crotalus viridis* from Park County, but elsewhere in the state this species ranges up to 2896 m elevation (Hammerson, 1986), nearly the elevation of Porcupine Cave. Apart from *Phrynosoma hernandesi,* no other reptile species are known to inhabit elevations above 2700 m elevation in Colorado.

Paleoenvironmental Significance

Given the fact that so few species seem to inhabit the region surrounding Porcupine Cave today, the relatively low abundance of amphibian and reptile remains at the site is not unexpected. Most of the specimens recovered thus far are from test pit excavations, surface samples, and unstratified or mixed deposits. Consequently, the majority of the reptile and amphibian records from the cave simply confirm the presence of these taxa in South Park (an intermontane basin in the southern Rocky Mountains of central Colorado) during the time intervals represented by the discrete deposits.

The number of identified vertebrate specimens in Porcupine Cave exceeds 13,000, out of a total number of vertebrate specimens that, by conservative estimate, exceeds 45,000. The primary taphonomic vectors most likely responsible for the accumulation of bones in Porcupine Cave seem to be wood rats, raptorial birds, and mammalian carnivorans. This combination of vectors was shown by Hadly (1999) to be an excellent means of sampling extant vertebrate communities, and it is unlikely that the Porcupine Cave herpetofauna was subjected to a taphonomic filter that would artificially inflate or deflate their abundance in the deposits. For these reasons we are confident that the relative abundance of these taxa in the deposits is an accurate reflection of their relative abundance in the communities at the time their remains were being incorporated into the deposits.

If long-distance transport (by raptorial birds or mammalian predators) of vertebrate remains from lower elevations was an important factor in bringing materials into the cave, we would expect to find other vertebrate taxa typical of such lower elevations. The absence of small mammals typical of lower elevations (especially heteromyid rodents) argues against such long-distance transport. In the absence of data to the contrary, we consider the herpetofaunal remains of Porcupine Cave to have been derived from within relatively short distances of the cave, almost certainly within the confines of South Park.

We attempted special analysis of herpetofaunal remains recovered from the Pit and the DMNH Velvet Room excavations, the two localities within the cave that were excavated with stratigraphic control and had at least a reasonable sample size. Our goal was to determine if any environmental data could be derived from the amphibian and reptile record that might complement (or contradict) the patterns revealed through studies of the mammalian fauna. Our analysis at higher taxonomic levels does reveal some information that can help in interpretation of climate change and the consequent effects on biodiversity of amphibians and reptiles.

The DMNH Velvet Room excavation (locality 644) contains 19 snake specimens including only one vertebra of non-Natricine Colubridae with no stratigraphic control, and a single viperid vertebra from level 7c in grid 20. All other specimens are natricines or unidentified colubroids. No meaningful interpretations are made for this locality.

Of the localities excavated in the cave thus far, the stratified sediments in the Pit locality (CM 1925 / UCMP V93173) provide the best information available on the effects of middle Pleistocene climate change on the vertebrate faunas in South Park. Biochronologic and paleomagnetic data indicate that the sediments in levels 4–8 date to between approximately 750,000 and 850,000 yr BP (Bell and Barnosky, 2000), or perhaps slightly older (chapter 7). The stratigraphic data for the Pit locality were summarized by Barnosky et al. (1996) and are further elaborated in chapters 7 and 23. These sources document the fact that several sedimentological changes in the Pit sequence represent times of climatic transition. The transition that is best documented is that at the level 4/3 boundary (Barnosky et al., 1996). Lithology of the sediments and changes in the relative abundance of sciurid and arvicoline rodents indicate that the sediments in levels 4 and 5 represented a glacial interval and those in levels 1–3, an interglacial (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996; Bell and Barnosky, 2000). Although the fossils are not abundant, the stratigraphic change in taxonomic diversity of amphibian and reptile remains from the Pit locality supports this interpretation (table 11.1).

TABLE 11.1
Stratigraphic Distribution of Amphibian and Reptile Remains from the Pit Locality

Taxon	*Level* 1–3	 4–5	 6	 7	 8A
Pelobatidae	1	—	—	—	—
Phrynosomatidae	1	—	—	—	—
Non-Natricine Colubridae	1	—	—	1	—
Natricinae	4	3	1	1	4
Viperidae	2	—	—	—	—
Indeterminate Colubroidea	5	2	—	1	3

NOTES: Levels 1–3 previously were interpreted to represent an interglacial deposit, and levels 4–5, a glacial deposit (Barnosky et al., 1996; Bell and Barnosky, 2000). Levels 6, 7, and 8A are interpreted in this book to represent an interglacial that was substantially cooler and moister than that represented by levels 1–3. Only specimens for which stratigraphic data are available (or can be inferred) are included. The single pelobatid specimen and the single phrynosomatid specimen most likely were deposited in levels 1–3, but a more precise determination cannot be made. See text for discussion.

Between levels 1–3 and the deeper levels of the Pit there is no indication of change in the taphonomic pathways responsible for bringing herpetofaunal remains into the deposit. The most abundant herpetofaunal taxon from the Pit locality is Natricinae, and all but one of the specimens recovered from the deeper levels of the Pit (a non-Natricine colubrid, represented by a single vertebra from level 7; table 11.1) are referred to this taxon or to undetermined Colubroidea. In the upper levels of the Pit (levels 1–3), the herpetofaunal remains include four natricine snake vertebrae, one vertebra of non-Natricine Colubridae, two vertebrae of a viperid snake, and five unidentified colubroids (table 11.1). In addition, a phrynosomatid lizard dentary and a sacrococcyx of a pelobatid frog are probably from levels 1–3 of the Pit. Precise stratigraphic data for these two specimens are not available, but the color and general preservation of the bones indicate that they were recovered from the upper levels of the Pit and not from deeper stratigraphic levels (Bell and Barnosky, 2000).

The change in herpetofaunal diversity from two taxa (Natricinae and non-Natricine Colubridae) in deeper levels of the Pit (8–4) to five taxa (Pelobatidae, Phrynosomatidae, Natricinae, non-Natricine Colubridae, Viperidae) is noteworthy. Although most paleoclimatic interpretations of fossil herpetofaunas are based on species-level identifications, it is clear that at least some tentative interpretations can be drawn from the material preserved in the Pit locality.

The pelobatid frog and viperid snake in the Pit fauna represent extralimital records in terms of both geography and elevation. No historical records of viperids or pelobatids are known from Park County (Hammerson, 1986, 1999). The only extant pelobatids in Colorado today *(Scaphiopus* and *Spea)* occur to the east and west of Park County, the closest records being from Jefferson, Douglas, El Paso, and Fremont counties (Hammerson, 1999). Two of these anurans *(S. bombifrons* and *S. intermontana)* currently range to above 2100 m elevation in Colorado, but no extant Colorado populations of pelobatids are found above 2440 m elevation (Hammerson, 1999).

Several North American viperid species have elevational ranges that approach or exceed the elevation of Porcupine Cave (e.g., *Crotalus intermedius, C. lepidus, C. molossus, C. pricei, C. scutulatus, C. transversus,* and *Sistrurus ravus,* all known from elevations above 2850 m, and *C. triseriatus,* which ranges as high as 4300 m; Lowe et al., 1986; Campbell and Lamar, 1989). *Crotalus viridis* is known from just outside Park County to the northeast and southeast, and it currently can be found as high as about 2896 m elevation (Hammerson, 1986, 1999).

The increased taxonomic diversity in the upper levels (1–3) of the Pit sequence supports previous interpretations that these levels represent an interglacial period and that at least levels 4 and 5 represent glacial intervals. In addition, the herpetofaunal diversity reflected in levels 1–3 in the Pit sequence exceeds that of the known extant diversity in the immediate vicinity of the cave (though not of Park County as a whole, which includes regions of considerably lower elevation than those represented in the immediate vicinity of the cave). This higher diversity suggests the possibility that the interglacial interval represented in the upper levels of the Pit was a warmer (though not necessarily a drier) interglacial than the one in which we currently live. This hypothesis is supported most strongly by the presence of a fossil pelobatid toad in the Pit. Extensive efforts to document the modern herpetofaunal communities in the vicinity of the cave are required to determine if the perceived temporal differences in overall diversity represent reality or are an artifact resulting from a lack of concerted effort to sample the local herpetofauna.

Appendix 11.1. Amphibian and Reptile Specimens Recovered from Porcupine Cave

Caudata

Ambystomatidae

MARK'S SINK (DMNH 1349)

DMNH 44765 trunk vertebra.

Anura

Pelobatidae

PIT (UCMP V93173)

Grid 3, level mixed (likely from levels 1–3): UCMP 399996 sacrococcyx.

Family Indeterminate

BADGER ROOM (DMNH 942/1351 AND UCMP V93176)

DMNH 44771 vertebral centrum; DMNH 44772 trunk vertebra; DMNH 44773 broken radioulna; UCMP 399997 tibiafibula.

GENERATOR DOME (DMNH 1347)

DMNH 44774 proximal tarsal.

MARK'S SINK (DMNH 1349)

DMNH 44755 urostyle; DMNH 44757 angulosplenial; DMNH 44758 trunk vertebra; DMNH 44759 trunk vertebra; DMNH 44760 sacral vertebra; DMNH 44761 humerus; DMNH 44762 humerus; DMNH 44763 tibiafibula; DMNH 44764 tibiafibula.

Squamata

Unidentified Lizard

MARK'S SINK (DMNH 1349)

DMNH 44756 vertebra; DMNH 44770 two fused vertebrae.

Non-acrodont Iguania

MARK'S SINK (DMNH 1349)

DMNH 33752 broken left maxilla; DMNH 44768 broken right maxilla; DMNH 44769 left dentary fragment.

Phrynosomatidae

Phrynosoma sp.

MARK'S SINK (DMNH 1349)

DMNH 44766 right maxilla; DMNH 44767 left dentary.

Genus Indeterminate

PIT (UCMP V93173)

Undifferentiated (likely from levels 1–3): UCMP 399995 left dentary.

Colubroidea

Colubridae

Natricinae

CM VELVET ROOM (UCMP V93175)

Grid 1, level 1B: UCMP 399992 pcv.

DMNH VELVET ROOM (DMNH 644)

Grid 16, level 6: DMNH 11971 pcv; grid 17, level 6: DMNH 14966; grid 11, level 7: DMNH 44775–44776 pcv; grid 7, level 8: DMNH 33756 pcv; grid 11, level 9: DMNH 44781 sphenoid; grid 11, level 10: DMNH 44777 pcv; grid 11, level 11: DMNH 44778 pcv; grid 12, level 11: DMNH 27888 pcv; grid 16, level 12: DMNH 12083 pcv; grid 11, level 13: DMNH 44779 pcv; grid 11, level 14: DMNH 44780 pcv; grid 6, level 15: DMNH 22171 pcv; grids 13–15, bilge: DMNH 44782 pcv.

GYPSUM ROOM (UCMP V93174)

Grid 1, level 4, UCMP 399962–399969 pcv, UCMP 399970–399971 maxilla fragment; grid and level undifferentiated: UCMP 399958–399961 pcv.

MARK'S SINK (DMNH 1349)

DMNH 44714–44735 pcv.

PIT (UCMP V93173)

Grid 1, level 1, UCMP 399942 pcv; grid 1, level 2: UCMP 399943–399944 pcv; grid 1, level 3: UCMP 399945 pcv; grid 1, level 4: UCMP 399946–39948 pcv; grid 3, level 6: UCMP 399949 pcv; grid 3, level 7: UCMP 399950 pcv; grid 3, level 8A: UCMP 399951 pcv; grid 7, level 8A: UCMP 399952–399954 pcv; grid 3, level mixed: UCMP 399955–399956 pcv; grid and level mixed: UCMP 399957 pcv.

Non-Natricine Colubridae

CM VELVET ROOM (UMCP V93175)

Grid 3/4, level mixed: UCMP 399993 large pcv.

DMNH VELVET ROOM (DMNH 644)

Grid 13–15, bilge: DMNH 27889 pcv.

GYPSUM ROOM (UCMP V93174)

Grid 1, level 4: UCMP 399974 pcv; UCMP 399975 pcv.

MARK'S SINK (DMNH 1349)

DMNH 44736 trunk vertebral fragment; DMNH 44737 pcv; DMNH 44738 pcv; DMNH 44739 pcv.

PIT (UCMP LOCALITY V93173)

Grid 1, level 2: UCMP 399972 pcv; grid 3, level 7: UCMP 399973 pcv.

Viperidae

CM VELVET ROOM (UCMP V93175)

Level mixed: UCMP 399998 vertebral centrum fragment with hypapophysis.

DMNH VELVET ROOM (DMNH 644)

Grid 20, level 7c: DMNH 33751 pcv.

MARK'S SINK (DMNH 1349)

DMNH 44750 anterior pcv; DMNH 44751 pcv; DMNH 27893 pcv.

PIT (CM 1925)

Grid 1, level 2: CM 65500 2 anterior pcv.

Indeterminate Colubroid

CM VELVET ROOM EAST EXTENSION (UCMP V93175)

Grid 3/4, level mixed: UCMP 399994 pcv fragment.

DMNH VELVET ROOM (DMNH LOCALITY 644)

Grid 21, level 9: DMNH 33753 trunk vertebra; grid 16, level 14: DMNH 33761 pcv; grid 7, level 20: DMNH 22698 trunk vertebra.

GYPSUM ROOM (UCMP V93174)

Grid 1, level 4: UCMP 399988 vertebral fragment, UCMP 399989 caudal vertebra, UCMP 399990 caudal vertebra, UCMP 399991 vertebral fragment; grid and level undifferentiated: UCMP 399987 trunk vertebra.

MARK'S SINK (DMNH 1349)

UCMP 44754 trunk vertebra; DMNH 44740–44749 caudal vertebra; DMNH 44752 trunk vertebral fragment; DMNH 44753 trunk vertebral fragment.

PIT (UCMP V93173)

Grid 1, level 1: UCMP 399976 trunk vertebra; grid 1, level 2: UCMP 399977–399978 trunk vertebra; grid 1, level 3: UCMP 399980 trunk vertebra; UCMP 399979 caudal vertebra; grid 3, level 4: UCMP 399981 trunk vertebra; UCMP 399982 caudal vertebra; grid 3, level 7: UCMP 399983 trunk vertebra; grid 7, level 8A: UCMP 399984 trunk vertebra; UCMP 399985 caudal vertebra; UCMP 399986 vertebral fragment.

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TWELVE

The Early and Middle Pleistocene Avifauna from Porcupine Cave

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Porcupine Cave is a multiroom limestone cave located in the southern Rocky Mountains of Park County, central Colorado, at an elevation of 2900 m. The cave was sealed for millennia until mining operations created an entrance in the late 1800s. Paleontological excavations, initiated by the Carnegie Museum of Natural History in 1986, were continued by the Denver Museum of Nature and Science. These excavations produced a rich collection of fossil vertebrates ranging in age from the early to the middle Pleistocene. Only fossils of the Carnivora and some of the rodent fauna have been reported previously (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Anderson, 1996; Barnosky et al., 1996; Bell and Barnosky, 2000).

Although mammalian remains dominate the vertebrate fauna, nearly 200 avian fossils were also recovered from the deposits. This avifauna is reported here and represents at least 45 taxa, the richest and most diverse assemblage of this age known from the intermountain western United States. Analysis of this avifauna provides new information on the composition of high-elevation avian communities in the early to middle Pleistocene in this region.

Materials and Methods

All fossil specimens were identified using comparative osteological collections at the U.S. National Museum, Washington, D.C., and the Florida Museum of Natural History (FLMNH), Gainesville. Terminology follows that of Howard (1929), and systematic presentation and taxonomy follow that of the American Ornithologists' Union (1998, 2000). Common names of most species mentioned below are noted in tables 10.1–10.13 and 12.1. Common names of birds not appearing in those tables are noted parenthetically after the first mention of the scientific name in the text. All fossil specimens are housed at the Carnegie Museum of Natural History (CM), the Denver Museum of Natural History (DMNH), and the University of California Museum of Paleontology (UCMP), and are catalogued with CM, DMNH, and UCMP numbers. DMNH numbers also refer to specimens that were catalogued in lots from specific locations in the cave. Thus the same catalogue number may appear repeatedly for multiple specimens from the same or different avian taxa. All specimens were measured with digital calipers, and values were rounded to the nearest 0.1 mm. Unless otherwise cited, all information on distribution and habitat of avian species in this chapter is taken from Bailey and Neidrach (1965) and Andrews and Righter (1992).

The ages of the deposits in Porcupine Cave are approximate because their determination relies almost entirely on biostratigraphic correlations based on arvicoline and sciurid rodents supplemented by magnetostratigraphic data; some of the latter data are equivocal. The best estimates place remains from the DMNH Velvet Room gray zone and below (horizons D–F at DMNH 644) in the middle Pleistocene (late to middle Irvingtonian, near and older than 780 Ka. Horizons A–C in the DMNH Velvet Room are placed at less than 780 Ka. Specimens from Mark's Sink (DMNH 1349, Velvet Room) probably are in part much older, possibly early Pleistocene (early Irvingtonian or latest Blancan, 1.3–1.6 Ma), as indicated by some of the arvicoline rodents. However, this is a mixed deposit with bones of different ages represented. Specimens from the Pit, levels 1–3, may equate with DMNH Velvet Room horizons D–F in age, and are estimated to lie somewhere in age between 600 and 800 Ka. Those from Pit levels 4–12 are at least in part older than 780 Ka, and probably are in the range of 800 Ka to possibly as old as 1.0 Ma. Deposits in the Badger Room (DMNH 942) probably correlate with levels 4–8 in the Pit. The Ferret Room (DMNH 1342) and Fissure Fill A (DMNH 1344) are also considered to be early middle Pleistocene in age, but they may be somewhat older than levels 8–12 in the Pit. (Chapter 20 reports a potential Blancan horse from Fissure Fill A, and chapter 19 recognizes two biostratigraphically old arvicolines in the Ferret Room.) A few specimens from Generator Dome

TABLE 12.1

Avian Taxa Identified from Early and Middle Pleistocene Deposits from Porcupine Cave

Taxon	*Number of Bones*	*MNI*
Early Pleistocene (earlier Irvingtonian and perhaps including Blancan)		
Pied-billed Grebe *(Podilymbus podiceps)*	2	1
Grebe (cf. *Podiceps* sp.)	1	1
Green-winged or Blue-winged Teal *(Anas crecca* or *A. discors)*	1	1
Anatidae, indeterminate	4	—
Hawk (*Buteo* sp.)	4	1
Accipitridae, indeterminate	1	—
Golden Eagle (cf. *Aquila chrysaetos*)	1	1
American Kestrel *(Falco sparverius)*	1	1
Falcon (*Falco* sp.)	1	1
Greater-sage Grouse *(Centrocercus urophasianus)*[a]	14	2
Spruce Grouse *(Falcipennis canadensis)*[a]	1	1
Blue Grouse *(Dendragopus cf. D. obscurus)*[a]	5	2
Phasianidae, indeterminate	2	—
Sora (cf. *Porzana carolina*)	1	1
Far Eastern or Eurasian Curlew *(Numenius madagascariensis or N. arquata)*[a]	1	1
Red-necked Phalarope *(Phalaropus cf. P. lobatus)*[a]	1	1
Scolopacidae, indeterminate	1	1
Gull (*Larus* sp.)	1	1
Great Horned Owl *(Bubo virginianus)*	1	1
Snowy Owl *(Nyctea scandiaca)*[a]	2	1
Long-eared or Short-eared Owl (*Asio* sp.)	1	1
Strigidae, indeterminate	1	1
Hairy Woodpecker *(Picoides villosus)*	1	1
Northern Flicker *(Colaptes auratus)*	7	2
American Crow *(Corvus brachyrhynchos)*	2	1
Common Raven *(Corvus corax)*[a]	2	1
Hirundinidae, indeterminate	1	1
Lark Sparrow *(Chondestes grammacus)*[a]	1	1
Lincoln's Sparrow *(Melospiza cf. M. lincolnii)*	2	2
White-crowned Sparrow *(Zonotrichia leucophrys)*	2	2
Sparrow (*Zonotrichia* sp.)	1	1
Dark-eyed Junco *(Junco hyemalis)*[a]	1	1
Lapland Longspur *(Calcarius lapponicus)*	3	3
Lapland Longspur *(Calcarius cf. C. lapponicus)*	1	1
Chestnut-collared Longspur *(Calcarius ornatus)*	2	2
Emberizidae, indeterminate	3	—
Gray-crowned Rosy-finch *(Leucosticte tephrocotis)*[a]	20	13
Black Rosy-finch *(Leucosticte atrata)*[a]	3	3
Rosy-finch (*Leucosticte* sp.)	1	1
Cassin's Finch *(Carpodacus cassinii)*[a]	1	1
Early middle Pleistocene (~1.0–0.78 Ma)		
Duck (*Anas* sp.)	1	1
Hawk (*Buteo* sp.)	1	1
Accipitridae, indeterminate	1	—
Virginia Rail *(Rallus cf. R. limicola)*	1	1
Black-billed Magpie *(Pica hudsonia)*[a]	1	1
Common Raven *(Corvus corax)*	2	1

TABLE 12.1 (continued)

Taxon	*Number of Bones*	*MNI*
Chipping Sparrow *(Spizella cf. S. passerina)*[a]	1	1
Song Sparrow *(Melospiza melodia)*	1	1
Emberizidae	1	1
Middle Pleistocene (stratigraphically younger than "early middle Pleistocene")		
Goose (cf. *Anser* sp. or *Chen* sp.)	1	1
Duck (*Anas* sp.)	1	1
Anatidae, indeterminate	2	—
Hawk (*Buteo* sp.)	1	1
Golden Eagle (cf. *Aquila chrysaetos*)	1	1
Accipitridae, indeterminate	1	—
Greater-sage Grouse *(Centrocercus urophasianus)*	1	1
White-tailed Ptarmigan *(Lagopus cf. L. leucurus)*	1	1
Black-billed Magpie *(Pica hudsonia)*	1	1
American Crow *(Corvus brachyrhynchos)*	2	1
White-breasted Nuthatch *(Sitta carolinensis)*[a]	1	1
Nuthatch (*Sitta* sp.)	1	1
White-crowned Sparrow *(Zonotrichea leucophrys)*[a]	1	1
Red-winged Blackbird *(Agelaius phoeniceus)*	1	1
Gray-crowned Rosy-finch *(Leucosticte tephrocotis)*	1	1
Late middle Pleistocene (? < 0.78 Ma)		
Duck (*Anas* sp.)	4	1
Redhead *(Aythya cf. A. americana)*	1	1
Anatidae, indeterminate	1	—
Hawk (*Buteo* sp.)	2	1
Accipitridae, indeterminate	1	—
Falcon (*Falco* sp.)	3	1
Greater-sage Grouse *(Centrocercus urophasianus)*	1	1
Pinyon Jay *(Gymnorhinus cyanocephalus)*	1	1
Horned Lark *(Eremophila alpestris)*[a]	4	3
Tree Swallow *(Tachycineta cf. T. bicolor)*[a]	1	1
Dark-eyed Junco *(Junco hyemalis)*	1	1
Brewer's Sparrow *(Spizella breweri)*[a]	1	1
Longspur (*Calcarius* sp.)	1	1
Gray-crowned Rosy-finch *(Leucosticte tephrocotis)*	2	2
Black Rosy-finch *(Leucosticte atrata)*	1	1
Total	154	95

[a] Earliest fossil records known from North America.

(DMNH 1347), Will's Hole (DMNH 1350), and the Crystal Room (DMNH 1345) cannot be dated reliably. However, the Generator Dome deposit is possibly at least as old as or older than the lower Pit levels 8–12 and is so treated here (but see chapter 2 for caveats). Age control for Will's Hole is poor, but in this chapter it is regarded as about the same age as horizons C–F of the DMNH Velvet Room.

Table 12.1 lists all avian taxa identified from these localities sorted into approximate relative-age bins: early Pleistocene (Mark's Sink); early middle Pleistocene (Pit levels 8–12, Badger Room, Fissure Fill A, Ferret Room, DMNH Velvet Room horizons G–I); middle Pleistocene (Pit levels 1–3, DMNH Velvet Room horizons C–F, Will's Hole); and late middle Pleistocene (DMNH Velvet Room horizons A–C). Specimens from mixed layers or provenances of unknown age (e.g., Crystal Room, Last Chance Pit) are not included in this table. Tables 10.1–10.13 list all avian taxa by locality. In the following section, the original excavation information in terms of numeric grid and level designations is provided for the DMNH Velvet Room specimens, with the correlated horizon information, when known, in parentheses. (See chapter 2 for information about how the grid level designations translate into horizon designations; only the horizon designations have stratigraphic meaning.)

Systematic Paleontology

Class Aves

Order Podicipediformes

Family Podicipedidae

PODILYMBUS PODICEPS *(LINNAEUS, 1758)*

REFERRED MATERIAL Left humerus missing proximal end, DMNH 41118; left carpometacarpus, DMNH 41206.

PROVENANCE Location 1349, Mark's Sink.

DESCRIPTION These specimens are identical to the living *P. podiceps* in size and characters. This species is one of the longest-lived of any extant bird with a fossil record, possibly extending to the early Pliocene (5.2–4.5 Ma; Becker, 1987; Emslie, 1998).

CF. PODICEPS *SP.*

REFERRED MATERIAL Distal right humerus, DMNH 41240.

PROVENANCE Location 1349, Mark's Sink, level 27.

DESCRIPTION This specimen is similar in size and most characters to the living *Podiceps auritus* (Horned Grebe) but differs in having a relatively shallower impression of brachialis anticus and deep fossa on the entepicondylar prominence. It may represent an extinct species. However, of the five known fossil species that have been described from North America, all are either larger and more robust than *P. auritus* or are not represented by the humerus (see Murray [1967] and Emslie [1995] for a review of these fossil species). It is unlikely that DMNH 41240 represents any of these species. One extinct genus and species, *Pliolymbus baryosteus* Murray, 1967, is smaller than *P. auritus* and has a deep impression of brachialis anticus (Murray, 1967). Additional material is needed to assess further the taxonomic position of this fossil specimen.

Order Anseriformes

Family Anatidae

CF. ANSER *SP. OR* CHEN *SP.*

REFERRED MATERIAL Partial premaxilla, DMNH 12807 (fig. 12.1A).

PROVENANCE Location 644, Velvet Room, grid 16, level 19 (I).

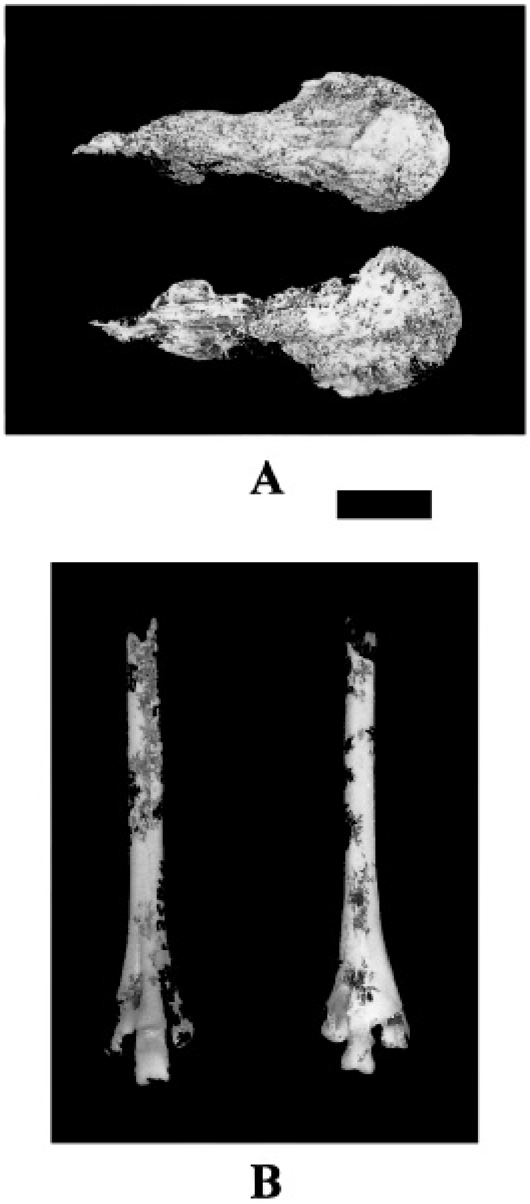

FIGURE 12.1 (A) Premaxilla (DMNH 12807) of an unidentifiable goose, cf. *Anser* or *Chen* sp., in dorsal (top) and ventral (bottom) views. (B) Right tarsometatarus (DMNH 35864) of *Numenius madagascariensis* or *N. arquata* (Far Eastern or Eurasian Curlew) in anterior (left) and posterior (right) views. Scale 1×, bar = 1 cm.

DESCRIPTION The relatively more posterior position of the nares on the premaxilla is one character that distinguishes *Anser* and *Chen* from *Branta,* which has nares placed farther anteriorly and nearer to the tip of the bill. The fossil is relatively larger than *A. albifrons, C. caerulescens,* and *C. rossi* and is too fragmentary for more specific identification. It may represent an undescribed species, but additional material is needed.

ANAS CRECCA *LINNAEUS, 1758,* *OR* A. DISCORS *LINNAEUS, 1766*

REFERRED MATERIAL Left tarsometatarsus, DMNH 30205.

PROVENANCE Location 1349, Mark's Sink (PC-10).

DESCRIPTION This specimen compares well in size to either of these two species, but no osteological characters of this element reliably distinguish either taxon.

ANAS *SP.*

REFERRED MATERIAL Humeral right and left coracoids, DMNH 30198; right coracoid missing sternal end, DMNH 12037; proximal right and left scapulae, DMNH 30198; right carpometacarpus, DMNH 30196.

PROVENANCE 30196: Location 1342, Ferret Room (PC-3); 30198: Location 644, Velvet Room, grid 21, level 2 (B); 12037: Location 644, Velvet Room, grid 7, below level 23 (no age correlation).

DESCRIPTION All specimens except DMNH 12037 are similar in size to *Anas clypeata.* DMNH 12037 is from a small duck and probably represents a species of teal.

AYTHYA *cf.* A. AMERICANA *(EYTON, 1838)*

REFERRED MATERIAL Humeral right coracoid, DMNH 30191.

PROVENANCE Location 644, Velvet Room, grid 26, level 1 (A).

ANATIDAE, INDETERMINATE

REFERRED MATERIAL Partial furculum, DMNH 12351; two right coracoids with ends damaged, DMNH 30205; partial right coracoid, DMNH 10895; sternal half of right coracoid, DMNH 43331; left coracoid missing ends, DMNH 30161; distal right humerus, DMNH 30078; distal right carpometacarpus, CM 75128.

PROVENANCE 10895: Location 644, Velvet Room, grid 7, level 23 (no age correlation); 12351: Location 644, Velvet Room, grid 17, level 3 (B); 30161: Location 644, Velvet Room, mixed; 30078, 30205: Location 1349, Mark's Sink (PC-10); DMNH 43331: Location 1349, Mark's Sink, level 11; CM 75128: Badger Room.

DESCRIPTION These specimens are too fragmentary for specific identification. The furculum (DMNH 12351) is most similar to *Oxyura jamaicensis,* while the other specimens represent either *Anas, Aythya,* or *Bucephala.*

Order Accipitriformes

Family Accipitridae

BUTEO *SP.*

REFERRED MATERIAL Tip of premaxilla, DMNH 30155; right distal tarsometatarsus, DMNH 35391; two pedal phalanges, DMNH 30188 and 35819; four ungual phalanges, DMNH 13799, 35810, 35815, and 35816.

PROVENANCE 30155: Location 644, Velvet Room, grid 4, level 3 (A/B mixed); 30188: Location 644, Velvet Room, grid 21, level 2 (B); 13799: Location 942, Badger Room, mixed level; 35810, 35815, 35816, 35819: Location 1349, Velvet Room, Mark's Sink; 35391: Will's Hole.

DESCRIPTION These specimens represent hawks near the size of *Buteo jamaicensis* or *B. regalis* and are too fragmentary, or lack diagnostic features, for species identification.

CF. AQUILA CHRYSAETOS *(LINNAEUS, 1758)*

REFERRED MATERIAL Distal left femur, DMNH 30165; distal right tarsometatarsus, CM 65325; pedal phalanx, DMNH 30183.

PROVENANCE 30165: Location 644, Velvet Room, grid 11, 60 in. below marker (no age correlation); 30183: Location 644, Velvet Room, grid 20, level 3 (C); 65325: CM 1925, Pit, grid 1, level 1.

DESCRIPTION These specimens compare well to *Aquila chrysaetos* in characters, but DMNH 30165 (distal breadth, 24.6 mm; breadth distal shaft, 13.0 mm) and CM 65325 (distal breadth, 19.6 mm; middle trochlea breadth and depth, 6.2 and 9.1 mm) are slightly smaller in size than those of the living species ($N = 3$ males, USNM) and distinctly larger than those of females of *Buteo jamaicensis* and *B. regalis.* In *Haliaeetus leucocephalus,* the distal femur is relatively narrower and deeper when viewed distally, and the external trochlea of the tarsometatarsus is relatively higher than in *A. chrysaetos* and the fossil specimens.

ACCIPITRIDAE, INDETERMINATE

REFERRED MATERIAL Distal right humerus, DMNH 30202; pedal phalanx with ends gnawed, DMNH 30205; ungual phalanx, DMNH 13798; ungual phalanx missing proximal end, DMNH 16094.

PROVENANCE 16094: Location 644, Velvet Room, grid 4, level 4 (A/B mixed); 13798: Location 644, Velvet Room, grid 16, level 7 (E); 30205: Location 1349, Velvet Room, Mark's Sink; 30202: Location 1347, Generator Dome (PC-8).

DESCRIPTION These specimens are similar in size to an eagle but are too fragmentary for identification.

Family Falconidae

FALCO SPARVERIUS *LINNAEUS, 1758*

REFERRED MATERIAL Distal half of right tibiotarsus, DMNH 35742.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

FALCO *SP.*

REFERRED MATERIAL Left ulna missing ends, DMNH 30189; proximal left femur, DMNH 35721; distal left tarsometatarsus, DMNH 9801; two ungual phalanges, DMNH 9924.

PROVENANCE 9801: Location 644, Velvet Room, grid 3, level 7 (mixed); 9924: Location 644, Velvet Room, grid 5, level 5 (B); 30189: Location 644, Velvet Room grid 25, level 2 (B); 35721: Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION The ulna, femur, and tarsometatarsus are within the size range of *Falco peregrinus* or *F. mexicanus,* but they are too fragmentary for positive identification. The phalanges (DMNH 9924) are from a large falcon, near the size of *F. rusticolus*.

Order GALLIFORMES

Family PHASIANIDAE

CENTROCERCUS UROPHASIANUS *(BONAPARTE, 1827)*

REFERRED MATERIAL Two premaxilla, DMNH 30204 and CM 73359; three distal mandibular symphyses, DMNH 8830, 8924, and 35383; two humeral ends of right coracoid, DMNH 30205 and 35743; humeral end of left coracoid, DMNH 30079; proximal right scapula, DMNH 30205; fragment of furculum, DMNH 30205; distal left humerus, DMNH 35385; two right carpometacarpi missing ends, DMNH 30205; two distal left tibiotarsi, DMNH 9849 and 30205; right and left tarsometatarsi with damaged proximal ends, DMNH 30205; right tarsometatarsus, DMNH 35817; right tarsometatarsus missing ends, DMNH 30205.

PROVENANCE 8830: Location 644, Velvet Room, grid 1, level 7 (mixed); 9849: Location 644, Velvet Room, grid 5, level 8 (C); 8924: Location 644, Velvet Room, grid 7, level 2 (A); 35385: Location 644, Velvet Room (no age correlation); 30204: Location 644, Mark's Sink; 30079, 30205, 35383, 35743, and 35817: Location 1349, Velvet Room, Mark's Sink; CM 73359: CM Velvet Room 1932, undifferentiated grid and level.

MEASUREMENTS See table 12.2.

DESCRIPTION These specimens compare well in size and characters to this species. The premaxilla (DMNH 30204) is slightly shorter than in modern specimens (approximately 14% shorter bill length and 7% smaller depth than the average for $N = 8$ females; table 12.2). The recently recognized *Centrocercus minimus* (Gunnison Sage-Grouse) (Young et al., 2000) has a culmen length 27% smaller than in *C. urophasianus* (Hupp and Braun, 1991), but no specimens of the former were available for comparison. Since *C. minimus* is distinguished by its smaller size, voice, and behavior (Young et al., 1994, 2000), acquisition and measurement of skeletal material from this population is warranted. *C. urophasianus* is resident in mountain parks and other areas where sagebrush is present. The fossils reported here represent the earliest record of this species in North America. It also has been reported from the late Pleistocene of Oregon, Nevada, and New Mexico (Brodkorb, 1964).

FALCIPENNIS CANADENSIS *(LINNAEUS, 1758)*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 6706; manubrium of sternum, DMNH 8830; proximal left humerus, DMNH 6706; distal right humerus, DMNH 8830; proximal right carpometacarpus, DMNH 30077.

PROVENANCE 6706: Location 644, Velvet Room, grid 1, level 4 (mixed); 8830: Location 644, Velvet Room, grid 1, level 7 (mixed); 30077: Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION These specimens are distinguished as *Falcipennis canadensis* from *Dendragapus obscurus* primarily by the relatively smaller size of the former. The manubrium of the sternum also is distinct in these species. DMNH 8830 has a relatively longer and narrower ventral manubrial spine, with a smaller foramen passing through the base of this spine, as found in *F. canadensis,* rather than exhibiting the condition found in *D. obscurus* (manubrium shorter and broader with a larger foramen). These specimens represent the first fossil record of this species in Colorado and the earliest known in North America. *F. canadensis* occurs in coniferous forests in Canada, Alaska, and south to Montana with one record of a bird shot near Palmer Lake, Colorado, in 1896 (Bailey and Niedrach, 1965). The fossils reported here indicate that this species occurred more commonly in the southern Rocky Mountains during the Pleistocene.

LAGOPUS *CF.* L. LEUCURUS *(RICHARDSON, 1831)*

REFERRED MATERIAL Right coracoid, DMNH 30206.

PROVENANCE Location 1350, Will's Hole (PC-11).

DESCRIPTION This specimen is recognized as *Lagopus,* and not *Bonasa,* by the morphology and relative size of the glenoid facet and head, which are more robust in the latter. It most closely resembles *Lagopus leucurus* in size; *L. mutus* and *L. lagopus* are larger and more robust in the shaft of the coracoid. *L. leucurus* is resident in alpine areas of Colorado today.

DENDRAGAPUS *CF.* D. OBSCURUS *(SAY, 1823)*

REFERRED MATERIAL Humeral left coracoid, DMNH 8530; two distal left humeri, DMNH 35759 and 35818; two distal right humeri, DMNH 35740 and 35809; right carpometacarpus, CM 73360; left carpometacarpus missing proximal end, DMNH 8530.

TABLE 12.2
Measurements of Premaxillae of *Centrocercus urophasianus*
Compared to the Fossil Specimen from Porcupine Cave

Specimens	*Length*	*Breadth*	*Depth*	*Breadth of Nasal Bar*
Males (*N* = 8)	12.8 ± 0.49	10.9 ± 0.31	8.23 ± 0.29	3.14 ± 0.29
	(11.9–13.4)	(10.6–11.5)	(7.8–8.6)	(2.9–3.6)
Females (*N* = 8)	11.1 ± 0.71	9.1 ± 0.64	7.1 ± 0.52	2.5 ± 0.32
	(10.0–12.4)	(8.2–9.8)	(5.9–7.6)	(1.8–2.7)
Fossil: DMNH 30204	9.5	9.8	6.6	2.3

NOTE: Measurements are in millimeters. Measurements are mean ± SD with range in parentheses.

PROVENANCE 8530: Location 644, Velvet Room, grid 1, level 10 (mixed); 35740, 35759, 35809, and 35818: Location 1349, Velvet Room, Mark's Sink; CM 73360: CM 1932, undifferentiated.

DESCRIPTION These specimens compare closely in size and characters to this species. CM 73360 measures length, 35.4 mm; proximal breadth and depth, 5.3 and 10.1 mm; least breadth and depth of shaft, 3.8 and 3.2 mm; and distal breadth and depth, 5.5 and 7.3 mm. It is similar in size to two female specimens of *Dendragapus obscurus* at USNM.

PHASIANIDAE, INDETERMINATE

REFERRED MATERIAL Distal mandibular symphysis, DMNH 41138; two right tarsometatarsi missing ends, DMNH 8849 and 41128.

PROVENANCE 8849: Location 644, Velvet Room, grid 1, level 2 (mixed); 41128: Location 1349, Mark's Sink, level 9; 41138: Location 1349, Mark's Sink, level 13.

Order Gruiformes

Family Rallidae

RALLUS *CF.* R. LIMICOLA

REFERRED MATERIAL Proximal right humerus, DMNH 30202.

PROVENANCE Location 1347, Generator Dome (PC-8).

DESCRIPTION This specimen compares well in characters to specimens of *Rallus limicola* from Florida examined at FLMNH but is slightly more robust in size. No specimens of this rail from more northern regions of North America were available for comparison. *R. limicola* is a common resident in Colorado in wet meadows and marshes in mountain parks and other regions.

CF. PORZANA CAROLINA *(LINNAEUS, 1758)*

REFERRED MATERIAL Right tarsometatarsus missing proximal end, DMNH 30205.

PROVENANCE Location 1349, Mark's Sink (PC-10).

DESCRIPTION The specimen also compares closely to *Rallus limicola* in size and features; however, the posterior proximal border of the middle trochlea is more pointed in *Porzana* and DMNH 30205 and more rounded and blunt in *Rallus*.

Order Charadriiformes

Family Scolopacidae

NUMENIUS MADAGASCARIENSIS *(LINNAEUS, 1766)* *OR* N. ARQUATA *(LINNAEUS, 1758)*

REFERRED MATERIAL Distal half of right tarsometatarsus, DMNH 35864 (fig. 12.1B).

PROVENANCE Location 1349, Velvet Room, Mark's Sink, level 19.

MEASUREMENTS See table 12.3.

DESCRIPTION DMNH 35864 is much larger and more robust than tarsometatarsi of male *Numenius americanus, N. borealis, N. minutus, N. tahitiensis,* and *N. phaeopus;* it is most similar in size and characters to *N. madagascariensis* and *N. arquata.* These species are both large curlews whose tarsometatarsi overlap in most measurements (table 12.3), and they cannot be distinguished by osteological characters. *N. madagascariensis* has been reported in North America from the Aleutian and Pribilof islands as a regular spring migrant and in British Columbia (accidental); it is found primarily in Siberia, Mongolia, and southeast Asia. *N. arquata* has occurred as accidental records in Newfoundland, New York, and Massachusetts (American Ornithologists' Union, 1998). The specimen reported here is the first fossil record of a large curlew representing a European or Asian species in North America.

DISCUSSION The identification of *N. madagascariensis* or *N. arquata* from the early Pleistocene of Colorado adds to a growing list of avian taxa with current European and Asiatic distributions that occurred in the late Pliocene or early Pleistocene of continental North America. Other taxa in this category include shelducks (Anatidae, Tribe Tadornini)

TABLE 12.3

Measurements of Tarsometatarsi of *Numenius* Species Compared to the Fossil Specimen from Porcupine Cave

Species	*LBS*	*LDS*	*DB*	*MTB*	*MTD*
Numenius arquata	3.9 ± 0.15	3.0 ± 0.18	10.3 ± 0.6	3.9 ± 0.23	4.7 ± 0.20
(*N* = 13; 6 M, 7 F)	(3.7–4.1)	(2.7–3.3)	(9.2–11.6)	(3.6–4.3)	(4.4–5.1)
Numenius americanus	3.6 ± 0.28	2.5 ± 0.21	9.1 ± 0.54	3.5 ± 0.16	4.2 ± 0.24
(*N* = 7; 6 M, 1 F)	(3.3–4.1)	(2.3–2.7)	(8.4–9.9)	(3.4–3.7)	(3.8–4.4)
Numenius madagascariensis (*N* = 2)					
USNM 500255 (M)	3.8	3.4	11.0	4.1	4.9
USNM 500254 (F)	4.1	3.3	11.1	4.1	4.7
Fossil: DMNH 35864	4.3	3.2	10.8	4.1	4.8

NOTES: Measurements are in millimeters. LBS, least breadth of shaft; LDS, least depth of shaft; DB, distal breadth; MTB, middle tarsus breadth; MTD, middle tarsus depth. Measurements for *N. arquata* and *N. americanus* are mean ± SD with range in parentheses.

represented by the extinct genera *Anabernicula* and *Brantadorna* from Florida and the western United States, pygmy geese (Anatidae, Tribe Anatini) represented by the extinct species *Helonetta brodkorbi* from Florida, and storks (Ciconiidae, *Ciconia*) represented by *C. maltha* from Florida and the western United States (Emslie, 1992, 1998). In addition, fossil birds from the early Pliocene of North Carolina include *Larus* aff. *L. minutus* (Little Gull), *Grus* aff. *G. antigone* (Sarus Crane), *Haematopus* aff. *H. ostralegus* (Common Oystercatcher), *Tringa* magn. *T. ochropus* (Green Sandpiper), and *Ardea* aff. *A. cinerea* (Gray Heron) (Olson and Rasmussen, 2001). Notably, all these taxa are affiliated with wetland environments, and it is possible that wetland species, owing to climatic conditions in the past, were able to extend their distributional ranges more easily during the ice ages than other avian taxa. *N. madagascariensis* currently nests in dry grasslands, near wetlands and sphagnum bogs where it prefers to forage, in Siberia and China and migrates to Australia in winter (Johnsgard, 1981; Ueta and Antonov, 2000). *N. arquata* breeds in similar habitat from northwestern Europe to central Asia (Johnsgard, 1981).

PHALAROPUS *CF.* P. LOBATUS *(LINNAEUS, 1758)*

REFERRED MATERIAL Right carpometacarpus, DMNH 35728.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen measures length, 18.5 mm; proximal breadth and depth, 2.2 and 4.8 mm; distal breadth and depth, 2.3 and 2.7 mm. This specimen was also compared to *Phalaropus tricolor* and *P. fulicaria,* both of which are relatively larger than *P. lobatus*. It is tentatively referred to this last species based on its small size and characters. *P. lobatus* is a common migrant in eastern Colorado and uncommon to rare in mountain parks and valleys, where it prefers wetlands, ponds, and streams.

CF. SCOLOPACIDAE, INDETERMINATE

REFERRED MATERIAL Distal half of right humerus (damaged), DMNH 35740.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is too fragmentary for generic identification, but it appears to represent a shorebird similar to a small *Numenius.*

Family Laridae

LARUS *SP.*

REFERRED MATERIAL Distal half of right tarsometatarsus missing external trochlea, DMNH 35758.

PROVENANCE Location 1349, Velvet Room, Mark's Sink, level 19.

DESCRIPTION This specimen is from a small gull, near the size of *Larus pipixcan,* but is too fragmentary for specific identification.

Order Strigiformes

Family Strigidae

BUBO VIRGINIANUS *(GMELIN, 1788)*

REFERRED MATERIAL Pedal phalange, DMNH 35819.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

NYCTEA SCANDIACA *(LINNAEUS, 1758)*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30153; three pedal phalanges, DMNH 30205 (2) and 30153.

PROVENANCE 30153: Location 644, Velvet Room, grid 2, level 3 (mixed); 30205: Location 1349, Velvet Room, Mark's Sink (PC-10).

DESCRIPTION The mandibular symphyses of *Nyctea scandiaca* and DMNH 30153 are relatively broader and larger than those in *Bubo* or *Strix*. The pedal phalanges are relatively shorter and more robust in *Nyctea* and the fossil specimens than in *Bubo virginianus* and are larger than in *Strix nebulosa*. *N. scandiaca* occurs primarily in Arctic tundra in Canada and Alaska, but it ranges southward sporadically and has been recorded in the northeastern plains and mountain parks of Colorado. The fossils reported here represent the earliest fossil record for the species. It has also been reported from the late Pleistocene of Wyoming (Emslie, 1985).

ASIO OTUS *(LINNAEUS, 1758)*

REFERRED MATERIAL Right femur with proximal end damaged, DMNH 30178.

PROVENANCE Location 644, Velvet Room, bilge level (mixed).

DESCRIPTION The specimen measures length, circa 51.5 mm; distal breadth, 9.1 mm. *Asio flammeus* is similar to *A. otus* but is slightly larger in size (Emslie, 1982). The measurements of DMNH 30178 more closely match those of *A. otus*. *A. otus* occurs in valleys and mountain parks throughout Colorado, including mixed coniferous forests near marshes or wet meadows.

ASIO *SP.*

REFERRED MATERIAL Humeral end of left coracoid, DMNH 43341.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is too fragmentary for specific identification but is similar in size and characters to either *Asio flammeus* or *A. otus*.

STRIGIDAE, INDETERMINATE

REFERRED MATERIAL Distal mandibular symphysis, DMNH 35730.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is most similar in size and characters to *Surnia ulula*, but it differs in position and size of foramina on the external surfaces. It is too fragmentary for more positive identification.

Order Piciformes

Family Picidae

PICOIDES VILLOSUS *(LINNAEUS, 1766)*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30080.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is referred to *Picoides*, and not *Colaptes*, by its relatively longer symphysis (short in *Colaptes*). In addition, *Melanerpes* has a shallower symphysis than *Picoides;* in *Sphyrapicus*, the proximal opening to a middle canal in the symphysis is more open and excavated than in *Picoides*. The fossil is recognized as *P. villosus* by its similarity in symphyseal length and breadth (much broader in *P. tridactylus*, broader and longer in *P. arcticus*, smaller in *P. pubescens*).

COLAPTES AURATUS *(LINNAEUS, 1758)*

REFERRED MATERIAL Distal right humerus, DMNH 30205; left ulna, DMNH 30205; distal left ulna, DMNH 30077; proximal left carpometacarpus, DMNH 30205; distal left carpometacarpus, DMNH 43321; two distal right tarsometatarsi, DMNH 30203 and 41145.

PROVENANCE 30077, 30203, and 30205: Location 1349, Mark's Sink (PC-10); 41145: Location 1349, Mark's Sink, level 16; 43321: Location 1349, Mark's Sink.

Order Passeriformes

Family Corvidae

GYMNORHINUS CYANOCEPHALUS

REFERRED MATERIAL Proximal half of left mandible, DMNH 35392.

PROVENANCE Location 644, Velvet Room, grid 11, level 4 (B).

DESCRIPTION This specimen compares well in size and characters to the living species. It was also compared to *Cyanocitta stelleri, Aphelocoma californica, Nucifraga columbiana,* and *Perisoreus canadensis*. All these genera are distinct, especially in their relative size and the morphology of the postarticular and articular processes of the mandible. DMNH 35392 most closely matches *Gymnorhinus cyanocephalus* in these features.

DISCUSSION This specimen represents the earliest fossil record of this species. It has also been reported from the late Pleistocene of Mexico and New Mexico and from archaeological sites in Utah and Arizona (Brodkorb, 1978; Steadman et al., 1994a). *G. cyanocephalus* is found primarily in pinyon-juniper forests in Colorado today, at an elevational range of 1680–2440 m.

PICA HUDSONIA *(SABINE, 1823)*

REFERRED MATERIAL Left humerus missing proximal end, DMNH 11332; left carpometacarpus, DMNH 30195.

PROVENANCE 11332: Location 644, Velvet Room, grid 9, level 6 (C); 30195: Location 1342, Ferret Room.

DESCRIPTION These specimens compare closely in size and characters to the living species. *Pica hudsonia* occurs in riparian zones and mountain parks throughout Colorado today.

CORVUS BRACHYRHYNCHOS *BREHM, 1822*

REFERRED MATERIAL Left coracoid missing ends, DMNH 30205; distal right tibiotarsus, DMNH 41100; distal right tarsometatarsus, DMNH 43342; distal left tarsometatarsus, CM 75132.

PROVENANCE 30205: Location 1349, Mark's Sink (PC-10); 43342: Location 1349, Mark's Sink, level 25; 41100: Location 644, Velvet Room, grid 7, level 16 (E); CM 75132: Badger Room.

DESCRIPTION The specimen is distinctly smaller than *Corvus corax* and compares well in size and characters to *C. brachyrhynchos*.

CORVUS CORAX *LINNAEUS, 1758*

REFERRED MATERIAL Right humerus missing distal end, UCMP 175013; proximal half of left carpometacarpus, CM 73316; humeral half of right coracoid, DMNH 30197; proximal right femur, DMNH 30205; left tibiotarsus missing proximal end, CM 73315; right tarsometatarsus missing portion of proximal end, DMNH 30198; distal right tarsometatarsus, DMNH 10974.

PROVENANCE CM 73315, 73316: Location CM 2203, Crystal Room (no age correlation); 30197 and 30198: Location 942, Badger Room (PC-1); 30205: Location 1349, Mark's Sink (PC-10); 10974: Location 644, Velvet Room, grid 7, level 22 (no age correlation); 175013: Location 1349, Mark's Sink, grid 1, level 1, 2, or 3.

DESCRIPTION These specimens are slightly smaller and more slender than modern specimens of *Corvus corax* but are distinctly larger than *C. cryptoleucus*. They probably represent a slightly smaller temporal form of the living species. Magish and Harris (1976) described an extinct raven, *C. neomexicanus,* from the late Pleistocene of New Mexico. Later, additional material was tentatively referred to this species from the late Pleistocene of Utah (Emslie and Heaton, 1987). This extinct raven is distinguished from *C. corax* only by its smaller size, and Brodkorb (1978) considered it to be synonymous with *C. corax*. The tarsometatarus (DMNH 30198) has an approximate length of 64.1 mm and depth of the distal middle trochlea of 5.1 mm; DMNH 10974 is 5.5 mm in the latter measurement. These measurements more closely approximate *C. corax* in size, as documented by Magish and Harris (1976:table 1), although the trochlea depth of DMNH 30198 is small. Based on these comparisons, the Porcupine Cave material is not considered to represent the extinct species *C. neomexicanus*.

Family Alaudidae

EREMOPHILA ALPESTRIS *(LINNAEUS, 1758)*

REFERRED MATERIAL Three premaxillae, DMNH 30160, 30171, and 30179; distal mandibular symphysis, DMNH 30082.

PROVENANCE 30160: Location 644, Velvet Room, grid 7, level 5 (B); 30171: Location 644, Velvet Room, grid 15, level 2 (B); 30179: Location 644, Velvet Room, grid 20, level 2 (B); 30082: Location 644, Velvet Room, grid 12, level 5 (B).

Family Hirundinidae

TACHYCINETA *CF.* T. BICOLOR *VIEILLOT, 1808*

REFERRED MATERIAL Premaxilla, DMNH 30097.

PROVENANCE Location 644, Velvet Room, grid 9, level 2 (B).

DESCRIPTION The specimen differs from *Hirundo rustica* and *Riparia riparia,* which have a slightly longer and narrower bill, and from *H. pyrrhonota,* which has a nasal bar that rises more steeply posteriorly from the premaxilla than in *Tachycineta bicolor. T. bicolor* is a common summer resident throughout Colorado today.

HIRUNDINIDAE, INDETERMINATE

REFERRED MATERIAL Right humerus, DMNH 30203.

PROVENANCE Location 1349, Velvet Room, Mark's Sink (PC-10).

Family Sittidae

SITTA CAROLINENSIS *LATHAM, 1790*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30207.

PROVENANCE Location 1350, Will's Hole (PC-11).

DESCRIPTION This specimen compares well in size and characters to *Sitta carolinensis;* the mandibular symphyses of *S. canadensis* and *S. pygmaea* are smaller than that in *S. carolinensis*.

SITTA *SP.*

REFERRED MATERIAL Distal mandibular symphysis missing tip, DMNH 43317.

PROVENANCE Location 644, Velvet Room, grid 21, level 7A (C).

DESCRIPTION This specimen is similar to *Sitta carolinensis* and *S. canadensis* in size and characters but it cannot be reliably distinguished to either species.

Family Troglodytidae

CF. THRYOTHORUS *SP.*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 8528.

PROVENANCE Location 644, Velvet Room, grid 1, level 10 (mixed).

DESCRIPTION This specimen is larger than those in *Salpinctes obsoletus, Troglodytes aedon, T. troglodytes, Thryomanes bewickii, Catherpes mexicanus, Cistothorus platensis,* and *C. palustris,* and distinctly smaller than that in *Campylorhynchus brunneicapillus.* It compares most closely in size and features to *Thryothorus ludovicianus,* but in lateral view the dentary in this species begins curving downward sooner than that in the fossil specimen. This specimen may represent an extinct species of wren, but additional material and further comparisons to living taxa are needed.

Family Emberizidae

SPIZELLA *CF.* S. PASSERINA *(BECHSTEIN, 1798)*

REFERRED MATERIAL Premaxilla, DMNH 30195.

PROVENANCE Location 1342, Ferret Room.

DESCRIPTION This specimen compares well in size and characters to this species; among other species in this genus, the premaxilla is slightly smaller and narrower *(Spizella breweri, S. pusilla,* and *S. pallida)* or larger and broader *(S. arborea).*

SPIZELLA BREWERI *CASSIN, 1856*

REFERRED MATERIAL Mandible missing proximal right end, DMNH 30164.

PROVENANCE Location 644, Velvet Room, grid 8/8A, level 2 (A).

DESCRIPTION This specimen is smaller and broader at the symphysis than those in *Spizella pallida* and *S. passerina,* smaller and narrower at the symphysis than those in *S. arborea, S. atrogularis,* and *S. pusilla,* and compares well in size and characters to *S. breweri,* including in the size and shape of the mandibular foramen. *S. breweri* is common in sagebrush and rabbitbrush habitats, but also occurs in pinyon-juniper forest throughout Colorado today (Rising, 1996).

CHONDESTES GRAMMACUS *(SAY, 1823)*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30081.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION *C. grammacus* is a common summer resident in valleys and foothills throughout Colorado today but is uncommon in mountain parks. It prefers grasslands and shrublands for breeding.

MELOSPIZA MELODIA *(WILSON, 1810)*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 35389.

PROVENANCE Location 1347, Generator Dome (PC-8).

DESCRIPTION *M. melodia* is a common breeding bird in mountain parks near rivers and wetlands, and in riparian zones, throughout Colorado.

MELOSPIZA *CF.* M. LINCOLNII *(AUDUBON, 1834)*

REFERRED MATERIAL Two premaxillae, DMNH 43307 and 43338.

PROVENANCE 43307: Location 1349, Velvet Room, Mark's Sink; 43338: Location 1349, Velvet Room, Mark's Sink, level 24.

DESCRIPTION These specimens compare best in size and features to this species. *Melospiza georgiana* has a longer and narrow beak, while *M. melodia* is longer and more robust. Specimens of *Zonotrichia leucophrys, Z. querula,* and *Z. albicollis* also are much larger and more robust than the fossil material.

ZONOTRICHIA LEUCOPHRYS *(FORSTER, 1772)*

REFERRED MATERIAL Right proximal mandible, DMNH 12765; two distal mandibular symphyses, DMNH 35753 and 41119.

PROVENANCE 12765: Location 644, Velvet Room, grid 8/8A, level 11 (E); 35753 and 41119: Location 1349, Mark's Sink.

DESCRIPTION These specimens compare well in size and characters to those in the living species except for a slightly higher ramus in DMNH 12765. *Zonotrichia leucophrys* occurs at all elevations in Colorado today, frequenting alpine tundra, riparian zones, and mountain parks for breeding, and wintering in the foothills and plains.

ZONOTRICHIA *SP.*

REFERRED MATERIAL Distal mandibular symphyses, DMNH 43343.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is similar to *Zonotrichia leucophrys* but is too fragmentary for specific identification.

JUNCO HYEMALIS *(LINNAEUS, 1758)*

REFERRED MATERIAL Premaxilla, DMNH 30164; distal mandibular symphysis, DMNH 35754.

PROVENANCE 30164: Location 644, Velvet Room, grid 8/8A, level 2 (A); 35754: Location 1349, Velvet Room, Mark's Sink, level 19.

DESCRIPTION The ventral surface of the premaxilla in *Junco* and DMNH 30164 has more distinct concavities and a more distinct midline ridge compared to *Zonotrichia* and *Melospiza. J. hyemalis* occurs throughout Colorado today.

CALCARIUS LAPPONICUS *(LINNAEUS, 1758)*

REFERRED MATERIAL Three premaxillae, DMNH 35722, 41207, and 41220.

PROVENANCE 35722: Location 1349, Mark's Sink, level 16; 41207: Location 1349, Mark's Sink, level 19; 41220: Location 1349, Mark's Sink, level 22.

DESCRIPTION These specimens were also compared to *Calcarius ornatus, C. pictus,* and *C. mccownii.* In *C. lapponicus* and *C. pictus,* the premaxillae are slightly smaller and narrower at the base than in *C. ornatus. C. mccownii* is distinctly larger, with a longer and more robust bill, than *C. ornatus, C. lapponicus,* and *C. pictus.* Compared to *C. pictus, C. lapponicus* has a slightly longer and narrower bill. *C. lapponicus* occurs primarily in the eastern plains of Colorado during winter, but it also has been reported from mountain parks and valleys. It prefers grassland and prairie habitats.

CALCARIUS *CF.* C. LAPPONICUS

REFERRED MATERIAL Premaxilla, DMNH 35729.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION The specimen is too fragmentary for positive identification but most closely matches *Calcarius lapponicus* in size and characters.

CALCARIUS *CF.* C. PICTUS *(SWAINSON, 1832)*

REFERRED MATERIAL Premaxilla, DMNH 43452.

PROVENANCE Last Chance Pit, unit 2, level 7.

DESCRIPTION This specimen is larger and more robust than *Calcarius lapponicus,* narrower at the base than in *C. ornatus,* and smaller than *C. mccownii.* It most closely matches the characteristics of *C. pictus* and is tentatively referred to that species. *C. pictus* previously has not been reported from Colorado. It prefers dry, grassy environments and tundra and breeds in Alaska and Canada. It migrates primarily through the Great Plains to Kansas and Oklahoma in winter (American Ornithologists' Union, 1998).

CALCARIUS ORNATUS *(TOWNSEND, 1837)*

REFERRED MATERIAL Two premaxillae, DMNH 35760 and 43311.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION These specimens compare well in size and features to this species as described previously. *C. ornatus* is a common summer resident in the plains of eastern Colorado and a migrant in western valleys. It prefers short- and mixed-grass prairie habitats that are frequently disturbed by fires or grazing (Hill and Gould, 1997).

CALCARIUS *SP.*

REFERRED MATERIAL Proximal left mandible, DMNH 30160.

PROVENANCE Location 644, Velvet Room, grid 7, level 5 (B).

DESCRIPTION This specimen is most similar to *Calcarius lapponicus* in characters but is slightly smaller than those in three females (FLMNH); no male specimens were available.

EMBERIZIDAE, INDETERMINATE

REFERRED MATERIAL Four distal mandibular symphysis, DMNH 35724, 35736, 41106, and 41119.

PROVENANCE 35724, 35736, and 41119: Location 1349, Velvet Room, Mark's Sink; 41106: Location 1347, Generator Dome, level 1.

DESCRIPTION These specimens are too fragmentary for identification.

Family Icteridae

AGELAIUS PHOENICEUS *(LINNAEUS, 1766)*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 8742.

PROVENANCE Location 644, Velvet Room, grid 7, level 6 (C).

Family Fringillidae

LEUCOSTICTE TEPHROCOTIS *(SWAINSON, 1832)*

REFERRED MATERIAL Ten premaxillae, DMNH 10552, 30081, 30097, 35747, 35749, 35801, 35806, 41119, 43313, and 43450; 14 distal mandibular symphyses, DMNH 30081 (2), 35383, 35397, 35746, 35812, 35813, 41119 (2), 41130, 41210, 43312, 43315, and 43327.

PROVENANCE 30097: Location 644, Velvet Room, grid 9, level 2 (B); 35397: Location 644, Velvet Room, grid 11, level 5 (C); 10552: Location 644, Velvet Room, grid 6, level 1 (A); 30081, 35383, 35746, 35747, 35749, 35801, 35806, 35812, 35813, 41119, 41130, 41210, 43312, 43313, 43315, and 43327: Location 1349, Velvet Room, Mark's Sink; 43450: Location 2433, Last Chance Pit.

DESCRIPTION This species is recognized by the premaxilla, which narrows toward the distal tip and is slightly broader and more robust in *Leucosticte tephrocotis* as opposed to a slightly more convex margin to the tip and narrower shape in *L. atrata,* and by a slightly shorter mandibular symphysis as compared to the latter species; no specimens of *L. australis* were available for comparison. *L. tephrocotis* is a winter resident in the foothills and mountain parks of Colorado, where it prefers meadows and shrublands.

LEUCOSTICTE ATRATA *RIDGWAY, 1874*

REFERRED MATERIAL Four distal mandibular symphyses, DMNH 30080 (2), 30081, and 30097.

PROVENANCE 30080 and 30081: Location 1349, Velvet Room, Mark's Sink; 30097: Location 644, Velvet Room, grid 9, level 2 (B).

DESCRIPTION The symphyses are slightly longer in these fossils and in *Leucosticte atrata* compared to a shorter symphysis in *L. tephrocotis*. *L. atrata* is an irregular to common winter resident in mountain parks and meadows of western Colorado.

LEUCOSTICTE *SP.*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 43316.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is too fragmentary for specific identification.

CARPODACUS CASSINII *BAIRD, 1854*

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30080.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION The symphysis is longer and narrower in this species and the fossil specimen compared to shorter and broader symphyses in *Carpodacus purpureus* and *C. mexicanus. Carpodacus cassinii* is a common resident throughout the mountains of Colorado, where it breeds primarily in coniferous forests.

PASSERIFORMES, INDETERMINATE

REFERRED MATERIAL Two right coracoids, DMNH 30190 and 35811; three right coracoids, DMNH 30203; right coracoid missing sternal end, DMNH 35757; left coracoid, DMNH 35744; humeral half left coracoid, DMNH 30203; three left and one right humeri, DMNH 30203; three right humeri, DMNH 30202; four right humeri, DMNH 30190, 35745, 35804, and 35807; distal right humerus, DMNH 35752; distal right humerus, shaft of left humerus, DMNH 30202; two left humeri, DMNH 35802 and 35814; distal left and proximal right humeri, DMNH 30203; two distal left humeri, DMNH 35740; distal half left humerus, DMNH 35751; two right ulnae, DMNH 30203; two right ulnae, DMNH 35761 and 35800; proximal half right ulna, DMNH 35755; proximal right and proximal left ulnae, DMNH 30203; distal half right ulna, DMNH 30203; proximal left and two distal right ulnae, distal left ulna, DMNH 35762; right carpometacarpus, DMNH 35803; two right and one left carpometacarpi, DMNH 30203; left carpometacarpus, DMNH 35808; left carpometacarpus missing ends, DMNH 30190; left femur, DMNH 30203; left tibiotarsus missing distal end, DMNH 30203; right tarsometatarsus, DMNH 30203.

PROVENANCE These specimens were recovered from various excavated areas of the cave.

Discussion

Prior to the discovery of Porcupine Cave, little information existed about early and middle Pleistocene avifauna from the intermountain West. Rogers et al. (2000) provided useful information with the report of 10 taxa from SAM Cave: *Tachybaptus* cf. T. *dominicus* (Least Grebe), *Phasianus colchicus* (Ring-Necked or Common Pheasant), *Troglodytes* cf. *T. troglodytes* (Winter Wren), Corvini, *Ammodramus* sp. (sparrow), *Junco* sp. (junco), *Passerculus* cf. *P. sandwichensis* (Savannah Sparrow), *Parus* sp. (tit), *Vireo* sp. (vireo), and *Asio* cf. *A. flammeus* (Short-eared Owl). The new records from Porcupine Cave add considerably to the diversity of birds known from the region and provide important information on the composition of avian communities in the Rocky Mountains of Colorado. The taxa identified include species reported as fossils for the first time in North America (e.g., the curlew *Numenius madagascariensis* or *N. arquata*), as well as many earlier fossil records than previously known (table 12.1).

The environment surrounding the cave today consists of a mountain park (Herring Park) with grasses, shrubs, and scattered open stands of ponderosa pine, Douglas-fir, and juniper. The lower valley is drained by Herring Creek, and although no riparian forests occur along this creek, there are some moderately large stands of aspen in the vicinity. Many of the avian taxa identified from the cave currently occur in the area either seasonally or year round and represent a diversity of habitats, including wetlands and ponds, alpine tundra, and subalpine forest. Although all these habitats currently occur within a 100-km radius of Porcupine Cave, the avifauna in general suggests that, during the time the fossils accumulated, the environment surrounding the cave was characterized by cooler temperatures and moister conditions than today. Probably within the vicinity of the cave there were more extensive wet meadows or marshes. Many of the avian species recovered from the deposits (e.g., shorebirds, ducks, rails) may have been brought to the cave by avian predators (e.g., eagles, hawks, falcons, owls) that have also been identified from this site. Although the sample size is small, the larger number of grouse bones from the deposits (table 12.1) is similar to findings by Steadman et al. (1994b) at Rattlesnake Cave, Idaho. Those authors considered roosting raptors as the primary agent for bone deposition in Rattlesnake Cave, where the nonpasserine avifauna was dominated by *Centrocercus urophasianus* (Greater Sage-Grouse). A similar interpretation may be applied here.

The avifauna from the early Pleistocene deposits (e.g., Mark's Sink) in particular indicate that wetlands, ponds, marshes, or a combination thereof were located near the cave in association with dry grassland, sagebrush shrubland, and subalpine forest (table 12.1). The presence of sora, phalarope, and gull, taxa not found in the other dated levels, suggests that aquatic and wetland environments may have been more extensive during the early Pleistocene than now. In addition, the abundance of sage grouse bones in these deposits further indicates that large areas of sagebrush shrubland occurred near the cave. Sage grouse are restricted primarily to sagebrush habitats today (Johnsgard, 1973). Species indicative of dry grasslands and tundra include the curlew, longspurs, and rosy-finch, whereas the presence of spruce grouse, blue grouse, and woodpeckers implies that subalpine coniferous forest was located near the site. These interpretations are complicated by the possibility that raptors identified from the cave, including falcon (*Falco* sp.) and owls, may have brought prey items to the cave from a few kilometers away.

Fewer avian fossils are identified from the early middle (~1.0–0.78 Ma) and middle (~780 Ka and somewhat younger) Pleistocene deposits compared to the early Pleistocene ones (table 12.1). However, taxa from the middle Pleistocene are similar to those of the early Pleistocene except that they lack some of the aquatic and wetland species. Only one bone of an unidentifiable goose and three of ducks were recovered from these layers, although the Red-winged Blackbird from the same deposits may also be associated with ponds and wetland environments. Most of the other taxa recovered from the middle Pleistocene are indicative of subalpine forest and shrubland. These differences may be due to excavation sample sizes and could change as new material is recovered from the cave and processed.

Additional fossils from middle to late middle Pleistocene deposits (table 12.1) represent environmental conditions similar to those of the middle Pleistocene with two exceptions. Pinyon Jay and Brewer's Sparrow are more restricted today to lower-elevation shrublands and pinyon-juniper forests, where they currently breed in Colorado. These two species suggest that climatic conditions were warmer than today during the deposition of sediments in the upper levels of the Velvet Room, though rosy-finch also occur in these levels. It is possible that these sediments accumulated during a relatively warm interglacial interval when more extensive sagebrush shrubland and pinyon-juniper forests may have existed near the cave. Supportive evidence for this interpretation comes from the mammalian record, which includes *Lemmiscus curtatus* (sagebrush vole), *Cynomys* sp. (prairie dog), and *Mustela nigripes* (black-footed ferret) from the upper levels of the cave deposits (Wood and Barnosky, 1994; Anderson, 1996). Anderson (1996:279), following Barnosky and Rasmussen (1988), suggested that sediments from one room in the cave, the Pit, show that "alternation of fine-grained, light-coloured loess in the upper layers with dark brown, organic-rich clay pellets in the lower layers indicated dry interglacial and wetter glacial intervals, respectively." Uppermost sediments from the Velvet Room have characteristics similar to those of the upper interglacial intervals of the Pit. Lower Velvet Room layers do not have the brown clay pellets, though they are different in character than the upper Velvet Room layers. It is quite probable that long-term climatic cycles were responsible for the diversity of species and environments represented by the fossil vertebrate fauna (Wood and Barnosky, 1994).

Several taxa from the cave represent range extensions from their modern distributions. The presence of a large curlew in the early Pleistocene of Colorado is notable; it is the only Eurasian species in the avifauna. The expansion of wetland habitats during glacial intervals probably facilitated the expansion of this and other aquatic and wetland species during the Pliocene and Pleistocene. Cooler conditions during glacial intervals may also have favored the expansion of alpine tundra and subalpine forests in this part of the Rocky Mountains, allowing for Snowy Owls and Spruce Grouse to reside in Colorado and Wyoming during the Pleistocene. Additional fossils recovered from the extensive deposits at Porcupine Cave will undoubtedly refine these interpretations and continue to add to our knowledge of early and middle Pleistocene avifaunas in Colorado.

Acknowledgments

Assistance with museum collections was provided by E. Anderson and K. Goulette (DMNH), D. W. Steadman and T. Webber (FLMNH), and S. Olson (USNM). I thank D. W. Steadman, T. Stidham, and A. D. Barnosky for their helpful comments on the manuscript.

THIRTEEN

The Carnivora from Porcupine Cave

ELAINE ANDERSON (deceased)
Denver Museum of Nature and Science

Anderson (1996) reported 22 species and 144 specimens of carnivores from nine areas in Porcupine Cave. Since then, *Ursus americanus* has been added to the faunal list, 774 specimens of carnivores have been identified, and three new areas (Mark's Sink, Will's Hole, and Generator Dome) have been excavated. These new sites are rich in carnivores, with 376 specimens identified so far. Remains of *Taxidea taxus, Canis latrans,* and *Spilogale putorius* are the most numerous and account for 570 specimens. Noteworthy finds are diagnostic teeth of *Martes* species A*, the oldest known true marten.

Fossils were discovered in Porcupine Cave in 1981 by Donald L. and Dalton (Larry) Rasmussen. Since 1986 field parties from the Carnegie Museum of Natural History (1986–88), the Denver Museum of Natural History (1989–98), and the Western Interior Paleontological Society (1993–98) have conducted excavations every summer, assisted by crews from the University of Kansas (1994) and the University of California, Berkeley (1993–94). Early excavations took place in the Pit, the Badger Room, and the Velvet Room, with sampling performed in other areas. In 1994 excavations began in Mark's Sink (named after Mark Stevens, a teenage volunteer), in Will's Hole (named after William Raynolds, Robert G. Raynolds's son), and in Generator Dome (named for the sound of the generator that could be heard in the room). As of 1998 work was continuing in these areas as well as in the Velvet Room and the Camel locality (named for a large camel bones that were found there). Deposits in the Pit and Velvet Room are stratified. The meaning of stratification in Generator Dome is equivocal. For the age of the localities mentioned in this chapter, refer to chapter 2 and to the discussion of locality ages in chapter 12.

The only other Irvingtonian site in Colorado is Hansen Bluff in the San Luis Valley in Alamosa County (Rogers et al., 1985, 1992). The only specimen of a carnivore in that fauna is the phalanx of a canid; the site also contains arvicolines and salamanders. The Hansen Bluff fauna ranges in age between 690 and 900 Ka. In nearby New Mexico, Irvingtonian carnivores are known from SAM Cave and include *Canis* cf. *C. latrans, C. rufus, Lutra canadensis, Mephitis mephitis, Mustela erminea, Spilogale putorius, Taxidea taxus,* and *Vulpes vulpes* (Rogers et al., 2000).

Systematic Paleontology

Class Mammalia

Order Carnivora

Family Mustelidae

MARTES DILUVIANA *COPE, 1889*

REFERRED MATERIAL Velvet Room: DMNH 10967 R m1 talonid (G11, L10, F). Mark's Sink: DMNH 38867 R m1 talonid (L29, 7/97), 40264 R glenoid fossa (L19, 7/97), 40265 L p4 (L19, 7/97), 40379 L p3 (8/96), 40380 L P2 (8/96), 40381 L M1 (L26, 7/97). Will's Hole: DMNH 39565 L c. Badger Room: DMNH 22768 fragmentary R jaw with alveoli p1-4; 22769 fragmentary R jaw with alveoli p1-4; 33461 proximal L ulna. CM 49108 L jaw with p4-m1. Generator Dome: DMNH 27037 fragmentary L maxilla with alveoli P4 (L1).

DESCRIPTION AND COMMENTS The extinct fisher *Martes diluviana* is represented by 13 specimens from Porcupine Cave. This is the only Irvingtonian occurrence of the species in the western United States. *Martes diluviana* has been reported from Port Kennedy Cave, Pennsylvania (type locality);

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* *Editor's Note:* The author intended to formally name this taxon as a new species of *Mustela* in a different publication, but she died before she was able to do so. She also intended to name a new species of *Martes,* fossils of which are reported in this chapter. For these two taxa the designation "species A" is used here to indicate that the material probably represents hitherto unnamed species; formal naming must await additional work.

Cumberland Cave, Maryland; Conard Fissure, Arkansas; and Hamilton Cave, West Virginia. Sexual dimorphism is evident in the measurements of p3, p4, the talonid of m1, and the depth of the mandible. *Martes diluviana* was probably ancestral to the extant *M. pennanti,* the fisher, which makes its first appearance in the late Rancholabrean and has been reported from 20 faunas.

MARTES *SPECIES A*

REFERRED MATERIAL Velvet Room: DMNH 33949 fragmentary R jaw with alveoli p1-4 (G 0, 5, 6, 7, L30); 34570 R M1 (G 0, 5, 6, 7, L 30). Mark's Sink: 34569 fragmentary R maxilla with P4 (8/96); 36681 L jaw with alveoli c-m1 (L19, 7/97); 39563 fragmentary L M1 (124, 7/97); 40243 R c (8/96); 40244 R C (8/96); 40266 R c (L22, 7/97). Ferret Room: DMNH 22771 skull fragments. Generator Dome: DMNH L c (L1). Gypsum Room: CM 48439 L m1.

DESCRIPTION AND COMMENTS Two diagnostic teeth, P4 and M1, of a true marten (subgenus *Martes*) were identified in 1996 from Mark's Sink and the Velvet Room, respectively (Anderson, 1997). Since then, several additional specimens including an m1 have been found. This material represents the oldest Pleistocene marten in North America. In size and morphology (figure 13.1), the specimens are similar to those of *M. americana,* the extant American marten. The P4 (DMNH 34569) lacks an external median rootlet, which is characteristic of the subgenus *Pekania* (fishers); the M1s (DMNH 34570 and 39563) show the characteristic expansion of the inner lobe; and the m1 has a small, distinct metaconid and a basined talonid. A preserved parietal (DMNH 22771) shows the broad tabletlike band bordered by two faint lines, the temporal ridges, which distinguish a young adult marten (in adults the ridges unite to form the sagittal crest).

In his genetic study of *M. zibellina,* the sable, and *M. americana,* Hicks (1996) showed that the two species are not closely related, as had formerly been thought (Anderson, 1994), and that the American marten has had a long, independent history in North America. The discovery of a true marten at Porcupine Cave confirms his conclusions.

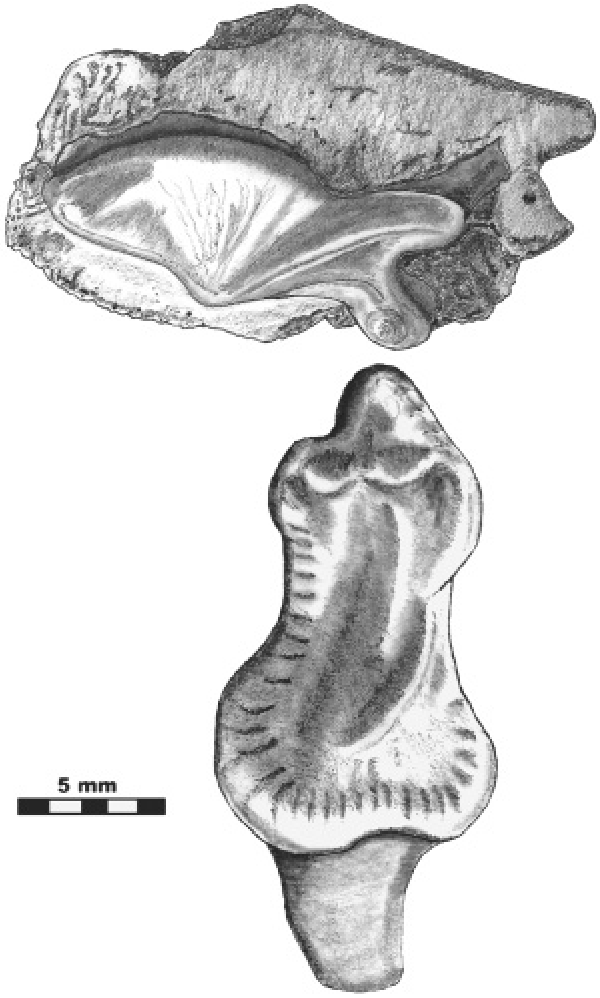

FIGURE 13.1 *Martes* species A, DMNH 34569, fragment of right maxilla with P4 from Mark's Sink (top), and DMNH 34570, right M1 from the Velvet Room (bottom).

MUSTELA FRENATA *LICHTENSTEIN, 1831*

REFERRED MATERIAL See appendix 13.1.

DESCRIPTION AND COMMENTS Fossils of long-tailed weasels are common in Porcupine Cave, especially in the Velvet Room (33 specimens) and Mark's Sink (39 specimens). Other Irvingtonian records of *M. frenata* include Conard Fissure, Arkansas, and Leisey Shell Pit, Florida, and the species has been recognized in 45 late Rancholabrean faunas ranging from California to Florida and south to Nuevo Léon, Mexico. Today the long-tailed weasel has the broadest geographic range of any American weasel, and its wide ecological tolerances enable it to inhabit plains, brushy areas, open woodlands, coniferous forests, and alpine regions. Specimens from Porcupine Cave are indistinguishable in size and morphology from other Pleistocene and Recent samples.

MUSTELA ERMINEA *LINNAEUS, 1858*

REFERRED MATERIAL See appendix 13.1.

DESCRIPTION AND COMMENTS *Mustela erminea* is the smallest extant mustelid in Colorado. Although there can be some overlap in measurements between female *M. frenata* and male *M erminea,* this was not a problem in the Porcupine Cave specimens. In the Velvet Room, remains of *M. erminea* (27 specimens) and *M. frenata* (33 specimens) are both common and are found together in several grids and levels (G1, L8; G8/8A, L2; G8/8A, L3; G12, L5; G16, L3). In contrast, in Mark's Sink, remains of *M. frenata* outnumber those of *M. erminea* 39 to 11. Whether this situation is an artifact of collecting or deposition, or reflects ecological conditions less favorable to ermine, is unknown.

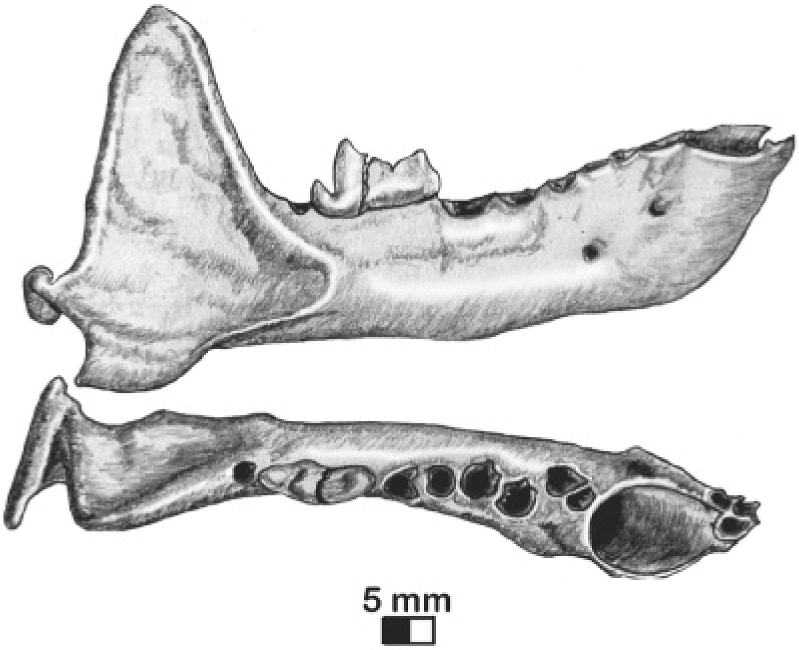

FIGURE 13.2 *Mustela nigripes,* DMNH 11017, right mandible with m1 from the Velvet Room (G3, L6).

Mustela erminea has been recognized at Cudahy, Kansas, and Conard Fissure, Arkansas, both Irvingtonian in age, and from 20 late Rancholabrean faunas. In Colorado the species currently ranges from the foothills to the tundra in timbered areas.

MUSTELA NIGRIPES *(AUDUBON AND BACHMAN, 1851)*

REFERRED MATERIAL See appendix 13.1.

DESCRIPTION AND COMMENTS Anderson (1996) reported the first Irvingtonian record of *Mustela nigripes,* four specimens from the Velvet Room (figure 13.2) and the Pit in Porcupine Cave. Since then, an additional 12 specimens have been identified, including postcranial elements. Compared with *M. vison,* the American mink, *M. nigripes* is characterized by auditory bullae that are more inflated, a smaller infraorbital foramen, a thicker mandible, relatively larger canines, an m1 that lacks a metaconid, and a smaller m2. Ferret postcranial elements are heavier and more rugose than those of mink. The specimens from the cave are nearly identical in size and morphology to recent samples.

Mustela nigripes and their preferred prey, *Cynomys* spp. (prairie dogs), have been found in the Badger Room, Velvet Room, Mark's Sink, Will's Hole, and the Pit. So far, ferrets have not been found in Generator Dome. The only other Irvingtonian site with *M. nigripes* is Cathedral Cave, Nevada (J. I. Mead, pers. comm., 1998).

MUSTELA VISON *SCHREBER, 1777*

REFERRED MATERIAL See appendix 13.1.

DESCRIPTION AND COMMENTS In 1994 *Mustela vison* was identified in Porcupine Cave, and the species is now represented by 16 specimens recovered from the Velvet Room, Mark's Sink, Will's Hole, and the Ferret Room (figure 13.3). Compared with those of *Mustela nigripes,* crania of *M. vison* have a larger inner lobe on M1, a larger infraorbital foramen, a wider occipital region, less inflated auditory bullae, an incipient metaconid and a wider talonid on m1, and a much larger m2. The postcranial skeleton of *M. vison* is less rugose than that of *M. nigripes.*

As Kurtén and Anderson (1980) noted, the fossil history of *M. vison* extends back to the Irvingtonian (Cumberland Cave, Conard Fissure, Cudahy, and now Porcupine Cave). The species has been recognized in 30 late Rancholabrean faunas. In Colorado *M. vison* currently has a wide distribution from the plains to above 3000 m, but the species is nowhere abundant (Armstrong, 1972). Semiaquatic in habits, mink den along stream banks and feed on riparian animals. The presence of *M. vison* in a fauna indicates the nearby presence of permanent water, and thus the species is an important environmental indicator.

MUSTELA *SPECIES A*

REFERRED MATERIAL Velvet Room: DMNH 18152 L maxilla with P4, associated R maxilla (G8/8A, L mixed). Mark's Sink: DMNH 41403 R jaw with p4-m1 (L27, 7/97); 41405 L jaw with p4-m1 (8/96); 41406 R jaw with m1 (8/96); 41407 R jaw with p3, m1 (L20, 7/97); 41408 L jaw with p4-m1 (L20, 7/97). Will's Hole: DMNH 41404 R P4; 41409 L maxilla with P4-M1. Badger Room: DMNH 10951 R m1. Generator Dome: DMNH 27038 L jaw with p3-m2 (L1). Pit: CM 48427 fragmentary R maxilla with P3-M1 (surface); 48446 fragmentary L jaw with p4-m2 (G1, L2); 49134 fragmentary L jaw with p4-m2 (G1, L3); 49170 partial skull with R P3-4, L P2-3, M1 (G mixed, L1,2,3);

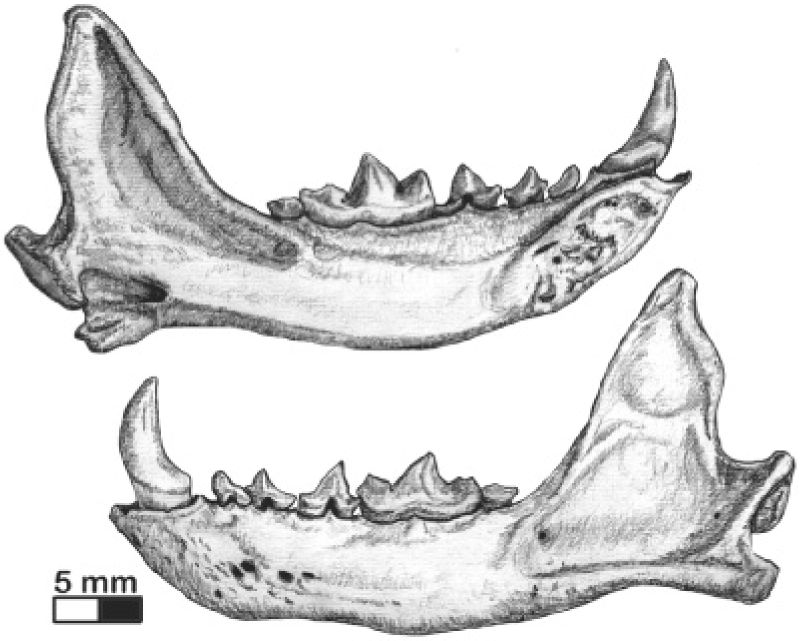

FIGURE 13.3 *Mustela vison,* DMNH 27767, left mandible with c-m2 from Will's Hole.

49171 partial skull with R I2-3, M1, L P4-M1 (G mixed, L1,2,3); UCMP 140550 R jaw with p4-m2 (G1, L2). Ferret Room: CM 49172 partial skull with R and L P3-M1.

DESCRIPTION AND COMMENTS Additional material of this new extinct mustelid has been recovered from Mark's Sink, Will's Hole, and Generator Dome. All of the specimens are the size of minks or ferrets but differ from both of those animals in a number of characters, including a shorter tooth row, the size and shape of the infraorbital foramen, and the configuration of P3, P4, M1, and m1.

GULO *CF.* G. SCHLOSSERI *KORMOS, 1914*

REFERRED *MATERIAL* Will's Hole: DMNH 28334 distal L tibia. Undifferentiated: CM 49107 fragmentary R jaw with p4 and alveoli of p1-3.

DESCRIPTION AND COMMENTS *Gulo,* the wolverine, is one of the rarest carnivores in Porcupine Cave, and this is the only Irvingtonian record of the species from the western United States. Bryant (1987) suggested that *G. schlosseri* is conspecific with *G. gulo,* but until direct comparisons are made with the European material, I am retaining the extinct name of the species. The distal tibia has a prominent medial malleolus that is characteristic of *Gulo.* The distal breadth, 23.9 mm, is close to that of an early Holocene sample from Idaho. (O.R. 17.3–23.7, $N=30$; Anderson, 1998). The jaw fragment shows the distinctive p4 and the alveoli of p1-3. Irvingtonian wolverines are known from Port Kennedy and Cumberland Caves. These three records are slightly older than the European ones, an observation that may indicate that *Gulo* arose in North America.

LUTRA (LONTRA) CANADENSIS *(SCHREBER, 1777)*

REFERRED MATERIAL Pit: CM 49168 L p3 (G3, L4).

DESCRIPTION AND COMMENTS Only a single tooth, a left p3, from the Pit is referable to *Lutra (Lontra) canadensis.* Other Irvingtonian records of the species include Cumberland Cave, Maryland; Port Kennedy Cave, Pennsylvania; Courtland Canal, Kansas; Leisey Shell Pit, Florida; and Vallecito, California; it has been found in 20 Rancholabrean faunas. Aquatic in habits and feeding on freshwater invertebrates, amphibians, and fish, the river otter is a good indicator of nearby permanent water.

INDETERMINATE OTTER

REFERRED MATERIAL Badger Room: DMNH 18151 R P3.

DESCRIPTION AND COMMENTS No additional specimens have been found of this large, unknown lutrine.

TAXIDEA TAXUS *(SCHREBER, 1777)*

REFERRED MATERIAL See appendix 13.1.

DESCRIPTION AND COMMENTS To date, remains of badgers outnumber those of all other carnivores in Porcupine Cave, with at least 213 specimens identified. Badger bones are most common in the appropriately named Badger Room (122 specimens) and in Generator Dome (37 specimens from the test trench). Both of these areas are close to an ancient cave entrance and were probably used by badgers for shelter and denning. Remains of *Taxidea taxus* are uncommon in the Velvet Room, Mark's Sink, and the Pit. Ten limb bones missing epiphyses are from juveniles; no deciduous teeth have

TABLE 13.1
Taxidea taxus: Measurements of P4, M1, and m1 from the Badger Room and a Recent Sample

	Badger Room	*Recent*
Length P4	12.08 (10.4–14.3) (*N* = 15)	11.73 (10.3–13.5) (*N* = 19)
Width M1	10.63 (9.8–11.9) (*N* = 12)	10.28 (9.3–11.6) (*N* = 19)
Length m1	13.63 (12.8–14.5) (*N* = 19)	13.55 (12.3–14.6) (*N* = 19)

NOTES: Measurements are in millimeters. Measurements are mean with observed range in parentheses.

TABLE 13.2
Spilogale putorius: Measurements of P4, M1, and m1 from Porcupine Cave and a Recent Sample

	Velvet Room	*Mark's Sink*	*Badger Room*	*Recent*
Length P4	6.25 (5.9–6.6) (*N* = 2)	5.98 (5.3–6.5) (*N* = 15)	5.64 (5.3–6.2) (*N* = 4)	6.04 (5.1–7.1) (*N* = 23)
Width M1	6.76 (5.7–6.6) (*N* = 2)	7.13 (5.1–7.2) (*N* = 12)	7.18 (5.8–6.3) (*N* = 7)	7.21 (4.8–7.3) (*N* = 22)
Length m1	6.76 (6.1–7.3) (*N* = 5)	7.13 (6.2–8.6) (*N* = 24)	7.18 (6.1–7.5) (*N* = 7)	7.21 (6.2–8.6) (*N* = 23)

NOTES: Measurements are in millimeters. Measurements are mean with observed range in parentheses.

been found. Measurements of the teeth, mandibles, and limb bones fall within ranges for Rancholabrean and Recent samples (table 13.1). The huge badgers from the late Pleistocene near Fairbanks, Alaska (Anderson, 1977), remain the largest known representatives of *Taxidea taxus.* Badgers, as well as their extensive diggings, are frequently encountered around the cave and camp today.

SPILOGALE PUTORIUS *(LINNAEUS, 1758)*

REFERRED MATERIAL See appendix 13.1.

DESCRIPTION AND COMMENTS *Spilogale putorius* is the most common mephitine and the third most abundant carnivore found in Porcupine Cave. Of the 172 specimens identified, 85 of them come from Mark's Sink. Other Irvingtonian occurrences include Inglis 1A, Coleman 2A, and Leisey Shell Pit, Florida; Conard Fissure, Arkansas; Trout Cave, West Virginia; Cumberland Cave, Maryland; and Curtis Ranch, Arizona, and the species has been found in more than 50 Rancholabrean faunas. Measurements of the Porcupine Cave specimens fall within those of other Pleistocene and Recent samples (table 13.2). Inhabitants of brushy, rocky, and wooded areas, *Spilogale putorius* is primarily insectivorous. The species is not found in South Park today.

Based on geographic and reproductive isolation, some workers (Kinlaw, 1995) recognize two species of *Spilogale* (spotted skunks) in the United States. *Spilogale putorius,* found from the Great Plains eastward, has a chromosome number of 64 and no delayed implantation. *Spilogale gracilis,* found in the western half of the country, has a chromosome number of 60 and a long (210–230 days) delayed implantation. Osteologically, the two species appear to be identical, and since it is unknown when they attained reproductive isolation, I am referring the specimens from Porcupine Cave to *S. putorius* on biogeographic grounds.

BRACHYPROTOMA OBTUSATA *(COPE, 1889)*

REFERRED MATERIAL Velvet Room: DMNH 10969 associated skull fragments with L P4 and R M1 (G16, L19, I); 11013 R jaw with m1 (G8/8A, L mixed); 11014 anterior half skull with L I3, C, P3-M1, R I3, P3-M1 (G11-12, L mixed); 40229 palate with L I1-3 (G21, L20). Mark's Sink: DMNH 36669 L M1 (7/94); 36672 L jaw with p4-m1 (8/96). Will's Hole: DMNH 27847 anterior half skull with RP3-M1. Badger Room: DMNH 27050 fragmentary L jaw with p4. Generator Dome: DMNH 21470 R maxilla with P3, M1 (L1); 21471 fragmentary R jaw with m1 (L1). Pit: CM 48429 anterior half skull with RP3-4 (G1, L3); 49112 anterior half skull with LI3, P4-M1, RP4 (G1, L1-3).

DESCRIPTION AND COMMENTS In addition to the five specimens reported previously from the Velvet Room and the Pit (Anderson, 1996), remains of the short-faced skunk have now been recovered from Mark's Sink, Will's Hole, Badger Room, and Generator Dome. *Brachyprotoma* (figure 13.4) differs from other skunks in having only two upper premolars (other genera have three). The short face and jaws; crowded, overlapping premolars; and curved toothrows are characteristic features. The canines show deep striations (figure 13.4; Youngman, 1986). *Brachyprotoma* was the size of a small *Spilogale,* and its trenchant dentition indicates a probable diet of hard-shelled insects. The stratigraphic range of *B. obtusata,* the only recognized species, extends from the Irvingtonian (Port Kennedy Cave, Pennsylvania; Cumberland Cave, Maryland;

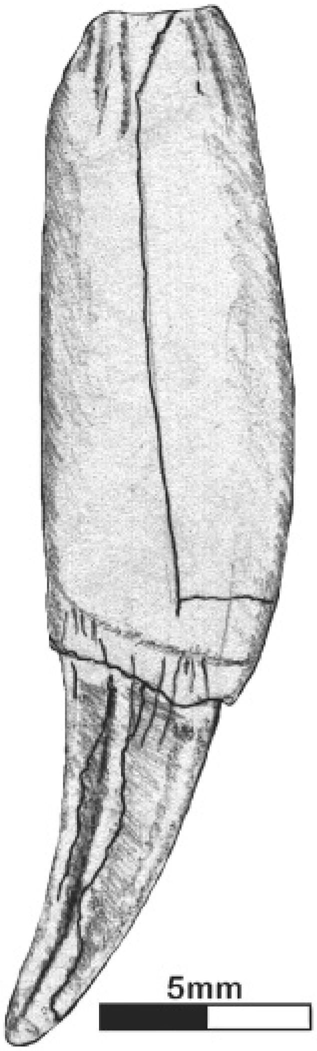

FIGURE 13.4 *Brachyprotoma obtusata,* DMNH 33778, left upper canine (showing the characteristic grooves) from Mark's Sink.

Hamilton Cave, West Virginia; and Conard Fissure, Arkansas) to the end of the Rancholabrean. It was one of the few small mammals to become extinct at that time, although the cause of its extinction is unknown.

MEPHITIS MEPHITIS *(SCHREBER, 1776)*

REFERRED MATERIAL Will's Hole: DMNH 27209 L m1. Badger Room: UCMP 140541 R m1 trigonid. Generator Dome: DMNH 40383 L P4 (L 1). Fissure Fill A: CM 49141 fragmentary R jaw with p4-m1.

DESCRIPTION AND COMMENTS In addition to the two specimens previously reported (Anderson, 1996), a left m1 (DMNH 27209) was found in Will's Hole and a left P4 (DMNH 40383) was recovered in Generator Dome. Both teeth show slight wear, and their morphology and measurements are similar to late Rancholabrean and Recent specimens. Other Irvingtonian occurrences of *Mephitis mephitis* include Inglis 1A and Coleman 2A, Florida; Conard Fissure, Arkansas; and Angus, Nebraska. In Colorado today, *M. mephitis* has the widest distribution and the broadest ecological tolerances, and in many areas it is the most common mephitine. Yet in the Irvingtonian at Porcupine Cave it was the rarest of the three skunks.

Family Canidae

CANIS LATRANS *SAY, 1823*

REFERRED MATERIAL See appendix 13.1.

DESCRIPTION AND COMMENTS The coyote *Canis latrans* is the most common canid and the second most abundant carnivore in Porcupine Cave. At least 180 specimens have been identified from eight areas in the cave, with most of the remains coming from the Badger Room, Mark's Sink, Generator Dome, and Fissure Fill A. All age classes are represented. Two fragmentary maxillae with deciduous dentitions (DMNH 36589 and 36590), representing different age classes as shown by the tooth eruption stages, were found in the Badger Room and indicate that the area was used as a den. A partial skull (DMNH 30076) belonged to an old animal, as shown by the heavily worn teeth. The canine puncture marks on its premaxilla, frontal, and palate are discussed in chapter 9. Adults are also represented; for example, in Generator Dome, an associated left p4, m1, and m2 (DMNH 27203), showing slight tooth wear, were found. Postcranial elements are numerous and include those of juvenile, young adult, and adult animals. A baculum of *C. latrans* (DMNH 20134) identical to that of extant coyotes was found in the Badger Room.

Coyotes are first recognized in the Irvingtonian and have been identified at Cumberland Cave, Maryland; Angus, Hay Springs, and Mullen, Nebraska; and Irvington, California. They are common in Rancholabrean faunas, especially in trap sites. Coyotes are frequently seen and heard in the vicinity of the cave today.

CANIS EDWARDII *GAZIN, 1942*

REFERRED MATERIAL See appendix 13.1.

DESCRIPTION AND COMMENTS *Canis edwardii,* a canid that was larger than a coyote but smaller than a gray wolf, is now represented by 34 specimens from Porcupine Cave. The most complete and diagnostic specimen is DMNH 18353, a left mandible with p1, p3-m2 that was found in the Badger Room in 1994 (figure 13.5).

Canis edwardii has been identified at Curtis Ranch, Arizona (the type locality; Gazin, 1942); Anita, Arizona; Vallecito, California; Minaca Mesa, Chihuahua, Mexico; USGS Vert. Loc. M1367, Owyhee County, Idaho (Repenning, pers. comm., 1994); Arkalon, Kansas; Gilliland, Oklahoma; Port Kennedy Cave, Pennsylvania; and Leisey Shell Pit, Haile 21A, and Rigby Shell Pit, Florida. All of these sites are late Blancan/Irvingtonian

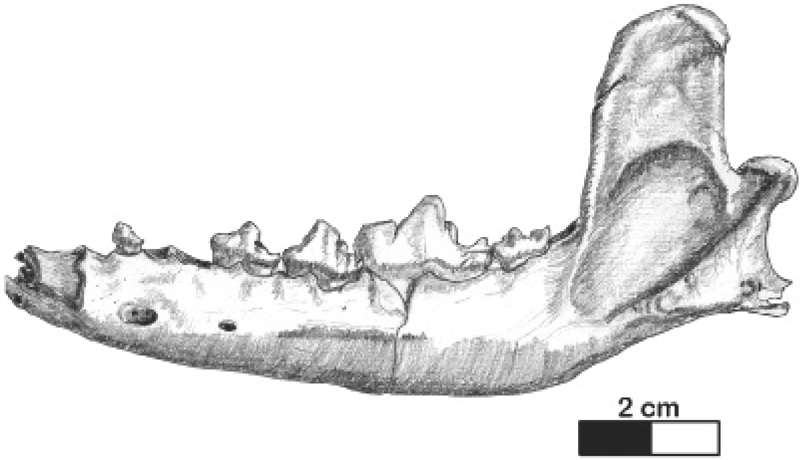

FIGURE 13.5 *Canis edwardii,* DMNH 18353. Left mandible with p1, p3-m2 from the Badger Room.

in age. At Leisey Shell Pit, *C. edwardii* was the most common canid (Berta, 1995). This species (including *C. priscolatrans*) was formerly thought to be ancestral to the extant red wolf, *C. rufus* (Nowak, 1979), but recent studies by Tedford (reported by R. M. Nowak at the Red Wolf Symposium, April 1999, Hays, Kansas) place *C. edwardii* at the base of the *C. armbrusteri–C. dirus* line.

CANIS *SP.*

REFERRED MATERIAL Badger Room: DMNH 11571 R p4. Pit: CM 48437 fragmentary L jaw with p2, p3-4, m1 broken.

DESCRIPTION AND COMMENTS These two specimens are too small to be *C. latrans* and too large to be fox; they may represent an extinct canid. The dentary is thick (7.6 mm below p3-4), and the ventral border is straight. The p4 is smaller and narrower than that of *C. latrans.* Small coyote-like canids have been reported from late Blancan to late Rancholabrean faunas, but they have not been described or compared (Kurtén and Anderson, 1980).

VULPES VELOX *(SAY, 1823)*

REFERRED MATERIAL See appendix 13.1.

DESCRIPTION AND COMMENTS *Vulpes velox* is the most common fox in Porcupine Cave, with a minimum of 47 specimens identified. Other Irvingtonian occurrences include Angus, Nebraska, and Berends, Oklahoma. An inhabitant of open, arid areas, this small, delicate canid is not found anywhere near the cave today, and it is becoming increasingly rare throughout its range.

VULPES VULPES *(LINNAEUS, 1758)*

REFERRED MATERIAL Velvet Room: DMH 6554 R P1 (G1, L5); 8717 fragmentary R jaw with m2 (G4, L3); 35775 proximal L ulna (G11, L3). Mark's Sink: DMNH 33472 L P4 (8/96); 33511 R M1 (7/94); 38869 R M1 (L 29, 7/97). Will's Hole: DMNH 21437 R P4. Generator Dome: DMNH 22045 L m1 trigonid (L 2). Badger Room: CM 49166 L proximal tibia. Pit: 48426 fragmentary R jaw with m1-2 (G mixed, L 1-3).

DESCRIPTION AND COMMENTS Several more specimens of *Vulpes vulpes* have been recovered since the first report of the species in the Irvingtonian (Anderson, 1996). All the specimens are larger than *V. velox* and *Urocyon cinereoargenteus* and much smaller than those of *Canis latrans.* In size and morphology, this sample closely resembles Recent *Vulpes vulpes.* This is the only Irvingtonian record of the species; it has been reported from 35 Rancholabrean faunas. The red fox is primarily associated with wooded areas, and in Colorado it is most common in the mountains.

UROCYON CINEREOARGENTEUS *(SCHREBER, 1775)*

REFERRED MATERIAL Pit: CM 48436 fragmentary R jaw with p4, p2-3, m1 broken (G5/6, L1). Velvet Room: DMNH 12318 R p3 (G1, L10).

DESCRIPTION AND COMMENTS No additional specimens of *Urocyon cinereoargenteus,* the gray fox, have been found since Anderson (1996) reported on the two specimens. The species is not known historically from Park County, although there are a few records from neighboring Chaffee County. Other Irvingtonian occurrences include Port Kennedy Cave, Pennsylvania; Cumberland Cave, Maryland; Conard Fissure, Arkansas; and Coleman IIA, Inglis 1A, and Leisey Shell Pit, Florida. Smaller than *Vulpes vulpes, Urocyon cinereoargenteus* has widely spaced cheek teeth, and the mandible has a straight ventral border and a prominent step below the angle. Found in brushy areas and deciduous forests, the gray fox, unlike other canids, frequently climbs trees, leaping from branch to branch (Nowak, 1991).

Family Ursidae

URSUS AMERICANUS *PALLAS, 1780*

REFERRED MATERIAL Generator Dome: DMNH 41411 L I1 (L1). Undifferentiated: UCMP 155908 MT III.

TABLE 13.3
Most Common Species (MNI) of Carnivores in Five Areas of Porcupine Cave

Badger Room	*Mark's Sink*	*Velvet Room*	*Generator Dome*	*Pit*
Taxidea taxus (122)	*Spilogale putorius* (85)	*Mustela frenata* (33)	*T. taxus* (37)	*T. taxus* (16)
Canis latrans (73)	*C. latrans* (40)	*Mustela erminea* (27)	*C. latrans* (26)	*S. putorius* (13)
S. putorius (45)	*M. frenata* (39)	*S. putorius* (10)	*C. edwardii* (9)	*M. frenata* (13)
C. edwardii (14)	*Vulpes vulpes* (29)	*V. velox*(9)	*S. putorius* (8)	*V. velox* (7)

DESCRIPTION AND COMMENTS So far, only two specimens, an upper first incisor and an immature third metatarsal, are referable to ursids. Both specimens compare favorably in size and morphology with *Ursus americanus*. Irvingtonian occurrences of *U. americanus* include Conard Fissure, Arkansas; Cumberland Cave, Maryland; Port Kennedy Cave, Pennsylvania; and Trout and Hamilton Caves, West Virginia. Although several species and subspecies of Pleistocene black bears have been named, Graham (1991) referred all of them to *U. americanus* and did not recognize any extinct subspecies, noting that, when the pronounced sexual dimorphism and individual variation of black bears are considered, measurements of the fossil material fall within samples of Recent *U. americanus*. Black bears frequent the hillsides and meadows around Porcupine Cave today.

Family Felidae

LYNX RUFUS *(SCHREBER, 1777)*

REFERRED MATERIAL Velvet Room: UCMP 140509 L P3 (G5-6, L 1). Mark's Sink: DMNH 33909 R C (8/96); 37163 L C unerupted (L 26, 7/97). Will's Hole: DMNH 40215 R c. Badger Room: DMNH 13924 L C; 41033 R m1; CM 49133 R C; 49138 L c. Generator Dome: DMNH 27044 L c (L 2). Crystal Room: DMNH 36667 R c; CM 49158 R C; 49159 middle phalanx. Cramped Quarters: CM 49154 fragmentary R jaw with canine, p3-4. Undifferentiated: CM 49125 L P4.

DESCRIPTION AND COMMENTS Felids are rare in Porcupine Cave. Except for CM 49154 from Cramped Quarters, the bobcat *Lynx rufus* is represented by isolated teeth, mainly canines. Measurements of the material fall within a recent sample from Colorado. The stratigraphic range of *Lynx rufus* extends back to the late Blancan (Cita Canyon, Texas), and the species has been identified from several Irvingtonian sites, including Inglis 1A, Coleman 2A, and Leisey Shell Pit, Florida; Conard Fissure, Arkansas; Trout Cave, West Virginia; and Port Kennedy Cave, Pennsylvania. Werdelin (1985) referred Blancan and Irvingtonian bobcats to an extinct subspecies, *L. r. calcaratus*. Bobcats are common in the foothills and canyons of the western three-fifths of Colorado (Armstrong, 1972), and individuals have been seen in the vicinity of the cave.

MIRACINONYX *CF.* M. INEXPECTATUS *(COPE, 1895)*

REFERRED MATERIAL Badger Room: DMNH 11016 R m1. Undifferentiated: CM 49167 L P4.

DESCRIPTION AND COMMENTS These two teeth represent the only record of *Miracinonyx* from Porcupine Cave. Irvingtonian cheetahs have been identified from Port Kennedy Cave, Pennsylvania (type locality); Cumberland Cave and Cavetown, Maryland; Hamilton Cave, West Virginia; Inglis 1A, Florida; Conard Fissure, Arkansas; and Santa Clara County, California (Van Valkenburgh et al., 1990). The genus *Miracinonyx* includes two species of large, small-headed, slender-limbed cats, the Irvingtonian *M. inexpectatus* and the late Rancholabrean *M. trumani.*

Discussion

With 23 species and 918 specimens, Porcupine Cave contains the richest Irvingtonian carnivore assemblage known. Today in South Park, 11 species of carnivores inhabit the area; 3 others *(Canis lupus, Ursus arctos,* and *Mustela nigripes)* have been extirpated within historic times. Remains of *Spilogale putorius* and *Vulpes velox* are common in the cave, but these species have not been reported from South Park or Park County. The 12 areas in the cave where carnivores have been found were not all open nor did they close at the same time, so the 23 species were not all faunal associates. The most productive areas in the cave for carnivores are the Badger Room, Mark's Sink, the Velvet Room, Generator Dome, and the Pit. Table 13.3 lists the most abundant species in each of these areas. The Badger Room and Generator Dome are close to the surface and had natural openings in the past; badgers, coyotes, skunks, and weasels probably denned there. The abundance of carnivores and their prey (rodents, lagomorphs) in Mark's Sink suggests a carnivore trap into which animals fell and then could not get out. If so, the cries and struggles of trapped animals would have attracted carnivores, which also would have fallen in and become entrapped; thus, over time, a talus cone would have been built below the natural opening. Carnivores in the Pit and Velvet Room tend to be small, and their remains may have been brought in by wood rats (*Neotoma* spp.) and in raptor pellets.

Remains of *Taxidea taxus, Canis latrans,* and *Spilogale putorius* outnumber all other carnivores. *T. taxus* (badgers) and

C. latrans (coyotes) are common in the area today. Other species—for example, *Lutra canadensis, Mephitis mephitis, Urocyon cinereoargenteus, Ursus americanus,* and *Lynx rufus*—are represented by only a few specimens. Whether this is an artifact of preservation or collecting, or indicative of actual rarity in the fauna, is unknown. Extinct species include *Martes diluviana, Martes* species A, *Gulo schlosseri, Mustela* species A, *Brachyprotoma obtusata, Canis edwardii, Canis* sp., and *Miracinonyx inexpectatus.*

The diverse habitats around Porcupine Cave today include wet meadows, high and dry steppe, montane shrub, and montane forest. In the Irvingtonian, grasslands and alpine tundra as well as the other habitats supported a heterogeneous fauna; the presence of mink, otter, and muskrat indicates nearby permanent streams and ponds. At least 35 species of rodents and lagomorphs and 12 species of equids and artiodactyls provided an ample prey base for the carnivores. Eurychores like the coyote, red fox, long-tailed weasel, and bobcat lived and hunted in all these communities (Armstrong, 1972). Other species are restricted to one or two of them, for example, mink and river otter in riparian areas, black-footed ferret and kit fox in grasslands, and marten and ermine in montane forests. Many species of rodents are even more habitat specific. Correlating presence and abundance with known habitat preferences and requirements of the different species helps in interpreting the paleoecology and climatic conditions during the Irvingtonian in south-central Colorado.

Work is continuing at Porcupine Cave—excavating new areas, interpreting the geology, mapping the cave and its environs, studying the extant flora and fauna—and at the museums—picking matrix, identifying specimens, describing new species, drawing and photographing specimens (including scanning electron microscope work), interpreting what has been found, and comparing the data with that for other Irvingtonian faunas. Porcupine Cave is just starting to reveal its secrets.

Appendix 13.1. Carnivore Specimens from Porcupine Cave

Mustela frenata

VELVET ROOM (DMNH 644)

DMNH 6555 LM1 (G1, L5); 6577 L p3 (G1, L7); 6578 R C (G1, L7); 6610 L scapula (G1, L7); 6637 R p3 (G1, L8); 6639 R jaw (G1, L8); 8531 L jaw with m1 (G1, L10); 8532 L M1 (G1, L10); 8675 L jaw with m1 (G4, L3); 8676 fragmentary L jaw with m1 (G4, L3); 8689 R c (G1, L6); 9847 fragmentary R jaw with m1 (G5, L8); 10500 L c (G5, L12); 10957 L jaw with p3-m1 (G10, L4, B); 10958 fragmentary R jaw with p4-m1 (G17, L7, D); 13813 L p4 (G16, L2, B); 14047 L P4 (G16, L3, B); 14048 R m1 (G16, L3, B); 21236 R jaw with dp4 (G15, L2, B); 22015 L P4 (G7, L4, B); 22132 L P4 (G15, L2, B); 22159 R jaw (G8/8A, L2, A); 22781 L P4 (G12, L6, C); 22782 R P4 (G12, L5, B); 29024 L p3 (G13-14, L10B, F); 29707 L jaw with p2-m1 (G8/8A, L17, F); 33776 R m1 (G8/8A, L3, B); 35771 R P4 (G11, L3B); 36497 R jaw with p3-m2 (G mixed, L28); 39553 R m1 (G16, L4, B); unnumbered R jaw fragment (G21, L20, below I).

CM VELVET ROOM (UCMP V93175)

UCMP 140511 fragmentary R and L jaws with c, p3-m1 (G4, L mixed).

MARK'S SINK

DMNH 21474 R innominate (7/94); 27036 R c (7/94); 27099 posterior half skull (7/94); 27771 R maxilla with M1 (7/94); 27772 L jaw with p3, m1-2 (7/94); 27773 R jaw with p3-m1 (7/94); 27774 R jaw with m1 (7/94); 27850 L jaw with p3 (7/94), p4 broken, m1-2 (7/94); 27851 R innominate (7/94); 27924 R maxilla with P4-M1 (7/94); 29304 L P4 (7/94); 33465 R c (7/94); 40387 L jaw (7/94). DMNH 33466 fragmentary R jaw with m1 (8/96); 33467 R jaw with p4-m2 (8/96); 33468 L maxilla with P4-M1 (8/96); 35772 R P4 (8/96); 38880 L M1 (8/96); 40386 L C (8/96); 40388 L condyle of jaw (8/96); 40389 fragmentary L jaw with m1 talonid (8/96); unnumbered fragmentary L jaw. DMNH 35773 R jaw with p4-m1 (L25, 7/97); 36003 L jaw with m1 (L19, 7/97); 38872 L M1 (L18, 7/97); 38879 fragmentary R jaw with m1 (L9, 7/97); 39548 R c (L9, 7/97); 39549 fragmentary L maxilla (L22, 7/97); 39550 L M1 (L24, 7/97); 39551 fragmentary palate (L26, 7/97); 39552 R M1 (L32, 7/97); 39555 L c (L12, 7/97); 40390 R c (L27, 7/97); 40275 fragmentary L jaw with m1 (L28, 7/97); 40385 R c (L30, 7/97); 40392 R P4 (L27, 7/97); 41266 fragmentary R jaw with p3-m1 (L22, 7/97); unnumbered L c (L34, 7/97).

BADGER ROOM

DMNH 20148 fragmentary L jaw with m1-2; 21238 R humerus, R radius. UCMP 147067 anterior half skull.

PIT

CM 48421 L jaw with p3-m2 (G5-6, L1); 48424 R jaw with p4-m2 (G5-6, L1); 48441 L c (G1, L5); 49119 fragmentary L jaw with m1 (S of G3, 50 mm below surface); 65319 R jaw with m1 (G1, L1); 65320 anterior half skull with R P4 (G1, L1); 66459 L C (G1, L1); 65493 L M1 (G1, L1); 66632 L M1 (G1, L1); 75500 L m1 (G1, L1); 75501 R c (G1, L1); 75502 L M1 (G1, L1B).

FISSURE FILL A

DMNH 41029 L jaw.

UNDIFFERENTIATED

CM 49120 L jaw with p4-m1.

Mustela erminea

VELVET ROOM (DMNH 644)

DMNH 6563 L P4 (G1, L6); 6638 R jaw with m1 (G1, L8); 6711 C (G1, L9); 6712 R humerus (G1, L9); 9934 L jaw with m1-2 (G5, L5); 10569 C (G16, L16, G); 10699 L femur (G6, L5, B); 10960 L jaw with m1 (G8/8A, L3, B); 10961 L jaw with m1 (G8/8A, L1-6, A-B-C); 10962 R jaw with m1 (G7, L below 23, below H); 10963 L innominate, L femur, L tibia (G7, L 22, below H); 12639 R femur (G11-12, L mixed); 13821 R c (G16, L1, A); 14047 L P4 (G16, L3, B); 15184 R tibia (G8/8A, L mixed); 22108 fragmentary R jaw with m1 (G16, L17, H); 22816 R C (G8/8A, L2, A); 27326 condyle R jaw (G4, L10); 27770 fragmentary R jaw (G12, L4, B); 27852 R c (G12, L5, B); 27853 fragmentary L m1 (G12, L5, B); 40206 fragmentary L jaw (G8/8A, L2, A); 41268 fragmentary L jaw with p3-m1 (G11, L16, H).

MARK'S SINK

DMNH 35824 L jaw with p4-m2 (L15, 7/97); 36499 L femur (8/96); 36522 fragmentary L jaw (8/96); 39559 R c (8/96); 39560 R c (8/96); 39561 2 R c (7/94); 39562 2 c (L29, 7/97); 40375 L maxilla with P4-M1 (L5, 7/97); 40384 L jaw with p4-m2 (L13, 7/97).

WILL'S HOLE

DMNH 27854 L jaw with p2-m2.

GENERATOR DOME

DMNH R femur (L1).

FERRET ROOM

DMNH 21440 R femur, L innominate.

PIT

CM 48442 fragmentary L jaw with m1 (G5/6N and 5/8N); 48447 L jaw with p3-m1 (G1, L2). UCMP 140531 R c (G3, L6); 140551 R jaw with m1 (G1, L3) .

Mustela nigripes

VELVET ROOM (DMNH 644)

DMNH 6610 L scapula (G1, L7); 9848 fragmentary L jaw with c, p3-m1 (G5, L8); 10959 L jaw with m1 (G11, L4, B–C); 11017 R jaw with m1 (G3, L6); 41034 L m1 (G12, L6, C).

MARK'S SINK

DMNH 27769 R jaw with p2, p4 (7/95); 35774 R femur (8/96); 37167 L maxilla with P4 broken (L26, 7/97); 40207 R C (7/93); 40273 R glenoid fossa (L17, 7/97).

WILL'S HOLE

DMNH 27768 fragmentary L jaw with p3-m1; 29307 L auditory bulla.

BADGER ROOM

DMNH 27047 proximal L femur; 41032 L radius.

PIT

CM 48448 L jaw with m1 (G3, L4); 66463 L M1 (G1, L1).

Mustela vison

VELVET ROOM (DMNH 644)

DMNH 6553 L P4 broken (G1, L5); 8848 fragmentary axis (G1, L7); 8948 L C (G7, L8, C).

MARK'S SINK

DMNH 33462 L jaw with c-m1 (8/96); 39556 R c (L24, 7/97); 39557 R c (8/96); 39558 L glenoid fossa (8/96); 40241 R C (8/96); 40242 fragmentary R jaw (L29, 7/97); 40242 fragmentary R jaw (8/96); 40274 L glenoid fossa (L26, 7/97); 40276 condyle L jaw (L26, 7/97); 40277 R coronoid process (L29).

WILL'S HOLE

DMNH 27767 L jaw with c-m2; 29306 R maxilla.

FERRET ROOM

DMNH 40209 R jaw with p2-3, m1.

Taxidea taxus

VELVET ROOM (DMNH 644)

DMNH 33457 terminal phalanx (G2, L6); 33458 fragmentary m1 (G10, L1, A); 35770 terminal phalanx (G mixed, L26); 41270 R P4 unerupted (G11, L5, C); 41271 distal L ulna (G20, L9, E).

MARK'S SINK

DMNH 36458 R C (L20, 7/97); 38868 fragmentary L M1 (L29, 7/97); 39497 proximal R ulna (L19, 7/97); 39530 fragmentary talonid R m1 (L24, 7/97); 39531 L P3 (L26, 7/97); 40240 R maxilla (8/96); 40245 distal L radius (L26, 7/97); 40246 R p2 (L22); 40249 talonid L m1 (L26, 7/97); 40248 fragmentary m1 (L33).

WILL'S HOLE

DMNH 23513 talonid R m1.

BADGER ROOM

DMNH 10954 L M1; 10955 R M1; 10956 R m1; 11569 R P4; 11570 R M1; 11917 R c; 14649 L femur, juvenile, R calcaneum, scapholunar, 4 middle phalanges; 14650 L p3; 14651 R p3; 14728 proximal phalanx; 20136 R maxilla with P4; 20137 R jaw with m1-2; 20138 R M1; 20139 L M1; 20140 L M1; 20141 L m1; 20142 L P4; 20143 L P4; 20144 L jaw with p4-m1; 20145 2 L jaws, 4 R jaws, all edentulous; 20146 L maxilla, R maxilla, L maxilla, juvenile, all edentulous; 20147 L humerus, L scapula, L ulna, L ulna (juvenile), proximal L ulna; radius, distal R. radius, fragmentary radius (juvenile), R femur, 2 metacarpals; 22085 fragmentary L maxilla; 23081 talonid L m1; 23082 talonid R m1; 23083 8 terminal phalanges; 27001 L premaxilla; 27005 talonid L m1; 27010 fragmentary L maxilla; 27011 R c; 27012 R astragalus; 27013 L C, R p4; 27014 L P3; 27015 L p4; 27016 R I3; 27017 R p4; 27018 L c; 27019 6 MC III, 3 MC IV; 29309 terminal phalanx; 29310 L c; 29311 L C; 29312 R calcaneum; 35370 skull fragmentary; 39533 L m1; 39534 6 metapodials; 39536 fragmentary R m1; 39537 L C; unnumbered L occipital condyle; unnumbered scapholunar.

CM VELVET ROOM (CM 1927)

CM 41414 middle phalanges (7); 41415 proximal phalanges (7); 41441 distal epiphysis-ulna; 49100 R jaw with m1; 49102 L maxilla with P4-M1; 49103 fragmentary R jaw with m1; 49104 baculum; 49106 fragmentary L jaw; 49153 R jaw; 49165 proximal L radius, distal R femur, distal L femur, R tibia; 49202 skull with R and L P4.

GENERATOR DOME

DMNH 21324 R tibia (L1); 21325 fragmentary L jaw (L1); 21331 R tibia (L1-2); 21441 R astragalus (L2); 21458 fragmentary L maxilla with P4 (L1); 21459 proximal L femur (juvenile), fragmentary tibia (juvenile), distal tibia (L1); 21460 2 L ulnae (L1); 21461 R maxilla (L1); 21462 L m1 (L1); 21463 L P4 (L1); 21464 R P4 (L1); 23430 L humerus (L2); 27000 fragmentary R condyle (L1); 27002 L calcaneum (L2); 27003 proximal R scapula, proximal L scapula (L1); 27004 R c (L1); 27006 MC I (L2); 27007 R glenoid fossa (L2); 28339 MC II (L1); 33460 L c (L2); 39535 R c (L1); 40391 2 i (L1); unnumbered R premaxilla (L1); unnumbered proximal phalanx (L1-2); unnumbered R I3 (L1-2); unnumbered 2 terminal phalanges (L1); unnumbered 3 middle phalanges (L1); unnumbered proximal phalanx (L1); unnumbered distal epiphysis ulna (L1); 41402 distal epiphysis-ulna (L1); 41413 terminal phalanges (2) (L1); 41429 R I 3 (L1-2); 41435 proximal phalanx (L1-2); 41438 R premaxilla (L1); 41449 phalanges (4) (L1).

BADGER DOME

DMNH 21453 proximal L ulna, proximal L femur, fragmentary radius (juvenile); 21454 L c.

PIT

CM 48419 L maxilla (G1, L mixed); 48425 R c (G5/6, L1); 48433 L c (surface); 48435 fragmentary R maxilla with P4 broken (G5/6, L2); 48451 R c (W of G1, L1); 48452 fragmentary R jaw with p3, p4-m1 broken (surface between G6 and G7); 49105 R jaw with p4-m1 broken (G1, L1); 49129 R m1 (nodule pile); 49160 R m1 (surface); 65317 R maxilla P4 (G1, L1); 65323 R maxilla (G1, L1). UCMP 140557 L premaxilla (G5/6, L1); 154464 distal R humerus (G1, L3); 154467 L radius (G1, L1-3); 154475 distal L humerus (G3, L4); 175017 distal R femur.

FISSURE FILL A

DMNH 23311 fragmentary R jaw; 40211 fragmentary R maxilla; 41028 fragmentary R ulna; 41030 fragmentary L ulna. CM 49142 fragmentary R jaw with m1; 49143 L P4; 49144 fragmentary m1; 49145 fragmentary m1; 49146 talonid R m1; 49147 L C.

CRYSTAL ROOM

CM 49157 L M1.

GYPSUM ROOM

CM 49162 L m1 (G1, L2).

UNDIFFERENTIATED

CM 49130 R m1; 49131 L c.

Spilogale putorius

VELVET ROOM (DMNH 644)

DMNH 10501 R jaw with p4-m1 (G5, L12); 10964 R jaw with dp4 (G16, L3, B); 10965 R jaw with p4-m1 (G16, L19, I); 35375 L M1 (G21, L21, below I); 35764 L C (G mixed, L27); 35768 L jaw with p2-m2 (G15, L28, below L); 38893 L jaw with c, p2, p4-m2 (G combined, L26); 39515 fragmentary R jaw with p4-m1 (G15, L8, D); 40228 L P4 (G21, L20, below I).

CM VELVET ROOM (CM 1927)

CM 48444 L C (G3, L3).

MARK'S SINK

DMNH 27210 fragmentary R jaw with m1 (7/94); 35502 proximal humerus (7/94); 36662 fragmentary R maxilla with P4 (7/94); 36665 L M1 (7/94); 40214 L P4 (7/94). DMNH 33469 fragmentary L jaw with m1 (8/96); 33470 L c (8/96); 33500 R jaw with c-m1 (8/96); 33501 R jaw with p3-m1 (8/96); 33505 L jaw with c, p4-m1 (8/96); 33506 L P4 (8/96); 33507 R jaw with p3, m1 (8/96); 33706 R P4 (8/96); 35374 R jaw with p3-m1 (8/96); 35766 L jaw with p4-m1 (8/96); 35767 fragmentary R jaw with m1 (8/96); 36663 R M1 (8/96); 36664 L c (8/96); 36665 L M1 (8/96); 36911 L M1 (8/96); 37099 R C (8/96); 38885 L P4 (8/96); 38887 R M1 (8/96); 38888 R jaw with p4-m1 (8/96); 38889 fragmentary L jaw with p4-m1 (8/96); 38891 R M1 (8/96); 38892 R P4 (8/96); 39513 fragmentary L jaw with p3 (8/96); 39529 R P4 (8/96); 40232 R jaw (8/96); 40233 R P4 (8/96); 40234 L p4 (8/96); 40235 R c (8/96); 40236 3 L c (8/96); 40237 R P4 (8/96); unnumbered L C (8/96). DMNH 35769 L jaw with p2-m2 (L17, 7/97); 35591 R m1 (L19, 7/97); 35821 L jaw with m1 (L15, 7/97); 35952 R P4 (L19, 7/97); 36658 L jaw with p4-m1 (L24, 7/97); 36659 L maxilla P4 (L24, 7/97); 36660 R jaw with p4-m1 (L28, 7/97); 36661 R jaw with p4-m1 (L31, 7/97); 36909 R jaw with m1 (L25, 7/97); 36910 L C (L25, 7/97); 37087 L P4 (L27, 7/97); 37159 R P4 (L20, 7/97); 37161 L M1 (L26, 7/97); 38873 R M1 (L26, 7/97); 38874 L P4 (L26, 7/97); 38875 L jaw with p2, p4, fragmentary m1 (L28, 7/97); 38876 R jaw with p4-m2 (L20, 7/97); 38877 R jaw with i2-3, p2-m2 (L22, 7/97); 38878 R jaw with p4-m1 (L28, 7/97); 39495 R C (L18, 7/97); 39496 R humerus (L19, 7/97); 39498 L C (L20, 7/97); 39499 L C (L21, 7/97); 39500 fragmentary L jaw (L22, 7/97); 39501 fragmentary L jaw with m1 trigonid (L22, 7/97); 39502 R p4 (L24, 7/97); 39503 R C (L24, 7/97); 39504 R jaw with p4 (L26, 7/97); 39505 L M1 (L26, 7/97); 39506 R P4 (L26, 7/97); 39507 R jaw (L26, 7/97); 39508 L maxilla with M1 (L29, 7/97); 39509 fragmentary L jaw with p3-m1 (L29, 7/97); 40247 R p3 (L29, 7/97); 40254 L P4 (L27, 7/97); 40255 R p4 (L4, 7/97); 40256 L m1 trigonid (L28, 7/97); 40257 R c (L17, 7/97); 40258 L M1 (L33, 7/97); 40259 L c (L19, 7/97); 40260 L C (L23, 7/97); 40261 R p4 (L16, 7/97); 40262 R jaw with p4-m1 (L16, 7/97); 40263 fragmentary L jaw (L21, 7/97); 40619 R maxilla with P4-M1 (L18, 7/97); 40620 L maxilla with P4 (L18, 7/97); unnumbered L P4 (L28, 7/97).

WILL'S HOLE

DMNH 23512 L M1; 28925 R ulna; 38899 R jaw; 39802 R C (G7, L26).

BADGER ROOM

DMNH 10950 fragmentary L maxilla with P4; 10952 L M1; 10953 L M1; 13923 L M1; 14725 distal R humerus; 14964 fragmentary L jaw; 15275 distal L humerus; 16006 fragmentary L jaw; 20149 fragmentary L jaw with m1; 20200 fragmentary L jaw with m1; 20201 fragmentary R jaw with m1; 20202 fragmentary L jaw with m1; 20203 L jaw with m1; 20204 fragmentary L jaw; 20205 L jaw with p4-m1; 20206 L jaw with p4-m2; 20207 L jaw with p2-m1; 20208 R maxilla with P2-M1; 20209 skull with L P4-M1, R M1; 20433 L maxilla with M1; 21240 R radius, proximal R radius, fragmentary L innominate; 27048 L M1; 27049 R C; 27862 L m1; 33503 proximal L humerus; 33503 fragmentary R innominate; 33504 L c; 39514 4 C; 39516 L P4; 40204 R c; 40205 L p4; 40212 R m1 trigonid; 40213 R c. 41401 L humerus; CM 49113 fragmentary L jaw with m1; 49115 L jaw with c, p3-m2; 49137 R jaw with c, p3-m1; 49139 fragmentary L jaw with p4.

GENERATOR DOME

DMNH 21443 fragmentary R innominate (L2); 21469 R jaw with p4-m1 (L1); 27039 3 c (L1); 27040 L M1 (L1); 27042 L auditory bulla (L1); 28329 fragmentary R jaw with p4 (L1).

PIT

DMNH 48422 L C (G3, L3); 49114 partial skull with L P4 broken (G1, L3); 49115 skull (crushed) with L P3-M1 (G7, L10 bottom); 49116 L m1 (nodule dump); 49161 R M1 (surface); 49293 R P4 (G1, L1); 49294 L P4 (G1, L1); 49295 fragmentary L P4 (G1, L1); 49296 fragmentary L P4 (G1, L1). UCMP 140516 L m1 trigonid (G7, L10); 140547 L M1 (G3, L5); 182170 R M1 (G3, L4); 182174 L M1 (G6, L7).

FERRET ROOM

DMNH 21695 R P4; 27211 fragmentary R jaw with m1; 41031 proximal L humerus.

GYPSUM ROOM

CM 49163 distal L humerus.

FISSURE FILL A

DMNH 38898 R jaw with m1.

UNDIFFERENTIATED

CM 49109 R jaw with m1; 49110 fragmentary R jaw with m1; 49111 R jaw with m1; 49117 L P4; 49118 R P3.

Canis latrans

VELVET ROOM (DMNH 644)

DMNH 12319 R m3 (Gl, L10); 12320 L DP3 (G1, L10); 22382 R m2 (G20, L7B, E); 23453 fragmentary petrosal (G5, L12) .

MARK'S SINK

DMNH 23428 R MT II (7/94); 40225 terminal phalanx (7/94); 40227 jaw fragmentary (7/94). DMNH 33451 R P3 (8/96);

33452 L astragalus (8/96); 37092 5 middle phalanges (8/96), proximal MC, MT IV (juvenile, 8/96), 2 distal metapodials (8/96); 38881 fragmentary L P4 (8/96); 38882 L P2 (8/96); 38883 L i3 (8/96); 38884 R i3 (8/96); 39517 2 c (8/96); 39518 2 fragmentary premolars (8/96); 39519 L p3 (8/96); 39520 proximal MT IV (8/96); 39528 fragmentary L c (8/96); 40230 terminal phalanx (8/96); 40231 proximal R tibia (8/96). DMNH 35823 R m1 (L21, 7/97); 35953 fragmentary L innominate (L19, 7/97); 36546 MT III (L31, 7/97); 38870 L m1 talonid (L24, 7/97); 38871 R m2 (L28, 7/97); 39489 fragmentary R P4 (L18, 7/97); 39490 R occipital condyle (L26, 7/97); 39491 cuboid (L26, 7/97); 39492 fragmentary L occipital condyle (L29, 7/97); 39494 fragmentary L jaw (L26, 7/97); 40251 distal metapodial (L15, 7/97); 40252 terminal phalanx (L34, 7/97); 40253 fragmentary M1 (L2, 7/97); 40393 R P3 split (L19, 7/97).

WILL'S HOLE

DMNH 21476 proximal R scapula; 27032 fragmentary R P4; 27033 L p1; 27034 L C; 27401 MT III.

BADGER ROOM

DMNH 11571 R p4; 12321 R I3; 14317 condyle L jaw; 20131 R m1; 20132 R m1 talonid; 20133 L M1; 20134 baculum; 26646 R femur (pathological); 27025 L p4; 27026 R M2; 27027 R p3; 27028 R premaxilla; 27029 R p3; 27030 condyle L jaw; 27031 atlas, sacrum, cervical vertebra, distal L humerus, fragmentary distal humerus, fragmentary ulna, MT IV, proximal MT III; 27402 R tibia; 27765 proximal radius, proximal epiphysis radius, proximal epiphysis humerus, caudal vertebra, distal metapodial; 30076 skull with R P2-M2, L P3-M2; 33454 R I1, L I2; 33509 distal epiphysis tibia; 36589 R maxilla with fragmentary Dp4, M1; 36590 R P4 unerupted; 38896 L p4; 38897 R P1; 39522 distal epiphysis femur; distal fibula, MT IV, distal metapodial, proximal MT IV, proximal calcaneum, 3 terminal phalanges; 39523 MT IV, distal metapodial; 39524 R C; 39526 R m3; 39527 L P3; 40222 2 terminal phalanges; 40223 P2 broken; 40224 distal metapodial; 40226 L occipital condyle; 41416 proximal phalanges (2); 41417 middle phalanges (7); 41431 vertebrae (2); 41433 MT III; 41448 head of femur; 46647 proximal tibia, distal R tibia, proximal L radius, proximal R humerus, R astragalus, lumbar vertebra.

GENERATOR DOME

DMNH 21326 distal epiphysis humerus (L1); 21327 proximal R tibia (L1); 21328 distal R tibia (L1); 21329 R innominate (L1-2); 21441 L astragalus (L2); 21442 R c (L2); 21465 R MT IV, R MC IV, scapholunar, R proximal epiphysis humerus (L1); 21466 fragmentary L p4 (L1); 21467 L p3 (L1); 27021 2 L jaw fragments (L2); 27022 R and L premaxillae (L1); 27023 cervical vertebra (L1); 27203 L p4, L m1, Lm2 associated (L2); 39525 fragmentary L jaw (L1-2); 40394 2 dist metapodials (L1); 41436 middle phalanx (L1); 41439 phalanges (2) (L1-2); 41444 MC IV, MT IV.

FERRET ROOM

DMNH 27205 fragmentary L maxilla with P3; 27207 R p3.

FISSURE FILL A

DMNH 27027 2 proximal L ulnae; 27200 R and L c; 27201 L M2; 27202 L M1; 27204 fragmentary R P4; 27766 cuboid, 2 phalanges, fragmentary p4, fragmentary p3; 33453 fragmentary L p2; 33768 fragmentary L maxilla; 33770 fragmentary L P4; 39521 MT III; 39803 fragmentary p3; 39804 L p4; 40217 L i2; 40218 fragmentary L p2; 40219 R P1; 40221 proximal MC IV; 40270 fragmentary L c; CM 49169 L m2.

PIT

CM 48437 fragmentary L jaw with p2, p3-4 broken (G5/6, L1); 49122 fragmentary L jaw (mixed); 49123 fragmentary R jaw with m1 trigonid (G1, L1-3); 49124 R m2 (surface). UCMP 140524 L i3 (surface); 154483 distal R radius.

UNDIFFERENTIATED

UCMP 155918 squamosal.

Canis edwardii

VELVET ROOM (DMNH 644)

DMNH 33508 fragmentary proximal ulna (G2, L3).

MARK'S SINK

DMNH 33456 L i2 (8/96); 36912 R I3 (L17, 7/97); 39493 L p4 (L25, 7/97); 40250 carpal (L29, 7/97); 40852 R MC IV (L31, 7/97).

BADGER ROOM

DMNH 11015 fragmentary m1; 18353 L jaw with p1, p3-m2; 27024 MC III; 33455 L premaxilla; 38894 R p4; unnumbered R p1; 41430 2 distal metapodials; 41432 terminal phalanx; 41442 4 proximal phalanges; 41443 lumbar vertebra. CM 49132 fragmentary R jaw with p2-p4.

GENERATOR DOME

DMNH 21330 fragmentary R jaw with p4, m1 trigonid (L 1-2); 27020 fragmentary R ilium (L1-2); 41434 terminal phalanx (L1); 41437 tarsal (L1); 41440 proximal MT III (L1-2); 41445 MC II (L1); 41446 MC IV (L1-2); 41447 proximal phalanx (L1-2).

WILL'S HOLE

DMNH 27035 L P4 talon.

FISSURE FILL A

DMNH 33769 LP4. CM 49140 fragmentary L jaw with m2, m3 broken.

CRYSTAL ROOM

DMNH 40899 fragmentary tibia.

PIT

CM 49292 L calcaneum (G1, L2).

Vulpes velox

VELVET ROOM (DMNH 644)

DMNH 10966 L P4 (G12, L3, B); 10968 fragmentary L max with P4 (G16, L19, I); 15087 proximal fibula (G16, L5, C); 19851 proximal R ulna, caudal vertebra (bilge); 20818 L jaw with p1-m2 (G26, L2, B); 21223 R c (bilge); 33471 R M1 (G21, L 20, below I); Unnumbered fragmentary L max with alveoli P3-4 (G7, below 23).

MARK'S SINK

DMNH 21499 proximal R radius (7/94); 22770 L dp4 (7/94); 23431 L jaw with m2 (7/94); 33510 L M1 (8/96); 39540 proximal R ulna; 39541 L P3 (8/96); 39542 fragmentary R jaw (8/96); 40208 R P2 (7/93); 40238 proximal R ulna (8/96); 40239 L maxilla (8/96). DMNH 35825 L jaw with p4-m1 (L21, 7/97); 36913 L p3 (L 11, 7/97); 36914 L p2 (L11, 7/97); 37169 L jaw (L26, 7/97); 39539 L m1 trigonid (L24, 7/97); 39543 L P3 (L7, 7/97); 39544 fragmentary P4 (L9, 7/97); 39545 fragmentary palate (L9, 7/97); 39546 fragmentary R jaw (L9, 7/97); 39547 R p3 (L22, 7/97); 40267 R M1 (L16, 7/97); 40268 R p2 (L21, 7/97); 40269 fragmentary R p4 (L29, 7/97); 40270 R P2 (L16, 7/97); 40271 proximal L ulna (L25, 7/97); 40272 proximal R ulna (L24, 7/97); 41002 fragmentary R P4 (L29, 7/97); 41004 L M1 (L24, 7/97).

GENERATOR DOME

DMNH 40210 R C (L1).

PIT

CM 48417 L jaw with p3 (G1, L1-3); 48418 fragmentary R jaw with m1-2 (G1, L1-3); 48443 L m1 (G3, L3); 48450 fragmentary R jaw with p4 (W of G1, L1); 49126 fragmentary L jaw with p4-m2 (G1, L3); 49127 fragmentary R maxilla with M1 (G1, L3). UCMP 140556 R jaw with m2 (mixed).

FISSURE FILL A

CM 49152 proximal R ulna.

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For stimulating discussions about the fauna, the geology, and the Pleistocene, I thank Lou Taylor, Bob Raynolds, Don Rasmussen, Jim Mead, C. A. Repenning, Russ Graham, Tom Goodwin, Dave Armstrong, Colleen Baxter, Craig Childs, Philip Pratt, Sue Ware, and Heidi Schutz. Very special thanks are owed to PJ Kremer for her drawings, and to George Dennison, who gave us all courage. Frank and Connie McMurry let us camp on their land and permitted us access to the cave.

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FOURTEEN

Middle Pleistocene (Irvingtonian) *Ochotona* (Lagomorpha: Ochotonidae) from Porcupine Cave

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The lagomorph family Ochotonidae, represented today by a single living genus (*Ochotona* [pika]), originated in the middle Oligocene of Asia. During the late Miocene and into the Pliocene, the family flourished throughout Eurasia and migrated into North America. Beginning in the late Pliocene and throughout the Pleistocene, the group has declined, survived only by the genus *Ochotona* (Erbajeva, 1988, 1994, 1996; Erbajeva and Tyutkova, 1997).

Today more than 23 species of *Ochotona* live in Asia, and only 2 live in North America (Hoffmann, 1993). Smith et al. (1990:14) rightly pointed out that the "Pikas are . . . a very poorly known group of mammals"; researchers are still uncertain of the alignment of many of the species and related forms. Corbet (1978) synonymized the two North American forms (*O. princeps* [American pika] and *O. collaris* [collared pika]) along with the northern Asian pika (*O. hyperborea*) with *O. alpina* (alpine pika) that lives in the mountainous Altai region of southern Siberia and northern Xinjian (China) and in Mongolia (Smith et al., 1990). Weston (1981) determined that *O. alpina* is distinct from the American forms, and that the American species are more closely similar to *O. hyperborea,* which is distributed through eastern to northeastern Siberia (Smith et al., 1990).

Gureev (1964) divided the living *Ochotona* of Asia into four morphological groups, all considered to be small forms of pikas (as are the American species). Large forms of *Ochotona* known from northern Eurasia *(O. tologoica, O. gromovi, O. zazhigini,* and *O. zasuchini)* were extinct by the end of the Pliocene (Erbajeva, 1985, 1988). The extinct *O. whartoni* (Guthrie and Matthews, 1971) is the only large species of *Ochotona* known from North America. It seems to have persisted in more northern latitudes, occurring as far east and south as southern Ontario until the earliest Holocene (Mead and Grady, 1996). This large form in North America persisted long after the large morphs lived in Eurasia.

The modern habitat requirements of the various species are described in Smith et al. (1990) and are seemingly well defined and understood for the North American *O. princeps* (Hafner, 1993, 1994; Hafner and Sullivan, 1995). Although it is assumed that the habitat requirements ascribed for *O. princeps* in the interglacial climate of today are relevant ecological templates for the form during the most recent Wisconsinan Glaciation, fossil data from dry cave deposits in the intermountain West might suggest a different paradigm (Mead and Spaulding, 1995).

The European and Asian Neogene stratigraphic record of all ochotonids, including *Ochotona,* is fairly detailed, with many localities of varying levels of chronological certainty (Sych, 1980; Bishop, 1982; Erbajeva, 1985, 1988, 1994). The North American Neogene record is far less complete (figure 14.1; table 14.1).

Shotwell (1956) described the earliest record of *Ochotona (O. spanglei)* for North America, with remains from Oregon of latest Hemphillian (early Pliocene) age. No other fossil ochotonids are described from Pliocene deposits (Hemphillian or Blancan), so one can only assume that pikas were exceedingly rare in North America throughout the Pliocene. Philip Bjork (pers. comm.; Bjork, 1997) has indicated that he has an apparent Blancan record of a small morph of *Ochotona* from the Black Hills, South Dakota (figure 14.1 at Unwily Coyote).

The North American record of *Ochotona* is sparse until the early Pleistocene Irvingtonian, when a more widespread occurrence is indicated (table 14.1; figure 14.1). At least two morphological forms of *Ochotona* lived in North America during the Irvingtonian, one large and one small. Guilday (1979), Mead (1987), and Mead and Grady (1996) provided an overview of the Irvingtonian record of *Ochotona* of North America, with emphasis on the eastern region. Irvingtonian-age *Ochotona* are known from Cumberland, Hamilton, and Trout caves in eastern North America (figure 14.1). *Ochotona* (large and small morphs) of purported Irvingtonian age are known

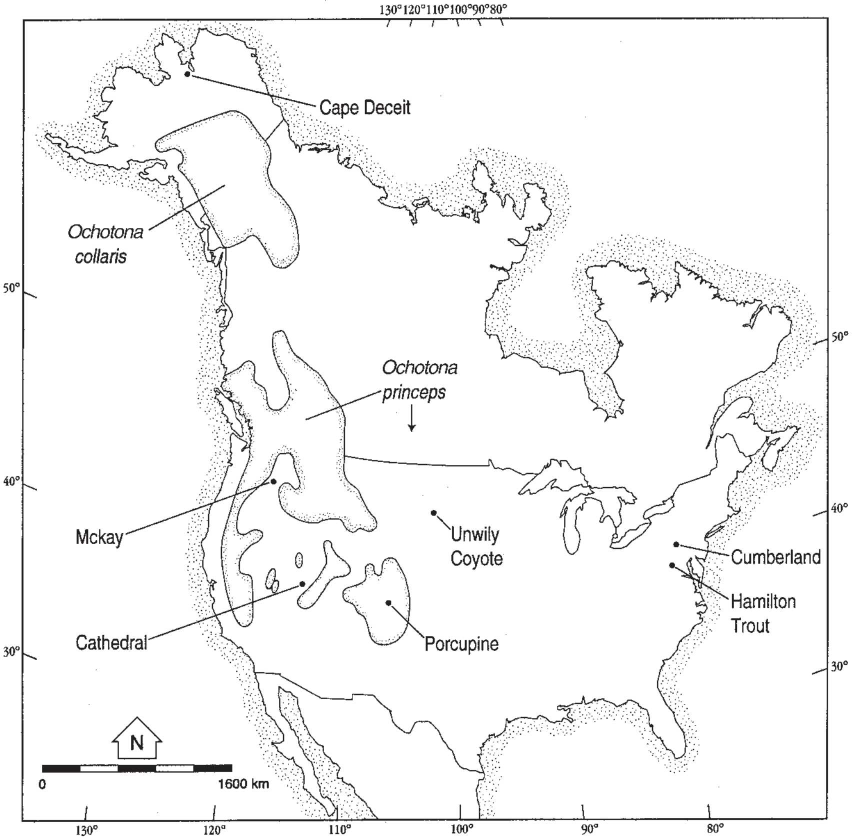

FIGURE 14.1 Map of North America showing fossil localities containing *Ochotona* of Hemphillian, Blancan, and definite Irvingtonian age (from table 14.1). Rancholabrean-age localities are numerous, and descriptions of them can be found in Mead (1987) and Mead and Spaulding (1995). A number of localities at high latitudes in Canada and Alaska are of equivocal age assignment and lack precision, and therefore are omitted here (see Mead, 1987; Morlan, 1996). The approximate Recent distributions of *O. princeps* and *O. collaris* are shown.

from a number of localities in the Arctic high latitudes in the West (Mead, 1987; Morlan, 1996). The small form (similar to *O. princeps*) occurred in the East to more southern latitudes. An unpublished account occurs from Cathedral Cave, Great Basin, Nevada (J. I. Mead and C. J. Bell, unpublished). Here we present the first record of Irvingtonian *Ochotona* from the intermountain West, a record from high-elevation Porcupine Cave, Colorado.

Porcupine Cave

As noted in earlier chapters, Porcupine Cave is situated at 2900 m elevation in South Park, in the Rocky Mountains of central Colorado (figure 14.1). Deposits in the cave provide one of the highest-elevation vertebrate fossil sites of Pleistocene age in North America and have the most taxonomically diverse high-elevation fauna on the continent, as documented in this volume and as first reported by Barnosky and Rasmussen (1988). Details of the stratigraphy, chronology, and faunas are provided elsewhere (Barnosky and Rasmussen, 1988; Bell and Barnosky, 2000). Of the 26 separate localities in Porcupine Cave, most were test pits or exploratory probes, but at least four extensive excavations have been conducted (Pit, DMNH Velvet Room, Mark's Sink, and Badger Room). In these four cases and at several other localities, sediments were removed and screened for microvertebrates (in part by us) as described in chapter 2. Only the Pit and the DMNH Velvet Room excavation are known to be meaningfully stratified. Ochotonid remains from all units were made available to us for this study.

Systematic Paleontology

Class Mammalia

Order Lagomorpha

Family Ochotonidae

OCHOTONA

Specimens of *Ochotona* were recovered from six sites in Porcupine Cave (appendix 14.1): Badger Room, Generator Dome,

TABLE 14.1

North American fossil *Ochotona* of Pliocene (Latest Hemphillian and Blancan) and Early Pleistocene (Irvingtonian) Age

Location	*Species/Morph*	*Reference; Remark*
		Hemphillian
McKay Reservoir	*spanglei*	Shotwell (1956); type
		Blancan
Unwily Coyote	Small	P. Bjork (pers. comm., 1997)
		Irvingtonian
Cape Deceit	*whartoni*/large	Guthrie and Matthews (1971); type
Cathedral Cave	Small	C. J. Bell and J. I. Mead (field notes)
Cumberland Cave	Small	Guilday (1979); Mead and Grady (1996)
Hamilton Cave	Small	Mead and Grady (1996)
Porcupine Cave	Small	This chapter
Trout Cave	Small	Guilday (1979); Pfaff (1990, 1991); Mead and Grady (1996)

NOTE: Rancholabrean-age localities are numerous, and descriptions of them can be found in Mead (1987) and Mead and Spaulding (1995). The small morph may also be referred to as *O. princeps*–like.

Mark's Sink, the Pit, Velvet Room, and Will's Hole. This chapter makes available the preliminary information about *Ochotona* from these localities. We are not positive that we have any taxon other than *O. princeps*. We have taken a liberal approach in describing these specimens by emphasizing subtle differences, particularly isolated teeth. The statistical study necessary to unequivocally differentiate the species has not been carried out and is beyond the scope of this chapter. Clearly what is needed for a satisfactory statistical analysis is abundant specimens from well-dated stratigraphic layers, but this is not possible for the present study. Examination of additional specimens may support the validity of the differences we highlight here, signaling a more complex evolutionary history of the pikas in North America. Alternatively, further material may indicate that the differences we note are merely geographic variation within a slowly evolving taxon.

OCHOTONA *CF.* O. PRINCEPS *(RICHARDSON, 1828)*

DESCRIPTION AND COMMENTS The specimens from Mark's Sink are from a medium to small pika, perhaps smaller than most of the extant *O. princeps*. The following are characteristics observed on all the mandibles from Mark's Sink. The ascending ramus of the mandible is somewhat short and wide, inclined slightly posteriorly. The coronar tubercle is well developed. The upper surface of the ascending ramus is wide anteriorly and becomes sharply narrow posteriorly. The angular part of the mandible is rather wide at its base. There is a well-developed crest on the base of the labial side. The angular opening is not deep and wide. Specimens DMNH 41347, 36492, and 37095 are small (alveolar lengths of p3–m3, respectively: 7.1, 7.2, 7.3 mm); however, some specimens from upper levels in Mark's Sink are about the same size, as is typical of *O. princeps* (see Mead and Grady, 1996:figure 2A). It appears that the pikas from deeper in the excavation might belong to a smaller form; however, this has not yet been documented statistically.

The size of the Lp3 (UCMP 173763) from the Pit corresponds to that of recent *O. princeps*. The anteroconid of the p3 is large, with wide confluence with the posteroconid (figure 14.2A). The anterointeral side of the anteroconid is much longer than on the other side. The rather short anteroexternal side has a very shallow depression. The enamel is developed on the anterior side of the anteroconid, being of almost the same thickness on both the anterointernal and anteroexternal sides. The anteroexternal and anterointernal folds between anteroconid and posteroconid are of the same depth and are filled with thin cement. The posteroconid is wider than long. Its lingual side, with a very shallow depression, is much shorter than the labial side. The posteroexternal fold of the tooth is filled with thick cement. Thick enamel surrounds the posteroconid, which is thin on its posterointernal portion (figure 14.2A).

Specimens from Will's Hole are all from a small ochotonid, as large as the extant *O. princeps*. The diastema of the specimens is short in comparison with that of modern specimens.

Specimens from the DMNH Velvet Room excavation are nearly identical in proportions to those from extant *O. princeps*. The ascending ramus is rather high with a developed coronar tubercle on the anterior face. The upper surface is wide on the anterior portion and becomes sharply narrow

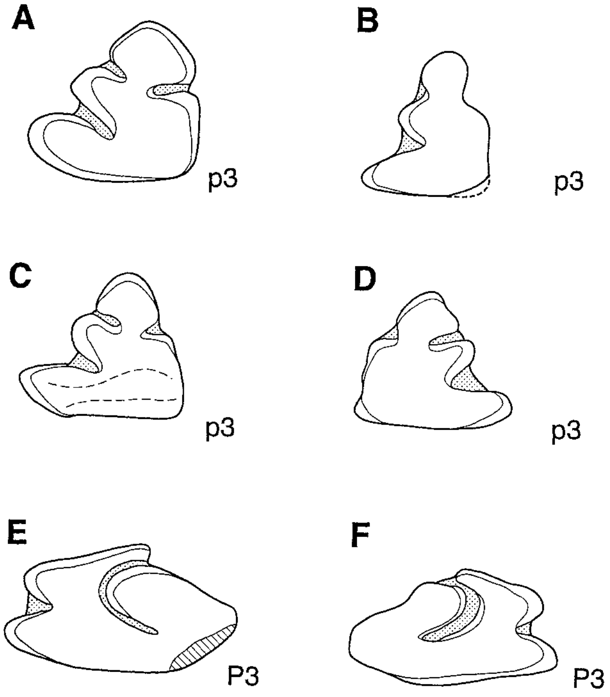

FIGURE 14.2 Drawings of select *Ochotona* teeth from Porcupine Cave. (A) *Ochotona* cf. *princeps,* Lp3 (UCMP 173763) from the Pit (G2 L10). (B) *Ochotona* sp. Trout Cave form, Lp3 (UCMP 173773) from the Pit (G1 L3). (C) *Ochotona* sp. Trout Cave form, Lp3 (in mandible; DMNH 10397) from the Velvet Room (G5 L7). (D) *Ochotona* sp. Trout Cave form, Rp3 (UCMP 173765) from the Pit (G1 L3). (E) *Ochotona* sp. Trout Cave form, LP3 (UCMP 173764) from the Pit (G3 L4). (F) *Ochotona* sp. Trout Cave form, RP3 (UCMP 173766) from the Pit (G3 L6).

posteriorly. In modern specimens this upper surface of the ramus is not as wide and gradually narrows posteriorly.

OCHOTONA *SP. NEAR TROUT CAVE FORM*

DESCRIPTION AND COMMENTS The Lp3 from the Pit G1 L3 is from a small pika with a curved lingual side (versus the typical straight walls; figure 14.2B). The anteroconid and posteroconid are widely confluent. The anteroconid is rounded (as has been observed in some *O. collaris*). The anterointernal fold is short, shallow, and without cement. The anteroexternal fold is slightly deeper than the former and is filled with cement (figure 14.2B). The posteroconid is moderately long with a slightly inclined internal wall. The posterior border of the tooth is straight. These characters are not observed in typical *O. princeps,* and only one character is observed in *O. collaris,* but similar characteristics are observed in *Ochotona* from Cumberland Cave and Trout Cave (Trout Cave Entrance locality; see Pfaff, 1990; M. Erbajeva, pers. obs.). This specimen is unusual, and if there was any pika fossil from Porcupine Cave that could be relegated to a new taxon, it would be this one from Pit level 3. This morph appears to have occurred in the East and West during the Irvingtonian.

All the other p3s have a wide to somewhat wide confluence between the anteroconid and the posteroconid. The anteroconid is rounded on the anterior edge with relatively thick enamel. The anterointernal and anteroexternal folds are the same depth and contain a thin amount of cement on the specimen from the Velvet Room (figure 14.2C). The posteroconid is long with a trapezoidal shape. The enamel is thick on the anterior and external borders, but thin to absent on the posterior border (figure 14.2C,D).

The two P3s have a short and narrow anteroloph, which begins in the middle of the tooth and is directed inward and turns posteroexternally, ending at about a third of the width of the tooth (figure 14.2E,F). All of the p3/P3s resemble those teeth from Trout Cave (M. Erbajeva, pers. obs.).

OCHOTONA *SP. SMALL MORPH A*

DESCRIPTION AND COMMENTS Morph A is a small pika with a thin, low, and gracile jaw. Its ascending ramus is short and slightly inclined posteriorly. The anterior face of the ascending ramus is rather wide in its lower portion and very narrow on the upper area. The base of the angular processus is of moderate width. The lower jaw ends below the lower incisor, forming a distinctive tubercle on the lingual side of the jaw and a relatively small tubercle on the labial side.

OCHOTONA *SP.*

DESCRIPTION AND COMMENTS The predominant remains recovered either were too fragmented or lacked sufficient definition to permit identification beyond the genus level.

Discussion

Ochotona was recovered in 6 of the 26 sites known in Porcupine Cave. Each excavated area presents its own set of chronological problems (see review in Bell and Barnosky, 2000). The age of most deposits in Porcupine Cave appears to be Irvingtonian, although some sediments within Mark's Sink might actually be Blancan (based on the presence of *Hypolagus, Ophiomys parvus, Mictomys vetus,* and *Pliolemmus antiquus;* C. J. Bell, pers. comm.). The majority of pika remains come from the DMNH Velvet Room excavation ($n = 50$ specimens), with equal numbers coming from the Pit ($n = 34$) and Mark's Sink ($n = 34$) (appendix 14.1). Probably the best chronological control is that for the excavations in the Pit. Table 14.2 demonstrates that the number of pika specimens increases as one progresses higher in the deposit; the greatest number (19) are from the surface. One speculation is that pikas were becoming increasingly more numerous in the local environment during the time of this late deposition. However, in all well-

TABLE 14.2
Numbers of Specimens of *Ochotona* from the Stratigraphic Units in the Pit

Location (Grid, Level)	*Taxon*	n
G1 L1	*Ochotona* sp.	19
G1 L2	*Ochotona* sp.	4
G1 L3	*Ochotona* sp. near Trout Cave form	1
G1 L5	*Ochotona* sp.	4
G2 L10	*Ochotona* cf. *princeps*	1
G3 L4	*Ochotona* sp. near Trout Cave form	1
G3 L6	*Ochotona* sp. near Trout Cave form	2
G5/6 L1–3	*Ochotona* sp.	1
G6 L1–3	*Ochotona* sp.	1

TABLE 14.3
Locations within Porcupine Cave for the Unusual Form of Pika Here Termed *Ochotona* sp. near Trout Cave Form

Location (Grid, Level)	*Assigned Age in Years Based on Stratigraphy*[a]
The Pit	
G1 L3	Within the range 600–850 Ka
G3 L4	Within the range 750–900 Ka
G3 L6	Within the range 750–900 Ka
DMNH Velvet Room excavation	
Below horizon C	>780 Ka

[a] See text and chapters 6 and 7.

sampled levels in the Pit (levels 1–7), pikas occur in about equal relative abundance in comparison with the total sample of small mammals (see figure 23.4).

We have not been able to readily discern distinct species and do not see clear-cut distinctions between the various fossils. We have divided the pika specimens into four categories: (1) *Ochotona* cf. *princeps,* (2) *Ochotona* sp. near Trout Cave form, (3) *Ochotona* sp. small morph A, and (4) *Ochotona* sp. What all this means is that the pikas of North America (other than *O. spanglei* and the large O. *whartoni*) are not readily changing in dental form and size, compared with other groups such as arvicoline rodents (Bell and Barnosky, 2000). The p3s from the Pit and the Velvet Room (table 14.3) show some promise for understanding possible subtle changes in small *Ochotona* of North America. It may be that with a better understanding of *Ochotona* from the Pliocene, the specimens from Trout Cave and some of the p3s from the Pit and the Velvet Room will be described as a new taxon.

Whether represented by different species or as one species *(Ochotona princeps)* with morphologically variable populations, pikas seem to have been established in the Rocky Mountains as far south as central Colorado by the middle Irvingtonian. *Ochotona* is recorded no lower than level 10 (G2 L10) in the Pit. Levels 4–8 seem to date to somewhere between 900 and 780 Ka (chapter 7). The higher stratigraphic levels of the Pit (levels 1–3, where most of the *Ochotona* are found) probably are no younger than about 600 Ka and could be as old as about 800 Ka, although Bell and Barnosky (2000) regarded them as dating to somewhere between 750 and 252 Ka. *Ochotona* is recorded from the Velvet Room excavation from as low as horizon M, which would be older than 780 Ka and possibly approaching 1 Ma. The conservative estimation would place *Ochotona* in this excavation area by at least 780 Ka.

Conclusions

The more complete fossil record of ochotonids in the Palearctic (versus that of the Nearctic) has allowed greater elucidation of their evolutionary history in Asia and Europe. The first record of *Ochotona* in North America seems to indicate the arrival of the small pika, *O. spanglei,* in the late Hemphillian, earliest Pliocene. The record of *Ochotona* for the Blancan is unknown, with only an undocumented record from South Dakota (Bjork, 1997). If the chronological assignment of Mark's Sink (lower levels) is correct, then these pika remains are the first documented *Ochotona* from the Blancan. Irvingtonian deposits in North America record both the large pika *(O. whartoni)* and the small species (*O. princeps*–like; Mead, 1987; Mead and Grady, 1996). If the Porcupine Cave record is representative of the greater intermountain West for the early and middle Pleistocene, then the large *Ochotona whartoni* was not in the region and may well have been restricted during this time to the western Arctic (see Mead and Grady, 1996; Morlan 1996). Given this overall sparse record of pikas for the North American Irvingtonian, the deposits in Porcupine Cave have provided the best opportunity so far to study the evolutionary history of *Ochotona* on this continent. Additional study of specimens from this site—especially if more specimens from well-stratified and well-dated sites become available—holds the promise of elucidating evolutionary and biogeographic patterns during a critical time in the North American evolution of pikas.

Appendix 14.1. *Ochotona* Specimens from Porcupine Cave, Reported by Location and Stratigraphic Unit

Specimen No.	*Specimen*	*Provenance*	*Taxon*	*Alveolar Length p3–m3 (mm)*
Badger Room (*n* = 5)				
DMNH 14315	R mandible; edentulous	L mixed	*O.* cf. *princeps*	
DMNH 14316	L mandible: m1–2	L mixed	*O.* cf. *princeps*	
DMNH 17682	L mandible: p4–m2	L mixed	*O.* cf. *princeps*	8.0
DMNH 20435	L mandible: p4–m3	L mixed	*O.* cf. *princeps*	7.3
DMNH 20436	R mandible: p3–m2	L mixed	*O.* cf. *princeps*	7.5
Generator Dome (*n* = 2)				
DMNH 28338	R humerus	PC-8 L2	*O.* cf. *princeps*	
DMNH 29118	R humerus; distal	PC-8 L1	*O.* cf. *princeps*	
Mark's Sink (*n* = 34)				
DMNH 21431	R mandible: p4–m2	PC-10	*O.* cf. *princeps*	8.3
DMNH 21432	L mandible: p4–m2	PC-10	*O.* cf. *princeps*	8.4
DMNH 21433	L mandible: m1–3	PC-10	*O.* cf. *princeps*	7.2
DMNH 21435	L/R mandibles; edentulous; *n* = 4	PC-10	*O.* cf. *princeps*	7.5, 8.2, 8.5
DMNH 27546	R mandible; edentulous	Mixed	*O.* cf. *princeps*	
DMNH 27547	L mandible: m1–2	Mixed	*O.* cf. *princeps*	8.4
DMNH 33474	L mandible: m1–2	Mixed	*O.* cf. *princeps*	8.4
DMNH 36039	L mandible: m1	Mixed	*O.* cf. *princeps*	
DMNH 36130	Premaxilla	Mixed	*O.* cf. *princeps*	
DMNH 36131	R mandible: m2–3	Mixed	*O.* cf. *princeps*	
DMNH 36132	L mandible: p4–m1	L21	*O.* cf. *princeps*	7.3
DMNH 36133	R mandible	Mixed	*O.* cf. *princeps*	7.7
DMNH 36427	Mandible fragment	L28	*O.* cf. *princeps*	
DMNH 36490	Fragment of R mandible: m1–m3	Mixed	*O.* cf. *princeps*	
DMNH 36491	Fragment of R mandible: m1–m3	Mixed	*O.* cf. *princeps*	
DMNH 36492	L mandible: p4–m2	Mixed	*O.* cf. *princeps*	7.2
DMNH 36674	R mandible; edentulous	L24	*O.* cf. *princeps*	
DMNH 36916	L mandible: m1–2	L11	*O.* cf. *princeps*	
DMNH 36917	L premaxilla	L11	*O.* cf. *princeps*	
DMNH 36918	Premaxilla	L30	*O.* cf. *princeps*	
DMNH 36924	Lm1	Mixed	*O.* cf. *princeps*	
DMNH 36925	L mandible; edentulous	Mixed	*O.* cf. *princeps*	8.5
DMNH 37095	Ulna; proximal	Mixed	*O.* cf. *princeps*	7.3
DMNH 37096	R mandible: p4	L17	*O.* cf. *princeps*	7.6
DMNH 37097	L mandible: p4	L42–44	*O.* cf. *princeps*	
DMNH 41347	R mandible: p4–m3	L6	*O.* cf. *princeps*	7.1
DMNH 41369	R mandible: p4–m3	Mixed		
DMNH 41370	Rm1	L28	*O.* cf. *princeps*	
DMNH 41371	LP4	L25	*O.* cf. *princeps*	
DMNH 41372	R mandible: m1–2	L29	*O.* cf. *princeps*	
DMNH 41373	L mandible; edentulous	L29	*O.* cf. *princeps*	
DMNH 41374	R mandible: m1–3	Bilge	*O.* cf. *princeps*	
DMNH 41375	R mandible: p4–m1	Mixed	*O.* cf. *princeps*	
DMNH 41376	L mandible: m1	L29	*O.* cf. *princeps*	

Specimen No.	*Specimen*	*Provenance*	*Taxon*	*Alveolar Length p3–m3 (mm)*
The Pit (*n* = 34)				
CM 65145	Rm2	G1 L1	*Ochotona* sp.	
CM 65311	R mandible; edentulous	G1 L1	*Ochotona* sp.	8.2
CM 65312	L mandible; edentulous	G1 L1	*Ochotona* sp.	8.2
CM 66410	Lp4	G1 L1	*Ochotona* sp.	
CM 66411	Lm1	G1 L1	*Ochotona* sp.	
CM 66413	Lm1	G1 L1	*Ochotona* sp.	
CM 66414	Rm1	G1 L1	*Ochotona* sp.	
CM 66415	Rm1	G1 L1	*Ochotona* sp.	
CM 66416	Molar fragment	G1 L1	*Ochotona* sp.	
CM 66417	RP4	G1 L1	*Ochotona* sp.	
CM 66418	RP4	G1 L1	*Ochotona* sp.	
CM 66420	Rp4	G1 L1	*Ochotona* sp.	
CM 66421	LM2	G1 L1	*Ochotona* sp.	
CM 66422	LM2	G1 L1	*Ochotona* sp.	
CM 66423	RP4	G1 L1	*Ochotona* sp.	
CM 66424	Lower molar fragment	G1 L1	*Ochotona* sp.	
CM 66606	Mandible fragment	G1 L2	*Ochotona* sp.	
CM 66607	Rm2	G1 L2	*Ochotona* sp.	
CM 66609	LP4	G1 L2	*Ochotona* sp.	
UCMP 173763	Lp3	G2 L10	*O.* cf. *princeps;* figure 14.2A	
UCMP 173764	LP3	G3 L4	*O.* sp. near Trout Cave form; figure 14.2E	
UCMP 173765	Rp3	G3 L6	*Ochotona* near sp. Trout Cave form; figure 14.2D	
UCMP 173766	RP3	G3 L6	*Ochotona* sp. near Trout Cave form; figure 14.2F	
UCMP 173767	R mandible: m1–2	G5/6N + 5/8N L1–3	*Ochotona* sp.	
UCMP 173768	LP4	G6 L1–3	*Ochotona* sp.	
UCMP 173769	L mandible: m1	Surface W of G8	*Ochotona* sp.	
UCMP 173770	RP4	G1 L1	*Ochotona* sp.	
UCMP 173771	Lp3	G1 L1	*Ochotona* sp.	
UCMP 173772	RP4	G1 L1	*Ochotona* sp.	
UCMP 173773	Lp3	G1 L3	*Ochotona* sp. near Trout Cave form	
UCMP 173774	LP4	G1 L5	*Ochotona* sp.	
UCMP 173775	Lp4	G1 L5	*Ochotona* sp.	
UCMP 173776	LM2	G1 L5	*Ochotona* sp.	
UCMP 173777	RM2	G1 L5	*Ochotona* sp.	
Velvet Room (*n* = 50)				
Carnegie Museum test pit (UCMP V93175)				
UCMP 173778	R mandible: p4–m3	Test Pit L2	*Ochotona* sp.	
UCMP 173779	LP4	G1 L1B	*Ochotona* sp.	
UCMP 173780	RP4	G1 L1B	*Ochotona* sp.	
UCMP 173781	Mandible; juvenile	G3 L3	*Ochotona* sp.	
UCMP 173782	R mandible: p4–m3	G4 L3	*Ochotona* sp.	7.4

(continued)

Specimen No.	Specimen	Provenance	Taxon	Alveolar Length p3–m3 (mm)
DMNH excavation[a]				
DMNH 6668	L mandible: m2	G1 L9	*Ochotona* sp.	8.0
DMNH 8224	L mandible: p4–m2	G2 L5	*Ochotona* sp.	7.8
DMNH 8525	R premaxilla	G1 L10	*Ochotona* sp.	
DMNH 8526	L mandible: p4–m3	G1 L10	*O.* cf. *princeps*	
DMNH 8527	L mandible: p4–m2	G1 L10	*O.* cf. *princeps*	8.3
DMNH 8859	L mandible; edentulous	G1 L2	*Ochotona* sp.	9.0
DMNH 9819	L humerus	G3 L5	*Ochotona* sp.	
DMNH 10397	L mandible: p3–m3	G5 L7	*Ochotona* sp. near Trout Cave form; figure 14.2C	7.7
DMNH 10875	Maxilla fragment	G7 L13	*Ochotona* sp.	
DMNH 10890	R mandible: m1	G7 L2	Morph A	7.2
DMNH 11316	Humerus; distal	G9 L14	*Ochotona* sp.	
DMNH 11829	R mandible: p4–m2	G8/8A L4	*Ochotona* sp.	8.1
DMNH 11893	L mandible: p4–m2	G8/8A mixed	*Ochotona* sp.	7.8
DMNH 11894	L mandible: m1	G8/8A mixed	*Ochotona* sp.	
DMNH 12021	R maxilla; edentulous	G15 L2	*Ochotona* sp.	
DMNH 12047	L maxilla; edentulous	G7 L below 23	*Ochotona* sp.	
DMNH 12048	L mandible; edentulous	G7 L below 23	*Ochotona* sp.	7.0
DMNH 20673	L ulna	G17 L1	*Ochotona* sp.	
DMNH 20957	Humerus; distal	G13–14 L10C	*Ochotona* sp.	
DMNH 21195	Fragment of R mandible: m2–m3 A	G15 L10A	*Ochotona* sp.	
DMNH 22381	L mandible; edentulous	G20 L7B	*O.* cf. *princeps*	7.3
DMNH 22392	R mandible: m1–2	Bilge	*Ochotona* sp.	7.6
DMNH 22916	Premaxilla	G20 L2	*Ochotona* sp.	
DMNH 23229	R mandible; edentulous	G2 L3	*Ochotona* sp.	8.0
DMNH 23230	R mandible: m1–3	G2 L3	*Ochotona* sp.	7.8
DMNH 23440	Premaxilla	G2 L2	*Ochotona* sp.	
DMNH 27545	Maxilla fragment	G17 L17	*Ochotona* sp.	
DMNH 27860	R mandible: m2–3	G12 L13	*Ochotona* sp.	
DMNH 28949	Premaxilla	G13–14 L10	*Ochotona* sp.	
DMNH 29710	Premaxilla	G25 L2	*Ochotona* sp.	
DMNH 30071	R humerus	G20 L14	*Ochotona* sp.	
DMNH 35438	R mandible: p4–m2	G11 L4	*Ochotona* sp.	
DMNH 35443	R mandible: m1–3	G21 L21	*Ochotona* sp.	
DMNH 36129	Rp4	G16 L13	*Ochotona* sp.	
DMNH 36494	R mandible; edentulous	G0.5, 6, 7 L30	*Ochotona* sp.	7.3
DMNH 36495	L mandible: p4–m2	G0.5–0.6 L30	*Ochotona* sp.	
DMNH 36496	L mandible: p4–m2	G mixed L26	*Ochotona* sp.	7.5
DMNH 36926	Rp4	G12 L5	*Ochotona* sp.	
DMNH 36927	p3	G12 L6	*Ochotona* sp.	
DMNH 41359	LM3	G12 L5	*Ochotona* sp.	
DMNH 41360	R mandible: p4–m3	G11 L18	Morph A	7.2
DMNH 41361	L mandible: p4–m1	G11 L18	Morph A	7.1
DMNH 41362	Palate: p3–m2	Bilge	*Ochotona* sp.	
DMNH 41363	Palate: RP4, M2	Bilge	*Ochotona* sp.	
No number	L mandible: m1–2	G11 L18	*Ochotona* sp.	

Specimen No.	*Specimen*	*Provenance*	*Taxon*	*Alveolar Length p3–m3 (mm)*
Will’s Hole (*n* = 7)				
DMNH 21710	R mandible: p4–m2	PC-11	*O.* cf. *princeps*	8.4
DMNH 21711	L mandible: p4–m2	PC-11	*O.* cf. *princeps*	8.3
DMNH 41364	L mandible: m1–2	PC-11 G7 L26	*O.* cf. *princeps*	
DMNH 41365	R maxilla: M2	PC-11 G7 L26	*O.* cf. *princeps*	
DMNH 41366	Maxilla; juvenile	PC-11 G7 L26	*O.* cf. *princeps*	
DMNH 41367	L mandible; juvenile	PC-11 G7 L26	*O.* cf. *princeps*	
DMNH 41368	R mandible; juvenile	PC-11 G7 L26	*O.* cf. *princeps*	

Provenance abbreviations: G, grid; L, level.

[a] Grid and level information must be converted to lettered horizons according to table 2.2 before it has stratigraphic meaning.

FIFTEEN

Leporidae of the DMNH Velvet Room Excavations and Mark's Sink

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This chapter establishes the presence of certain leporid taxa in the DMNH Velvet Room excavations and in Mark's Sink, which here collectively are called the DMNH Velvet Room sites. As noted in chapter 2, the taphonomy of Porcupine Cave is complex. Some rooms were carnivore dens, and in others, such as the Velvet Room, wood rats (*Neotoma* spp.) seem to have been the principal agent for accumulation. These animals built their nests within the room, scavenging outside for bones, twigs, and other matter suitable for incorporating into their nests. Often the bones came from raptor kills and owl pellets. Over spans of time up to thousands of years (Finley, 1990), wood rat dens deteriorate, in some cases scattering their contents over the floor, perhaps to be reused by other wood rats. Thus there is potential for some recycling of bone in such deposits, complicating interpretations of the degree of time averaging in the fossil assemblage of any particular stratigraphic level. However, in Holocene wood rat accumulations similar to those of the Pit and presumably to the Velvet Room deposits, analogously thick stratigraphic levels span no more than 1400 years (Hadly, 1999). The leporids of the DMNH excavations in the Velvet Room must be interpreted with such potential for time averaging in mind.

The leporid remains of the DMNH Velvet Room sites consist mostly of isolated teeth, fragments of dentaries and maxillae, and numerous postcranial remains. The postcranial remains were identified to genus only. Dentaries with p3 present allowed the most confident identifications (Ramos, 1999). Tables 10.6, 10.12, and 10.13 show the presence or absence of the various genera of leporids identified in the DMNH Velvet Room sites.

Localities

DMNH 644

DMNH 644 is the most comprehensive excavation in the Velvet Room, with more than 2 m of stratified material excavated. Paleomagnetic dating indicates that horizons A–C are younger than the Brunhes-Matuyama boundary, which dates to about 780 Ka; horizons D and below appear to predate 780 Ka. Horizon A is composed of a modern assortment of packrat fecal pellets, bone, and plant material. Horizon B is a rich brown layer. Horizon C is gray in color. A tan layer, horizon D, lies atop a brown laminated zone, horizon E. Horizons F–K subdivide a rocky, light brown layer. As one progresses down, horizons L–R become progressively redder. Wood rats seem to have been a major taphonomic agent in this locality, although fluvial deposition is evidenced by the presence of intact, freshwater snail shells in some horizons. In general, however, the strata are layered in a talus cone, the apex of which is near a purported sealed entrance into the room. (See chapter 2 for additional details.)

Mark's Sink

Mark's Sink (DMNH 1349) is located in the Velvet Room apart from locality 644. It is a small sink filled with bone and debris. It was originally thought to be stratified, but further work suggested that it was badly bioturbated, and deposition was so complex that it is currently regarded as a mixed sample, even though the lowest sections were differentiated into more than

33 levels as they were excavated. The source of this very rich bone deposit is unclear.

Leporid remains were identified using the information and methods outlined in a previous study (Ramos, 1999). Not all specimens were studied; therefore it was impossible to determine meaningful minimum numbers of individuals and numbers of identifiable specimens. All conclusions therefore are based on presence-absence data.

Systematic Paleontology

Class Mammalia

Order Lagomorpha

Family Leporidae

HYPOLAGUS

DESCRIPTION The defining character of this genus is the p3, which has a posterior external reentrant (PER; figure 15.1) extending no more than halfway across the tooth, a very shallow anterior external reentrant (AER), and usually no other reentrants. Species in this genus show a wide range of size, from that of a small cottontail to that of a large hare. The degree of cursoriality ranges from less cursorial than *Sylvilagus* to typical jackrabbit ecomorph (Dawson, 1958; Campbell, 1969; White, 1984).

GEOGRAPHIC DISTRIBUTION This extinct genus was widespread throughout North America and Europe in the Pleistocene.

TEMPORAL DISTRIBUTION Species of this genus are known from the early Miocene to the early Pleistocene in North America, but only from the Late Miocene in Asia and the Late Pliocene in Europe (White, 1984, 1991b).

HYPOLAGUS *SPP.*

REFERRED SPECIMENS DMNH 33269, 38978, 38983, 38988, 38997, 39060, 39081, 39111, 39150, 39168, 39172, 39175, 39194, 39300, 39304, 39349, 39362.

COMMENTS This genus was a surprise at Porcupine Cave because it was thought to have gone extinct at the end of the Pliocene (White, 1987). However, Repenning et al. (1995) reported *Hypolagus* from the earliest Irvingtonian at Froman Ferry Fauna. In addition to the p3 characteristics noted previously, the P2 has a single anterior reentrant (AR), which is similar to that in *Brachylagus*. There may be three species of *Hypolagus* present in the DMNH Velvet Room sites. One is represented by two jaws with teeth present, as well as numerous p3s. This is a small rabbit, about the size of *Sylvilagus bachmani* and somewhat larger than *Brachylagus coloradoensis*. Of the two larger potential species, one is about the size of a large *Sylvilagus* or *L. americanus* and has a triangular p3 with very thick enamel. It is known from a few scattered p3s. The other is known from a single p3. It is large, nearly the size of that in *Lepus townsendii*.

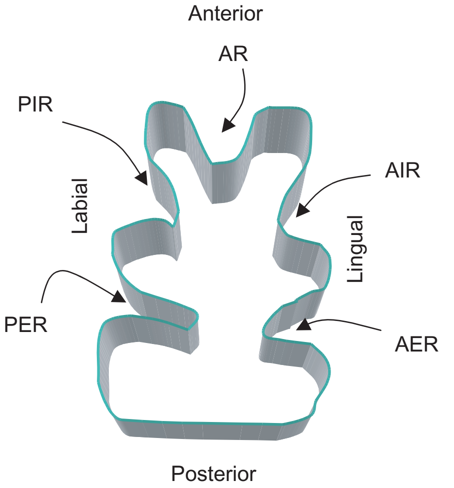

FIGURE 15.1 Terminology for leporid p3 morphology. AER, anterior external reentrant; AIR, anterior internal reentrant; AR, anterior reentrant; PER, posterior external reentrant; PIR, posterior internal reentrant.

LEPUS

DESCRIPTION These are medium to large leporids, of which there are approximately 29 species (Chapman and Flux, 1990). The interparietal is lacking in adults, and the postorbital processes are triangular and arched over the orbits ($2n = 48$; Robinson et al., 1983). These hares are typically somewhat cursorial *(L. americanus)* to highly cursorial *(L. alleni),* and most prefer open habitats.

GEOGRAPHIC DISTRIBUTION Extant species of *Lepus* are found throughout Europe, Asia, Africa, Greenland, and North America (Flux and Angermann, 1990).

TEMPORAL DISTRIBUTION Specimens referable to *Lepus* are known from the early Pliocene to the present (Kurtén and Anderson, 1980).

LEPUS AMERICANUS *ERXLEBEN, 1777*

REFERRED SPECIMENS DMNH 6709, 8932, 9402, 10700, 11067, 11153, 11199, 11911, 14697, 37076, 37079, 39052, 39080, 39103, 39106, 39119, 39137, 39198, 39308, 39318, 39367.

DESCRIPTION *Lepus americanus,* the snowshoe hare, is the smallest of the North American species of *Lepus*. Its skull is small, the size of that in some *Sylvilagus,* arched over the orbits and lacking anterior supraorbital processes. The p3 is simple, with a single AR and with little to no crenulation in the PER. This species molts into a pale or white winter pelage, a trait also expressed by *L. arcticus, L. othus, L. townsendii,* and *L. timidus.*

GEOGRAPHIC DISTRIBUTION *Lepus americanus* is found throughout much of Canada and Alaska, and in the Sierra Nevadas, Cascades, Rocky Mountains, and Appalachian Mountains of the coterminous United States. It prefers the dense understory of subclimax forests but can be found in a variety of forest types. *L. americanus* is still present in South Park, although not in areas immediately adjacent to the site.

TEMPORAL DISTRIBUTION This species has a fairly long history. Besides being known from the middle Irvingtonian sediments of the Velvet Room, *L. americanus* has been reported from several late Rancholabrean sites, some of which are well south of its current distribution (Kurtén and Anderson, 1980).

COMMENTS This species is very common in the DMNH Velvet Room sites and is easily distinguished from most other leporids, even with fragmentary material. *L. americanus* has a p3 pattern that places it in the Arctic hare clade, but many extant specimens exhibit a greater degree of crenulation in the posterior fold of the PER than in any other species in this clade. However, most of the *L. americanus* specimens from Porcupine Cave either lack this crenulation or have very little.

LEPUS CALIFORNICUS *GRAY, 1837*

REFERRED SPECIMENS DMNH 39059, 39324.

DESCRIPTION *Lepus californicus,* the black-tailed jackrabbit, is a large, lean, highly cursorial hare that is well adapted to both deserts and plains. Molecular and morphological evidence indicates that it is more closely related to *L. alleni* and its allies than to *L. townsendii* (Nelson, 1909; Halanych and Robinson, 1997; Ramos, 1999). The skull is long and narrow with a flattened profile. The p3 is quite crenulated, more so than in *L. townsendii* and its allies but less so than in *L. alleni* or *L. callotis.*

GEOGRAPHIC DISTRIBUTION *L. californicus* can be found from the Pacific Coast of Baja California and California, across the Great Basin, and into the Great Plains, reaching south into central Mexico.

TEMPORAL DISTRIBUTION This species is reported from both early Irvingtonian (Curtis Ranch, southern Arizona) and late Irvingtonian sites (Slaton, west Texas), and is common in Rancholabrean sites within its present range (Kurtén and Anderson, 1980).

COMMENTS *L. californicus* is an inhabitant of open grasslands and shrub desert. This highly cursorial hare is present in Colorado but is not found in South Park today. It is distinguished from *L. townsendii* by having a more slender dentary, slightly smaller teeth, and more crenulation on the enamel reentrants of the p3. This hare is known from the early Irvingtonian, and possibly earlier (Kurtén and Anderson, 1980).

LEPUS TOWNSENDII *BACHMAN, 1839*

REFERRED SPECIMENS DMNH 9630, 9923, 11202, 11769, 20776, 23436, 27078, 38982, 38986, 38996, 39053, 39058, 39063, 39073, 39074, 39095, 39115, 39118, 39178, 39183, 39196, 39302, 39317, 39322, 39330, 39339, 39340, 39351, 39354, 39358, 39369.

DESCRIPTION This is a medium to large hare with a heavy body and moderately long ears. Its skull shape and p3 patterns closely resemble those of *L. arcticus, L. othus,* and *L. timidus.* There is geographic variation in the shapes of the supraorbital processes and incisors. Specimens from the northernmost reaches of the range lack an anterior supraorbital process. In addition, northern specimens have the *Sylvilagus* pattern of incisor, in which the groove is simple and divides the tooth into rounded, anterior surfaces that are roughly equal in size. This pattern of incisor is also found in *L. arcticus, L. timidus,* and *L. othus* (Ramos, 1998, 1999).

GEOGRAPHIC DISTRIBUTION *Lepus townsendii,* the white-tailed jackrabbit, is found from above treeline to the plains. Its range extends from the Sierra Nevada and Cascade Mountains, across the northern Great Basin, through the Rocky Mountains and the Great Plains. The southern limits of its range have been receding since the turn of the century, while the range of the black-tailed jackrabbit has been expanding. Ramos (1998) reported evidence of this trend dating from the Rancholabrean.

TEMPORAL DISTRIBUTION The oldest record for the white-tailed jackrabbit comes from Mullen II and is late Irvingtonian. The species is also known from several Rancholabrean sites within it present range (Kurtén and Anderson, 1980).

COMMENTS The white-tailed jackrabbit still inhabits areas immediately surrounding the cave site. Its presence in the early and middle Irvingtonian sediments of Porcupine Cave is a temporal extension of its known distribution.

SYLVILAGUS

DESCRIPTION Cottontails are small to medium or large rabbits with agouti coloring and complex p3 patterns. They retain many ancestral characters, such as keeping the interparietal into adulthood, short limbs, and less specialization for locomotion than is found in jackrabbits. Cottontails are often confused with the European rabbit *(Oryctolagus cuniculus)* but differ in that true cottontails do not burrow, do not live in social groups, and generally have shorter ears.

GEOGRAPHIC DISTRIBUTION Species of this genus are known only from North and South America (Chapman and Ceballos, 1990).

TEMPORAL DISTRIBUTION The oldest known *Sylvilagus* species are reported from Blancan sites in southern California, southern Arizona, northern Texas, and Florida (White, 1984, 1991a).

SYLVILAGUS AUDUBONII *(BAIRD, 1857)*

REFERRED SPECIMENS DMNH 27084, 39146.

DESCRIPTION This rather small rabbit has relatively longer ears and legs than other cottontails, reflecting its adaptation for arid, open terrain. However, there is a significant amount of geographic variation in these traits. The skull is arched posterior to the orbits as in *S. nuttallii,* and the p3 has moderate crenulation.

GEOGRAPHIC DISTRIBUTION This species is found throughout the Great Plains, Great Basin, and Southwest and down into the central and western regions of northern Mexico. It can be found in sagebrush plains and pinyon-juniper stands. This cottontail is the most cursorial of its congeners and will tolerate less cover than other cottontails. Genetically it is closely related to *S. nuttallii* (Robinson et al., 1984), and its skull and p3 morphology substantiate this relationship because these two cottontails are the most difficult to distinguish from one another using only skull fragments (Ramos, 1999).

TEMPORAL DISTRIBUTION The species was known only from Recent and Rancholabrean sites (Kurtén and Anderson, 1980) until it was identified in Porcupine Cave deposits.

COMMENTS It is quite difficult to distinguish *S. audubonii* from *S. nuttallii.* Enamel patterns of the p3 between the two show a high degree of variation and overlap and cannot be relied upon for confident identifications. Much of the material was assigned to *S. nuttallii* based upon size. However, some specimens were significantly larger than the usual range for *S. nuttallii.* These were assigned to *S. audubonii,* which is somewhat larger. The desert cottontail does not inhabit South Park at present and, owing to the apparently close phylogenetic and geographic proximity between it and the mountain cottontail (Findley et al., 1975; Robinson et al., 1984; Chapman and Ceballos, 1990), it is possible that the two had not completely diverged by the early and middle Irvingtonian.

SYLVILAGUS NUTTALLII *(BACHMAN, 1837)*

REFERRED SPECIMENS DMNH 10555, 11200, 39056, 39065, 39068, 39077, 39087, 39092, 39141, 39158, 39321.

DESCRIPTION This is a small cottontail, genetically and morphologically similar to *S. audubonii.* Cranial characters do not easily distinguish this species from *S. audubonii.* The skull is arched posterior to the orbits with small anterior supraorbital processes that do not fuse with the skull, and the auditory bullae tend to be small. The p3 shows a fair amount of variation, but in general it is not nearly so complex as that of *S. aquaticus* or *S. palustris,* but not so simple as that of *S. floridanus.* It has relatively short ears and a more grayish pelage than *S. floridanus.*

GEOGRAPHIC DISTRIBUTION The mountain cottontail is a small rabbit that occurs in the intermountain region of North America. Its distribution includes much of the southern and central Rocky Mountains, north across the Great Basin to the Sierra Nevada and Cascade Mountains, where it can be found in rocky areas with brush, sagebrush (*Artemisia* spp.), or both.

TEMPORAL DISTRIBUTION The species is known from late Rancholabrean deposits within its current range (Kurtén and Anderson, 1980).

COMMENTS The mountain cottontail currently inhabits South Park, but it is not common in the Porcupine Cave sediments. The distinction between this species and *S. audubonii* is not clear from the fragmentary remains, and it may reflect a taxonomic indistinction during the time frame represented at Porcupine Cave.

AZTLANOLAGUS *SPP.*

REFERRED SPECIMENS DMNH 39054, 39057, 39061, 39066, 39067, 39071, 39072, 39075, 39078, 39093, 39100, 39104, 39108, 39113, 39114, 39120, 39124, 39129, 39133, 39134, 39136, 39149, 39154, 39169, 39173, 39182, 39186–39191, 39195, 39197, 39306, 39307, 39309, 39313, 39319, 39320, 39323, 39327, 39329, 39331, 39334, 39335, 39347, 39348, 39350, 39353, 39356, 39359, 39361, 39363–39366.

COMMENTS This genus is represented by remains that are significantly larger than those of the single described species, *Aztlanolagus agilis* (Russell and Harris, 1986). It is the most common leporid found in the Mark's Sink deposits but is very rare in DMNH 644. It is a small leporid, approximately the size of *S. nuttallii,* and it is found in association with both extant taxa, such as *L. americanus* and *S. nuttallii,* and extinct forms, such as *Hypolagus* spp. and *Brachylagus coloradoensis* (Ramos, 1999). Winkler and Tomida (1988) noted that Blancan and Irvingtonian specimens of *Aztlanolagus* have less crenulation in their reentrants than do the younger specimens from the Wisconsinan. The *Aztlanolagus* material found at Porcupine Cave contains both the highly crenulated, though larger, specimens, and also less crenulated specimens, which are even larger. The latter appear in the lower parts of Mark's Sink.

BRACHYLAGUS

DESCRIPTION This genus is characterized by small size, a rudimentary tail, and the lack of an AR in the simplistic p3. The P2 has a single AR, a character unique among the living North American leporids. Only one living species is known, and it has short, rounded ears and very short hind legs. This genus was alternately considered part of *Lepus* and *Sylvilagus* before finally being separated out owing to its genetic and morphological differences.

GEOGRAPHIC DISTRIBUTION Two species are known, a living species found only in the Great Basin region and an extinct species recently described from central Colorado.

TABLE 15.1

Matrix of Species Presence and Absence for the Horizons of the Main Dig Site in the Velvet Room

Species	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*
Hypolagus sp.	—	—	—	—	—	—	•	—
Lepus americanus	•	•	•	•	•	•	—	•
Lepus californicus	—	•	—	—	—	—	—	—
Lepus townsendii	•	•	•*	—	—	—	—	—
Lepus sp.	—	•	—	—	—	—	—	•
Sylvilagus audubonii	•	—	—	•	—	—	—	•
Sylvilagus nuttallii	•	•*	•*	—	—	—	—	—
Sylvilagus sp.	•	—	—	•	—	—	—	—
Brachylagus coloradoensis	—	—	—	—	—	—	—	—
Aztlanolagus sp.	—	—	—	•	•	•	—	—

NOTE: •, present; *, tentative identification.

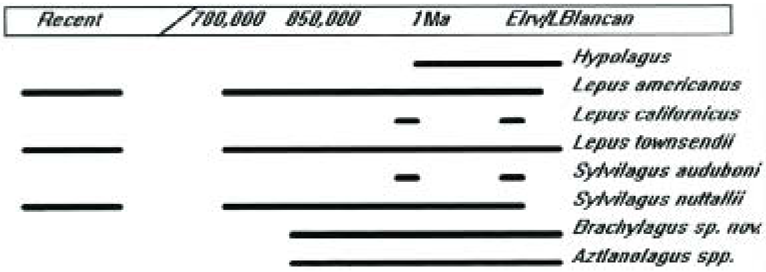

FIGURE 15.2 Temporal range of species identified in the DMNH Velvet Room sites. EIrv/Lblancan, early Irvingtonian / late Blancan boundary. The 780 Ka calibration is the Brunhes-Matuyama boundary.

TEMPORAL DISTRIBUTION Species of *Brachylagus* are known from the Irvingtonian of eastern Nevada (C. J. Bell, pers. comm.) and the early Irvingtonian of central Colorado (Ramos, 1999).

BRACHYLAGUS COLORADOENSIS *RAMOS, 1999*

REFERRED SPECIMENS DMNH 28901, 33250, 33255, 33257, 33260, 33261, 33270–33272, 39062, 39079, 39109, 39116, 39117, 39121–39123, 39144, 39147, 39161, 39176, 39305, 39315, 39316. See also Ramos (1999).

COMMENTS This is a small leporid, only slightly more robust than the extant species, *Brachylagus idahoensis.* The p3 is simple, with a PER extending one-half to two-thirds of the way across the width of the tooth. A slight posterior internal reentrant (PIR) is often present, but there is no AR. The P2 has a single AR as in *Hypolagus.* The initial excavators of the Pit identified the remains as *B. idahoensis* (Barnosky and Rasmussen, 1988); however, the dental differences are significant, and these fossils are now allocated to a new species of *Brachylagus* (Ramos, 1999).

Discussion and Conclusions

At least 7, and possibly 10 (see the descriptions of *Hypolagus* spp. and *Aztlanolagus* spp.), species of Leporidae are herein identified from the DMNH Velvet Room sites. Of these, three are still found in the vicinity, three (possibly six) are extinct, and two have current distributions that do not include the South Park area of Colorado. All species were identified from the mixed strata of Mark's Sink. Table 15.1 gives the distribution of identified species through DMNH Velvet Room 644. Figure 15.2 shows the temporal distribution elsewhere.

Based on the information in table 15.1 and figure 15.2, horizon G and below in DMNH 644 could be as old as 1 Ma because *Hypolagus* is present. However, chapter 7 discusses the possibility of an upward range extension for *Hypolagus. Aztlanolagus* suggests an age of at least 850 Ka for horizons D–F. Only the lagomorphs identified as extant species occur above horizon D. These data are consistent with other biostratigraphic information.

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SIXTEEN

Identification of Miscellaneous Mammals from the Pit Locality

Including Soricidae, Leporidae, Geomyoidea

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Several taxa in the Pit are represented by very few specimens or by material that is presently impossible to identify to the species level. Nevertheless, these taxa are important in characterizing the Pleistocene fauna. This chapter summarizes the criteria that were used to identify these specimens, which include soricids (shrews), leporids (rabbits and hares), and geomyoid rodents (gophers).

IDENTIFICATION CRITERIA FOR MISCELLANEOUS SPECIES

Class Mammalia

Order Insectivora

Family Soricidae

REFERRED MATERIAL CM 65487–65489; UCMP 165581.

DESCRIPTION AND COMMENTS Soricidae (shrews) may be possible to identify further and are under study by Russell Graham. The general morphology of the teeth and jaws resembles that of *Sorex.*

Order Lagomorpha

Family Leporidae

The leporids from the Pit were identified by A. D. Barnosky. It was not possible to confidently identify leporine specimens to the level of species, or in most cases even genus, on the basis of qualitative traits of isolated teeth. The only moderately diagnostic tooth is the p3, but even that tooth is subject to wide variation within species and exhibits broad overlap in morphology between *Lepus* and *Sylvilagus.* In view of the potential for error in ascribing too great a level of taxonomic detail to identification of isolated leporine teeth, a conservative approach was taken in identifying specimens from the Pit. Leporids from the Badger Room were identified by Faysal Bibi using the criteria noted later in this chapter. Leporid specimens from localities other than the Pit and Badger Room were identified by C. Baxter using criteria noted in chapter 15.

HYPOLAGUS *SP.*

REFERRED MATERIAL UCMP 164573, 164595.

DESCRIPTION AND COMMENTS *Hypolagus* was recognized on the basis of the p3 morphology, which is characterized by a posterior external reentrant that extends only about 50% of the width of the tooth, no anterior reentrant, and size range similar to *Lepus* or large *Sylvilagus.*

LEPUS *SP.*

REFERRED MATERIAL CM 63615, 65200, 65607, 66400; UCMP 164000–164003, 164013, 164018, 164019, 164022–164024, 164032, 164043, 164048–164052, 164130, 164203, 164224, 164258, 164263–164265, 164267, 164357, 164358, 164375, 164376, 164388, 164415, 164450, 164516, 164604–164607.

DESCRIPTION AND COMMENTS Specimens with a p3 that fell within the largest two-thirds of the size range of the Pit sample, with an anterior reentrant composed of only one inflection and a noncrenulated anterior margin of the posterior external reentrant, were referred to *Lepus.* In relatively few cases, upper or lower cheek teeth were referred to *Lepus* solely on the basis of very large size (e.g., upper 5% of sampled size range). Specimens were also assigned to *Lepus* if the distance between the alveoli for the I and p3 was greater than 21 mm or if the p3 itself had the *Lepus* or *Sylvilagus* enamel pattern but measured greater than 3.7 mm anterior-posterior, following White (1991a, 1991b).

All of the specimens referred to *Lepus* and *Sylvilagus* are characterized by a posterior external reentrant that extends at least 70–95% of the width of the tooth. This, the presence of an anterior reentrant, and the absence of such features as a pronounced anterior internal or posterior internal reentrant, precluded reference to such genera as *Hypolagus, Alilepus, Brachylagus, Aluralagus, Romerolagus,* and *Aztlanolagus*.

SYLVILAGUS *SP.*

REFERRED MATERIAL CM 63673, 63684, 63688, 63691, 63692, 66602; UCMP 164021, 164047, 164057, 164142, 164199, 164201, 164202, 164266, 164378, 164467, 164509.

DESCRIPTION AND COMMENTS Specimens were designated as *Sylvilagus* if they had a p3 that fell in the middle (e.g., all but the largest 5% or smallest 5%) of the size range for Porcupine Cave Pit specimens and also had an anterior reentrant that contained at least two inflections. Most of these specimens also exhibited some crenulation of the enamel band that composes the anterior margin of the posterior external reentrant.

Because it was not possible to confidently distinguish between several species of *Sylvilagus* or *Lepus* solely on the basis of isolated teeth, most of the specimens referred to one of these genera carry the species designation "sp." With detailed quantitative work it may eventually be possible to distinguish which species are present at Porcupine Cave Pit, but such work is beyond the scope of the present treatment.

AZTLANOLAGUS *SP.*

REFERRED MATERIAL CM 63679; UCMP 164256, 164257, 164260, 164355, 164356, 164379, 164389, 164390, 164416–164420, 164451, 164452, 164461–164464, 164490, 164491, 164498, 164499, 164520, 164539, 164540, 164544, 164545, 164555–164567, 164584, 164585, 164596, 164597, 164599, 164602.

DESCRIPTION AND COMMENTS Assignment to *Aztlanolagus* required a p3 characterized by a deep anterior internal reentrant, anterior external reentrant, posterior internal reentrant, and posterior external reentrant, as well as a prominent anterior reentrant, as figured by Winkler and Tomida (1988) and White (1991a, 1991b). Mandibles of small to intermediate size that lacked p3, but exhibited molars with a highly crenulated anterior enamel band on the talonid, also were referred to *Aztlanolagus,* as were isolated lower molars with the highly crenulated anterior enamel band on the talonid.

BRACHYLAGUS COLORADENSIS *RAMOS, 1999*

REFERRED MATERIAL CM 63666, 63670, 63671, 63677, 63694, 65146, 65486, 65604, 66120, 66405, 66408, 66409, 66431, 66432, 66603, 66604; UCMP 158150, 164044–164046, 164062, 164068-164071, 164096–164102, 164141, 164193, 164194–164198, 164259, 164261, 164262, 164352–164354, 164377, 164409, 164465, 164466, 164468, 164482, 164521.

DESCRIPTION AND COMMENTS *Brachylagus coloradensis* is relatively easy to recognize based on its diminutive size and simple P2 (with only one deep anterior reentrant) and p3 (with no anterior reentrant and a posterior external reentrant that commonly extends less than 75% of the width of the tooth). P2s and p3s that featured characteristics deemed diagnostic by Ramos (1999) were therefore referred to *B. coloradensis*. Very small (e.g., those in the smallest 5% of the sample size range) leporine teeth and edentulous jaws and maxillaries were assumed to belong to *B. coloradoensis* by their stratigraphic association with the diagnostic teeth, since no other diminutive leporines are known from the deposits.

LEPORINAE SP.

REFERRED MATERIAL CM 63607–63614, 63616–63663, 63665, 63667–63669, 63672, 63674–63676, 63678, 63680, 63681–63683, 63685–63687, 63689, 63690, 63693, 63695–63700, 65025–65035, 65192, 65194, 65216, 65313–65315, 65485, 65592–65594, 65605, 65606, 66399, 66401–66404, 66425–66430, 66463, 66464, 66600, 66601; UCMP 164004–164012, 164014–164017, 164020, 164025–164031, 164033–164042, 164053–164056, 164058–164061, 164063–164067, 164072–164095, 164103–164129, 164131–164140, 164143–164192, 164200, 164204–164223, 164225–164255, 164268–164351, 164359, 164360–164374, 164380–164387, 164391–164408, 164410–164414, 164421–164449, 164453–164460, 164469–164481, 164483–164489, 164492–164497, 164500, 164501–164508, 164510–164515, 164517–164519, 164522–164538, 164541–164543, 164546–164554, 164557–164566, 164568–164572, 164623–164625.

DESCRIPTION AND COMMENTS All specimens of leporines that fell within the upper 95% of the sample size range and that could not be directly associated with a p3 were given the designation "Leporinae sp." It is likely that some of these specimens represent *Lepus,* some *Sylvilagus,* and some *Aztlanolagus,* but at present there is no reliable way to differentiate this nondiagnostic material.

LEPORIDAE, SPECIES INDETERMINATE

REFERRED MATERIAL UCMP 164574–164583, 164586–164594, 164598, 164600, 164601, 164603.

DESCRIPTION AND COMMENTS Teeth that were clearly leporid but that exhibited none of the diagnostic traits noted previously are listed in this category.

Order Rodentia

Superfamily Geomyoidea

GEOMYOID, SPECIES INDETERMINATE

REFERRED MATERIAL UCMP 158080, 158081.

DESCRIPTION AND COMMENTS *Dipodomys* specimens were reported as possibly present in the Pit by Bell and Barnosky (2000). That possibility was based on one isolated m3 (UCMP 158080) from level 7. This tooth, although superficially similar to *Dipodomys* lower third molars, is substantially larger (length 1.4 mm, posterior width 1.3 mm, anterior width 0.9 mm) than in *D. ordii* or *D. microps*. It compares favorably with *Geomys bursarius* in overall morphology, but it is slightly smaller and has enamel all the way around the occlusal surface, whereas *G. bursarius* has dentine tracts. A p4 (UCMP 158081) from the same level also resembles *G. bursarius,* except for much smaller size and a slightly more anteroposteriorly compressed anterior loph. In these respects the tooth closely resembles *Pliogeomys;* however, the Porcupine Cave specimens are unrooted and hence cannot be assigned to that genus. The separation between the anterior and posterior lophs is too pronounced and the anterior loph too rounded to be *Dipodomys*. Given the occurrence of the p4 and m3 in the same level, and their resemblance to *Geomys,* it seems likely that they indicate a related geomyoid; however, there are several geomyoid genera, including *Cratogeomys, Nerterogeomys,* and *Geomys,* which share similar p4 and m3 morphology and are distinguished by characters of skull and jaw morphology. Unfortunately, only these two isolated cheek teeth record the presence of this geomyoid species. Therefore, the material is presently considered nondiagnostic at the generic level, but it does indicate the presence of a geomyoid rodent other than *Thomomys*.

Family Geomyidae

THOMOMYS *SP.*

REFERRED MATERIAL CM 65590, 65839–65841, 66119, 66123–66144, 66263, 66395–66398, 66447–66450, 66623, 66625–66627; UCMP 158000–158009, 158012–158018, 158021, 158023–158030, 158032, 158034–158045, 158047–158055, 158057, 158059, 158060–158071, 158074–158079, 158083, 158085–158089, 158091–158095, 158097–158106, 158108–158111, 158113–158115, 158119–158124, 158127–158132, 158134, 158136–158141, 158143–158147, 164626–164631, 164671, 164680, 164696–164700, 164702, 164704–164706, 165501, 165502, 165541–165543.

THOMOMYS *AFF. T.* TALPOIDES

REFERRED MATERIAL CM 65484; UCMP 158010, 158019, 158022, 158031, 158033, 158046, 158056, 158058, 158072, 158073, 158082, 158084, 158090, 158096, 158107, 158116, 158117, 158125, 158126, 158133.

THOMOMYS *AFF.* T. BOTTAE

REFERRED MATERIAL UCMP 158011, 158112, 158118, 158135, 164701, 164703.

DESCRIPTION AND COMMENTS Species of *Thomomys* in the Pit were identified by S. S. B. Hopkins and assigned to *Thomomys* sp., *T.* aff. *T. talpoides,* or *T.* aff. *T. bottae*. Dentally the species can only be distinguished by characters of the lower fourth premolar. Thus all teeth other than p4 were assigned to *Thomomys* sp. The p4 in *T. bottae* and closely related species is characterized by an anterior loph that is rounded or ovate on its anterior margin. In *T. talpoides* and related species, the anterior loph of p4 is triangular and asymmetrical (Thaeler, 1980). Two specimens of the anterior part of the skull exhibited the asymmetrically arched palatal outline in lateral view that Thaeler (1980) noted as diagnostic of *T. talpoides* and allied species. Designations are to species groups (indicated by "aff.") because of the difficulties of distinguishing between most species within the *bottae* or *talpoides* groups based solely on dental remains.

Family Muridae

PEROMYSCUS *SP.*

REFERRED MATERIAL CM 65304–65429, 65527, 65528, 65835, 65836, 66110–66118, 66523; UCMP 158116–158173, 158175–158181, 158183–158200, 164679, 165503–165530, 165532–165540, 165544–165548, 165550, 165551, 165556–165559, 165562–165569, 165571–165580.

DESCRIPTION AND COMMENTS These specimens were assigned to *Peromyscus* on the basis of similarity of the cheek teeth to those of modern specimens of the genus. It may be possible with more detailed work to determine which species are present.

Family Erethizontidae

ERETHIZON *SP.*

REFERRED MATERIAL CM 65023; UCMP 165583, 165584.

DESCRIPTION AND COMMENTS Referral was based on similarity of the cheek teeth to those of modern specimens of *Erethizon dorsatum*.

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SEVENTEEN

Systematics and Faunal Dynamics of Fossil Squirrels from Porcupine Cave

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Squirrels (Rodentia, Sciuridae) are diverse taxonomically and ecologically in the extant North American fauna (Hall, 1981). On a broad scale, the roots of sciurid diversity extend deeply in time, with fossils known as far back as the early Oligocene (e.g., Sutton and Black, 1975; Emry and Thorington, 1984), but adaptive radiation leading to modern species and species groups was probably concentrated in the late Neogene. Details of this radiation remain sketchy. It is tempting to seek causation in Plio-Pleistocene environmental fluctuations associated with glacial-interglacial variation (e.g., Vrba, 1992), but testing this hypothesis is difficult. Although the latest Pleistocene record of sciurids is dense (see Kurtén and Anderson, 1980; Harris, 1985), the earlier record (Blancan through early Rancholabrean) is relatively sparse, primarily documenting ground-dwelling species from the Great Plains (e.g., Hibbard, 1941a; Hazard, 1961; Paulson, 1961; Skinner and Hibbard, 1972; Eshelman, 1975; Goodwin and Hayes, 1994; Goodwin, 1995a, 1995b) and usually lacking sufficiently precise chronological control to reconstruct glacial-interglacial transitions.

The fossil assemblage from Porcupine Cave provides rich documentation of Irvingtonian faunal diversity at high elevations in the central Rocky Mountains (Barnosky and Rasmussen, 1988). Samples from various sites in the cave probably span a significant period of time within the Irvingtonian, and at least one site (the Pit) may document one and perhaps more glacial-interglacial cycles. This record may allow investigation of faunal response to glacial-interglacial transitions prior to the Pleistocene-Holocene boundary (Wood and Barnosky, 1994; Barnosky et al., 1996). Prior to this report, information on Irvingtonian sciurids from the vicinity of Colorado and northern New Mexico was known only from Hansen Bluff (Rogers et al., 1985) and SAM Cave, with the latter locality producing at least seven species, including one species each of *Cynomys, Tamias,* and *Sciurus,* and four species of *Spermophilus,* according to the faunal list in Rogers et al. (2000).

Previous work on sciurids from Porcupine Cave demonstrated that they are diverse (more than seven species [Barnosky and Rasmussen, 1988; Anderson, 1996]); showed that some sciurids exhibited marked changes in relative abundance within the stratified Pit sequence (Wood and Barnosky, 1994; Barnosky et al., 1996); and permitted paleoclimatic interpretation based in part on the sciurid assemblage (Wood and Barnosky, 1994; Barnosky et al., 1996; Rouse, 1997). The primary purposes of the present study are twofold. First, I characterize more completely the taxonomic diversity and patterns of variation of the sciurid assemblage from various sites in Porcupine Cave. Second, I explore implications of the sciurid assemblage for biostratigraphic reconstructions, understanding temporal environmental variation, and working out the adaptive history of the Sciuridae.

Materials and Methods

Sites and Chronology

Porcupine Cave includes numerous fossil-bearing sites that exhibit significant faunal and presumably chronological variation. Geochronologic and biostratigraphic evidence indicates that most sites fall within the Irvingtonian (early to middle Pleistocene). The following sites yielded fossils examined in the present study: Badger Room (BR), Come-A-Long Room (CAR), Fissure Fill A (FFA), Generator Dome (GD), Mark's Sink (MS), Pit, Velvet Room–CM excavation (VR-CM), Velvet Room–DMNH excavation (VR-DMNH), and Will's Hole (WH). The Pit and VR-DMNH samples were divided into stratigraphic subsamples, using field levels (Pit) or composite horizons (VR-DMNH). Samples from other sites could not be subdivided into stratigraphic levels.

Materials Examined

I studied all sciurid taxa exclusive of *Marmota;* information on the latter genus, as included in this chapter, was kindly provided by A. D. Barnosky. Site collections were sampled with the following coverage:

1. Incomplete but extensive samples of mostly well-preserved specimens (partial to complete skulls, maxillae and dentaries with teeth) from VR-DMNH and MS, with fragmentary specimens of poorly represented taxa and horizons also included.
2. Incomplete sample from VR-CM.
3. Large, nearly exhaustive sample from the Pit (all specimens known to us from stratified contexts in the Pit; surface collections were incompletely studied).
4. Small but exhaustive (insofar as I could determine) samples from other sites (BR, CAR, FFA, GD, and WH).

Analyses

Qualitative and quantitative comparisons with extant and extinct species allowed taxonomic assignment of most specimens. Most quantitative comparisons were based on the following variables:

1. *Length of the maxillary alveolar row (LMAX).* Front edge of alveolus of P3 to back edge of alveolus of M3.
2. *Length of lower alveolar row (LMAND).* All but *Cynomys:* front surface of anterior root on p4, in line with alveolar border (lateral view), to back edge of alveolus of m3. For *Cynomys:* same except anterior boundary was front edge of alveolar row of p4, to be consistent with Goodwin (1995b). In both cases, recorded length is the average of two replicates.
3. *Dimensions of p4 length (Lp4), trigonid width (WTrp4), and talonid width (WTlp4).* Lengths and widths of upper cheek teeth, and lengths and trigonid widths of other lower cheek teeth, were taken in selected cases.

In selected cases, quantitative variation within and across taxa was explored graphically and statistically (ANOVA) using Systat 5 for the Macintosh (Systat, Inc., Evanston, Illinois). For *Cynomys,* quantitative comparisons were done with all lower cheek teeth. Adult specimens with unworn to moderately worn teeth were measured. Relative abundances were estimated using minimum numbers of individuals per taxon (MNI), calculated separately for each site (small sites and MS), individual level (in the Pit), or horizon (VR-DMNH). Variation in relative abundance was examined graphically.

Systematic Paleontology

At least 11 sciurid phena were observed in this study, ranging in size from chipmunks *(Tamias)* to marmots *(Marmota).* I interpret these phena as distinct species: at least one species each of chickaree *(Tamiasciurus),* chipmunk, and marmot; five species of ground squirrels *(Spermophilus);* and three species of prairie dogs *(Cynomys)* or prairie dog–like ground squirrels. The taxonomic sequence of the following accounts follows presumed phylogenetic relationships among sciurids in general (Hafner, 1984) and ground-dwelling sciurids in particular (Hafner, 1984; Goodwin and Hayes, 1994).

Class Mammalia

Family Sciuridae

Subfamily Sciurinae

TAMIASCIURUS HUDSONICUS *(ERXLEBEN, 1777); FIGURE 17.1A,B*

REFERRED MATERIAL Pit level 1–R M1-2 (CM 66103); level 2–L M1-2 (UCMP 175231); L M3 (CM 66506); 2 R m1-2 (UCMP 180964–180965); level 3–L M1-2 (UCMP 180968); L, R m1-2 (UCMP 180966–180967); level 4–L, R P4 (UCMP 180973–180974); R M1-2 (UCMP 180975); L, R m1-2 (UCMP 180969–180970); L, R m3 (UCMP 180971–180972); level 5–L, R M1-2 (UCMP 180977–180978); L m1-2 (UCMP 180976); level 6–R M1-2 (UCMP 180980); R m1-2 (UCMP 180979); level 7–L m1-2 (UCMP 180981); L, R m3 (UCMP 180982–180983). NISP = 23, MNI = 7.

IDENTIFICATION AND DISCUSSION Fossils referred to *Tamiasciurus* clearly represent a small tree squirrel. Upper cheek teeth bear a broad, mesiodistally expanded protocone; low metaloph and protoloph; and prominent mesostyle (figure 17.1A). Lower cheek teeth are likewise low crowned, bear a conspicuous entoconid notch, exhibit a prominently swollen ectolophid, and usually have a distinct mesostylid (on m1-m2; figure 17.1B). This combination of features is shared by *Tamiasciurus* and *Sciurus,* is never found in ground squirrels, and is not typical of *Glaucomys* (flying squirrels). Teeth of the latter commonly lack mesostyles and mesostylids, and furthermore they bear a distinct groove on the mesial face of the protoconid of lower cheek teeth at the junction of protolophid and protoconid. A preliminary faunal list reported cf. *Glaucomys* from Porcupine Cave (Anderson, 1996), but I did not observe the *Glaucomys* morphotype in this survey.

The Porcupine Cave specimens are referred to *Tamiasciurus,* not *Sciurus,* on the basis of small size and morphology of the trigonid on m1-m3. In *Tamiasciurus* and fossil specimens, the trigonid pit is characteristically bounded mesially by a protolophid at least as high as or higher than the distally bounding metalophid. In contrast, *Sciurus* characteristically exhibits a very low protolophid adjacent to this pit. The trigonid pit on *Sciurus* thus often opens mesially, especially with wear. Both *Sciurus* (Barnosky and Rasmussen, 1988) and *Tamiasciurus* (Barnosky and Rasmussen, 1988; Anderson, 1996) were previously listed from the cave, but I found no evidence of the former in my study.

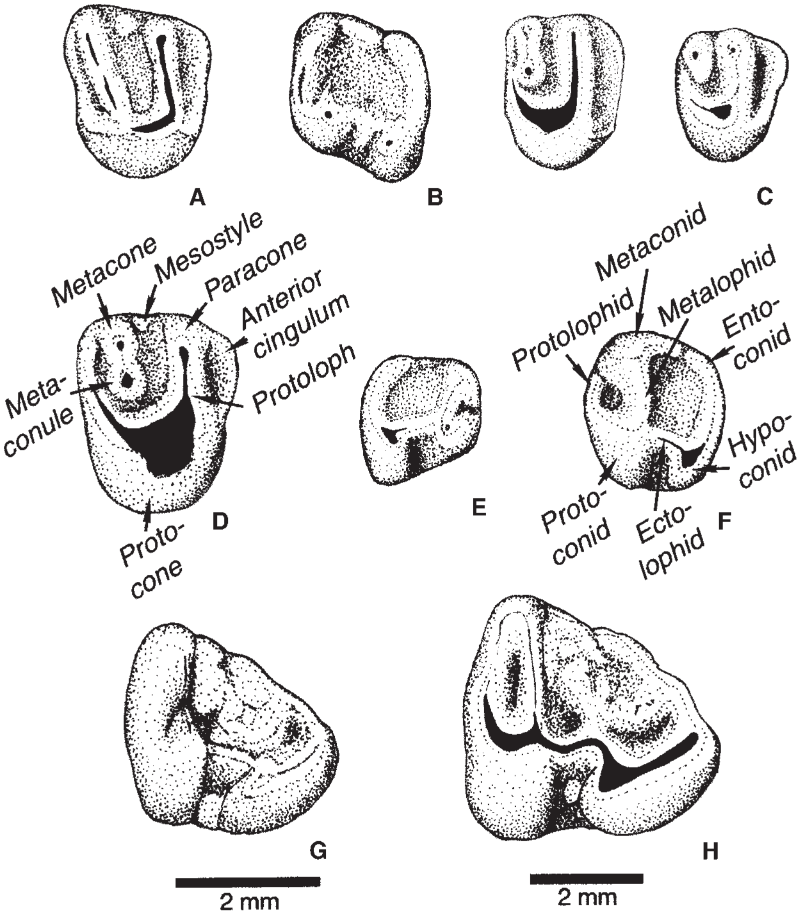

FIGURE 17.1 Fossil teeth of *Tamiasciurus, Spermophilus,* and *Cynomys.* (A) R M1-2 (UCMP 180980) and (B) L m1-2 (UCMP 180966) of *Tamiasciurus hudsonicus* (both from the Pit). (C) R P4 and M2 of *Spermophilus,* possibly near *S. meadensis* (DMNH 28335, Generator Dome). (D) R P4 of *Spermophilus* (?*Otospermophilus*) sp. (UCMP 180950, Pit level 10). (E) R p4 of *S. lateralis* (DMNH 37288, Will's Hole) and (F) L p4 of *S.* cf. *S. elegans* (UCMP 180193, Pit level 8A). (G) L m3 of *S.* cf. *S. elegans* (UCMP 180493, Pit level 3) and (H) R m3 (reversed) of *Cynomys* cf. *C. leucurus* (180155, Pit level 3). Scale bar beneath G applies to all but H, with its own scale bar. Morphological terms are labeled on D and F.

T. hudsonicus is one of two extant species in the genus and the only one found in Colorado (Armstrong, 1972), or, for that matter, east of the Pacific states (Hall, 1981). Referral of fossil specimens to this lineage is thus very probable on biogeographic grounds. This species has previously been documented in the Irvingtonian (Conard Fissure, Cumberland Cave, Trout Cave; Kurtén and Anderson, 1980) as well as in numerous Rancholabrean sites (Kurtén and Anderson, 1980).

Of all Porcupine Cave sciurids, *T. hudsonicus* is the strongest indicator of forest habitat within the sampling range of the cave. The species is characteristic of subalpine and montane forests in Colorado (Armstrong, 1972; Fitzgerald et al., 1994) but avoids ponderosa pine forests with *Sciurus aberti,* a species not observed in the Porcupine Cave assemblage. *T. hudsonicus* may also utilize riparian stands of cottonwood, although it is less abundant in such habitat (Armstrong, 1972; Fitzgerald et al., 1994).

TAMIAS *CF.* T. MINIMUS *BACHMAN, 1839*

REFERRED MATERIAL Velvet Room (DMNH): R maxillae with P4-M1 (DMNH 29100); M1-M3 (DMNH 38866); R dentary with m1-m3 (DMNH 10487); L dentary with p4-m1 (DMNH 12014). Velvet Room (CM)–L maxilla with P4-M3 (CM 49237). Pit level 1–R dentary with p4-m1 (CM 65327); R m1-2 (UCMP 180952); level 2–2 R M1-2 (UCMP 180954–180955); L M1-2 (CM 66524); R edentulous dentary (CM 65502); R m1-2 (UCMP 180953); level 3–L M3 (UCMP 180957); R m1-2 (UCMP 180956); level 4–L P4 (UCMP 180960); R M1-2 (UCMP 180961); R M3 (UCMP 180962); L p4 (UCMP 180958); L m1-2 (UCMP 180959); level 5–R M1-2 (UCMP 180963). NISP = 20, MNI = 11.

IDENTIFICATION AND DISCUSSION Chipmunks *(Tamias)* can be distinguished from all other North American sciurids based on a combination of small size, the presence of a notch mesiobuccal to the protoconid on m1-m3, and other dental details. Three species occur today in or near the vicinity of Porcupine Cave. The least chipmunk *(Tamias minimus)* and Colorado chipmunk *(T. quadrivittatus)* are mapped as locally present, and the Uinta chipmunk *(T. umbrinus)* occurs less than 50 km to the west (Armstrong, 1972).

Definitive identification of chipmunk species based on dental remains is difficult, but *T. minimus* is typically smaller than other species (e.g., Goodwin and Reynolds, 1989). Measurement of the alveolar row on three Porcupine Cave dentaries (mean = 5.07 mm, SD = 0.07, minimum–maximum = 5.00–5.14 mm) indicates a very small chipmunk. Armstrong (1972) reported lower tooth row (not alveolar) measurements for modern chipmunks in Colorado (ranges: *T. minimus,* 4.4–

5.5 mm; *T. quadrivittatus,* 5.5–6.3 mm; *T. umbrinus,* 5.5–5.9 mm). These values are probably less than equivalent measurements of the alveolar row, yet fossils still fall within the range of *T. minimus* but outside the range of other species. On this basis, I refer the fossil specimens to *T. minimus.*

T. minimus has been reported from a number of late Quaternary sites (e.g., Harris, 1985; Goodwin and Reynolds, 1989) but, to my knowledge, has not previously been reported from the Irvingtonian. This species is the most widespread extant species of North American chipmunk, ranging across much of Canada and southward across large regions of the western United States (Hall, 1981). In Colorado today, *T. minimus* is common, widespread geographically, and eurytopic: it occurs from greasewood flats to habitats above treeline (Armstrong, 1972). The paleoecological significance of its occurrence is thus difficult to assess.

MARMOTA *SP. (AUDUBON AND BACHMAN), 1841*

REFERRED MATERIAL Fossil material was not surveyed systematically for this chapter. However, detailed phylogeographic studies on *Marmota* from the Pit were performed by Polly (2003), and the response of *Marmota* populations to climate change was examined in his paper and in chapters 24 and 25; the material referred to *Marmota* is listed in appendix 25.1.

IDENTIFICATION AND DISCUSSION Cursory examination indicates the presence of marmot specimens at several sites in Porcupine Cave (listed from the Pit, Gypsum Room, VR-CM, and BR [Barnosky and Rasmussen, 1988]; observed in the VR-DMNH and MS assemblages). The species there today is *Marmota flaviventris,* which occupies a broad geographic range and a variety of habitats in the montane West (Hall, 1981), ranging from semidesert to alpine meadows (Frase and Hoffmann, 1980). Although the species does not require mesic conditions, it is evidently sensitive to a lack of winter-spring precipitation because of its dependence on green fodder in spring and early summer (Harris, 1970). The species is common and abundant in late Pleistocene sites of the montane West (e.g., Harris, 1985). Previous work has documented sharp changes in relative abundance of marmot in the Pit sequence (Barnosky et al., 1996).

There is doubt that *M. flaviventris* is the species represented in the Pit sequence. Polly's work (2003) placed the Pit specimens in the *M. monax* clade based on a morphometric study of the m3. However, it still is not clear whether the Porcupine Cave specimens represent *M. monax* or a species that is too distantly related to be placed in the *M. monax* crown group. Until this situation is resolved the marmots here are simply assigned to *Marmota* sp.

GENUS SPERMOPHILUS

Five sciurid taxa from Porcupine Cave are assigned to the genus *Spermophilus,* a large and extremely successful group of ground-dwelling squirrels especially diverse today in western North America (Hall, 1981). One species is of uncertain subgeneric placement; others represent the subgenera *S. (Callospermophilus),* probably *S. (Otospermophilus),* and *S. (Spermophilus)* (two species). Three of these five taxa are known from only one or two specimens; the other two are well represented.

Subgenus Uncertain

SPERMOPHILUS *SP. POSSIBLY* S. MEADENSIS *(HIBBARD, 1941A); FIGURE 17.1C*

REFERRED MATERIAL Generator Dome: R maxilla with P4, M2 (DMNH 28335).

IDENTIFICATION AND DISCUSSION Known from a single specimen, this ground squirrel dentition is distinguished from that of other Porcupine Cave sciurids by a combination of small size and incomplete metaloph on P4 and M2 (figure 17.1C). The specimen falls within size variation of extant thirteen-lined *(Spermophilus tridecemlineatus)* and spotted *(S. spilosoma)* ground squirrels, species of the subgenus *Spermophilus (Ictidomys)* that exhibit an incomplete metaloph and today occur in Colorado (Armstrong, 1972). It differs from both species in possessing a vertically oriented, versus a ventrolaterally sloping, lateral wall of the infraorbital foramen, and from most specimens of *S. tridecemlineatus* in the lesser mesiodistal compression of the protocone. It resembles some specimens of *S. tereticaudus* (subgenus *Xerospermophilus*) in general dental form and the shape of the infraorbital foramen, but referral to this taxon seems unlikely on biogeographic grounds: the taxon is restricted to very arid regions of the Mojave, Sonoran, and Chihuahuan Deserts of the American Southwest (Hall, 1981). The fossil can be distinguished from *Ammospermophilus,* because the latter exhibits a relatively narrow M2 and a smaller, less buccally expanded anterior cingulum.

The Porcupine Cave specimen closely resembles two Blancan species: *S. meadensis* (known from the Blancan-Irvingtonian transition in Meade County, Kansas, Borchers local fauna; Hibbard, 1941a), and *S. howelli* (known from early Blancan sites in Meade County, Rexroad 3, Fox Canyon; Hibbard, 1941b, 1941c; Hazard, 1961; geochronology summarized in Lundelius et al., 1987). It is slightly smaller than all specimens of these two species that were measured (mean (SD) minimum–maximum (*n*) for length P4: fossil, 1.62 mm; *S. meadensis,* 1.82 mm (0.06) 1.74–1.93 mm (12); *S. howelli,* 1.81 mm (0.08) 1.65–1.95 mm (14)). I do not offer a definitive species identification, but referral to *S. meadensis* seems the more probable of the two; *S. howelli* is otherwise unknown after the early Blancan. The Generator Dome sample appears old on other evidence (discussed later in this chapter), consistent with a late Blancan or earliest Irvingtonian taxon in that sample.

Subgenus *Otospermophilus* Brandt, 1844

SPERMOPHILUS *(?*OTOSPERMOPHILUS*) SP.; FIGURE 17.1D*

REFERRED MATERIAL Pit level 10: R P4 (UCMP 180950); level 11–R M1-2 (UCMP 180951).

IDENTIFICATION AND DISCUSSION Two specimens deep in the Pit sequence represent a relatively large, narrow-toothed ground squirrel with broad protocone and incomplete metaloph on upper cheek teeth (P4 illustrated; figure 17.1D). This combination of features is characteristic of the subgenus *Spermophilus (Otospermophilus)* but may be primitive for the genus; thus I refer specimens to *S. (Otospermophilus)* with question.

Limited metric and qualitative data are consistent with two taxonomic interpretations:

1. Specimens represent *S. variegatus,* an extant member of *S. (Otospermophilus)* that today occurs within 50 km east, south, and southwest of Porcupine Cave (Armstrong, 1972), or
2. Fossils document the presence of an extinct species.

The complete absence of this morph in large collections from higher in the Pit, and from younger sites in the cave (especially VR-DMNH), is most consistent with the latter interpretation.

This sciurid compares favorably in size (P4 length = 2.35 mm, width = 2.99 mm) and form with the early Blancan *S. rexroadensis* (sample from Fox Canyon: P4 length [mean (SD)] = 2.28 mm (0.07), width = 2.92 mm (0.14), *n* = 4). However, it exhibits a slightly broader protocone and lesser buccal expansion of the paracone than is typical for that taxon. This sciurid also resembles a published description of *S. bensoni,* especially in the well-developed metaconule of P4-M2. The latter probably is smaller (based on extrapolation from a lower tooth row measurement, dental measurements not reported; Gazin, 1942). *S. bensoni* is reported from the early to late Blancan of Arizona and the middle Irvingtonian of California (Kurtén and Anderson, 1980; Tomida, 1987). The Porcupine Cave sciurid is less similar to other extinct Pleistocene species. It exhibits a substantially more robust protocone on the upper teeth than in similar-sized *S. meltoni* (Skinner and Hibbard, 1972); is larger than *S. howelli* (Hibbard, 1941c) and *S. meadensis* (Hibbard, 1941a); is smaller than *S. boothi* and *S. johnsoni* (Skinner and Hibbard, 1972), *S. mcgheei* and probably *S. finlayensis* (Strain, 1966); and is much less derived morphologically than *S. cochisei* (Gazin, 1942) or ?*S. cragini* (Goodwin and Hayes, 1994).

Subgenus *Callospermophilus* Merriam, 1897

SPERMOPHILUS LATERALIS *(SAY, 1823); FIGURE 17.1E*

REFERRED MATERIAL See appendix 17.1. NISP = 327, MNI = 66.

IDENTIFICATION AND DISCUSSION The third most abundant sciurid in the composite Porcupine Cave assemblage represents the golden-mantled ground squirrel *(Spermophilus lateralis).* Numerous features support this assignment: oval infraorbital foramen with vertical lateral wall; small P3 relative to P4; swept-back coronoid process of dentary; gradual drop in dorsal surface of dentary anterior to the p4; less strongly angled angular process of dentary (about 60° versus 90° in posterior view); narrow trigonid relative to talonid, especially on p4 (figures 1E, 2A); characteristically less elongate distal molars (m3 and M3) than seen in *S. elegans;* and M3 lacking a developed metaloph. Fossils assigned to *S. lateralis* average significantly smaller in size than fossils assigned to *S.* cf. *S. elegans* (table 17.1; $p < 0.00001$ for both lower and upper alveolar rows). Fossils can be distinguished from those of other dentally primitive ground squirrels of small size, such as *Ammospermophilus* and *S. (Xerospermophilus),* by the complete metaloph on P4 through M2. I did not make comparisons with other species in the subgenus *Spermophilus (Callospermophilus),* but on biogeographic grounds *S. lateralis* is probably the lineage at Porcupine Cave; other species in the subgenus are restricted to either the Pacific Northwest *(S. saturatus)* or the mountains of central Mexico *(S. madrensis)* (Hall, 1981).

S. lateralis today occupies large areas of the montane West (Hall, 1981) and, in Colorado, occurs across much of the western half of the state (Armstrong, 1972). The species prefers open woodland, forest edge, or shrubland habitats but typically avoids dense forests (Armstrong, 1972; Fitzgerald et al., 1994). The fossil record for *S. lateralis* is dense for the latest Pleistocene, with numerous records documenting occurrence in regions that today are arid and have unsuitable habitat (e.g., Harris, 1985). The Porcupine Cave record roots this lineage deeply in the Pleistocene of the Rocky Mountains.

Subgenus *Spermophilus* Cuvier, 1825

SPERMOPHILUS *CF.* S. ELEGANS *KENNICOTT, 1863; FIGURE 17.1F,G*

REFERRED MATERIAL See appendix 17.1. NISP = 1953, MNI = 400.

SUPRASPECIFIC ASSIGNMENT By far the most abundant sciurid in the Porcupine Cave assemblage represents the morphologically derived ground squirrel subgenus, *Spermophilus (Spermophilus).* Evidence supporting this assignment includes a triangular infraorbital foramen, relatively high-crowned cheek teeth, large P3 relative to P4, elongate M3 typically with metaloph, abrupt drop in dorsal surface of the dentary anterior to p4, strong dorsal projection of the coronoid process, strongly angled angular process (about 90° in posterior view), transversely widened trigonid on p4 (figure 17.2A) with incomplete protolophid (figure 17.1F), high trigonid on p4-m3, and elongate m3 (figure 17.1G). The species is on average significantly larger than *S. lateralis* (table 17.1).

The Porcupine Cave taxon is allied with the "big-eared" species group (*S. beldingi, S. armatus, S. elegans, S. richardsonii;* Nadler et al., 1984). It is larger and displays greater development of the metaloph on M3 than "small-eared" species (*S. brunneus, S. townsendii* complex; Nadler et al., 1984), and is smaller than "long-eared" forms (*S. columbianus, S. parryii;* Nadler et al., 1984). "Big-eared" species show broad overlap odontometrically (figure 17.2B) and are similar qualitatively, even with complete skulls. Porcupine Cave specimens differ

TABLE 17.1

Comparison of *S. lateralis* and *S.* cf. *S. elegans* on Lower and Upper Alveolar Row Measurements

		Lower Alveolar Row		*Upper Alveolar Row*	
Taxon	*Sample*	*Mean (SD)*	*Minimum–Maximum (Sample Size)*	*Mean (SD)*	*Minimum–Maximum (Sample Size)*
S. lateralis	Total	8.64 (0.44)	8.00–9.52 (24)	8.84 (0.41)	8.39–9.46 (9)
S. cf. *S. elegans*	Total	9.32 (0.29)	8.47–10.22 (239)	10.23 (0.35)	9.29–11.08 (132)
	Velvet Room (A–B)	9.38 (0.30)	8.79–10.22 (46)	10.33 (0.35)	9.60–11.08 (35)
	Velvet Room (C–F)	9.25 (0.31)	8.47–9.90 (18)	10.37 (0.48)	9.80–11.05 (9)
	Velvet Room (CMNH)	9.39 (0.26)	8.82–9.91 (28)	10.10 (0.27)	9.74–10.46 (10)
	Pit	9.16 (0.27)	8.73–9.52 (9)	10.01 (0.19)	9.71–10.29 (7)
	Will's Hole	9.24 (0.32)	8.82–10.04 (16)	10.15 (0.42)	9.55–10.95 (10)
	Mark's Sink	9.31 (0.30)	8.68–10.20 (66)	10.15 (0.38)	9.29–10.91 (32)

NOTE: *S.* cf. *elegans* is given as totals and as selected subsamples.

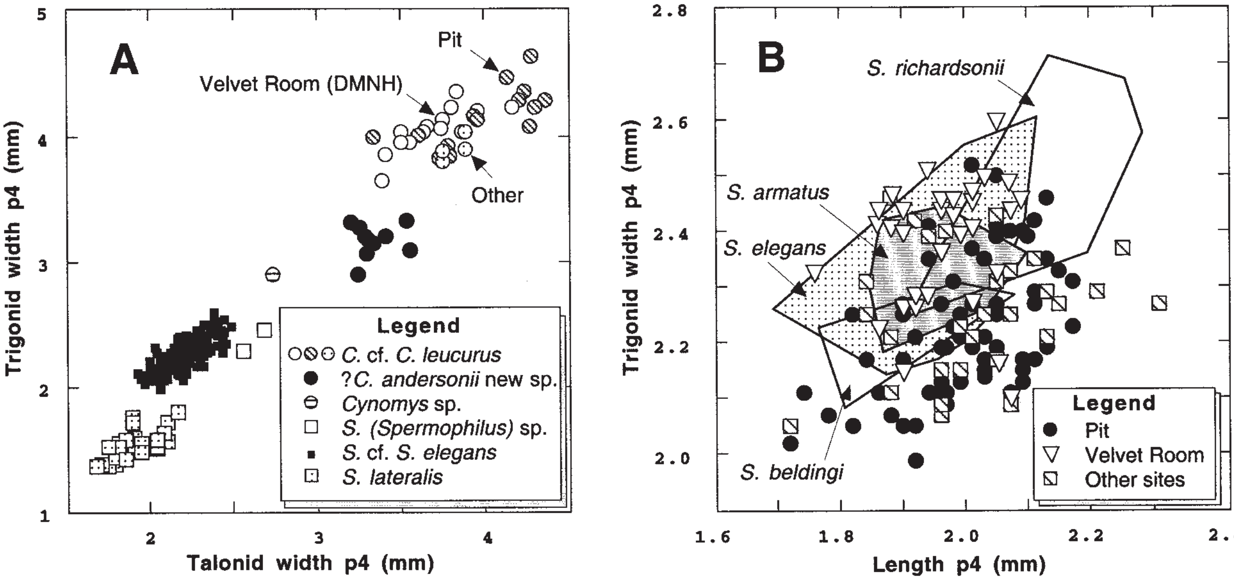

FIGURE 17.2 (A) Scatterplot of trigonid and talonid width, p4, showing morphometric relationships among ground squirrels and prairie dogs. (B) Scatterplot of trigonid width versus length of p4, showing relationships among various Porcupine Cave samples of *S.* cf. *S. elegans* and envelopes of variation of samples of modern "big-eared" ground squirrels.

from *S. beldingi* and *S. armatus* in typically displaying a prominent trench lingual to the ectolophid and hypoconid of m3 (figure 17.1G) and distinctly raised lateral margins of the skull roof across the interorbital region. Both of these features are shared with *S. elegans* and *S. richardsonii,* closely related species of the northern Great Plains (*S. richardsonii;* Michener and Koeppl, 1985) and appropriate habitats in the central Rocky Mountains and northern Great Basin (*S. elegans;* Zegers, 1984). *S. elegans* is present today in the vicinity of Porcupine Cave (Armstrong, 1972).

MORPHOMETRIC VARIATION AND SPECIFIC ASSIGNMENT The derived Porcupine Cave morph did not vary significantly across samples (tests done on samples as indicated in table legends) in measures of alveolar (table 17.1) or p4 length (table 17.2; $F = 0.85$), suggesting little temporal variation in body size and consistent with a single taxon present across sites. In contrast, two measures of p4 width (trigonid width: $F = 7.38$, $p < 0.00001$; talonid width: $F = 3.93$, $p < 0.001$) varied significantly across sites (subdivided where possible into stratigraphic samples; table 17.2). For both variables, all significant pairwise differences (Tukey's post-hoc test) distinguished the VR-DMNH (horizon A–B) sample from other samples. Graphic comparison between fossils and extant members of the big-eared species group demonstrated that, on average, fossils exhibit a narrower p4 (figure 17.2B). The

TABLE 17.2

Dimensions of p4 for Samples of *S.* cf. *S. elegans*

	Length p4		*Trigonid Width p4*		*Talonid Width p4*	
Locality	*Mean (SD)*	*Minimum–Maximum (Sample Size)*	*Mean (SD)*	*Minimum–Maximum (Sample Size)*	*Mean (SD)*	*Minimum–Maximum (Sample Size)*
Velvet Room (A–B)	1.95 (0.08)	1.76–2.07 (22)	2.42 (0.09)	2.23–2.60 (22)	2.31 (0.09)	2.13–2.48 (22)
Velvet Room (C+)	1.99 (0.08)	1.88–2.09 (11)	2.29 (0.13)	2.11–2.46 (11)	2.23 (0.12)	2.05–2.42 (11)
Pit (1)	2.02 (0.09)	1.86–2.17 (28)	2.24 (0.11)	2.07–2.46 (28)	2.16 (0.10)	2.01–2.39 (28)
Pit (2)	1.98 (0.13)	1.74–2.13 (16)	2.23 (0.11)	2.05–2.35 (16)	2.20 (0.15)	1.92–2.45 (16)
Pit (3)	2.00 (0.06)	1.90–2.07 (7)	2.30 (0.09)	2.15–2.40 (7)	2.17 (0.08)	2.03–2.27 (7)
Pit (4)	2.01 (0.07)	1.92–2.09 (8)	2.16 (0.10)	1.99–2.31 (8)	2.12 (0.09)	2.02–2.27 (8)
Pit (5)	1.95 (0.11)	1.72–2.05 (7)	2.18 (0.09)	2.02–2.27 (7)	2.15 (0.11)	1.96–2.33 (7)
Pit (6)	2.01 (0.08)	1.84–2.09 (7)	2.28 (0.18)	2.11–2.52 (7)	2.18 (0.15)	1.99–2.37 (7)
Pit (7–9)	1.96 (0.06)	1.90–2.01 (3)	2.11 (0.07)	2.05–2.19 (3)	2.11 (0.09)	2.05–2.21 (3)
Pit (10–11)	2.02 (0.12)	1.88–2.17 (4)	2.14 (0.07)	2.07–2.23 (4)	2.12 (0.16)	1.94–2.29 (4)
Will's Hole	2.02 (0.12)	1.88–2.25 (10)	2.20 (0.10)	2.07–2.37 (10)	2.16 (0.10)	2.03–2.42 (10)
Mark's Sink	1.98 (0.12)	1.72–2.21 (17)	2.27 (0.13)	2.05–2.46 (17)	2.22 (0.12)	1.96–2.37 (17)
Badger Room	2.10 (0.04)	2.07–2.13 (2)	2.27 (0.08)	2.21–2.33 (2)	2.31 (0.11)	2.23–2.39 (3)
Generator Dome	2.13 (—)		2.29 (—)		2.25 (—)	

NOTE: Interlocality statistical comparisons pooled Pit levels 7–11 and excluded samples from the Badger Room and Generator Dome because of small sample size.

sample from VR-DMNH falls almost entirely within the envelope of variation of modern *S. elegans* but is smaller than average for *S. richardsonii;* other Porcupine Cave samples clustered below these taxa (figure 17.2B).

Stratigraphic variation in the Pit and VR-DMNH sequences further complicates systematic interpretation (figure 17.3A). The sample from Pit level 6 exhibits two size clusters. Larger specimens seem anomalous compared to adjacent stratigraphic samples, breaking what otherwise might be viewed as a progressive if irregular trend toward increasing p4 width through time (assuming that VR-DMNH is younger than the Pit, a point that is discussed later in this chapter).

Given available evidence, three species level interpretations deserve consideration:

1. Fossils may represent a single, evolving lineage continuous with extant *S. elegans* and should thus be assigned to that species, an interpretation suggesting a long history for *S. elegans* distinct from *S. richardsonii.* In contrast, Neuner (1975) inferred post-Pleistocene divergence of *S. richardsonii* and *S. elegans* based in part on morphological intermediacy of the widespread fossil representative of the lineage, known primarily from the Great Plains (Neuner, 1975).
2. Fossils may represent a single lineage, as described previously, but the lineage should be subdivided into two chronospecies: one for older samples, with samples from upper VR-DMNH assigned to *S. elegans.* This interpretation again conflicts with that of Neuner (1975) and is complicated by the presence of *S. elegans*–type specimens from level 6 in the Pit.
3. The fossil sample includes two distinct but related lineages: an older lineage dominant in the Pit (and other old sites), and *S. elegans,* which shows up at least by level 6 but which is never dominant until the time represented by the upper horizons of VR-DMNH. This interpretation is intriguing, but it is complicated by the absence of other clear evidence for two morphological clusters at any given time horizon.

At present, the taxonomic status of the fossil samples remains unresolved. Pending further study, involving additional characters and comparisons with other Pleistocene samples of the *S. richardsonii–S. elegans* group, I assign these fossils to *S.* cf. *S. elegans.**

In addition to the material already described, notes of A. D. Barnosky written in 1991 document the presence of 29 isolated *Spermophilus* teeth from level 8 in the Pit, at least 24 of which (MNI = 3) may have been referable to *S.* cf. *S. elegans* according to Barnosky, as inferred from the descriptions and sketches that were recorded. Unfortunately, these specimens

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* *Editor's Note:* Since this chapter was written, the author has published a quantitative analysis that supports the identification of the Porcupine Cave specimens as an "early, temporally variable segment in the lineage [of *S. elegans*]" (Goodwin, 2002:185).

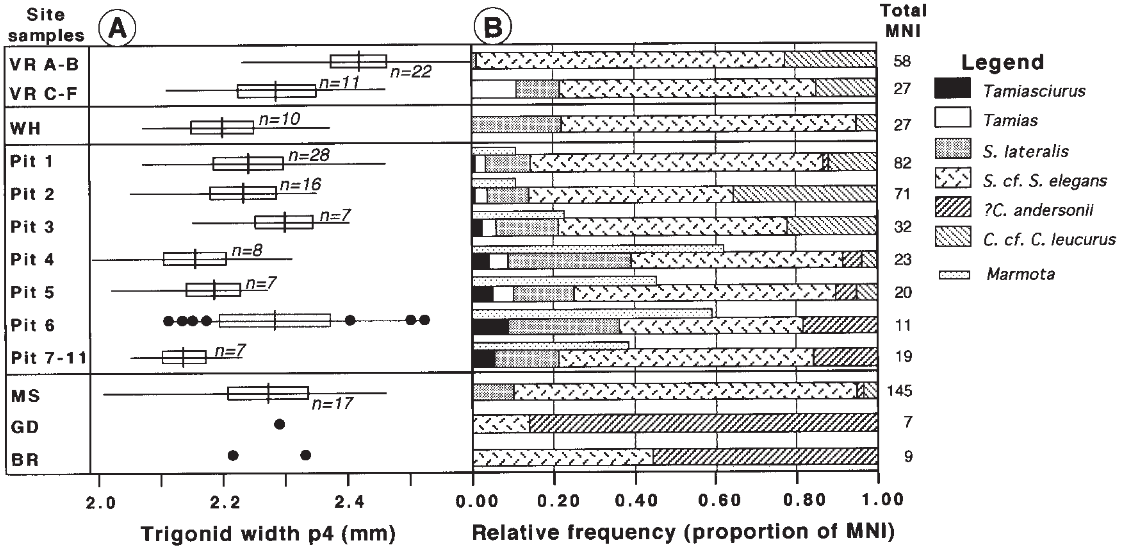


FIGURE 17.3 Stratigraphic and interlocality patterns in (A) trigonid width of p4 of *S.* cf. *S. elegans* (showing mean, standard deviation, and range; displaying individual specimens in some cases) and (B) relative frequency of selected sciurid taxa (as proportion of MNI). Locality abbreviations are given in the Materials and Methods section.

were subsequently lost and so were unavailable for examination in preparing this chapter. Noting their presence, however, is important in that the specimens document the presence of *Spermophilus* in level 8 as well as in the sub- and superjacent levels.

DISCUSSION A ground squirrel related to the *S. richardsonii–S. elegans* species group was widely distributed across the Great Plains in the Pleistocene (Neuner, 1975), apparently present from the middle Irvingtonian (Cudahy local fauna; Paulson, 1961) to the end of the Pleistocene. The Porcupine Cave record indicates that this lineage was also present (and apparently extremely abundant) in appropriate habitats of the central Rocky Mountains well back in the Pleistocene. Ongoing study may clarify the relationships between the Great Plains and Porcupine Cave populations of this lineage.

Goodwin (1998) reported a dental abnormality present in modern members of the *S. richardsonii–S. elegans* lineage, concentrated in an interspecific hybrid zone in Montana, and known from a fossil in Nebraska. The abnormality involves bilateral expression of a supernumerary distal upper molar and always results in abnormal development of the two distal upper teeth ("M3A" and "M3B"). This abnormality was not observed in a large sample of M3s from Porcupine Cave assigned to *S.* cf. *S. elegans* ($n > 500$).

Porcupine Cave is near the southeastern limit of the current range for *S. elegans* (Armstrong, 1972). In Colorado, the species occupies grassland and semiarid shrubland and has a diet consisting principally of grasses and forbs (Armstrong, 1972; Fitzgerald et al., 1994). *S. elegans* is reported to displace *S. lateralis* when they co-occur (Fitzgerald et al., 1994), a relationship that may partially explain the greater representation of the former in almost all samples taken from the cave.

SPERMOPHILUS (SPERMOPHILUS) *SP.*

REFERRED MATERIAL Badger Room: L p4 (DMNH 34201). Mark's Sink: R dentary with p4-m2 (DMNH 37054). NISP = 2, MNI = 2.

IDENTIFICATION AND DISCUSSION This sciurid is distinguished from *S.* cf. *S. elegans* by its larger size; substantially greater buccal expansion of the hypoconid on p4, resulting in a relatively greater ratio of talonid width to trigonid width (figure 17.2A); bulging mesial margin of p4; and more robust dentary. However, it is linked with advanced ground squirrels, *S. (Spermophilus),* by the widened trigonid on p4 and the strongly angled angular process (circa 90° in posterior view). Both sites with this sciurid appear to be old on the basis of other evidence (summarized later in this chapter), but specimens differ from all described Blancan or Irvingtonian sciurids.

Genus *Cynomys*

Prairie dogs *(Cynomys)* are large, derived ground squirrels endemic to North America throughout their history (Goodwin, 1995b). Morphological evidence suggests a close relationship with derived ground squirrels (subgenus *Spermophilus;* Bryant, 1945; Goodwin, 1995b); some late Blancan–early Irvingtonian taxa are morphologically intermediate between these taxa, complicating taxonomic assignment (e.g., ?*S. cragini;* Goodwin and Hayes, 1994).

Two subgenera and five extant species currently are recognized (Pizzimenti, 1975). The subgenus *C. (Cynomys),* referred to as black-tailed prairie dogs, includes *C. mexicanus,* today restricted to a small area in northeastern Mexico, and *C. ludovicianus,* which ranges widely across the Great Plains. The subgenus *C. (Leucocrossuromys),* referred to as white-tailed prairie dogs, includes three species. All three occur on high-elevation basins or plateaus associated with the Rocky Mountains (*C. parvidens,* southwestern Utah; *C. leucurus,* central Rocky Mountains and Wyoming Basin; *C. gunnisoni,* southern Rocky Mountains).

A recent systematic review of fossil *Cynomys* recognized seven or possibly eight species in pre-Holocene contexts (Goodwin, 1995b), with the lineage known as early as the late Pliocene. A striking feature of the Pleistocene record for the genus was the common and apparently persistent co-occurrence of both subgenera at sites on the central Great Plains and far southern Rocky Mountains. White-tails only occurred to the north of (and at higher elevations than) this zone of overlap; black-tails only were found to the south and east (Goodwin, 1995a). This pattern contrasts with the limited subgeneric overlap evident today. Previous work on *Cynomys* from Porcupine Cave has suggested the presence of at least two species representing both subgenera (Barnosky et al., 1996; Rouse, 1997). The present study recognizes three prairie dogs or prairie dog–like sciurids from the cave, describes one new species, and reinterprets subgeneric identifications.

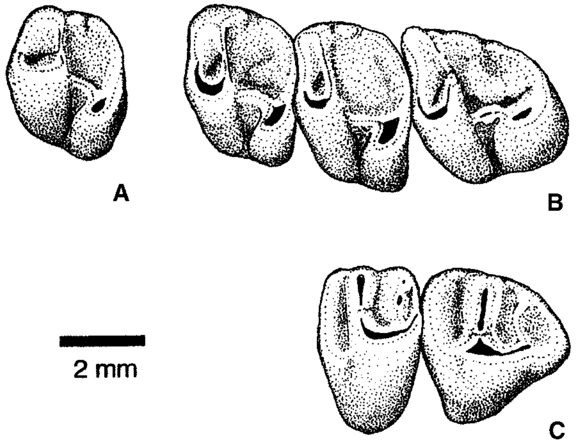


FIGURE 17.4 (A–C) Specimens of ?*Cynomys andersoni* sp. nov. (A) L p4 (DMNH 14303, Badger Room); (B) holotype, occlusal view of m1-m3 (DMNH 28320, Generator Dome); (C) R M2 and M3 (reversed) (DMNH 28317, Generator Dome).

?CYNOMYS ANDERSONI, *SP. NOV.; FIGURE 17.4A–C*

HOLOTYPE DMNH 28320, left dentary with m1-m3 (figure 17.4B).

REFERRED MATERIAL See appendix 17.1. NISP = 82, MNI = 23.

TYPE LOCALITY AND AGE Generator Dome locality, Porcupine Cave, Park County, Colorado. Irvingtonian.

DIAGNOSIS Distinguished from *Spermophilus (Spermophilus)* by complete protolophid on p4; from ?*Spermophilus cragini* by smaller size, distally expanded M3, and prominent metaloph on M3; and from all extant and adequately known fossil *Cynomys* by smaller size, lesser development of the metalophid on m3, rounded P3, and lack of buccodistal accessory lophule of protoloph on M3.

ETYMOLOGY Named in honor of Elaine Anderson, whose enthusiasm for Pleistocene mammals in general, and for the study of Porcupine Cave specimens in particular, has contributed greatly to knowledge of Pleistocene mammals. Her encouragement was instrumental in getting the author involved in this study.

DESCRIPTION The maxilla bears a triangular infraorbital foramen, but not so strongly as is typical of *Cynomys.* P3 is subequal in length and width (mean [SD] minimum–maximum *[n]:* L, 2.22 mm [0.04] 2.20–2.27 mm [3]; W, 2.26 mm [0.11] 2.15–2.37 mm [3]), not nearly as wide as is characteristic of ?*S. cragini* (Goodwin and Hayes, 1994) or extant *Cynomys.* The mesiobuccal face of the tooth is not flattened, as is typical of *Cynomys.* The anterior and posterior cingula resemble those of ?*S. cragini* in most respects (Goodwin and Hayes, 1994), but the anterior cingulum does not extend as far apically at its buccal juncture with the prominent oblique loph of P3.

P4 is poorly represented in the Porcupine Cave sample. Two adequately preserved specimens bear a somewhat compressed protocone, giving a subtriangular appearance. The anterior cingulum, mesiodistally expanded near its buccal end, tapers lingually to its terminus along the mesial surface of the protocone.

M1 and M2 (M2 shown in figure 17.4C) bear a progressively more robust protocone than does P4. The anterior cingulum does not taper as strongly lingually as on P4. In several specimens, the parastyle of M1 (but not M2) extends buccally beyond the margin of the paracone, a feature also seen on the type of ?*S. cragini* (Goodwin and Hayes, 1994). None of these teeth bears a mesostyle. The buccal half of the protoloph on P4 to M2 usually lacks the prominent distal expansion, bounded distolingually by a prominent notch, that is characteristic of *Cynomys.* However, one specimen (M1 or M2; UCMP 180186) exhibits this attribute incipiently, and several specimens display a notch on the distal surface of the protoloph but lack distal expansion of the protoloph buccal to the notch (figure 17.4C).

M3 (figure 17.4C) averages slightly longer (mean [SD] minimum–maximum *[n]:* 3.64 mm [0.17] 3.38–3.98 mm [10]) than wide (3.57 mm [0.22] 3.23–3.93 mm [8]); relative M3 length is greater than that exhibited by ?*S. cragini* (Goodwin and Hayes, 1994). Tooth shape is characteristically subtriangular with somewhat flattened mesial, buccal, and distolingual surfaces joined at rounded corners. The distolingual surface often bears a distinct notch at the distal terminus of the protocone. The anterior cingulum is shaped much as that of M1 or M2. The protoloph is well developed but never bears the prominent, buccodistal accessory lophule characteristic of *Cynomys.* A prominent metaloph, usually present, extends mesiobuccally from the distobuccal margin of the protocone, then turns buccally to parallel the protoloph. The metaloph

TABLE 17.3

Comparison of ?*Cynomys andersoni* with Other Primitive Prairie Dogs and Prairie Dog–Like Ground Squirrels Based on Lower Dental Variables

	?Cynomys andersoni		?Spermophilus cragini			
Variable	*Mean (SD)*	*Minimum–Maximum (Sample Size)*	*Mean (SD)*	*Minimum–Maximum (Sample Size)*	Cynomys hibbardi [a]	Cynomys sappaensis[a]
Lower alveolar row	12.40 (0.24)	12.24–12.75 (4)	—	13.65	—	
Length p4	2.70 (0.23)	2.07–2.90 (11)	2.83 (0.11)	2.69–2.95 (9)	—	3.05
Trigonid width p4	3.15 (0.15)	2.89–3.33 (11)	3.45 (0.17)	3.10–3.67 (9)	—	3.64
Talonid width p4	3.28 (0.22)	2.72–3.55 (11)	Not measured		—	3.88
Length m1	2.56 (0.10)	2.43–2.65 (5)	2.82 (0.17)[b]	2.59–3.06 (12)[b]	2.91	2.88
Width m1	3.49 (0.16)	3.25–3.70 (5)	3.81 (0.21)[b]	3.53–4.14 (12)[b]	3.80	3.92
Length m2	2.78 (0.08)	2.65–2.90 (10)		—	3.06	3.10
Width m2	3.62 (0.18)	3.33–3.88 (10)		—	4.04	4.20
Length m3	3.76 (0.14)	3.55–4.13 (16)	3.93 (0.17)	3.69–4.32 (12)	4.11	4.08
Width m3	3.75 (0.11)	3.51–3.93 (16)	4.05 (0.11)	3.84–4.17 (12)	4.09	3.89

SOURCES: Data for ?*S. cragini* are from Goodwin and Hayes (1994) and represent data for left teeth (right teeth with similar statistics). Data for *C. hibbardi* and *C. sappaensis* are from Goodwin (1995b).

[a] $n = 1$.

[b] Includes both m1 and m2 (undifferentiated sample of isolated teeth).

is absent from one referred specimen from Mark's Sink (DMNH 36336).

?*C. andersoni* is distinctly smaller than other primitive prairie dogs *(C. hibbardi, C. sappaensis)* or prairie dog–like ground squirrels (?*Spermophilus cragini*) on lower dental variables (table 17.3). The dentary is not well preserved in the Porcupine Cave assemblage but exhibits an abrupt drop of the dorsal surface anterior to the p4. On p4, width across the trigonid is subequal to or less than width across the talonid (figure 17.2A), resembling black-tailed *(C. [Cynomys])* but not white-tailed *(C. [Leucocrossuromys])* prairie dogs (Goodwin, 1995b). This results from prominent buccal expansion of the hypocone (figure 17.4A). A prominent protolophid and metalophid, defining a distinct trigonid basin, unite the protoconid and metaconid. As in *Cynomys* but not *Spermophilus,* the protolophid is typically complete and is not separated from the metaconid by a distinct notch; a rudimentary notch is present on a few specimens. The talonid basin bears little if any rugosity and is deepest along its buccal margin, typically exhibiting a trench lingual to the ectolophid. The ectolophid bears a slight swelling midway along its length on a few specimens. The lingual margin of the talonid is somewhat flattened in some specimens, then curves buccally at the entoconid, merging into the gently curving posterolophid. In other specimens (figure 17.4A), the lingual and distal margins form a nearly continuous curve. The entoconid is delimited mesially by a small but clear notch; this notch is absent or indistinct in ?*S. cragini.*

The m1 and m2 (figure 17.4B) take the shape of a rough parallelogram; the talonid is distinctly offset buccally relative to the trigonid. The protoconid and metaconid are not strongly expanded basally, giving the trigonid a somewhat gracile appearance. The metalophid is characteristically complete, bounding a distinct trigonid pit, but is prominently V-shaped when observed in distal view. On specimens with associated m1 and m2, the metalophid is higher and exhibits a more prominent lingual arm on m1. The talonid basin is slightly rugose in some specimens; one specimen (DMNH 23335) exhibits a low, oblique "mesolophid" on m2. The talonid is deepest along the ectolophid, forming an indistinct trench that characteristically deepens and expands as a pit at its mesial terminus, adjacent to the trigonid (figure 17.4B). The outline of the talonid varies in shape. Some specimens have flattened lingual and distal margins, connected at a rounded entoconid; other specimens exhibit a more continuous arc from metaconid to hypoconid. The entoconid is commonly not as distinct as on p4, and the hypoconid is not strongly expanded basally. It invariably projects buccomesially, often constricting the buccal entrance to the hypoflexid.

The m3 (figure 17.4B) is relatively elongate and usually subtriangular. Bases of the protoconid and metaconid are not strongly expanded. The metalophid is variably developed. In most specimens (figure 17.4B) it extends ventrolingually from the protoconid, terminating along the distal wall of the trigonid, and lacks the prominent lingual arm characteristic of modern *Cynomys.* In others, a rudimentary lingual arm is evident, completely bounding a shallow but distinct trigonid pit. When present, this pit is placed less apically than it is in other *Cynomys.* The talonid basin is raised, forming a platform with characteristic rugosity. A prominent crescent-shaped trench separates this platform from the hypoconid, ectolophid, and protoconid and sometimes continues lingually along the distal wall of the trigonid (figure 17.4B). It usually is unobstructed or only slightly constricted along its length, as in *C. (Cynomys),* but in one specimen (DMNH 22829B) it is blocked by a bridge, as is characteristic of *C. (Leucocrossuromys).* The trench commonly expands and deepens at a point distolingual to the protoconid (figure 17.4B). The ectolophid is typically expanded slightly near its midpoint (figure 17.4B), and in several specimens the swelling forms a small conulid. The hypoconid projects strongly mesially in all specimens, as in *C. (Cynomys),* constricting the buccal opening of the hypoflexid.

DISCUSSION Several sciurids, possibly representing multiple lineages, approached the prairie dog morphotype during the late Blancan and early Irvingtonian. *C. hibbardi* (Eshelman, 1975) and *C. sappaensis* (Goodwin, 1995b) appear to represent the *Cynomys* lineage. Other taxa (e.g., ?*C. vetus,* ?*S. cragini,* and ?*C. andersoni*) are morphologically mosaic (Goodwin and Hayes, 1994; Goodwin, 1995b; this chapter): they combine derived features otherwise known only in *Cynomys* (e.g., the complete protolophid on p4 in ?*S. cragini* and ?*C. andersoni*) with primitive features otherwise known in *Spermophilus* but not *Cynomys* (e.g., the incomplete metalophid on m3). The taxonomic position of these taxa remains uncertain. I tentatively ally ?*C. andersoni* with prairie dogs.

?*C. andersoni* is clearly distinguished from other prairie dog–like taxa based on smaller size (table 17.3) and morphological details. It is distinctly more primitive, especially in the development of the metalophid on m3, than *C. hibbardi* and *C. sappaensis,* and it differs from ?*S. cragini* in possessing a more elongate M3 with well-developed metaloph. ?*C. vetus* is known only from a partial skull with extremely worn teeth, but it is clearly larger than ?*C. andersoni* with a less elongate M3. It is more difficult to establish phylogenetic relationships among these forms. A possible relationship among ?*S. cragini, S. cochisei* (a smaller taxon known from Arizona; Gazin, 1942), and ?*C. vetus* has been suggested (Goodwin and Hayes, 1994). In contrast to these three species, ?*C. andersoni* has a more elongate M3 with a better-developed metaloph and typically lacks strong buccal expansion of the parastyle on M3.

?CYNOMYS *SP.*

REFERRED MATERIAL Mark's Sink: L dentary with I, p4-m1 (DMNH 36933).

IDENTIFICATION AND DISCUSSION A single specimen from Mark's Sink falls at or near the upper size limit of *S.* cf. *S. elegans* in length (Lp4 = 2.21 mm; compare with table 17.2) but differs from that taxon in the much greater width of the trigonid and talonid (figure 17.2A). In addition, p4 bears a complete protolophid with only rudimentary constriction at its contact with the metaconid, a morphology I have not observed in *S. elegans* or related species in the subgenus *S. (Spermophilus)* but one that resembles *Cynomys.* Both p4 and m1 are extremely hypsodont and exhibit a distinct notch mesial to the entoconid. This combination of size and morphology is not present in any fossil or Recent species of which I am aware. I tentatively interpret the fossil to represent the smallest prairie dog yet known, but forego formal description in hopes of finding additional material in the fragmentary component of the Mark's Sink sample. Regardless, the great trigonid and talonid width of p4 resembles that of *C. (Leucocrossuromys)* more closely than that of *C. (Cynomys).*

Subgenus *Leucocrossuromys* Hollister, 1916

CYNOMYS *CF.* C. LEUCURUS *MERRIAM, 1890; FIGURE 17.1H*

REFERRED MATERIAL See appendix 17.1. NISP = 427, MNI = 83.

IDENTIFICATION AND DESCRIPTION Several Porcupine Cave sites (Pit, VR-DMNH, VR-CM, MS, and WH) include fossils of undoubted prairie dogs *(Cynomys).* Characters supporting this assignment include great hypsodonty (for sciurids), large size, the presence of an accessory lophule along the buccodistal margin of the protoloph on M3, a complete protolophid on p4, a complete metalophid on m3 (figure 17.1H), and the presence of deep trigonid trenches lingual to the ectolophid on m1-m3 (especially m3). All diagnostic specimens from these sites represent white-tailed prairie dogs, *C. (Leucocrossuromys),* based on the following characters (Goodwin, 1995b): anterior cingular ridge on P3 terminates along the mesiobuccal face of the oblique loph in a distinct notch; presence of a prominent bridge connecting the ectolophid and talonid platform on most specimens of m3 (figure 17.1H); and hypoconid of m3 deflected anteriorly less strongly than is typical in black-tailed prairie dogs (figure 17.1H). Other typical "white-tailed" characters—notably the less buccal expansion of the hypoconid on p4 and the greater trigonid width of p4-m2 than in black-tails—are more variably developed in the Porcupine Cave assemblage.

Site samples of white-tailed prairie dogs vary morphometrically (e.g., figure 17.2A) and qualitatively. In contrast to fossils from relatively old sites (Pit, MS, WH), the VR-DMNH prairie dogs (mostly from horizon B) show less extensive and less frequent anterior deflection of the hypoconid on m3 (figure 17.5A), exhibit a significantly shorter and narrower p4 (across the talonid), and display wider m1-m2 (table 17.4). In degree of anterior deflection of the hypoconid on m3, the two Porcupine Cave samples form a series linking *C. gunnisoni* (displaying the primitive morphotype for white-tailed prairie dogs; Pizzimenti, 1975; Goodwin, 1995b) with *C. leucurus* (a member of the crown group of the subgenus). Both samples more closely resemble *C. leucurus* than small *C. gunnisoni* on most univariate comparisons (table 17.4). A multivariate discriminant function model, built to discriminate *C. leucurus* from *C. gunnisoni* on measures of p4-m2, likewise classifies most fossils in both samples with *C. leucurus* (figure 17.5B). This model correctly classified 90% of modern specimens.

TABLE 17.4

Comparison of Four Samples of *Cynomys* on Lower Dental Variables

	C. gunnisoni		C. leucurus		*Velvet Room (DMNH)* C. (Leucocrossuromys)		*"Old" Porcupine Cave* C. (Leucocrossuromys)	
Variable	*Mean (SD)*	*Minimum–Maximum (Sample Size)*	*Mean (SD)*	*Minimum–Maximum (Sample Size)*	*Mean (SD)*	*Minimum–Maximum (Sample Size)*	*Mean (SD)*	*Minimum–Maximum (Sample Size)*
Lp4	2.80 (0.10)	2.63–2.95 (26)	3.04 (0.12)	2.85–3.18 (15)•	2.92 (0.15)	2.55–3.10 (16)	3.13 (0.12)	2.93–3.43 (19)•
WTrp4	3.87 (0.18)	3.50–4.15 (26)	4.08 (0.13)	3.88–4.33 (15)•	4.06 (0.18)	3.65–4.35 (14)•	4.11 (0.23)	3.80–4.63 (19)•
WTlp4	3.58 (0.22)	3.13–3.98 (26)•	3.87 (0.16)	3.58–4.18 (15)*†	3.69 (0.22)	3.38–4.16 (14)•*	3.96 (0.28)	3.33–4.36 (19)†
Lm1	2.72 (0.13)	2.53–3.00 (26)•	2.80 (0.10)	2.68–2.95 (15)•*	2.85 (0.12)	2.65–3.05 (23)*†	2.97 (0.17)	2.80–3.28 (8)†
Wm1	4.27 (0.15)	3.93–4.56 (26)	4.51 (0.16)	4.13–4.78 (15)•	4.78 (0.20)	4.28–5.16 (22)	4.57 (0.14)	4.26–4.68 (7)•
Lm2	2.94 (0.11)	2.75–3.15 (26)•	3.03 (0.10)	2.88–3.21 (15)•*	3.02 (0.12)	2.80–3.20 (25)•*	3.12 (0.19)	2.90–3.53 (10)*
Wm2	4.48 (0.17)	4.15–4.78 (26)	4.84 (0.23)	4.30–5.18 (15)•*	4.93 (0.23)	4.43–5.36 (25)•	4.71 (0.13)	4.55–4.98 (10)*
Lm3	4.54 (0.21)	4.21–5.03 (26)•	4.70 (0.15)	4.35–5.01 (15)•*	4.64 (0.19)	4.18–4.88 (21)•*	4.76 (0.24)	4.20–4.76 (26)*
Wm3	4.31 (0.18)	3.93–4.68 (26)	4.83 (0.20)	4.26–5.08 (15)*	4.67 (0.20)	4.33–5.06 (21)•	4.64 (0.21)	4.10–4.93 (26)•*

NOTES: Significant differences were found for all variables (ANOVA). Cells sharing a symbol (•, *, or †) are not significantly different (Tukey's post-hoc test). Variable abbreviations indicate length (L) of p4, length (L) and width (W) of m1-m3, and trigonid (WTr) and talonid (WTl) widths of p4.

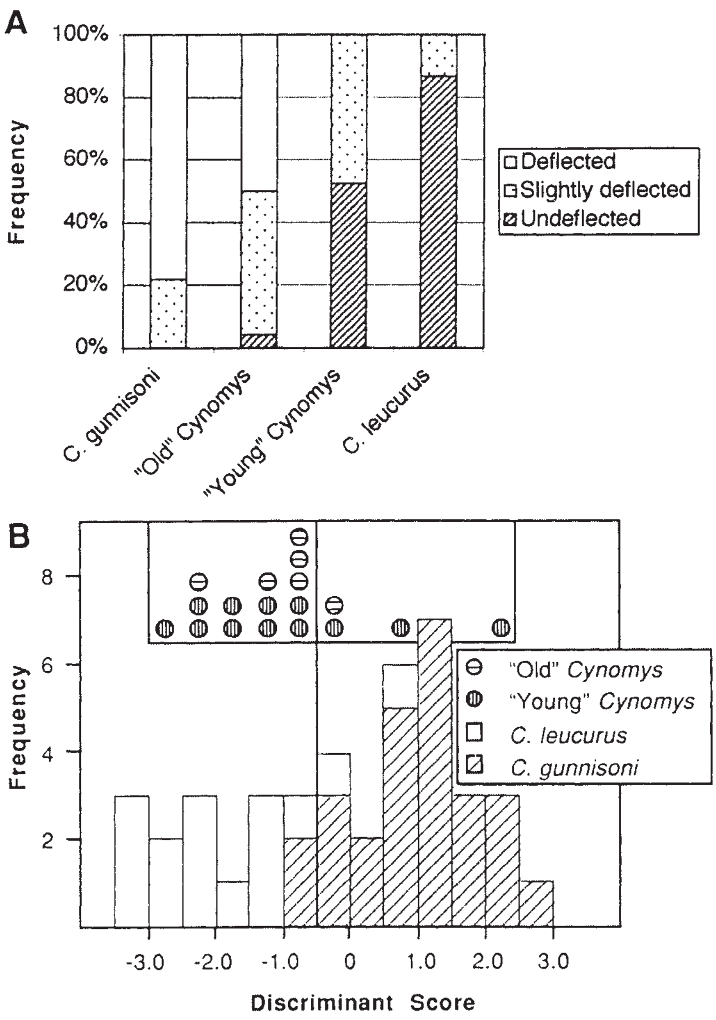


FIGURE 17.5 (A) Relative frequency of three classes of anterior deflection of hypoconid on m3 among four samples of prairie dogs: modern *Cynomys gunnisoni,* "Old" *Cynomys* from Porcupine Cave (Pit, WH, MS specimens), "Young" *Cynomys* from Porcupine Cave (VR-DMNH sample), and extant *C. leucurus.* (B) Discrimination of modern *C. gunnisoni* and *C. leucurus* based on discriminant function model using variables of p4-m2. Specimens left of the vertical line are classified by the model as *C. leucurus;* those right of the line are classified as *C. gunnisoni.* Fossils of "Old" and "Young" Porcupine Cave *Cynomys* are depicted as dots and are classified by the discriminant model based on their position relative to the vertical line.

Fossils also cluster with derived white-tails in typically displaying a bridge connecting the ectolophid with the talonid platform of m3, a feature less consistently developed in *C. gunnisoni.* A few fossil specimens lack this bridge but are otherwise indistinguishable from typical specimens.

These patterns of variation indicate the presence of an evolving lineage probably related to extant *Cynomys leucurus,* with dental morphology becoming more "modern" up through the sequence. Work is ongoing to determine if variation in the fossil sequence warrants subdivision at the species level.

DISCUSSION The systematic interpretation offered in the present study does not recognize black-tailed prairie dogs in the Pit sequence, as opposed to previous studies (Barnosky et al., 1996; Rouse, 1997). Paleoclimatic inferences hinging on co-occurrence of both subgenera may require revision (Barnosky et al., 1996; Rouse, 1997).

Occurrence of *C.* cf. *C. leucurus* in the Porcupine Cave assemblage suggests the presence of that lineage since the Irvingtonian. This conclusion falsifies a phylogenetic hypothesis that treats *C. niobrarius* as ancestral to *C. leucurus* and *C. parvidens,* with the latter species pair originating during range restriction and fragmentation at the end of the Pleistocene (Goodwin, 1995b). *C. niobrarius* was significantly larger in size than any other white-tail (Goodwin, 1995b). It was abundant and widespread across the northern and central Plains at least from the late Irvingtonian, extending west onto the Snake River Plain at times during this interval (Goodwin, 1995a, 1995b). The Porcupine Cave record indicates that *C. leucurus* was probably likewise present from the middle Irvingtonian, living in the high-elevation habitats of the Rocky Mountains.

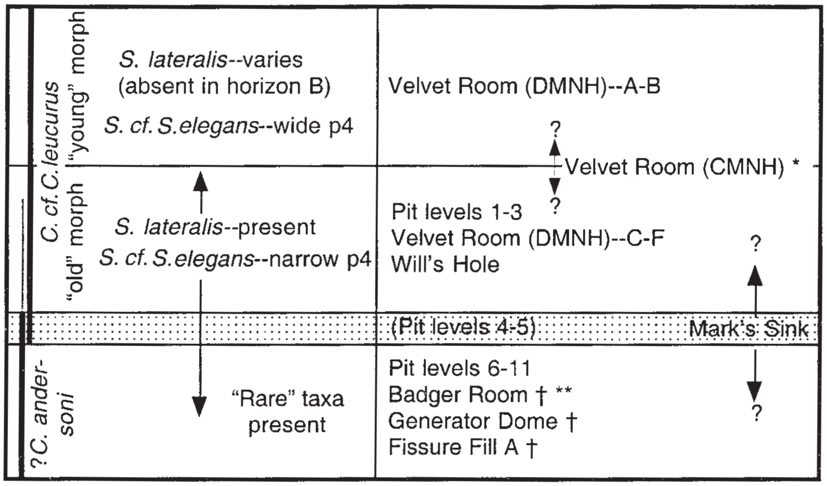
C. leucurus is not present today in the vicinity of Porcupine Cave but occurs some 80 km to the northwest (Armstrong, 1972). *C. gunnisoni* is regionally present today, but was evidently absent within the sampling range of the cave during fossil accumulation. As reviewed by Goodwin (1995b), *C. gunnisoni* was identified from the Hansen's Bluff local fauna, a middle Irvingtonian site located in south central Colorado (Rogers et al., 1985).

Historical Implications

Site Correlation and Biochronology

Variation in taxonomic composition, morphology, and relative frequency of sciurids was used to generate an age corre-

FIGURE 17.6 Preliminary age correlation hypothesis for Porcupine Cave sites based on the sciurid fauna. *, *S.* cf. *S. elegans* not measured; †, *S. lateralis* not present (but samples were small); **, single specimen may represent *C.* cf. *C. leucurus,* suggesting a mixed age.



lation hypothesis for Porcupine Cave sites with sciurids (figure 17.6). Using the stratified Pit sequence as a reference, three temporal zones can be recognized based on the presence or absence and the abundance of two prairie dog species (figure 17.6): Pit levels 6 and deeper (?*C. andersoni* only), levels 4–5 (both species subequal in abundance), and levels 1–3 (almost exclusively the "old" morph of *C.* cf. *C. leucurus;* one of more than 330 *Cynomys* specimens was ?*C. andersoni*). Three additional sites (BR, GD, FFA) have ?*C. andersoni* but not *C.* cf. *C. leucurus* and may be roughly equivalent with deeper levels in the Pit; age relationships among these sites are not clarified by sciurid data. MS includes both prairie dogs, with confusing distribution: ?*C. andersoni* is found as high as level 13, and *C.* cf. *C. leucurus* as low as level 26. This site appears to be mixed, spanning several zones as documented in the Pit sequence (figure 17.6). All rare sciurids from Porcupine Cave (those documented by fewer than three specimens each) occur in "old" sites: *Spermophilus* possibly *S. meadensis* (GD), *S.* (?*Otospermophilus*) sp. (deep in the Pit, levels 10 and 11), *S. (Spermophilus)* sp. (MS, BR), and ?*Cynomys* sp. (MS).

Two additional sciurid assemblages (VR-DMNH below horizon B, WH) are suggested as roughly age equivalent with upper levels of the Pit. The presence of *C.* cf. *C. leucurus* with deflected hypoconid on m3, and of narrow-toothed *S.* cf. *S. elegans* (figure 17.3A), clearly links WH with the upper section of the Pit. The other site, VR-DMNH (deep), exhibits *S.* cf. *S. elegans* with a relatively narrow p4 (figure 17.3A) but has little *Cynomys* material. The few specimens examined from these deeper levels suggest equivalence with the upper Pit.

The youngest Porcupine Cave fauna with sciurids appears to be the upper horizons (A–B) of VR-DMNH, postdating the entire Pit sequence (figure 17.6). *Cynomys* fossils from this sample are more derived (*C.* cf. *C. leucurus* with a less deflected hypoconid on m3); specimens of *S.* cf. *S. elegans* are more modern in aspect with significantly greater trigonid width of p4 (figure 17.3A); and *S. lateralis* is conspicuously absent in a large ground squirrel sample (125 specimens of *S.* cf. *S. elegans*) from horizon B of this site (figure 17.3B). *S. lateralis* is present in a small sample from horizon A of the VR-DMNH, indicating recolonization of the Porcupine Cave vicinity. One other site with an adequate sample (VR-CM) has not been studied morphometrically. One reasonably preserved m3 from the site seems to suggest "young" *C.* cf. *C. leucurus.*

Sciurids may provide clues for broader biochronologic interpretation. ?*C. andersoni* most closely resembles a suite of primitive prairie dogs and prairie dog–like taxa present in the latest Blancan and earliest Irvingtonian (?*S. cragini,* ?*C. vetus, C. hibbardi*). Two of the rare taxa found in "old" sites also show resemblance to Blancan taxa: *Spermophilus* possibly *S. meadensis* (possible link with late Blancan Borchers local fauna; Hibbard, 1941a), and *S. (Otospermophilus)* sp. (possible link with *S. rexroadensis* from early Blancan Fox Canyon and Rexroad local faunas; Hibbard, 1941c). Sciurids provide fewer constraints on younger Porcupine Cave sites.

Environmental Interpretation

The Pit sequence may document at least two glacial-interglacial cycles, with most study to date having focused on one putative glacial-interglacial couplet (levels 4–5 and 1–3, respectively) (Barnosky et al., 1996). Sedimentary and faunal variation is consistent with a model of wet glacial–dry interglacial environmental fluctuation for this upper couplet (Barnosky et al., 1996). Environmental conditions at other sites in Porcupine Cave have not been investigated adequately.

Substantial variation among sites and strata in relative abundance of most common sciurid taxa (exclusive of *Marmota,* which has not been studied other than in the Pit) probably reflects broader environmental history (figure 17.3B), although further work is needed to rule out taphonomic biases. Striking fluctuations in relative frequency of *Marmota* (determined only for the Pit sequence; calculated as percent total sciurid MNI) are also evident (figure 17.3B). *Tamiasciurus hudsonicus* is present but never dominant through the well-sampled parts of the Pit sequence (see figure 23.4), the clearest sciurid indicator of persistent woodland habitat within sampling range of the cave. It decreases in relative abundance upsection from level 6 and is rare above level 3 (MNI = 2 of 153 exclusive of *Marmota*), consistent with the hypothesis of interglacial drying (Barnosky et al., 1996). Absence from other well-sampled sites—especially Mark's Sink, which has some constituents that appear to overlap in time with portions of the Pit sequence (figure 17.6)—may reflect sampling bias. As of this writing, I have not examined all fragmentary material from Mark's Sink, and all specimens of *Tamiasciurus* known from the Pit are isolated teeth.

T. minimus and *S. lateralis* are often associated with woodland but do not strictly require this habitat. When grouped with *Tamiasciurus* as potential "woodland" indicators, a substantial decrease in relative abundance upsection from level 4 (figure 17.3B) may indicate a decrease in woodland-shrubland habitat and, by extension, increasing aridity. However, variation within the presumed glacial interval (levels 4–5) complicates simple modeling. Perhaps most significantly, potential "woodland" indicators show sharp contrast in the VR-DMNH sequence—constituting more than 20% of the sciurid assemblage (exclusive of *Marmota*) in composite horizon C–F (deep in VR-DMNH), but less than 2% in composite horizon A–B (completely absent from the well-sampled horizon B). Faunally (at least in terms of the sciurid assemblage), horizon B of VR-DMNH reflects the least wooded (and, by extension, perhaps the driest) environment of any well-sampled site within the cave.

"Grassland" indicators in the sciurid assemblage include *S.* cf. *S. elegans, Cynomys,* and (perhaps) ?*C. andersoni. S.* cf. *S. elegans* is present and abundant at all well-sampled sites, but prairie dogs show marked variation in relative abundance. Stratigraphic variation in the Pit sequence is complicated by taxonomic turnover. However, relatively low frequencies of *Cynomys* in presumed glacial deposits (levels 4–5) contrast with sharply higher frequencies in levels 1–3 and with peak abundance (circa 35% of the non-*Marmota* sciurid assemblage) at level 2. This is, again, consistent with regional drying and local expansion of the relatively open habitat favorable for *Cynomys*. Not surprisingly, prairie dogs are relatively abundant in the upper horizons of the VR-DMNH. The numerical dominance of ?*C. andersoni* in two old sites (GD, BR) may partially be an artifact of the small sample sizes from these sites (NISP = 41 and 24, respectively).

Dramatic fluctuations in the relative abundance of *Marmota* sp. have been noted elsewhere (Wood and Barnosky, 1994; Barnosky et al., 1996) and interpreted as consistent with the glacial-interglacial hypothesis: *Marmota* is numerically dominant in levels 4–5 (glacial) but much less abundant higher in the sequence (interglacial) (figure 17.3B). Further work is needed to clarify the variation in frequency of marmots among other sites in Porcupine Cave.

Pleistocene Evolutionary History of Rocky Mountain Sciurids

The appearance of *C.* cf. *C. leucurus* coincides with the onset of presumed glacial environments (the species first appears in Pit level 5), and the virtual disappearance of ?*C. andersoni* coincides with the shift to an interglacial (the Pit level 4/3 transition, based on the model of Barnosky et al. [1996]). Taxonomic turnover may be linked with local environmental history.

The Porcupine Cave record indicates morphological modernization of m3 in *C.* cf. *C. leucurus* (taking *C. gunnisoni* as indicative of primitive morphology; figure 17.5A), possibly associated with habitat drying. Similarly, the record documents modernization of p4 morphology in *S.* cf. *S. elegans* through time, with the youngest measured samples in the Porcupine Cave sequence (upper VR-DMNH) essentially indistinguishable in width from modern *S. elegans* (figure 17.2B). Two incidents of increased tooth width (Pit level 4/3 boundary, VR-DMNH horizon C/B boundary) correspond with episodes of habitat change (decreasing woodland–increasing grassland) that may reflect climatic drying. These results are preliminary and restricted in scope, but they suggest that further detailed studies of morphological variation, especially in the Pit and VR-DMNH sequences, would be fruitful in elucidating associations between habitat change and morphological evolution.

A striking feature of the sciurid record from Porcupine Cave is its "modern" aspect. Older samples in the cave (figure 17.6) include extinct taxa (?*C. andersoni,* various rare taxa noted previously), but they also encompass apparent representatives of lineages that occur in the vicinity of Porcupine Cave today. For example, *Tamiasciurus, S. lateralis,* and *S.* cf. *S. elegans* are all documented at or below Pit level 7. Younger samples (figure 17.6) lose the early extinct forms, retain extant lineages that appeared earlier, and incorporate representatives of additional lineages present today in the Rocky Mountains *(C.* cf. *C. leucurus, Tamias).*

This aspect of the Porcupine Cave sciurid assemblage bears on two broader issues. First, it is clear that the existing Rocky Mountain sciurid fauna has deep roots in time. Whereas some taxa exhibit evolutionary change in the sequence (e.g., *S.* cf. *S. elegans, C.* cf. *C. leucurus*), they probably represent the same lineages as modern species. Much of the radiation that produced modern diversity in Sciuridae, at least as reflected in the Rocky Mountain region, apparently predated the Porcupine Cave record. Second, the modern high-elevation sciurid assemblage has been virtually intact at least since the middle Irvingtonian. The only extant lineage that is out of range is *C.* cf. *C. leucurus,* but this represents a relatively minor range shift. Non-analogue associations, so common elsewhere in the Pleistocene (e.g., Lundelius et al., 1983; Graham, 1985) and documented for other groups at Porcupine Cave (Wood and Barnosky, 1994), are not evident in the sciurid assemblage.

Appendix 17.1. List of Specimens Examined for the Four Most Abundant Sciurids Studied

Specimens are ordered by locality and element (skulls, palates, maxillae, and upper cheek teeth first; dentaries and lower cheek teeth last). Pit specimen numbers have CM and UCMP prefixes, which are listed separately. Specimens from the CM Velvet Room Excavation have CM prefixes. Catalogue numbers from other localities have DMNH prefixes. See chapter 25 for a listing of *Marmota* specimens.

Spermophilus lateralis

MARK'S SINK

R maxilla I, P3-M3 (23369); L maxilla P4-M3 (23379); 2 R maxillae P4-M3 (22288, 37202); L maxilla P4-M2 (33665); 2 R maxillae P4-M2 (37215, 37217); L maxilla M1-M3 (33846.2); 3 R maxillae M1-M3 (29725, 33682, 36306); L maxilla M3 (36688); 2 L dentaries I, p4-m3 (22468, 22474); 2 R dentaries I, p4-m3 (22871, 33516); 3 L dentaries p4-m3 (22479, 22483, 33534); 3 R dentaries p4-m3 (27516, 33539, 37120); L dentary I, p4-m2 (35831); 2 R dentaries I, p4-m2 (22595, 27905); L dentary p4-m2 (22490); 5 R dentaries p4-m2 (21366, 22862, 33543, 33695, 37115); R dentary p4-m1, m3 (37200); 2 L dentaries p4-m1 (21378, 22504); R dentary p4-m1 (33538); R dentary m1-m3 (33694); L dentary I, m1-m2 (37234); R dentary I, m1-m2 (22553); 2 L dentaries m1-m2 (33838, 37118); 3 R dentaries m1-m2 (27512, 33664, 37216); L dentary I, p4 (33686); R dentary m1 (36303).

PIT (CM CATALOGUE NUMBERS)

LEVEL 1 R maxilla P4, M2-M3 (65289); L maxilla M1-M2 (66454); L maxilla M2-M3 (65277); 4 L maxillae P4 (61859); L maxilla M1 (65284); L P4 (66082); 2 R P4 (65908, 66083); 6 L M1 or M2 (65861, 65864, 65879, 66102, 66104, 66377); 6 R M1 or M2 (65911, 65944, 65952, 66085, 66101, 66381); 2 L M3 (65109, 66077); 4 R M3 (65971, 65973, 66086, 66087); L p4 (66108); 3 L m1 or m2 (66057, 66392, 66393); 2 R m1 or m2 (65087, 66050); L m3 (66078).

LEVEL 2 L maxilla P3-M3 (65372); L maxilla P4-M3 (65375); L maxilla P4-M1 (65373); R maxilla M1-M2 (65377); 2 R maxillae M2-M3 (65390, 65403); L maxilla M2 (65389); R maxilla M3 (65393); R P4 (66504); 2 L M1 or M2 (66508); 6 R M1 or M2 (64920, 64922, 66506, 66507); 2 L M3 (65378, 66497); R M3 (66496); 2 L dentaries p4-m2 (65384, 65400); R dentary p4-m2 (65399); L dentary p4-m1 (65383); L dentary m1-m3 (65385); R dentary m1-m3 (65402); R dentary m1-m2 (65401); R dentary p4 (65397); L p4 (66490); R p4 (66493); 2 L m1 or m2 (64866, 64896); 2 R m1 or m2 (64893, 64898); L m3 (65760).

LEVEL 3 2 L P4 (65615, 65616); R P4 (65651); 3 L M1 or M2 (65627, 65631, 65756); 3 R M1 or M2 (65650, 65661, 65665); 2 L M3 (65636, 65640); L dentary m1-m2 (65524); R p4 (65601); 3 L m1 or m2 (65620–65622); 2 R m1 or m2 (65647, 65658); L m3 (65633).

PIT (UCMP CATALOGUE NUMBERS)

LEVEL 1 L, R maxillae P4-M1 (180806, 180807); R maxilla M1-M3 (180808); 2 L, 3 R M3 (180809–180813); L dentary I, p4-m3 (180796); R dentary I p4-m2 (180797); R dentary p4 (180798); 2 R dentaries m1-m3 (180799, 180800); L p4 (180801); 2 L, R m1-2 (180802–180804); R m3 (180805).

LEVEL 2 L maxilla M1 (180824); R maxilla M3 (180825); 2 L, 2 R M3 (180825–180829); L dentary I, p4-m2 (180822); R m3 (180823).

LEVEL 3 2 R maxillae P4-M1(180851, 180852); L, 3 R P4 (180853–180856); 7 L, 3 R M1-2 (180857–180866); 3 L, 4 R M3 (180867–180873); L dentary p4-m2 (180830); L dentary p4, m1 (180831); L dentary m2 (180832); 3 L, 3 R p4 (180833–180838); 2 L, 5 R m1-2 (180839–180845); L, 4 R m3 (180846–180850).

LEVEL 4 R M1-2 (180886); 7 L, 7 R M3 (180887–180900); 3 L, 3 R P4 (180874–180878); R m1-2 (180879); 7 L, 2 R m3 (180880–180885).

LEVEL 5 P3 (180910); L, R P4 (180911, 180912); 4 L, 2 R M1-2 (180913–180918); 3 L, 2 R M3 (180919–180923); L p4 (180901); 2 L m1-2 (180902, 180903); 3 L, 3 R m3 (180904–180909).

LEVEL 6 R P4 (180931); 3 L M1-2 (180932–180934); L M3 (180935); L p4 (180924); 3 L, 2 R m3 (180925–180929); isolated lowers/uppers (180930).

LEVEL 7 P3, M3 (180936); 2 R M1-2 (180937, 180938); L M3 (180935).

LEVEL 8A P3 (180941); L M1-2 (180942); L m3 (180940).

LEVEL 10 3 P3 (180817–180819); L, R M1-2 (180820, 180821); L, R p4 (180814, 180815); R m3 (180816).

VELVET ROOM (DMNH)

HORIZON A R dentary I, p4-m3 (10618).

HORIZON A–C L dentary p4-m2 (27554).

HORIZON C R maxilla P3-M3 (20886).

HORIZON D L maxilla P4-M3 (20545); R maxilla P4-M3 (12003).

HORIZON D–E R dentary I, p4-m3 (20463).

HORIZON F OR BELOW R dentary p4-m3 (10807).

UNCERTAIN HORIZON L maxilla M1-M3 (33846); L dentary I, p4-m3 (27303); R dentary I, p4-m3 (8203); 2 R dentaries p4-m3 (6533, 8442).

VELVET ROOM (CM)

2 R P4 (66098, 66107); R dentary I, p4-m3 (49278); L dentary p4-m3 (49215); R dentary p4-m3 (49210); R dentary I, m1-m2 (49217).

WILL'S HOLE

Skull I, P4-M3 (37298); L maxilla P3-M1 (37260); L maxilla P4-M2 (37266); R maxilla P4-M2 (37270); L maxilla P4-M1 (37296); L maxilla M1, M3 (22889); R maxilla M1, M3 (22892); 2 R dentaries I, p4-m2 (37262, 37288); L dentary p4-m2 (37275); R dentary p4-m1, m3 (38850); R dentary p4-m1 (22859); 2 R dentaries m1-m2 (35635, 37268); 3 L dentaries I, p4 (37250, 37253, 37286).

Spermophilus cf. *S. elegans*

BADGER ROOM

Skull P4 (28928); L maxilla P3-M3 (13951); L maxilla P4-M1 (17559); 2 R maxillae P4-M1 (16004, 20448); R maxilla M1-M3 (17560); L dentary I, p4-m3 (17556); L dentary I, p4-m2 (20446); L dentary I, m1-m2 (17557); L dentary m2-m3 (20450).

COME-A-LONG ROOM

L maxilla M2 (22305).

GENERATOR DOME

R maxilla M1-M2 (28026); R dentary p4 (28325).

MARK'S SINK

2 skulls P3-M3 (21357, 21358); skull I, P4-M3 (36019); skull P4-M3 (21356); skull R P4-M3 (21360); skull P4, M2-M3 (21359); 3 palates P4-M3 (21374, 21375, 22281); palate R P4-M3 (22278); palate P4-M2 (22281); 2 palates P4-M1, M3 (22277, 22282); palate M1-M3 (22283); palate M1-M2 (22276); palate L M2 (27505); palate M3 (22279); 2 palates edentulous (27825, 33521); 3 L maxillae P3-M3 (21376, 23374, 33837); 2 R maxillae P3-M3 (23358, 33549); L maxilla P3-M2 (23378); R maxilla P3, M1 (35631); 15 L maxillae P4-M3 (21377, 23354, 23355, 23360, 23370, 23375–23377, 33532, 33678, 33833, 33843, 36021, 36930, 37210); 27 R maxillae P4-M3 (21361, 22284, 22285, 22289, 22290, 22292–22298, 23371, 27520, 27532, 33515, 33533, 33649, 33663, 33666, 33669, 33674.2, 33676, 33699, 33844, 36152, 37113); 3 L maxillae P4-M2 (23357, 27168, 33544); 7 R maxillae P4-M2 (22896, 29726, 33698, 33845, 37064, 37207); 3 L maxillae P4-M1, M3 (23352, 23359, 28326); 2 R maxillae P4-M1, M3 (21363, 22286); 2 L maxillae P4, M2-M3 (23361, 37114); R maxilla P4, M2-M3 (33523); 3 L maxillae P4-M1 (23351, 33681, 36614); 4 R maxillae P4-M1 (22299, 23373, 27509, 37206); 4 L maxillae P4, M3 (21379, 23372, 33674, 33830); 5 L maxillae M1-M3 (23350, 23353, 33531, 35837, 37117); 5 R maxillae M1-M3 (21362, 23356, 23368, 33672, 33834); L maxilla M1-M2 (21381); R maxilla M1, M3 (33667); 2 L maxillae M2-M3 (21382, 33498); 3 R maxillae M2-M3 (23367, 33671, 37051); 2 L maxillae P4 (36685, 37204); L maxilla M2 (33513); 3 L maxillae M3 (33496, 33697, 33835); 12 L dentaries I, p4-m3 (22467, 22469–22473, 27531, 27904, 33518, 33519, 33668, 33848); 19 R dentaries I, p4-m3 (22543–22549, 22575–22579, 22594, 22872, 27506, 33512, 33525, 33536, 36025); 15 L dentaries p4-m3 (22475–22478, 22480–22482, 22484, 22485, 27534, 33547, 33685, 33696, 36149, 36921); 19 R dentaries p4-m3 (21364, 22580–22589, 22863, 22864, 27529, 27907, 33514, 33520, 35828, 37112); 7 L dentaries I, p4-m2 (22496, 22497, 22593, 27535, 33517, 33691, 37109); 4 R dentaries I, p4-m2 (22592, 33527, 33535, 35841); 15 L dentaries p4-m2 (21367, 22486–22489, 22491–22495, 22499, 22875, 33540, 36881, 36928); 7 R dentaries p4-m2 (22590, 22591, 33688, 36879, 36919, 37211); L dentary I, p4, m2-m3 (22886); L dentary I, p4-m1, m3 (22513); R dentary I, p4-m1, m3 (22550); 2 L dentaries p4, m2-m3 (22535, 22536); R dentary p4, m2-m3 (33545); 2 L dentaries p4-m2, m3 (22512, 22877); R dentary p4-m1, m3 (33522); 5 L dentaries p4-m1 (22500, 22502, 27508, 29729, 37136); 6 R dentaries p4-m1 (22597–22599, 27510, 27517, 38860); R dentary I, p4, m3 (22551); 2 L dentaries p4, m2 (22534, 33499); 5 L dentaries p4, m3 (22514, 22529, 22532, 22533, 36932); 2 R dentaries p4, m3 (22516, 33528); 2 L dentaries I, m1-m3 (22531, 37063); 7 L dentaries m1-m3 (22518, 22520–22523, 33530, 33541); 8 R dentaries m1-m3 (21365, 22554, 27167, 27533, 33670, 33692, 33841, 36300); 8 L dentaries m1-m2 (21368, 22501, 22525, 22526, 33690, 36617, 37214, 38854); 6 R dentaries m1-m2 (21369, 22596, 33497, 33546, 33689, 33847); 2 R dentaries I, m2-m3 (22556, 36920); 9 L dentaries m2-m3 (21373, 22517, 22524, 22528, 22537, 27507, 33677, 33836, 38855); 10 R dentaries m2-m3 (21372, 22555, 24728, 27514, 27518, 29724, 33684, 36683, 37209); 2 L dentaries m1, m3 (22515, 22538); L dentary I, p4 (37208); 2 R dentaries I, p4 (36922, 37116); 15 L dentaries p4 (22498, 22503, 22505–22511, 27523, 27551, 27555, 27865, 33495, 33840); 13 R dentaries p4 (22539, 22540, 22542, 22557, 27522, 27528, 27863, 27864, 29727, 33548, 33693, 36929, 37111); L dentary I, m1 (37213); 5 L dentaries m1 (22541, 27513, 27515, 33841, 36693); 3 R dentaries m1 (36618, 36684, 37110); 2 L dentaries m2 (33537, 36682); R dentary m2 (37203); 4 L dentaries m3 (22527, 22530, 27526, 33839); 4 R dentaries m3 (22552, 33680, 33683, 35633).

PIT (CM CATALOGUE NUMBERS)

LEVEL 1 Skull P4-M3 (65290); 3 palates, edentulous (66455–66457); L maxilla P4, M2-M3 (66452); R maxilla P4-M1 (65286); R maxilla M1-M2 (65816); 2 R maxillae P4 (65288, 66453); 2 R maxillae M3 (65283, 65287); R maxilla edentulous (65281); 17 L P4 (65092, 65093, 65886, 65887, 65889, 65890, 65895–65897, 65900, 66080, 66088, 66092–66095, 66378); 11 R P4 (65082, 65091, 65902, 65904, 65907, 65909, 65912, 65915, 66089, 66096, 66097); 29 L M1 or M2 (65096, 65097, 65859, 65860, 65863, 65866, 65867–65878, 65880–65884, 65891–65893, 65899, 65903, 66091); 46 R M1 or M2 (65090, 65095, 65099–65102, 65905, 65906, 65913, 65914, 65916–65931, 65933–65935, 65937–65943, 65945, 65947–65951, 65953, 66084, 66379, 66383); 21 L M3 (65108, 65110–65112, 65842–65848, 65850–65855, 65954, 66374–66376); 29 R M3 (65103, 65104, 65106, 65285, 65405, 65858, 65949, 65955–65968, 65970, 65972, 65974–65977, 66373, 66384); L dentary p4, m3 (65272); R dentary m1-m3 (66451); R dentary I, m1-m2 (65278); L dentary m1-m2 (65274); L dentary m2-m3 (65276); R dentary p4 (65280); L dentary m1 (65273); R dentary m3 (65107); 14 L p4 (65083, 66053, 66056, 66060–66063, 66066, 66067, 66068, 66075, 66076, 66100, 66105); 9 R p4 (65079, 65089, 66025, 66029, 66041, 66045, 66046, 66049, 66389); 23 L m1 or m2 (65071, 65073, 65077, 65084, 65086, 65275, 65988, 65992, 65993, 65995–65997, 65999, 66000, 66003, 66054, 66055, 66058, 66059, 66069, 66071, 66386, 66387); 30 R m1 or m2 (65075, 65076, 65088, 65279, 66018–66020, 66023, 66026–66028, 66030–66038, 66042–66044, 66047, 66048, 66051, 66052, 66388, 66390, 66391); 13 L m3 (65069, 65070, 65072, 65978–65981, 65983–65986, 65990, 66394); 18 R m3 (65078, 65080, 65081, 66004–66016, 66385, 65079).

LEVEL 2 Skull edentulous (65406); R maxilla P4-M3 (65388); L maxilla P4, M2-M3 (65374); R maxilla M1-M3 (65380); L maxilla M1-M2 (65391); R maxilla M1-M2 (65392); L maxilla M2-M3 (65379); L maxilla M2 (65376); R maxilla M3 (65394); L maxilla edentulous (65371); 3 L P3 (66500); R P4 (64907); 3 L M1 or M2 (64868, 64870, 64923); 10 R M1 or M2 (66495); 24 L M3 (64885, 64886, 64925, 64926, 66497); 28 R M3 (64909–64911, 64913–64915, 66496, 66502, 66503); R dentary p4-m1 (65398); R dentary m1-m2 (65404); L dentary m2-m3 (65386); L dentary p4 (65381); R dentary p4 (65395); L dentary m1 (65382); R dentary m1 (65396); L dentary m3 (65387); R dentary m3 (65405); 7 L p4 (64862–64865, 64872, 66490, 66501); 6 R p4 (64888–64890, 64895, 66493, 66500); 4 L m1 or m2 (64869, 64871, 64873, 64906); 6 R m1 or m2 (64867, 64887, 64891, 64892, 64894, 64897); 9 L m3 (64874–64881, 66488); 10 R m3 (64899–64905, 66491, 66501, 66503).

LEVEL 3 Skull edentulous (65523); palate edentulous (65522); R maxilla M2-M3 (65521); R P4 (65652); 5 L M1 or M2 (65623, 65628, 65629, 65632, 65664); 5 L M3 (65637–65639, 65641, 65642); R M3 (65672); R dentary, edentulous (65520); L p4 (65613); 2 R p4 (65643, 65644); L m1 or m2 (65614); 5 R m1 or m2 (65645, 65646, 65648, 65656, 65659); 2 L m3 (65634, 65755); 6 R m3 (65666–65671).

PIT (UCMP CATALOGUE NUMBERS)

LEVEL 1 Palate M3 (180368); R maxilla P3-M3 (180347); R maxilla P4-M2 (175229); L maxilla P3 (180348); 2 L maxillae P4-M2 (180350, 180351); L maxilla P4-M1, M3 (180352); 2 L maxillae P4-M1 (180353, 180354); R maxilla 2 P4, M3 (180355); L maxilla P4 (180356); L maxilla M1-M3 (180357); R maxilla M1-M2 (180358); 3 L maxillae M2-3 (180359–180361); R maxilla M2 (180362); 2 R maxillae M3 (180363, 180364); 2 L 2 R maxillae edentulous (180365–180367); 2 R P3 (180369–180370); 25 L, 20 R M3 (175230, 180370–180402); R dentary I, p4-m2 (180213); L, R dentaries I p4-m1 (180214, 180215); 3 L, 2 R dentaries p4-m3 (180216–180220); 2 R dentaries p4-m2 (180221, 180222); L, R dentaries p4-m1 (180223, 180224); L, 3 R dentaries p4 (180225–180228); 3 R dentaries m1-m3 (180229–180231); L, R dentaries m1 (180232, 180233); 2 L, R dentaries m2-m3 (180234–180236); R dentary m3 (180237); 8 L, 7 R p4 (180240–180254); 30 L, 20 R m1-2 (180255–180304); 33 L, 24 Rm3 (180305–180346); 2 isolated lower/upper (180238, 180239).

LEVEL 2 Skull P3-M3 (180447); skull P4-M3 (180448); skull P4, M3 (180449); L maxilla P4 (180446); R P3 (180450); L, R M1-2 (180451, 180452); 6 L 10 R M3 (180453–180464); R dentary I, p4-m1 (180422); R dentary m2-m3 (180423); 7 R p4 (180424–180430); 2 L, 2 R m1-2 (180431–180434); 9 L, 15 R m3 (180435–180445).

LEVEL 3 2 L, 2 R P3 (180508–180511); 3 L, 5 R P4 (180512–180519); 7 L, 6 R M1-2 (180520–180532); 5 L, 6 R M3 (180533–180543); L, R dentaries I, p4-m3 (180465); R dentary I, p4 (180466); R dentary p4, m3 (180467); R dentary p4 (180468); L 2 R p4 (180469–180471); 9 L, 7 R m1-2 (180472–180487); 11 L, 11 R m3 (180488–180506).

LEVEL 4 2 L M1-2 (180574, 180575); 11 L, 12 R M3 (180576–180592); 2 R dentaries p4-m3 (180544); 5 L, 14 R p4 (180547–180559); 2 L, 3 R m1-2 (180560–180564); 12 L, 6 R m3 (180565–180573); 3 isolated lower/upper (180545, 180546).

LEVEL 5 8 L, 3 R P3 (180639–180649); 6 L, 4 R P4 (180650–180656); 9 L, 8 R M1-2 (180657–180670); 6 L, 2 R M3 (180671–180678); 5 L, 4 R p4 (180593–180601); 7 L, 12 R m1-2 (180602–180619); 12 L, 9 R m3 (180620–180638).

LEVEL 6 3 R P3 (180703–180705); 2 L P4 (180706, 180707); 5 L, 4 R M1-2 (180708–180716); 6 L, 7 R M3 (180717–180729); 3 L, 4 R p4 (180680–180686); 5 L, 2 R m1-2 (180687–180693); 5 L, 3 R m3 (180694–180701); 21 isolated lower/upper (180679, 180702).

LEVEL 7 3 L P3 (180735–180737); 2 L, 5 R P4 (180738–180743); 2 L, 7 R M1-2 (180744–180750); 5 L, 5 R M3 (180751–180760); L, R p4 (180730, 180731); L, R m1-2 (180732, 180733); R m3 (180734).

LEVEL 8 R P3, L P3, R P4, 2 L P4, 5 RM1 or M2, 3 L M1 or M2, R M3, L M3, R p4, 3L p4, Rm 1 or 2, Lm1 or 2, 2 R m3, L m3. These specimens were in UCMP collections and were examined by A. D. Barnosky in 1991 but were subsequently lost; thus they are uncurated and were not available for my examination. They were questionably referred to *S.* cf. *S. elegans* by Barnosky based on the notes recorded at the time they were examined, but their referral to this species is by no means certain.

LEVEL 8A 3 L P3 (180777–180779); L, 4 R P4 (180780–180783); 5 L, 4 R M1-2 (180784–180786); 2 L M3 (180787, 180788); L, R p4 (180763, 180764); 4 L, 5 R m1-2 (180765–180773); 2 L, R m3 (180774–180776); isolated lowers/uppers (180762).

LEVEL 9 L P3 (180789); 2 L, RM1-2 (180790–180792); L M3 (180793).

LEVEL 10 L P3 (180414); L, R P4 (180415, 180416); 2 L, 2 R M1-2 (180417–180420); L M3 (180421); 2 L, 2 R p4 (180403–180406); 4 L m1-2 (180407–180410); 2 L, R m3 (180411–180413).

VELVET ROOM (DMNH)

HORIZON A Skull P4, M2-M3 (10621); palate P4-M3 (10568); palate P4-M3 (11272); R maxilla P3-M3 (29699); L maxilla P4-M3 (10566); 2 R maxillae P4-M3 (10561, 36027); L dentary I, p4-m3 (11211); 2 R dentaries I, p4-m3 (22403, 22404).

HORIZON A–C 3 palates P4-M3 (12207, 12208, 21581); palate L P4-M3 (8379); palate R P4-M3 (8316); palate M3 (8350); L maxilla P4-M3 (8658); R maxilla P4, M2-M3 (8416); 3 L dentaries I, p4-m3 (8318, 8322, 12209); R dentary I, p4-m3 (8420); 2 L dentaries p4-m3 (12217, 21586); R dentary p4-m3 (8413); 2 L dentaries p4-m2 (8661, 27305); L dentary p4-m1, m3 (8324).

HORIZON B Skull I, P4-M3 (11168); skull P4-M3 (11280); skull, partial, P4-M3 (11095); skull P4, M3 (12340); skull L P4, M3 (11097); 7 palates P4-M3 (10660, 11169, 11253, 11942, 20617, 20762, 21822); palate R P4-M3 (10571); palate P4-M1, M3 (12127); palate M1-M3 (21821); 3 L maxillae P3-M3 (11094, 20766, 20863); L maxilla P3-P4, M2-M3 (36017); L maxilla P3-M2 (29674); 16 L maxillae P4-M3 (10573, 10661, 11248, 11811, 11816, 11936, 12135, 12136, 12301, 12565, 12569, 13804, 13805, 20765, 20866, 23414); 20 R maxillae P4-M3 (9935, 10511, 10650, 10725, 11092, 11245, 11282, 11803, 11804, 12123, 12562, 12564, 20742, 20770, 20771, 20861, 21852, 22146, 27835); L maxilla P4-M2 (12140); 2 L maxillae P4-M1, M3 (20864, 27157); 2 R maxillae P4-M1, M3 (9974, 12124); 18 L dentaries I, p4-m3 (9937, 10516, 11256, 11262, 11820, 11934, 12066, 12143, 12150, 12151, 12298, 12540, 12544, 20760, 20761, 20801, 21853); 10 R dentaries I, p4-m3 (10526, 11171, 12172, 12337, 12361, 12377, 12555, 20851, 20852, 20985); 8 L dentaries p4-m3 (9946, 10654, 10712, 11172, 11295, 12334, 15150, 21999); 13 R dentaries p4-m3 (10522, 10709, 10710, 11085, 11270, 12068, 12333, 20697, 20736, 20769, 20854–20856); 2 R dentaries I, p4-m2 (10708, 10723); L dentary I, p4-m1, m3 (11173); 3 R dentaries I, p4-m1, m3 (9968, 12241, 12556); 2 L dentaries p4-m1, m3 (11255, 20803); 2 R dentaries I, p4, m3 (11077, 12174); R dentary I, m1-m3 (12551); 2 L dentaries m1-m3 (10711, 38851); L dentary I, p4 (9945).

HORIZON B–E Palate L P4-M1, M3 (20709).

HORIZON C 2 palates P3-M3 (8553, 22375); palate P4-M3 (9877); palate P4-M1, M3 (9870); 2 L maxillae P3-M3 (10461, 21116); R maxilla P3-M3 (9860); 2 L maxillae P4-M3 (9864, 9865); 2 R maxillae P4-M3 (9852, 9859); L maxilla P4-M1, M3 (9866); 3 L dentaries I, p4-m3 (8548, 8549, 9875); 7 R dentaries I, p4-m3 (8543, 9861, 9868, 9872, 9878, 12773, 20973); L dentary p4-m3 (22301); 3 R dentaries p4-m3 (9851, 9853, 9874); R dentary I, p4, m2-m3 (9869); L dentary I, p4-m1, m3 (20710); R dentary I, p4-m1, m3 (8544); L dentary p4, m2-m3 (20503).

HORIZON C–D L maxilla P4-M3 (27843).

HORIZON D 3 R maxillae P4-M3 (8432, 20544, 27315); 2 L dentaries I, p4-m3 (10747, 12218); R dentary I, p4-m3 (10746).

HORIZON E AND BELOW R dentary I, p4-m3 (12225); R dentary I, p4, m3 (12805).

UNCERTAIN HORIZON Skull L P3-M3 (6556); 2 skulls P4-M3 (11900, 21555); skull, partial, L P4-M3 (6729); skull P4, M2-M3 (10389); 2 palates P3-M3 (6565, 11903); 4 palates P4-M3 (9831, 21554, 23214, 23444); palate R P4-M3 (21609); 2 palates P4-M2 (6487, 21553); 2 L maxillae P3-M3 (6594, 11887); R maxilla P3-M3 (6544); R maxilla P3-M1, M3 (6445); 13 L maxillae P4-M3 (6425, 6442, 6451, 6478, 6479, 6537, 8239, 8243, 9669, 9718, 9805, 9826, 11891); 13 R maxillae P4-M3 (6481, 6503, 6512, 6548, 6599, 6603, 8435, 8439, 9641, 9659, 9679, 9721, 27308); R maxilla P4-M2 (11885); L maxilla P4-M1, M3 (10391); 2 R maxillae P4-M1, M3 (9642, 21563); 2 R maxillae P4, M2-M3 (6597, 8244); 4 L maxillae M1-M3 (11888, 21380, 33529, 33832); 10 L dentaries I, p4-m3 (6492, 6508, 6616, 6730, 8445, 9707, 9716, 11874, 21605, 23217); 17 R dentaries I, p4-m3 (6444, 6489, 6494, 6596, 6614, 6685, 6727, 8204, 8206, 8232, 9646, 9715, 9807, 10612, 10909, 11879, 21559); 8 L dentaries p4-m3 (6443, 6490, 6493, 8448, 9648, 21606, 23443, 23446); 20 R dentaries p4-m3 (6404, 6506, 6531, 6532, 6617, 6622, 9644, 9652, 9657, 9712, 9806, 9808, 9823, 9824, 9832, 10489, 11899, 21556, 21607, 21620); 2 L dentaries I, p4, m2-m3 (9650, 21561); L dentary I, p4-m1, m3 (23215); R dentary I, p4-m1, m3 (9653); L dentary p4-m1, m3 (11897); R dentary p4-m1, m3 (6488); L dentary m1-m3 (11888.2); R dentary m2-m3 (36683.1); L dentary I, p4 (8202).

VELVET ROOM (CM) skull M1-M3 (49248); skull M2-M3 (49249); skull M3 (49209); 5 palates P4-M3 (49226, 49260, 49262, 49267, 49271); 2 palates P4-M2 (49231, 49271); 2 palates P4-M1, M3 (49201, 49257); palate M2 (49258); palate M3 (49200); L maxilla P3-M3 (49261); R maxilla P3-M3 (49211); L maxilla P4-M3 (49275); R maxilla P4-M3 (49263); R maxilla P4-M2 (49203); L maxilla P4-M1 (49235); L maxilla M1-M3 (49276); R maxilla P4 (49222); R maxilla M2 (49264); 3 L dentaries I, p4-m3 (49223, 49250, 49281); 7 R dentaries I, p4-m3 (49220, 49224, 49230, 49251, 49266, 49268, 49272); 8 L dentaries p4-m3 (49202, 49207, 49233, 49243, 49252, 49265, 49274, 49277); 7 R dentaries p4-m3 (49206, 49208, 49214, 49216, 49218, 49232, 49273); 3 L dentaries I, p4-m2 (49227, 49269, 49279); L dentary p4-m2 (49225); L dentary p4, m2-m3 (49245); 2 L dentaries p4-m1 (49212, 49254); L dentary I, p4, m3 (49204); L dentary p4, m2 (49219); R dentary p4, m3

(49261); 2 L dentaries I, m1-m3 (49221, 49280); 3 L dentaries I, p4 (49205, 49244, 49247); R dentary I, p4 (49213); 3 L dentaries p4 (49228, 49253, 49256); R dentary p4 (49255); L dentary I, m3 (49234); L dentary m3 (49246); L dentary I (49229); L dentary, edentulous (21384).

WILL'S HOLE Skull P4-M3 (37292); skull edentulous (23484); palate P4, M3 (37299); palate M1 (23491); L maxilla P4-M3 (37285); 2 R maxillae P4-M3 (37258, 37280); 2 L maxillae P4-M2 (37252, 37276); R maxilla P4-M2 (37271); R maxilla P4-M1, M3 (37283); L maxilla P4, M2-M3 (37257); R maxilla P4, M2-M3 (22893); 2 R maxillae P4, M3 (22894, 37281); R maxilla M1-M3 (37284); L maxilla M2-M3 (22891); R maxilla M2-M3 (22897); L maxilla P4 (22888); L maxilla M3 (22890); 2 R maxillae M3 (22898, 22899); 2 L dentaries I, p4-m3 (22885, 37287); 3 R dentaries I, p4-m3 (37256, 37269, 37282); 4 L dentaries p4-m3 (22876, 37255, 37267, 37274); 2 R dentaries p4-m3 (37251, 37259); L dentary I, p4-m2 (37291); 2 L dentaries p4-m1 (22883, 37278); 5 R dentaries p4-m1 (22860, 22861, 37261, 37264, 37279); R dentary I, m1-m3 (37290); 3 L dentaries m1-m3 (22879–22881); R dentary m1-m3 (22867); R dentary I, m1-m2 (37295); L dentary m1-m2 (22878); L dentary m2-m3 (37272); R dentary m2-m3 (22868); 4 L dentaries I, p4 (22882, 22884, 37289, 37297); 2 R dentaries I, p4 (22869, 22870); L dentary I, m1 (22887); 4 R dentaries m1 (22865, 22866, 37277).

?*Cynomys andersoni*

BADGER ROOM

R maxilla P4-M2 (36153); 2 L, 3 R M3 (22829, 33910); R dentary m1 (20443); R dentary m3 (22834); L dentary m1-m2 (20447); 2 L, 2 R p4, 5 L, 5 R m3 (14303, 22829, 33910).

FISSURE FILL A

R dentary m1-m3 (23335); L dentary I, m1 (23334); L dentary m3 (23332).

GENERATOR DOME

R maxilla P3-M1 (28024); R maxilla M1-M3 (28317); 2 R dentaries m1-m3 (28027, 28320); 3 L dentaries m1-m2 (28047, 28048, 28323); R dentary m1-m2 (28319); 2 L dentaries p4 (28025, 28318); 2 R dentaries m2 (28022, 28327); R dentary m3 (28321); L p4, L, 4 R m1 or m2, 3 L m3 (28316).

MARK'S SINK

R maxilla P3-M2 (36880); R maxilla M1-M3 (36336); L M3 (37247); R dentary m1-m2 (36886); R m1 or m2 (38861); R m3 (37247).

PIT (CM CATALOGUE NUMBERS)

LEVEL 1 R p4 (65112).

PIT (UCMP CATALOGUE NUMBERS)

LEVEL 4 R M3 (180185); L, R p4 (180182, 180183); L m3 (180184).

LEVEL 5 R M1-2 (180186).

LEVEL 6 R m1-2 (180187); 2 L m3 (180188, 180189).

LEVEL 7 R P4 (180190); L, R M1-2 (180191, 180192).

LEVEL 8A R P3 (180197); L P4 (180198); L, R M1-2 (180199, 180200); L M3 (180201); L p4 (180193); 2 L m1-2 (180194, 180195); L m3 (180196).

LEVEL 11 R p4 (180180); L m1-2 (180181).

Cynomys cf. *C. leucurus*

MARK'S SINK

L P3 (35502); L M1 or M2 (37247); L dentary I, p4-m3 (37164); L dentary p4-m3 (37170); R dentary p4-m2 (36887); L dentary m1, m3 (37140); L dentary m3 (37168); L m3 (37247).

PIT (CM CATALOGUE NUMBERS)

LEVEL 1 Palate P4 (65265); palate R M3 (66438); L maxilla M2-M3 (65261); 2 R maxillae M2-M3 (65262, 66439); L, R maxillae P4 (66440, 66441); 2 L, R maxillae M3 (65259, 65263, 66443); L maxilla edentulous (65260); 3 L M3 (65140, 65856, 66372); L dentary p4-m2 (65257); R dentary m1-m2 (65258); 3 R p4 (61119, 65117, 65125); L, 3 R m1 or m2 (65114, 65118, 65121, 66371); L m3 (65113).

LEVEL 2 R palate P4-M2 (65361); 4 L, 6 R P3 (64937, 64938, 66486); 6 L P4 (64942, 64943, 64944, 65002, 66485); 7 R P4 (64996, 65003, 65004, 65769, 66480); 23 L M1 or M2 (64941, 64946, 64948, 64950, 64951, 64952, 64953, 64954, 64955, 64956, 64958, 64960, 64961, 64962, 64985, 64995, 66484); 18 R M1 or M2 (64984, 64985, 64987, 64988, 64989, 64990, 64991, 64992, 64994, 65000, 65765, 66481); 16 L M3 (64963, 64964, 64965, 64966, 64967, 64969, 64970, 64971, 64972, 64973, 64974, 64975, 66483); 12 R M3 (64908, 64912, 64976–64983, 66482); 2 L, 4 R p4 (64926, 64927, 64930, 65017, 65019, 65020); 5 L m1 or m2 (64929, 64931, 64932, 65016, 65773); 11 R m1 or m2 (65010–65015, 65018, 66476); 6 L m3 (64933, 64935, 64936, 66474, 66476); 12 R m3 (64930, 64934, 65005–65009, 65762, 65763, 66476B, 66477).

LEVEL 1 OR 2 Palate P4-M2 (65266); palate R P4-M2 (65267); R maxilla edentulous (65260).

LEVEL 3 R maxilla P4-M3 (65509); L, R P4 (175227, 175228); L M1 or M2 (65600); R, L dentaries p4-m3 (65506, 65507); R dentary p4-m2 (65505); L dentary fragment m2 (65510).

PIT (UCMP CATALOGUE NUMBERS)

SURFACE Palate edentulous (180004); palate P4-M3 (180003); R maxilla M1-M2 (180002); R P4 (180005); L dentary m1 (180000); L dentary m2-m3 (180001).

LEVEL 1 R maxilla P3 (180038); R maxilla M1-M3 (180036); R P3 (180037); L, R P4 (180039, 180040); 4 L, 5 R M3 (180041–180049); 2 R dentaries p4-m2 (180006, 180007); R dentary m1-m2 (180008); R dentary m2-m3 (180009); L dentary m2 (180010); 4 R p4 (180011–180014); 5 L, 9 R m1-2 (180015–180026); 3 L, 5 R m3 (180027–180034); L lower cheek tooth (180035).

LEVEL 2 Palate M1 (180088); palate M1-M3 (180087); palate P4-M2 (180086); R maxilla P4, M3 (180084); L maxilla M2-M3 (180085); L P3 (180089); 4 R, 4 L P4 (180090–180098); 11 R, 10 L M1-2 (180099–180121); 9 R, 8 L M3 (180122–180137); R dentary p4-m2 (180050); L dentary m2-m3 (180054); L dentary m1 (180053); L dentary m1-m2 (180052); L dentary m1-m3 (180051); 3 R, 2 L p4 (180055–180059); 12 R, 4 L m1-2 (180060–180075); 6 R, 2 L m3 (180076–180083).

LEVEL 3 R maxilla M1 (180157); 2 R, 2 L P4 (180158–180161); 6 R, 2 L M1-2 (180162–180169); 2 R, 6 L M3 (180170–180177); R dentary p4-m1 (180138); R, L p4 (180139, 180140); 2 R, 3 L m1-2 (180141–180145); 6 R, 5 L m3 (180146–180156).

LEVEL 4 R dentary p4-m3 (180178).

LEVEL 5 L P4 (180179).

WILL'S HOLE

L dentary I, p4-m3 (23485); R dentary m2-m3 (23483).

VELVET ROOM (DMNH)

HORIZON A L maxilla P4-M2 (10627).

HORIZON A–C R dentary I, p4-m3 (12202); 3 L dentaries p4-m3 (8297, 8383, 8710); R dentary p4-m3 (8295); 2 L dentaries m1-m3 (8382, 27882).

HORIZON B L maxilla P3-M3 (13797); 2 L maxillae P4-M3 (11955, 21858); L maxilla P4-M2 (29628); R maxilla P4-M2 (22010); R maxilla M1-M2 (12114); L maxilla M2-M3 (20755); L maxilla M1 (20657); R maxilla M3 (11240); 4 L dentaries p4-m3 (9950, 10508, 20507, 20511); 6 R dentaries p4-m3 (11121, 11241, 11242, 12240, 20658, 20815); L dentary p4-m2 (20660); 2 R dentaries p4-m2 (20512, 20657); 3 L dentaries m1-m3 (11122, 11243, 21859); 2 R dentaries m1-m3 (11793, 11794); 2 L dentaries m1-m2 (12112, 20660); R dentary m1-m2 (12113); L dentary m2-m3 (22009); R dentary m1 (11792); L m3 (20657).

HORIZON B–C 2 L maxillae P4-M3 (20689, 20711); L dentary p4 (21533).

HORIZON C L maxilla M1-M2 (9881); L dentary m2-m3 (9886).

HORIZON D L dentary p4-m3 (15403); L m3 (9916); R m1 or m2, R m3 (10752).

UNCERTAIN HORIZON L palate P4-M3 (6568); 3 L maxillae P4-M3 (9814, 20479, 23227); R maxilla P4-M3 (8385); L maxilla P4-M2 (6566); R maxilla P4-M2 (6497); R maxilla P4-M1 (6424); R maxilla M1-M2 (6569); R maxilla M2-M3 (6643); L dentary I, p4-m3 (6640); L dentary p4-m3 (6567); R dentary p4-m3 (21576); L dentary p4-m2 (8221); L dentary p4, m2-m3 (11865); R dentary p4-m1 (6641); 3 L dentaries m1-m3 (9722, 11867, 21568); R dentary m3 (21566); L, R m3 (8248).

VELVET ROOM (CM)

Palate M2 (49241); L maxilla M2 (19236); 2 R dentaries p4-m3 (49238, 49242); L dentary m1-m3 (49240); R dentary m2 (49239).

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EIGHTEEN

Fossil Wood Rats of Porcupine Cave

Tectonic or Climatic Controls?

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The evolution and paleobiogeography of wood rats (packrats), genus *Neotoma,* is poorly known, not because they are uncommon as fossils, but because their teeth all look alike. Living species are identified by features that are seldom preserved in fossils. Usually all that is mentioned of the teeth is the anterointernal reentrant (or "groove," as it is most frequently called in the description of modern forms) of the M1, the alveolar length of the tooth row, and the nature of the m3. The great majority of fossil records consist only of isolated teeth, which generally have not been considered sufficient to identify species.

Thus, at present, all that can be said of the history of *Neotoma* is that it belongs to a New World lineage first known in the late Miocene (circa 5.5–5.3 Ma ago) of central Mexico. These early Mexican representatives (Caranza-Castañeda and Walton, 1992) are very small forms that appear to be only slightly more derived than the generalized sigmodontine condition. Similar early Pliocene forms have a wide distribution over the southwestern quarter of the United States. Such late Miocene and early Pliocene forms are universally placed in the extinct genus *Paraneotoma* and are diagnosed as having an S-shaped m3.

Near the Pliocene-Pleistocene transition (circa 1.8 Ma ago), the S of the m3 is almost universally altered to an 8 that is present in all but one living species of *Neotoma, N. (Hodomys) alleni,* which retains the S-shaped last lower molar and is found in the western part of central Mexico (southern Sinaloa to northern Oaxaca). It thus seems that wood rats probably evolved in Mexico or Central America and dispersed northward into the southwestern United States near the beginning of the Pliocene. From there they appear to have continued dispersing northward along the eastern and western sides of the Rocky Mountains. Today the recognized species on either side of the Rocky Mountains are distinct, with little hybridization between them except just north of Mexico, south and southwest of the Colorado Rockies.

With the exception of the bushy-tailed wood rat, *Neotoma cinerea,* which has adapted to cooler habitats, the northernmost range of wood rats reaches coastal northern Oregon west of the Rockies and southwestern South Dakota to the east. Most species seem never to have crossed the Rocky Mountains. In the eastern United States *Neotoma* extends into southern New York; in the Mississippi Valley it ranges northward only to the southern tip of Illinois. East of the Rocky Mountains the northern limit of the wood rat is strikingly close to the former extreme southern limits of continental glaciation, a situation that has a parallel record with mountain glaciation in the Rocky Mountains. *Neotoma cinerea* ranges along the Rocky Mountains as far north as southern Yukon Territory and adjacent Northwest Territories.

Neotoma largely avoids full tropical regions but extends southward to northern Nicaragua in the mountains of Central America. Following the nomenclature of Hall (1981), the subgenera *N. (Hodomys)* and *N. (Teanopus),* each monospecific, are the primary exceptions and live in a small tropical area on the Pacific coast of Mexico. Thus, except for the bushy-tailed wood rat, *Neotoma cinerea,* the modern ranges of most species of *Neotoma* are found in warm-temperate to subtropical areas, with about half the living species preferring dry regions or deserts.

Neotoma cinerea, which currently lives in the vicinity of Porcupine Cave at about 2900 m elevation, and as low as 1800 m near Colorado Springs, is found as fossils in the cave. At the latitude of Porcupine Cave, 1800 m is about the upper elevational limit of the other species present in the fauna of the Pit: *N. floridana, N. micropus, N. mexicana,* and *N. stephensi.* Finley (chapter 8) describes the modern habitat of these species.

Of these, only *N. stephensi* is not currently widely ranging in Colorado. It occurs throughout most of northern Arizona and the western third of New Mexico practically to the Colorado state line southeast of Durango. Throughout its range this wood rat is closely associated with juniper bushes or small trees, on which it depends for food, water, and shelter. It builds its nests near (within 10 m), beneath, or in junipers (Vaughan, 1980, 1982). Its former range was apparently much greater, as evidenced by Porcupine Cave and a few other fossil localities, and the relict nature of its modern distribution was pointed out by Vaughan (1982).

The enamel structure (Schmelzmuster) of species of *Neotoma* is not well known. Descriptions are available only for *Neotoma fuscipes* (Koenigswald, 1980:63). From that study it seems that the enamel structure is basically quite primitive in the genus, and it is possible that a wider examination might prove of value. But it is also possible, to judge from arvicolines with similar primitive enamel, that the enamel structure will not prove diagnostic of species.

Materials and Methods

More than 2500 specimens, mostly isolated teeth, of *Neotoma* were examined from Porcupine Cave. Material from the Pit included 1650 specimens (appendix 18.1). An additional batch of specimens catalogued by 550 DMNH numbers was examined from the DMNH Velvet Room sample (DMNH 644); the great majority were isolated teeth, and some DMNH numbers included many teeth.

Part of this study focused on defining taxonomically useful dental characters. All teeth were examined, but only the m1, M1, and m2 (if only slightly worn) could be confidently assigned to a species. The author's collection of modern and fossil species of *Neotoma* was used as comparative material. Throughout the identification process, a sample of 25 specimens of modern wood rats was kept on the microscope desk for comparison, including at least two specimens for the species that seemed most distinctive *(N. micropus),* and six specimens for the species in which variation seemed conspicuous *(N. cinerea).*

The comparative material represented all the extant species found in Colorado east of the Rocky Mountains, including *N. albigula,* which was expected as a possible part of the fauna but was not found, and *N. stephensi.* The latter has not been reported from Colorado, but Fitzgerald et al. (1994) listed it as a probable occurrence near the state's extreme southwestern border. The modern range of *Neotoma albigula* overlaps parts of the distribution of *N. mexicana, N. floridana,* and *N. micropus* in southeastern Colorado.

Additional specimens of all other species from west of the Rocky Mountains were also available for comparison, but those species were not found to be present in the Porcupine Cave fossil sample. All species from the United States were represented in the reference collection and initially were compared with the Porcupine Cave fossils. Approximately a dozen fossil localities in the western United States were represented as fossil comparative material, and fossil localities in the eastern United States were represented by specimens or epoxy casts made from borrowed specimens.

In the discussions that follow, identifications were not considered firm unless at least two definitive characters affirmed them. Questionable identifications were those made on the basis of only one character.

The diagnostic characters employed in this study should be verified in known modern specimens whenever possible. Although they seem valid, future work may show variation more pronounced than that recognized here.

Paleontological Descriptions

Class Mammalia

Order Rodentia

Family Muridae

NEOTOMA

GENERAL COMMENTS Zakrzewski (1993) provided an overall summary of the fossil record of the wood rats and discussed their dental characters. The terminology he used is not the same as that used herein, although in many cases it refers to the same features. There is no generally accepted terminology for the features that are called by different names in his report and in this chapter. Both reports include illustrations that define the terms. Zakrzewski's intent was to cover all known species of *Neotoma,* fossil and living, whereas only those involved in the fossil faunas of Porcupine Cave are discussed here; all of the Porcupine Cave fossils represent extant species.

USEFUL DENTAL CHARACTERISTICS *Neotoma* is a high-crowned cricetid rodent with roots on its teeth. The configuration of the occlusal surface changes dramatically with increasing wear, and it appears impossible to characterize species without taking this fact into account. The most reliable characters are those that remain when the tooth is greatly worn. These characters include the following:

1. The rootward extent and depth at a particular point in wear of the anteromedial groove on the M1 and m1 (figure 18.1, no. 3).
2. The presence or absence of pits (figure 18.1, no. 1) at the base of the reentrants (figure 18.1, no. 5) and, to a limited extent, which reentrants have them.
3. The form of the basal margin of the enamel crown (dentine tract) of m1 (figure 18.1, no. 4).
4. The relative anteroposterior dimension of the buccal reentrants of the lower first molar in occlusal view. (For example, in figure 18.1, center, the posterior reentrant is longer than the anterior one.)
5. The configuration of the occlusal surface on teeth showing little wear, including the position of the commissures between lophids and the configuration of the joined anteroconid-metaconid complex of m1 (which varies with wear, with the depth of the anteromedial groove, and with the presence or absence of an anterior cingulum).

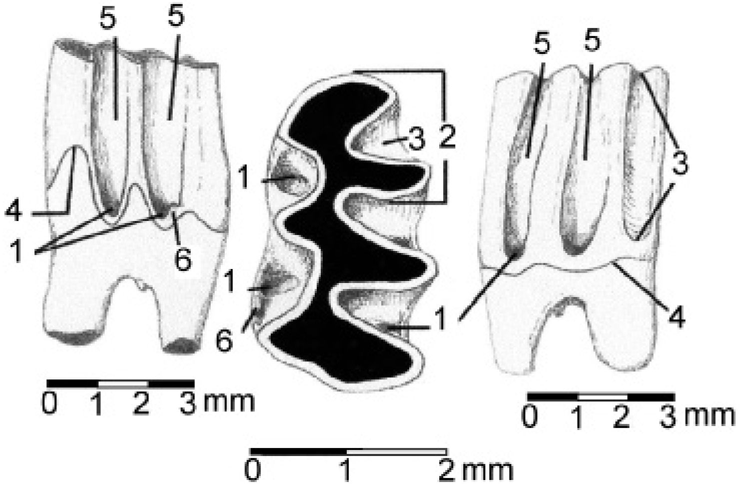

FIGURE 18.1 Left, buccal view (anterior to left); center, occlusal view (anterior up); right, lingual view (anterior to right) of the left m1 of *Neotoma cinerea,* showing dental features discussed. 1, Pits; 2, anteroconid-metaconid complex (anteroconid is most anterior; metaconid posterior to 3); 3, anteromedial groove; 4, base of the enamel crown-dentine tract (ascending the anterobuccal face of the anteroconid, left in the buccal view); 5, reentrants; 6, stylid. The tooth shows minor wear. The anterior cingulum projects posteriorly low along the buccal margin of the tooth from the posterobuccal corner of the anteroconid external to the anterobuccal pit. The posterior cingulum is a broad dentine field extending lingually from the hypoconid, which is the posterior buccal salient angle; these are seen in the occlusal view. Elevation of the dentine tract is moderate for the species (buccal view, left, 4) but is distinctly more wavy that in some other species.

Unless the tooth is fully erupted, the first three of these dental characters cannot be observed in modern dried specimens without dissection of some of the alveolar bone. There is, of course, no such problem with isolated fossil teeth or with modern specimens with fully erupted cheek teeth. The configuration of the occlusal surface of all species changes rapidly with wear and simulates that of other species at different stages of wear. As an example, the configuration of the occlusal surface of the m1 of *Neotoma cinerea* with considerable wear can be quite similar to that of *N. floridana* or *N. stephensi* with slight wear. An estimation of the approximate degree of wear is thus important, and this is often not possible on museum specimens in which the tooth is not fully erupted.

The m3 of all extant species of *Neotoma* in the United States consists of anterior and posterior dentine fields that are joined by a necklike commissure. Variation includes three conditions: the neck is lingual, central, or buccal. The same form of m3 is found in different species. Thus isolated m3s, like M2s and M3s, cannot be identified to species. When wear is great enough that the entire base of the enamel crown is no longer intact, identification is impossible, except in the case of *Neotoma cinerea,* which has enamel pits at the base of all or most reentrants of m1 and m2 that remain as islets even in very worn teeth.

Recognition of the dentine tract (character no. 3 in the previous list) is frequently difficult in dried modern specimens and in some fossil specimens. Helpful clues result from the fact that periodontal fibers do not adhere to tooth enamel, and, where they appear in modern dried specimens (below the alveolar rim in dissected specimens), the base of the enamel crown is indicated by their absence. In most fossil specimens (where the fibers are no longer preserved) differential secondary discoloration of enamel and dentine often indicates the position of the enamel crown base (but care is necessary because fossil enamel is often translucent). In other fossil specimens the tooth must be manipulated under the microscope to achieve incidental reflection such that the limit of enamel deposition on the tooth becomes evident in the surface topography of the tooth.

The incidental reflection technique requires practice to achieve proficiency. When one looks at the buccal side of the tooth where the dentine tract is present (with the tooth oriented so that the microscope light reflects off it), in many cases the enamel appears higher than the dentine (being deposited on the dentine). However, in some cases it appears that the dentine continues to be deposited after enamel deposition has ended, so the dentine appears to be higher. In either case, the base of the enamel shows up as a slightly different elevation than the dentine on the surface revealed by reflected light. In high-crowned wood rats, waviness of the dentine tract is minor in comparison to fully hypsodont rodents, such as voles and lemmings. In some publications, especially European ones, the dentine tract is called the "linea sinuosa" (Rabeder, 1981; Fejfar and Repenning, 1998:text figure 1). In wood rats, it has been called the dentine tract by Lundelius (1979), Harris (1984), and Zakrzewski (1993). As in all rooted hypsodont taxa, the undulations of the base of the enamel crown vary slightly between individuals of the same species, and therefore the taxonomic utility of this character is most reliable where the tract is most developed, that is, where it ascends the buccal face of the anteroconid. In the wood rats, as in the arvicolines, this greatest waviness is on the buccal face of the anteroconid (anteroconid complex in arvicolines) of m1. In those wood rats that have at least incipient dentine tracts, the height of the tracts is very diagnostic. In the species of the present study, an anterobuccal dentine tract is absent only in *Neotoma floridana* and is most extreme in *N. stephensi* and *N. cinerea.* In most wood rats the anterobuccal dentine tract is eventually cut as the crown wears, causing a discontinuity of the enamel band on the occlusal surface of the anteroconid-metaconid complex.

DIFFERENTIATION OF *NEOTOMA* TAXA All species are semihypsodont. The m1 metaconid (most anterior lingual salient angle) is broadly confluent with the anteroconid (most anterior field of the occlusal surface), varyingly separated by a shallow anteromedial reentrant, or groove; these two dentine fields are herein called the "anteroconid-metaconid complex" (figure 18.1, center, no. 2). The protoconid (medial buccal salient angle) is broadly confluent with the entoconid (medial lingual salient angle), and the two varyingly approach a transverse loph; the hypoconid (posterior buccal salient angle) is completely confluent with a posterior cingulum (posterior lingual salient angle) and forms a second (more posterior) transverse loph.

Lophs and the anteroconid-metaconid complex (figure 18.1, no. 2) are all connected by open commissures except in teeth with no or very slight wear. The commissure may be centrally located or have buccal displacement from the midline of the tooth (figure 18.1, center), with the feature varying with wear. The connection is more nearly closed in the very similar subgenera *Hodomys* and *Teanopus* (application of names follows that of Hall, 1981). The m2 consists of three lophs formed by the metaconid and anterior cingulum, the entoconid and protoconid, and the hypoconid and the posterior cingulum; it lacks the anteroconid of m1.

The m3 has anterior and posterior dentine fields united by a necklike commissure that may be located lingually, medial, or buccally. The subgenus *Hodomys* has an S-shaped m3, as does the Pliocene genus *Paraneotoma.* The generalization that the S-shaped m3 of *Paraneotoma* distinguishes it from the 8-shaped m3 of *Neotoma* is true and convenient. But the difference is gradational. Many examples of mid-Pliocene specimens of *Paraneotoma* (e.g., from the Taunton fauna of eastern Washington, circa 3 million years old) exhibit little-worn m3s with a clear S pattern, but after about half the crown is worn away, they assume the 8 pattern of *Neotoma.*

Such gradation has not been observed in early Pleistocene faunas. The S pattern is absent in the earliest forms of *Neotoma* except, possibly, in the completely unworn m3. *Parahodomys spelaeus* Gidley and Gazin from the circa 830,000-year-old Cumberland Cave fauna of Maryland (and a few unstudied records) bears some resemblance to *Paraneotoma,* but even it has a less clear S pattern on m3 than extant *Neotoma (Hodomys)* from Mexico.

The upper teeth of *Neotoma* superficially resemble the lowers except that the lophs are oriented more anterobuccally. On the M1 the anterocone joins the protocone to form the first loph (the "anterior loop"), which in many species is partly separated by a shallow anteromedial groove. This groove varies in depth from essentially lacking in *N. stephensi* and most subspecies of *N. floridana* to maximum development in species such as *N. cinerea, N. mexicana,* and *N. micropus;* it also varies in vertical extent and is variable in *N. floridana.*

The paracone and hypocone form the second loph of M1, and the metacone forms the third and shortest loph, the posterior cingulum being weak in the upper teeth.

The difference in orientation of the lophs of the lower teeth (nearly transverse) and the upper teeth (about 45° from transverse) allows the lophs of the opposing teeth to pass each other in propalinal chewing with much the same action as the blades of a pair of scissors. The pattern is the same in M2 and M3. The upper teeth usually have three roots, whereas the lower ones have only two. As pointed out by Zakrzewski (1993) the puzzling Mexican species *Neotoma (Hodomys) alleni* has a pronounced primitive S-shaped m3 but seems advanced in having an abnormally great number of roots on its teeth.

In many species, the lower teeth and less commonly the upper teeth possess a sloping crest that may extend posteriorly from the ends of the lophs (the ancestral position of the conids, as is evident in *Neotomodon*). With greater development, these sloping crests form a low wall across the bottom of the reentrants behind the cusp. In less hypsodont murids this crest, as developed at the posterolateral corner of the anteroconid, has been called the anterior cingulum (e.g., Lindsay, 1972:figure 40). This crest leaves the lowermost part of the reentrant walled off from the side of the tooth, producing a "pit" at the base of the reentrant (figure 18.1, no. 1). Pits occur in the bottom of many reentrants, caused by similar crests projecting posteriorly from this and other cusps and cuspids. They occur in many species as individual variations, but in a few species the pits characterize the majority of individuals and thus serve to help recognize species.

Pits form in the buccal and less frequently in the lingual reentrants of the teeth. On extremely worn teeth the pits remain as enamel islets and thus are one of the most persistent characters throughout the wear of the tooth. Pits cannot be observed without dissection in dried modern specimens that do not have fully erupted teeth. In some species, depending upon the relative openness of the reentrant, the development of an external wall at the reentrant base results in a depressed valley rather than a conical pit, as is most conspicuous in *N. floridana* and *N. micropus,* which do not have conical pits.

Excessive development of the lateral walls at the base of the reentrants frequently results in the development of a low cusp, a style or stylid. These form most frequently on the wall across the base of the posterobuccal reentrant of the m1 and m2 (figure 18.1, no. 6). Development of a style or stylid is random, although it may be present more frequently in some species.

If the crest on the buccal side of the anteroconid of the m1 extends upward to the occlusal surface, it forms a buccal spur on the surface's posterobuccal corner. This structure (not illustrated) is more typical of some species in which the crest is higher. Its total absence is typical of species in the western faunal region west of the Rocky Mountains (for example, *Neotoma fuscipes*). The feature varies with wear in many species; the spur, if present, becomes more prominent with wear.

The development of hypsodonty may be thought of as a delay in root formation. The periodontal fibers that hold the tooth in its alveolus do not adhere to tooth enamel, but do attach to either tooth dentine or tooth cementum. Increasing hypsodonty is therefore accompanied by the increasing exposure of dentine and cementum. *Neotoma* is only semi-hypsodont; thus no cementum is present in the reentrants between the lophs, and the degree of exposure of dentine (where enamel is not deposited) varies with the species. Some exposure of the dentine is present in most wood rat species and produces a waviness in the basal margin of the enamel, that is, "dentine tracts," which are most conspicuous on the buccal side of the anteroconid-metaconid complex of the m1. The degree of this development appears to be a consistent diagnostic character of the species of *Neotoma* and persists with wear.

The root pattern on the teeth of *Neotoma* exhibits the usual condition of low-crowned murids. Two roots are on the lower teeth and three are on the uppers; Ml has a lingual third root at its longitudinal midpoint, whereas M2 and M3 have two anterior roots and one posterior root. Supernumerary roots are rare (except in *N. [Hodomys] alleni*).

Table 18.1 summarizes the dental differences between species found as fossils in Porcupine Cave. Relevant characters are compared in the following diagnostic summary. Referred specimens for the Pit locality are listed in appendix 18.1.

NEOTOMA CINEREA *(ORD, 1815)*

MODERN DISTRIBUTION Today the bushy-tailed wood rat, *Neotoma cinerea,* is the only wood rat species known from the Porcupine Cave area. It was also present throughout the history of the deposits in the cave. In addition to occurring at higher elevations (above 1830 m) at the latitude of Porcupine Cave today, *N. cinerea* is the only species that ranges north of Oregon and into northwestern Canada.

DISTINGUISHING CHARACTERS Although *Neotoma cinerea* includes some of the largest individuals known, the size range of its teeth varies widely and overlaps that of other species. Its most distinctive feature is the presence of pits in most reentrants.

ANTEROMEDIAL GROOVE OF m1: Usually prominent to about the base of the enamel cap, but may be only a relatively inconspicuous swale (a shallow and broadly open valley) when the tooth is about half worn. With little wear the groove is uniquely deep, making the anteroconid appear greatly enlarged; this trait is shared with *N. mexicana,* especially in specimens in which the swale extends half way to the enamel base. The condition in *N. cinerea* differs from that in *N. stephensi* and from *N. micropus,* in which the groove lacks great depth, and from *N. floridana* in extending to the enamel base.

PITS: Always prominent at the bottom of most reentrants. Always present in the two buccal and posterior lingual reentrants of m1, sometimes present in the anterior lingual reentrant. Some pits are always present on other lower teeth, and pits are present in the reentrants of the great majority of upper teeth. *N. cinerea* is unique in its many consistently present pits; *N. mexicana* has none on the lingual side of m1. In some individuals of *N. cinerea* a depressed valley, rather than a pit, is present at the base of the anterobuccal reentrant of the upper M1, as in *N. floridana,* but the other reentrants of this tooth retain conspicuous pits, unlike *N. floridana.*

POSTERIOR BUCCAL REENTRANT OF m1: At least as wide and often noticeably wider in an anteroposterior direction than is the anterior buccal reentrant. The latter condition is unique to the species, but the former condition is shared with most other species. *N. cinerea* differs from *N. mexicana* in the width of this reentrant.

DENTINE TRACT OF m1: Variation of this tract is great in *N. cinerea,* possibly more than in any other species, but exposed dentine runs at least halfway up the buccal face of the anteroconid-metaconid complex. This character is shared with *N. stephensi* and *N. mexicana,* but it differs from the condition in *N. floridana,* which has no dentine tract, and in *N. micropus,* which has only a slight rise up this face.

BUCCAL CREST FORMS A SPUR: When the m1 is about half worn, the crest running posteriorly from the anteroconid across the buccal base of the anterobuccal reentrant, forming the pit, is met by the occlusal surface and begins forming a posterior spur on the occlusal surface. The degree of development of this spur is shared with *N. mexicana* and exceeded by *N. floridana,* in which the spur appears with little wear. The character differs in *N. micropus* and *N. stephensi,* in which the crest is very low or absent.

ANTEROMEDIAL GROOVE OF M1: Uniformly deep to the enamel base. Some individuals have a small pit at the base of the groove. This feature is shared with *N. mexicana* and *N. micropus* but differs from the condition in *N. floridana* and *N. stephensi.*

NEOTOMA MEXICANA *BAIRD, 1855*

MODERN DISTRIBUTION Today *Neotoma mexicana* occupies intermediate elevations between *N. cinerea* (high) and *N. floridana* (low), occurring in the lower foothills of the Colorado Front Range but also on the Great Plains to the extreme southwest corner of Colorado. The species is rather rare in the fossil record of Porcupine Cave.

DISTINGUISHING CHARACTERS On average *N. mexicana* is smaller than *N. cinerea* (Hall, 1981). The teeth, although resembling those of *N. cinerea* more than those of other species, have unique characters, most distinctive of which is the greatly elongate anterobuccal reentrant.

ANTEROMEDIAL GROOVE OF m1: As in *N. cinerea,* this groove extends to the base of the enamel cap and may be shallow to an inconspicuous swale when about half worn. The

TABLE 18.1

Summary of Dental Differences among the Species of *Neotoma* Represented in the Porcupine Cave Fauna

Species	*Groove, m1*	*Buccal Pits, Lower*	*Dentine Tract*	*Groove, M1*	*Buccal Pits, Upper*	*Posterobuccal Reentrant Occlusal Length, m1*	*Anterobuccal Renentrant Occlusal Length, m1*
N. cinerea	To enamel base; may shallow to a swale in lower half; upper half very deep.	Present; posterior style frequent.	High relief up buccal face.	To enamel base, uniformly deep.	Present, also on lingual side.	Frequently elongate.	Not elongate.
N. mexicana	To enamel base; may shallow to a swale in lower half; upper half deep.	Posterior reentrant only. No style.	High relief.	To enamel base, uniformly deep.	Present, only on buccal side. Tendency to form valleys.	Not elongate.	Very elongate.
N. floridana	About four-fifths to one-half to enamel base, uniformly deep.	Lacking, but posterobuccal reentrant with valley. Styles very rare.	Flat with no relief up buccal face.	Very shallow and well short of reaching enamel base. Not visible on occlusal surface with modest wear.	Valleys only.	Not elongate.	Not elongate.
N. micropus	One-half to three-quarters to enamel base.	Lacking, but with valleys.	Moderate relief, one-quarter up buccal face.	Deep and bottoms at enamel base in small pit.	Valleys only.	Not elongate.	Not elongate.
N. stephensi	To enamel base, fairly deep with no shallowing and no basal pit.	Pits in most reentrants, similar to *N. cinerea.* Styles very rare.	Possibly the greatest relief of all, not variable as in *cinerea.*	Essentially lacking with slight wear, as in *N. floridana.*	Present, no lingual pits.	Not elongate.	Not elongate.

development of the swale is shared with *N. cinerea,* but the species differs from *N. stephensi* and *N. floridana* in having the shallow swale extend to the enamel base, and from *N. micropus* in having a shallow swale but no pit at the bottom.

PITS: Fewer than in *N. cinerea.* Pits are limited to the posterior buccal reentrant of m1, and no lingual pits are present in the lower or upper teeth. The pits have a tendency to appear in the form of elongate valleys, and this differs from the condition in *N. cinerea.*

POSTERIOR BUCCAL REENTRANT OF m1: Resembles other species; reentrant is not great in anteroposterior width. However, the anterobuccal reentrant is greatly elongated anteroposteriorly, and this condition is unique to the species.

DENTINE TRACT: The tract is as wavy as in *N. cinerea,* and exposed dentine runs halfway or more up the buccal face of the anteroconid-metaconid complex. This trait is shared with *N. stephensi* and *N. cinerea;* it differs from the condition in *N. floridana,* which lacks dentine tracts, and from that in *N. micropus,* in which the dentine track rises only slightly up this face.

BUCCAL CREST NOT PRESENT: When m1 is over three-fourths worn, a weak crest running posteriorly from the anteroconid across the buccal base of the anterobuccal reentrant may (or, more usually, may not) be present, but it is never prominent enough to form a pit. *N. mexicana* differs in this character from *N. floridana* and *N. cinerea* (which have a crest) but is indistinguishable from *N. micropus* and *N. stephensi.*

ANTEROMEDIAL GROOVE OF M1: Uniformly deep to the enamel base. No swale and no small pit at base, as in most *N. cinerea;* differs from *N. micropus* (which has a small pit) and from *N. floridana* and *N. stephensi,* in which the pit does not extend to the base.

NEOTOMA FLORIDANA *(ORD, 1818)*

MODERN DISTRIBUTION *Neotoma floridana,* the eastern wood rat, today is a resident of the southern parts of the central and eastern United States. Its westernmost records in the modern fauna are at Pueblo and Colorado Springs, Colorado, and it ranges into the northern part of eastern Colorado. In eastern Texas and eastward it is present in warm temperate to subtropical areas, with the exception of the subspecies *N. f. magister,* which occupies the area of southern Indiana, Ohio, nearly all of Pennsylvania, southern New York, and southeastward to the eastern side of the Appalachian Mountains. Including *N. f. magister, N. floridana* is the most widely distributed wood rat species in the United States, living even on the delta south of New Orleans and New Iberia, Louisiana.

N. f. magister is geographically distinct and somewhat unique in dental characters, requiring that considerable dental variation be ascribed to the species *N. floridana.* It is perhaps arguable whether *N. magister* Baird, 1858, should be considered a subspecies of *N. floridana* (Schwartz and Odum, 1957).

DISTINGUISHING CHARACTERS This species is unique in having no dentine tract. Its specific separation from *Neotoma micropus* has been questioned (Hall, 1981:748).

ANTEROMEDIAL GROOVE OF m1: Prominent to about four-fifths of the distance to the base of the enamel cap, but uniformly deep, a trait shared with *N. f. magister* and *N. micropus.* Differs from other species in not clearly extending to the enamel base.

PITS ARE LACKING: The posterior buccal reentrants of the lower molars and all buccal reentrants of the upper molars have elongate valleys at their bottoms; these may be slightly depressed. The distinction between a pit, which is a conical depression in the bottom of the reentrant, and a valley, which is an elongate depression in the bottom of the reentrant along its axis, is gradational but distinctive. The condition of pits in this species is shared with *N. micropus* and *N. mexicana* (in which the distinction of pits from valleys is equivocal) but is distinct from other species.

POSTERIOR BUCCAL REENTRANT OF m1: About equal in anteroposterior length to anterior buccal reentrant, as in most species and with some *N. cinerea;* differs from *N. mexicana,* which has the anterior buccal reentrant elongate, and from some individuals of *N. cinerea* with elongate posterior reentrant.

DENTINE TRACT LACKING: The basal margin of the enamel crown is flat with no irregularity (also true in *N. floridana magister*), differing conspicuously from the other species discussed. No dentine tract rises up the buccal face of the anteroconid-metaconid complex, a condition that differs slightly from that in *N. micropus* and greatly from that in other species discussed.

BUCCAL CREST FORMS A SPUR WITH SLIGHT WEAR: Very early in wear the buccal crest makes a prominent, backward-projecting spur on the occlusal surface of the anteroconid. A spur also forms on the protocone of m2. This trait is shared with subspecies *N. f. magister* and with *N. micropus,* although the crest is smaller in the latter; it differs from the condition in *N. cinerea* and *N. stephensi,* both of which exhibit less prominence of the crest, and from that in *N. mexicana,* which lacks the crest until the tooth is nearly worn away.

ANTEROMEDIAL GROOVE OF M1: Very short and shallow. It disappears with little wear, ending well short of the base of the enamel cap. The groove is even shorter in *N. stephensi. N. floridana* differs from other species considered here, and also from *N. f. magister,* in its weak development of the groove.

NEOTOMA MICROPUS *BAIRD, 1855*

MODERN DISTRIBUTION Commonly known as the southern plains wood rat, *Neotoma micropus* appears to prefer hotter regions than *Neotoma floridana* and seems better able to endure drier climates; it widely overlaps the range of *Neotoma albigula,* a real "desert rat," over vast areas from the Arizona–New Mexico state line eastward nearly as far as Austin, Texas. This range includes the southeastern quarter of Colorado. *N. micropus* abuts against the southern limit of *N. floridana* along the Arkansas River from Pueblo, Colorado, across Kansas to Arkansas City. From there the mutual boundary runs past Enid and Seiling, Oklahoma, to the Canadian River and then southward to Wichita Falls, Texas, to the Gulf of Mexico near

Victoria, Texas (Hall, 1981). The species range continues along the Gulf Coast to Veracruz and San Luis Potosi, Mexico, suggesting that heat rather than aridity controls the range.

Along this boundary between the geographic ranges of *N. floridana* and *N. micropus,* Hall (1981:748) mentioned only one place "less than one mile [2.6 km] in diameter" where the two species ranges overlap. In view of the vast area in which *N. micropus* shares the range of *N. albigula,* this almost complete allopatry of *N. micropus* and *M. floridana* seems curious.

This sharp separation of their modern ranges contrasts with the record from the Pit locality in Porcupine Cave, in which both *N. floridana* and *N. micropus* are present in most of the fossiliferous levels from level 3 to level 10 (see table 18.2; see also tables 10.9, 10.10).

DISTINGUISHING CHARACTERS Only specimens of *N. micropus* from the type area in Meade County, Kansas, were examined during this study, and these seem from dental characters to be fairly distinct from *N. floridana.* The most distinguishing character of *N. micropus* is the pit found at the base of the anteromedial groove of M1.

ANTEROMEDIAL GROOVE OF m1: Moderately deep but bottoms between one-half and two-thirds of the distance to the base of the enamel crown. This character is shared only with *N. floridana.*

PITS: Lacking; the bottoms of many reentrants are elongate and form a valley that may be depressed below the outer margin of the tooth. Valleys are present in the posterior buccal reentrant of m1 and m2 and in all buccal reentrants of the upper teeth. This condition is shared with *N. floridana* and *N. mexicana,* although few valleys are sunken below the outer margin of the teeth in *N. mexicana.* The trait differs from that in other species here considered.

POSTERIOR BUCCAL REENTRANT OF m1: Slightly narrower anteroposteriorly than the anterior buccal reentrant, but difference is minor, unlike the condition in *N. mexicana* and some *N. cinerea.* The character generally resembles that in the other species considered.

DENTINE TRACT: Very slightly developed. Base of enamel crown on m1 slightly wavy and rises slightly across the anterior and buccal face of the anteroconid-metaconid complex to form a rudimentary dentine tract, which is not greatly different from that in *N. floridana* but is a meaningful difference upon detailed comparison. Tract development is intermediate between that in *N. floridana* and that in other species considered, and in this respect it appears unique.

BUCCAL CREST FORMS A SMALL SPUR WITH SLIGHT WEAR: Posterobuccal spur on the occlusal surface of the anteroconid-metaconid complex is present but small, and it does not increase in size down the tooth, but appears early in wear. The crest is somewhat similar to that in *N. floridana,* including *N. f. magister,* but is not as prominent. The crest differs from that in *N. stephensi, N. cinerea,* and *N. mexicana.*

ANTEROMEDIAL GROOVE OF M1: Bottoms at enamel base in a small pit. This condition of the M1 groove is very unusual and is unique in having a pit. In these respects the species differs greatly from *N. floridana.*

NEOTOMA STEPHENSI *GOLDMAN, 1905*

MODERN DISTRIBUTION *Neotoma stephensi,* the Stephens' wood rat, today does not occur anywhere near Porcupine Cave nor in southeastern Colorado. Instead it is confined almost entirely to northern Arizona and western New Mexico. *N. stephensi* is uniquely specialized in its diet of juniper leaves, a specialization that allows it to live in areas where it could not otherwise survive.

Vaughan (1982) documented the highly selective feeding of the species, noting that it avoids those junipers—and those branches on a single juniper—that contain a higher concentration of defensive chemicals that inhibit digestion (turpentines). His data suggested that the species lives in a state of constant stress because of this diet, resulting in a small litter size and slow recovery rate from major disturbances. In the spring when other plants are green, individuals will eat other vegetation as well as juniper.

Vaughan suggested also that wood rat feeding may cause the juniper plant itself to react, down to the level of specific branches on a single tree, by increasing its production of defensive chemicals. This hypothesis seemed to be supported by the declining conditions of laboratory animals fed juniper clippings from branches that free animals avoided.

DISTINGUISHING CHARACTERS The presence of a high dentine tract on m1 with virtually no anteromedial groove on M1 distinguishes the species.

ANTEROMEDIAL GROOVE OF m1: Moderately deep, shallowing slightly nearly to the base of the enamel but not forming a shallow swale. The groove differs from that in *N. cinerea* and *N. mexicana* in its lack of a swale and from that in *N. floridana* and *N. micropus* in shallowness.

PITS: Present in the buccal reentrants of m1 and in the posterior buccal reentrant of m2; the same pattern persists in the upper M1 and M2. This condition is shared with *N. cinerea* except for having no medial pits. The pits differ from those of *N. floridana, N. mexicana,* and *N. micropus,* all of which have valleys rather than well-developed pits.

Discussion

The Fossil Records of the Pit Locality

The Pit locality (UCMP V93173, CM 1925) is well sampled, with 1650 *Neotoma* specimens examined (appendix 18.1). Interesting variation in the numbers and species of wood rat specimens occurs through the different stratigraphic levels, and those differences do not seem to arise from collection biases (see chapter 2, Barnosky and Rasmussen [1988], and Wood and Barnosky [1994] for information on excavation and processing procedures). The number of specimens per level varies greatly, from a maximum of 500 specimens in level 2 to a min-

TABLE 18.2

Numbers of Identified Specimens (NISP) and Percentages of NISP by Level for *Neotoma* Fossils in the Pit Locality

	NISP												
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*8A*	*9*	*10*	*11*	*12*
Neotoma cinerea (bushy-tailed wood rat)	278	432	17	9	30	10	8	0	3	—	4	2	—
Neotoma mexicana (Mexican wood rat)	—	5	6	—	—	—	—	—	—	—	—	—	—
Neotoma floridana (Florida wood rat)	1	15	81	15	2	2	6	—	1	1	1	—	—
Neotoma micropus (southern plains wood rat)	—	—	2	—	3	4	1	—	1	3	9	2	—
Neotoma stephensi (Stephens' wood rat)	11	4	4	—	—	—	1	—	—	—	—	—	—
Neotoma sp. (wood rat)	65	44	221	154	63	43	22	15	13	4	18	—	1
Total	355	500	331	178	98	59	38	15	18	8	32	4	1

	Percentage												
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*8A*	*9*	*10*	*11*	*12*
Neotoma cinerea	78	86	5	5	31	17	21	0	17	0	13	50	0
Neotoma mexicana	0	1	2	0	0	0	0	0	0	0	0	0	—
Neotoma floridana	0	3	24	8	2	3	16	0	6	13	1	—	—
Neotoma micropus	0	0	1	0	3	7	3	0	6	38	9	50	—
Neotoma stephensi	3	1	1	0	0	0	3	0	0	0	0	0	—
Neotoma sp.	18	9	66	87	64	73	58	100	72	50	18	0	100
Total	100	100	100	100	100	100	100	100	100	100	41	100	100

imum of one specimen in level 12. Below level 7, sample sizes decrease substantially, as is the case for all taxa in the Pit.

All levels contain some *Neotoma* species that do not live in the area today. Percentages of species show marked change at or above level 3 (table 18.2).

The age of the Pit deposits probably ranges from around 780 Ka or perhaps slightly older at the top to at least 900 Ka at the bottom. Because levels 1–3 represent interglacial deposits as inferred from sediments and fauna, they therefore either correlate with oxygen isotope stage 19 of Shackleton and Opdyke (1976) or, more likely, with stage 21. During glacial stage 18, which in now outdated terminology* correlated with the "Nebraskan" ice accumulation in North America (several ice advances were encompassed by the "Nebraskan"), there was no mountain glaciation in the South Park region (Richmond, 1986). Presumably this held for earlier glaciations within the so-called "Nebraskan" as well. It is most likely that one or more of these earlier glaciations correlate with the glacial interval inferred for Porcupine Cave Pit levels 4 and 5. Near Porcupine Cave the only potentially correlative sediments are gravel deposits in the Upper Arkansas Graben containing the Bishop ash about 18 km south of Buena Vista, Colorado, 8 km north of the "Christmas 1806" rest stop on U.S. Highway 285. Within the Upper Arkansas Graben, these "Nebraskan" gravels (circa 0.78 Ma) overlie the Dry Union Formation (circa 7 Ma), indicating a gap of more than 6 Ma that is represented, locally, only by erosion.

Neotoma cinerea, the species that is currently the local resident, is represented in all levels except for levels 12 and 9, which have samples so small that the addition of one more specimen would dramatically alter the percentages (table 18.2). This species is represented by highest percentages in all well-sampled levels, except for levels 3 and 4, which have a minimum percentage of this species (despite very high sample sizes). *N. cinerea* reaches its highest percentages in levels 1 and 2.

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* Sibrava, Bowen, and Richmond (1986) abandoned the glacial terms Kansan and Nebraskan as being too vague for practical use. I use the term "Nebraskan" informally as a shorthand way of referring to the glacial advances that took place between about 850 and 718 Ka ago. Similarly, I use "Kansan" informally to refer to glacial advances that took place between 687 and about 338 Ka ago.

Neotoma floridana, now limited to the plains below the Front Range and eastward to the southern Atlantic coast, is also present in nearly all levels with a peak percentage in level 3, where *N. cinerea* has its minimum percentage and *N. micropus* has its youngest record.

Neotoma micropus now has a range in the southern plains adjacent to but almost entirely distinct from the range of *N. floridana* (Hall, 1981). *N. micropus* overlaps widely the range of *N. albigula* (which is not present in Porcupine Cave) and also extends well down the Gulf of Mexico coast beyond the more arid range of *N. albigula. N. micropus* is represented by low percentages in levels 3–8A and level 10. It is found in relatively high percentages in levels 9 and 11, although the increase in those levels could be an artifact of sample size. The presence of *N. micropus* might indicate conspicuously warm habitats, but not as dry as would be indicated by the missing *N. albigula.*

Neotoma stephensi is present in low percentages in levels 1–3 and 7, all of which are interpreted as interglacial levels. Interpreting its presence in the Porcupine Cave area requires consideration of its dietary specialization and possible overstimulation of juniper defenses. However, in its modern range some 500 km to the southwest it has an altitudinal range of 1200–2591 m (Hoffmeister and de la Torre, 1960), suggesting that it is able to exist in cooler climates than typify most of its modern range.

Neotoma mexicana in Porcupine Cave is barely out of its modern range and was found only in levels 2 and 3. Thus its absence, rather than its presence, is the relevant point in interpretation.

The Fossil Record of the DMNH Velvet Room Excavation

DMNH 644 produced a large sample of wood rats. About 1386 specimens were examined; these correspond to about 550 DMNH catalogue numbers, many of which refer to more than one specimen. As with the Pit fauna, most specimens were isolated teeth, and roughly half were not identifiable to species level. Detailed provenance data were not available, but the specimens are distributed through most horizons of the excavation. These specimens would benefit from further study in the context of proper stratigraphic placement, but at this point it is safe to say that *Neotoma cinerea* dominates in the DMNH Velvet Room excavation. In the entire sample, only 13 specimens were identified to a species other than *N. cinerea:* two *N. floridana,* one *N. mexicana,* five *N. micropus,* and five *N. stephensi.* The very low percentage of these other species is in contrast to data from the lower levels in the Pit (table 18.2). The strong dominance of *N. cinerea* is consistent with the DMNH Velvet Room excavation being at least as young as the uppermost two levels in the Pit, a conclusion supported by increasing evidence of glacial and interglacial conditions in adjacent areas. Because the provenance data on the Velvet Rooms wood rats has not yet been compiled and more than 99% of the identified specimens represent *N. cinerea,* the DMNH Velvet Room excavation is not considered further in this chapter.

Environmental Controls

The wood rat fauna from the Pit includes four of the five species of wood rats that now live in southeastern Colorado. Four of the five southeastern Colorado species live in the vicinity of Pueblo, about 120 km to the southeast of Porcupine Cave at an elevation of 1489 m, and extend eastward across the Great Plains. The fifth *(Neotoma cinerea)* is the species that makes up the majority of the Porcupine Cave sample and now lives in the cave area, as well as elsewhere in the mountains at elevations as low as 1830 m. Three other southeastern Colorado species found in the cave deposits are *N. micropus, N. mexicana,* and *N. floridana.* A southeastern Colorado species that does not occur as fossils in the cave is *Neotoma albigula.* Instead *N. stephensi* is the fifth wood rat species in the Pit fauna. Given the age interpreted for the Pit sequence (circa 780,000 to as old as 1 million years), the wood rat fossils represent the earliest known occurrence of the five *Neotoma* species.

As noted previously, *N. albigula* now lives in the deserts from the Imperial Valley of California eastward across Arizona and New Mexico (avoiding the high Mogollon Rim and the southern Sangre de Cristo Mountains) almost to Austin, Texas, and southward to Michoacán in central Mexico. Only its northernmost range is in extreme southwest and southeast Colorado. It is a species of hot deserts with hot summers and little or no winter snow. Its absence in the Pit fauna suggests that at least one of these conditions did not exist around Porcupine Cave during deposition of the Pit fauna.

N. stephensi now lives between about 1200 m and 2440 m elevation and about 200 km farther south (latitudinally) than Porcupine Cave. Except for *N. stephensi,* all the wood rat species of the Pit fauna live nearby, around 80 km to the east near Colorado Springs and at or below 1830 m elevation.

Climate and Orogeny

The difference in wood rat species composition between the time represented through the Pit sequence and the present suggests major biogeographic changes in the Porcupine Cave area. Three causes seem possible: orogenic elevation of the South Park area since the Pit fauna was deposited, causing the loss of a Great Plains–like habitat that once had been continuous with South Park; climate change; or a combination of the two.

The climate change that would permit wood rats, now living on the Great Plains of southeastern Colorado below 1830 m elevation, to live near Porcupine Cave would seem to include increased warmth and dryness. The paleomagnetic correlations detailed in chapter 7 indicate a time equivalence to the mid-"Nebraskan" glacial advances across the northeastern Great Plains. Although this would result in warmer winters, it would also result in cooler summers with more moisture.

Tectonic uplift in the Colorado Rocky Mountains in the last 780,000 years would be consistent with the occurrence of *Neotoma* species in the Pit fauna, and it is consistent with correlative glacial history in the nearby Upper Arkansas Graben. This graben lies 16 km west of Porcupine Cave and is part of the Rio Grande Rift that runs south from Leadville to Salida, Colorado (see figure 4.1). At Salida the Upper Arkansas Graben is separated from the remainder of the Rio Grande Rift by a northwest-trending transference from the Sangre de Cristo Mountains. Poncha Pass carries highway traffic across this uplifted transference and into the San Luis Valley, now continuous, as the Rio Grande Rift, all the way to Mexico. Since the Upper Arkansas Graben began sinking as a result of tension caused by uplift of the Colorado Plateau, some 7 Ma ago, deposits have accumulated in it, leaving a record of the history of regional uplift and glaciation. The Wagon Tongue Formation that overlies the Rocky Mountain Peneplain (Lee, 1923), forming most of South Park (De Voto, 1971), contains vertebrate fossils that are about 15 million years old and predate the Upper Arkansas Graben.

There are three points of time control within the graben: the circa 7-million-year-old fossils found in the lake or marsh beds near Salida, which were the first deposits in the developing graben; the 780,000-year-old Bishop Ash, which was deposited in the graben on the floodplain of the ancestral Arkansas River (it is also deposited on river floodplains in the San Luis Valley; Rogers et al., 1985, 1992); and the 670,000-year-old Lava Creek ash between glacial outwash gravels. The Bishop Ash has been used to date the beginning of the Brunhes normal-polarity interval (Obradovich and Izett, 1992) and thus provides a minimum age for the reversed parts of the Pit sequence, that is, levels 8 and below. It also was deposited during the "Nebraskan" (glaciations E [normal], F [reversed], and G [reversed] of Richmond, 1986).

Although the "Nebraskan" featured the most extensive continental ice sheet that covered the Great Plains, no indication of mountain glaciation during this time has been found in the Upper Arkansas Graben (Richmond, 1986). Instead, the oldest mountain glaciation recorded in the Upper Arkansas Graben is "Kansan" glaciation represented by deposits that straddle the Lava Creek Ash, dating from about 670 Ka.

Mountain glaciation occurs in mountains because of cooler and wetter climates at higher elevation, and one possibility is that the Upper Arkansas Graben, 16 km west of Porcupine Cave, and the areas surrounding it were at a lower elevation when the Pit fauna lived in that area. This hypothesis would be consistent with the elevation indicated by the unusual assemblage of wood rat species. The other possibility is that elevations were the same as today, but that the glacial climates of the earlier part of the "Nebraskan" were not as cool and moist in South Park as those coeval with the Lava Creek Ash. Because chapters 7 and 23 discuss climatic scenarios in more detail, the remainder of this discussion focuses on possible tectonic interpretations.

Today, about 24 km west of the Upper Arkansas Graben, the Continental Divide, averaging between 3650 and 3960 m in elevation with many peaks higher than 4370 m, drains into the graben (see figure 4.1). These mountains were clearly glaciated during the later glacial episodes, but there is no indication that this was so when the wood rats of the Pit fauna lived. This too would be consistent with lower elevations during the "Nebraskan" glaciations.

The modern route of the Arkansas River passes southward down the Upper Arkansas Graben to the west of South Park and Porcupine Cave, and then south of them toward the Great Plains at Canon City (see figure 4.1). Because of its depth of incision, the Arkansas River is now capturing, through Badger Creek, the drainage of some of the southernmost part of South Park. The immediate area of Porcupine Cave is drained by Badger Creek today. However, the cave is not far removed from the modern headwaters of Cottonwood Creek, which flows southeastward from South Park to the Arkansas River near Canon City. Recent uplift may have enabled Badger Creek to capture the drainage of this part of South Park, and the Arkansas River is deeply incised between Canon City and Salida. These geomorphic features are also consistent with uplift of the Porcupine Cave region since the Pit fauna lived.

Conclusions

The wood rats of the Pit fauna of Porcupine Cave (2900 m elevation) include three species *(Neotoma mexicana, N. micropus, N. floridana)* that now live in the vicinity of Pueblo, Colorado (1420 m elevation) and in southeastern Colorado in the western part of the Great Plains. A fourth *(N. stephensi)* now lives farther southwest than Colorado, and a fifth *(N. cinerea)* is characteristic of elevations above 1800 m in the Rocky Mountain region. The wood rats of the DMNH Velvet Room excavation have not yet been examined in stratigraphic context, but in general they seem to more closely resemble the modern fauna in yielding *N. cinerea* with very rare exceptions.

The cave itself is on a ridge of Paleozoic rock protruding above a beveled surface that truncates older rocks and appears to represent a preserved part of the Tertiary Rocky Mountain Peneplain (Lee, 1923). Faulting before 780 Ka ago elevated the ridge above the plain to make the cave available to the wood rats.

The wood rat fauna of the Pit locality indicates that what is now considered Great Plains habitat was continuous with South Park prior to and possibly around 780 Ka ago. This situation would be consistent with an elevation of the cave no higher than 1830 m at the time the fossil deposits accumulated. This is the lowest modern elevation of *Neotoma cinerea* and the approximate highest modern elevation of the other wood rats of the Pit fauna where they occur around Pueblo. The wood rat assemblage would also be consistent with differing glacial climatic patterns in the "Nebraskan" as compared to the "Kansan" and later glacial advances.

At perhaps the same time as the uppermost Pit levels were deposited, or more probably slightly more recent in time than the Pit sequence, the Bishop Ash was deposited in silts, sands, and gravels in the Upper Arkansas Valley west of Porcupine Cave. The Bishop Ash was also deposited at the same time that the "Nebraskan" glacial advances E, F, and G of Richmond (1986), as correlated to Shackleton and Opdyke (1976), flowed across the northeastern part of the Great Plains. At this time and presumably during earlier "Nebraskan" glaciations, the Porcupine Cave region lacked mountain glaciers. One explanation is that the elevation of the cave was lower then; another is differing glacial climatic patterns in the "Nebraskan" as compared to "Kansan" and later glaciations, when mountain glaciers did exist in the Porcupine Cave region. Also consistent with some degree of uplift since the Porcupine Cave Pit fauna lived is the potential piracy of Badger Creek and the deep incision of the Arkansas River between Salida and Canon City.

Appendix 18.1. Specimens of *Neotoma* from the Pit

Neotoma cinerea

LEVEL 1

CM 64600, 64604, 64605, 64607, 64609, 64610, 64612, 64613, 64616, 64620, 64621, 64623, 64625, 64626, 64628, 64630, 64632, 64634, 64638, 64640, 64644, 64645, 64647, 64653, 64655, 64658, 64661, 64668, 64674, 64678, 64679, 64680, 64681, 64684, 64689, 64708, 64710, 64711, 64714, 64719, 64722, 65056, 65059–65066, 65068, 65221–65225, 65227, 65229, 65291, 65292, 65295, 65296, 65298, 65299–65302, 65329–65339, 65341–65353, 65355–65358, 65429, 66149, 66151, 66152, 66159–66162, 66164–66166, 66168, 66169, 66171, 66351–66356, 66359–66445, 66698, 69688. UCMP 172500–172506, 172545, 172575, 172730, 172731, 172734–172739, 172741, 172742, 172744–172772, 172775, 172777, 172778, 172780–172783, 172786–172794, 172797–172801, 172803, 172804, 172806, 172808, 172813–172817, 172821–172823, 172826, 172829–172833, 172835, 172837–172842, 172844–172871, 172873–172883, 172885, 172887, 172890, 172891, 172893–172900, 172905–172909.

LEVEL 2

CM 63634, 64601–64603, 64606, 64609, 64611, 64612, 64614, 64615, 64617, 64622, 64624, 64627, 64629, 64631, 64633, 64635, 64637, 64642, 64643, 64646, 64648–64652, 64654, 64657, 64660, 64662–64667, 64669, 64671–64673, 64675–64677, 64682, 64683, 64685, 64686, 64690–64693, 64694–64697, 64699, 64701–64707, 64709, 64713, 64715–64718, 64723, 64725–64734, 64739–64741, 64743, 64744, 64748, 64749, 64751, 64753, 64754, 64756, 64759, 64761–64769, 64771–64787, 64795–64797, 64809–64815, 64817–64833, 64836, 64839, 64841–64853, 64855–64858, 64860, 64861, 65426, 65430–65434, 65436, 65437, 65439, 65440, 65442–65444, 65446–65449, 66145–66147, 66509–66511, 66514, 66515, 66517, 66520. UCMP 172524–172606, 172608–172623, 172625–172648, 172650–172668, 172670–172682, 172684–172691, 172693, 172698, 172707–172721, 172724, 172726, 172728.

LEVEL 3

CM 64745, 64844, 65712, 65717, 65722. UCMP 172507, 172511–172513, 172515–172518.

LEVEL 4

UCMP 172996–173004.

LEVEL 5

UCMP 172508, 172510, 172917, 172920, 172922, 172973, 172974, 172976, 172986, 172988, 172989, 172990, 172991, 173005–173017.

LEVEL 6

UCMP 172915, 172927–172929, 172981, 172982, 172984, 172985.

LEVEL 7

UCMP 172950, 172952, 172956, 172957, 172992–172995.

LEVEL 8A

UCMP 172967, 172970, 172971.

LEVEL 10

UCMP 172932, 172935, 172963.

LEVEL 11

UCMP 172930?, 172931?, 172945.

Neotoma mexicana

LEVEL 2

CM 64742, 64752, 64760, 64808, 64837.

LEVEL 3

CM 65745. UCMP 213487, 213766.

Neotoma floridana

LEVEL 1

CM 65057.

LEVEL 2

CM 64618, 64666, 64724, 64755, 64757, 64770, 64771, 64774, 64777, 64792, 64793, 64803–64806.

LEVEL 3

CM 65676, 65677, 65682, 65737, 65741–65744, 65746, 65747, 65749, 65752. UCMP 213451, 213452, 213454–213463.

LEVEL 4

UCMP 213524–213528, 213678–213680.

LEVEL 5

UCMP 172974, 172976.

LEVEL 6

UCMP 172980.

LEVEL 7

UCMP 172951, 172953, 172954, 172958, 172960.

LEVEL 8A

UCMP 172969.

LEVEL 9

UCMP 172966.

LEVEL 10

UCMP 172940.

Neotoma micropus

LEVEL 3

CM 64816, 65732.

LEVEL 5

UCMP 172923, 172924, 172926.

LEVEL 6

UCMP 172910–172912, 172914.

LEVEL 7

UCMP 172948.

LEVEL 8A

UCMP 172968.

LEVEL 9

UCMP 172935, 172936, 172965.

LEVEL 10

UCMP 172933, 172937–172939, 172941–172944, 172962.

LEVEL 11

UCMP 172946, 172947.

Neotoma stephensi

LEVEL 1

UCMP 172740, 172774, 172776, 172779, 172784, 172785, 172809, 172820, 172884, 172889.

LEVEL 2

CM 64636, 64798, 64799, 64801.

LEVEL 3

CM 65681, 65697, 65702, 65707.

LEVEL 7

UCMP 172949.

Neotoma sp.

LEVEL 1

CM 65057, 65058, 65067, 65226, 65230, 65252, 65303, 65340, 65837, 66148, 66154–66158, 66163, 66167, 66170, 66173–66179, 66182–66185, 66187, 66189, 66349, 66350, 66357, 66358. UCMP 172722, 172723, 172725, 172727, 172732, 172743, 172810–172812, 172818, 172819, 172824, 172825, 172827, 172836, 172843, 172892, 172901–172904, 172918, 172959, 172961, 213386, 213387, 213423, 213425, 213453, 213465, 213842–213854.

LEVEL 2

CM 64619, 64758, 64788, 64789, 64807, 64834, 64840, 64854, 64859, 65435, 65441, 65445, 65450, 65512, 66513, 66516, 66518, 66519. UCMP 164695, 172520–172523, 172607, 172624, 172649, 172669, 172683, 172692, 172694–172697, 172699–172706, 172983, 213418.

LEVEL 3

CM 65525, 65526, 65587, 65673–65675, 65678–65680, 65683–65686, 65688–65696, 65698–65701, 65703–65706, 65708–65711, 65713, 65715, 65716, 65718–65721, 65723–65731, 65733–65736, 65738, 65739, 65748, 65750, 65751, 65753.

UCMP 172509, 172514, 172805, 213351–213385, 213389–213417, 213421, 213422, 213426–213450, 213464, 213466–213486, 213488–213490, 213599–213607, 213609, 213751–213765.

LEVEL 4

UCMP 172978, 172979, 172987, 213419, 213420, 213424, 213491–213523, 213573–213598, 213616–213677, 213681–213704.

LEVEL 5

UCMP 164670, 164672, 172919, 172921, 172925, 213501, 213502, 213529–213544, 213705–213800.

LEVEL 6

UCMP 172913, 172916, 172926, 213500, 213545–213549, 213713–213730, 213801–213807.

LEVEL 7

UCMP 172955, 213550, 213551, 213731–213734, 213808–213822.

LEVEL 8

UCMP 213552–213567.

LEVEL 8A

UCMP 213735–213737, 213829–213838.

LEVEL 9

UCMP 213824, 213826–213828.

LEVEL 10

UCMP 213568, 213569, 213738–213742, 213745–213750, 213823, 213825, 213839–213841.

LEVEL 11

Four teeth, not assigned separate numbers.

LEVEL 12

UCMP 213570.

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The loan of specimens from the National Museum of Natural History, the American Museum of Natural History, the University of California Museums of Vertebrate Zoology and Paleontology, the Californian Academy of Sciences, and the Denver Museum of Natural History is gratefully acknowledged.

I was not greatly familiar with the geology of the Rocky Mountains, and considerable time was involved in integrating this geological history with the record of fossil wood rats from Porcupine Cave. I thank Robert G. H. Raynolds of the Denver Museum, for sharing his greater knowledge of Rocky Mountain geology, and Gerald M. Richmond, formerly of the U.S. Geological Survey, for sharing his expertise on the history of continental glaciation. Without their help I could still be unraveling a very complicated tectonic history to explain the presence of a Great Plains wood rat fauna in the Pit.

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NINETEEN

Arvicoline Rodents from Porcupine Cave

Identification, Spatial Distribution, Taxonomic Assemblages, and Biochronologic Significance

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The arvicolines are a taxonomically diverse assemblage of rodents that includes the voles, lemmings, and muskrats and their extinct kin. The importance accorded by paleontologists to arvicoline rodents stems in large part from the widespread recognition of their utility as biochronologic tools. The accelerated evolutionary rates within at least some lineages of arvicolines, their impressive capacity for rapid reproduction and dispersal, and their consequent abundance in the fossil record combine to provide temporal resolution on a finer scale than is available through the biostratigraphic study of other terrestrial faunal groups. It is for this reason that, throughout the history of excavation of the various deposits in Porcupine Cave, special attention was paid to the recovery and identification of arvicoline remains. The documentation of these remains is the primary focus of this chapter.

Here we present a summary of the fossil arvicoline rodent specimens recovered from each locality in the cave and explain the dental characteristics that were used to identify them. The Carnegie Museum of Natural History and University of California Museum of Paleontology excavations have been completed, but the Denver Museum of Nature and Science maintained an active excavation and research program in Porcupine Cave until recently; we include DMNH materials that were picked, sorted, and made available to us as of May 1998. For all collections, only those specimens identified to at least the generic level are included. The stratigraphic distribution of taxa in the localities for which stratigraphic control is available and a complete list of all specimens identified to at least the generic level are provided in appendix 19.1. A listing of which species occur in which sites, presented as minimum numbers of individuals (MNI) and number of identifiable specimens (NISP), appears in tables 10.1–10.13. Nondiagnostic teeth and postcranial elements are not included in this chapter, but they amount to thousands of additional specimens.

This chapter supersedes all previously published accounts of occurrence and taxonomic assemblages of arvicolines in Porcupine Cave (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996; Bell and Barnosky, 2000). The taxonomic identifications for individual specimens, which in some cases may differ from those listed in previous publications, are listed in appendix 19.1. The biochronologic implications of the arvicolines are discussed in chapter 7.

The wealth of material from Porcupine Cave prevents us from presenting detailed quantitative analyses for all arvicoline groups at this time. In some cases we note our observations and perceptions of patterns discernible in the Porcupine Cave record, but there is clearly much work yet to be done with these fossils. The abundant sample sizes of some taxa certainly offer opportunities for further research on morphological variation, morphological change through time, and patterns of variation in enamel microstructure. Similarly, future workers studying mammalian community structure and the impacts of climate change on the faunas preserved in Porcupine Cave will find the arvicolines a fertile area for continued investigation.

The significance of the Porcupine Cave material extends beyond the sheer numbers of specimens and their inherent value for this and other studies. The occurrence at 2900 m elevation of such diverse assemblages of taxa both constitutes a fascinating insight into the biogeographic history of these animals in Colorado and presents new challenges for the biochronologic interpretation of high-elevation faunas. Moreover, the Porcupine Cave faunas include taxonomic associations of many species not previously known to have been sympatric in distribution, and they provide new elevational records, geographic range extensions, or both for some species. At least three of the taxa reported here *(Pliolemmus* *antiquus, Ophiomys parvus,* and *Mictomys vetus/M. landesi)* are not known from cave-derived faunas elsewhere.

Materials and Methods

Details of excavation history for the many localities within Porcupine Cave are presented in chapter 2. All specimens were examined under magnification. Identifications were made with reference to previously published descriptions, and from comparisons with fossil and modern skeletal material.

Specimens reported here are housed at three institutions: the Carnegie Museum of Natural History (CM), Denver Museum of Nature and Science (DMNH), and University of California Museum of Paleontology (UCMP). Batch cataloguing was not performed for the arvicoline collections; every specimen reported is given an independent catalogue number so that future studies can refer to specific specimens where our judgment of taxonomic affinity is questioned or revised.

Although occasional upper or lower tooth rows were preserved intact, the vast majority of arvicoline material recovered from the cave consists of isolated teeth. Arvicoline teeth generally are relatively hypsodont, with cusps arranged as alternating more or less triangular prisms (Repenning et al., 1990). Molars may be rooted or rootless. The number of triangles, their degree of confluence or closure relative to one another and to the anterior portion of the tooth, enamel microstructure, the degree of enamel differentiation, dentine tract height, and the presence of various dental structures are all features that play a role in taxonomic allocation. For most arvicoline species, the lower first molar (m1) is the most diagnostic tooth; for some taxa it is the only tooth that can confidently be identified. A posterior loop, at least three alternating triangles, and an anterior cap are common features of the lower first molar of all arvicolines. The unique and diverse taxonomic associations found in some localities in Porcupine Cave (e.g., the Pit, Mark's Sink) make it impossible in most cases to reliably associate isolated teeth, which in other circumstances might be identifiable, with the diagnostic m1s. This is especially true of the upper third molars (M3s), which figure prominently in some other arvicoline faunal reports (e.g., Van der Meulen, 1978; Morlan, 1984). In the case of the bog lemmings of the genus *Mictomys* and the voles of the genera *Phenacomys* and *Mimomys,* every molar from Porcupine Cave is identified at least to genus. The sagebrush voles of the genus *Lemmiscus* also have several identifiable teeth, including at least two of the upper molars (M2-3).

Taxonomic Inventory

At least 13 arvicoline species are recorded from the localities within Porcupine Cave. No single locality contains all 13 species, but as many as nine are recorded from a single stratigraphic layer within the Pit locality (Bell and Barnosky, 2000). In addition to the distribution of each taxon within Porcupine Cave, the known geographic and temporal distribution derived from other localities is provided in a brief comment section.

Class Mammalia

Order Rodentia

Family Muridae

PLIOLEMMUS ANTIQUUS *HIBBARD, 1937*

IDENTIFICATION This species is readily identifiable; it is one of the few North American arvicolines that has rootless molars that lack cement in the reentrant angles. The m1 consists of a posterior loop and usually seven alternating, closed triangles, with a somewhat variable, but always relatively simplistic, anterior cap. Dentine tracts usually break the occlusal enamel surface on all salient angles in advanced stages of wear (Hibbard, 1938, 1956, 1972). The m1 of *Guildayomys hibbardi* is also rootless and lacks cement, but the posterior triangles are usually slightly confluent, and the sixth and seventh triangles are broadly confluent with each other and with the anterior cap (Zakrzewski, 1984).

DISTRIBUTION WITHIN PORCUPINE CAVE Only three specimens of *Pliolemmus antiquus* were recovered from Porcupine Cave, all from DMNH 1349, Mark's Sink.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION The recovery of *Pliolemmus* in Porcupine Cave was completely unexpected. Prior to its discovery here, its known distribution was limited to only a few localities in the Great Plains. It was previously reported from Kansas in Rexroad Locality 2 (from a sandy pocket in the clay; see Hibbard, 1941b:288, 1941d: 91–92), Deer Park (=Deer Park A of Martin et al., 2000; formerly Rexroad 1 of Hibbard, 1938, 1941b; see Hibbard, 1956), Dixon and Sanders (Hibbard, 1956), and the Bender fauna (Hibbard, 1972). Additional records were reported from the Sand Draw fauna in Nebraska (Hibbard, 1972) and Cita Canyon in Texas (Schultz, 1977). Radiometric age control is lacking for these localities, but paleomagnetic and biochronologic age assignments suggest that its earliest occurrence is in the Bender fauna (possibly 3.2 Ma; Martin et al., 2000). Its youngest occurrence is either in the Sanders fauna (between 3.0 and approximately 2.6 Ma; Martin et al., 2000) or at Cita Canyon (near the boundary between the Gauss and Matuyama Chrons at approximately 2.58 Ma; Berggren et al., 1995). Its highest known elevation was in the Sanders fauna at approximately 786 m; the Porcupine Cave record thus extends the known geographic range of this species 480 km to the west and the known elevational range by approximately 2114 m.

OPHIOMYS PARVUS *(WILSON, 1933)*

IDENTIFICATION The molars are rooted, lack cementum in the reentrant angles, and generally have enamel of uniform thickness. The m1 has well-developed dentine tracts on the labial side, a posterior loop, and five alternating triangles, the last two of which are broadly confluent in most specimens but are themselves only narrowly connected with the anterior cap.

DISTRIBUTION WITHIN PORCUPINE CAVE *Ophiomys* was recovered only from DMNH 1349, Mark's Sink and Kate's Cupola. Only 15 specimens were obtained.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION *Ophiomys parvus* fossils are widely distributed across the western United States. The only reported Irvingtonian record of *O. parvus* is from the Froman Ferry fauna in Idaho (Repenning et al., 1995), where it extended into earliest Irvingtonian sediments (as defined by Repenning et al., 1995, by the first appearance of *Phenacomys* in the section). The species is known from the Grand View and related faunas along Jackass Butte in Idaho (Wilson, 1933; Hibbard and Zakrzewski, 1967; Repenning, in press), Wild Horse Butte (Idaho; Repenning, 1987), 20 localities along the Snake River collectively referred to as the Froman Ferry Sequence in Idaho (Repenning et al., 1995), the Birch Creek fauna (Owyhee County, Idaho; Hearst, 1999), Boyle Ditch in Wyoming (identified as *Ophiomys meadensis* by Barnosky, 1985; transferred to *O. parvus* by Repenning, in press), the Thayne Fauna in Wyoming (identified as *Mimomys [Ophiomys] meadensis* by Repenning, 1987; transferred to *O. parvus* by Repenning, in press), six localities in an unnamed sandstone formation in the Elsinore Fault Zone (Riverside County, California; Pajak et al., 1996), locality 1357 in the Vallecito Creek faunal sequence in the Anza-Borrego Desert State Park in southern California (Repenning et al., 1995:30), Beaver, Utah (reported as *Mimomys [Ophiomys] meadensis* by Repenning, 1987:264; transferred to *O. parvus* by Repenning, in press), the Seneca fauna in Nebraska (Martin and Schultz, 1985), the Dixon fauna in Kansas (identified as *Pliophenacomys meadensis* by Hibbard, 1956; transferred to *O. parvus* by Repenning, in press), and the White Rock fauna in Kansas (identified as *Mimomys meadensis* by Eshelman, 1975; transferred to *O. parvus* by Repenning, in press). The oldest record of *Ophiomys parvus* is probably from the Birch Creek fauna in Idaho at approximately 2.4 ± 0.1 Ma (Hearst, 1999). The youngest known record is from Froman Ferry at approximately 1.6 Ma (Repenning et al., 1995).

MIMOMYS *CF.* M. VIRGINIANUS *REPENNING AND GRADY, 1988*

IDENTIFICATION Molars referred to *Mimomys* cf. *M. virginianus* are rooted and also have cementum in the reentrant angles. A "*Mimomys* Kante" is usually present on the fourth triangle or slightly anterior to it. Five triangles are usually present on the m1; the fifth is broadly confluent with a highly variable anterior cap. *Mimomys virginianus* was described from the Cheetah Room fauna in Hamilton Cave, West Virginia (Repenning and Grady, 1988). Shortly thereafter a closely related species, *M. dakotaensis,* was described from the Java fauna in South Dakota (R. A. Martin, 1989). *Mimomys virginianus* and *M. dakotaensis* differ in size, in the relative proportions of cementum in the reentrant angles, and in the height of dentine tracts at the position of the *Mimomys* Kante. Only two m1 specimens of *M. dakotaensis* are known; measurements of only one (broken) specimen were provided in the original description, and it is larger than specimens in the type collection of *M. virginianus* (R. A. Martin, 1989). *Mimomys dakotaensis* has less cementum in the reentrant angles than does *M. virginianus,* but it has a better-developed dentine tract at the position of the *Mimomys* Kante. The amount of cementum in the Porcupine Cave fossils (when considered as a composite assemblage) varies considerably. Within the Pit fauna, the amount of cementum is more similar to that in *M. virginianus,* and this was the primary basis for the tentative identification of the Pit fossils as *Mimomys* cf. *M. virginianus* (Bell and Barnosky, 2000). Some specimens from Mark's Sink (e.g., DMNH 37750, 37791, 37799, 37801) seem to approach the minimal amounts seen in *M. dakotaensis,* and this suggests the possibility that the two species may be conspecific. The mixed nature of the Mark's Sink deposit prevents any detailed analysis of potential gradual change in this feature. Until a thorough analysis of the Porcupine Cave material can be completed (including a Schmelzmuster analysis), we refrain from definitive species identification. The greater overall similarity with *M. virginianus* is the basis for our tentative referral of all material to that species.

DISTRIBUTION WITHIN PORCUPINE CAVE DMNH1347, Generator Dome; DMNH 1349, Mark's Sink; DMNH 1349, Kate's Cupola; DMNH 644, Velvet Room; DMNH 942, Badger Room; UCMP V93175, Velvet Room; UCMP V98022, Fissure Fill A; UCMP V93174, Gypsum Room; UCMP V93173, Pit.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION *Mimomys virginianus* is reported from Hamilton Cave, West Virginia (Repenning and Grady, 1988), localities CRH44 and CRH47 from the Old Crow Basin, Yukon Territory (Repenning, in press), and Cape Deceit, Alaska (Repenning, in press). *Mimomys* sp. was reported from Cathedral Cave in Nevada (Bell, 1995) and was reidentified as *Mimomys* cf. *M. virginianus* by Bell and Barnosky (2000).

Mimomys dakotaensis is known only from the type locality in the Java fauna in South Dakota (R. A. Martin, 1989); a single *Mimomys* m1 from the Little Dell Locality 2 fauna in Utah was identified as *Mimomys* cf. *M. dakotaensis* on the basis of reduced cementum in the reentrant angles (Gillette et al., 1999). External age control is lacking for all these localities, but the Hamilton Cave material was reported to be approximately 840,000 years old (Repenning and Grady, 1988). The Java fauna lacks age control but is generally considered to be early Irvingtonian in age (R. A. Martin, 1989; Repenning, 1992).

PHENACOMYS GRYCI *REPENNING, 1987*

IDENTIFICATION Molars are rooted and lack cementum in the reentrant angles. Lingual alternating triangles and reentrants on m1 are asymmetrically elongated, and usually only five triangles are present on m1; the fourth (second labial) triangle usually has at least some indication of a *Mimomys* Kante and the fifth (third lingual) triangle is broadly confluent with a highly variable anterior cap. Dentine tracts were noted to be short by Repenning et al. (1987), a condition further clarified by Repenning and Grady (1988).

The proposed subgenus *Paraphenacomys* Repenning and Grady is recognized by the dentine tract on the posterior loop on m1 being shorter than that on the labial face of the anteroconid complex. That subgenus includes *P. gryci, P. brachyodus* (currently known only from the type locality in Hamilton Cave, West Virginia; Repenning and Grady, 1988), and the extant *P. albipes*. *Phenacomys brachyodus* is distinguished from *P. gryci* by having better-developed additional wings on the anteroconid complex (Repenning and Grady, 1988). The type population of *P. gryci* displays considerable variation in the morphology of the anteroconid complex, in part due to differential wear (Repenning et al., 1987). The Porcupine Cave material most closely resembles USNM specimens 264298 and 264299 from the type population (see figure 6D,E in Repenning et al., 1987) and USNM 264317 (illustrated by Repenning and Grady, 1988:9, figure 3A). Porcupine Cave m1 specimens generally conform well with the diagnosis of *P. gryci* provided by Repenning et al. (1987), but they show a very reduced (occasionally absent) *Mimomys* Kante. These specimens are among the most advanced morphotypes known of *P. gryci;* it is possible they actually represent a different species, but more detailed analyses would be required to demonstrate this. Only m1 specimens are identified to species.

DISTRIBUTION WITHIN PORCUPINE CAVE DMNH 1347, Generator Dome; DMNH 1349, Mark's Sink; DMNH 1342, Ferret Room; DMNH 942, Badger Room; DMNH 644, Velvet Room, 0-6, 0-5 level 29; UCMP V93176, Badger Room; UCMP V98022, Fissure Fill A; UCMP V93174, Gypsum Room; UCMP V93173, Pit, level 3, level 4, level 10.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION The type population of *P. gryci* was reported from the Fish Creek fauna in Alaska, dating to approximately 2.4 Ma (Repenning et al., 1987). It was subsequently reported from high in the Froman Ferry faunal sequence (between 1.6 and 1.5 Ma; Repenning et al., 1995) and Cathedral Cave in Nevada (no age control; Bell, 1995; Bell and Barnosky, 2000). *Phenacomys* cf. *P. gryci* was reported from the Little Dell Dam Locality 2 fauna in Utah by Gillette et al. (1999), but no external age is available for that material.

PHENACOMYS *SP. (NOT* P. GRYCI*) MERRIAM, 1889*

IDENTIFICATION Molars are rooted and lack cementum in the reentrant angles. The lingual triangles and reentrant angles show a pronounced asymmetrical elongation; there are five or more fully closed triangles on m1, often with a sixth triangle well developed and confluent with the anterior cap. There is no indication of a *Mimomys* Kante.

Only m1 specimens are identified here (other specimens are listed under "*Phenacomys* sp."). These specimens differ from *P. gryci* in having a greater number of closed triangles on m1 and in lacking any indication of a *Mimomys* Kante. A few morphologically intermediate forms between these relatively "advanced" *Phenacomys* morphotypes and those of *P. gryci* were found in Porcupine Cave. In an effort to preserve our friendship, we made no effort to identify these specimens beyond generic level. The reliance on labial dentine tracts to identify *Phenacomys* m1s to a finer taxonomic level holds great promise (Repenning and Grady, 1988), but the variation in this feature within the extant and fossil species of *Phenacomys* is in need of further exploration (Bell and Barnosky, 2000). The *Phenacomys* material from Porcupine Cave should be reexamined as part of a comprehensive revision of North American Pleistocene *Phenacomys*.

DISTRIBUTION WITHIN PORCUPINE CAVE CM 1925, Pit; DMNH 644, Velvet Room; DMNH 1349, Mark's Sink; DMNH 1349, Kate's Cupola; UCMP V93173, Pit.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION No *Phenacomys* are known in North America prior to the Irvingtonian. Early records of *Phenacomys* other than *P. gryci* include *P. brachyodus* from Hamilton Cave, West Virginia (approximately 840–830 Ka; Repenning and Grady, 1988), *Phenacomys* cf. *P. intermedius* from the LB1 locality in SAM Cave in New Mexico (reversed sediments, thus older than 780 Ka; Rogers et al., 2000), and *Phenacomys* sp. from Cumberland Cave in Maryland (Guilday, 1971; approximately 830 Ka according to Repenning, 1992), the Little Sioux fauna in Iowa (Guilday and Parmalee, 1972; referred to as the "County Line" fauna by Repenning, 1987; this fauna underlies the Hartford Ash, the age of which was given as approximately 740 Ka by Boellstorff, 1978), and Wilson Valley in Kansas (Hibbard, 1944; Guilday and Parmalee, 1972; this is probably the record Hibbard [1970] referred to from the "Cudahy fauna" [see Hibbard, 1976]; it is closely associated with the Lava Creek B Ash dated to between 602 and 670 Ka; see Izett and Honey, 1995; Gansecki et al., 1998). The reports of *Phenacomys* sp. from the Java fauna in South Dakota (Martin, 1973; Van der Meulen, 1978; Repenning, 1987) were based on the material subsequently identified as *Hibbardomys* by R. A. Martin (1989). Several species of *Phenacomys* are extant in North America.

PHENACOMYS *SP. MERRIAM, 1889*

IDENTIFICATION Most specimens identified as *Phenacomys* sp. are isolated molars other than intact or slightly damaged m1s. These specimens are rooted and lack cementum in the reentrant angles and probably belong to *Phenacomys gryci* as well as other species of *Phenacomys,* but they are not identifiable beyond the generic level. It is possible that some of this material could belong to *Ophiomys parvus,* definitively identified only from the Mark's Sink locality in Porcupine Cave.

DISTRIBUTION WITHIN PORCUPINE CAVE Specimens were recovered from many localities within Porcupine Cave and are summarized in appendix 19.1 and chapter 10.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION See "Known Geographic and Temporal Distribution" sections for *Phenacomys gryci* and *Phenacomys* sp. (not *P. gryci*).

ONDATRA *SP. LINK, 1795*

IDENTIFICATION The relatively large size of muskrat specimens distinguished them from other arvicolines in Porcupine Cave. Molars are rooted, and cementum is usually present in the reentrant angles, but it is somewhat reduced and has a network pattern when viewed from the side. Species identification of muskrats is based primarily on the m1, and only three m1 specimens are known from the cave. The single m1 specimen from the Pit is a badly fragmented juvenile and cannot be identified beyond *Ondatra.* The specimens from the Velvet Room and Fissure Fill A are also unidentified at the species level.

DISTRIBUTION WITHIN PORCUPINE CAVE DMNH 644, Velvet Room; UCMP V93173, Pit; UCMP V98022, Fissure Fill A.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION Only 14 specimens of muskrat were recovered from Porcupine Cave (12 from the Pit, and one each from the DMNH Velvet Room and Fissure Fill A). Although muskrats are not common in the Porcupine Cave faunas, they are reported from many late Pliocene and Pleistocene faunas elsewhere in North America. The earliest record of North American muskrat is from the Kettleman Hills in California (Repenning et al., 1995). The original identification of *Dolomys* (Eurasian muskrat) was changed to *Pliopotamys* by Repenning (1998: 49); that specimen comes from beneath a volcanic tuff identified as the Lawlor Tuff, which elsewhere was dated at 4.1 ± 0.2 Ma (Sarna-Wojcicki et al., 1991). Muskrats are still extant and have a widespread distribution in North America (Hall, 1981). The earliest *Ondatra* specimens are from the late Blancan in Idaho (Birch Creek fauna), at approximately 2.4 Ma (Repenning et al., 1995; Hearst, 1999).

MICTOMYS VETUS *(WILSON, 1934)* *OR* M. LANDESI *(HIBBARD, 1954)*

IDENTIFICATION *Mictomys vetus* has rootless molars with cementum in at least the posterior reentrant angles. The lower first molar has a posterior loop, a well-developed triangle 1 that is confluent with a greatly reduced triangle 2, and a well-developed and closed triangle 3. Labial and lingual reentrant angles are present; reentrant angles on the anterior cap are with or without cement. The axis of the tooth is shifted labially, but not to the degree seen in other *Mictomys* species (Koenigswald and Martin, 1984; Repenning and Grady, 1988). In an emended diagnosis, the anterior cap of the m1 of *M. vetus* was reported by Zakrzewski (1972) to have a deep and angular lingual reentrant angle and a shallow labial one; the labial edge of the second triangle was reported to be somewhat rounded as a result of a flattening where the dentine tract intercepts the occlusal surface. *Mictomys landesi* was reported to differ in having shallow reentrant angles on both the labial and lingual sides of the anterior cap, with a more triangularly shaped labial edge on the second triangle (Zakrzewski, 1972), presumably resulting from a lesser degree of flattening at the labial apex.

Of the 26 specimens from Porcupine Cave, 25 are from a mixed deposit (Mark's Sink and Kate's Cupola) and cannot be placed in any reliable stratigraphic context. When we sorted the many specimens from this locality, we took only the m1 sample for identification, and therefore the morphology of *Mictomys* M3s from that deposit is not known at this time. It is possible that the morphology of the M3 will help to determine the specific identity of the *Mictomys* from Mark's Sink (no M3 is available from the Ferret Room). Of the 26 m1s available for study, five have a somewhat flattened second triangle (more "rounded" condition of Zakrzewski, 1972), and one has a more or less triangular second triangle (with the apex only slightly truncated at the labial edge). All other specimens have a distinctly flattened labial edge on triangle 2. The lingual reentrant angles of the anterior cap vary from very deep (DMNH 37739) to deep (e.g., DMNH 37672) to shallow (e.g., DMNH 37876). Cement is absent in the anterior reentrant angles of most specimens but is present in two specimens (DMNH 37672, 37862). The labial reentrant angles of the anterior cap also vary in morphology, from relatively deep (e.g., DMNH 37672) to absent (e.g., DMNH 38315). The anterior cap morphology also varies considerably.

This mixed assemblage displays an assortment of characters that make reliable species identification impossible at this time. The differences between *M. vetus* and *M. landesi* are subtle, and the two species may be conspecific (Fejfar and Repenning, 1998), but confirmation of this hypothesis will require additional investigations. Preliminary Schmelzmuster analysis (Koenigswald and Martin, 1984) revealed subtle differences between the two species, but only one specimen of each species was examined, and the *M. vetus* specimen was a tentatively identified specimen from the Seneca fauna.

DISTRIBUTION WITHIN PORCUPINE CAVE Specimens referable to *M. vetus* or *M. landesi* are known only from DMNH 1349, Mark's Sink and Kate's Cupola, and DMNH 1342, Ferret Room.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION *Mictomys landesi* is known only from the Borchers fauna (Kansas; Hibbard, 1954; given as "*Synaptomys (Mictomys)* cf. *vetus*" by Hibbard, 1941a, and as *Synaptomys vetus* by Hibbard, 1949); it was considered a junior synonym of *M. vetus* by Fejfar and Repenning (1998). *Mictomys vetus* was reported from California Wash (Arizona; Repenning, 1987; given as *Synaptomys* by Lindsay and Tessman, 1974); the Tusker fauna, 111 Ranch (Arizona; Galusha et al., 1984; Repenning, 1987; Tomida, 1987; given as *Synaptomys* by Lindsay and Tessman, 1974); nine localities in the Froman Ferry faunal sequence (Idaho; Repenning et al., 1995); the Grand View faunas, including Castle Butte, Wild Horse Butte, and Jackass Butte (Idaho; Wilson, 1933; Shotwell, 1970; Repenning, 1987; Repenning et al., 1995); an unnamed butte 11 km northwest of Jackass Butte (Idaho; Fejfar and Repenning, 1998:178); Ninefoot Rapids (Idaho; Repenning, 1987); Seneca (Nebraska; tentative referral by Koenigswald and Martin, 1984, and Martin and Schultz, 1985; listed as *Synaptomys (Metaxyomys)* sp. by Schultz et al., 1978, and L. D. Martin, 1989); Beaver (Utah; Repenning et al., 1995; Fejfar and Repenning, 1998); Boyle Ditch (Wyoming; identified as *Synaptomys* sp. by Barnosky, 1985; transferred to *M. vetus* by Fejfar and Repenning, 1998); and the Thayne fauna (Wyoming; Repenning, 1987). A possibly closely related species, *M. anzaensis,* is known only from the Vallecito Creek sequence in the Anza-Borrego Desert in California (Zakrzewski, 1972); this species was considered a junior synonym of *M. vetus* by Repenning et al. (1995) and Fejfar and Repenning (1998).

Mictomys landesi from the Borchers fauna is directly associated with the Huckleberry Ridge Ash, which dates to between 2.003 ± 0.014 Ma (Gansecki et al., 1998) and 2.10 ± 0.02 Ma (Honey et al., 1998). Radiometric dates are not available for *M. vetus* populations, but paleomagnetic calibrations indicate that the earliest known occurrences are just below the Gauss-Matuyama boundary, currently dated to 2.581 Ma (Berggren et al., 1995). The youngest reported occurrence of *M. vetus* is in the Froman Ferry section, dated to between 1.6 and 1.5 Ma (Repenning et al., 1995).

MICTOMYS KANSASENSIS *(HIBBARD, 1952)* *OR* M. MELTONI *(PAULSON, 1961)*

IDENTIFICATION Molars are rootless, with cementum in at least the lingual reentrant angles of the lower molars. The axis of the lower tooth row is shifted strongly to the labial edge of the teeth, resulting in the pronounced elongation of the lingual triangles (Koenigswald and Martin, 1984). The m1s have a posterior loop, two closed but not alternating triangles (resulting from loss of triangle 2), and a moderately variable anterior cap. Enamel is positively differentiated, with the anterior enamel band of each triangle thicker than the posterior band on the lower molars.

Mictomys kansasensis was first recognized in the Kentuck faunal assemblage, and it was diagnosed primarily by the posterior extension of the lower incisor to a position about equal to the posterior edge of the m3 (Hibbard, 1952). *Mictomys meltoni* was named from the Cudahy Ash Pit in Kansas and diagnosed by a combination of characters, including positively differentiated enamel, lack of a cement-filled labial reentrant on m3, posterior extension of the lower incisor to a point just anterior to the anterior edge of the m3, and an anteriorly convex (rather than concave) posterior edge of the first triangle on m1 (Paulson, 1961).

The majority of the m1 specimens from the Pit fauna in Porcupine Cave were previously reported to be similar to *M. meltoni* in having a convex or flat posterior margin of the first triangle of m1 (Bell and Barnosky, 2000). The overall expression of this character has not been critically evaluated for most *M. kansasensis* specimens, but it is present in at least some populations referred to that species (e.g., Wathena; see comment by Bell and Barnosky, 2000). In addition, in the few specimens in the Pit that preserved the relevant portion of the jaw, the incisor terminates anterior to m3. This feature is also subject to some variation (Repenning and Grady, 1988), and its reliability as a character to separate *M. meltoni* and *M. kansasensis* is not established.

No Porcupine Cave materials have yet been investigated for Schmelzmuster morphology, which may ultimately be a useful feature in separating the species. The utility of Schmelzmuster morphology for differentiating higher-level taxa seems indisputable (e.g., Koenigswald, 1980), and rigorous application may have promise for finer taxonomic resolution (e.g., Wallace, 1999). Preliminary analysis of lemming enamel indicated that species determination in this group may be possible (Koenigswald and Martin, 1984). Triangles on the m1 of *M. kansasensis* were reported to have an extremely thin posterior enamel margin that consists almost entirely of radial enamel, although some lamellar enamel is present at the extreme lingual border of the triangle (Koenigswald and Martin, 1984). The only existing comparison of the Schmelzmuster of these species was restricted to one specimen of *M. kansasensis* from each of three localities and one specimen of *M. meltoni* from Cudahy (Koenigswald and Martin, 1984). A critical evaluation of the Schmelzmuster in *Mictomys* species is now needed. For Schmelzmuster to be convincing as a systematically informative character at the species level, a much more systematic and thorough approach must be undertaken. Schmelzmuster samples must be taken from homologous portions of the dentition from multiple individuals within a fauna (i.e., the same location of the same tooth in multiple specimens from a single locality). Multiple populations of the same purported species should be subjected to analysis to establish the range of intraspecific variation, and analysis of all nominal species must be completed to document interspecific variation and evaluate the utility of enamel microstructure for differentiating species-level taxa. Such a study is under way for the genus *Microtus* (Wallace, 1999) but has not yet been undertaken for lemmings.

DISTRIBUTION WITHIN PORCUPINE CAVE CM 1925, Pit; DMNH 644, Velvet Room; DMNH 942, Badger Room; DMNH 1347, Generator Dome; DMNH 1349, Mark's Sink and Kate's Cupola; UCMP V93173, Pit; UCMP 93174, Gypsum Room; UCMP V93175, CM Velvet Room; UCMP V98022, Fissure Fill A.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION *Mictomys kansasensis* was previously reported from the El Casco fauna (California; Repenning, 1987; Repenning and Grady, 1988; Albright, 1999; given as *Synaptomys kansasensis* by Reynolds and Reeder, 1991); the Hansen Bluff sequence (Colorado; Repenning, 1987, given as "Alamosa, Colorado";

but identified as *Synaptomys meltoni* by Rogers et al., 1985); Kentuck (Kansas; Hibbard, 1952; Semken, 1966), Nash fauna (Kansas; Eshelman and Hibbard, 1981, as *Synaptomys (Mictomys) kansasensis*), Rick Forester (Kansas; Martin et al., 2000), Wathena (Kansas; Van der Meulen, 1978; Koenigswald and Martin, 1984), McCook fauna (Nebraska; Koenigswald and Martin, 1984:134); Sappa (Nebraska; Koenigswald and Martin, 1984; Martin and Schultz, 1985; this material was listed as *Mictomys meltoni* by Schultz and Martin, 1970, and Repenning, 1987); the LB4, Pink Solid, Bot 4, and Under Arch localities in SAM Cave (New Mexico; Rogers et al., 2000); Java (South Dakota; R. A. Martin, 1973, 1989; Repenning, 1987); and Wellsch Valley (Saskatchewan; Stalker and Churcher, 1982; Repenning, 1987). If the proposed stratigraphic placement of the Nash fauna (somewhat younger than 2.1 Ma; Martin et al., 2000) is correct, then the oldest occurrence of *M. kansasensis* is probably from there. The species thus appears to have persisted for something less than one million years and to have been contemporaneous with *M. vetus* (see "Known Geographic and Temporal Distribution" section for *Mictomys vetus* or *M. landesi*).

Mictomys meltoni was reported from reversed sediments in the PP2 locality in the Hansen Bluff faunal sequence (Colorado; Rogers et al., 1985, as *Synaptomys meltoni;* identified as *Synaptomys (Mictomys) kansasensis* by Repenning, 1987, who also named the locality "Alamosa, Colorado"), Cudahy Ash Pit (Kansas; Paulson, 1961; given as *Synaptomys (Mictomys) borealis* by Hibbard, 1944), Wilson Valley (Kansas; given as *Synaptomys (Mictomys) borealis* by Hibbard, 1944), Bull Draw (Texas; Dalquest and Schultz, 1992:29), Deadman's Creek (Texas; Dalquest and Schultz, 1992:31), and Mayfield Ranch (Texas; Dalquest and Schultz, 1992:33). *Mictomys* cf. *M. meltoni* was reported from the Courtland Canal and Hall Ash faunas (Kansas; Eshelman and Hager, 1984) and the Horse Room in Salamander Cave (South Dakota; Mead et al., 1996). Most of the localities are closely associated with the Lava Creek B Ash, dated to between 670 Ka (Izett et al., 1992; Izett and Honey, 1995) and 602 Ka (Gansecki et al., 1998). The exceptions are Hansen Bluff (approximately 820 Ka, but with uncertain species assignment) and Salamander Cave in South Dakota, dated at 252 ± 30 Ka (Mead et al., 1996).

Specimens identified as *Mictomys kansasensis* or *M. meltoni* were reported from Cathedral Cave (Nevada; Bell, 1995; given as *Mictomys borealis* by Mead et al., 1992). Specimens with possible affinity with *Mictomys meltoni* are known from Cumberland Cave (Maryland; given as *Synaptomys (Myctomys)* [*sic*] cf. *borealis* by Gidley, 1913; as *Synaptomys (Mictomys)* sp. by Gidley and Gazin, 1938, and Van der Meulen, 1978:130; and as *Mictomys* n. sp. by Repenning and Grady, 1988), Snowville (Utah; Repenning, 1987; Repenning and Grady, 1988; given as *Synaptomys (Mictomys) meltoni-borealis* by Repenning, 1987), and the Kennewick Roadcut (Washington; identified as *Mictomys borealis* by Rensberger et al., 1984; a more tentative identification was reported by Rensberger and Barnosky, 1993). As noted previously, the specific identity of the *Mictomys* from Hansen Bluff, Colorado, is uncertain.

Undetermined species of *Mictomys* are also known from Yucca Flats (Nevada; perhaps greater than 400,000 years old, discovered by Repenning and reported by Mead et al., 1992: 230), the LB3 and Tight Spot localities in SAM Cave (New Mexico; Rogers et al., 2000), the Beaver fauna (Utah; identified as *Mictomys,* but species not given; Repenning et al., 1995:29), Little Dell Locality 2 (Utah; Gillette et al., 1999), and the Cheetah Room fauna in Hamilton Cave (West Virginia; Repenning and Grady, 1988).

MICTOMYS *SP. TRUE, 1894*

IDENTIFICATION Specimens identified as *Mictomys* sp. are isolated molars other than intact or slightly damaged m1s.

DISTRIBUTION WITHIN PORCUPINE CAVE Specimens were recovered from many localities within Porcupine Cave and are summarized in appendix 19.1.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION See "Known Geographic and Temporal Distribution" sections for *Mictomys vetus* or *M. landesi* and *Mictomys kansasensis* or *M. meltoni.*

ALLOPHAIOMYS PLIOCAENICUS *KORMOS, 1933*

IDENTIFICATION Molars are rootless; the m1 consists of a posterior loop, three alternating closed triangles, and well-developed primary wings (triangles 4 and 5; terminology following Repenning, 1992) that are broadly confluent with a very simple anterior cap. Only m1s are identifiable as *Allophaiomys*.

TAXONOMIC BACKGROUND The complicated Old and New World history of *Allophaiomys* was reviewed by Repenning (1992) and Martin and Tesakov (1998a). Fossils are reported from across much of the Holarctic; traditionally these fossils were considered to represent one or two extinct species with an extremely wide geographic distribution. Recent analyses of large samples of *Allophaiomys,* especially from Europe, indicate that the evolutionary history may be much more complex and that multiple closely related species may be erroneously assigned to a single taxon (Agustí, 1992; Agustí et al., 1993; Nadachowski and Zagorodnyuk, 1996; Martin and Tesakov, 1998b; Nadachowski and Garapich, 1998). A growing body of evidence strongly suggests that an *Allophaiomys* morphotype was present ancestrally in several, and perhaps many, early lineages of arvicolines allied to the extant genus *Microtus* (sensu lato). These morphotypes persist in populations of several extant, Old World arvicoline species (Nadachowski and Zagorodnyuk, 1996; Nadachowski and Garapich, 1998) but are no longer found among North American species.

The status of the North American fossils with an *Allophaiomys* morphotype is not certain, but the traditional conceptualization was that *Allophaiomys* in North America gave rise to multiple independent lineages that still have extant representatives in the North American fauna (e.g., Martin, 1975; Repenning, 1992; Martin and Tesakov, 1998b). In light of this interpretation, we find perplexing the direct stratigraphic association of *Allophaiomys* with several of its purported descendants (*Microtus meadensis, M. paroperarius,* and *Microtus* sp. with five closed triangles on m1) in the Pit fauna (Bell and Barnosky, 2000) and the CM Velvet Room excavation (level 3) in Porcupine Cave, and in Cathedral Cave (Bell, 1995; Bell and Barnosky, 2000).

A recent phylogenetic analysis of 24 *Microtus* species based on mtDNA sequence data (Conroy and Cook, 2000) resulted in recognition of a monophyletic North American clade of endemic *Microtus* species. This result challenges the traditional hypothesis that the diversity of extant North American *Microtus* species is the result of multiple independent dispersal events from Asia via the Bering Land Bridge. These data provide an interesting challenge for paleontologists seeking to unravel the complexities of arvicoline evolution and biogeography in North America because they suggest that all extant, endemic North American *Microtus* species are descended from a single common ancestor.

It is not clear what this means for interpreting the taxonomic, much less the phylogenetic, status of populations traditionally referred to *Allophaiomys.* The recommendation to refer all *Allophaiomys* morphotypes to the genus *Microtus* (Martin, 1987) seems premature, and treatment of *Allophaiomys* as an arbitrarily defined "metaregion" as suggested by Martin and Tesakov (1998b) offers little in the way of resolution to the problem. We continue to refer these North American morphotypes to the nominal species *A. pliocaenicus,* but we acknowledge that this is a somewhat arbitrary assignment.

DISTRIBUTION WITHIN PORCUPINE CAVE DMNH 942, Badger Room; UCMP V98022, Fissure Fill A; DMNH 1347, Generator Dome; UCMP V93174, Gypsum Room; UCMP V93173, Pit; UCMP V93175, CM Velvet Room; DMNH 644, DMNH Velvet Room; DMNH 1349, Mark's Sink.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION The fossil record of *Allophaiomys* was reviewed by Repenning (1992) and Martin and Tesakov (1998a). It was reported previously from the drill core at Hansen Bluff (Colorado; Rogers et al., 1992), Aries A fauna (Kansas; Izett and Wilcox, 1982 [as *Phaiomys*]; Martin et al., 2000 [as *Microtus pliocaenicus*]), Courtland Canal (Kansas; Zakrzewski, 1985 [as *Pitymys* sp.]; Repenning, 1992), Kentuck (Kansas; Martin, 1975; Zakrzewski, 1985 [as *Pitymys* sp.]; Repenning, 1992), Nash fauna (Kansas, Zakrzewski, 1985 [as *Pitymys* sp.]; Martin et al., 2000 [as *Microtus pliocaenicus*]), Rick Forester (Kansas; Martin et al., 2000 [as *Microtus pliocaenicus*]), Short Haul locality (Kansas; Martin et al., 2000:7 [as *Microtus pliocaenicus*]), Wathena (Kansas; Van der Meulen, 1978; Zakrzewski, 1985 [as *Pitymys* sp.], McCook fauna (Nebraska; Koenigswald and Martin, 1984:134), Sappa (Nebraska; Van der Meulen, 1978; Martin and Schultz, 1985; Repenning, 1987), Cathedral Cave (Nevada; Bell, 1995; Bell and Barnosky, 2000), SAM Cave (New Mexico; Repenning, 1992; Rogers et al., 2000), Java (South Dakota; R. Martin, 1975, 1989), Little Dell Dam Locality 2 (Utah; Gillette et al., 1999), Cheetah Room fauna of Hamilton Cave (West Virginia; Repenning, 1992), and Wellsch Valley (Saskatchewan, Canada; Stalker and Churcher, 1982; Churcher, 1984; Repenning, 1992). *Allophaiomys guildayi* was reported from Cumberland Cave (Maryland; Van der Meulen, 1978 [as "*Microtus (Pedomys) guildayi*"]; Repenning, 1992), Hanover Quarry No. 1 Fissure (Pennsylvania; Guilday et al., 1984 [as *Pedomys guildayi*]; Repenning, 1992), and Fyllan Cave (Texas; Taylor, 1982 [as *Pitymys guildayi*]; Repenning, 1987). "*Allophalomys* [*sic*] sp. (lg)" was included without comment in a list of the mammalian taxa from Olive Dell in the upper San Timoteo Formation of southern California (Reynolds and Reeder, 1991: 47), but this record cannot be verified. The presence of *Allophaiomys* in Porcupine Cave was first recognized by Keesing (1992).

Many of the localities that produced *Allophaiomys* lack external age control, but the oldest known occurrence of *Allophaiomys pliocaenicus* is probably in the Nash fauna, where it is probably slightly younger than 2.1 Ma (Martin et al., 2000). Its youngest record may be from the Cheetah Room fauna in Hamilton Cave, which was assigned an age of 840 Ka by Repenning (1992).

MICROTUS PAROPERARIUS *HIBBARD, 1944*

IDENTIFICATION Molars are rootless, with cementum in the reentrant angles. The m1 consists of a posterior loop followed by four closed alternating triangles; a fifth triangle is well developed but is confluent with the anterior cap. Triangle 2 is smaller than triangle 1 on m1. Only m1s are identifiable as *M. paroperarius.*

The original diagnosis of this species (Hibbard, 1944) was amended by Paulson (1961), who noted that approximately 20% of m1 specimens in the type population had a closed fifth triangle. This altered diagnosis traditionally presented no problems because in virtually all localities with *M. paroperarius* it was the only species of *Microtus* reported to be present. However, a second species of *Microtus* may be present in the Cudahy Ash Pit fauna (Bell and Repenning, 1999), and there are several localities in Porcupine Cave where specimens readily assignable to *M. paroperarius* are associated with more complex m1s with a fully closed fifth triangle; the latter specimens fall outside the designated morphological range given in the original diagnosis for *M. paroperarius.* All specimens reported here conform with the primary criterion noted by Hibbard (1944) for recognition of the species (the fifth triangle is confluent with the anterior cap).

A more complicated problem is whether *M. paroperarius* can be differentiated reliably from *M. oeconomus,* an extant vole whose range in North America is now restricted to Alaska, the northwest portion of the Northwest Territories, British Columbia, and the Yukon in Canada (Hall, 1981). Characters reported to differentiate these species (see Hibbard, 1944; Paulson, 1961) must be carefully reevaluated, with large population sizes of both species examined. Hibbard clearly recognized the morphological similarity between the two species (*M. operarius* is a junior synonym of *M. oeconomus,* and the name "*paroperarius*" indicates his assessment of their similarity), but he was somewhat inconsistent in his statements of characters to differentiate them (Bell and Repenning, 1999:758). The differentiating characters listed by Paulson (1961:144) must be evaluated with larger sample sizes; he himself suggested that the close morphological similarity of the two species was indicative of close relationship (Paulson, 1961:146), and Van der Meulen (1978) suggested that the two species cannot be separated on the basis on dentition. Until recently, *M. paroperarius* was reported only from localities east of the Rocky Mountains. The original report of Porcupine Cave material documented its presence at high elevation in the central Rockies (Barnosky and Rasmussen, 1988), and subsequent publications documented its presence in Utah (Little Dell Dam Locality 1; Gillette et al., 1999) and Nevada (Cathedral Cave; Bell, 1995; Bell and Barnosky, 2000). An unpublished record of a single m1 from Oregon (Natural History Museum of Los Angeles County specimen 105914 from locality 4188) further reduces the geographic separation of the two taxa. The Oregon material is catalogued as "Irvingtonian," but no external age control is available.

A single m1 specimen showing a "*Lasiopodomys*" morphology was reported from the Pit locality by Bell and Barnosky (2000). A second specimen (UCMP 213018) from Porcupine Cave was recovered from the Fissure Fill A locality.

Measurements of the *M. paroperarius* from the Pit fauna were provided by Bell and Barnosky (2000). None of the Porcupine Cave specimens (from the Pit or other localities) approach the very large sizes of teeth reported from the base of the nearby Hansen Bluff sequence in southern Colorado (Rogers et al., 1985; Repenning, 1992:57).

DISTRIBUTION WITHIN PORCUPINE CAVE UCMP V94014, Crystal Room; UCMP V98022, Fissure Fill A; DMNH 1349, Mark's Sink; UCMP V93173 and CM 1925, Pit; UCMP V93175, CM Velvet Room; DMNH 644, DMNH Velvet Room main excavation.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION *Microtus paroperarius* is reported from Conard Fissure (Arkansas; Brown, 1908; Graham, 1972), normal and reversed sediments at Hansen Bluff (Colorado; Rogers et al., 1985, 1992), the County Line fauna (Illinois; Miller et al., 1994), Little Sioux (Iowa; Zakrzewski, 1985), Cudahy Ash Pit (Kansas; Hibbard, 1944; Paulson, 1961), Hall Ash Pit (Kansas; Eshelman and Hager, 1984), Holzinger (Kansas; Zakrzewski, 1985), Sunbright Ash Pit (Kansas; Hibbard, 1944), Tobin (Kansas; Hibbard, 1944), Wilson Valley (Kansas; Hibbard, 1944), Cumberland Cave (Maryland; Van der Meulen, 1978), Mullen Locality Cr-10, Pit 3 (Nebraska; Martin, 1972:178), Shoemaker Ranch (Nebraska; Paulson, 1961:145), Cathedral Cave (Nevada; Bell, 1995; Bell and Repenning, 1999), Hanover Quarry No. 1 Fissure (Pennsylvania; Guilday et al., 1984), Horse Room of Salamander Cave (South Dakota; Mead et al., 1996), Bull Draw (Texas; Dalquest and Schultz, 1992:29), Deadman's Creek (Texas; Dalquest and Schultz, 1992:31), Gilliland (Texas; Dalquest and Carpenter, 1988; Dalquest and Schultz, 1992:18), Mayfield Ranch (Texas; Dalquest and Schultz, 1992:33), Woody Draw (Texas; Dalquest and Schultz, 1992:27), Vera (Texas; Getz and Hibbard, 1965; Hibbard and Dalquest, 1966; Dalquest and Carpenter, 1988), Little Dell Locality 1 (Utah; Gillette et al., 1999), Hamilton Cave (West Virginia; Repenning and Grady, 1988), and Trout Cave No. 2 (West Virginia; Pfaff, 1990).

The earliest record was reported from Hamilton Cave by Repenning and Grady (1988) and was assigned an age of approximately 840 Ka by Repenning (1992). The youngest dated specimens referred to *M. paroperarius* are from Salamander Cave in South Dakota (252 ± 30 Ka; Mead et al., 1996).

MICROTUS MEADENSIS *(HIBBARD, 1944)* *OR* TERRICOLA MEADENSIS *(HIBBARD, 1944)*

IDENTIFICATION This species exhibits rootless molars with cementum present in the reentrant angles. The m1 consists of a posterior loop and three closed triangles, followed by triangles 4 and 5 (the primary wings of Repenning, 1992), which are confluent in a rhombus that is either closed off from the anterior cap or connected to it by a narrow confluence. Secondary wings (incipient triangles 6 and 7) are well developed, with labial reentrant angle 4 and lingual reentrant angle 5 also well developed.

TAXONOMIC BACKGROUND Specimens from Porcupine Cave were reported previously as *Pitymys meadensis* by Barnosky and Rasmussen (1988) and as *Terricola meadensis* by Repenning (1992), Bell (2000), and Bell and Barnosky (2000). Proper generic allocation is difficult to assess at this time. The mtDNA data presented by Conroy and Cook (2000), supplemented by unpublished data (C. Conroy, pers. comm.) support previous studies (Repenning, 1983; Moore and Janecek, 1990; Repenning, 1992) in which North American "pitymyine" species, variably classified in the genera *Pitymys, Pedomys, Terricola,* and *Microtus,* were found to be paraphyletic and nested among species traditionally placed in *Microtus.* The extant species traditionally classified in these genera that are clearly members of a morphologically variable clade that is taxonomically treated most efficiently as *Microtus* include *M. pinetorum* ("*Pitymys*") and *M. ochrogaster* ("*Pedomys*") (Conroy and Cook, 2000).

In an unpublished mtDNA analysis that included *M. quasiater,* that species was also grouped with other North American endemic *Microtus* species (C. Conroy, pers. comm.). *Microtus quasiater* was placed in *Terricola* by Repenning (1992), but it now appears to be more appropriately placed with *Microtus.* DNA evidence for the placement of the Eurasian *T. savii* and *T. subterraneus* is not available yet, and several evolutionary and taxonomic scenarios are thus possible. On one hand, the extinct species *meadensis* could belong to a monophyletic Eurasian clade of voles that penetrated the North American continent during the middle Pleistocene but subsequently became extinct here (resulting in an appropriate "*Terricola meadensis*" taxonomy). Alternatively, *meadensis* could be a member of a monophyletic North American endemic *Microtus* clade (sensu Conroy and Cook, 2000), but was a species that was morphologically convergent with Eurasian *Terricola* (resulting in an appropriate "*Microtus meadensis*" taxonomy). A third alternative is that all Eurasian species placed within *Terricola* by Repenning (1992) are actually part of a more expansive *Microtus* clade (in which case *meadensis* would be best placed within *Microtus* as well). Molecular data will provide an opportunity to resolve the placement of the extant species, but recovery of ancient DNA from *meadensis* seems unlikely at present, and dental synapomorphies permitting the recognition of a monophyletic *Terricola* are currently unknown. We present two taxonomic alternatives here because we could not reach a consensus on this issue. In other chapters in this volume *Microtus meadensis* is adopted as the appropriate taxonomy for this species.

DISTRIBUTION WITHIN PORCUPINE CAVE UCMP V93174 and CM 1926, Gypsum Room; UCMP V93177, New Passage; V93173 and CM 1925, Pit; DMNH 644, Velvet Room main excavation; DMNH 1349, Mark's Sink; DMNH 1350, Will's Hole.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION Specimens of *meadensis* were reported from Anza-Borrego Desert (California; Repenning, 1992), North Livermore Avenue (California; Repenning, 1983), Olive Dell Ranch (California; Repenning, 1983), Hansen Bluff (Colorado; Rogers et al., 1995), Sunbright Ash Pit (Kansas; Hibbard, 1944; Paulson, 1961), Cudahy Ash Pit (Kansas; Paulson, 1961), Tobin fauna (Kansas; Hibbard, 1944), Cathedral Cave (Nevada; Bell, 1995), Horse Room of Salamander Cave (South Dakota; Mead et al., 1996), Bull Draw (Texas; Dalquest and Schultz, 1992:29), Deadman's Creek (Texas; Dalquest and Schultz, 1992:31), Mayfield Ranch (Texas; Dalquest and Schultz, 1992:33), Woody Draw (Texas; Dalquest and Schultz, 1992:27), Kennewick (Washington; Rensberger et al., 1984; Rensberger and Barnosky, 1993), and El Tajo de Tequixquiac (Mexico; Repenning, 1983).

The oldest occurrence appears to be at Hansen Bluff in Colorado (approximately 820 Ka; Repenning, 1992:72). The youngest reported occurrence is from Salamander Cave at approximately 252 Ka (Mead et al., 1996).

MICROTUS *SP. (NOT* M. PAROPERARIUS *OR* M. MEADENSIS*)*

IDENTIFICATION Molars are rootless and have cementum in the reentrant angles. The m1 consists of a posterior loop followed by at least five (occasionally six) closed, alternating triangles; triangle 2 is distinctly smaller than triangle 1. Triangles 6 and 7 (secondary wings of Repenning, 1992) are well developed.

At least 12 *Microtus* species extant in North America have an m1 with five or six closed alternating triangles: *M. breweri, M. californicus, M. chrotorrhinus, M. longicaudus, M. mexicanus, M. miurus, M. montanus, M. oregoni, M. pennsylvanicus, M. richardsoni*, *M. townsendii,* and *M. xanthognathus* (Hall, 1981). The search for reliable dental characters that will permit species-level identification of isolated fossil *Microtus* teeth continues, but in general species identification remains an elusive goal. Studies applying discriminant analysis (Smartt, 1972, 1977) were successful at discriminating teeth of five species, but they were never extended to all North American taxa. Promising preliminary results based on enamel microstructure suggest the possibility that Schmelzmuster can be effective for identification of species (Wallace, 1999); we eagerly await expansion of this study. Many species identifications of *Microtus* fossils reported in the literature are ultimately based on modern geographic distribution, but this practice can potentially generate misleading information that is incorporated into subsequent studies of biochronology, biostratigraphy, and paleobiogeography (see discussions in Bell and Mead, 1998; Bell and Barnosky, 2000). We were not able to identify any reliable dental characteristics that would permit species-level differentiation among the many known species with at least five closed triangles (not to mention any potentially extinct species with similar morphology).

Some of these specimens previously were identified as "*Microtus montanus* or *Microtus longicaudus*" by Barnosky and Rasmussen (1988), Wood and Barnosky (1994), and Barnosky et al. (1996) and as "*Microtus* sp. (not *M. paroperarius*)" by Bell and Barnosky (2000). Only m1 specimens are included in the material listed in the appendix and in the tables of chapter 10, where they are identified as "*Microtus* 5T." Other molars cannot be identified reliably even to genus, and could represent teeth of *Lemmiscus, Allophaiomys,* or any of many species of *Microtus*.

The original report of *M. pennsylvanicus* from Porcupine Cave (Barnosky and Rasmussen, 1988) was based on the presence in the CM Velvet Room excavation of an upper second molar (M2) with a well-developed posterolingual dentine field ("*pennsylvanicus* loop" or "posterior internal loop" of some authors). This structure was for many years taken to be indicative of the presence of *M. pennsylvanicus,* but several authors previously acknowledged that it is regularly present in *M. californicus;* its expression in approximately 50% of specimens examined of *M. montanus* and *M. richardsoni* and in occasional specimens of *M. longicaudus* and *M. mexicanus* was noted by Bell and Repenning (1999). No definitive identification of *M. pennsylvanicus* can be made from the Porcupine Cave fauna at this time. Only two M2 specimens in the collection examined thus far have a well-developed posterolingual dentine field (UCMP 213332 from level 6 of the Pit, and UCMP 213333 from an undetermined level in the CM Velvet Room fauna).

DISTRIBUTION WITHIN PORCUPINE CAVE CM 1925, Pit; CM 1926, Gypsum Room; DMNH 644, DMNH Velvet Room; DMNH 942, Badger Room; DMNH 1349, Kate's Cupola and Mark's Sink; UCMP V93173, Pit; UCMP V93174, Gypsum Room; UCMP V93175, CM Velvet Room; UCMP V94014, Crystal Room.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION *Microtus* species with five or six triangles are quite common in Irvingtonian and especially Rancholabrean faunas; at least 12 species are still extant in North America (listed in the previous section). In addition to Porcupine Cave, other early North American specimens known to show this morphology are from the Anza-Borrego Desert (California; Zakrzewski, 1972; Repenning, 1992), the Elsinore Fault Zone (California; Pajak et al., 1996), the Irvington fauna (California; Savage, 1951), Hansen Bluff (Colorado; Bell and Repenning, 1999), SAM Cave (New Mexico; Rogers et al., 2000), and Wellsch Valley (Saskatchewan, Canada; Stalker and Churcher, 1982; Churcher, 1984; illustrated by Repenning, 1992:37).

The oldest reported record is from the Anza-Borrego Desert, where it may be as old as 1.4 Ma (Repenning, 1992), but locality data for that material may be problematic (L. K. Murray, pers. comm.). The Wellsch Valley record also seems to have a great antiquity, but age control for those materials is lacking, and reliable temporal placement is not possible at this time. The SAM Cave record is probably the next oldest and is estimated to be as old as approximately 840 Ka (Rogers et al., 2000).

LEMMISCUS CURTATUS *THOMAS, 1912: FIVE- AND SIX-TRIANGLE MORPHOTYPES*

IDENTIFICATION The molars are rootless with cementum in the reentrant angles. The m1 consists of a posterior loop and five or six closed, alternating triangles; in the majority of specimens (fossil and modern) the sixth triangle is confluent with the anterior cap. Incipient development of a seventh triangle is very rare. Triangle 2 of the m1 is as long as or longer than triangle 1.

DISTRIBUTION WITHIN PORCUPINE CAVE CM 1925, Pit; CM 1926, Gypsum Room; CM 1927, CM Velvet Room; DMNH 644, DMNH Velvet Room; DMNH 1349, Mark's Sink; UCMP V93173, Pit; UCMP V93174, Gypsum Room; UCMP V93175, CM Velvet Room; UCMP V97002, undifferentiated cave deposits.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION *Lemmiscus curtatus* m1s with five or six closed triangles are common in many Rancholabrean-age deposits in the western United States (Kurtén and Anderson, 1980; Barnosky and Rasmussen, 1988; Harris, 1993; Bell and Mead, 1998; Bell and Glennon, 2003) but are relatively rare in Irvingtonian faunas. All fossil occurrences are west of the Great Plains. Irvingtonian records outside Porcupine Cave include Cathedral Cave (Nevada; Bell, 1995), the Under Arch and LB5 localities in SAM Cave (New Mexico; Rogers et al., 2000), and possibly the Kennewick Roadcut locality (Washington; Rensberger et al., 1984; Rensberger and Barnosky, 1993), but the Kennewick sequence may be entirely Rancholabrean (Rensberger and Barnosky, 1993). In most of these localities the five-triangle *Lemmiscus* are found in association with the four-triangle forms listed subsequently as *Lemmiscus* four-triangle morphotype. Barnosky and Bell (2003) discussed these associations and their implications for species concepts. The SAM Cave material has an estimated age of approximately 840 Ka (Rogers et al., 2000). Cathedral Cave lacks external age control. The five-triangle morphotypes are dominant in extant populations of *L. curtatus.*

LEMMISCUS CURTATUS *THOMAS, 1912: FOUR-TRIANGLE MORPHOTYPE*

IDENTIFICATION Molars are rootless with cementum in the reentrant angles. The m1 consists of a posterior loop and four closed triangles; the fifth triangle is well developed, open, and confluent with the anterior cap. Only the labial secondary wing (triangle 6) is developed. Otherwise the morphology is similar to that of *Lemmiscus curtatus*. Only m1 specimens were identified.

DISTRIBUTION WITHIN PORCUPINE CAVE CM 1925, Pit; CM 1926, Gypsum Room; DMNH 644, DMNH Velvet Room; DMNH 1349, Kate's Cupola; DMNH 1349, Mark's Sink; DMNH 1342, Ferret Room; DMNH 1350, Will's Hole; UCMP V93173, Pit; UCMP V93174, Gypsum Room; UCMP V93175, CM Velvet Room.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION Irvingtonian localities include Cathedral Cave (Nevada; Bell, 1995; Bell and Mead, 1998), SAM Cave (New Mexico; Repenning, 1992; Rogers et al., 2000), and possibly the Kennewick locality (Washington; Rensberger et al., 1984; Rensberger and Barnosky, 1993); however, the Kennewick sequence may be entirely Rancholabrean (Rensberger and Barnosky, 1993). With an estimated age of approximately 840 Ka (Rogers et al., 2000), SAM Cave may be one of the oldest record of this morphotype, the other being the levels below level 4 in the Pit in Porcupine Cave. Specimens of *Lemmiscus* with only four closed triangles on m1 are also reported from two late Pleistocene localities, where the morphotype persisted until possibly as late as 9.5 Ka: Kokoweef Cave (California; Bell and Jass, in press) and Snake Creek Burial Cave (Nevada; Bell and Mead, 1998). This morphotype does not appear to be expressed in any extant *Lemmiscus* populations; here we reserve judgment on whether or not it should be regarded as the same species as *L. curtatus.*

LEMMISCUS *SP.*

IDENTIFICATION The M2 and M3 of *Lemmiscus* are also identifiable. The M2 shows pronounced anteroposterior enlargement of the lingual reentrant angle, often resulting in a "squared" appearance of this reentrant angle. M3 has an anterior loop, usually two alternating triangles, and an anteroposteriorly elongated posterior loop. The M2 and M3 specimens listed in the appendix could be from individuals showing both the four- and five-triangle morphologies on m1 (discussed previously).

DISTRIBUTION WITHIN PORCUPINE CAVE *Lemmiscus* specimens are reported from many localities and levels within Porcupine Cave; these are summarized in the appendix.

KNOWN GEOGRAPHIC AND TEMPORAL DISTRIBUTION See "Known Geographic and Temporal Distribution" sections for both *Lemmiscus curtatus* morphotypes.

Discussion and Conclusions

Arvicoline Biodiversity and Biogeography

With no fewer than 13 species, the overall diversity of arvicoline rodents within Porcupine Cave exceeds that of any other North American locality. Moreover, arvicoline diversity within discrete stratigraphic horizons in some localities within the cave (e.g., Pit, level 4, with at least nine species) presents a unique example not only of taxonomic diversity, but also of species associations. Perhaps most notable in this regard is the stratigraphic co-occurrence of *Allophaiomys* with at least three of its purported descendants *(Microtus* sp. with five closed triangles, *M. paroperarius,* and *M. meadensis).* This stratigraphic co-occurrence is seen in the Pit (level 4) and in the CM Velvet Room excavation (level 3) and provides an interesting challenge to the purported ancestor-descendant relationship between these taxa. Perhaps the simplest explanation is that *Allophaiomys* persisted for a longer period of time in the higher elevations of Colorado than in the Great Plains, where most of the fossil occurrences are known. This refugium hypothesis should be tested in other relatively high-elevation localities (when they are identified and excavated). The recognition of significant taxonomic differences in contemporaneous faunas at high- and midlatitude localities through the Pliocene and Pleistocene clearly demands independent biochronologies for high-latitude sites (Bell et al., in press); in view of this, region-specific arvicoline biochronologies may well be required for high mountain sites as well (Bell and Barnosky, 2000).

Faunal provinciality along longitudinal gradients is difficult to document for early through middle Pleistocene faunas, in part because of the relative paucity of faunas of an appropriate age throughout much of North America. The Rocky Mountains have long been recognized to be a significant boundary between arvicoline rodent faunas in North America, and beginning in the 1980s Repenning and his colleagues began to discuss the separate arvicoline faunal histories east and west of the Rockies (e.g., Repenning, 1987, 1992; Repenning et al., 1995). Formal recognition of an Eastern United States Faunal Province and a Western United States Faunal Province was proposed by Fejfar and Repenning (1992); the proposal was based primarily on arvicoline rodent faunal histories. The Porcupine Cave faunas are uniquely situated in a high-elevation intermontane basin in the central Rockies and thus provide important insight into faunal dynamics across this significant boundary in the middle Pleistocene. Prior to their discovery in Porcupine Cave, *Microtus paroperarius* and *Allophaiomys pliocaenicus* were not known to occur west of the Great Plains. Their discovery in Porcupine Cave was followed by additional discoveries of both taxa in Utah (Gillette et al., 1999) and Nevada (Bell, 1995; Bell and Barnosky, 2000), thus lessening the differences between eastern and western U.S. arvicoline faunas in the Irvingtonian. The recognition of *Pliolemmus antiquus* in the Mark's Sink locality of Porcupine Cave also represents a significant westward range extension (and a significant elevational extension) of an arvicoline previously known only from the Great Plains.

Chronologic Significance

The chronologic significance of arvicoline rodents is well established. The known temporal ranges of arvicolines recovered from Porcupine Cave are summarized in table 19.1 and are based on localities outside Porcupine Cave. The biochronology and age interpretations of the stratified sequences from Porcupine Cave are discussed in chapter 7, but a few comments are in order here.

One of the most interesting (and frustrating) arvicoline assemblages from the Cave is from the Mark's Sink locality (DMNH 1349). Although the fossils from Mark's Sink are mixed, it is clear from the species recovered that this is the oldest deposit yet located within the cave. *Pliolemmus antiquus* is known elsewhere only from Pliocene deposits in the Great Plains. Its presence, combined with that of *Ophiomys parvus* and *Mictomys vetus* or *M. landesi,* argues strongly that at least part of the Mark's Sink sediments contain a Pliocene (mid- to late Blancan) fauna. No other localities in Porcupine Cave include these three taxa together.

The Badger Room and Generator Dome appear to represent the next oldest assemblages of arvicolines within the cave. They include *Mimomys* cf. *M. virginianus, Phenacomys gryci,* and *Allophaiomys pliocaenicus.* Fissure Fill A is probably somewhat younger because, in addition to those three taxa, it contains *Microtus paroperarius.* Sample sizes are adequate in the Badger Room and Fissure Fill A, and low in Generator Dome, but it is intriguing that none of these localities contains any specimens of *Lemmiscus,* which is quite abundant in other localities. It is possible that these localities predate the arrival of *Lemmiscus* in the vicinity of Porcupine Cave. However, *Lemmiscus* is present in the Ferret Room in association with *Phenacomys gryci* and *Mictomys vetus* or *M. landesi.* It may also be that taphonomic and sample size considerations result in the apparent absence of *Lemmiscus* in some localities.

When *Lemmiscus* occurs, it is generally represented by both four- and five-triangle morphotypes. The exception is the Ferret Room, where only a single four-triangle specimen is known; but only three arvicoline teeth were recovered from this locality, so sample size is prohibitively small. This is true of the other Irvingtonian localities of *Lemmiscus* as well (Cathedral Cave and SAM Cave). The clear indication from studies of the change in relative abundance of the two morphotypes from the Pit (Barnosky et al., 1996; Bell and Barnosky, 2000; see figure 23.8), as well as from the Kennewick locality in Washington (Rensberger et al., 1984; Rensberger

TABLE 19.1

Known Temporal Range of Arvicoline Rodent Taxa Recovered from Porcupine Cave

Taxon	*Oldest Reported Occurrence*	*Youngest Reported Occurrence*
Pliolemmus antiquus	~3.2 Ma	~2.58 Ma
Ophiomys parvus	2.4 Ma	1.5 Ma
Mictomys vetus / *M. landesi*	2.58 Ma	1.5 Ma
Ondatra sp.	2.4 Ma	Extant
Phenacomys gryci	2.4 Ma	1.5 Ma
Mictomys kansasensis	Slightly younger than 2.1 Ma	~1.2 Ma
Allophaiomys pliocaenicus	Slightly younger than 2.1 Ma	~840 Ka
Mimomys cf. *M. virginianus*	"Early Irvingtonian"	~840 Ka
Microtus sp. five-triangle morphotype	1.4 Ma? Alternatively ~840 Ka	Extant
Phenacomys sp. (not *P. gryci*)	~840 Ka	Extant
Microtus paroperarius	~840 Ka	252 ± 30 Ka
Lemmiscus curtatus five-triangle morphotype	840 Ka	Extant
Lemmiscus curtatus four-triangle morphotype	840 Ka	~9.5 Ka
Microtus/Terricola meadensis	820 Ka	252 ± 30 Ka
Mictomys meltoni	670 Ka	252 ± 30 Ka

NOTES: Oldest and youngest known reliable dates are provided for each taxon and are based on radiometric dating, paleomagnetics, or biochronologic correlation of localities outside Porcupine Cave. See text for references and details on localities. *Mictomys kansasensis* and *M. meltoni* are both shown, but the species identification from Porcupine Cave is not established.

and Barnosky, 1993), is that the early populations of *Lemmiscus* have more four-triangle than five-triangle morphotypes, but this relative abundance shifts through time in favor of the five-triangle morphology. In modern populations, the five-triangle morphology predominates, but six-triangle forms are not uncommon (particularly from northern Nevada; Barnosky and Bell, unpubl. data). No four-triangle morphotypes are known from extant populations, and that morphology appears to have become extinct in the latest Pleistocene or early Holocene (Bell and Mead, 1998; Bell and Jass, in press). Presumably populations of *Lemmiscus* existed that were older than those now known, and when they are found we predict that they will contain only four-triangle morphotypes. Early reports of the fauna from SAM Cave in New Mexico (Repenning, 1992; Bell and Barnosky, 2000) indicated that only four-triangle morphotypes were known from that site. Those reports were based on an incomplete sample; a more thorough report on the fauna confirms the presence of five-triangle morphotypes there (Rogers et al., 2000). None of the well-sampled localities within Porcupine Cave records a *Lemmiscus* population with only four-triangle morphotypes.

Clearly the work on Porcupine Cave arvicolines is still in its early stages. The wealth of material from this unique site guarantees that the faunas from the cave will play a key role in helping us reshape our thoughts on arvicoline biochronology in the western United States.

Appendix 19.1. Specimens of Arvicoline Rodents from Porcupine Cave

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
DMNH	15078	*Allophaiomys*	*pliocaenicus*	Left	Dentary fragment with m1-2	942	Badger Room			
DMNH	38292	*Allophaiomys*	*pliocaenicus*	Left	Dentary with m1-2	942	Badger Room			
DMNH	38293	*Allophaiomys*	*pliocaenicus*	Left	m1	942	Badger Room			
DMNH	38294	*Allophaiomys*	*pliocaenicus*	Left	m1	942	Badger Room			
DMNH	38295	*Allophaiomys*	*pliocaenicus*	Right	m1 (partially digested)	942	Badger Room			
DMNH	38296	*Allophaiomys*	*pliocaenicus*	Right	m1	942	Badger Room			
DMNH	38297	*Allophaiomys*	*pliocaenicus*	Right	m1	942	Badger Room			
DMNH	38309	Microtinae			m1 (partially digested)	942	Badger Room			
DMNH	38274	*Microtus*	5T	Left	Dentary fragment with m1	942	Badger Room			
DMNH	15075	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1	942	Badger Room			
DMNH	38273	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with i1, m1	942	Badger Room			
DMNH	38281	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	942	Badger Room			
DMNH	38282	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	942	Badger Room			
DMNH	38283	*Mictomys*	*kansasensis/meltoni*	Left	m1	942	Badger Room			
DMNH	38284	*Mictomys*	*kansasensis/meltoni*	Left	m1	942	Badger Room			
DMNH	38285	*Mictomys*	*kansasensis/meltoni*	Left	m1	942	Badger Room			
DMNH	38286	*Mictomys*	*kansasensis/meltoni*	Left	m1	942	Badger Room			
DMNH	38287	*Mictomys*	*kansasensis/meltoni*	Left	m1	942	Badger Room			
DMNH	15076	*Mictomys*	*kansasensis/meltoni*	Right	m1	942	Badger Room			
DMNH	38288	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	942	Badger Room			
DMNH	38289	*Mictomys*	*kansasensis/meltoni*	Right	m1	942	Badger Room			
DMNH	38290	*Mictomys*	*kansasensis/meltoni*	Right	m1	942	Badger Room			
DMNH	38291	*Mictomys*	*kansasensis/meltoni*	Right	m1	942	Badger Room			
DMNH	38358	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	942	Badger Room			
DMNH	15079	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	942	Badger Room			
DMNH	38298	*Mimomys*	*virginianus*	Left	m1	942	Badger Room			
DMNH	38299	*Mimomys*	*virginianus*	Left	m1	942	Badger Room			
DMNH	38300	*Mimomys*	*virginianus*	Left	m1 (broken)	942	Badger Room			
DMNH	38301	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	942	Badger Room			
DMNH	38302	*Mimomys*	*virginianus*	Right	m1	942	Badger Room			
DMNH	38303	*Mimomys*	*virginianus*	Right	m1	942	Badger Room			
DMNH	38304	*Mimomys*	*virginianus*	Right	m1	942	Badger Room			
DMNH	38305	*Mimomys*	*virginianus*	Right	m1	942	Badger Room			
DMNH	38306	*Mimomys*	*virginianus*	Right	m1	942	Badger Room			
DMNH	38307	*Mimomys*	*virginianus*	Right	m1	942	Badger Room			
DMNH	38308	*Mimomys*	*virginianus*	Right	m1 (broken)	942	Badger Room			
DMNH	38359	*Mimomys*	*virginianus*	Right	m1	942	Badger Room			
DMNH	38360	*Mimomys*	*virginianus*	Right	m1	942	Badger Room			
DMNH	15080	*Phenacomys*	*gryci*	Left	Dentary fragment with m1-2	942	Badger Room			
DMNH	38275	*Phenacomys*	*gryci*	Left	m1	942	Badger Room			
DMNH	38276	*Phenacomys*	*gryci*	Right	m1	942	Badger Room			
DMNH	38277	*Phenacomys*	*gryci*	Right	m1	942	Badger Room			
DMNH	38278	*Phenacomys*	*gryci*	Right	m1	942	Badger Room			
DMNH	38279	*Phenacomys*	*gryci*	Right	m1	942	Badger Room			
DMNH	38280	*Phenacomys*	*gryci*	Right	m1 (broken)	942	Badger Room			
UCMP	213037	*Phenacomys*	*gryci*	Right	Dentary with i1, m1-3	V93176	Badger Room			
UCMP	213188	*Allophaiomys*	*pliocaenicus*	Right	Dentary with m1	V93175	CM Velvet Room	3	3	
UCMP	213187	*Allophaiomys*	*pliocaenicus*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213189	*Allophaiomys*	*pliocaenicus*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213190	*Allophaiomys*	*pliocaenicus*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213191	*Allophaiomys*	*pliocaenicus*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213256	*Lemmiscus*	(4T)	Right	Dentary with i1, m1	V93175	CM Velvet Room	3	2	
UCMP	213257	*Lemmiscus*	(4T)	Left	Dentary with i1, m1	V93175	CM Velvet Room	3	3	
UCMP	213258	*Lemmiscus*	(4T)	Right	Dentary with i1, m1-2	V93175	CM Velvet Room	3	3	
UCMP	213259	*Lemmiscus*	(4T)	Right	m1	V93175	CM Velvet Room	3	3	
UCMP	213322	*Lemmiscus*	(4T)	Right	m1 (broken)	V93175	CM Velvet Room	1	3	
UCMP	213324	*Lemmiscus*	(4T)	Right	Dentary fragment with i1, m1	V93175	CM Velvet Room	1	3	

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	213271	*Lemmiscus*	(4T)	Right	Dentary fragment with m1 (broken)	V93175	CM Velvet Room	3/4	Mixed; east extension	
UCMP	213270	*Lemmiscus*	(4T)	Right	Dentary fragment with m1-2	V93175	CM Velvet Room	3/4	Mixed; east extension	
UCMP	213260	*Lemmiscus*	(4T)	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213261	*Lemmiscus*	(4T)	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213262	*Lemmiscus*	(4T)	Right	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213263	*Lemmiscus*	(4T)	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213264	*Lemmiscus*	(4T)	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213265	*Lemmiscus*	(4T)	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213266	*Lemmiscus*	(4T)	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213267	*Lemmiscus*	(4T)	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213268	*Lemmiscus*	(4T)	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213269	*Lemmiscus*	(4T)	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213272	*Lemmiscus*	(4T)	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213273	*Lemmiscus*	cf. (4T)	Left	m1 (broken)	V93175	CM Velvet Room	3	3	
UCMP	213274	*Lemmiscus*	cf. (4T)	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213275	*Lemmiscus*	(4T)	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213276	*Lemmiscus*	cf. (4T)	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213232	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	1	1B	
UCMP	213233	*Lemmiscus*	*curtatus*	Left	m1	V93175	CM Velvet Room	1	1B	
UCMP	213234	*Lemmiscus*	*curtatus*	Left	m1	V93175	CM Velvet Room	1	1B	
UCMP	213235	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	1	1B	
UCMP	213320	*Lemmiscus*	*curtatus*	Right	m1 (juvenile)	V93175	CM Velvet Room	1	1B	
UCMP	213238	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1	V93175	CM Velvet Room	3	2	
UCMP	213236	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	3	2	
UCMP	213237	*Lemmiscus*	*curtatus*	Left	m1	V93175	CM Velvet Room	3	2	
UCMP	213255	*Lemmiscus*	*curtatus*	Right	Dentary with m1-3	V93175	CM Velvet Room		2	
UCMP	213323	*Lemmiscus*	*curtatus*	Left	Dentary fragment with i1, m1	V93175	CM Velvet Room	1	3	
UCMP	213243	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1	V93175	CM Velvet Room	1	3	
UCMP	213240	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-2	V93175	CM Velvet Room	3	3	
UCMP	213244	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-2	V93175	CM Velvet Room	1	3	
UCMP	213239	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-3	V93175	CM Velvet Room	3	3	
UCMP	213241	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-3	V93175	CM Velvet Room	3	3	
UCMP	213242	*Lemmiscus*	*curtatus*	Left	Dentary with m1-3	V93175	CM Velvet Room	3	3	
UCMP	213245	*Lemmiscus*	*curtatus*	Left	m1	V93175	CM Velvet Room	3	3	
UCMP	213321	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	1	3	
CM	45478	*Lemmiscus*	*curtatus*	Right	m1	1927	CM Velvet Room		3	
UCMP	213246	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	3		
UCMP	213247	*Lemmiscus*	*curtatus*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213248	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213249	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213250	*Lemmiscus*	*curtatus*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213251	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213252	*Lemmiscus*	*curtatus*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213253	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213254	*Lemmiscus*	*curtatus*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
CM	45479	*Lemmiscus*	sp.	Left	M2	1927	CM Velvet Room		3	
UCMP	213101	*Lemmiscus*	sp.	Left	M1	V93175	CM Velvet Room	1	1B	
UCMP	213106	*Lemmiscus*	sp.	Right	M1	V93175	CM Velvet Room	1	1B	
UCMP	213114	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	1	1B	
UCMP	213115	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	1	1B	
UCMP	213107	*Lemmiscus*	sp.		Palate with left I1 and right M1	V93175	CM Velvet Room	3	2	
UCMP	213116	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room		2	
UCMP	213135	*Lemmiscus*	sp.		Palate with left M2-3	V93175	CM Velvet Room	3	3	
UCMP	213141	*Lemmiscus*	sp.	Right	M3	V93175	CM Velvet Room	3	3	
CM	45477	*Lemmiscus*	sp.		Anterior skull with left M2	1927	CM Velvet Room		Mixed	
UCMP	213102	*Lemmiscus*	sp.	Left	M1	V93175	CM Velvet Room	3/4	3	
UCMP	213103	*Lemmiscus*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213104	*Lemmiscus*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213105	*Lemmiscus*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213108	*Lemmiscus*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213109	*Lemmiscus*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	213110	*Lemmiscus*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213111	*Lemmiscus*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213112	*Lemmiscus*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213113	*Lemmiscus*	sp.	Right	M1-2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213117	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213118	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213119	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213120	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213121	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213122	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213123	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213124	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213125	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213126	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213127	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213128	*Lemmiscus*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213129	*Lemmiscus*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213130	*Lemmiscus*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213131	*Lemmiscus*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213132	*Lemmiscus*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213133	*Lemmiscus*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213134	*Lemmiscus*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	399900	*Lemmiscus*	sp.	Left	M2	V93175	CM Velvet Room	Mixed	Mixed	
UCMP	213136	*Lemmiscus*	sp.	Left	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213137	*Lemmiscus*	sp.	Left	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213138	*Lemmiscus*	sp.	Left	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213139	*Lemmiscus*	sp.	Left	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213140	*Lemmiscus*	sp.	Left	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213142	*Lemmiscus*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213143	*Lemmiscus*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213144	*Lemmiscus*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213145	*Lemmiscus*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213146	*Lemmiscus*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213147	*Lemmiscus*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213279	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3	3	
UCMP	213280	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3	3	
UCMP	213283	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3	3	
UCMP	213284	*Microtus*	*meadensis*	Left	m1 (broken)	V93175	CM Velvet Room	3	3	
UCMP	213289	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3	3	
UCMP	213305	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room		3	
UCMP	213326	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	1	3	
UCMP	213277	*Microtus*	*meadensis*	Right	m1 (broken)	V93175	CM Velvet Room	3	3	
UCMP	213281	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3	3	
UCMP	213292	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3	3	
UCMP	213319	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room		3	
UCMP	213278	*Microtus*	*meadensis*	Right	Dentary with i1, m1	V93175	CM Velvet Room		Mixed	
UCMP	213282	*Microtus*	*meadensis*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213285	*Microtus*	*meadensis*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213286	*Microtus*	*meadensis*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213287	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213288	*Microtus*	*meadensis*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213290	*Microtus*	*meadensis*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213291	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213293	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213294	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213295	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213296	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213297	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213298	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213299	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213300	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213301	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213302	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213303	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213304	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213306	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213307	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213308	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213309	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	213310	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213311	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213312	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213313	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213314	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213315	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213316	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213317	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213318	*Microtus*	*meadensis*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213325	*Microtus*	*meadensis*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213192	*Microtus*	*paroperarius*	Left	Dentary with i1, m1-2	V93175	CM Velvet Room		3	
UCMP	213193	*Microtus*	*paroperarius*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213194	*Microtus*	*paroperarius*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213195	*Microtus*	*paroperarius*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213196	*Microtus*	*paroperarius*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213218	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	1	1B	
UCMP	213219	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	3	2	
UCMP	213202	*Microtus*	5T	Left	Dentary fragments, i1, m1	V93175	CM Velvet Room	3	3	
UCMP	213200	*Microtus*	5T	Left	Dentary with i1, m1-2	V93175	CM Velvet Room	3	3	
UCMP	213201	*Microtus*	5T	Left	Dentary with i1, m1-2	V93175	CM Velvet Room	3	3	
UCMP	213198	*Microtus*	5T	Left	Dentary with m1-2 (juvenile)	V93175	CM Velvet Room	3	3	
UCMP	213199	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3	3	
UCMP	213203	*Microtus*	5T	Left	m1 (broken)	V93175	CM Velvet Room	1	3	
UCMP	213217	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3	3	
UCMP	213220	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	3	3	
UCMP	213221	*Microtus*	5T	Right	Dentary with i1, m1-2	V93175	CM Velvet Room	3	3	
UCMP	213204	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213205	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213206	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213207	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213208	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213209	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213210	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213211	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213212	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213213	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213214	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213215	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213216	*Microtus*	5T	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213222	*Microtus*	5T	Right	m1 (juvenile)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213223	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213224	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213225	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213226	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213227	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213228	*Microtus*	5T	Right	m1 (partially digested)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213229	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213230	*Microtus*	5T	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213231	*Microtus*	5T	Right	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213333	*Microtus*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213148	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	1	1B	
UCMP	213044	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	1	1B	
UCMP	213092	*Mictomys*	*kansasensis/meltoni*	Left	Dentary with i1, m2-3	V93175	CM Velvet Room	3	3	
UCMP	213149	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	3	3	
UCMP	213150	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3	3	
UCMP	213151	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3	3	
UCMP	213169	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	1	3	
UCMP	213170	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93175	CM Velvet Room	3	3	
UCMP	213152	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213153	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213154	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213155	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213156	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213157	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213158	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	Mixed	Mixed	
UCMP	213159	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93175	CM Velvet Room	Mixed	Mixed	

(continued)

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
UCMP	213160	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213161	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213162	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213163	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213164	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213165	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213166	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213167	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213168	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213171	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213172	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213173	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213174	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213175	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213176	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213177	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213178	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213179	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213180	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213181	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213182	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213183	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93175	CM Velvet Room	Mixed	Mixed	
UCMP	213184	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213185	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213186	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	399908	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	1	3	
UCMP	399905	*Mictomys*	sp.	Right	m2	V93175	CM Velvet Room	1	3	
UCMP	399940	*Mictomys*	sp.	Left	m2	V93175	CM Velvet Room	3	3	
UCMP	399906	*Mictomys*	sp.	Left	m3	V93175	CM Velvet Room	1	3	
UCMP	399907	*Mictomys*	sp.	Right	m3	V93175	CM Velvet Room	1	3	
UCMP	399939	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3	3	
UCMP	399941	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3	3	
UCMP	213061	*Mictomys*	sp.	Right	palate with M1	V93175	CM Velvet Room	3	3	
UCMP	213045	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213046	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213047	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213048	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213049	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213050	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213051	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213052	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213053	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213054	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213055	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213056	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213057	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213058	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213059	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213060	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213062	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213063	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213064	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213065	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213066	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213067	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213068	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213069	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213070	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213071	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213072	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213342	*Mictomys*	sp.	Right	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	399904	*Mictomys*	sp.	Left	M1	V93175	CM Velvet Room	Mixed	Mixed	
UCMP	213093	*Mictomys*	sp.	Left	m2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213094	*Mictomys*	sp.	Left	m2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213095	*Mictomys*	sp.	Right	m2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213334	*Mictomys*	sp.	Left	m2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213335	*Mictomys*	sp.	Left	m2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213336	*Mictomys*	sp.	Left	m2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213337	*Mictomys*	sp.	Left	m2	V93175	CM Velvet Room	3/4	Mixed	

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
UCMP	213338	*Mictomys*	sp.	Right	m2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213339	*Mictomys*	sp.	Right	m2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	399903	*Mictomys*	sp.	Left	m2	V93175	CM Velvet Room	Mixed	Mixed	
UCMP	213096	*Mictomys*	sp.	Left	m3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213097	*Mictomys*	sp.	Right	m3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213098	*Mictomys*	sp.	Right	m3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213099	*Mictomys*	sp.	Right	m3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213100	*Mictomys*	sp.	Right	m3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213340	*Mictomys*	sp.	Left	m3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213341	*Mictomys*	sp.	Left	m3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	399901	*Mictomys*	sp.	Right	m3	V93175	CM Velvet Room	Mixed	Mixed	
UCMP	213073	*Mictomys*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213074	*Mictomys*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213075	*Mictomys*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213076	*Mictomys*	sp.	Left	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213077	*Mictomys*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213078	*Mictomys*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213079	*Mictomys*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213080	*Mictomys*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213081	*Mictomys*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213082	*Mictomys*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213083	*Mictomys*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213343	*Mictomys*	sp.	Left	M2 (broken)	V93175	CM Velvet Room	3/4	Mixed	
UCMP	399902	*Mictomys*	sp.	Left	M2	V93175	CM Velvet Room	Mixed	Mixed	
UCMP	213084	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213085	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213086	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213087	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213088	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213089	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213090	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213091	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213344	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213345	*Mictomys*	sp.	Right	M3	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213197	*Mimomys*	*virginianus*	Left	m1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213041	*Phenacomys*	sp.	Left	M1	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213042	*Phenacomys*	sp.	Right	M2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	213043	*Phenacomys*	sp.	Right	m2	V93175	CM Velvet Room	3/4	Mixed	
UCMP	399909	*Phenacomys*	sp.	Right	M3	V93175	CM Velvet Room	Mixed	Mixed	
UCMP	213039	*Microtus*	*paroperarius*	Left	m1	V94014	Crystal Room	Surface		
UCMP	213040	*Microtus*	5T	Right	m1	V94014	Crystal Room	Surface		
DMNH	37610	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 644	DMNH Velvet Room	Mixed	29	Mixed
DMNH	38352	*Allophaiomys*	*pliocaenicus*	Right	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	Mixed	27	Mixed
DMNH	44702	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 644	DMNH Velvet Room	(0–5, 6–7)	31	Mixed
DMNH	44704	*Allophaiomys*	*pliocaenicus*	Left	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	(0–5, 6–7)	30	Mixed
DMNH	44709	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 644	DMNH Velvet Room	(0–5, 0–6)	30	Mixed
DMNH	9403	*Lemmiscus*	(4T)	Left	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	6	2	A
DMNH	37599	*Lemmiscus*	(4T)	Left	m1	DMNH 644	DMNH Velvet Room	21	17	Below I
DMNH	37513	*Lemmiscus*	(4T)	Right	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	11	8	E
DMNH	37591	*Lemmiscus*	(4T)	Left	Dentary fragment with i1, m1	DMNH 644	DMNH Velvet Room	20	7B	E
DMNH	37564	*Lemmiscus*	(4T)	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	15	10B	F
DMNH	10838	*Lemmiscus*	(4T)	Left	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	6 or 7	22	H
DMNH	37573	*Lemmiscus*	(4T)	Right	m1	DMNH 644	DMNH Velvet Room	15	10G	H
DMNH	37574	*Lemmiscus*	(4T)	Right	m1	DMNH 644	DMNH Velvet Room	15	10G	H
DMNH	37584	*Lemmiscus*	(4T)	Right	m1	DMNH 644	DMNH Velvet Room	16	18	H
DMNH	38342	*Lemmiscus*	(4T)	Right	m1	DMNH 644	DMNH Velvet Room	16	17	H
DMNH	38347	*Lemmiscus*	(4T)	Right	Dentary with m1-2	DMNH 644	DMNH Velvet Room	17	17	H
DMNH	37509	*Lemmiscus*	(4T)	Left	m1	DMNH 644	DMNH Velvet Room	11	17	H or I
DMNH	37472	*Lemmiscus*	(4T)	Left	m1	DMNH 644	DMNH Velvet Room	10	29	I
DMNH	37512	*Lemmiscus*	(4T)	Left	m1	DMNH 644	DMNH Velvet Room	11	18	I or J

(continued)

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
DMNH	6671	*Lemmiscus*	(4T)	Right	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	1	9	Mixed
DMNH	14983	*Lemmiscus*	(4T)	Left	m1	DMNH 644	DMNH Velvet Room	1	5	Mixed
DMNH	37360	*Lemmiscus*	(4T)	Left	m1	DMNH 644	DMNH Velvet Room	1	4	Mixed
DMNH	37402	*Lemmiscus*	(4T)	Left	m1	DMNH 644	DMNH Velvet Room	2	4	Mixed
DMNH	37413	*Lemmiscus*	(4T)	Left	m1	DMNH 644	DMNH Velvet Room	4	4	Mixed
DMNH	37609	*Lemmiscus*	(4T)	Right	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	Mixed	28	Mixed
DMNH	38353	*Lemmiscus*	(4T)	Left	m1	DMNH 644	DMNH Velvet Room	Mixed	27	Mixed
DMNH	11205	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	8	1	A
DMNH	15067	*Lemmiscus*	*curtatus*	Left	Dentary fragment with i1, m1	DMNH 644	DMNH Velvet Room	16	1	A
DMNH	37445	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	8 or 8A	2	A
DMNH	37446	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	8 or 8A	2	A
DMNH	37447	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	8 or 8A	2	A
DMNH	37448	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	8 or 8A	2	A
DMNH	37449	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	2	A
DMNH	37450	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	2	A
DMNH	37451	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	2	A
DMNH	37452	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	2	A
DMNH	37474	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	11	2	A
DMNH	37475	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	11	2	A
DMNH	37476	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	11	2	A
DMNH	37544	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	15	1	A
DMNH	37576	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	1	A
DMNH	44667	*Lemmiscus*	sp.	Right	M2	DMNH 644	DMNH Velvet Room	7	2	A
DMNH	44668	*Lemmiscus*	sp.	Right	M3	DMNH 644	DMNH Velvet Room	7	2	A
DMNH	44669	*Lemmiscus*	sp.	Right	M3	DMNH 644	DMNH Velvet Room	7	2	A
DMNH	44671	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	7	2	A
DMNH	37431	cf. *Lemmiscus*	sp.	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	7	2	A
DMNH	10641	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	6	3	B
DMNH	10691	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	6	4	B
DMNH	11779	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	4	B
DMNH	11780	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	4	B
DMNH	12246	*Lemmiscus*	*curtatus*	Right	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	17	4	B
DMNH	37434	*Lemmiscus*	*curtatus*	Left	m1 (partially digested)	DMNH 644	DMNH Velvet Room	7	3	B
DMNH	37435	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	7	3	B
DMNH	37436	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	7	3	B
DMNH	37437	*Lemmiscus*	*curtatus*	Left	m1 (juvenile)	DMNH 644	DMNH Velvet Room	7	3	B
DMNH	37438	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	7	3	B
DMNH	37439	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	7	5	B
DMNH	37440	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	7	5	B
DMNH	37453	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	8 or 8A	3	B
DMNH	37454	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	8 or 8A	3	B
DMNH	37455	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	3	B
DMNH	37456	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	3	B
DMNH	37457	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	8 or 8A	4	B
DMNH	37469	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	10	3	B
DMNH	37470	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	10	3	B
DMNH	37479	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	37480	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	37516	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	12	3	B
DMNH	37517	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	12	4	B
DMNH	37518	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	12	4	B
DMNH	37531	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	13 or 14	2	B
DMNH	37548	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37549	*Lemmiscus*	*curtatus*	Left	Dentary fragment with i1, m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37550	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37551	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37552	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37553	*Lemmiscus*	*curtatus*	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37554	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37555	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37556	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37603	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	25	2	B

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37604	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	25	2	B
DMNH	37607	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1	DMNH 644	DMNH Velvet Room	26	2	B
DMNH	38316	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38317	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38318	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38319	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38320	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38321	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38322	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38323	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38324	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38325	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38326	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38327	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38328	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	38329	*Lemmiscus*	*curtatus*	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	16	3	B
DMNH	38330	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	3	B
DMNH	38331	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	3	B
DMNH	38333	*Lemmiscus*	*curtatus*	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	16	4	B
DMNH	38334	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	16	4	B
DMNH	38335	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	16	4	B
DMNH	38336	*Lemmiscus*	*curtatus*	Right	m1 (partially digested)	DMNH 644	DMNH Velvet Room	16	4	B
DMNH	44674	*Lemmiscus*	sp.	Left	M2	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	44675	*Lemmiscus*	sp.	Right	M2	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	44676	*Lemmiscus*	sp.	Left	M3	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	44677	*Lemmiscus*	sp.	Left	M3	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	44678	*Lemmiscus*	sp.	Left	M3	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	44679	*Lemmiscus*	sp.	Right	M3	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	37482	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37483	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37484	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37485	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37486	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37487	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37488	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37489	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37490	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37520	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	12	5	B or C
DMNH	37521	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1	DMNH 644	DMNH Velvet Room	12	5	B or C
DMNH	37522	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	12	5	B or C
DMNH	44680	*Lemmiscus*	sp.	Left	M2	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	44681	*Lemmiscus*	sp.	Right	M2	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37441	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	7	6	C
DMNH	37442	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	7	6	C
DMNH	37524	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	12	6	C
DMNH	37589	*Lemmiscus*	*curtatus*	Right	Dentary fragment with i1, m1-2 (juvenile)	DMNH 644	DMNH Velvet Room	20	3	C
DMNH	37590	*Lemmiscus*	*curtatus*	Right	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	20	3	C
DMNH	10758	*Lemmiscus*	*curtatus*	Right	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	6	11	D
DMNH	37539	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	13 or 14	8	D or E
DMNH	11831	*Lemmiscus*	*curtatus*	Right	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	8 or 8A	13A	E
DMNH	37577	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	16	9	E
DMNH	44682	*Lemmiscus*	sp.	Left	M2	DMNH 644	DMNH Velvet Room	11	9	E
DMNH	37562	*Lemmiscus*	*curtatus*	Left	m1 (juvenile)	DMNH 644	DMNH Velvet Room	15	10A	E or F
DMNH	37429	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	6	15	F
DMNH	37497	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37578	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1 (juvenile)	DMNH 644	DMNH Velvet Room	16	11A	F
DMNH	37594	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	21	11	F
DMNH	38341	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	16	14	G
DMNH	10846	*Lemmiscus*	*curtatus*	Right	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	6 or 7	21	H
DMNH	10885	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	7	below 23	H

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	12245	*Lemmiscus*	*curtatus*	Left	Dentary fragment with i1, m1	DMNH 644	DMNH Velvet Room	7	below 23	H
DMNH	6672	*Lemmiscus*	*curtatus*	Right	Dentary with m1-3	DMNH 644	DMNH Velvet Room	1	9	Mixed
DMNH	9633	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	3	4	Mixed
DMNH	10282	*Lemmiscus*	*curtatus*	Right	Dentary fragment with i1, m1	DMNH 644	DMNH Velvet Room	5	7	Mixed
DMNH	10534	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	5	4	Mixed
DMNH	10598	*Lemmiscus*	*curtatus*	Right	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	5	Mixed	Mixed
DMNH	14980	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	2	Mixed
DMNH	14982	*Lemmiscus*	*curtatus*	Right	m1 (partially digested)	DMNH 644	DMNH Velvet Room	1	4	Mixed
DMNH	37354	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	2	Mixed
DMNH	37355	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	2	Mixed
DMNH	37356	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	2	Mixed
DMNH	37357	*Lemmiscus*	*curtatus*	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	1	3	Mixed
DMNH	37358	*Lemmiscus*	*curtatus*	Right	m1 (juvenile)	DMNH 644	DMNH Velvet Room	1	3	Mixed
DMNH	37359	*Lemmiscus*	*curtatus*	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	1	3	Mixed
DMNH	37361	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	5	Mixed
DMNH	37362	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	5	Mixed
DMNH	37363	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	5	Mixed
DMNH	37364	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	5	Mixed
DMNH	37365	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	6	Mixed
DMNH	37366	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	6	Mixed
DMNH	37372	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	8	Mixed
DMNH	37373	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	8	Mixed
DMNH	37374	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	8	Mixed
DMNH	37375	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	8	Mixed
DMNH	37376	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	8	Mixed
DMNH	37377	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	8	Mixed
DMNH	37384	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	9	Mixed
DMNH	37385	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	9	Mixed
DMNH	37386	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37387	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37388	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37389	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37390	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37391	*Lemmiscus*	*curtatus*	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37392	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37393	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37394	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37403	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	4	2	Mixed
DMNH	37409	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	4	3	Mixed
DMNH	37410	*Lemmiscus*	*curtatus*	Left	m1 (partially digested)	DMNH 644	DMNH Velvet Room	4	3	Mixed
DMNH	37411	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	4	3	Mixed
DMNH	37412	*Lemmiscus*	*curtatus*	Right	m1 (juvenile)	DMNH 644	DMNH Velvet Room	4	3	Mixed
DMNH	37414	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	4	4	Mixed
DMNH	37415	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	4	4	Mixed
DMNH	37416	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	4	4	Mixed
DMNH	37417	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	4	4	Mixed
DMNH	37418	*Lemmiscus*	*curtatus*	Left	m1	DMNH 644	DMNH Velvet Room	4	4	Mixed
DMNH	37419	*Lemmiscus*	*curtatus*	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	4	4	Mixed
DMNH	37420	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room		Mixed	
DMNH	37421	*Lemmiscus*	*curtatus*	Right	m1	DMNH 644	DMNH Velvet Room	4	4	Mixed
DMNH	37460	*Lemmiscus*	*curtatus*	Right	Dentary fragment with i1, m1	DMNH 644	DMNH Velvet Room	8 or 8A	Mixed	Mixed
DMNH	44672	*Lemmiscus*	*curtatus*	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	11	2	Mixed
DMNH	44659	*Lemmiscus*	sp.	Left	M2	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	44660	*Lemmiscus*	sp.	Left	M2	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	44661	*Lemmiscus*	sp.	Left	M2	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	44662	*Lemmiscus*	sp.	Right	M2	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	44663	*Lemmiscus*	sp.	Right	M2	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	44664	*Lemmiscus*	sp.	Left	M3	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	44665	*Lemmiscus*	sp.	Left	M3	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	44666	*Lemmiscus*	sp.	Right	M3	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	44673	*Lemmiscus*	sp.	Right	M3	DMNH 644	DMNH Velvet Room	11	2	Mixed
DMNH	44700	*Lemmiscus*	sp.	Left	M3	DMNH 644	DMNH Velvet Room	(0–4, 0–5)	32	Mixed
DMNH	12244	*Microtus*	*meadensis*	Left	Dentary fragment with i1, m1	DMNH 644	DMNH Velvet Room	7	23	Below H

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37464	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	9	6	C
DMNH	37465	*Microtus*	*meadensis*	Right	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	9	6	C
DMNH	37466	*Microtus*	*meadensis*	Right	m1 (partially digested)	DMNH 644	DMNH Velvet Room	9	6	C
DMNH	37523	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	12	6	C
DMNH	37533	*Microtus*	*meadensis*	Left	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	13 or 14	6	C
DMNH	37534	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	13 or 14	6	C
DMNH	37535	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	13 or 14	6	C
DMNH	37587	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	20	3	C
DMNH	37588	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	20	3	C
DMNH	37606	*Microtus*	*meadensis*	Left	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	25	7A	C
DMNH	37557	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	15	7A	C or D
DMNH	37558	*Microtus*	*meadensis*	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	15	7– 8	C or D
DMNH	10742	*Microtus*	*meadensis*	Left	Dentary with m1, m3	DMNH 644	DMNH Velvet Room	6	10	D
DMNH	10870	*Microtus*	*meadensis*	Right	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	7	12	D
DMNH	10881	*Microtus*	*meadensis*	Left	Dentary with i1, m1	DMNH 644	DMNH Velvet Room	7	14	D
DMNH	37424	*Microtus*	*meadensis*	Right	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	6	9	D
DMNH	37467	*Microtus*	*meadensis*	Left	m1 (juvenile)	DMNH 644	DMNH Velvet Room	9	8	D
DMNH	37525	*Microtus*	*meadensis*	Left	Dentary with i1, m1	DMNH 644	DMNH Velvet Room	12	7	D
DMNH	37527	*Microtus*	*meadensis*	Right	Dentary with m1-2	DMNH 644	DMNH Velvet Room	12	8	D
DMNH	38338	*Microtus*	*meadensis*	Right	Dentary fragment with i1, m1	DMNH 644	DMNH Velvet Room	16	7	D
DMNH	37538	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	13 or 14	8	D or E
DMNH	12006	*Microtus*	*meadensis*	Left	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	16	10	E
DMNH	37459	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	14	E
DMNH	37492	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	11	8	E
DMNH	37493	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	11	9	E
DMNH	37494	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	11	9	E
DMNH	37495	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	11	9	E
DMNH	37559	*Microtus*	*meadensis*	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	15	8A	E
DMNH	37560	*Microtus*	*meadensis*	Left	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	15	8	E
DMNH	37496	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	11	10	E or F
DMNH	37528	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	12	11	E or F
DMNH	37540	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	13 or 14	10A	E or F
DMNH	10972	*Microtus*	*meadensis*	Left	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	7	18	F
DMNH	37502	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37503	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37504	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37505	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37506	*Microtus*	*meadensis*	Right	m1 (partially digested)	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37507	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	11	12	F
DMNH	37530	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	13	12	F
DMNH	37579	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	16	12	F
DMNH	37585	*Microtus*	*meadensis*	Right	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	17	12	F
DMNH	38346	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	17	12	F
DMNH	10757	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	Mixed		Mixed
DMNH	37422	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	4	11	Mixed
DMNH	37430	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	6	Mixed	Mixed
DMNH	37461	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	8 or 8A	Mixed	Mixed
DMNH	37608	*Microtus*	*meadensis*	Left	m1	DMNH 644	DMNH Velvet Room	Mixed	28	Mixed
DMNH	37615	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	Mixed		Mixed
DMNH	38354	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	Mixed	27	Mixed
DMNH	38355	*Microtus*	*meadensis*	Right	m1	DMNH 644	DMNH Velvet Room	Mixed	27	Mixed
DMNH	37458	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	8 or 8A	5	B
DMNH	37602	*Microtus*	*paroperarius*	Left	Dentary fragment with i1, m1-3	DMNH 644	DMNH Velvet Room	25	2	B
DMNH	37598	*Microtus*	*paroperarius*	Right	Dentary with m1	DMNH 644	DMNH Velvet Room	21	17	Below I
DMNH	37600	*Microtus*	*paroperarius*	Right	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	21	18	Below I
DMNH	37462	*Microtus*	*paroperarius*	Right	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	9	6	C
DMNH	37425	*Microtus*	*paroperarius*	Right	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	6	9	D
DMNH	37561	*Microtus*	*paroperarius*	Left	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	15	8	E
DMNH	37529	*Microtus*	*paroperarius*	Right	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	12	12	F
DMNH	37586	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	17	16	G
DMNH	37595	*Microtus*	*paroperarius*	Left	Dentary with i1, m1	DMNH 644	DMNH Velvet Room	21	12	G
DMNH	37443	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	7	20	H

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37471	*Microtus*	*paroperarius*	Left	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	10	23	H
DMNH	37508	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	11	16	H
DMNH	37543	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	14	10G	H
DMNH	37566	*Microtus*	*paroperarius*	Left	m1	DMNH 644	DMNH Velvet Room	15	10E	H
DMNH	37567	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	15	10E	H
DMNH	37569	*Microtus*	*paroperarius*	Left	m1	DMNH 644	DMNH Velvet Room	15	10G	H
DMNH	37570	*Microtus*	*paroperarius*	Right	m1 (partially digested)	DMNH 644	DMNH Velvet Room	15	10G	H
DMNH	37571	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	15	10G	H
DMNH	37572	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	15	10G	H
DMNH	37575	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	15	10G	H
DMNH	37582	*Microtus*	*paroperarius*	Right	m1 (juvenile)	DMNH 644	DMNH Velvet Room	16	18	H
DMNH	37542	*Microtus*	*paroperarius*	Left	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	14	10H	I
DMNH	38345	*Microtus*	*paroperarius*	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	16	19	I
DMNH	11845	*Microtus*	*paroperarius*	Left	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	Mixed		Mixed
DMNH	14810	*Microtus*	*paroperarius*		2 m1s (missing)	DMNH 644	DMNH Velvet Room	1	2	Mixed
DMNH	37395	*Microtus*	*paroperarius*	Right	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37614	*Microtus*	*paroperarius*	Right	Dentary fragment with i1, m1	DMNH 644	DMNH Velvet Room	Mixed		Mixed
DMNH	37432	*Microtus*	5T	Left	m1 (juvenile)	DMNH 644	DMNH Velvet Room	7	2	A
DMNH	37473	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	11	2	A
DMNH	37433	*Microtus*	5T	Left	m1 (juvenile)	DMNH 644	DMNH Velvet Room	7	3	B
DMNH	37468	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	10	3	B
DMNH	37477	*Microtus*	5T	Left	m1 (juvenile)	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	37478	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	11	3	B
DMNH	37515	*Microtus*	5T	Left	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	12	2	B
DMNH	37545	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37546	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	37547	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	15	2	B
DMNH	38332	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	16	3	B
DMNH	37481	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	37519	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	12	5	B or C
DMNH	37532	*Microtus*	5T	Left	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	13 or 14	3	B or C
DMNH	37463	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	9	6	C
DMNH	37536	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	13 or 14	6	C
DMNH	37605	*Microtus*	5T	Left	Dentary with i1, m1-2	DMNH 644	DMNH Velvet Room	25	7A	C
DMNH	10741	*Microtus*	5T	Right	Dentary with m1-2	DMNH 644	DMNH Velvet Room	6	10	D
DMNH	37526	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	12	8	D
DMNH	38337	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	16	6	D
DMNH	38339	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	16	8	D
DMNH	38340	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	16	8	D
DMNH	37592	*Microtus*	5T	Left	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	21	7B	E
DMNH	37427	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	6	15	F
DMNH	37428	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	6	15	F
DMNH	9628	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	3	1	Mixed
DMNH	9920	*Microtus*	5T	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	5	10	Mixed
DMNH	10497	*Microtus*	5T	Right	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	5	12	Mixed
DMNH	11846	*Microtus*	5T	Left	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	8 or 8A	Mixed	Mixed
DMNH	14816	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	1	3	Mixed
DMNH	14979	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	1	1	Mixed
DMNH	37350	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	1	1	Mixed
DMNH	37351	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	1	2	Mixed
DMNH	37352	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	1	2	Mixed
DMNH	37353	*Microtus*	5T	Left	m1 (juvenile)	DMNH 644	DMNH Velvet Room	1	2	Mixed
DMNH	37367	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	1	7	Mixed
DMNH	37368	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	1	7	Mixed
DMNH	37369	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	1	7	Mixed
DMNH	37371	*Microtus*	5T	Left	m1 (partially digested)	DMNH 644	DMNH Velvet Room	1	8	Mixed
DMNH	37378	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	1	9	Mixed
DMNH	37379	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	1	9	Mixed
DMNH	37380	*Microtus*	5T	Left	m1 (juvenile)	DMNH 644	DMNH Velvet Room	1	9	Mixed
DMNH	37381	*Microtus*	5T	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	1	9	Mixed
DMNH	37382	*Microtus*	5T	Right	m1 (partially digested)	DMNH 644	DMNH Velvet Room	1	9	Mixed
DMNH	37383	*Microtus*	5T	Right	m1 (partially digested)	DMNH 644	DMNH Velvet Room	1	9	Mixed

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37396	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37397	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37398	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37399	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37400	*Microtus*	5T	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37404	*Microtus*	5T	Left	m1	DMNH 644	DMNH Velvet Room	4	3	Mixed
DMNH	37405	*Microtus*	5T	Left	m1 (juvenile)	DMNH 644	DMNH Velvet Room	4	3	Mixed
DMNH	37406	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	4	3	Mixed
DMNH	37407	*Microtus*	5T	Right	m1	DMNH 644	DMNH Velvet Room	4	3	Mixed
DMNH	37408	*Microtus*	5T	Right	m1 (juvenile)	DMNH 644	DMNH Velvet Room	4	3	Mixed
DMNH	38350	*Microtus*	5T	Right	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	Mixed	27	Mixed
DMNH	38357	*Microtus*	5T	Right	m1 (juvenile)	DMNH 644	DMNH Velvet Room	Mixed		Mixed
DMNH	37370	cf. *Microtus*	sp.	Left	m1 (partially digested)	DMNH 644	DMNH Velvet Room	1	7	Mixed
DMNH	37596	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 644	DMNH Velvet Room	21	17	Below I
DMNH	37597	*Mictomys*	*kansasensis/meltoni*	Right	Dentary with m1-2	DMNH 644	DMNH Velvet Room	21	17	Below I
DMNH	37601	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	21	20	Below I
DMNH	37426	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	6	10	D
DMNH	37537	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	13 or 14	8	D or E
DMNH	37563	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	DMNH 644	DMNH Velvet Room	15	10A	E or F
DMNH	37498	*Mictomys*	*kansasensis/meltoni*	Left	Dentary with m1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37499	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37500	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37501	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	37541	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 644	DMNH Velvet Room	13 or 14	10B	F
DMNH	37565	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	15	10C	F
DMNH	37580	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 644	DMNH Velvet Room	16	12	F
DMNH	37593	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	21	11	F
DMNH	37444	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	7	21	H
DMNH	37568	*Mictomys*	*kansasensis/meltoni*	Left	m1-2	DMNH 644	DMNH Velvet Room	15	10G	H
DMNH	37583	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 644	DMNH Velvet Room	16	18	H
DMNH	38343	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 644	DMNH Velvet Room	16	17	H
DMNH	37510	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with i1, m1-2	DMNH 644	DMNH Velvet Room	11	17	H or I
DMNH	37511	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	11	17	H or I
DMNH	38349	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 644	DMNH Velvet Room	20	15	H or I
DMNH	38344	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	16	19	I
DMNH	37611	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1	DMNH 644	DMNH Velvet Room	Mixed	31	Mixed
DMNH	37613	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	Mixed	31	Mixed
DMNH	38356	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room	Mixed	28	Mixed
DMNH	44683	*Mictomys*	sp.	Left	M1	DMNH 644	DMNH Velvet Room	11	9	E
DMNH	44684	*Mictomys*	sp.	Right	M1	DMNH 644	DMNH Velvet Room	11	9	E
DMNH	44685	*Mictomys*	sp.	Right	M3	DMNH 644	DMNH Velvet Room	11	9	E
DMNH	44686	*Mictomys*	sp.	Left	M1	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	44687	*Mictomys*	sp.	Left	M2	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	44688	*Mictomys*	sp.	Right	M3	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	44689	*Mictomys*	sp.	Left	m2	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	44690	*Mictomys*	sp.	Left	m3	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	44691	*Mictomys*	sp.	Left	m3	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	44692	*Mictomys*	sp.	Left	m3	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	44693	*Mictomys*	sp.	Right	m3	DMNH 644	DMNH Velvet Room	11	11	F
DMNH	44694	*Mictomys*	sp.	Right	M3 (broken)	DMNH 644	DMNH Velvet Room	11	12	F
DMNH	44695	*Mictomys*	sp.	Left	m2	DMNH 644	DMNH Velvet Room	11	12	F
DMNH	38348	*Mictomys*	sp.	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	17	18	H
DMNH	44670	*Mictomys*	sp.	Left	Dentary with i1, m3	DMNH 644	DMNH Velvet Room	10	26	H or I
DMNH	44696	*Mictomys*	sp.	Left	m3	DMNH 644	DMNH Velvet Room	11	17	H or I
DMNH	44697	*Mictomys*	sp.	Left	m3	DMNH 644	DMNH Velvet Room	11	18	I or J
DMNH	44705	*Mictomys*	sp.	Left	M3	DMNH 644	DMNH Velvet Room	Mixed	Mixed	Mixed
DMNH	44707	*Mictomys*	sp.	Right	m1 fragment	DMNH 644	DMNH Velvet Room	(0–5, 0–6)	30	Mixed
DMNH	44708	*Mictomys*	sp.	Right	M1	DMNH 644	DMNH Velvet Room	(0–5, 0–6)	30	Mixed
DMNH	44710	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 644	DMNH Velvet Room	(0–4, 0–3)	?	Mixed

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	44713	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 644	DMNH Velvet Room	(0–4, 0–3)	?	Mixed
DMNH	37612	*Mimomys*	*virginianus*	Left	m1	DMNH 644	DMNH Velvet Room	Mixed	31	Mixed
DMNH	38351	*Mimomys*	*virginianus*	Right	Dentary with m1-3	DMNH 644	DMNH Velvet Room	Mixed	27	Mixed
DMNH	44699	*Mimomys*	*virginianus*	Left	M2	DMNH 644	DMNH Velvet Room	(0–4, 0–5)	32	Mixed
DMNH	44701	*Mimomys*	*virginianus*	Right	M2	DMNH 644	DMNH Velvet Room	(0–4, 0–5)	32	Mixed
DMNH	44711	*Mimomys*	*virginianus*	Left	m1	DMNH 644	DMNH Velvet Room	(0–4, 0–3)	?	Mixed
DMNH	44712	*Mimomys*	*virginianus*	Left	m1	DMNH 644	DMNH Velvet Room	(0–4, 0–3)	?	Mixed
DMNH	37514	*Ondatra*	sp.	Left	Dentary fragment with m1-2	DMNH 644	DMNH Velvet Room		>8	Mixed
DMNH	44703	*Phenacomys*	*gryci*	Left	Dentary with i1, m1	DMNH 644	DMNH Velvet Room	(0–6, 0–5)	29	Mixed
DMNH	15069	*Phenacomys*	sp.	Left	Dentary with m1-2	DMNH 644	DMNH Velvet Room	16	2	B
DMNH	12242	*Phenacomys*	sp.	Left	Dentary with i1, m1-3	DMNH 644	DMNH Velvet Room	12	5	B or C
DMNH	37581	*Phenacomys*	sp.	Left	m1	DMNH 644	DMNH Velvet Room	16	16	G
DMNH	14817	*Phenacomys*	sp.	Right	m1	DMNH 644	DMNH Velvet Room	1	4	Mixed
DMNH	37401	*Phenacomys*	sp.	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	1	10	Mixed
DMNH	37423	*Phenacomys*	sp.	Right	m1 (broken)	DMNH 644	DMNH Velvet Room	5	26 mix	Mixed
DMNH	44698	*Phenacomys*	sp.	Left	M3	DMNH 644	DMNH Velvet Room	(0–5, 6–7)	31	Mixed
DMNH	44706	*Phenacomys*	sp.	Right	M2	DMNH 644	DMNH Velvet Room	(0–5, 0–6)	30	Mixed
DMNH	37491	indeterminate	indeterminate	Left	m1 fragment	DMNH 644	DMNH Velvet Room	11	4	B or C
DMNH	38268	*Lemmiscus*	(4T)	Left	Dentary fragment with m1	DMNH 1342	Ferret Room			
DMNH	38267	*Mictomys*	*vetus/landesi*	Left	Dentary fragment with m1	DMNH 1342	Ferret Room			
DMNH	38266	*Phenacomys*	*gryci*	Left	Dentary fragment with i1, m1	DMNH 1342	Ferret Room			
UCMP	213031	*Allophaiomys*	*pliocaenicus*	Left	m1	V98022	Fissure Fill A			
UCMP	213032	*Allophaiomys*	*pliocaenicus*	Left	m1	V98022	Fissure Fill A			
UCMP	213033	*Allophaiomys*	*pliocaenicus*	Left	m1	V98022	Fissure Fill A			
UCMP	213034	*Allophaiomys*	*pliocaenicus*	Right	m1	V98022	Fissure Fill A			
UCMP	213035	*Allophaiomys*	*pliocaenicus*	Right	m1 (broken)	V98022	Fissure Fill A			
UCMP	213018	*Microtus*	*paroperarius*	Right	m1	V98022	Fissure Fill A			
UCMP	213019	*Mictomys*	*kansasensis/meltoni*	Left	m1	V98022	Fissure Fill A			
UCMP	213020	*Mictomys*	*kansasensis/meltoni*	Left	m1	V98022	Fissure Fill A			
UCMP	213021	*Mictomys*	*kansasensis/meltoni*	Left	m1	V98022	Fissure Fill A			
UCMP	213022	*Mictomys*	*kansasensis/meltoni*	Left	m1	V98022	Fissure Fill A			
UCMP	213023	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V98022	Fissure Fill A			
UCMP	213024	*Mictomys*	*kansasensis/meltoni*	Left	m1	V98022	Fissure Fill A			
UCMP	213025	*Mictomys*	*kansasensis/meltoni*	Left	m1	V98022	Fissure Fill A			
UCMP	213026	*Mictomys*	*kansasensis/meltoni*	Right	m1	V98022	Fissure Fill A			
UCMP	213027	*Mictomys*	*kansasensis/meltoni*	Right	m1	V98022	Fissure Fill A			
UCMP	213028	*Mictomys*	*kansasensis/meltoni*	Right	m1	V98022	Fissure Fill A			
UCMP	213029	*Mictomys*	*kansasensis/meltoni*	Right	m1	V98022	Fissure Fill A			
UCMP	213030	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V98022	Fissure Fill A			
UCMP	213036	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V98022	Fissure Fill A			
UCMP	213327	*Mictomys*	sp.	Right	M3	V98022	Fissure Fill A			
UCMP	213328	*Mictomys*	sp.	Right	M3	V98022	Fissure Fill A			
UCMP	213329	*Mictomys*	sp.	Right	M3	V98022	Fissure Fill A			
UCMP	213348	*Mictomys*	sp.	Right	M3	V98022	Fissure Fill A			
UCMP	399910	*Mictomys*	sp.	Left	M1 (partially digested)	V98022	Fissure Fill A			
UCMP	399911	*Mictomys*	sp.	Right	M1	V98022	Fissure Fill A			
UCMP	399912	*Mictomys*	sp.	Right	M1	V98022	Fissure Fill A			
UCMP	399913	*Mictomys*	sp.	Right	M1	V98022	Fissure Fill A			
UCMP	399914	*Mictomys*	sp.	Right	M1	V98022	Fissure Fill A			
UCMP	399915	*Mictomys*	sp.	Right	M1	V98022	Fissure Fill A			
UCMP	399916	*Mictomys*	sp.	Right	M1	V98022	Fissure Fill A			
UCMP	399917	*Mictomys*	sp.	Right	M1	V98022	Fissure Fill A			
UCMP	399918	*Mictomys*	sp.	Left	M1	V98022	Fissure Fill A			
UCMP	399919	*Mictomys*	sp.	Right	M1	V98022	Fissure Fill A			
UCMP	399920	*Mictomys*	sp.	Right	M2	V98022	Fissure Fill A			
UCMP	399921	*Mictomys*	sp.	Left	m3	V98022	Fissure Fill A			
UCMP	399922	*Mictomys*	sp.	Right	m2	V98022	Fissure Fill A			

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	399923	*Mictomys*	sp.	Left	m2	V98022	Fissure Fill A			
UCMP	399924	*Mictomys*	sp.	Left	m2	V98022	Fissure Fill A			
UCMP	399925	*Mictomys*	sp.	Left	M3	V98022	Fissure Fill A			
UCMP	399926	*Mictomys*	sp.	Left	M2	V98022	Fissure Fill A			
UCMP	399927	*Mictomys*	sp.	Left	M2	V98022	Fissure Fill A			
UCMP	399928	*Mictomys*	sp.	Left	M2	V98022	Fissure Fill A			
UCMP	399929	*Mictomys*	sp.	Left	M2	V98022	Fissure Fill A			
UCMP	399930	*Mictomys*	sp.	Right	M2	V98022	Fissure Fill A			
UCMP	399931	*Mictomys*	sp.	Right	M2	V98022	Fissure Fill A			
UCMP	399932	*Mictomys*	sp.	Right	M2	V98022	Fissure Fill A			
UCMP	399933	*Mictomys*	sp.	Right	M2	V98022	Fissure Fill A			
UCMP	213011	*Mimomys*	*virginianus*	Left	m1	V98022	Fissure Fill A			
UCMP	213012	*Mimomys*	*virginianus*	Left	m1	V98022	Fissure Fill A			
UCMP	213013	*Mimomys*	*virginianus*	Right	m1 (broken)	V98022	Fissure Fill A			
UCMP	213014	*Mimomys*	*virginianus*	Right	m1	V98022	Fissure Fill A			
UCMP	213015	*Mimomys*	*virginianus*	Right	m1 (broken)	V98022	Fissure Fill A			
UCMP	399896	*Mimomys*	*virginianus*	Left	m1 (broken)	V98022	Fissure Fill A			
UCMP	213346	*Mimomys*	*virginianus*	Left	m3	V98022	Fissure Fill A			
UCMP	213347	*Mimomys*	*virginianus*	Right	m2	V98022	Fissure Fill A			
UCMP	399895	*Mimomys*	*virginianus*	Left	m2	V98022	Fissure Fill A			
UCMP	399934	*Mimomys*	*virginianus*	Left	M2	V98022	Fissure Fill A			
UCMP	399935	*Mimomys*	*virginianus*	Left	M2	V98022	Fissure Fill A			
UCMP	399936	*Mimomys*	*virginianus*	Left	M2	V98022	Fissure Fill A			
UCMP	213330	*Ondatra*	sp.	Right	m1 (broken)	V98022	Fissure Fill A			
UCMP	213017	*Phenacomys*	*gryci*	Right	m1	V98022	Fissure Fill A			
UCMP	213016	*Phenacomys*	sp.	Left	m1 (broken)	V98022	Fissure Fill A			
UCMP	213349	*Phenacomys*	sp.	Left	M2	V98022	Fissure Fill A			
UCMP	213350	*Phenacomys*	sp.	Left	m2	V98022	Fissure Fill A			
UCMP	399937	*Phenacomys*	sp.	Right	M2	V98022	Fissure Fill A			
UCMP	399938	*Phenacomys*	sp.	Left	M3	V98022	Fissure Fill A			
DMNH	44655	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1347	Generator Dome			
DMNH	44656	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1347	Generator Dome			
DMNH	44657	*Allophaiomys*	*pliocaenicus*	Right	m1 (juvenile)	DMNH 1347	Generator Dome			
DMNH	44658	*Mictomys*	sp.	Right	m1 (broken)	DMNH 1347	Generator Dome			
DMNH	44652	*Mimomys*	*virginianus*	Left	m1 (partially digested)	DMNH 1347	Generator Dome			
DMNH	44653	*Mimomys*	*virginianus*	Left	m1	DMNH 1347	Generator Dome			
DMNH	44654	*Mimomys*	*virginianus*	Left	m1 (partially digested)	DMNH 1347	Generator Dome			
DMNH	44651	*Phenacomys*	*gryci*	Right	m1	DMNH 1347	Generator Dome			
UCMP	212937	*Allophaiomys*	*pliocaenicus*	Left	m1	V93174	Gypsum Room	1	2	
UCMP	212935	*Allophaiomys*	*pliocaenicus*	Left	m1	V93174	Gypsum Room	1	4	
UCMP	212936	*Allophaiomys*	*pliocaenicus*	Left	m1	V93174	Gypsum Room	1	4	
UCMP	212938	*Allophaiomys*	*pliocaenicus*	Left	m1	V93174	Gypsum Room			
UCMP	212939	*Allophaiomys*	*pliocaenicus*	Right	m1	V93174	Gypsum Room			
CM	45475	*Lemmiscus*	(4T)	Left	m1	1926	Gypsum Room			
UCMP	212941	*Lemmiscus*	(4T)	Left	m1 (broken)	V93174	Gypsum Room	1	4	
UCMP	212942	*Lemmiscus*	(4T)	Left	m1 (broken)	V93174	Gypsum Room	1	4	
UCMP	212943	*Lemmiscus*	(4T)	Right	m1 (broken)	V93174	Gypsum Room	1	4	
UCMP	212977	*Lemmiscus*	(4T)	Right	m1	V93174	Gypsum Room	1	4	
UCMP	212940	*Lemmiscus*	cf. (4T)	Right	m1 fragment	V93174	Gypsum Room			
CM	45476	*Lemmiscus*	*curtatus*	Right	m1	1926	Gypsum Room			
UCMP	212944	*Lemmiscus*	*curtatus*	Left	m1	V93174	Gypsum Room			
UCMP	212945	*Lemmiscus*	*curtatus*	Right	m1	V93174	Gypsum Room			
UCMP	212946	*Lemmiscus*	*curtatus*	Left	m1	V93174	Gypsum Room			
UCMP	212978	*Lemmiscus*	sp.	Left	M1	V93174	Gypsum Room			
UCMP	212979	*Lemmiscus*	sp.	Right	M1	V93174	Gypsum Room			
UCMP	212980	*Lemmiscus*	sp.	Left	M2	V93174	Gypsum Room			
UCMP	212981	*Lemmiscus*	sp.	Left	M2	V93174	Gypsum Room			
UCMP	212982	*Lemmiscus*	sp.	Left	M2	V93174	Gypsum Room			
UCMP	212983	*Lemmiscus*	sp.	Right	M2	V93174	Gypsum Room			
UCMP	212984	*Lemmiscus*	sp.	Left	M3	V93174	Gypsum Room			
UCMP	212985	*Lemmiscus*	sp.	Right	M3	V93174	Gypsum Room			
UCMP	212986	*Lemmiscus*	sp.	Right	M3	V93174	Gypsum Room			
UCMP	212987	*Lemmiscus*	sp.	Right	M3	V93174	Gypsum Room	1	4	
CM	45424	*Microtus*	*meadensis*	Right	Dentary with m1-2	1926	Gypsum Room			
UCMP	155857	*Microtus*	*meadensis*	Right	m1	V93174	Gypsum Room			
UCMP	212952	*Microtus*	*meadensis*	Right	m1	V93174	Gypsum Room			
UCMP	212953	*Microtus*	*meadensis*	Right	m1	V93174	Gypsum Room			
UCMP	212954	*Microtus*	*meadensis*	Right	m1	V93174	Gypsum Room			

(continued)

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
UCMP	212955	*Microtus*	*meadensis*	Right	m1	V93174	Gypsum Room			
UCMP	212956	*Microtus*	*meadensis*	Left	m1	V93174	Gypsum Room			
UCMP	212957	*Microtus*	*meadensis*	Left	m1	V93174	Gypsum Room			
UCMP	212958	*Microtus*	*meadensis*	Left	m1	V93174	Gypsum Room			
UCMP	212959	*Microtus*	*meadensis*	Left	m1	V93174	Gypsum Room			
UCMP	212960	*Microtus*	*meadensis*	Right	m1 (broken)	V93174	Gypsum Room	1	4	
UCMP	212961	*Microtus*	*meadensis*	Right	Dentary with i1, m1-2	V93174	Gypsum Room	1	2	
CM	45500	*Microtus*	5T	Right	m1	1926	Gypsum Room			
UCMP	212962	*Microtus*	5T	Right	m1	V93174	Gypsum Room			
UCMP	212963	*Microtus*	5T	Left	m1	V93174	Gypsum Room			
UCMP	212964	*Microtus*	5T	Left	m1	V93174	Gypsum Room			
UCMP	212965	*Microtus*	5T	Left	m1	V93174	Gypsum Room			
UCMP	212966	*Microtus*	5T	Left	m1	V93174	Gypsum Room			
UCMP	212967	*Microtus*	5T	Left	m1	V93174	Gypsum Room			
UCMP	212968	*Microtus*	5T	Left	m1	V93174	Gypsum Room			
UCMP	212969	*Microtus*	5T	Left	m1	V93174	Gypsum Room	Surface	1	
UCMP	212947	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93174	Gypsum Room			
UCMP	212948	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93174	Gypsum Room			
UCMP	212949	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93174	Gypsum Room			
UCMP	212950	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93174	Gypsum Room	1	4	
UCMP	212951	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93174	Gypsum Room	1	4	
UCMP	212988	*Mictomys*	sp.	Left	M1	V93174	Gypsum Room	1	4	
UCMP	212989	*Mictomys*	sp.	Left	M1	V93174	Gypsum Room	1	4	
UCMP	212990	*Mictomys*	sp.	Left	M1	V93174	Gypsum Room			
UCMP	212991	*Mictomys*	sp.	Left	M1 (broken)	V93174	Gypsum Room			
UCMP	212992	*Mictomys*	sp.	Left	M1	V93174	Gypsum Room			
UCMP	212993	*Mictomys*	sp.	Right	M1	V93174	Gypsum Room	1	4	
UCMP	212994	*Mictomys*	sp.	Right	M1	V93174	Gypsum Room	1	4	
UCMP	212995	*Mictomys*	sp.	Right	M1	V93174	Gypsum Room	1	4	
UCMP	212996	*Mictomys*	sp.	Right	M1	V93174	Gypsum Room	1	4	
UCMP	212997	*Mictomys*	sp.	Left	M2	V93174	Gypsum Room			
UCMP	212998	*Mictomys*	sp.	Left	M2	V93174	Gypsum Room	1	4	
UCMP	212999	*Mictomys*	sp.	Right	M2	V93174	Gypsum Room			
UCMP	213000	*Mictomys*	sp.	Left	M3	V93174	Gypsum Room	1	4	
UCMP	213001	*Mictomys*	sp.	Left	M3	V93174	Gypsum Room	1	4	
UCMP	213002	*Mictomys*	sp.	Left	M3	V93174	Gypsum Room			
UCMP	213003	*Mictomys*	sp.	Left	M3	V93174	Gypsum Room			
UCMP	213004	*Mictomys*	sp.	Right	M3	V93174	Gypsum Room	1	4	
UCMP	213005	*Mictomys*	sp.	Left	m2	V93174	Gypsum Room	1	4	
UCMP	213006	*Mictomys*	sp.	Left	m2	V93174	Gypsum Room	1	4	
UCMP	213007	*Mictomys*	sp.	Left	m2	V93174	Gypsum Room			
UCMP	213008	*Mictomys*	sp.	Left	m2	V93174	Gypsum Room			
UCMP	213009	*Mictomys*	sp.	Right	m3	V93174	Gypsum Room	1	4	
UCMP	213010	*Mictomys*	sp.	Left	m3	V93174	Gypsum Room	1	4	
UCMP	213331	*Mictomys*	sp.	Right	m2	V93174	Gypsum Room	1	4	
UCMP	212933	*Mimomys*	*virginianus*	Left	m1	V93174	Gypsum Room			
UCMP	212934	*Mimomys*	*virginianus*	Left	m1	V93174	Gypsum Room			
UCMP	212931	*Phenacomys*	*gryci*	Left	m1	V93174	Gypsum Room	1	4	
UCMP	212932	*Phenacomys*	sp.	Left	m1 fragment	V93174	Gypsum Room	1	4	
UCMP	212970	*Phenacomys*	sp.	Left	m3	V93174	Gypsum Room	1	4	
UCMP	212971	*Phenacomys*	sp.	Left	m2	V93174	Gypsum Room	1	4	
UCMP	212972	*Phenacomys*	sp.	Right	m2	V93174	Gypsum Room	1	4	
UCMP	212973	*Phenacomys*	sp.	Left	M1	V93174	Gypsum Room			
UCMP	212974	*Phenacomys*	sp.	Right	M2	V93174	Gypsum Room	1	4	
UCMP	212975	*Phenacomys*	sp.	Right	M2	V93174	Gypsum Room			
UCMP	212976	*Phenacomys*	sp.	Left	M3	V93174	Gypsum Room	1	4	
CM	45501	Indeterminate	Indeterminate	Right	m1 (broken)	1926	Gypsum Room			
DMNH	38258	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Kate's Cupola			
DMNH	38257	*Microtus*	5T	Right	Dentary fragment with m1-2	DMNH 1349	Kate's Cupola			
DMNH	38259	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Kate's Cupola			
DMNH	38260	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Kate's Cupola			
DMNH	38261	*Mictomys*	*vetus/landesi*	Right	m1	DMNH 1349	Kate's Cupola			
DMNH	38262	*Mictomys*	*vetus/landesi*	Right	m1	DMNH 1349	Kate's Cupola			
DMNH	44650	*Mictomys*	sp.	Right	m1 (broken)	DMNH 1349	Kate's Cupola			
DMNH	38256	*Mimomys*	*virginianus*	Left	Dentary with i1, m1-2	DMNH 1349	Kate's Cupola			
DMNH	38263	*Ophiomys*	*parvus*	Left	m1	DMNH 1349	Kate's Cupola			
DMNH	38264	*Phenacomys*	sp. (not *P. gryci*)	Right	Dentary fragment with m1-2	DMNH 1349	Kate's Cupola			

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	38265	*Phenacomys*	sp. (not *P. gryci*)	Right	m1	DMNH 1349	Kate's Cupola			
DMNH	37630	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37648	*Allophaiomys*	*pliocaenicus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37658	*Allophaiomys*	*pliocaenicus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37725	*Allophaiomys*	*pliocaenicus*	Right	Dentary with m1-3	DMNH 1349	Mark's Sink			
DMNH	37740	*Allophaiomys*	*pliocaenicus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37754	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37755	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37756	*Allophaiomys*	*pliocaenicus*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37761	*Allophaiomys*	*pliocaenicus*	Right	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37769	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37782	*Allophaiomys*	*pliocaenicus*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37783	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37784	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37785	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37786	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37787	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37788	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37797	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37818	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37819	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37820	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37821	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37855	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37856	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37857	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37858	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37859	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37867	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37868	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37869	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37870	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37907	*Allophaiomys*	*pliocaenicus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37934	*Allophaiomys*	*pliocaenicus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37935	*Allophaiomys*	*pliocaenicus*	Left	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37936	*Allophaiomys*	*pliocaenicus*	Right	Dentary fragment with i1, m1	DMNH 1349	Mark's Sink			
DMNH	38031	*Allophaiomys*	*pliocaenicus*	Right	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	38061	*Allophaiomys*	*pliocaenicus*	Left	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	38062	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38063	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38064	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38065	*Allophaiomys*	*pliocaenicus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38066	*Allophaiomys*	*pliocaenicus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38242	*Allophaiomys*	*pliocaenicus*	Right	m1 (partially digested)	DMNH 1349	Mark's Sink			
DMNH	37619	*Lemmiscus*	(4T)	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37634	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37644	*Lemmiscus*	(4T)	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37647	*Lemmiscus*	(4T)	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37653	*Lemmiscus*	(4T)	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37666	*Lemmiscus*	(4T)	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37686	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37687	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			

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	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
DMNH	37689	*Lemmiscus*	(4T)	Right	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37696	*Lemmiscus*	(4T)	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37697	*Lemmiscus*	(4T)	Right	Dentary with i1, m1	DMNH 1349	Mark's Sink			
DMNH	37698	*Lemmiscus*	(4T)	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37711	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37719	*Lemmiscus*	(4T)	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37747	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37758	*Lemmiscus*	(4T)	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37759	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37762	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37816	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37817	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37854	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37908	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37979	*Lemmiscus*	(4T)	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37980	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37981	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37982	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37983	*Lemmiscus*	(4T)	Right	Dentary fragment with i1, m1	DMNH 1349	Mark's Sink			
DMNH	37984	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38036	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38074	*Lemmiscus*	(4T)	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38075	*Lemmiscus*	(4T)	Left	Dentary fragment with i1, m1	DMNH 1349	Mark's Sink			
DMNH	38076	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38077	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38078	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38079	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38080	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38081	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38239	*Lemmiscus*	(4T)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38244	*Lemmiscus*	(4T)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38245	*Lemmiscus*	(4T)	Right	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37616	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37643	*Lemmiscus*	*curtatus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37654	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37665	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37684	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37685	*Lemmiscus*	*curtatus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37757	*Lemmiscus*	*curtatus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37796	*Lemmiscus*	*curtatus*	Left	m1-2	DMNH 1349	Mark's Sink			
DMNH	37871	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37985	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37986	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37987	*Lemmiscus*	*curtatus*	Left	Dentary with m1-3	DMNH 1349	Mark's Sink			
DMNH	37988	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1	DMNH 1349	Mark's Sink			
DMNH	37989	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37990	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37991	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37992	*Lemmiscus*	*curtatus*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37993	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37994	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37995	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37996	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37997	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1	DMNH 1349	Mark's Sink			
DMNH	37998	*Lemmiscus*	*curtatus*	Right	m1-2	DMNH 1349	Mark's Sink			

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37999	*Lemmiscus*	*curtatus*	Right	m1-2	DMNH 1349	Mark's Sink			
DMNH	38000	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38001	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38002	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38003	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38004	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38005	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38006	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38007	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38008	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38037	*Lemmiscus*	*curtatus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38038	*Lemmiscus*	*curtatus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38039	*Lemmiscus*	*curtatus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38082	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	38083	*Lemmiscus*	*curtatus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38084	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38085	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38086	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38087	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38088	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38089	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38090	*Lemmiscus*	*curtatus*	Right	Dentary fragment with i1, m1	DMNH 1349	Mark's Sink			
DMNH	38091	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38092	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38093	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38249	*Lemmiscus*	*curtatus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38250	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1-2 (m1 broken)	DMNH 1349	Mark's Sink			
DMNH	38251	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38252	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38253	*Lemmiscus*	*curtatus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38254	*Lemmiscus*	*curtatus*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38255	*Lemmiscus*	*curtatus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38310	*Lemmiscus*	*curtatus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37623	*Microtus*	*meadensis*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37624	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37625	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37626	*Microtus*	*meadensis*	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37632	*Microtus*	*meadensis*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37640	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37641	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37642	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37649	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37650	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37663	*Microtus*	*meadensis*	Left	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	37664	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37673	*Microtus*	*meadensis*	Left	Dentary fragment with i1, m1	DMNH 1349	Mark's Sink			
DMNH	37674	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37676	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37690	*Microtus*	*meadensis*	Left	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37691	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37703	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37704	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37705	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			

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	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37706	*Microtus*	*meadensis*	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37715	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37728	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37729	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37730	*Microtus*	*meadensis*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37731	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37732	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37733	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37748	*Microtus*	*meadensis*	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37779	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37889	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37906	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38009	*Microtus*	*meadensis*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38010	*Microtus*	*meadensis*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38011	*Microtus*	*meadensis*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38012	*Microtus*	*meadensis*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38013	*Microtus*	*meadensis*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38014	*Microtus*	*meadensis*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38015	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38016	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38017	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38018	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38019	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38020	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38021	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38022	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38023	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38024	*Microtus*	*meadensis*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38025	*Microtus*	*meadensis*	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38026	*Microtus*	*meadensis*	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38027	*Microtus*	*meadensis*	Right	Dentary fragment with i1, m1	DMNH 1349	Mark's Sink			
DMNH	38028	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38029	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38030	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38094	*Microtus*	*meadensis*	Left	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	38095	*Microtus*	*meadensis*	Left	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	38096	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38097	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38098	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38099	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38100	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38101	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38102	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38103	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38104	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38105	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38106	*Microtus*	*meadensis*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38107	*Microtus*	*meadensis*	Left	m1 (partially digested)	DMNH 1349	Mark's Sink			
DMNH	38108	*Microtus*	*meadensis*	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	38109	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38110	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38111	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38112	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38113	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	38114	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38115	*Microtus*	*meadensis*	Right	m1 (juvenile)	DMNH 1349	Mark's Sink			
DMNH	38116	*Microtus*	*meadensis*	Right	m1 (partially digested)	DMNH 1349	Mark's Sink			
DMNH	38234	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38235	*Microtus*	*meadensis*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38236	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38246	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38247	*Microtus*	*meadensis*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38248	*Microtus*	*meadensis*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37618	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37627	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37655	*Microtus*	*paroperarius*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37668	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37679	*Microtus*	*paroperarius*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37693	*Microtus*	*paroperarius*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37708	*Microtus*	*paroperarius*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37709	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37710	*Microtus*	*paroperarius*	Right	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37734	*Microtus*	*paroperarius*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37942	*Microtus*	*paroperarius*	Left	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37943	*Microtus*	*paroperarius*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37944	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37945	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37946	*Microtus*	*paroperarius*	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37947	*Microtus*	*paroperarius*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37948	*Microtus*	*paroperarius*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38067	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38068	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38069	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38070	*Microtus*	*paroperarius*	Left	m1 (partially digested)	DMNH 1349	Mark's Sink			
DMNH	38071	*Microtus*	*paroperarius*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38072	*Microtus*	*paroperarius*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38073	*Microtus*	*paroperarius*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38232	*Microtus*	*paroperarius*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38233	*Microtus*	*paroperarius*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37617	*Microtus*	5T	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37620	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37621	*Microtus*	5T	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37622	*Microtus*	5T	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37628	*Microtus*	5T	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37638	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37639	*Microtus*	5T	Right	Dentary with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37646	*Microtus*	5T	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37656	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37659	*Microtus*	5T	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37660	*Microtus*	5T	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37661	*Microtus*	5T	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37662	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37680	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37681	*Microtus*	5T	Left	Dentary with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37682	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37683	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37694	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37695	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37707	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37717	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37718	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37726	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37727	*Microtus*	5T	Left	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37735	*Microtus*	5T	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37949	*Microtus*	5T	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37950	*Microtus*	5T	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37951	*Microtus*	5T	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37952	*Microtus*	5T	Left	i1, m1	DMNH 1349	Mark's Sink			
DMNH	37953	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37954	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37955	*Microtus*	5T	Right	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37956	*Microtus*	5T	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37957	*Microtus*	5T	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37958	*Microtus*	5T	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37959	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37960	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37961	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37962	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37963	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37964	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37965	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37966	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37967	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37968	*Microtus*	5T	Right	m1 (juvenile)	DMNH 1349	Mark's Sink			
DMNH	37969	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38033	*Microtus*	5T	Left	Dentary with i1, m1	DMNH 1349	Mark's Sink			
DMNH	38117	*Microtus*	5T	Left	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	38118	*Microtus*	5T	Left	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	38119	*Microtus*	5T	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	38120	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38121	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38122	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38123	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38124	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38125	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38126	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38127	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38128	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38129	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38130	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38131	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38132	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38133	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38134	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38135	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38136	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38240	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38241	*Microtus*	5T	Right	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38311	*Microtus*	5T	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38312	*Microtus*	5T	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37633	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37645	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37688	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37692	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37712	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37713	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37722	*Mictomys*	*kansasensis/meltoni*	Right	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37723	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37724	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37736	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37737	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	37738	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37751	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37752	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37753	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37764	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37765	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37766	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	37767	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37768	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37772	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37773	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37774	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37775	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37776	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37777	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37806	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37807	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37808	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37809	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37810	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37811	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37812	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37813	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37814	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37815	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37834	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37835	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37836	*Mictomys*	*kansasensis/meltoni*	Left	Dentary with m1-3	DMNH 1349	Mark's Sink			
DMNH	37837	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37838	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37839	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37840	*Mictomys*	*kansasensis/meltoni*	Left	m1 (partially digested)	DMNH 1349	Mark's Sink			
DMNH	37841	*Mictomys*	*kansasensis/meltoni*	Right	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37842	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37843	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37844	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37845	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37846	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37850	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37851	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37863	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37864	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37865	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37866	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37877	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37878	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37884	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37885	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37886	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37887	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37888	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37898	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37899	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37900	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37901	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37902	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37903	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37910	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37919	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37920	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37921	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37922	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37923	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37924	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37925	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37928	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37929	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37930	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37931	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37932	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37933	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38040	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38185	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38186	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38187	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38188	*Mictomys*	*kansasensis/meltoni*	Right	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	38189	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38190	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38191	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38192	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38193	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38194	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38195	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38196	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38197	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38198	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38199	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38200	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38201	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38202	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38203	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38204	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38205	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38206	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38207	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38208	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38209	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38210	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38211	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38212	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38213	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38214	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38215	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38216	*Mictomys*	*kansasensis/meltoni*	Left	m1 (partially digested)	DMNH 1349	Mark's Sink			
DMNH	38217	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38218	*Mictomys*	*kansasensis/meltoni*	Right	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	38219	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38220	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38221	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38222	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38223	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38224	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38225	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38226	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38227	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	38228	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38229	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38230	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38231	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38237	*Mictomys*	*kansasensis/meltoni*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38238	*Mictomys*	*kansasensis/meltoni*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38313	*Mictomys*	*kansasensis/meltoni*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37657	*Mictomys*	*vetus/landesi*	Right	Dentary with i1, m1, m3	DMNH 1349	Mark's Sink			
DMNH	37672	*Mictomys*	*vetus/landesi*	Right	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37700	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37739	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37763	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37778	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37833	*Mictomys*	*vetus/landesi*	Left	Dentary with m1-3	DMNH 1349	Mark's Sink			
DMNH	37861	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37862	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37875	*Mictomys*	*vetus/landesi*	Left	Dentary with m1-3	DMNH 1349	Mark's Sink			
DMNH	37876	*Mictomys*	*vetus/landesi*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37882	*Mictomys*	*vetus/landesi*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37883	*Mictomys*	*vetus/landesi*	Right	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37897	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37926	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37927	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38179	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38180	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38181	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38182	*Mictomys*	*vetus/landesi*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38183	*Mictomys*	*vetus/landesi*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38184	*Mictomys*	*vetus/landesi*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38315	*Mictomys*	*vetus/landesi*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37629	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37635	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37636	*Mimomys*	*virginianus*	Right	Dentary fragment with m-2	DMNH 1349	Mark's Sink			
DMNH	37637	*Mimomys*	*virginianus*	Right	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37651	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37652	*Mimomys*	*virginianus*	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37669	*Mimomys*	*virginianus*	Left	Dentary with i1, m1	DMNH 1349	Mark's Sink			
DMNH	37670	*Mimomys*	*virginianus*	Right	Dentary with i1, m1	DMNH 1349	Mark's Sink			
DMNH	37671	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37677	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37678	*Mimomys*	*virginianus*	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37701	*Mimomys*	*virginianus*	Left	Dentary with m1-3	DMNH 1349	Mark's Sink			
DMNH	37702	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37716	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37720	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37721	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37742	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37743	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37744	*Mimomys*	*virginianus*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37745	*Mimomys*	*virginianus*	Right	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37746	*Mimomys*	*virginianus*	Right	Dentary fragment with i1, m1	DMNH 1349	Mark's Sink			
DMNH	37750	*Mimomys*	*virginianus*	Right	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37760	*Mimomys*	*virginianus*	Left	Dentary with m1-2	DMNH 1349	Mark's Sink			

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	37770	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	37771	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37789	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37790	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1	DMNH 1349	Mark's Sink			
DMNH	37791	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37792	*Mimomys*	*virginianus*	Right	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37793	*Mimomys*	*virginianus*	Right	Dentary with m1-3	DMNH 1349	Mark's Sink			
DMNH	37794	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37795	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37798	*Mimomys*	*virginianus*	Left	Dentary with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37799	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37800	*Mimomys*	*virginianus*	Right	m1 (partially digested)	DMNH 1349	Mark's Sink			
DMNH	37801	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37802	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37803	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37804	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37805	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37825	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37826	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37827	*Mimomys*	*virginianus*	Left	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37828	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37829	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37830	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37831	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37832	*Mimomys*	*virginianus*	Right	Dentary with m1-2	DMNH 1349	Mark's Sink			
DMNH	37847	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37848	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37849	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37860	*Mimomys*	*virginianus*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37873	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37874	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37879	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37880	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37881	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37895	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37896	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37916	*Mimomys*	*virginianus*	Left	Dentary with m1-3	DMNH 1349	Mark's Sink			
DMNH	37917	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37970	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37971	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37972	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37973	*Mimomys*	*virginianus*	Right	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	37974	*Mimomys*	*virginianus*	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37975	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37976	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37977	*Mimomys*	*virginianus*	Right	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37978	*Mimomys*	*virginianus*	Right	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38034	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38035	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	38137	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	38138	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	38139	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38140	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38141	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38142	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38143	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38144	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38145	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38146	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38147	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38148	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38149	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38150	*Mimomys*	*virginianus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38151	*Mimomys*	*virginianus*	Left	Dentary fragment with i1, m1	DMNH 1349	Mark's Sink			
DMNH	38152	*Mimomys*	*virginianus*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	38153	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38154	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38155	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38156	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38157	*Mimomys*	*virginianus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38158	*Mimomys*	*virginianus*	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38159	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	38160	*Mimomys*	*virginianus*	Right	Dentary fragment with i1, m1-3	DMNH 1349	Mark's Sink			
DMNH	38161	*Mimomys*	*virginianus*	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38162	*Mimomys*	*virginianus*	Right	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	38163	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38164	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38165	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38166	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38167	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38168	*Mimomys*	*virginianus*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38169	*Mimomys*	*virginianus*	Right	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	38170	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38171	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38172	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38173	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38174	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38175	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38176	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38177	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			

(continued)

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
DMNH	38178	*Mimomys*	*virginianus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37822	*Ophiomys*	*parvus*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37893	*Ophiomys*	*parvus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37909	*Ophiomys*	*parvus*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37937	*Ophiomys*	*parvus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37941	*Ophiomys*	*parvus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37667	*Ophiomys*	*parvus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37741	*Ophiomys*	*parvus*	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37824	*Ophiomys*	parvus	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37894	*Ophiomys*	*parvus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37904	*Ophiomys*	*parvus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37913	*Ophiomys*	*parvus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37914	*Ophiomys*	*parvus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37915	*Ophiomys*	*parvus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38054	*Ophiomys*	*parvus*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37699	*Phenacomys*	*gryci*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37749	*Phenacomys*	*gryci*	Right	Dentary fragment with m1-3	DMNH 1349	Mark's Sink			
DMNH	37780	*Phenacomys*	*gryci*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37781	*Phenacomys*	*gryci*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37823	*Phenacomys*	*gryci*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37905	*Phenacomys*	*gryci*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37939	*Phenacomys*	*gryci*	Left	Dentary fragment with m1	DMNH 1349	Mark's Sink			
DMNH	37940	*Phenacomys*	*gryci*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38032	*Phenacomys*	*gryci*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38044	*Phenacomys*	*gryci*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38045	*Phenacomys*	*gryci*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38046	*Phenacomys*	*gryci*	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	38047	*Phenacomys*	*gryci*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38048	*Phenacomys*	*gryci*	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38049	*Phenacomys*	*gryci*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38050	*Phenacomys*	*gryci*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38314	*Phenacomys*	*gryci*	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37631	*Phenacomys*	sp. (not *P. gryci*)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37675	*Phenacomys*	sp. (not *P. gryci*)	Left	Dentary fragment with i1, m1-2	DMNH 1349	Mark's Sink			
DMNH	37714	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37890	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37853	*Phenacomys*	sp. (not *P. gryci*)	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	37872	*Phenacomys*	sp. (not *P. gryci*)	Right	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37892	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37911	*Phenacomys*	sp. (not *P. gryci*)	Left	Dentary fragment with m1-2	DMNH 1349	Mark's Sink			
DMNH	37912	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37891	*Phenacomys*	sp.	Left	m1	DMNH 1349	Mark's Sink			
DMNH	37938	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38051	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38052	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38053	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38055	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	DMNH 1349	Mark's Sink			
DMNH	38056	*Phenacomys*	sp. (not *P. gryci*)	Left	m1 (broken)	DMNH 1349	Mark's Sink			
DMNH	38057	*Phenacomys*	sp. (not *P. gryci*)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38058	*Phenacomys*	sp. (not *P. gryci*)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38059	*Phenacomys*	sp. (not *P. gryci*)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38243	*Phenacomys*	sp. (not *P. gryci*)	Right	m1	DMNH 1349	Mark's Sink			
DMNH	37918	*Phenacomys*	sp.	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38060	*Phenacomys*	sp.	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38041	*Pliolemmus*	*antiquus*	Left	m1	DMNH 1349	Mark's Sink			

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
DMNH	38042	*Pliolemmus*	*antiquus*	Right	m1	DMNH 1349	Mark's Sink			
DMNH	38043	*Pliolemmus*	*antiquus*	Right	m1	DMNH 1349	Mark's Sink			
UCMP	213038	*Microtus*	*meadensis*	Left	Dentary with i1, m1-3	V93177	New Passage			
UCMP	155000	*Allophaiomys*	*pliocaenicus*	Left	m1	V93173	Pit	7	4	
UCMP	155001	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	3	4	
UCMP	155002	*Allophaiomys*	*pliocaenicus*	Right	m1 (broken)	V93173	Pit	3	4	
UCMP	155003	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	3	4	
UCMP	155004	*Allophaiomys*	*pliocaenicus*	Left	m1	V93173	Pit	3	4	
UCMP	155005	*Allophaiomys*	*pliocaenicus*	Left	m1	V93173	Pit	3	4	
UCMP	155006	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	2	5	
UCMP	155007	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	7	5	
UCMP	155008	*Allophaiomys*	*pliocaenicus*	Left	m1	V93173	Pit	7	5	
UCMP	155009	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	6	6	
UCMP	155010	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	7	6	
UCMP	155564	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	6	6	
UCMP	155011	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	2	7	
UCMP	155012	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	3	7	
UCMP	155013	*Allophaiomys*	*pliocaenicus*	Left	m1	V93173	Pit	3	7	
UCMP	155014	*Allophaiomys*	*pliocaenicus*	Left	m1	V93173	Pit	3	7	
UCMP	155015	*Allophaiomys*	*pliocaenicus*	Right	Dentary with i1, m1-2	V93173	Pit	3	8A	
UCMP	155016	*Allophaiomys*	*pliocaenicus*	Right	Dentary with i1, m1-3	V93173	Pit	3/7	8A	
UCMP	155017	*Allophaiomys*	*pliocaenicus*	Left	Dentary with i1, m1-2	V93173	Pit	3/7	8A	
UCMP	155018	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	7	8A	
UCMP	155019	*Allophaiomys*	*pliocaenicus*	Left	m1	V93173	Pit	7	8A	
UCMP	155020	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	2	11	
UCMP	155021	*Allophaiomys*	*pliocaenicus*	Right	m1	V93173	Pit	2	11	
CM	45460	*Lemmiscus*	(4T)	Left	m1	1925	Pit	1	1	
CM	45462	*Lemmiscus*	(4T)	Left	m1	1925	Pit	1	1	
CM	45463	*Lemmiscus*	(4T)	Right	m1	1925	Pit	1	1	
CM	45464	*Lemmiscus*	(4T)	Right	m1	1925	Pit	1	1	
CM	65233	*Lemmiscus*	(4T)	Right	m1	1925	Pit	1	1	
CM	66214	*Lemmiscus*	(4T)	Left	m1	1925	Pit	1	1	
UCMP	155333	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	1	1	
UCMP	155334	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	1	1	
UCMP	155335	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	1	
UCMP	155336	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	1	
UCMP	155337	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	1	
UCMP	155338	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	1	
UCMP	155339	*Lemmiscus*	(4T)	Right	Dentary with i1, m1-2	V93173	Pit	5/6	1	
CM	45466	*Lemmiscus*	(4T)	Right	m1	1925	Pit	1	2	
CM	45467	*Lemmiscus*	(4T)	Right	m1	1925	Pit	1	2	
CM	65481	*Lemmiscus*	(4T)	Right	Dentary with i1, m1-2	1925	Pit	1	2	
CM	66547	*Lemmiscus*	(4T)	Left	m1	1925	Pit	1	2	
CM	66588	*Lemmiscus*	(4T)	Right	m1	1925	Pit	1	2	
UCMP	155340	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	1	2	
UCMP	155341	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	1	2	
UCMP	155342	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	2	
UCMP	155343	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	2	
CM	45470	*Lemmiscus*	(4T)	Right	m1	1925	Pit	1	3	
CM	65556	*Lemmiscus*	(4T)	Left	m1	1925	Pit	1	3	
CM	65557	*Lemmiscus*	(4T)	Left	mi (broken)	1925	Pit	1	3	
CM	65562	*Lemmiscus*	(4T)	Right	m1	1925	Pit	1	3	
CM	65579	*Lemmiscus*	(4T)	Right	m1	1925	Pit	1	3	
UCMP	155344	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	1	3	
UCMP	155346	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	3	
UCMP	155347	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	3	
UCMP	155349	*Lemmiscus*	(4T)	Left	Dentary with m1-3	V93173	Pit	5/6	3	
UCMP	155350	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	5/6	3	
UCMP	155351	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	5/6	3	
CM	65053	*Lemmiscus*	(4T)	Right	Dentary with i1, m1-3	1925	Pit	1	1 to 3	
CM	45506	*Lemmiscus*	(4T)	Left	m1 (broken)	1925	Pit	1	3	
UCMP	155348	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	1	3?	
UCMP	155345	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	3?	
UCMP	155352	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	1	4	
UCMP	155353	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	1	4	
UCMP	155354	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	4	
UCMP	155355	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	4	
UCMP	155356	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	4	

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	155357	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	4	
UCMP	155358	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	4	
UCMP	155359	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	1	4	
UCMP	155360	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	2	4	
UCMP	155361	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	2	4	
UCMP	155362	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	3	4	
UCMP	155363	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	3	4	
UCMP	155364	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	3	4	
UCMP	155365	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	3	4	
UCMP	155366	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	3	4	
UCMP	155367	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	3	4	
UCMP	155368	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	3	4	
UCMP	155369	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	3	4	
UCMP	155370	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	3	4	
UCMP	155371	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	3	4	
UCMP	155372	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	3	4	
UCMP	155373	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	3	4	
UCMP	155374	*Lemmiscus*	(4T)	Right	m1 (broken)	V93173	Pit	3	4	
UCMP	155386	*Lemmiscus*	(4T)	Left	m1 (partially digested)	V93173	Pit	1	4	
UCMP	155387	*Lemmiscus*	(4T)	Left	m1 (broken)	V93173	Pit	1	4	
UCMP	155388	*Lemmiscus*	(4T)	Left	m1 (broken)	V93173	Pit	1	4	
UCMP	155389	*Lemmiscus*	(4T)	Right	m1 (broken)	V93173	Pit	3	4	
UCMP	155375	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	2	5	
UCMP	155376	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	6	5	
UCMP	155377	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	6	5	
UCMP	155378	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	7	5	
UCMP	155379	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	3	6	
UCMP	155380	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	3	6	
UCMP	155381	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	6	7	
UCMP	155382	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	2	8	
UCMP	155383	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	2	8	
UCMP	155384	*Lemmiscus*	(4T)	Left	m1	V93173	Pit	3	10	
UCMP	155385	*Lemmiscus*	(4T)	Right	m1	V93173	Pit	6	10	
CM	66194	*Lemmiscus*	cf. (4T)	Right	m1 (broken)	1925	Pit	1	1	
UCMP	155265	*Lemmiscus*	*curtatus*	Right	Dentary with i1, m1-2	V93173	Pit	1/7	Surface	
CM	45457	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1	1925	Pit	1	1	
CM	45458	*Lemmiscus*	*curtatus*	Right	Dentary with m1-2	1925	Pit	1	1	
CM	45459	*Lemmiscus*	*curtatus*	Right	Dentary with m1-2	1925	Pit	1	1	
CM	45461	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	45465	*Lemmiscus*	*curtatus*	Right	Dentary with m1-2	1925	Pit	1	1	
CM	66190	*Lemmiscus*	*curtatus*	Right	m1 (broken)	1925	Pit	1	1	
CM	66201	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66220	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66239	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	66242	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	66267	*Lemmiscus*	*curtatus*	Right	m1 (broken)	1925	Pit	1	1	
CM	66268	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66277	*Lemmiscus*	*curtatus*	Left	m1 (broken)	1925	Pit	1	1	
CM	66279	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	66281	*Lemmiscus*	*curtatus*	Right	m1 (broken)	1925	Pit	1	1	
CM	66282	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66283	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	66301	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66304	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	66308	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66310	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	66323	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66324	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66328	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66330	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	66334	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	1	
CM	66343	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	66346	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
CM	66347	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	1	
UCMP	155266	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	1	
UCMP	155267	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	1	
UCMP	155268	*Lemmiscus*	*curtatus*	Left	m1 (partially digested)	V93173	Pit	1	1	
UCMP	155269	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	1	
UCMP	155270	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	1	

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	155271	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	1	
UCMP	155272	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	1	
UCMP	155273	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	1	
UCMP	155274	*Lemmiscus*	*curtatus*	Left	m1 (partially digested)	V93173	Pit	1	1	
UCMP	155275	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	1	
UCMP	155276	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	1	
UCMP	155277	*Lemmiscus*	*curtatus*	Left	m1 (broken)	V93173	Pit	1	1	
UCMP	155278	*Lemmiscus*	*curtatus*	Left	m1 (broken)	V93173	Pit	1	1	
UCMP	155279	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155280	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155281	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155282	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155283	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155284	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155285	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155286	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155287	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155288	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155289	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
UCMP	155290	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	1	
CM	66562	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	2	
CM	66570	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	2	
CM	66572	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	2	
CM	66581	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	2	
CM	66597	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	2	
UCMP	155291	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	2	
UCMP	155292	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	2	
UCMP	155293	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	2	
UCMP	155294	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	2	
UCMP	155295	*Lemmiscus*	*curtatus*	Right	m1 (broken)	V93173	Pit	1	2	
CM	45468	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	3	
CM	45469	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	3	
CM	45471	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	3	
CM	45472	*Lemmiscus*	*curtatus*	Right	m1	1925	Pit	1	3	
CM	65578	*Lemmiscus*	*curtatus*	Left	m1	1925	Pit	1	3	
UCMP	155296	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	3	
UCMP	155297	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	1	3	
CM	65169	*Lemmiscus*	*curtatus*	Left	Dentary fragment with m1-2	1925	Pit	1	1 to 3	
UCMP	155320	*Lemmiscus*	*curtatus*	Left	Dentary with m1-3	V93173	Pit	5/6N	1 to 3	
UCMP	155321	*Lemmiscus*	*curtatus*	Left	Dentary with m1-2	V93173	Pit	5/6N	1 to 3	
UCMP	155322	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	5/6N	1 to 3	
UCMP	155298	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	4	
UCMP	155299	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	1	4	
UCMP	155300	*Lemmiscus*	*curtatus*	Left	m1 (partially digested)	V93173	Pit	1	4	
UCMP	155301	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	3	4	
UCMP	155302	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	3	4	
UCMP	155303	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	3	4	
UCMP	155304	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	3	4	
UCMP	155305	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	3	4	
UCMP	155306	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	3	4	
UCMP	155307	*Lemmiscus*	*curtatus*	Right	m1 (broken)	V93173	Pit	3	4	
UCMP	155308	*Lemmiscus*	*curtatus*	Right	m1 (broken)	V93173	Pit	3	4	
UCMP	155309	*Lemmiscus*	*curtatus*	Right	m1 (broken)	V93173	Pit	3	4	
UCMP	155310	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	2	5	
UCMP	155311	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	6	5	
UCMP	155312	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	6	5	
UCMP	155313	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	3	6	
UCMP	155314	*Lemmiscus*	*curtatus*	Left	m1 (broken)	V93173	Pit	6	6	
UCMP	155315	*Lemmiscus*	*curtatus*	Left	m1 (broken)	V93173	Pit	6	7	
UCMP	155316	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	2	8	
UCMP	155317	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit	2	8	
UCMP	155318	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit	6	9	
UCMP	155319	*Lemmiscus*	*curtatus*	Right	m1 (broken)	V93173	Pit	6	10	
UCMP	155323	*Lemmiscus*	*curtatus*	Left	Dentary with i1, m1-2	V93173	Pit	South extension	Mixed	
UCMP	155324	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit		Mixed	

(continued)

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
UCMP	155325	*Lemmiscus*	*curtatus*	Left	m1	V93173	Pit		Mixed	
UCMP	155326	*Lemmiscus*	*curtatus*	Left	m1 (broken)	V93173	Pit		Mixed	
UCMP	155332	cf. *Lemmiscus*	*curtatus*	Left	m1 (broken)	V93173	Pit		Mixed	
UCMP	155327	*Lemmiscus*	*curtatus*	Right	m1	V93173	Pit		Mixed	
CM	66255	cf. *Lemmiscus*	*curtatus*	Left	m1 (broken)	1925	Pit	1	1	
UCMP	155329	cf. *Lemmiscus*	*curtatus*	Left	m1 (broken)	V93173	Pit	1	1	
UCMP	155331	cf. *Lemmiscus*	*curtatus*	Right	m1 (broken)	V93173	Pit	6	7	
UCMP	155390	*Lemmiscus*	sp.	Right	M1	V93173	Pit	3/4	Surface south of wall	
UCMP	155391	*Lemmiscus*	sp.	Left	M1	V93173	Pit	3/4	Surface south of wall	
UCMP	155407	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3/4	Surface south of wall	
UCMP	155408	*Lemmiscus*	sp.	Left	M2	V93173	Pit	3/4	Surface south of wall	
UCMP	155495	*Lemmiscus*	sp.	Left	M3	V93173	Pit	3/4	Surface south of wall	
UCMP	155496	*Lemmiscus*	sp.	Right	M3	V93173	Pit	3/4	Surface south of wall	
CM	45410	*Lemmiscus*	sp.	Right	M3	1925	Pit	1	1	
CM	45411	*Lemmiscus*	sp.	Right	M3	1925	Pit	1	1	
CM	45412	*Lemmiscus*	sp.	Left	M3	1925	Pit	1	1	
CM	45413	*Lemmiscus*	sp.	Left	M3 (broken)	1925	Pit	1	1	
CM	66191	*Lemmiscus*	sp.	Left	M3	1925	Pit	1	1	
CM	66210	*Lemmiscus*	sp.	Right	M2	1925	Pit	1	1	
CM	66217	*Lemmiscus*	sp.	Left	M2	1925	Pit	1	1	
CM	66233	*Lemmiscus*	sp.	Left	M2	1925	Pit	1	1	
CM	66260	*Lemmiscus*	sp.	Left	M3	1925	Pit	1	1	
CM	66265	*Lemmiscus*	sp.	Right	M3	1925	Pit	1	1	
CM	66271	*Lemmiscus*	sp.	Right	M2	1925	Pit	1	1	
CM	66278	*Lemmiscus*	sp.	Right	M2 (broken)	1925	Pit	1	1	
CM	66286	*Lemmiscus*	sp.	Left	M3	1925	Pit	1	1	
CM	66299	*Lemmiscus*	sp.	Right	M2	1925	Pit	1	1	
CM	66337	*Lemmiscus*	sp.	Right	M3	1925	Pit	1	1	
UCMP	155392	*Lemmiscus*	sp.	Left	M1	V93173	Pit	1	1	
UCMP	155393	*Lemmiscus*	sp.	Left	M1	V93173	Pit	1	1	
UCMP	155394	*Lemmiscus*	sp.	Right	M1	V93173	Pit	1	1	
UCMP	155409	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	155411	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	155412	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	155413	*Lemmiscus*	sp.	Left	M2 (broken)	V93173	Pit	1	1	
UCMP	155414	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	155415	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	155416	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	155417	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	155418	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	155419	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	1	
UCMP	155420	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	1	
UCMP	155421	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	1	
UCMP	155422	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	1	
UCMP	155423	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	1	
UCMP	155494	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	155497	*Lemmiscus*	sp.	Left	M3	V93173	Pit	1	1	
UCMP	155498	*Lemmiscus*	sp.	Left	M3	V93173	Pit	1	1	
UCMP	155499	*Lemmiscus*	sp.	Left	M3	V93173	Pit	1	1	
UCMP	155500	*Lemmiscus*	sp.	Left	M3	V93173	Pit	1	1	
UCMP	155501	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	1	
UCMP	155424	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	2	
UCMP	155425	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	2	
UCMP	155426	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	2	
UCMP	155427	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	2	
UCMP	155502	*Lemmiscus*	sp.	Left	M3	V93173	Pit	1	2	
UCMP	155503	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	2	

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	155504	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	2	
CM	65582	*Lemmiscus*	sp.	Right	M3	1925	Pit	1	3	
CM	65583	*Lemmiscus*	sp.	Left	M3	1925	Pit	1	3	
CM	65584	*Lemmiscus*	sp.	Left	M2	1925	Pit	1	3	
CM	65585	*Lemmiscus*	sp.	Left	M2	1925	Pit	1	3	
CM	65586	*Lemmiscus*	sp.	Left	M3	1925	Pit	1	3	
UCMP	155428	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	3	
UCMP	155505	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	3	
UCMP	399897	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	3	
UCMP	399898	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	3	
UCMP	399899	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	3	
UCMP	155395	*Lemmiscus*	sp.	Left	M1	V93173	Pit	2	4	
UCMP	155396	*Lemmiscus*	sp.	Left	M1	V93173	Pit	2	4	
UCMP	155397	*Lemmiscus*	sp.	Right	M1	V93173	Pit	2	4	
UCMP	155398	*Lemmiscus*	sp.	Right	M1	V93173	Pit	2	4	
UCMP	155399	*Lemmiscus*	sp.	Right	M1	V93173	Pit	2	4	
UCMP	155400	*Lemmiscus*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155401	*Lemmiscus*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155402	*Lemmiscus*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	155429	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	4	
UCMP	155430	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	4	
UCMP	155431	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	4	
UCMP	155432	*Lemmiscus*	sp.	Left	M2	V93173	Pit	1	4	
UCMP	155433	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	4	
UCMP	155434	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	4	
UCMP	155435	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	4	
UCMP	155436	*Lemmiscus*	sp.	Right	M2 (broken)	V93173	Pit	1	4	
UCMP	155437	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	4	
UCMP	155438	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	4	
UCMP	155439	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	4	
UCMP	155440	*Lemmiscus*	sp.	Left	M2	V93173	Pit	2	4	
UCMP	155441	*Lemmiscus*	sp.	Left	M2	V93173	Pit	2	4	
UCMP	155442	*Lemmiscus*	sp.	Left	M2	V93173	Pit	2	4	
UCMP	155443	*Lemmiscus*	sp.	Left	M2	V93173	Pit	2	4	
UCMP	155444	*Lemmiscus*	sp.	Right	M2	V93173	Pit	2	4	
UCMP	155445	*Lemmiscus*	sp.	Right	M2	V93173	Pit	2	4	
UCMP	155446	*Lemmiscus*	sp.	Right	M2	V93173	Pit	2	4	
UCMP	155447	*Lemmiscus*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155448	*Lemmiscus*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155449	*Lemmiscus*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155450	*Lemmiscus*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155451	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155452	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155453	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155454	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155455	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155456	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155457	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155506	*Lemmiscus*	sp.	Left	M3	V93173	Pit	1	4	
UCMP	155507	*Lemmiscus*	sp.	Left	M3 (partially digested)	V93173	Pit	1	4	
UCMP	155508	*Lemmiscus*	sp.	Left	M3	V93173	Pit	1	4	
UCMP	155509	*Lemmiscus*	sp.	Left	M3	V93173	Pit	1	4	
UCMP	155510	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155511	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155512	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155513	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155514	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155515	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155516	*Lemmiscus*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155517	*Lemmiscus*	sp.	Left	M3	V93173	Pit	2	4	
UCMP	155518	*Lemmiscus*	sp.	Left	M3	V93173	Pit	2	4	
UCMP	155519	*Lemmiscus*	sp.	Left	M3	V93173	Pit	3	4	
UCMP	155520	*Lemmiscus*	sp.	Right	M3	V93173	Pit	3	4	
UCMP	155521	*Lemmiscus*	sp.	Right	M3	V93173	Pit	3	4	
UCMP	155522	*Lemmiscus*	sp.	Right	M3	V93173	Pit	3	4	
UCMP	155523	*Lemmiscus*	sp.	Right	M3	V93173	Pit	3	4	
UCMP	155524	*Lemmiscus*	sp.	Right	M3	V93173	Pit	3	4	
UCMP	155525	*Lemmiscus*	sp.	Right	M3	V93173	Pit	3	4	

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
CM	45473	*Lemmiscus*	sp.	Left	M3	1925	Pit	1	5	
CM	45474	*Lemmiscus*	sp.	Left	M2	1925	Pit	1	5	
UCMP	155403	*Lemmiscus*	sp.	Left	M1	V93173	Pit	2	5	
UCMP	155404	*Lemmiscus*	sp.	Right	M1	V93173	Pit	6	5	
UCMP	155458	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	5	
UCMP	155459	*Lemmiscus*	sp.	Right	M2	V93173	Pit	1	5	
UCMP	155460	*Lemmiscus*	sp.	Right	M2	V93173	Pit	2	5	
UCMP	155461	*Lemmiscus*	sp.	Right	M2	V93173	Pit	2	5	
UCMP	155462	*Lemmiscus*	sp.	Left	M2	V93173	Pit	3	5	
UCMP	155463	*Lemmiscus*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155464	*Lemmiscus*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155465	*Lemmiscus*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155466	*Lemmiscus*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155467	*Lemmiscus*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155468	*Lemmiscus*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155469	*Lemmiscus*	sp.	Right	M2	V93173	Pit	6	5	
UCMP	155470	*Lemmiscus*	sp.	Right	M2	V93173	Pit	6	5	
UCMP	155471	*Lemmiscus*	sp.	Right	M2	V93173	Pit	6	5	
UCMP	155526	*Lemmiscus*	sp.	Left	M3	V93173	Pit	2	5	
UCMP	155527	*Lemmiscus*	sp.	Left	M3	V93173	Pit	2	5	
UCMP	155528	*Lemmiscus*	sp.	Left	M3	V93173	Pit	2	5	
UCMP	155529	*Lemmiscus*	sp.	Left	M3	V93173	Pit	6	5	
UCMP	155530	*Lemmiscus*	sp.	Right	M3	V93173	Pit	6	5	
UCMP	155531	*Lemmiscus*	sp.	Right	M3	V93173	Pit	6	5	
UCMP	155532	*Lemmiscus*	sp.	Right	M3	V93173	Pit	7	5	
UCMP	155533	*Lemmiscus*	sp.	Right	M3	V93173	Pit	7	5	
UCMP	155405	*Lemmiscus*	sp.	Left	M1	V93173	Pit	2	6	
UCMP	155406	*Lemmiscus*	sp.	Left	M1	V93173	Pit	3	6	
UCMP	155472	*Lemmiscus*	sp.	Left	M2	V93173	Pit	2	6	
UCMP	155473	*Lemmiscus*	sp.	Left	M2	V93173	Pit	3	6	
UCMP	155474	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	6	
UCMP	155475	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	6	
UCMP	155476	*Lemmiscus*	sp.	Left	M2	V93173	Pit	6	6	
UCMP	155477	*Lemmiscus*	sp.	Right	M2	V93173	Pit	6	6	
UCMP	155478	*Lemmiscus*	sp.	Right	M2	V93173	Pit	7	6	
UCMP	155534	*Lemmiscus*	sp.	Left	M3	V93173	Pit	7	6	
UCMP	155535	*Lemmiscus*	sp.	Right	M3	V93173	Pit	7	6	
UCMP	155536	*Lemmiscus*	sp.	Right	M3	V93173	Pit	7	6	
UCMP	155537	*Lemmiscus*	sp.	Right	M3	V93173	Pit	7	6	
UCMP	155479	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	7	
UCMP	155480	*Lemmiscus*	sp.	Left	M2	V93173	Pit	6	7	
UCMP	155538	*Lemmiscus*	sp.	Left	M3	V93173	Pit	6	7	
UCMP	155539	*Lemmiscus*	sp.	Left	M3	V93173	Pit	7	7	
UCMP	155481	*Lemmiscus*	sp.	Left	M2	V93173	Pit	2	8	
UCMP	155482	*Lemmiscus*	sp.	Right	M2 (broken)	V93173	Pit	2	8	
UCMP	155483	*Lemmiscus*	sp.	Right	M2	V93173	Pit	3	8A	
UCMP	155484	*Lemmiscus*	sp.	Right	M2	V93173	Pit	7	8A	
UCMP	155485	*Lemmiscus*	sp.	Right	M2	V93173	Pit	7	8A	
UCMP	155486	*Lemmiscus*	sp.	Right	M2	V93173	Pit	7	8A	
UCMP	155544	*Lemmiscus*	sp.	Left	M1 or M2 (broken)	V93173	Pit	6	9	
UCMP	155487	*Lemmiscus*	sp.	Right	M2	V93173	Pit	2	10	
UCMP	155488	*Lemmiscus*	sp.	Left	M2	V93173	Pit	3	10	
UCMP	155489	*Lemmiscus*	sp.	Right	M2	V93173	Pit	7	10	
UCMP	155540	*Lemmiscus*	sp.	Left	M3	V93173	Pit	3	10	
UCMP	155541	*Lemmiscus*	sp.	Left	M3	V93173	Pit	3	10	
UCMP	155542	*Lemmiscus*	sp.	Left	M3	V93173	Pit	3	10	
UCMP	155490	*Lemmiscus*	sp.	Right	M2	V93173	Pit	2	11	
CM	65580	*Lemmiscus*	sp.	Right	M2	1925	Pit		Mixed	
UCMP	155491	*Lemmiscus*	sp.	Left	M2	V93173	Pit		Mixed	
UCMP	155543	*Lemmiscus*	sp.	Left	M3	V93173	Pit		Mixed	
UCMP	212930	*Lemmiscus*	sp.	Right	M3	V93173	Pit		Mixed	
UCMP	155022	*Microtus*	5T	Left	m1	V93173	Pit	1/7	Surface	
CM	45485	*Microtus*	5T	Left	m1	1925	Pit	1	1	
CM	45486	*Microtus*	5T	Right	m1	1925	Pit	1	1	
CM	45497	*Microtus*	5T	Left	m1	1925	Pit	1	1	
CM	45498	*Microtus*	5T	Right	m1	1925	Pit	1	1	
CM	45502	*Microtus*	5T	Right	m1	1925	Pit	1	1	
CM	65232	*Microtus*	5T	Right	m1	1925	Pit	1	1	
CM	66202	*Microtus*	5T	Right	m1 (broken)	1925	Pit	1	1	

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
CM	66276	*Microtus*	5T	Right	m1	1925	Pit	1	1	
CM	66284	*Microtus*	5T	Left	m1 (broken)	1925	Pit	1	1	
CM	66303	*Microtus*	5T	Right	m1	1925	Pit	1	1	
CM	66319	*Microtus*	5T	Left	m1 (broken)	1925	Pit	1	1	
CM	66338	*Microtus*	5T	Left	m1	1925	Pit	1	1	
CM	66348	*Microtus*	5T	Right	m1	1925	Pit	1	1	
UCMP	155025	*Microtus*	5T	Left	m1	V93173	Pit	1	1	
UCMP	155026	*Microtus*	5T	Left	m1	V93173	Pit	1	1	
UCMP	155027	*Microtus*	5T	Left	m1	V93173	Pit	1	1	
UCMP	155028	*Microtus*	5T	Left	m1	V93173	Pit	1	1	
UCMP	155029	*Microtus*	5T	Left	m1	V93173	Pit	1	1	
UCMP	155030	*Microtus*	5T	Left	m1	V93173	Pit	1	1	
UCMP	155031	*Microtus*	5T	Left	v	V93173	Pit	1	1	
UCMP	155032	*Microtus*	5T	Right	m1	V93173	Pit	1	1	
UCMP	155033	*Microtus*	5T	Right	m1	V93173	Pit	1	1	
UCMP	155034	*Microtus*	5T	Right	m1	V93173	Pit	1	1	
UCMP	155035	*Microtus*	5T	Right	m1	V93173	Pit	1	1	
UCMP	155036	*Microtus*	5T	Right	m1	V93173	Pit	1	1	
UCMP	155037	*Microtus*	5T	Right	m1 (broken)	V93173	Pit	1	1	
UCMP	155038	*Microtus*	5T	Right	m1	V93173	Pit	1	1	
UCMP	155080	*Microtus*	5T	Right	m1 (juvenile)	V93173	Pit	1	1	
CM	45445	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	45487	*Microtus*	5T	Left	m1	1925	Pit	1	2	
CM	45488	*Microtus*	5T	Left	m1	1925	Pit	1	2	
CM	45489	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	45490	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	45491	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	45492	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	45493	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	45494	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	45499	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	45503	*Microtus*	5T	Left	m1	1925	Pit	1	2	
CM	63606	*Microtus*	5T	Left	m1	1925	Pit	1	2	
CM	66534	*Microtus*	5T	Left	m1	1925	Pit	1	2	
CM	66567	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	66569	*Microtus*	5T	Right	m1	1925	Pit	1	2	
CM	66593	*Microtus*	5T	Left	m1	1925	Pit	1	2	
UCMP	155039	*Microtus*	5T	Left	m1	V93173	Pit	1	2	
UCMP	155040	*Microtus*	5T	Left	m1	V93173	Pit	1	2	
UCMP	155041	*Microtus*	5T	Left	m1	V93173	Pit	1	2	
UCMP	155042	*Microtus*	5T	Left	m1	V93173	Pit	1	2	
UCMP	155043	*Microtus*	5T	Left	m1	V93173	Pit	1	2	
UCMP	155044	*Microtus*	5T	Left	m1	V93173	Pit	1	2	
UCMP	155045	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155046	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155047	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155048	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155049	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155050	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155051	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155052	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155053	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155054	*Microtus*	5T	Right	m1	V93173	Pit	1	2	
UCMP	155055	*Microtus*	5T	Right	Dentary with m1-2	V93173	Pit	5/6	2	
UCMP	155056	*Microtus*	5T	Right	Dentary with m1-2	V93173	Pit	5/6	2	
UCMP	155057	*Microtus*	5T	Left	m1	V93173	Pit	5/6 or 1/6	2	
UCMP	155261	*Microtus*	5T	Right	Dentary fragment with m1	V93173	Pit	1	2	
CM	45495	*Microtus*	5T	Left	m1	1925	Pit	1	3	
CM	45496	*Microtus*	5T	Right	m1	1925	Pit	1	3	
UCMP	155058	*Microtus*	5T	Left	Dentary with i1, m1	V93173	Pit	1	3	
UCMP	155059	*Microtus*	5T	Right	m1	V93173	Pit	1	3	
UCMP	155060	*Microtus*	5T	Right	m1	V93173	Pit	1	3	
UCMP	155061	*Microtus*	5T	Right	m1	V93173	Pit	1	3	
UCMP	155064	*Microtus*	5T	Left	m1	V93173	Pit	5/6	3	
UCMP	155062	*Microtus*	5T	Left	m1	V93173	Pit	1	3?	
UCMP	155063	*Microtus*	5T	Left	m1	V93173	Pit	1	3?	

(continued)

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
UCMP	155561	*Microtus*	5T	Right	m1	V93173	Pit	1	3?	
UCMP	155071	*Microtus*	5T	Left	m1	V93173	Pit	5/6N	1–3	
UCMP	155072	*Microtus*	5T	Left	m1	V93173	Pit	5/6N	1–3	
UCMP	155073	*Microtus*	5T	Right	Dentary with m1-2	V93173	Pit	5/6N	1–3	
UCMP	155074	*Microtus*	5T	Right	Dentary with m1-2	V93173	Pit	5/6N	1–3	
UCMP	155066	*Microtus*	5T	Left	m1	V93173	Pit	1	4	
UCMP	155067	*Microtus*	5T	Right	m1	V93173	Pit	1	4	
UCMP	156154	*Microtus*	5T	Left	m1	V93173	Pit	3	4	
UCMP	156155	*Microtus*	5T	Left	m1	V93173	Pit	3	4	
UCMP	156156	*Microtus*	5T	Right	m1	V93173	Pit	3	4	
UCMP	155068	*Microtus*	5T	Right	m1	V93173	Pit	6	5	
UCMP	155069	*Microtus*	5T	Left	m1	V93173	Pit	7	5	
UCMP	155070	*Microtus*	5T	Right	m1	V93173	Pit	2	6	
UCMP	155023	*Microtus*	5T	Left	Dentary with i1, m1-2	V93173	Pit	West of grid 1	Mixed	
UCMP	155024	*Microtus*	5T	Left	m1	V93173	Pit	South extension	Mixed	
UCMP	155075	*Microtus*	5T	Left	m1	V93173	Pit		Mixed	
UCMP	155076	*Microtus*	5T	Left	m1	V93173	Pit		Mixed	
UCMP	155077	*Microtus*	5T	Left	m1	V93173	Pit	1	Mixed	
UCMP	155078	*Microtus*	5T	Right	m1	V93173	Pit		Mixed	
UCMP	155079	*Microtus*	5T	Right	m1	V93173	Pit	1	Mixed	
CM	66317	cf. *Microtus*	5T	Left	m1 (broken)	1925	Pit	1	1	
UCMP	155065	cf. *Microtus*	5T	Left	m1 (partially digested)	V93173	Pit	1	4	
CM	45402	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	1	
CM	45403	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	1	
CM	45404	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	1	
CM	45405	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	1	
CM	45428	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	1	
CM	45429	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	1	
CM	45430	*Microtus*	*meadensis*	Right	m1 (broken)	1925	Pit	1	1	
CM	66199	*Microtus*	*meadensis*	Right	m1 (broken)	1925	Pit	1	1	
CM	66307	*Microtus*	*meadensis*	Left	m1 (broken)	1925	Pit	1	1	
CM	66325	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	1	
CM	66335	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	1	
UCMP	155196	*Microtus*	*meadensis*	Left	Dentary with m1-2	V93173	Pit	1/7	Surface	
UCMP	155197	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1/7	Surface	
UCMP	155198	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1/7	Surface	
UCMP	155199	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1/7	Surface	
UCMP	155200	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	1	
UCMP	155201	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	1	
UCMP	155202	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	1	
UCMP	155203	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	1	
UCMP	155204	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	1	
UCMP	155205	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	1	
UCMP	155206	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	1	
CM	45431	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	2	
CM	45432	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	2	
CM	45433	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	2	
CM	45434	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	2	
CM	45435	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45436	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45437	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45438	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45439	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45440	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45441	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45442	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45443	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45444	*Microtus*	*meadensis*	Right	m1 (partially digested)	1925	Pit	1	2	
CM	45446	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	45447	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	63601	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	2	
CM	66530	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	66542	*Microtus*	*meadensis*	Left	m1	1925	Pit	1	2	
CM	66560	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
CM	66571	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	2	
UCMP	155207	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	2	

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	155208	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	2	
UCMP	155209	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	2	
UCMP	155210	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	2	
UCMP	155211	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	2	
UCMP	155212	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155213	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155214	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155215	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155216	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155217	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155218	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155219	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155220	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155221	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	2	
UCMP	155222	*Microtus*	*meadensis*	Right	Dentary with m1-2	V93173	Pit	5/6	2	
UCMP	156153	*Microtus*	*meadensis*	Right	Dentary with i1, m1-2	V93173	Pit	5/6	2	
CM	65558	*Microtus*	*meadensis*	Left	m1 (broken)	1925	Pit	1	3	
CM	65563	*Microtus*	*meadensis*	Right	m1 (broken)	1925	Pit	1	3	
CM	65587	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	3	
CM	65588	*Microtus*	*meadensis*	Right	m1	1925	Pit	1	3	
UCMP	155223	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	3	
UCMP	155224	*Microtus*	*meadensis*	Right	Dentary with m1	V93173	Pit	1	3	
UCMP	155225	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	3	
UCMP	155226	*Microtus*	*meadensis*	Right	m1	V93173	Pit	5/6	3	
UCMP	155227	*Microtus*	*meadensis*	Right	Dentary with m1-2	V93173	Pit	5/6	3	
UCMP	155228	*Microtus*	*meadensis*	Left	m1	V93173	Pit	5/6	3	
UCMP	155229	*Microtus*	*meadensis*	Right	Dentary with i1, m1-3	V93173	Pit	5/6	3	
UCMP	155264	*Microtus*	*meadensis*	Left	Dentary with i1, m1	V93173	Pit	5/6	3	
UCMP	155230	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	3?	
UCMP	155231	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	3?	
UCMP	155255	*Microtus*	*meadensis*	Left	m1	V93173	Pit	5/6N	1–3	
UCMP	155232	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	4	
UCMP	155233	*Microtus*	*meadensis*	Left	m1 (broken)	V93173	Pit	1	4	
UCMP	155234	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	4	
UCMP	155235	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	4	
UCMP	155236	*Microtus*	*meadensis*	Right	m1 (broken)	V93173	Pit	1	4	
UCMP	155237	*Microtus*	*meadensis*	Right	m1	V93173	Pit	1	4	
UCMP	155238	*Microtus*	*meadensis*	Right	m1 (broken)	V93173	Pit	1	4	
UCMP	155239	*Microtus*	*meadensis*	Right	m1 (broken)	V93173	Pit	2	4	
UCMP	155240	*Microtus*	*meadensis*	Right	m1	V93173	Pit	2	4	
UCMP	155241	*Microtus*	*meadensis*	Right	m1	V93173	Pit	3	4	
UCMP	155242	*Microtus*	*meadensis*	Left	m1 (broken)	V93173	Pit	3	4	
UCMP	155243	*Microtus*	*meadensis*	Left	m1	V93173	Pit	3	4	
UCMP	155565	*Microtus*	*meadensis*	Right	m1	V93173	Pit	3	4	
UCMP	155244	*Microtus*	*meadensis*	Left	m1	V93173	Pit	2	5	
UCMP	155245	*Microtus*	*meadensis*	Left	m1	V93173	Pit	6	5	
UCMP	155247	*Microtus*	*meadensis*	Right	m1	V93173	Pit	6	5	
UCMP	155248	*Microtus*	*meadensis*	Right	m1	V93173	Pit	6	5	
UCMP	155250	*Microtus*	*meadensis*	Right	m1 (broken)	V93173	Pit	6	6	
UCMP	155253	*Microtus*	*meadensis*	Right	m1	V93173	Pit	2	7	
UCMP	155847	*Microtus*	*meadensis*	Right	m1 (broken)	V93173	Pit	2	8	
UCMP	155254	*Microtus*	*meadensis*	Right	m1	V93173	Pit	3	8A	
UCMP	155256	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	Mixed	
UCMP	155257	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	Mixed	
UCMP	155258	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	Mixed	
UCMP	155259	*Microtus*	*meadensis*	Left	m1	V93173	Pit	1	Mixed	
CM	45421	cf. *Microtus*	*meadensis*	Left	m1 (broken)	1925	Pit	1	1	
UCMP	155263	cf. *Microtus*	*meadensis*	Right	m1 (broken)	V93173	Pit	1	1	
UCMP	155246	cf. *Microtus*	*meadensis*	Left	m1 (broken)	V93173	Pit	6	5	
UCMP	155249	cf. *Microtus*	*meadensis*	Left	m1 (broken)	V93173	Pit	3	6	
UCMP	155251	cf. *Microtus*	*meadensis*	Right	m1 (broken)	V93173	Pit	7	6	
UCMP	155252	cf. *Microtus*	*meadensis*	Right	m1 (broken)	V93173	Pit	7	6	
CM	66345	*Microtus*	*paroperarius*	Left	m1	1925	Pit	1	1	
UCMP	155081	*Microtus*	*paroperarius*	Left	m1	V93173	Pit	1	1	
UCMP	155082	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	1	1	
UCMP	155083	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	1	1	
UCMP	155084	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	1	1	
CM	45482	*Microtus*	*paroperarius*	Left	m1	1925	Pit	1	2	

(continued)

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
CM	45483	*Microtus*	*paroperarius*	Left	m1	1925	Pit	1	2	
CM	45484	*Microtus*	*paroperarius*	Right	m1	1925	Pit	1	2	
UCMP	155085	*Microtus*	*paroperarius*	Right	Dentary with m1-2	V93173	Pit	1	2	
CM	45507	*Microtus*	*paroperarius*	Left	m1	1925	Pit	1	3	
CM	65559	*Microtus*	*paroperarius*	Left	m1 (broken)	1925	Pit	1	3	
UCMP	155086	*Microtus*	*paroperarius*	Left	m1	V93173	Pit	1	3	
UCMP	155087	*Microtus*	*paroperarius*	Left	m1	V93173	Pit	5/6	3	
UCMP	155088	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	5/6	3	
UCMP	155089	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	5/6	3	
UCMP	155090	*Microtus*	*paroperarius*	Left	m1	V93173	Pit	1	3?	
UCMP	155091	*Microtus*	*paroperarius*	Left	m1	V93173	Pit	3	4	
UCMP	155092	*Microtus*	*paroperarius*	Left	m1	V93173	Pit	1	4	
UCMP	155093	*Microtus*	*paroperarius*	Left	m1	V93173	Pit	2	4	
UCMP	155094	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	1	4	
UCMP	155095	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	1	4	
UCMP	155262	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	1	4	
UCMP	156152	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	3	4	
UCMP	155096	*Microtus*	*paroperarius*	Right	m1 (partially digested)	V93173	Pit	6	5	
UCMP	155098	*Microtus*	*paroperarius*	Left	m1	V93173	Pit	6	7	
UCMP	155099	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	6	7	
UCMP	155562	*Microtus*	*paroperarius*	Right	m1	V93173	Pit	2	7	
UCMP	155100	*Microtus*	*paroperarius*	Left	Dentary with i1, m1-2	V93173	Pit		Mixed	
UCMP	155101	*Microtus*	*paroperarius*	Right	m1 (broken)	V93173	Pit		Mixed	
UCMP	155097	cf. *Microtus*	*paroperarius*	Left	m1 (broken)	V93173	Pit	7	6	
UCMP	213332	*Microtus*	sp.	Left	M2	V93173	Pit	7	6	
UCMP	155102	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	1/7	Surface	
CM	45414	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with i1, m1-2	1925	Pit	1	1	
CM	45415	*Mictomys*	*kansasensis/meltoni*	Left	m1 (missing)	1925	Pit	1	1	
CM	45416	*Mictomys*	*kansasensis/meltoni*	Left	m1	1925	Pit	1	1	
CM	45509	*Mictomys*	*kansasensis/meltoni*	Right	m1	1925	Pit	1	2	
CM	45510	*Mictomys*	*kansasensis/meltoni*	Right	m1	1925	Pit	1	2	
UCMP	155103	*Mictomys*	*kansasensis/meltoni*	Right	Dentary with i1, m1-2	V93173	Pit	5/6	2	
UCMP	155104	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	1	2	
CM	65572	*Mictomys*	*kansasensis/meltoni*	Right	m1	1925	Pit	1	3	
UCMP	155106	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	1	3	
UCMP	155107	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	1	3	
UCMP	155108	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	5/6	3	
UCMP	155109	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	1	3	
UCMP	155110	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	1	3	
UCMP	155111	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	1	3	
UCMP	155112	*Mictomys*	*kansasensis/meltoni*	Right	Dentary with i1, m1-2	V93173	Pit	1	3	
UCMP	155113	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	1	3	
UCMP	155841	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	1	3	
UCMP	155842	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	1	3	
UCMP	155105	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	4?	3?	
UCMP	155186	*Mictomys*	*kansasensis/meltoni*	Left	Dentary with m1-2	V93173	Pit	5/6N	1–3	
UCMP	155114	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	2	4	
UCMP	155115	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	1	4	
UCMP	155116	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	4	
UCMP	155117	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	4	
UCMP	155118	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	4	
UCMP	155119	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	4	
UCMP	155120	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	4	
UCMP	155121	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	3	4	
UCMP	155122	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	4	
UCMP	155123	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	4	
UCMP	155124	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	1	4	
UCMP	155125	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	3	4	
UCMP	155126	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	2	4	
UCMP	155127	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	1	4	
UCMP	155128	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	2	4	
UCMP	155129	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	4	
UCMP	155130	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	2	4	
UCMP	155131	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	4	
UCMP	155132	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	4	
UCMP	155133	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	4	
UCMP	155134	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	2	4	
UCMP	155135	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	1	4	

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	155136	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	3	4	
UCMP	155137	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	1	4	
UCMP	155138	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	4	
UCMP	155139	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	2	4	
UCMP	155140	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	4	
UCMP	155141	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	4	
UCMP	155142	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	3	4	
UCMP	155143	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	3	4	
UCMP	155563	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	4	
UCMP	155144	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	7	5	
UCMP	155145	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	7	5	
UCMP	155146	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	5	
UCMP	155147	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	7	5	
UCMP	155148	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	6	5	
UCMP	155149	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	3	5	
UCMP	155150	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	6	5	
UCMP	155151	*Mictomys*	*kansasensis/meltoni*	Left	Dentary with m1-2	V93173	Pit	1	5	
UCMP	155844	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	2	5	
UCMP	155845	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	2	5	
UCMP	155846	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	2	5	
UCMP	155152	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	2	6	
UCMP	155153	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	2	6	
UCMP	155154	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	7	6	
UCMP	155155	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	2	6	
UCMP	155156	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	2	6	
UCMP	155157	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	6	6	
UCMP	155158	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	7	7	
UCMP	155159	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	3	7	
UCMP	155160	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	7	7	
UCMP	155161	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	6	7	
UCMP	155162	*Mictomys*	*kansasensis/meltoni*	Right	Dentary fragment with broken m1	V93173	Pit	6	7	
UCMP	155163	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	7	7	
UCMP	155164	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	3	7	
UCMP	155165	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	6	7	
UCMP	155843	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	2	7	
UCMP	155166	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	2	8	
UCMP	155167	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	2	8	
UCMP	155168	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	2	8	
UCMP	155169	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	2	8	
UCMP	155170	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	2	8	
UCMP	155171	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	2	8	
UCMP	155172	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	3	8A	
UCMP	155173	*Mictomys*	*kansasensis/meltoni*	Left	m1 (broken)	V93173	Pit	3	8A	
UCMP	155174	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	8A	
UCMP	155175	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	7	8A	
UCMP	155176	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	8A	
UCMP	155177	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	7	8A	
UCMP	155178	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	10	
UCMP	155179	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	3	10	
UCMP	155180	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	10	
UCMP	155181	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	7	10	
UCMP	155182	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	3	10	
UCMP	155183	*Mictomys*	*kansasensis/meltoni*	Right	m1	V93173	Pit	7	11	
UCMP	155184	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	7	11	
UCMP	155185	*Mictomys*	*kansasensis/meltoni*	Right	m1 (broken)	V93173	Pit	2	11	
UCMP	155187	*Mictomys*	*kansasensis/meltoni*	Left	m1	V93173	Pit	1	Mixed	
CM	45417	*Mictomys*	sp.	Left	M1	1925	Pit	1	1	
CM	45418	*Mictomys*	sp.	Left	M3	1925	Pit	1	1	
CM	45419	*Mictomys*	sp.	Right	M3	1925	Pit	1	1	
CM	66525	*Mictomys*	sp.	Right	M1	1925	Pit	1	2	
CM	66528	*Mictomys*	sp.	Left	M3	1925	Pit	1	2	
CM	66537	*Mictomys*	sp.	Left	m2	1925	Pit	1	2	
CM	66544	*Mictomys*	sp.	Right	m2	1925	Pit	1	2	
CM	66594	*Mictomys*	sp.	Right	M1	1925	Pit	1	2	
UCMP	155644	*Mictomys*	sp.	Left	M2	V93173	Pit	1	2	
UCMP	155645	*Mictomys*	sp.	Right	M2	V93173	Pit	1	2	
UCMP	155792	*Mictomys*	sp.	Right	m3	V93173	Pit	1	2	

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
CM	65568	*Mictomys*	sp.	Left	M1	1925	Pit	1	3	
CM	65569	*Mictomys*	sp.	Left	M1	1925	Pit	1	3	
CM	65570	*Mictomys*	sp.	Left	M1	1925	Pit	1	3	
CM	65571	*Mictomys*	sp.	Left	M2	1925	Pit	1	3	
CM	65574	*Mictomys*	sp.	Right	m3	1925	Pit	1	3	
CM	65575	*Mictomys*	sp.	Right	m3	1925	Pit	1	3	
CM	65576	*Mictomys*	sp.	Right	M2 (broken)	1925	Pit	1	3	
CM	65577	*Mictomys*	sp.	Left	M2	1925	Pit	1	3	
UCMP	155568	*Mictomys*	sp.	Right	M1	V93173	Pit	1	3	
UCMP	155698	*Mictomys*	sp.	Left	M3	V93173	Pit	5/6	3	
UCMP	155744	*Mictomys*	sp.	Left	m2	V93173	Pit	1	3	
UCMP	155745	*Mictomys*	sp.	Left	m2	V93173	Pit	1	3	
UCMP	155793	*Mictomys*	sp.	Right	m3	V93173	Pit	1	3	
UCMP	155569	*Mictomys*	sp.	Left	M1	V93173	Pit	1	4	
UCMP	155570	*Mictomys*	sp.	Left	M1 (partially digested)	V93173	Pit	1	4	
UCMP	155571	*Mictomys*	sp.	Left	M1	V93173	Pit	1	4	
UCMP	155572	*Mictomys*	sp.	Right	M1	V93173	Pit	1	4	
UCMP	155573	*Mictomys*	sp.	Right	M1	V93173	Pit	1	4	
UCMP	155574	*Mictomys*	sp.	Right	M1	V93173	Pit	1	4	
UCMP	155575	*Mictomys*	sp.	Right	M1	V93173	Pit	1	4	
UCMP	155576	*Mictomys*	sp.	Right	M1 (broken)	V93173	Pit	1	4	
UCMP	155577	*Mictomys*	sp.	Right	M1 (broken)	V93173	Pit	1	4	
UCMP	155578	*Mictomys*	sp.	Right	M1	V93173	Pit	2	4	
UCMP	155579	*Mictomys*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155580	*Mictomys*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155581	*Mictomys*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155582	*Mictomys*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155583	*Mictomys*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155584	*Mictomys*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155585	*Mictomys*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155586	*Mictomys*	sp.	Left	M1	V93173	Pit	3	4	
UCMP	155587	*Mictomys*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	155588	*Mictomys*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	155589	*Mictomys*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	155590	*Mictomys*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	155591	*Mictomys*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	155592	*Mictomys*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	155593	*Mictomys*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	155594	*Mictomys*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	155646	*Mictomys*	sp.	Left	M2	V93173	Pit	1	4	
UCMP	155647	*Mictomys*	sp.	Left	M2	V93173	Pit	1	4	
UCMP	155648	*Mictomys*	sp.	Left	M2	V93173	Pit	1	4	
UCMP	155649	*Mictomys*	sp.	Left	M2 (broken)	V93173	Pit	1	4	
UCMP	155650	*Mictomys*	sp.	Right	M2	V93173	Pit	1	4	
UCMP	155651	*Mictomys*	sp.	Left	M2	V93173	Pit	2	4	
UCMP	155652	*Mictomys*	sp.	Right	M2	V93173	Pit	2	4	
UCMP	155653	*Mictomys*	sp.	Right	M2	V93173	Pit	2	4	
UCMP	155655	*Mictomys*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155656	*Mictomys*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155657	*Mictomys*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155658	*Mictomys*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155659	*Mictomys*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155660	*Mictomys*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155661	*Mictomys*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	155662	*Mictomys*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155663	*Mictomys*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155664	*Mictomys*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155665	*Mictomys*	sp.	Right	M2	V93173	Pit	3	4	
UCMP	155699	*Mictomys*	sp.	Left	M3	V93173	Pit	1	4	
UCMP	155700	*Mictomys*	sp.	Left	M3	V93173	Pit	1	4	
UCMP	155701	*Mictomys*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155702	*Mictomys*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155703	*Mictomys*	sp.	Right	M3 (partially digested)	V93173	Pit	1	4	
UCMP	155704	*Mictomys*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155705	*Mictomys*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155706	*Mictomys*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155707	*Mictomys*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155708	*Mictomys*	sp.	Right	M3 (broken)	V93173	Pit	1	4	
UCMP	155709	*Mictomys*	sp.	Left	M3	V93173	Pit	2	4	

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	155710	*Mictomys*	sp.	Right	M3	V93173	Pit	2	4	
UCMP	155711	*Mictomys*	sp.	Left	M3	V93173	Pit	3	4	
UCMP	155712	*Mictomys*	sp.	Left	M3	V93173	Pit	3	4	
UCMP	155713	*Mictomys*	sp.	Right	M3	V93173	Pit	3	4	
UCMP	155714	*Mictomys*	sp.	Right	M3	V93173	Pit	3	4	
UCMP	155715	*Mictomys*	sp.	Right	M3	V93173	Pit	3	4	
UCMP	155743	*Mictomys*	sp.	?	Upper molar fragment	V93173	Pit	3	4	
UCMP	155746	*Mictomys*	sp.	Left	m2	V93173	Pit	1	4	
UCMP	155747	*Mictomys*	sp.	Right	m2	V93173	Pit	1	4	
UCMP	155748	*Mictomys*	sp.	Right	m2	V93173	Pit	1	4	
UCMP	155749	*Mictomys*	sp.	Right	m2	V93173	Pit	1	4	
UCMP	155750	*Mictomys*	sp.	Right	m2	V93173	Pit	1	4	
UCMP	155751	*Mictomys*	sp.	Right	m2	V93173	Pit	1	4	
UCMP	155752	*Mictomys*	sp.	Left	m2	V93173	Pit	2	4	
UCMP	155753	*Mictomys*	sp.	Left	m2	V93173	Pit	2	4	
UCMP	155754	*Mictomys*	sp.	Right	m2	V93173	Pit	2	4	
UCMP	155755	*Mictomys*	sp.	Right	m2	V93173	Pit	2	4	
UCMP	155756	*Mictomys*	sp.	Left	m2	V93173	Pit	3	4	
UCMP	155757	*Mictomys*	sp.	Left	m2	V93173	Pit	3	4	
UCMP	155758	*Mictomys*	sp.	Left	m2	V93173	Pit	3	4	
UCMP	155759	*Mictomys*	sp.	Left	m2	V93173	Pit	3	4	
UCMP	155760	*Mictomys*	sp.	Left	m2	V93173	Pit	3	4	
UCMP	155761	*Mictomys*	sp.	Left	m2	V93173	Pit	3	4	
UCMP	155762	*Mictomys*	sp.	Left	m2	V93173	Pit	3	4	
UCMP	155763	*Mictomys*	sp.	Left	m2	V93173	Pit	3	4	
UCMP	155764	*Mictomys*	sp.	Right	m2	V93173	Pit	3	4	
UCMP	155794	*Mictomys*	sp.	Left	m3	V93173	Pit	1	4	
UCMP	155795	*Mictomys*	sp.	Left	m3	V93173	Pit	1	4	
UCMP	155796	*Mictomys*	sp.	Right	m3	V93173	Pit	1	4	
UCMP	155797	*Mictomys*	sp.	Right	m3	V93173	Pit	2	4	
UCMP	155798	*Mictomys*	sp.	Right	m3	V93173	Pit	2	4	
UCMP	155799	*Mictomys*	sp.	Left	m3	V93173	Pit	3	4	
UCMP	155800	*Mictomys*	sp.	Right	m3	V93173	Pit	3	4	
UCMP	155801	*Mictomys*	sp.	Right	m3	V93173	Pit	3	4	
UCMP	155802	*Mictomys*	sp.	Right	m3	V93173	Pit	3	4	
UCMP	155816	*Mictomys*	sp.	Left	Lower molar fragment	V93173	Pit	1	4	
UCMP	155817	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	1	4	
UCMP	155818	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	1	4	
UCMP	155819	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	1	4	
UCMP	155820	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	2	4	
UCMP	155821	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	2	4	
UCMP	155822	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	3	4	
UCMP	155823	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	3	4	
CM	45511	*Mictomys*	sp.	Right	M3	1925	Pit	1	5	
UCMP	155595	*Mictomys*	sp.	Right	M1	V93173	Pit	1	5	
UCMP	155596	*Mictomys*	sp.	Left	M1	V93173	Pit	2	5	
UCMP	155597	*Mictomys*	sp.	Right	M1	V93173	Pit	2	5	
UCMP	155598	*Mictomys*	sp.	Right	M1	V93173	Pit	2	5	
UCMP	155599	*Mictomys*	sp.	Right	M1	V93173	Pit	2	5	
UCMP	155600	*Mictomys*	sp.	Right	M1	V93173	Pit	2	5	
UCMP	155601	*Mictomys*	sp.	Left	M1 (broken)	V93173	Pit	3	5	
UCMP	155602	*Mictomys*	sp.	Left	M1 (partially digested)	V93173	Pit	3	5	
UCMP	155603	*Mictomys*	sp.	Left	M1	V93173	Pit	6	5	
UCMP	155604	*Mictomys*	sp.	Left	M1	V93173	Pit	6	5	
UCMP	155605	*Mictomys*	sp.	Left	M1	V93173	Pit	6	5	
UCMP	155606	*Mictomys*	sp.	Right	M1	V93173	Pit	6	5	
UCMP	155607	*Mictomys*	sp.	Right	M1	V93173	Pit	6	5	
UCMP	155608	*Mictomys*	sp.	Right	m1 (broken)	V93173	Pit	6	5	
UCMP	155609	*Mictomys*	sp.	Left	M1	V93173	Pit	7	5	
UCMP	155666	*Mictomys*	sp.	Left	M2 (broken)	V93173	Pit	1	5	
UCMP	155667	*Mictomys*	sp.	Right	M2	V93173	Pit	2	5	
UCMP	155668	*Mictomys*	sp.	Right	M2	V93173	Pit	2	5	
UCMP	155669	*Mictomys*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155670	*Mictomys*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155671	*Mictomys*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155672	*Mictomys*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155673	*Mictomys*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	155674	*Mictomys*	sp.	Right	M2	V93173	Pit	6	5	

(continued)

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
UCMP	155675	*Mictomys*	sp.	Right	M2	V93173	Pit	6	5	
UCMP	155676	*Mictomys*	sp.	Left	M2	V93173	Pit	7	5	
UCMP	155716	*Mictomys*	sp.	Right	M3	V93173	Pit	2	5	
UCMP	155717	*Mictomys*	sp.	Right	M3	V93173	Pit	6	5	
UCMP	155718	*Mictomys*	sp.	Left	M3	V93173	Pit	7	5	
UCMP	155719	*Mictomys*	sp.	Left	M3	V93173	Pit	7	5	
UCMP	155720	*Mictomys*	sp.	Right	M3 (broken)	V93173	Pit	7	5	
UCMP	155765	*Mictomys*	sp.	Left	m2	V93173	Pit	1	5	
UCMP	155766	*Mictomys*	sp.	Right	m2	V93173	Pit	1	5	
UCMP	155767	*Mictomys*	sp.	Left	m2	V93173	Pit	3	5	
UCMP	155768	*Mictomys*	sp.	Right	m2	V93173	Pit	3	5	
UCMP	155769	*Mictomys*	sp.	Left	m2	V93173	Pit	6	5	
UCMP	155770	*Mictomys*	sp.	Left	m2	V93173	Pit	7	5	
UCMP	155803	*Mictomys*	sp.	Left	m3	V93173	Pit	1	5	
UCMP	155804	*Mictomys*	sp.	Right	m3	V93173	Pit	6	5	
UCMP	155805	*Mictomys*	sp.	Left	m3	V93173	Pit	7	5	
UCMP	155824	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	6	5	
UCMP	155825	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	7	5	
UCMP	212929	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	6	5	
UCMP	155610	*Mictomys*	sp.	Left	M1	V93173	Pit	2	6	
UCMP	155611	*Mictomys*	sp.	Right	M1	V93173	Pit	2	6	
UCMP	155612	*Mictomys*	sp.	Right	M1	V93173	Pit	2	6	
UCMP	155613	*Mictomys*	sp.	Left	M1	V93173	Pit	3	6	
UCMP	155614	*Mictomys*	sp.	Left	M1 (broken)	V93173	Pit	3	6	
UCMP	155615	*Mictomys*	sp.	Left	M1	V93173	Pit	7	6	
UCMP	155616	*Mictomys*	sp.	Left	M1	V93173	Pit	7	6	
UCMP	155677	*Mictomys*	sp.	Right	M2	V93173	Pit	2	6	
UCMP	155678	*Mictomys*	sp.	Right	M2	V93173	Pit	3	6	
UCMP	155679	*Mictomys*	sp.	Right	M2	V93173	Pit	6	6	
UCMP	155680	*Mictomys*	sp.	Left	M2	V93173	Pit	7	6	
UCMP	155681	*Mictomys*	sp.	Right	M2	V93173	Pit	7	6	
UCMP	155721	*Mictomys*	sp.	Right	M3	V93173	Pit	3	6	
UCMP	155722	*Mictomys*	sp.	Right	M3	V93173	Pit	3	6	
UCMP	155723	*Mictomys*	sp.	Right	M3 (broken)	V93173	Pit	3	6	
UCMP	155724	*Mictomys*	sp.	Left	M3	V93173	Pit	6	6	
UCMP	155725	*Mictomys*	sp.	Left	M3	V93173	Pit	6	6	
UCMP	155726	*Mictomys*	sp.	Left	M3	V93173	Pit	7	6	
UCMP	155727	*Mictomys*	sp.	Right	M3	V93173	Pit	7	6	
UCMP	155771	*Mictomys*	sp.	Left	m2 (broken)	V93173	Pit	7	6	
UCMP	155772	*Mictomys*	sp.	Left	m2	V93173	Pit	7	6	
UCMP	155773	*Mictomys*	sp.	Left	m2	V93173	Pit	7	6	
UCMP	155774	*Mictomys*	sp.	Left	m2	V93173	Pit	7	6	
UCMP	155775	*Mictomys*	sp.	Right	m2	V93173	Pit	7	6	
UCMP	155806	*Mictomys*	sp.	Right	m3	V93173	Pit	3	6	
UCMP	155807	*Mictomys*	sp.	Left	m3	V93173	Pit	6	6	
UCMP	155808	*Mictomys*	sp.	Right	m3	V93173	Pit	6	6	
UCMP	155809	*Mictomys*	sp.	Right	m3	V93173	Pit	7	6	
UCMP	155826	*Mictomys*	sp.	Right	m2 or m3	V93173	Pit	3	6	
UCMP	155827	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	3	6	
UCMP	155828	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	3	6	
UCMP	155617	*Mictomys*	sp.	Left	M1	V93173	Pit	6	7	
UCMP	155618	*Mictomys*	sp.	Right	M1 (broken)	V93173	Pit	6	7	
UCMP	155619	*Mictomys*	sp.	Right	M1 (partially digested)	V93173	Pit	6	7	
UCMP	155620	*Mictomys*	sp.	Left	M1	V93173	Pit	7	7	
UCMP	155682	*Mictomys*	sp.	Right	M2	V93173	Pit	2	7	
UCMP	155683	*Mictomys*	sp.	Right	M2	V93173	Pit	2	7	
UCMP	155684	*Mictomys*	sp.	Right	M2	V93173	Pit	3	7	
UCMP	155685	*Mictomys*	sp.	Right	M2	V93173	Pit	3	7	
UCMP	155686	*Mictomys*	sp.	Right	M2	V93173	Pit	6	7	
UCMP	155687	*Mictomys*	sp.	Right	M2	V93173	Pit	7	7	
UCMP	155728	*Mictomys*	sp.	Left	M3	V93173	Pit	2	7	
UCMP	155729	*Mictomys*	sp.	Right	M3	V93173	Pit	2	7	
UCMP	155730	*Mictomys*	sp.	Left	M3	V93173	Pit	3	7	
UCMP	155731	*Mictomys*	sp.	Right	M3	V93173	Pit	3	7	
UCMP	155732	*Mictomys*	sp.	Right	M3	V93173	Pit	6	7	
UCMP	155733	*Mictomys*	sp.	Left	M3 (broken)	V93173	Pit	7	7	
UCMP	155776	*Mictomys*	sp.	Right	m2	V93173	Pit	2	7	
UCMP	155777	*Mictomys*	sp.	Right	m2	V93173	Pit	2	7	
UCMP	155778	*Mictomys*	sp.	Right	m2	V93173	Pit	2	7	

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	155779	*Mictomys*	sp.	Left	m2	V93173	Pit	3	7	
UCMP	155780	*Mictomys*	sp.	Right	m2	V93173	Pit	3	7	
UCMP	155810	*Mictomys*	sp.	Right	m3	V93173	Pit	2	7	
UCMP	155811	*Mictomys*	sp.	Right	m3	V93173	Pit	3	7	
UCMP	155812	*Mictomys*	sp.	Left	m3	V93173	Pit	6	7	
UCMP	155829	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	3	7	
UCMP	155830	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	3	7	
UCMP	155831	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	3	7	
UCMP	155832	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	6	7	
UCMP	155833	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	6	7	
UCMP	155834	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	7	7	
UCMP	155835	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	7	7	
UCMP	155836	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	7	7	
UCMP	155621	*Mictomys*	sp.	Left	M1	V93173	Pit	2	8	
UCMP	155622	*Mictomys*	sp.	Left	M1	V93173	Pit	2	8	
UCMP	155623	*Mictomys*	sp.	Right	M1	V93173	Pit	2	8	
UCMP	155624	*Mictomys*	sp.	Right	M1	V93173	Pit	2	8	
UCMP	155625	*Mictomys*	sp.	Right	M1 (broken)	V93173	Pit	2	8	
UCMP	155643	*Mictomys*	sp.	Left	M1 or M2 (broken)	V93173	Pit	2	8	
UCMP	155688	*Mictomys*	sp.	Left	M2	V93173	Pit	2	8	
UCMP	155689	*Mictomys*	sp.	Right	M2	V93173	Pit	2	8	
UCMP	155690	*Mictomys*	sp.	Right	M2	V93173	Pit	2	8	
UCMP	155734	*Mictomys*	sp.	Left	M3	V93173	Pit	2	8	
UCMP	155735	*Mictomys*	sp.	Right	M3	V93173	Pit	2	8	
UCMP	155736	*Mictomys*	sp.	Right	M3	V93173	Pit	2	8	
UCMP	155781	*Mictomys*	sp.	Left	m2	V93173	Pit	2	8	
UCMP	155782	*Mictomys*	sp.	Left	m2	V93173	Pit	2	8	
UCMP	155783	*Mictomys*	sp.	Right	m2	V93173	Pit	2	8	
UCMP	155784	*Mictomys*	sp.	Right	m2	V93173	Pit	2	8	
UCMP	155785	*Mictomys*	sp.	Right	m2	V93173	Pit	2	8	
UCMP	155786	*Mictomys*	sp.	Right	m2	V93173	Pit	2	8	
UCMP	155837	*Mictomys*	sp.	Right	Lower molar fragment	V93173	Pit	2	8	
UCMP	155738	*Mictomys*	sp.	Right	M3 (broken)	V93173	Pit	6	9	
UCMP	155634	*Mictomys*	sp.	Left	M1	V93173	Pit	3	10	
UCMP	155635	*Mictomys*	sp.	Left	M1	V93173	Pit	3	10	
UCMP	155636	*Mictomys*	sp.	Left	M1	V93173	Pit	7	10	
UCMP	155637	*Mictomys*	sp.	Left	M1	V93173	Pit	7	10	
UCMP	155695	*Mictomys*	sp.	Left	M2	V93173	Pit	3	10	
UCMP	155696	*Mictomys*	sp.	Left	M2	V93173	Pit	3	10	
UCMP	155697	*Mictomys*	sp.	Left	M2	V93173	Pit	6	10	
UCMP	155739	*Mictomys*	sp.	Right	M3	V93173	Pit	7	10	
UCMP	155787	*Mictomys*	sp.	Left	m2	V93173	Pit	7	10	
UCMP	155814	*Mictomys*	sp.	Right	m3	V93173	Pit	3	10	
UCMP	155815	*Mictomys*	sp.	Left	m3	V93173	Pit	6	10	
UCMP	155838	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	3	10	
UCMP	155638	*Mictomys*	sp.	Right	M1	V93173	Pit	2	11	
UCMP	155639	*Mictomys*	sp.	Left	M1	V93173	Pit	3	11	
UCMP	155640	*Mictomys*	sp.	Right	M1	V93173	Pit	3	11	
UCMP	155641	*Mictomys*	sp.	Right	M1	V93173	Pit	6	11	
UCMP	155740	*Mictomys*	sp.	Right	M3	V93173	Pit	2	11	
UCMP	155741	*Mictomys*	sp.	Right	M3	V93173	Pit	3	11	
UCMP	155788	*Mictomys*	sp.	Left	m2	V93173	Pit	3	11	
UCMP	155789	*Mictomys*	sp.	Right	m2	V93173	Pit	3	11	
UCMP	155790	*Mictomys*	sp.	Left	m2	V93173	Pit	7	11	
UCMP	155839	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	2	11	
UCMP	155840	*Mictomys*	sp.	?	Lower molar fragment	V93173	Pit	7	11	
UCMP	155642	*Mictomys*	sp.	Right	M1	V93173	Pit	2	12	
UCMP	155626	*Mictomys*	sp.	Left	M1 (partially digested)	V93173	Pit	3	8A	
UCMP	155627	*Mictomys*	sp.	Left	M1 (partially digested)	V93173	Pit	3	8A	
UCMP	155628	*Mictomys*	sp.	Left	M1	V93173	Pit	3	8A	
UCMP	155629	*Mictomys*	sp.	Left	M1	V93173	Pit	3	8A	
UCMP	155630	*Mictomys*	sp.	Left	M1	V93173	Pit	7	8A	
UCMP	155631	*Mictomys*	sp.	Left	M1	V93173	Pit	7	8A	
UCMP	155632	*Mictomys*	sp.	Right	M1	V93173	Pit	7	8A	
UCMP	155633	*Mictomys*	sp.	Right	M1	V93173	Pit	7	8A	
UCMP	155691	*Mictomys*	sp.	Left	M2	V93173	Pit	3	8A	
UCMP	155692	*Mictomys*	sp.	Right	M2	V93173	Pit	3	8A	
UCMP	155693	*Mictomys*	sp.	Left	M2	V93173	Pit	7	8A	

(continued)

	Number	Genus	Species	Side	Element	Locality No.	Locality	Grid	Level	Horizon
UCMP	155694	*Mictomys*	sp.	Right	M2	V93173	Pit	7	8A	
UCMP	155737	*Mictomys*	sp.	Left	M3	V93173	Pit	3	8A	
UCMP	155742	*Mictomys*	sp.	Left	M1or M2 (broken)	V93173	Pit	3	8A	
UCMP	155813	*Mictomys*	sp.	Right	m3	V93173	Pit	3	8A	
UCMP	156167	*Mimomys*	*virginianus*	Right	m2	V93173	Pit	3	4	
UCMP	155188	*Mimomys*	*virginianus*	Right	m1 (broken)	V93173	Pit	6	5	
UCMP	156158	*Mimomys*	*virginianus*	Left	m2	V93173	Pit	2	5	
UCMP	156159	*Mimomys*	*virginianus*	Right	m2	V93173	Pit	6	5	
UCMP	156164	*Mimomys*	*virginianus*	Left	m2	V93173	Pit	3	5	
UCMP	155189	*Mimomys*	*virginianus*	Left	Dentary with m1-2	V93173	Pit	3	6	
UCMP	156160	*Mimomys*	*virginianus*	Left	M1	V93173	Pit	7	7	
UCMP	156161	*Mimomys*	*virginianus*	Right	M1	V93173	Pit	7	7	
UCMP	156165	*Mimomys*	*virginianus*	Right	M2	V93173	Pit	6	7	
UCMP	155190	*Mimomys*	*virginianus*	Left	M3	V93173	Pit	3	7	
UCMP	155191	*Mimomys*	*virginianus*	Left	M1 (broken)	V93173	Pit	7	8A	
UCMP	155566	*Mimomys*	*virginianus*	Left	m1	V93173	Pit	7	8A	
UCMP	156166	*Mimomys*	*virginianus*	Right	M2	V93173	Pit	3	8A	
UCMP	156168	*Mimomys*	*virginianus*	Left	m2	V93173	Pit	7	8A	
UCMP	156169	*Mimomys*	*virginianus*	Left	m3	V93173	Pit	7	8A	
UCMP	156162	*Mimomys*	*virginianus*	Left	M1	V93173	Pit	7	10	
UCMP	156163	*Mimomys*	*virginianus*	Right	M1	V93173	Pit	7	10	
CM	45409	*Ondatra*	sp.	Right	M3	1925	Pit	1	1	
CM	66522	*Ondatra*	sp.	Left	M2	1925	Pit	1	2	
UCMP	155567	*Ondatra*	sp.	Right	m1 (broken, juvenile)	V93173	Pit	5/6 or 1/5	2	
UCMP	155848	*Ondatra*	sp.	Right	M1	V93173	Pit	1	2	
UCMP	155850	*Ondatra*	sp.	Right	M2	V93173	Pit	1	1 or 2	
UCMP	155849	*Ondatra*	sp.	Left	M1	V93173	Pit	1	4	
UCMP	155851	*Ondatra*	sp.	Left	M2	V93173	Pit	2	4	
UCMP	155852	*Ondatra*	sp.	Right	M3	V93173	Pit	1	4	
UCMP	155853	*Ondatra*	sp.	Left	M3	V93173	Pit	2	4	
UCMP	155856	*Ondatra*	sp.	Left	Broken lower molar	V93173	Pit	1	4	
UCMP	155854	*Ondatra*	sp.	Left	M3	V93173	Pit	6	5	
UCMP	155855	*Ondatra*	sp.	Right	M3	V93173	Pit	3	8A	
UCMP	155194	*Phenacomys*	*gryci*	Left	m1	V93173	Pit	3	4	
UCMP	155195	*Phenacomys*	*gryci*	Right	m1	V93173	Pit	2	10	
UCMP	155193	*Phenacomys*	sp. (not *P. gryci*)	Left	m1	V93173	Pit	5/6	3	
CM	66365	*Phenacomys*	sp. (not *P. gryci*)	Right	m1	1925	Pit	1	1	
UCMP	155192	*Phenacomys*	sp. (not *P. gryci*)	Right	m1	V93173	Pit	1	2	
CM	45420	*Phenacomys*	sp.	Right	M1	1925	Pit	1	1	
CM	66364	*Phenacomys*	sp.	Left	M1	1925	Pit	1	1	
UCMP	212906	*Phenacomys*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	212907	*Phenacomys*	sp.	Left	M2	V93173	Pit	1	1	
UCMP	212914	*Phenacomys*	sp.	Right	m2	V93173	Pit	1	1	
UCMP	212915	*Phenacomys*	sp.	Right	m2	V93173	Pit	1	1	
UCMP	212920	*Phenacomys*	sp.	Left	M3	V93173	Pit	1	1	
UCMP	212921	*Phenacomys*	sp.	Left	m3	V93173	Pit	1	1	
CM	66521	*Phenacomys*	sp.	Left	m2	1925	Pit	1	2	
UCMP	212900	*Phenacomys*	sp.	Right	M1	V93173	Pit	3	4	
UCMP	212901	*Phenacomys*	sp.	Right	M1	V93173	Pit	1	4	
UCMP	212908	*Phenacomys*	sp.	Left	M2	V93173	Pit	3	4	
UCMP	212916	*Phenacomys*	sp.	Left	m2	V93173	Pit	3	4	
UCMP	212923	*Phenacomys*	sp.	?	Molar fragment	V93173	Pit	3	4	
UCMP	212927	*Phenacomys*	sp.	?	Molar fragment	V93173	Pit	3	4	
UCMP	212909	*Phenacomys*	sp.	Left	M2	V93173	Pit	6	5	
UCMP	212910	*Phenacomys*	sp.	Right	M2	V93173	Pit	2	5	
UCMP	212917	*Phenacomys*	sp.	Left	m2	V93173	Pit	7	5	
UCMP	212902	*Phenacomys*	sp.	Left	M1	V93173	Pit	7	6	
UCMP	212903	*Phenacomys*	sp.	Left	M1	V93173	Pit	3	6	
UCMP	212911	*Phenacomys*	sp.	Right	M2	V93173	Pit	2	6	
UCMP	212925	*Phenacomys*	sp.	Right	Molar fragment	V93173	Pit	3	6	
UCMP	212904	*Phenacomys*	sp.	Right	M1	V93173	Pit	2	7	
UCMP	212912	*Phenacomys*	sp.	Left	M2	V93173	Pit	6	7	
UCMP	212918	*Phenacomys*	sp.	Left	m2	V93173	Pit	3	7	
UCMP	212928	*Phenacomys*	sp.		Molar fragment	V93173	Pit	7	7	
UCMP	212924	*Phenacomys*	sp.	Left	Molar fragment	V93173	Pit	2	8	
UCMP	212922	*Phenacomys*	sp.	Left	m2 (broken, partially digested)	V93173	Pit	6	9	
UCMP	212919	*Phenacomys*	sp.	Left	m2	V93173	Pit	3	10	

	Number	*Genus*	*Species*	*Side*	*Element*	*Locality No.*	*Locality*	*Grid*	*Level*	*Horizon*
UCMP	212913	*Phenacomys*	sp.	Right	M2	V93173	Pit	7	11	
UCMP	212905	*Phenacomys*	sp.	Left	M1	V93173	Pit	7	8A	
UCMP	212926	cf. *Phenacomys*	sp.	?	Molar fragment	V93173	Pit	1	4	
DMNH	38269	*Lemmiscus*	(4T)	Right	Dentary with m1-2	DMNH 1350	Will's Hole			
DMNH	38270	*Microtus*	*meadensis*	Left	m1		Will's Hole			
DMNH	38271	*Microtus*	*meadensis*	Left	Dentary fragment with m1		Will's Hole			
DMNH	38272	*Microtus*	*meadensis*	Right	Dentary fragment with i1, m1		Will's Hole			
UCMP	155328	*Lemmiscus*	*curtatus*	Right	m1	V97002	Undifferentiated			
CM	45480	*Lemmiscus*	sp.	Left	M3	1932	Undifferentiated			
CM	45481	*Lemmiscus*	sp.	Left	M3	1932	Undifferentiated			
CM	45448	*Microtus*	*meadensis*	Right	Dentary with i1, m1	1932	Undifferentiated			
CM	45449	*Microtus*	*meadensis*	Left	m1	1932	Undifferentiated			
CM	45450	*Microtus*	*meadensis*	Left	m1	1932	Undifferentiated			
CM	45451	*Microtus*	*meadensis*	Right	m1	1932	Undifferentiated			
CM	45452	*Microtus*	*meadensis*	Right	m1	1932	Undifferentiated			
CM	45453	*Microtus*	*meadensis*	Right	m1	1932	Undifferentiated			
UCMP	155260	*Microtus*	*meadensis*	Left	m1	V97002	Undifferentiated			

Acknowledgments

We thank our colleagues interested in arvicolines for their stimulating conversations over the years, especially Robert A. Martin, Wigart von Koenigswald, and Richard Zakrzewski. We also offer thanks to Elaine Anderson for funneling specimens to us in a timely manner as they were picked from the DMNH excavation, and to Don Rasmussen for his hard work on many of the excavations that produced arvicolines, and for encouraging paleontological research in the cave. Betty Hill (CM), Pat Holroyd (UCMP), and Logan Ivy (DMNH) facilitated loans and remained patient while material was identified and curated. The research reported in this chapter was partially supported by NSF grant BSR-9196082. Financial and logistical support from the UCMP and from the University of Texas Geology Foundation is acknowledged. Because of ADB's participation, this chapter may be considered University of California Museum of Paleontology contribution 1813.

TWENTY

Pliocene and Pleistocene Horses from Porcupine Cave

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Perissodactyl fossils from Porcupine Cave are relatively rare, represented by only 56 fragments of horses (*Equus* spp.). Given this relative paucity of material, combined with the generally nondiagnostic nature of the remains and the confused systematics of North American Pleistocene horses, the equids from Porcupine Cave cannot be conclusively identified to species. However, in some cases the size or morphology of the recovered remains permits specific or subgeneric affinities to be suggested.

The equid fossils consist almost exclusively of isolated broken tooth portions or of distal limb elements. Most of this material was recovered from three distinct localities: the Badger Room (CM 1928, DMNH 942, UCMP V93176), the Pit (CM 1925,UCMP V93173), and the Velvet Room. The latter region has been the site of five distinct excavations; horse fossils have been recovered from the CM excavation (CM 1927, UCMP V93175), the DMNH excavation (DMNH 644), and Mark's Sink (DMNH 1349).

The deposits in the Pit are perhaps the most thoroughly dated so far, dating from as old as 1 Ma at the bottom to as young as 600 Ka at the top. Mark's Sink contains the oldest fossils from Porcupine Cave, perhaps dating to the late Blancan, but these fossils are stratigraphically mixed with younger material. Fissure Fill A may also be relatively old (Anderson, 1996), possibly Blancan or early Irvingtonian, and this hypothesis is discussed in more detail later in this chapter. The fossils from the Badger Room are thought to equate temporally with stratigraphic levels between levels 4 and 8 in the Pit. Velvet Room localities other than Mark's Sink seem younger than all but the uppermost Pit levels.

Materials, Methods, and Taxonomic Considerations

Three institutions house the Porcupine Cave fossils discussed in this chapter: the Carnegie Museum of Natural History (CM), the Denver Museum of Nature and Science (DMNH), and the University of California Museum of Paleontology (UCMP). Identifications were based on direct comparison with fossils representing the taxa listed in the subsequent sections. Much confusion exists about the names and conceptualization of these taxa; the following comments clarify how the taxonomic names are used in this chapter.

Equus (Plesippus) simplicidens Cope, 1893

The comparative sample included fossils from the Hagerman Horse Quarry, Twin Falls County, Idaho. Initially these specimens were referred to *Plesippus shoshonensis* by Gazin (1936), but they were subsequently synonymized with *E. (P.) simplicidens* (Skinner, 1972; McDonald, 1996). They are housed at the Hagerman Fossil Beds National Monument (HAFO) and at the Natural History Museum of Los Angeles County (LACM). The taxon *Plesippus* was originally proposed as a genus by Matthew (1924); Schultz (1936) followed this usage. *Plesippus* was later synonymized by Skinner (1972) with the extant zebra subgenus *Dolichohippus* Heller, 1912. More recent studies have preferred to separate *Plesippus* from *Dolichohippus* and to consider it a valid subgenus of *Equus* (Forsten and Eisenmann, 1995; Eisenmann and Baylac, 2000) or a valid genus (Repenning et al., 1995; Albright, 1999; but see Kelly, 1997, for a contrary view). For the purposes of this study *Plesippus* is considered a valid subgenus of *Equus*.

Equus (Asinus) cumminsi Cope, 1893

The comparative sample included fossils from the Blanco Local Fauna (type locality), Texas (Cope, 1893; Dalquest, 1975, 1988) and the Red Light Local Fauna, Hudspeth County, Texas (Akersten, 1972). Fossils from the Blanco and from the Red Light faunas are housed at the Texas Memorial Museum (TMM), University of Texas, Austin. The lectotype is not entirely diagnostic, but the type locality is well documented and topotypal fossils help augment the species diagnosis. For the purposes of the present study, *E. (A.) cumminsi* is considered a valid species designation for later Pliocene (and possibly early Pleistocene) small, asslike equines. The complicated history of the taxonomy of this species is discussed later in this chapter.

Equus conversidens **Owen, 1869**

The comparative sample included referred specimens from San Josecito Cave, Nuevo León, Mexico (*E. conversidens leoni* of Stock, 1950), which are housed at the LACM. Additional fossils were examined from Rancho La Brea, Los Angeles, California (Scott, 1990); they are housed at the George C. Page Museum of La Brea Discoveries (GCPM). Supplementary specimens of small horses from Fort Irwin, Kokoweef Cave, and the Piute Valley, San Bernardino County, California (Scott, 1996, 1997), housed at the San Bernardino County Museum (SBCM), were included in the comparisons. Published information (Harris and Porter, 1980) and unpublished data (A. Harris, pers. comm.) on fossils of *E. conversidens* from Dry Cave, New Mexico, were also employed.

The validity of *Equus conversidens* has been challenged (Winans, 1989; MacFadden, 1992) on the basis that the holotype specimen is not diagnostic. That holotype was named prior to the presently accepted strict codification of zoological naming procedures. Numerous species names proposed in the late 1800s and early 1900s for Pleistocene horses are based on insufficiently diagnostic material, yet many of the names continue to be employed. To reject these names, although perhaps technically advisable, would result in considerable taxonomic confusion and instability. Here the name *E. conversidens* (and some other equid taxa mentioned later) is maintained primarily because it has a long history of use and promotes taxonomic stability. The International Code of Zoological Nomenclature (International Committee on Zoological Nomenclature, 2000:article 75.5) and Simpson (1945) support such an approach, although eventual designation of a suitable neotype would be desirable and is recommended. In the interim, my consideration of *E. conversidens* as a valid species recognizes that its phylogenetic relationships have not yet been fully determined.

At present, at least three different, but potentially valid, diagnoses of the morphology and interpretations of the relationships of *Equus conversidens* are present in the literature (Scott, 1996). This chapter employs the most commonly used of the diagnoses, considering the species to be a small, stout-limbed equid, following the conventions of numerous previous investigations (Skinner, 1942; Stock, 1950; Hibbard, 1955; Slaughter, 1966a; Mooser and Dalquest, 1975; Dalquest, 1978, 1988; Harris and Porter, 1980; Kurtén and Anderson, 1980; Azzaroli, 1992, 1998; Dalquest and Schultz, 1992).

Equus (Hemionus) **spp.**

The comparative sample includes fossils from south of Dalhart in Hartley County, Texas, housed at the American Museum of Natural History (AMNH), which previously were referred to "*Equus (Hemionus) conversidens.*" *E. conversidens* as conceptualized in this chapter is not considered to be a hemionine equid taxon (see previous section). Azzaroli (1995, 1998) considered the Hartley County fossils better referred to the species *Equus semiplicatus* Cope, 1893 (which Azzaroli interpreted to include the large hemionine *E. calobatus* Troxell, 1915; see "Problems with Hemionine Taxonomy"). There is in fact some overlap between those Hartley County fossils and paralectotypal fossils of *E. (H.) calobatus* from Briscoe County, Texas, but the latter fossils are generally larger, and it is not clear if the two samples represent the same species. The Hartley County fossils are referred conservatively to *Equus (Hemionus)* sp. herein.

Also considered as *Equus (Hemionus)* sp. in this study are fossils from Sheridan County, Nebraska, that were used in comparisons and reside at the University of Nebraska State Museum (UNSM). These specimens were previously referred to *Equus (Hemionus) calobatus* (Troxell) 1915, but the sample has the same difficulties as that from Hartley County, so species assignment is not warranted.

Published measurements of a paralectotypal metacarpal (Troxell, 1915) and unpublished measurements of paralectotypal and topotypal phalanges (L. K. Murray, pers. comm.) of *E. (H.) calobatus* from the Yale Peabody Museum (YPM) were also used in deciding which Porcupine Cave fossils should be assigned to this subgenus.

PROBLEMS WITH HEMIONINE TAXONOMY

Hemionine equid species reported from North America include a large species and one or possibly two smaller species (Troxell, 1915; Savage, 1951; Winans, 1989; Dalquest and Schultz, 1992; Azzaroli, 1998). The taxonomy of these species is unclear. The large form is often referred to the taxon *Equus calobatus* Troxell, 1915, a species initially based on long, slender limb elements of a large equid from Rock Creek, Texas. Savage (1951:244) considered *E. calobatus* to be a *nomen vanum* but did not suggest any better species designation, concluding only that "equid remains [from Rock Creek], with the exception of *Equus scotti* Gidley, should pertain to only one species." The only other species from Rock Creek mentioned in this context, *Equus semiplicatus* Cope, 1893, was also considered a *nomen vanum* by Savage (1951), so it is not clear what name he preferred for the fossils, if any. Azzaroli (1995, 1998) seemingly followed Savage (1951) to some degree, preferring to consider *E. calobatus* a junior synonym of *Equus semiplicatus* Cope, 1893. Azzaroli (1995, 1998) based his interpretation in part on the fossils mentioned previously from south of Dalhart in Hartley County, Texas, in the collections of the AMNH. As noted previously, these fossils—and the holotype fossils of *E. semiplicatus*—may be too small to be confidently aligned with *E. calobatus.* The latter taxon is here preferred for large, stilt-legged Pleistocene horses from North America.

Smaller stilt-legged Pleistocene horses—*Equus (Hemionus)* sp.—have been referred with equal authority to *Equus tau* Owen, 1869 (Savage, 1951; Dalquest, 1978) or to *Equus francisi* Hay, 1915 (Lundelius and Stevens, 1970; Winans, 1989;

Azzaroli, 1998). Dalquest and Schultz (1992) proposed that perhaps both *E. tau* and *E. francisi* were valid species, the former slightly smaller than the latter.

Equus conversidens has also been interpreted by some researchers as a small stilt-legged equid. For example, Dalquest and Hughes (1965) proposed that slender small horse phalanges from Slaton Quarry, Texas, were best attributed to *E. conversidens,* but this conclusion was advanced at a time when *E. conversidens* and *E. francisi* were considered synonymous (following Savage, 1951, and Hibbard, 1955). The subsequent determination that *E. francisi* was a stilt-legged equid (Lundelius and Stevens, 1970) and the identification of teeth resembling *E. francisi* from the Slaton Quarry site (Dalquest and Schultz, 1992) suggest that the small, slender phalanges from that site—originally interpreted to be *E. conversidens* (Dalquest and Hughes, 1965)—are probably more correctly assigned to *E. francisi.* Skinner (1972) also proposed that *E. conversidens* was a stilt-legged hemionine, a reinterpretation of his earlier (1942) analysis of fossils from Papago Springs Cave, Arizona. Postcranial elements originally assigned to *E. conversidens* (Skinner, 1942) were later determined to "represent another form of *Equus* for which we found no dentition" (Skinner, 1972:125), whereas a slender phalanx originally referred to *Equus tau* Owen (1869) (Skinner, 1942) was reassigned to *E. conversidens* based on "studies of living and extinct *Equus* in the American Museum of Natural History Mammal and Frick Collections" (Skinner, 1972:125). No additional diagnosis or rationale for this new interpretation was advanced.

Bennett (1980) cited *E. conversidens* as having elongate metapodials, although specimens exhibiting this morphology were neither listed nor described. Bennett (1980) acknowledged unpublished data from Skinner as her "guidepost" during her investigation, and so this usage may reflect Skinner's influence to some degree. Similarly, Downs and Miller (1994:9) employed the "expertise, information, and written comments provided by Morris F. Skinner in the late 1980s," as well as Skinner's (1972) work, to establish characters for living and fossil subgenera of *Equus;* this work probably presents the morphologic criteria on which Skinner's (1972) efforts were based. Downs and Miller (1994) listed *E. conversidens* as *"Equus (Hemionus) conversidens,"* a small, stilt-legged equid. Additional features that further defined this interpretation of *E. conversidens* included a short rostrum, no ectoflexid penetration in m1-2 with occasional penetration in m3, broad U-shaped linguaflexids, and infundibulae in the lower incisors (Downs and Miller, 1994:6).

The foregoing discussion clearly illustrates that the taxonomy of the Pleistocene hemionine horses in North America is badly confused and in need of revision, which is beyond the scope of this chapter. For the present, these animals will be discussed simply as "*Equus (Hemionus)* spp."

Equus scotti Gidley, 1900

The comparative sample included fossils from Rock Creek, Briscoe County, Texas (Gidley, 1900), which are housed at the AMNH and the UCMP. Additional referred fossils are from Murrieta and Temecula, Riverside County, California (Scott, 1998), housed at the SBCM, and the American Falls Reservoir, southeastern Idaho (Pinsof, 1998), housed at the Idaho State Museum of Natural History, Pocatello, Idaho (IMNH). Azzaroli (1995, 1998) proposed that *Equus scotti* is best considered a junior synonym of *Equus excelsus* Leidy, 1858. This latter species, however, is based on a nondiagnostic lectotype. Furthermore, the type locality was not adequately described, the geologic age of the lectotype is indeterminate, and topotypal fossils are not available, so an expanded diagnosis of the species is not possible (Savage, 1951). *E. scotti* is considered the more appropriate name in this chapter, because it is better defined, based on several individuals from the well-reported type locality at Rock Creek, Texas.

Equus occidentalis Leidy, 1865 (sensu Merriam, 1913; hereafter termed *E. "occidentalis"*)

The comparative material included fossils from Rancho La Brea, Los Angeles, and Diamond Valley Lake in Riverside County, California. These fossils reside at the GCPM (Rancho La Brea fossils) and the SBCM (Diamond Valley Lake specimens). The name *Equus occidentalis* is technically a *nomen vanum* in that it was based on nondiagnostic cheek teeth from an unknown locality (Miller, 1971; Scott, 1992). Nevertheless it has been commonly employed to refer to the large horses from Rancho La Brea, following Merriam (1913). Winans (1989) placed the large Rancho La Brea horses in her "*Equus laurentius* species group," and some subsequent studies (e.g., MacFadden, 1992; Duckler and Van Valkenburgh, 1998) have seemed to treat this as a synonymy. In fact, *E. laurentius* is indistinguishable from *E. caballus* (Matthew, 1926; Savage, 1951), and so this name should not be used to refer to the large horse from Rancho La Brea. Until the taxonomy and systematics of the large horses from Rancho La Brea can be more thoroughly studied, they are best referred to *E. "occidentalis,"* with the quotation marks indicating that the name is used sensu Merriam (1913).

Choice of Morphological Characters in Taxonomic Assignments

There is currently no agreement as to the number of large and small equid species that roamed North America during the Pliocene and Pleistocene epochs. The most commonly adopted synonymy at present appears to be that of Winans (1989), who recognized five metrically defined "species groups" in North America. Winans (1989:295) clearly emphasized the possibility "that some of the [species] groups . . . defined encompass more than one species," yet subsequent studies have employed her species groups as if they were actual species—or at least as if the species names she employed were valid (e.g., MacFadden, 1992, 1998; Duckler and Van Valkenburgh, 1998; Pinsof, 1998). Other recent taxonomic revisions have focused more on morphology than on metrics, and have proposed estimates ranging from 9 (Dalquest, 1988) to 10 (Bennett, 1980) to 15 (Azzaroli and Voorhies, 1993; Azzaroli, 1995, 1998) species of extinct North American equids. All these revisions are hindered by the lack of agreement on how the Plio-Pleistocene species are defined.

Part of the problem is that the most common fossils, teeth and crania, have not yet been proven to reliably reflect real differences between species. This difficulty was made especially clear by studies of extant Old World equids. Klein and Cruz-Uribe (1996) attempted to use discriminant analyses of cranial characters to determine the affinities of subfossil skulls from South Africa. The groups yielded by the analysis of the cranial characters did not match species clusters of extant equids based on mtDNA (George and Ryder, 1986). If the mitochondrial data are correct, then it is clear that "biomolecular similarity . . . may not extend to the cranium" (Klein and Cruz-Uribe, 1996:626).

The same problem applies to isolated dental material, perhaps even more so. Hulbert (1995) recognized this in adopting a conservative taxonomic approach in his description of Pleistocene *Equus* from the Leisey Shell Pit site in Florida, preferring to assign letter designations (A, B, and C) to the equid morphospecies observed in the sample rather than making species referrals.

In light of these problems, the morphological criteria utilized in this chapter are those thought to be most helpful in elucidating the systematics of this difficult group, taking into account that the fossil record produces mostly isolated teeth and podial elements. The useful characters include the following:

1. Body size, inferred from postcranial elements (Von den Driesch, 1976; Harris and Porter, 1980; Eisenmann et al., 1988), particularly metapodials because they are weight-bearing elements (Guthrie, 1990) and are relatively common in many fossil assemblages.
2. Shape of the protocone, primarily in upper premolars (Eisenmann et al., 1988).
3. Depth of the molar ectoflexid relative to the molar isthmus in the lower molars (Skinner, 1972; Dalquest, 1978, 1988; Eisenmann et al., 1988; Downs and Miller, 1994; Hulbert, 1995).
4. Presence of infundibulae (enamel-lined cups) in some or all of the lower incisors (Cope, 1892; Gidley, 1901; Hoffstetter, 1950; Bennett, 1980; Eisenmann et al., 1988; Downs and Miller, 1994; Hulbert, 1995).
5. Length and stoutness of the metapodials and first phalanges (Bennett, 1980; Downs and Miller, 1994).

Missing from this list of features is the morphology of the linguaflexids of the lower molars. Students of European and African Plio-Pleistocene horses (e.g., Forsten, 1986; Eisenmann et al., 1988) have used this feature to reliably distinguish Old World caballine and zebrine (or "stenonid") equids. Caballine horses have U-shaped linguaflexids, whereas zebrine horses have V-shaped linguaflexids. However, the linguaflexids of North American Pleistocene horses are generally quite variable (Dalquest, 1988; Dalquest and Schultz, 1992) and therefore generally unreliable in phylogenetic analyses. For example, my own recent examination of lower molars of *Equus "occidentalis"* from Rancho La Brea revealed that, even when the study was confined to teeth rooted in the dentary, and to animals of the same sex (based on presence of canine teeth in the jaw) and approximately the same ontogenetic age (based on tooth eruption and wear), both U-shaped and V-shaped linguaflexids were observed in the lower molars. This observation strongly suggests that this feature is not useful in delineating phylogenetic relationships among North American Pleistocene equids.

The dental characters listed as useful here have been regarded by some authors (Groves and Willoughby, 1981:341) to be among the *least* useful traits for elucidating phylogenetic relationships among extinct equids. Groves and Willoughby (1981) advocated limb proportions as the primary basis for identifying fossil equids, followed by cranial characters (but see the contrary indication of Klein and Cruz-Uribe, 1996, discussed previously), and only third by dentition. Unfortunately, the sample of horse fossils from Porcupine Cave does not provide either substantial postcranial or cranial evidence, mandating that most conclusions derive from dental characters. Included in the suite of dental characters used in identifying the Porcupine Cave horses are those Groves and Willoughby (1981) cited as potentially useful, specifically the degree of penetration of the molar ectoflexid and the presence or absence of infundibulae in the lower incisors. The known problems of within-taxon variability of the other dental characters employed herein were reduced somewhat by taking the ontogenetic age of individuals into account.

Measurements

Measurements were taken following the procedures outlined by Von den Driesch (1976) and defined by Harris and Porter (1980). Data were acquired using Mitutoyo Digimatic calipers connected by a Mitutoyo MRS100 caliper interface cable to a Hitachi VisionBook Plus 5000 laptop running the CalExcel caliper interface program (32-bit version for Windows 95/NT; Timothy Heaton and Jim Bourdon, Vermillion, South Dakota). Graphic plots were generated using SigmaPlot 5.0 (SPSS, Inc., Richmond, California).

Taphonomy

Element Preservation and Representation

The equid fossils from the Badger Room (*N* = 10) consist of five partial teeth, a proximal scapula fragment, a distal metapodial, an astragalus, and two phalanges (II and III). The teeth include two slightly worn deciduous premolars (very likely from a single individual) and one worn adult premolar, all from a large horse species, as well as a partial lower deciduous premolar from a small equid. Both large and small horse species are also represented among the postcranial remains. With the exception of the second phalanx (CM 49283), all the bones and teeth from the Badger Room are broken to some degree. Breakage on the astragalus (DMNH 23073) and the terminal phalanx (DMNH 23072) appears to be recent. Breakage on the remaining fossils is primarily predepositional, although many specimens also exhibit some small degree of recent breakage. Of interest here is the broken midshaft region of the distal metapodial (CM 49179), which is spirally fractured and suggests "green" bone breakage (figure 20.1). This specimen lacks other indications of carnivore activity or trampling.

Equid fossils from the Pit (*N* = 15) include two teeth (one unworn deciduous premolar, one very worn adult premolar), five proximal sesamoids, one scaphoid, two first phalanges, four second phalanges, and one terminal phalanx. Both large and small horse species are represented in the sample. Breakage is minor on all elements, probably because of the small and sturdy nature of most of the specimens.

Fossils of extinct horses from the Velvet Room (*N* = 19; 1 from the CM excavation, 10 from the DMNH excavation, and 8 from Mark's Sink) are represented by 10 teeth or tooth fragments, a patella, a distal metapodial, two phalanges (I and II), sesamoids (two proximal, one distal), and two scaphoids. Deciduous and adult teeth are present; both large and small equids are represented.

Weathering

Three specimens from the Badger Room—a proximal scapula (CM 73356), the lunar (CM 49181), and a terminal phalanx (DMNH 23072)—appear to have been subaerially exposed prior to fossilization. The surface of the scapula is rounded and lightly polished, and the neck of the corocoid process is eroded to reveal cancellous bone; this abrasion appears to be the result of water wear. The inferior articular surface of the lunar is pitted, the body of the bone has suffered surficial flaking and rounding, and the dorsal face has a shallow transverse crack—features that are suggestive of weathering owing to subaerial exposure (Hill, 1980). The broken terminal phalanx is likewise surficially flaked, particularly on the plantar surface but also on the articulation, again indicating weathering. Damage to both elements accords closely with descriptions of stage 1 weathering as defined by Behrensmeyer (1978).

Only one equid bone from the Pit, a scaphoid (CM 49285), exhibits any firm evidence of climatic weathering, and again this damage resembles stage 1 weathering (Behrensmeyer, 1978). The inferior articular surface is lightly pitted, and the outer surface is coarse. Three of the proximal sesamoids (UCMP V93173/154469, UCMP V93173/154476, and UCMP 93173/154485) may also be weathered—and if so, it is stage 1 weathering—but the features may simply be the result of poor preservation. None of the equid fossils from the Velvet Room exhibits any evidence of weathering.

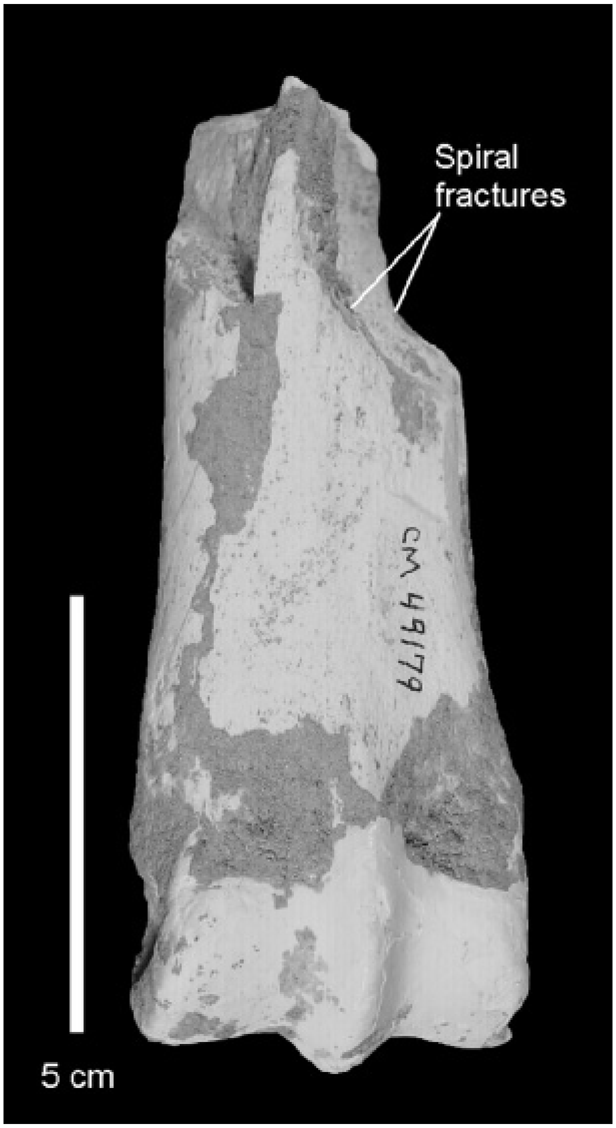

FIGURE 20.1 Distal metapodial, CM 49179, from the Badger Room, slightly oblique ventral view, indicating spiral fracturing.

The most weathered bone from the Porcupine Cave equid sample is a terminal phalanx, CM 73345, from the Gypsum Room. The plantar surface of this bone exhibits relatively deep cracking and pronounced flaking and spalling of surficial bone, corresponding with stage 2 weathering (Behrensmeyer, 1978). In contrast, the dorsal and articular surfaces of the fossil show only stage 0 or 1 weathering. Clearly this fossil was subaerially exposed somewhat longer than other equid fossils from Porcupine Cave, although the duration of this exposure was nevertheless not pronounced.

Rodent and Carnivore Damage

Damage inflicted by rodents is minimal on equid fossils from the Badger Room, an observation that contrasts somewhat

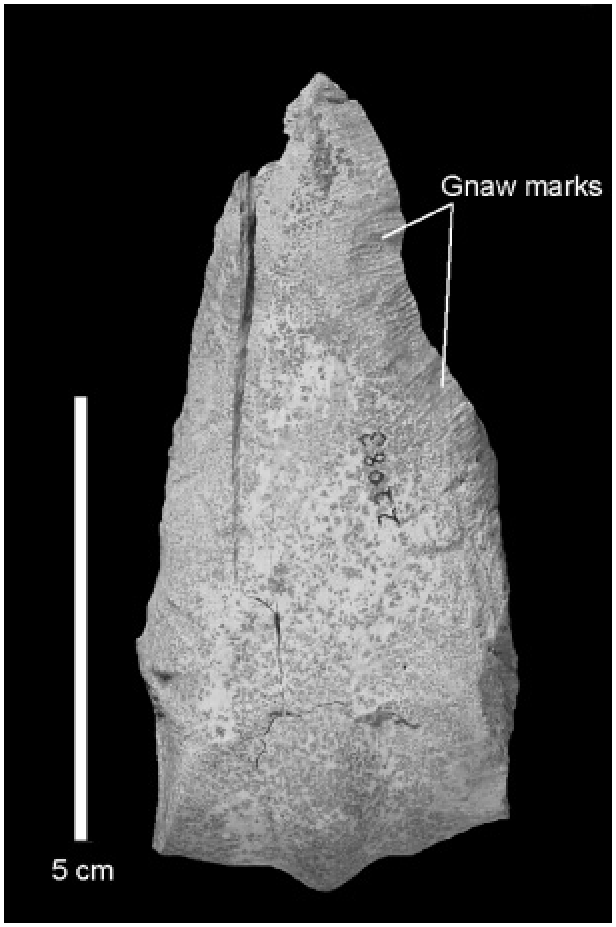

FIGURE 20.2 Rodent (wood rat?) gnawing of a distal metapodial (DMNH 22083) from the Velvet Room, dorsal view.

with previous reports suggesting that rodent damage was in general relatively common on fossil bones from this area of Porcupine Cave (Anderson, 1996). Only the second phalanx (CM 49283) exhibits substantial rodent gnawing; very slight rodent gnawing can also be discerned on the scaphoid (CM 49181). None of the fossils demonstrates conclusive evidence of carnivore activity. The proximal scapula portion has a broad punctate depression with radiating stress lines on the articular surface, as well as a thin, sharply defined puncture on the ventral surface of the neck of the corocoid process, but these may represent damage inflicted during excavation. The broken midshaft of the distal metapodial exhibits spiral fracturing but lacks other indications of carnivore activity or trampling.

In contrast, rodent gnawing is relatively common on equid fossils from the Pit area of Porcupine Cave. Of the 13 postcranial bones from this area, 9 have been gnawed by rodents. No evidence of other carnivorous or scavenging activity was observed on equid bones from the Pit.

All elements from the Velvet Room exhibit some degree of postmortem modification, primarily rodent gnawing that ranges from very slight to extreme (figure 20.2). A distal sesamoid (DMNH 38522) exhibits not only very light rodent gnawing, but also two more substantial grooves on the posterior superior edge. These grooves are spaced 5.53 mm apart (distance measured between the center point of each incision), and a corresponding notch is present on the posterior inferior edge. These features strongly suggest carnivore rather than rodent gnawing.

FIGURE 20.3 Oblique occlusal view of apparent etching on an isolated left p4 (DMNH 23074) from the Badger Room. Note that the etching is confined to that portion of the tooth that in life would have extended above the jaw line.

Etching

An isolated left p4 (DMNH 23074) of a young adult small horse found in the Badger Room exhibits very heavy etching, resembling acid etching. This etching is present on the occlusal surface and on all portions of the tooth that in life would have extended above the jaw line (figure 20.3). The root of the tooth lacks any such etching. Although the cause of this etching has not yet been identified, it is reasonable to suggest that the restricted nature of the modification is due to only the uppermost portion of the tooth having been exposed at

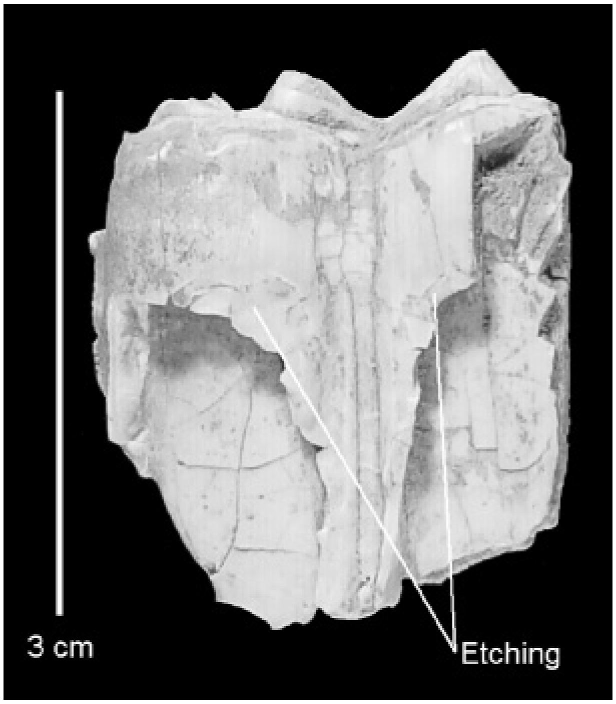

FIGURE 20.4 Etching on the labial surface of a deciduous lower premolar (CM 73357) from the Badger Room.

the time the damage was inflicted. This in turn suggests that this tooth was still in place in at least a portion of the dentary at the time the damage occurred. Another tooth from the Badger Room, a deciduous lower premolar (CM 73357), exhibits similar etching along the borders of arcuate breaks on the labial surface of the tooth root (figure 20.4).

Two teeth from the Velvet Room, a partial left DP2 (DMNH 12796) and an isolated broken m1 (DMNH 41172), also appear to have been acid etched. DMNH 12796 lacks the lingual enamel and the dentine of the protocone; the broken edges of the remaining labial enamel of the protocone are worn and smooth. The labial enamel and cementum along the length of the paracone are completely missing, and here too the broken edges of enamel left along the mesostyle and the metastyle are worn and smooth. The broken edges of the lingual enamel of the protoconule and the posterior border of the hypocone, broken approximately halfway down the length of the tooth, are similarly smoothly worn and taper to a thin edge. In contrast, the labial enamel of the metacone and the lingual enamel of the hypocone appear cleanly broken halfway down the length of the tooth. Etching on DMNH 12796 is most evident on the remaining enamel of the protoconule and the hypocone and on the posterior border of the tooth. Etching is also present to a lesser degree on the enamel of the metacone, as well as on the occlusal surface. No etching is evident along the exposed internal enamel of the pre- and postfossettes. A thin layer of calcium carbonate is present on the occlusal surface of the tooth and on the interior surfaces of the metacone, protoconule, and hypocone.

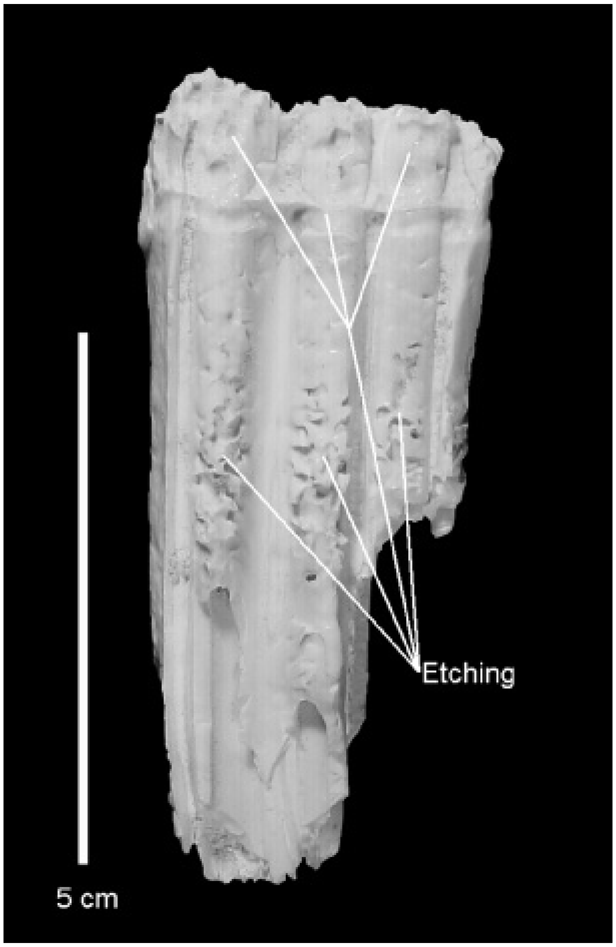

FIGURE 20.5 Etching on the lingual surface of a right m1 (DMNH 41172) from the Velvet Room. Etching is primarily on all portions of the tooth that once extended above the jaw line, including the occlusal surface, and also markedly on the lingual face of the root.

Etching on DMNH 41172 is evident primarily and extensively on all portions of the tooth that once extended above the former jaw line, including the occlusal surface, and also markedly on the lingual face of the root and to a lesser degree on the anterior and posterior faces of the tooth root (figure 20.5). As with DMNH 23074 from the Badger Room, this pattern of etching suggests that the tooth was initially attached to at least a portion of the dentary when the etching process was initiated. Later, after the tooth was no longer attached to the dentary, etching continued on the newly exposed faces of the tooth root.

The agent or agents responsible for the etching cannot be identified conclusively. The fact that several equid teeth from Porcupine Cave exhibit this etching suggests some process associated with being inside the cave rather than acidic conditions prior to deposition. The etching superficially resembles root damage (see Andrews, 1990:figures 1.11, 1.12 for comparison) but lacks the characteristic channel-like linearity. Acidic

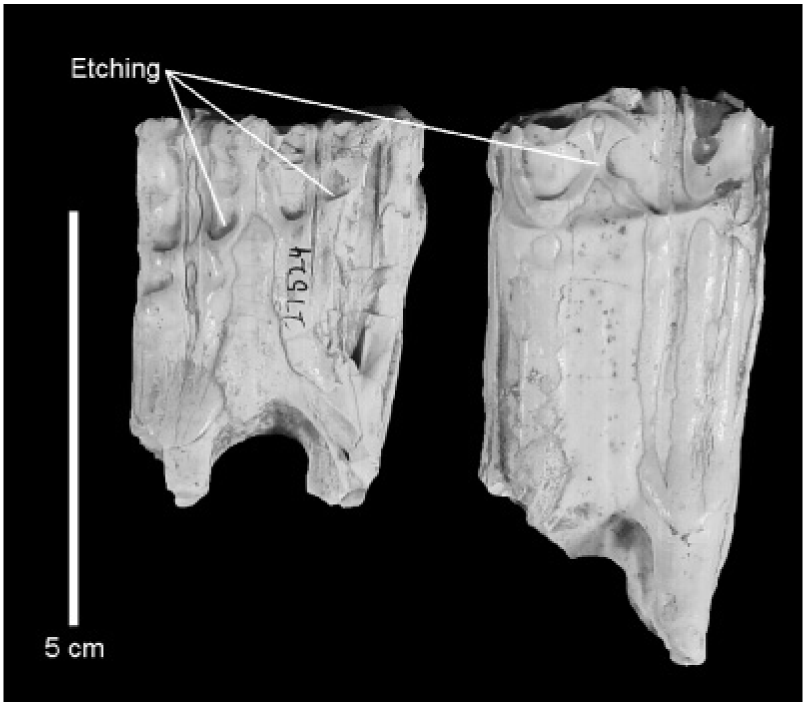

FIGURE 20.6 Etching on the lingual surface of adult lower premolars (right p2, DMNH 27524; right p3 or p4, CM 49180) from Fissure Fill A.

groundwater distributed widely in the relevant deposits is not indicated, because in that case etching would be expected on the entire surface of each of the affected specimens and would very likely be present on other specimens recovered nearby. Etching by urine or other organic excretory acids from wood rats or other inhabitants of the cave is considered unlikely for the same reasons. Etching caused by digestion by carnivores seems improbable, because carnivores do not normally consume equid teeth. It is conceivable that the etching resulted from mildly acidic water draining through portions of Porcupine Cave and coming into contact with the fossils, probably prior to the burial, but this is conjecture at best.

Also of interest are the fossils from Fissure Fill A (DMNH 1344, UCMP V98022) and the Fissure Dump Pile (DMNH 1348). The latter excavation is a dump pile of mine tailings located outside the mouth of Porcupine Cave, which is the backdirt from the excavation of the adit dug by miners. Fossils from the Fissure Dump Pile may have come from the vicinity of Fissure Fill A or B, both of which are exposed in the adit, or from any portion of the excavated adit. Biostratigraphic evidence suggests that Fissure Fill A correlates temporally with the lower or middle stratigraphic levels of the Pit. At least one juvenile and one older adult are represented in the equid dental sample from the Fissure Fill localities. Three of the adult teeth (left P3, DMNH 27098; right p2, DMNH 27524; right p3 or p4, CM 49180) exhibit etching similar to that previously described for teeth from the Badger Room and Mark's Sink. On DMNH 27098 this etching is relatively light, and, although present on all aspects of the fossil, it is most evident on the labial face of the tooth root. On the lower premolars this damage is generally more pronounced than on the upper premolar, is marked on the lingual side of both teeth, and is especially well developed on the uppermost portion of the teeth that in life extended above the dentary (figure 20.6). The etching on the teeth from Fissure Fill A differs from that on the teeth from the Badger Room and Mark's Sink in being more extensively distributed on all teeth, in being less strongly and sharply incised, in having a more definite orientation (primarily anteroposterior), and in being present only slightly on the occlusal surfaces of the teeth. It is not clear whether the agent responsible for the etching evident on the teeth from Fissure Fill A is the same as that responsible for the damage on the teeth from other areas of Porcupine Cave.

Other Skeletal Elements

Additional areas of Porcupine Cave that have yielded equid fossils include Generator Dome (DMNH 1347; *N* = 4), the Gypsum Room (CM 1926 / UCMP V93174; *N* = 2) and the Crystal Room (DMNH 1345 / UCMP V94014; *N* = 1). Generator Dome is stratigraphically mixed. The ages of the Gypsum Room and Crystal Room deposits are not certain, although they may equate to the lower or middle Pit layers. As with equid fossils from other areas of the cave, the few fossils from Generator Dome, the Gypsum Room, and the Crystal Room consist almost entirely of pedal elements and tooth fragments. An exception to this generalization is a lumbar vertebra (DMNH 41027) from the Generator Dome. This bone represents the only element from the axial skeleton recorded from the cave.

Given the preponderance of dental and pedal elements of horses from Porcupine Cave, it is likely that the bones were brought into the cave as isolated elements. They had not lain out in the open for very long, judging from the general lack of weathering damage and the absence of any weathering beyond stage 2 (and that stage only evident on a single specimen). Those few elements exhibiting evidence of weathering show damage on only one or two surfaces, not on the entire bone. This observation and the lack of tumbling abrasion on the majority of the equid fossils (the exception being CM 73356, the proximal scapula from the Badger Room, which is waterworn) indicate that none of the fossils had been transported far prior to their initial collection. The sizes of recovered elements, the abundance of rodent gnaw marks, and the paucity of verifiable carnivore damage all indicate that rodents dragged most of the horse bones into the cave. The small incisor impressions constituting most of the gnaw marks implicate wood rats rather than porcupines (R. L. Reynolds, pers. comm.). The etching evident on some of the teeth may be the result of mildly acidic water draining into portions of Porcupine Cave episodically prior to the burial of the fossils, in which case many of the teeth were still rooted in at least a portion of the jaw when the damage was inflicted.

Systematic Paleontology

Class Mammalia

Order Perissodactyla

Family Equidae

Genus *Equus*

Subgenus *Asinus* Gray, 1824

EQUUS (ASINUS) *SP. CF.* E. (A.) CUMMINSI *COPE, 1893*

REFERRED MATERIAL From DMNH 1344 / UCMP V98022: broken left P3, worn and etched, DMNH 27098; right p3 or p4, worn and etched, CM 49180; fragment of medial trochlea of left astragalus, DMNH 27097. From DMNH 1348: right p2, worn and etched, DMNH 27524.

REMARKS Three of these four specimens were recovered from Fissure Fill A; the p2 was recovered from DMNH 1348 (Fissure Dump Pile). The teeth exhibit remarkably similar preservation, and are all worn to approximately the same degree. Therefore they are interpreted to be derived from a single mature adult. Although worn, the teeth are virtually straight in the transverse plane. The occlusal surfaces exhibit an extremely simple enamel pattern. The protocone of the upper premolar, DMNH 27098, is of particular interest in that it is short and round with a very slight lingual flattening and has minimal anterior development (figure 20.7). The metaflexid of DMNH 27524 exhibits a small, columnar enamel "islet" embedded in the cementum (figure 20.8); this unusual feature runs the length of the tooth, and it may have been an invagination of the labial enamel wall of the metaflexid earlier in wear that pinched off as the animal aged. The astragalus fragment is extremely small, similar in size to astragali of *Equus (Hemionus)* sp., as well as to astragali referred to *Equus (Asinus) cumminsi* from the Love Formation in Hudspeth County, Texas (Akersten, 1972; see discussion of *Equus cumminsi* later in this section).

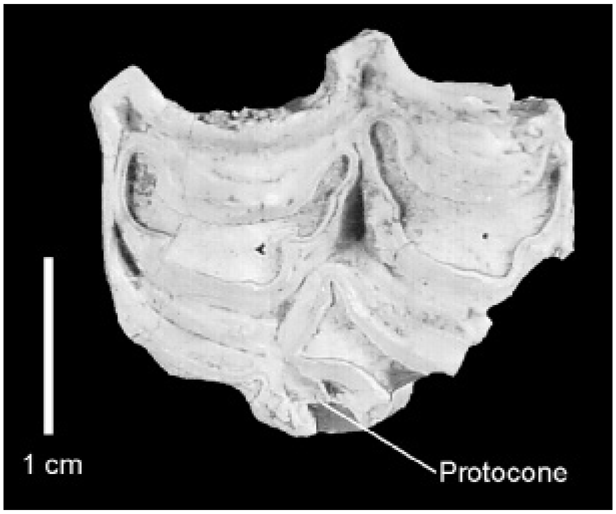

FIGURE 20.7 Occlusal view of left P3 (DMNH 27098) from Fissure Fill A. Note shortened and rounded protocone.

The small size and protocone morphology of DMNH 27098 are unlike any described for small species of North American Pleistocene *Equus,* but they closely resemble features described for two small Pliocene (Blancan North American Land Mammal Age) equids, *Equus (Asinus) cumminsi* Cope, 1893, and *Equus (Plesippus) francescana minor* (Frick), 1921 (originally reported as *Pliohippus francescana minor,* but subsequently referred to the subgenus *Plesippus* [Matthew and Stirton, 1930; Schultz, 1936]). However, equid upper premolars by themselves are generally not diagnostic to species, so specific assignment of the Porcupine Cave fossils must remain tentative.

DMNH 27098 is herein assigned to *Equus* sp. cf. *E. (Asinus) cumminsi.* CM 49180 and DMNH 27524 are similarly referred based on their small size, simple morphology, and presumed affinity with DMNH 27098. DMNH 27097 resembles referred specimens of *E. cumminsi* in size (see the next section) and so is also referred to *Equus* sp. cf. *E. cumminsi.* In order to fully justify these assignments, some discussion of both *Equus cumminsi* and *E. francescana minor* is required.

EQUUS CUMMINSI This taxon was initially described by Cope (1893) based on three upper cheek teeth from the Blanco Local Fauna in Texas that exhibited relatively small size and a simple enamel pattern with a small, rounded protocone that lacked a lingual groove—similar to the morphology evidenced by DMNH 27098 from Porcupine Cave. The lectotype tooth of *E. cumminsi,* a figured upper molar, was in fact so primitive that Gidley (1901) referred it to the genus *Protohippus* Leidy, 1858, whereas Merriam (1916) and Osborn (1918) assigned it to *Pliohippus* Marsh, 1874. Matthew and Stirton (1930) and Schultz (1936) proposed that *E. cumminsi* was better assigned to *Plesippus* Matthew, 1924, a taxon presently considered a subgenus of *Equus* (Forsten and Eisenmann, 1995;

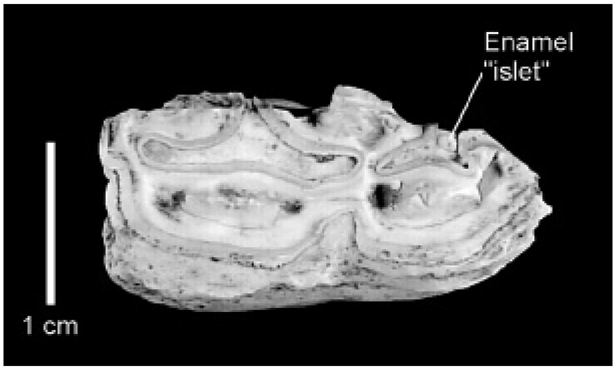

FIGURE 20.8 Occlusal view of right p2 (DMNH 27524) from Fissure Fill A. Small, columnar enamel "islet" is noted.

Eisenmann and Baylac, 2000) that is also characterized in part by upper cheek teeth with simple enamel patterns and small, rounded protocones in some individuals. *Plesippus* is further characterized dentally by lower molars in which the linguaflexids are generally V-shaped and the ectoflexids fully penetrate the molar isthmus (Skinner, 1972; Downs and Miller, 1994). No directly associated upper and lower dentitions of *Equus cumminsi* have been reported from the Blanco (Dalquest, 1988; but see the following discussion in this section), and therefore the morphology of the lower teeth of this species as defined from the type locality is not known for certain (Azzaroli and Voorhies, 1993).

Hibbard (1944) referred an M3 and a right dentary of a small equid from the Blancan Meade Formation in Kansas to *Equus (Plesippus)* sp. cf. *E. (P.) cumminsi.* The rationale behind this referral, not elaborated by Hibbard, probably relied on the geologic age, the small size of the referred fossils, and the relatively simple enamel of the M3 from the Meade Formation. Since no topotypal lower cheek teeth of *E. cumminsi* were reported by Cope (1893) from the Blanco, no comparisons were possible for the dentary from the Meade Formation. However, the lower molars figured by Hibbard also exhibit the shallow ectoflexids typical of *Asinus* rather than *Plesippus*—a fact not noted by Hibbard (1944) and observed subsequently by Dalquest (1978) and Azzaroli and Voorhies (1993).

Small horses from the Blancan Hudspeth Local Fauna, Camp Rice Formation, Hudspeth County, Texas, also possess lower molars with short ectoflexids. Strain (1966) recognized the importance of these short ectoflexids and referred those fossils to *Equus (Asinus)* sp. cf. *E. (A.) cumminsi,* a determination that was subsequently supported by Akersten (1972) and Azzaroli and Voorhies (1993). It is assumed that the specific referral was based on comparison with Hibbard's (1944) fossils from Kansas, since no upper teeth were reported by Strain (1966) and so no comparisons could be made with the holotype fossils described by Cope (1893).

Equus (Asinus) cumminsi was later reported from deposits dating to the Blancan elsewhere in Hudspeth County, from the Red Light Local Fauna of the Love Formation (Akersten, 1972). This report was based on isolated upper and lower cheek teeth and pedal elements including two astragali and three first phalanges. The lower molariform teeth (TMM 40664-2, left m1 or m2, and TMM 40964-1, right m1; Akersten, 1972:figure 16E,G) are small and exhibit V-shaped linguaflexids and ectoflexids that extend to very near the molar isthmus. Two of the three first phalanges are small, but they are so waterworn as to be virtually useless for measurements or more precise identification. The remaining phalanx (TMM 40856-3) is small, similar in size to phalanges of the small stout-limbed Pleistocene equid *E. conversidens* from San Josecito Cave, but also within the low end of the size range of the somewhat larger *E. (Plesippus) simplicidens* (figure 20.9). *Equus (Plesippus)* sp. cf. *E. (P.) simplicidens* was also reported from the Love Formation by Akersten (1972), and it is therefore not clear why TMM 40856-3, along with the other two waterworn phalanges from that formation, were referred to *E. (A.) cumminsi* rather than to *E. (P.) simplicidens.*

The astragali from the Love Formation (TMM 40856-7 and TMM 40891-13), in contrast, are substantially smaller than those of both *E. conversidens* and *Equus (Plesippus) simplicidens* (figure 20.10), and resemble in size astragali of small stilt-legged horses (possibly *Equus [Hemionus]* sp.) from the Shoshone paleontological site near the Tecopa lake beds in the Mojave Desert, California (Scott, 1997). The diminutive size of these astragali suggests that they are too small to be derived from the same species as that represented by the first phalanges. On the other hand, *Equus (Hemionus)* sp. is not known from Blancan deposits in North America, and so these astragali cannot easily be referred to that taxon. The small equid astragali from the Love Formation are therefore inferred herein to represent *E. (A.) cumminsi,* following the conclusions of Akersten (1972), whereas the first phalanx is thought to represent a small individual of *E. (P.) simplicidens.*

The upper molariform tooth (TMM 40664-227) referred to *Equus cumminsi* from the Love Formation, not figured by Akersten (1972), is also small and extremely worn, and it possesses a protocone that has a small but distinct anterior "heel" and a shallow but distinct lingual groove. These features differ somewhat from Cope's holotype of *E. cumminsi,* which has been figured (Cope, 1893; Gidley, 1901; Osborn, 1918) as possessing a more rounded protocone with a less-developed anterior projection and no apparent lingual grooving; in these characteristics it resembles some individuals of *Equus (Plesippus).* Both of these teeth are from old individuals; TMM 40664-227 is slightly more worn. The difference in wear is not great, however, and the observed variation in occlusal morphology between these two teeth is not thought to result from significantly different ontogenetic age between the respective individuals. The shape of the protocone of TMM 40664-227 is not sufficient to either confirm or reject the plesippine status of the specimen. Teeth of *E. (P.) simplicidens* from Hagerman exhibit small, rounded protocones in some individuals (see Schultz, 1936) as well as more triangular protocones with short anterior projections in other individuals; the latter morphology is shared with some later species of *Equus.* The small size of TMM 40664-227 is also insufficient to confirm Akersten's

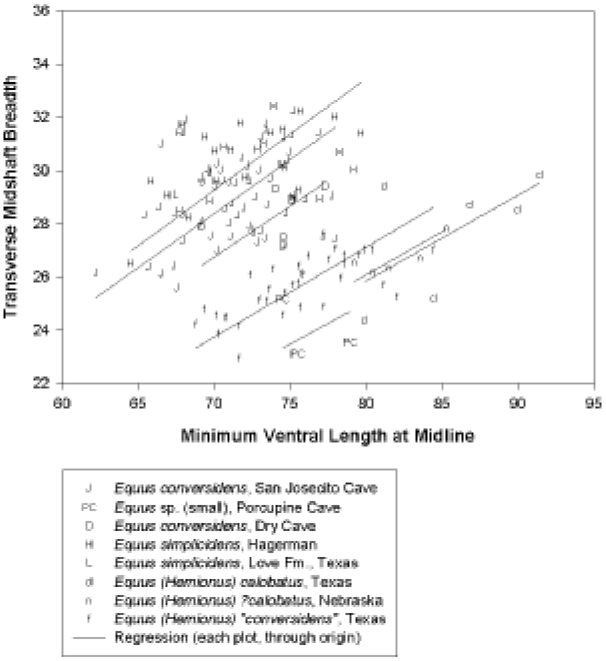

FIGURE 20.9 Bivariate plot of measurements of first phalanges from Porcupine Cave, compared with like elements of *Equus conversidens* from San Josecito Cave and Dry Cave, with *Equus simplicidens* from the Hagerman Fossil Beds and from the Love Formation, with paralectotypal *Equus calobatus* from Rock Creek, and with other smaller hemionines from Nebraska and Texas. The specimen from the Love Formation was assigned to *Equus cumminsi* by Akerston (1972) but clearly falls within the range of *E. simplicidens.* The phalanges from Porcupine Cave clearly fall within the size range of the smaller hemionines. Note that the phalanges from Porcupine Cave are gnawed; were the specimens complete, they would probably have plotted slightly to the right.

(1972) identification. Direct examination of the Love Formation tooth leads to the suggestion that its small size is quite possibly the result of the specimen's advanced stage of wear and is not necessarily indicative of specific affinities. Cheek teeth of the large horse species *E. scotti* from Murrieta and *E. "occidentalis"* from Rancho La Brea that are worn to the same degree closely approximate the Love Formation tooth in size, whereas similarly worn cheek teeth of the small Pleistocene horse *E. conversidens* from Fort Irwin, California—in life probably similar in size to *E. cumminsi*—are distinctly smaller. It seems reasonable to conclude that TMM 40664-227 cannot be assigned with any confidence to *E. cumminsi.*

To summarize the systematics of the fossils referred to *Equus (Asinus) cumminsi* from the Love Formation, it is clear that some of these fossils are better referred to other, larger Blancan equid taxa, such as *E. (P.) simplicidens.* However, those fossils that were correctly referred to *E. (A.) cumminsi* confirm the non-plesippine affinities of the species.

Dalquest (1978, 1988) reviewed the systematics of *Equus cumminsi* and noted that, although no lower teeth were directly associated with the holotype of the species, three lower

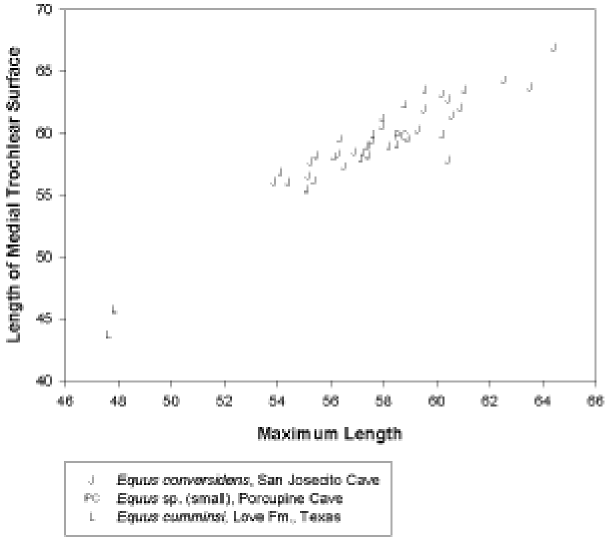

FIGURE 20.10 Bivariate plot of measurements of astragali from Porcupine Cave, compared with like elements of *Equus conversidens* from San Josecito Cave and *E. cumminsi* from the Love Formation. The astragalus clearly falls within the range of *E. conversidens.*

teeth (presumed to be p4, m1, and m2) of a single individual of a small horse from the Blanco, the type locality of *E. cumminsi,* exhibit ectoflexids that do not penetrate the molar isthmus. This feature allies these teeth with *Asinus* rather than *Plesippus.* Dalquest therefore proposed that these lower teeth were from the same small equid species as the upper teeth described by Cope, and considered *E. cumminsi* from the Blanco to be an ass, not a zebra. This interpretation, which conformed with the studies of referred lower teeth by Strain (1966) and Akersten (1972), was not endorsed by Azzaroli and Voorhies (1993:184), who noted simply that "there is no evidence that Cope's *E. cumminsi* had shallow ectoflexids." Direct examination of two of the three teeth (right p4 and m1, batch catalogued as TMM 31166-3; the remaining tooth was not available) mentioned by Dalquest (1978, 1988) confirmed the short, *Asinus*-like nature of the ectoflexid in each. The third tooth, figured as an m2 by Dalquest (1978:figure 3) and subsequently as an m1 by Kurtén and Anderson (1980: figure 14.2), is also clearly ass-like in the lack of penetration of the ectoflexid.

Given the small size, the simplicity of the enamel, and in particular the small, rounded protocone of the P3 (DMNH 27098) from Porcupine Cave, it seems reasonable to assign this tooth to *Equus* sp. cf. *E. cumminsi.* This species is here interpreted to belong in the subgenus *Asinus,* following the studies of Strain (1966), Akersten (1972), and Dalquest (1975, 1978, 1988). CM 49180 and DMNH 27524 are also assigned to *E.* sp. cf. *E. (A.) cumminsi* on the presumption that they are derived from the same individual as DMNH 27098. DMNH 27097 is also referred to *Equus* sp. cf. *E. (A.) cumminsi* on the basis of its presumed association with the above-mentioned cheek teeth and its similarity in size with like specimens from

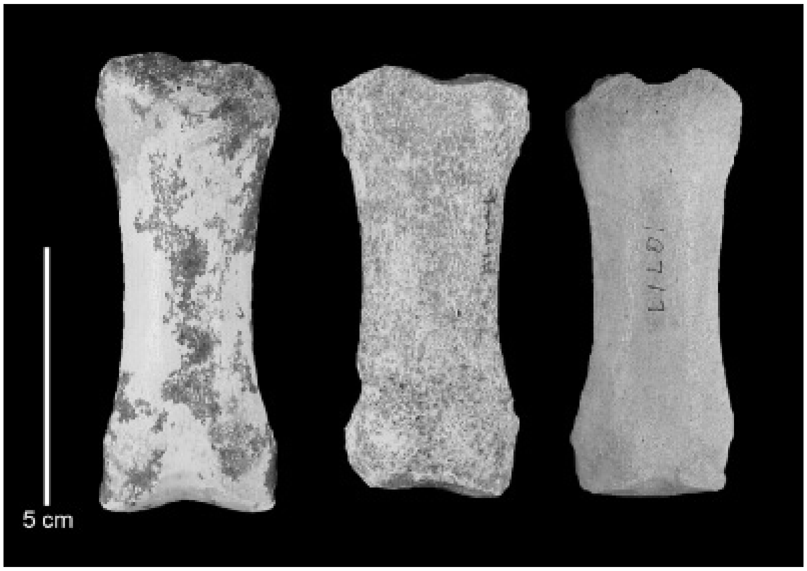

FIGURE 20.11 First phalanges of *Equus (Hemionus)* sp. from Porcupine Cave (left to right: CM 73317, UCMP 155921, DMNH 10717). Phalanges have been gnawed.

the Love Formation in Texas (Akersten, 1972) referred to this taxon. The recovery of additional specimens of this enigmatic species from Porcupine Cave, or elsewhere, will help test the validity of this assignment.

EQUUS (PLESIPPUS) FRANCESCANA MINOR This species is even less well known than *Equus cumminsi.* Originally described by Frick (1921) as "*Pliohippus francescana minor,*" the taxon was based on four closely associated upper cheek teeth (left P4 and M1 and right P3 and M1, UCMP 23262, 23264, 23266, and 26267, respectively) and some associated craniodental remains from the San Timoteo Formation in Riverside County, California. *Pliohippus francescana* was subsequently referred to the genus *Plesippus* by Matthew and Stirton (1930) and Schultz (1936), but the smaller subspecies was not mentioned and it is not clear if these authors considered it to be plesippine as well. The taxon has not been discussed in any detail since; the most recent review of plesippine horses from the San Timoteo Formation (Albright, 1999) did not make any mention of *E. (P.) francescana minor.* Frick (1921) considered *"Pliohippus" francescana minor* to be somewhat more primitive than Cope's *Equus cumminsi,* but the differences between the taxa are minor and well within the range of variation for a single species. *E. (P.) francescana minor* is here considered a junior synonym of *E. (A.) cumminsi,* since no metric or morphologic features distinguish these taxa. The recovery of additional small horse remains from the Blancan portion of the San Timoteo Formation in southern California will help test this interpretation.

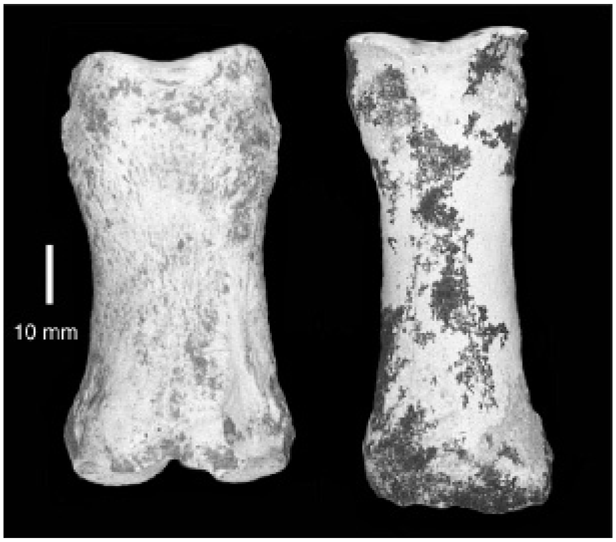

FIGURE 20.12 First phalanx of *Equus (Hemionus)* sp. from Porcupine Cave (right) compared with first phalanx of *E. conversidens.*

Subgenus *Hemionus* Stehlin and Graziosi, 1935

EQUUS (HEMIONUS) *SP. (SMALL)*

REFERRED MATERIAL From CM 1925 / UCMP V93173: from level 1, first phalanx, CM 73317; from surface, first phalanx, UCMP V93173/155921. From DMNH 644, level 4: first phalanx, DMNH 10717.

REMARKS These three specimens are all long and slender, suggesting affinity with the subgenus *Hemionus.* Unfortunately, all have been substantially gnawed, so few precise measurements are possible (figures 20.11, 20.12). Even so, these phalanges are clearly longer and narrower than like elements of the stout-limbed small equid *Equus conversidens* (figures 20.9, 20.12).

The slender phalanges from Porcupine Cave fall within or near the size range of the small hemionines (figure 20.9). Lacking more abundant and diagnostic fossils, and given the present uncertainty as to whether one or two small species of small hemionines were present in North America during the Pleistocene, no specific determinations are advanced for these fossils.

EQUUS *SP. (LARGE)*

REFERRED MATERIAL From DMNH 644: anterior fragment of left DP?2, DMNH 27400; from level 1, right DI3, DMNH 11915. From DMNH 942: left DP3, DMNH 27052; right DP4, DMNH 27053; partial right P3, worn, DMNH 27054. From DMNH 1349: right m1 or m2, DMNH 41172; dorsolateral fragment of right patella, DMNH 38526; proximal sesamoid, DMNH 41024; proximal sesamoid, DMNH 41025. From UCMP V94014: right lunar, CM 49181. From CM 1925 / UCMP V93173: from level 1, right scaphoid, CM 49285; from level 2, left p2, worn, UCMP 169163; from levels 1–3, proximal sesamoid, UCMP 154469; from levels 5–6, proximal sesamoid, UCMP 155903; from the mixed 1987 collection, proximal sesamoid, UCMP 154476; from mixed fossils, proximal sesamoid, UCMP 154485; and from an unrecorded level, proximal sesamoid, UCMP 154480. From Porcupine Cave, undifferentiated: left navicular, UCMP 155909.

REMARKS None of the specimens listed is sufficiently complete or diagnostic to merit specific identification. The size of the pedal elements compares favorably with like elements of *Equus "occidentalis"* from Rancho La Brea.

DMNH 27054, a right P3 from an elderly individual, is similar in size to like specimens of *Equus scotti* and *E. "occidentalis"* (figure 20.13). This specimen lacks the anterior third of the tooth as well as the labial surface, so measurements are not possible. The tooth exhibits a relatively simple enamel pattern with uncomplicated fossettes, although this appearance may be the result of the relatively advanced stage of wear. The pli caballin is reduced but present. The protocone is broad and triangular, reminiscent of like teeth of both *E. scotti* and *E. "occidentalis"* in later wear.

DMNH 41172, a right m1 or m2 from a young individual, has extensive acid etching all along the occlusal surface and has had the base of the tooth broken away, so measurements are not possible. The specimen is as long anteroposteriorly as like teeth of both *Equus scotti* and *E. "occidentalis"* but is buccolingually compressed, resulting in the entry of the short ectoflexid into the molar isthmus (with possible full penetration in later wear, had the animal lived longer) (figure 20.14). Full penetration of the isthmus by the ectoflexid is generally accepted as a characteristic of the extinct North American zebra taxon *Plesippus* Matthew, 1924 (as well as the present-day zebra subgenus *Dolichohippus* Heller, 1912), but in the case of DMNH 41172 the penetration is thought to result from buccolingual compression. The linguaflexid is broad, shallow, and narrowly U- or V-shaped. This feature combined with the short ectoflexid suggests affinity with asses (subgenus *Asinus* Gray, 1824) or hemionines (subgenus *Hemionus* Stehlin and Graziosi, 1935).

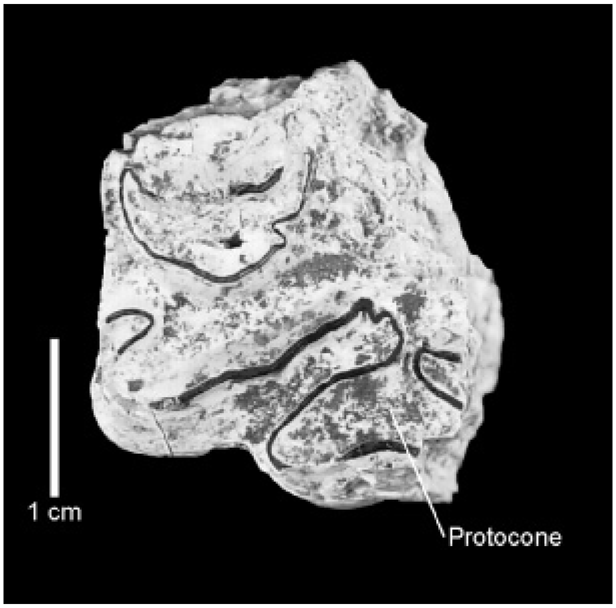

FIGURE 20.13 Right P3 (DMNH 27054) from the Badger Room, occlusal view. Note broad, triangular protocone.

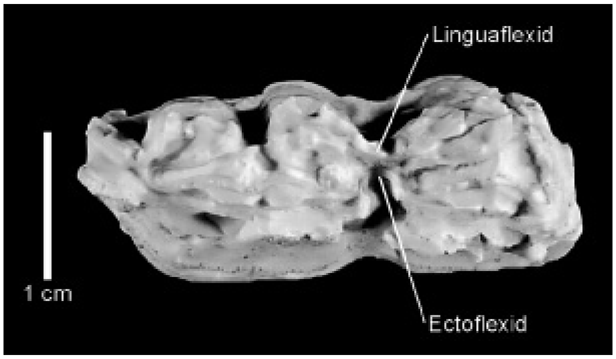

FIGURE 20.14 Right m1 or m2 (DMNH 41172) from Mark's Sink in the Velvet Room, occlusal view. The penetration of the ectoflexid into the molar isthmus is thought to result from buccolingual compression.

EQUUS *SP. (SMALL)*

REFERRED MATERIAL From CM 1928 / DMNH 942: right dp3 or dp4, broken and etched, CM 73357; left p4, etched, DMNH 23074; proximal portion of left scapula, CM 73356; right astragalus, DMNH 23073; distal metapodial, CM 49179; second phalanx, CM 49283; partial terminal phalanx, DMNH 23072. From CM 1927 / UCMP V93175: left scaphoid, UCMP 155899. From CM 1926 / UCMP V93174: second phalanx, UCMP 172483; terminal phalanx, CM 73345. From CM 1925 / UCMP V93173: from surface, second phalanx, UCMP 155904; second phalanx, UCMP 155920; from level 1, terminal phalanx, CM 49284; from levels 1–3, mixed, left DP3, UCMP 175016; from mixed fossils, second phalanx, UCMP 154484. From DMNH 644: from level 1, partial left DP2, DMNH 12796; posterior portion of prefossette and postfossette of right P4 or

M1, DMNH 11906; from level 2, right scaphoid, DMNH 21024; from level 3, partial right m1 or m2, DMNH 36426; distal metapodial, DMNH 22083; and from levels 1–6, partial right di2, unworn, DMNH 12197. From DMNH 1345 / UCMP V94014: left lunar, DMNH 41026. From DMNH 1347: left DI?3, DMNH 33903; lumbar vertebra, DMNH 41027. From DMNH 1349: second phalanx, DMNH 39004; distal sesamoid, DMNH 38522. From Porcupine Cave, undifferentiated: second phalanx, UCMP 155910.

REMARKS None of this material is sufficiently diagnostic to warrant definitive assignment to species. Measurements of an astragalus (DMNH 23073) fall within the size range of like elements of *Equus conversidens* from San Josecito Cave (figure 20.10), as do measurements of the second phalanges (figure 20.15). However, the phalanges from Porcupine Cave appear to group at opposite ends of the *E. conversidens* distribution. The possibility that more than one equid species is represented in the sample of second phalanges from Porcupine Cave—one very small, possibly akin to *Equus (Hemionus),* and the other medium-sized—cannot therefore be ruled out. An alternate explanation is that these phalanges differ in size because they are from fore- and hindlimbs. If this is the case the equine species represented would be quite small; regression lines plotted through the origins of each curve show that the Porcupine Cave fossils are somewhat smaller than the other fossils sampled (figure 20.15). Lacking more diagnostic fossils, a conservative view is adopted here and the phalanges are all considered to be simply "*Equus* sp. (small)."

A deciduous di2, DMNH 12197, is broken from the medial tip down through the center of the root, so measurements are not possible. However, direct comparison of the tooth with like specimens of *Equus conversidens* and *E. "occidentalis"* reveals that the Porcupine Cave fossil falls within the size range of deciduous incisors of the former taxon, but is smaller than the smallest deciduous incisors of the latter. This specimen lacks an infundibulum, a feature shared by numerous Pleistocene horse taxa, including *E. conversidens, E. "occidentalis," E. fraternus* Leidy, 1860 (sensu Azzaroli, 1998; including *E. leidyi*) and *E. francisi* Hay, 1915 (sensu Azzaroli, 1998; possibly including *E. tau*). Since DMNH 12197 is smaller than the smallest deciduous incisors of *E. "occidentalis"* from Rancho La Brea, it cannot be comfortably referred to this species. Of the remaining nominal species, *E. fraternus* was initially named without designation of either a holotype or a type locality and is best considered a *nomen vanum* (Savage, 1951; contra Azzaroli, 1998), whereas *E. leidyi* is characterized primarily by the complexity of its cheek tooth enamel, which is not sufficient to distinguish this form from other North American Pleistocene species (Savage, 1951). The size of DMNH 12197 from Porcupine Cave, and its lack of an infundibulum, suggest close affinity with either *E. conversidens* or *E. francisi.* Lacking additional, more diagnostic material from the same individual, and given that equids resembling both the small, stout-limbed *E. conversidens* and the small, stilt-legged *E. francisi* are present in the Porcupine Cave assemblage, no more specific determinations for DMNH 12197 can be advanced.

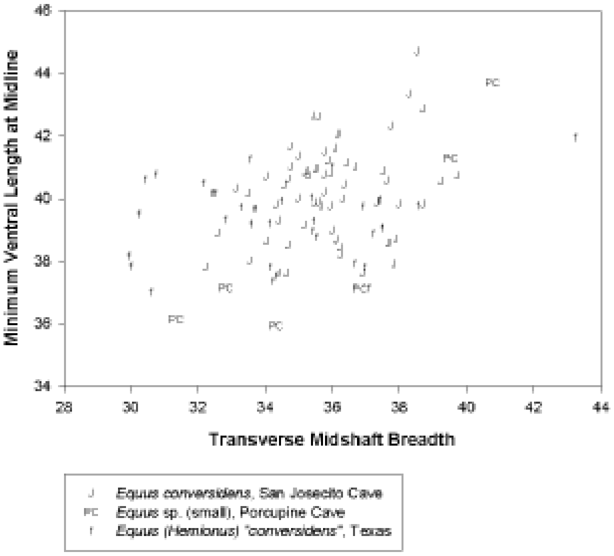

FIGURE 20.15 Bivariate plot of measurements of second phalanges of small *Equus* from Porcupine Cave, compared with like elements of *Equus conversidens* from San Josecito Cave and *Equus (Hemionus)* sp. from Texas.

DMNH 36426 is a lower first or second molar from a young adult animal. The tooth lacks the anterior third and is broken near the tooth root, precluding measurements. The tooth exhibits a broadly U-shaped linguaflexid and an ectoflexid that enters into but does not fully penetrate the molar isthmus. The latter feature is superficially reminiscent of the ectoflexid observed in DMNH 41172, described earlier as *Equus* sp. (large). However, in the case of DMNH 41172 the ectoflexid is short and enters the isthmus only because of the buccolingually compressed nature of the specimen. DMNH 36426 appears much shorter anteroposteriorly than DMNH 41172 and exhibits no buccolingual compression. The ectoflexid is long relative to the size of the tooth. This feature, combined with the broad U shape of the linguaflexid, suggests affinity with the caballine horses rather than with zebras, in which the linguaflexids are V shaped and the ectoflexids completely penetrate the molar isthmus, or with the asses or hemionines, in which the ectoflexids are short and do not enter the molar isthmus.

The small horse sample from Porcupine Cave therefore very possibly incorporates specimens representing more than one small horse species. The astragalus DMNH 23073 falls very comfortably within the range of the small stout-limbed equid *Equus conversidens,* and the molar tooth DMNH 36426 confirms that a small *E. conversidens*–like horse was present in the cave. On the other hand, the second phalanges can be interpreted in two ways. The conservative interpretation, preferred herein, is that the phalanges all represent a single species of indeterminate small equid. Another possible explanation is that two species are represented by the second phalanges: one very small, possibly hemionine, and the other somewhat larger, similar in size to large individuals of *E. conversidens* or to smaller individuals of an as-yet-indeterminate medium-sized equid. Unfortunately the fossils are not sufficiently diagnostic to permit any greater clarity in resolving the true number of small horses present in the sample.

Discussion

Although limited in sample size, the fossil horse assemblage from Porcupine Cave is significant, first, because of its high species diversity. At least one species of large horse and two species of small horse—one stout-limbed and one stilt-legged—are represented. This diversity resembles that reported for assemblages of extinct Pleistocene horses elsewhere in North America. For example, Dalquest and Schultz (1992) reported *Equus scotti, E. conversidens,* and *E. francisi* (and possibly a medium-sized horse as well) from the Irvingtonian assemblage recovered from Slaton Quarry, Texas. Hulbert (1995) described three distinct species from the Irvingtonian-age Leisey Shell Pit 1-A in Florida: a large caballine, a small hemionine, and an enigmatic third species with deep molar ectoflexids and compressed lower incisors. Scott (1996, 1997) reported both *E. conversidens* and an indeterminate species of small hemionine from the Mojave Desert of California, a region where large horses were also common during the Pleistocene (Jefferson, 1991). The diversity of horses from Porcupine Cave therefore accords well with that of equids from other Pleistocene sites throughout North America. Unfortunately, the Porcupine Cave sample size is not sufficiently robust to advance interpretations as to the relative frequency of these species in the region during the Pleistocene (Payne, 1972; Grayson, 1978).

Fossils resembling the Blancan ass *Equus (Asinus) cumminsi* are also present in the sample from Porcupine Cave, bringing the minimum number of equid species represented from the site to four. The possible presence of *E. (A.) cumminsi* is important in that it suggests a Blancan age for the faunal assemblage from Fissure Fill A, an area of Porcupine Cave that has previously been interpreted to have yielded some of the oldest fossils from the site (Anderson, 1996). Fossil remains of *E. (A.) cumminsi* from other sites in North America are so rare that it is yet unknown whether this species was confined to Blancan assemblages, or whether it might have also been present in early Irvingtonian faunas. The identification of fossils resembling *E. (A.) cumminsi* in association with early Irvingtonian indicator taxa from Porcupine Cave is very suggestive that the latter interpretation is correct; this interpretation would constitute a substantial temporal range extension for this species. However, more and better fossils of *E. cumminsi,* collected with precise stratigraphic control and associated with radiometric dates, a temporally diagnostic fauna, or both, will nevertheless be necessary to further detail its biochronologic range.

With the exception of the hemionines (see discussion later in this section), both large and small horses are present throughout the period of time during which deposition occurred in the various localities within Porcupine Cave. Large horses are recorded from both the lower (older) and the upper (younger) levels of the Pit. Small horses are less common from the Pit, being confined to the upper levels, but are fairly abundant from both the Badger Room (equivalent to the middle and lower levels of the Pit) and the Velvet Room (levels equating to or younger than the uppermost Pit levels). Both sizes of extinct equine have been recovered from Mark's Sink. Overall, small horses are better represented from Porcupine Cave than large horses, but this finding may very well be a sampling artifact, given that rodents are considered to be the prime accumulating agents.

The fossils of extinct hemionines recovered from the uppermost Pit and from the DMNH Velvet Room excavation are interesting from a paleoenvironmental perspective. The presence of stilt-legged equids in fossil assemblages has been proposed as useful in indicating relatively xeric conditions (Eisenmann, 1985). Extant hemionines (onagers and kiangs), once widespread over much of arid and semiarid Eastern Europe and Asia from Bulgaria and Romania in the west to Manchuria in the east, are presently restricted in the wild to semidesert grasslands in southern Mongolia, semidesert habitats on the high Tibetan plateau, and remote salt plains along the India-Pakistan border (Willoughby, 1974; Eisenmann, 1985; Nowak, 1991). Grevy's zebras, best considered "slender-limbed" rather than strictly stilt-legged, presently inhabit arid open bush grasslands in Ethiopia, Somalia, and northern Kenya (Willoughby, 1974; Mochi and MacClintock, 1976; Klingel, 1979; Rubenstein, 1986; Ginsberg, 1989; Nowak, 1991). If Eisenmann's (1985) interpretation is correct, then this ecological restriction of slender-limbed and stilt-legged equids to semiarid and arid environs could be a paleoenvironmental indicator for Pleistocene localities in which they are found.

Slender phalanges referred to *Equus (Hemionus)* sp. from the Pit and from the Velvet Room are consistent with their purported presence in semiarid environments. In the Pit, sediments in the middle levels (levels 4 and 5) are compact brown clays that may be coeval with an oxygen isotope glacial stage as young as stage 20 (Bell and Barnosky, 2000) or as old as stage 22 (chapter 7). Sediments higher in the excavation from levels 1–3 consist of loose, dry, tan dust, possibly associated with an oxygen isotope interglacial stage near stage 19 or 21 (Bell and Barnosky, 2000). The rodent and lagomorph fauna recovered from the Pit indicates climate change through time, from a relatively cool, moist interglacial (levels 6–9) to a cool glacial (levels 4–5) to a very warm interglacial (levels 1–3). Of the three first phalanges assigned herein to *Equus (Hemionus)* sp., two were recovered from the surface of the Pit and CM 73317 was recovered from level 1. Therefore, those fossils clearly come from interglacial deposits. This association of the xeric-adapted *Equus (Hemionus)* sp. with an interglacial time period, with loose, dusty sediments, and with a high proportion of xeric-adapted micromammals (Barnosky et al., 1996) accords well with Eisenmann's (1985) predictions concerning the environmental preferences of extinct stilt-legged equids. The remaining hemionine phalanx (DMNH 10717) was recovered from the Velvet Room grid 6, level 4, horizon B, which probably is even younger than the uppermost (interglacial) Pit levels, but of a similar sediment type. DMNH 10717 may therefore also conform to Eisenmann's (1985) observations. However, it will be necessary to confirm further such associations before we can firmly regard extinct hemionine species as strong predictors of semiarid paleoenvironments in the absence of other supporting evidence.

Conclusions

Fossil remains of extinct *Equus* from Porcupine Cave consist almost exclusively of isolated dental and distal limb elements. These fossils are interpreted to have been brought into the cave by rodents, probably wood rats. Juvenile, mature, and aged individuals are all represented in the sample. Some dental elements show damage resembling acid etching, and most limb elements have been gnawed.

A minimum of four taxa are represented in the sample: large horses, smaller caballine horses, small hemionine horses, and a small Blancan ass. Unfortunately the fossil remains are not sufficiently diagnostic to advance specific determinations, except in the case of the latter form, *Equus* sp. cf. *E. cumminsi*. This animal is associated with an early Irvingtonian micromammal fauna in Porcupine Cave; either a previously unrecognized Blancan faunal component is also present from this portion of the cave, or else this find constitutes a substantial temporal range extension for the species. The presence of stilt-legged equids from some areas within Porcupine Cave lends credence to interpretations of semiarid interglacial conditions in the region during part of the time period preserved in the fossil record from this important and unique Plio-Pleistocene site.

Acknowledgments

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Unpublished measurements of fossil specimens were graciously provided by Arthur Harris of the Centennial Museum, El Paso, Texas (*Equus conversidens* from Dry Cave) and Lyndon K. Murray of the YPM (*E. calobatus* from Rock Creek). Digital caliper and computer hardware was supplied by Fred Ferguson of Quality Control Company, Leslie Marcus of the American Museum of Natural History, and Tom Ross of Tekwerks; software was provided by Timothy Heaton of the University of South Dakota as shareware from his Web page.

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TWENTY-ONE

Pleistocene (Irvingtonian) Artiodactyla from Porcupine Cave

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This chapter documents the Artiodactyla recovered from various localities within Porcupine Cave. Details of the excavations, stratigraphy, and chronology are discussed in other chapters and will not be described here except when pertinent to the artiodactyls. Table 21.1 provides a summary listing of identified artiodactyls (see also chapter 10).

Taphonomy

All recovered artiodactyl fossils were isolated remains; articulated or semiarticulated specimens were conspicuously absent. There is definitely a selection bias by size. Most of the elements are less than 20 cm in length, and typically less than 10 cm, whether an entire bone or a fragment. Only in one instance was a larger skeletal element recovered: the partial cranium of a *Camelops* (camel) found in the talus cone in Tobacco Road. This is the only specimen of an artiodactyl from this area of the cave, a region that is inadequately excavated; the paleontological remains from here are not yet well understood and await further study. Some of the smaller, sturdier skeletal elements from the various deposits are entire. Rodents have gnawed on a number of the larger bones, some extensively (figure 21.1). The taphonomy of the cave and its various deposits is discussed in more detail in chapters 2, 8, 9, 20, and 22, and we augment those observations as they relate to the artiodactyl remains discussed here.

The accumulation of bones within the cave has several causes, and these may have changed through time as one entrance closed while another one opened. Entrances could have been steep and may have acted as natural traps, or they may have been easily accessible to those animals that would walk into the cave. Given the richness of the entire fauna, which tends to be biased toward small mammals, many of the entrances might have also been used as raptor roosts. The general lack of breakage of skeletal elements would further imply that most of the bones were not brought into the cave via carnivore dung, although clearly this did happen. The large number of carnivore remains in the cave indicates that denning possibly occurred in or near the entrances, that entrances were natural traps, or both. Such deadly pit-fall entrances are known to entrap a high percentage of carnivores (White et al., 1984). A natural trap entrance would be suitable for raptor roosting and would act as a funnel into the cave for slope wash during rain and snow runoff. Such slope wash would also account for the large number of molluscan remains (which have yet to be studied) found in various excavations within the Velvet Room (J. I. Mead, pers. obs.).

Based on the artiodactyl remains, it appears that the entrances to the cave were not large walk-in shelters. If peccaries (tayassuid artiodactyls) are common in a region, they often use walk-in cave entrances for retreat, and their skeletal remains (often entire or semiarticulated) are common (Lundelius, 1960; Guilday et al., 1971; Sowls, 1984). Caves with walk-in entrances often act as shelters for other artiodactyls. Antilocaprids and bovids use such shelters, and their skeletal remains are often abundant in the cave deposits (Skinner, 1942; Euler, 1984; Mead and Lawler, 1994; Czaplewski et al., 1999a, 1999b). The remains of artiodactyls so far recovered from Porcupine Cave are unlike those typically found in caves with sheltered, walk-in entrances.

Artiodactyl remains are relatively scarce in the overall record from Porcupine Cave (appendix 21.1). Based on the fragmented nature of the recovered remains, the elements of artiodactyls were introduced into the cave from the outside, and the animals do not appear to have been cave occupants. Their remains appear to have been transported into the cave, possibly pit-trapped on occasion (e.g., the camel skull), or both. The size bias of the artiodactyl remains implies that, for the most part, remains were either being washed into the cave or being carried in by smaller animals. Carnivores will amass bones (Brain, 1981; Bonnichsen and Sorg, 1989), but these bones will typically show extreme breakage, fracturing, carnasial gnawing,

TABLE 21.1

Artiodactyla Recovered from Porcupine Cave

	Locality within Porcupine Cave											
Taxon	*Bd*	*CAR*	*CR*	*FR*	*G*	*GDR*	*MS*	*Pt*	*TR*	*TS*	*VMX*	*WH*
						Tayassuidae						
Platygonus	×	—	×	×	—	—	×	×	—	—	×	×
						Camelidae						
Camelops	—	×	—	—	—	—	—	—	×	×	—	—
Hemiauchenia	—	—	—	×	—	—	—	—	—	—	—	—
						Cervidae						
cf. *Cervus*	—	—	—	—	—	—	—	—	—	—	×	—
Odocoileus	—	—	—	—	—	—	—	×	—	—	×	—
cf. *Odocoileus*	—	—	—	×	—	—	—	×	—	—	—	×
cf. *Navahoceros*	—	—	—	—	—	—	—	—	—	—	×	—
						Antilocapridae						
Stockoceros	—	—	—	—	—	—	—	—	—	—	×	—
Antilocapra/*Tetrameryx*	—	—	—	—	—	—	—	×	—	—	—	—
Gen. et sp. indet.	×	×	×	×	×	×	×	×	—	—	×	×
						Bovidae						
Oreamnos harringtoni	—	×	—	—	—	—		×	—	—	—	—
Ovis	—	—	—	—	—	—	×	×	—	—	—	—
Ovibovini indet.	×	—	—	—	—	—	—	×	—	—	—	—

NOTES: See text under species account to better understand locality designation. *Abbreviations:* Bd, Badger Room; CR, Crystal Room; FR, Ferret Room; G, General; GDR, Generator Dome; CAR, Come-A-Long Room, MS, Mark's Sink; Pt, the Pit; TS, Trailside Entrance; TR, Tobacco Road; VMX, Velvet Room main excavation; WH, Will's Hole.

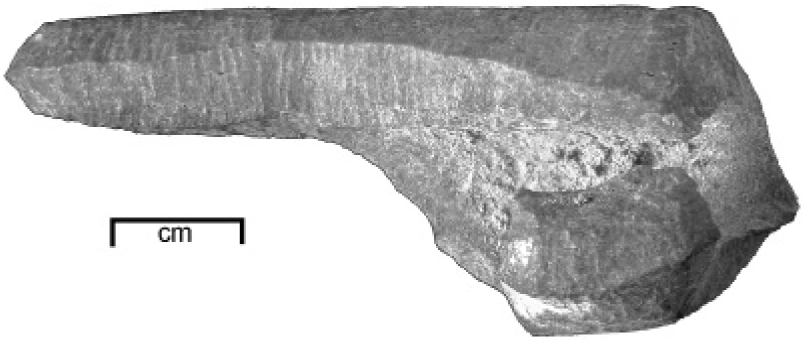

FIGURE 21.1 Extreme rodent gnawing on a broken mid-diaphysis of a long bone (DMNH 22021; Velvet Room).

puncturing, and dissolution. These effects are rarely observed in the artiodactyl remains from Porcupine Cave. Porcupines (*Erethizon,* Rodentia) collect bones but gnaw them extensively, and they often select bones of larger mass. This form of extensive gnawing is not apparent in the material recovered from Porcupine Cave.

Systematic Paleontology

Artiodactyl remains were recovered from the following localities: Badger Room, Come-A-Long Room, Crystal Room, Ferret Room, General (bones from the cave that cannot be placed at a particular locality), Generator Dome, Mark's Sink, the Pit, Tobacco Road, Trailside Entrance, Velvet Room, and Will's Hole. Appendix 21.1 provides a listing of all specimens described in this chapter, including the institution of curation and specimen number, identification, skeletal element, and location. Measurement terminology follows von den Driesch (1976); classification of mammals follows McKenna and Bell (1997).

Class Mammalia

Order Artiodactyla

Suborder Suiformes

Family Tayassuidae

PLATYGONUS *SP.*

IDENTIFICATION Only a few teeth were recovered (appendix 21.1). A portion of a left c1 (DMNH 9896: anterior-posterior diameter = 11.76 mm) is split longitudinally, but still illustrates the characteristic shape and morphology of the tayassuids (figure 21.2A). Canines of *Mylohyus* (forest peccary) are relatively and absolutely smaller than in *Platygonus* (Lundelius, 1960; Guilday et al., 1971). Although the Porcupine Cave specimen is split longitudinally, it does contain distinct surface grooves, indicating that the specimen belongs to *Platygonus* and not *Mylohyus.* The canine is not strongly curved, which is typical of *Platygonus* and the living *Tayassu* and unlike the strongly curved canines of *Mylohyus* (Lundelius, 1960; figure 21.2A).

Only a single cheek tooth was recovered, a right dp4 (DMNH 10640: anterior-posterior length = 12.03 mm). This deciduous tooth is lophodont and appears hypsodont, as in *Platygonus* and unlike *Mylohyus.*

A first phalanx (DMNH 40673: Glpe = 38.73 mm, SD = 15.02 mm) contains the ventral protrusion of the plateau post-articulaire (figure 21.2B). This bone is curved and convex, not flat as in *Odocoileus.* The medial articulation of the proximal end differs in length from the lateral articulation. This condition matches that in *Platygonus* but differs from that in *Odocoileus, Ovis, Antilocapra,* and *Oreamnos,* in which the respective features are the same length. The first phalanges—DMNH 20440 (Glpe = 34.03 mm, SD = 12.40 mm), DMNH 40673 (figure 21.2B), and DMNH 42203 (Glpe = 38.13 mm, SD = 13.42 mm)—have splayed distal articular facets and a wide articular groove that presumably allows for the deflected angle of the distal toe bones typical of the tayassuids.

The characteristic shape of the second phalanx belonging to *Platygonus* is shown in figure 21.2C (UCMP 154477: Glpe = 38.38 mm, SD = 14.29 mm; similar is CM 75503: Glpe = 27.43 mm, SD = 12.26 mm). The distal portion of the third phalanx (UCMP 155906) shows the characteristic flattened and spatulate shape typical of tayassuids (figure 21.2D; DLS = 33.06 mm, LD = 32.20 mm). The articular facet is angled and deflected to allow for the out-turned toes. There are no other North American ruminants with this orientation.

DISCUSSION Two tayassuid genera, *Platygonus* and *Mylohyus,* are represented in the North American Pleistocene. Comparisons indicate the presence of the smaller of the two genera, *Platygonus,* in Porcupine Cave. As noted by Kurtén and Anderson (1980), *Mylohyus* is mostly an eastern North American genus, not found west of Texas and Missouri.

Irvingtonian-age finds of *Platygonus* are rare, with some of the best samples coming from the Leisey Shell Pit (Florida), Cumberland Cave (Maryland), and Hay Springs (Nebraska; Wright, 1995). Slaughter (1966b) suggested that there are only two valid species of Pleistocene *Platygonus (P. vetus* and *P. compressus). P. vetus* (= *P. cumberlandensis* and *P. intermedius*) is one of the largest peccaries known, and is found in the Blancan and Irvingtonian. *P. compressus* is known only from the Rancholabrean. Although *P. vetus* is often shown to be significantly larger than *P. compressus,* the Irvingtonian-age samples from Florida represent a distinctly smaller animal than its more northerly representatives (Wright, 1995). Most of the analyses on *Platygonus* were conducted on the cranium and selected postcranial elements. Few comprehensive studies have been performed on the phalanges. All peccary phalanges recovered from Porcupine Cave are similar in size to those of *P. compressus* from Bat Cave, Missouri (Hawksley et al., 1973), and to those from Rancho La Brea (Merriam and Stock, 1921). Because there is a lack of data concerning the phalanges of Irvingtonian *Platygonus,* we are unable to adequately identify the Porcupine Cave samples to species. Their size indicates they could belong to *P. compressus* or to the small form of *P. vetus* (as in those from Florida).

Suborder Tylopoda

Family Camelidae

CAMELOPS *SP.*

IDENTIFICATION A first phalanx (CM 75512) has the insertion scar of the major suspensory ligaments and tendons (interosseus tendon and distal sesamoidean ligaments) at the mid-diaphysis. This scar is rounded in shape, as observed in *Camelops* and unlike those found in *Hemiauchenia* and *Titanotylopus* (Harrison, 1979). The measurements (GL = 116.5 mm, BP = 40.7 mm) are in agreement with those reported for other *Camelops* (Webb, 1965). The first phalanges of *Hemiauchenia* (and the diminutive *Palaeolama*) are narrower and shorter

FIGURE 21.2 Skeletal elements of *Platygonus.* (A) Lc1 (DMNH 9896); (B) first phalanx (DMNH 40673); (C) second phalanx (UCMP 154477); (D) third phalanx (UCMP 155906).

than those of *Camelops* (for a discussion of these genera, see Webb and Stehli, 1995).

A cranium (DMNH 38812) is in a poor state of preservation, with the bone being powdery and teeth broken or missing. The associated atlas has been repaired but shows distortion. Minimum measurements of the atlas include the following: GL = 145 mm and GBw ≈ 161 mm. The length of the M1 is 33.9 mm; the paracone is 27.5 mm wide and the protocone is 25.5 mm wide. Although in a poor state of repair, the specimen is identifiable to the genus *Camelops* because of its large size.

DISCUSSION According to Kurtén and Anderson (1980), six genera of camels lived in North America during the Pleistocene. The giant cameline, *Titanotylopus,* lived into the Irvingtonian, with *Blancocamelus* occurring only in the Blancan. The giant camelopines, *Megatylopus* and *Camelops,* and the smaller lamine forms, *Hemiauchenia* and *Palaeolama,* are known from the Irvingtonian and Rancholabrean. *Camelops* is known from Blancan to late Rancholabrean time in North America and is well documented in Colorado. Dalquest (1992), in contrast, contended that four or five genera of camels lived in North America in the Pleistocene *(Palaeolama, Palauchenia, Titanotylopus, Hemiauchenia,* and *Camelops).*

GENUS HEMIAUCHENIA *SP.*

IDENTIFICATION A 40.7-mm-long fragment represents the distal end of a metapodial (CM 75513). Although damaged, the greatest diameters of the diaphysis are 20.5 (transverse) and 13.5 mm. These measurements and the characteristic deep groove closely resemble those of *Hemiauchenia.*

DISCUSSION *Hemiauchenia* is a familiar genus of lamine camel in many areas of North America, especially California (Stock, 1928). The chronological range of *Hemiauchenia* extends from the end of the Rancholabrean back into the Hemphillian, with the evolutionary lineage progressing from *H. vera* through *H. blancoensis* and *H. seymourensis* to *H. macrocephala* (Webb and Stehli, 1995).

Suborder Ruminantia

Superfamily Cervoidea

Family Cervidae

Subfamily Cervinae

Tribe Cervini

CF. CERVUS *SP.*

IDENTIFICATION The labial pattern of the M3 (DMNH 28331; figure 21.3A) closely approximates that of *Cervus elaphus,* but it contains a broken anterior extension near the base, which is not seen on slightly worn *C. elaphus* M3. Interapex (paracone-metacone) length along the labial edge is 12.36 mm, compared with 12.68 mm in modern *C. elaphus.* The ridge on the posterolabial corner of the paracone is narrow, and it has an extremely narrow groove along the anterior edge, similar to that observed among modern *Cervus.* The size of the tooth is larger than observed in *Odocoileus* and *Navahoceros.*

DISCUSSION *Cervus,* a genus common to Holarctic faunas, is rare in the Porcupine Cave deposits. Presumably the specimens recovered represent *C. elaphus,* but this conclusion remains equivocal. It is possible that the specimen represents the Irvingtonian *Cervus? brevitrabalis,* known only from antler fragments; this species is still in need of careful assessment and characterization (Kurtén and Anderson, 1980).

Subfamily Odocoileinae

Tribe Odocoileini

ODOCOILEUS *SP.*

IDENTIFICATION The small fragment of maxilla with brachydont deciduous teeth (dP2-4; CM 65596; figure 21.3B)

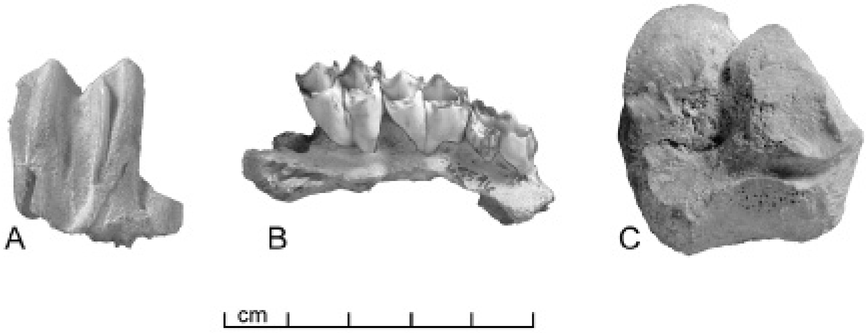

FIGURE 21.3 Cervids from Porcupine Cave. (A) M3 (DMNH 28331) of cf. *Cervus.* (B) dP2–4 (CM 65596) of *Odocoileus* sp. (C) naviculo-cuboid with entocuneiform (DMNH 27055) of cf. *Navahoceros.*

has an alveolar length of 35.58 mm. Size and tooth form compare closely with those of a juvenile *Odocoileus.* DMNH 8498 has a length of 8.93 mm and a GW of 4.74 mm. These remains are smaller than in *Cervus* and *Navahoceros.*

DISCUSSION *Odocoileus* appeared in North America in the Blancan (Pliocene) as *O. brachydontus.* Webb and Stehli (1995) recorded the living species, *O. virginianus,* in the Irvingtonian deposits at the Leisey Shell Pits of Florida. This species is also known from Blancan-age localities (Kurtén and Anderson, 1980). It is not surprising to find *Odocoileus* in the Irvingtonian deposits of Porcupine Cave. Unfortunately, the specimens recovered are inadequate to determine whether the species was *O. virginianus* or *O. hemionus.*

CF. ODOCOILEUS *SP.*

IDENTIFICATION These samples (DMNH 39805; UCMP 154481, 173745) of the first phalanges have all the delicate characters typical of the smaller, more gracile odocoilene deer and do not have the sharp edges characteristic of the antilocaprids. The following measurements were taken: UCMP 173745 (Gple = 56.30 mm, SD = 11.58 mm); UCMP 154481 (Gple ≈ 44.22 mm, SD = 12.93 mm); and DMNH 39805 (SD = 12.25 mm).

CF. NAVAHOCEROS *SP.*

IDENTIFICATION The greatest mediolateral width of the navicular-cuboid (DMNH 27055) is 40.37 mm, smaller than the same element observed in *Cervus,* and larger than observed in *Odocoileus, Ovis,* antilocaprids, or *Oreamnos.* The size matches that of the same element in *Euceratherium* and *Navahoceros.* Edges of the left naviculo-cuboid with entocuneiform (DMNH 27055; figure 21.3C) are gnawed on the plantar surface. The articular surface (on the distal face of the naviculo-cuboid where it contacts the lateral edge of the metatarsal) is dorsoplantarly long as in cervids and not short as in bovids (Lawrence, 1951; Heintz, 1970). Although the plantar edge is gnawed, the area appears to have a wide and long articular facet, similar to that found in cervids and unlike the short and more angular facet found in bovids (Lawrence, 1951; Heintz, 1970). Additional fragmentary left naviculo-cuboids (DMNH 10738) lack the entocuneiform, but otherwise closely resemble DMNH 27055.

DISCUSSION Cf. *Navahoceros* was known previously only from the Rancholabrean of the Rocky Mountain region of North America (Kurtén and Anderson, 1980), and its presence in Porcupine Cave extends the chronological range of the taxon into the Irvingtonian. *Navahoceros* is a large odocoilene deer represented by a single species, *N. fricki.* The genus is not well understood or adequately characterized (Kurtén, 1975; Blackford, 1995), and both the genus and the specimens presented here from Porcupine Cave warrant further study.

Family Antilocapridae

Subfamily Antilocaprinae

ANTILOCAPRA *SP. OR* TETRAMERYX *SP.*

IDENTIFICATION The LM2 (UCMP 173751) is hypsodont with no development of a root pattern. Morphologically, this tooth is similar to those of *Antilocapra americana.* The antero- and posterolabial ridges (parastyle, mesostyle, metastyle) are more distinct than those observed in living *Antilocapra americana* but otherwise similar (occlusal length is 17.07 mm; greatest width is 10.24 mm). At this time we cannot differentiate M2s of *Antilocapra* from those of large *Tetameryx.*

The adult humerus (CM 75504) is missing the proximal third, just below the epiphysis. The distal projection of the medial condyle is long and prominent in both *Oreamnos americanus* and *O. harringtoni.* This same projection is slight on *Ovis canadensis* and almost absent on antilocaprids and CM 75504. The diaphysis is straight on both the dorsal and volar sides in both *Oreamnos americanus* and *O. harringtoni,* whereas it is angular and curved in *Ovis canadensis,* antilocaprids, and CM 75504. The intercondyloid fossa is prominent and deep in antilocaprids and CM 75504 and shallow in *Ovis.* The shape and rugosity of the tendon attachments immediately above the lateral portion of the trochlea indicate that the specimen is an antilocaprid and not *Ovis* or *Oreamnos.* For these reasons, we have identified this specimen as belonging to an antilocaprid. Table 21.2 demonstrates that the humerus is about the same size as that of modern *Antilocapra americana* and the Rancholabrean-age *Antilocapra* from Natural Trap Cave, Wyoming (Chorn et al., 1988).

TABLE 21.2
Measurements of the Humerus and Radius
of Modern and Fossil *Antilocapra* and Fossils from Porcupine Cave

	BD	*SD*	*GL*	*BP*
		Humerus		
Porcupine Cave (*n* = 1)	38.5	19.6		
Natural Trap Cave (*n* = 5)	38.8	18.4		
	1.3	0.5		
	37.0–40.2	17.8–19.0		
Modern (*n* = 11)	38.7	19.1		
	1.2	0.1		
	367.9–40.5	17.1–20.1		
		Radius		
Porcupine Cave (*n* = 1)	36.2	22.7	210.1	39.8
Natural Trap Cave (*n* = 3)	33.7	19.6	204.0	37.0
	1.4	0.3	2.4	0.3
	32.0–35.4	19.3–20.1	201.0–207.0	34.7–39.7
Modern (*n* = 10)	32.8	21.2	210.9	37.4
	1.7	1.4	7.6	1.4

NOTES: Measurements are in millimeters; mean, standard deviation, and range are given. *Antilocapra* measurements are from Chorn et al. (1988). Abbreviations and method of measurement follow von den Driesch (1976).

The complete radius from Porcupine Cave (UCMP 173746; figure 21.4A) is morphologically identical to that of modern *Antilocapra* with respect to the distal end and carpal articulations, and it is distinct from the morphologies observed on *Ovis* and *Oreamnos.* The articular surface for the ulna at the proximal end is identical to that found on *Antilocapra,* including the deep V-notch for the internal articulation with the ulna on the volar surface, and it is distinct from those areas observed on *Ovis* and *Oreamnos.* For these reasons, we identify the radius as belonging to an antilocaprid. Table 21.2 lists various measurements of the fossil radius in comparison with those found on modern *Antilocapra americana* and the fossil *Antilocapra* from Natural Trap Cave, Wyoming (Chorn et al., 1988). The specimen from Porcupine Cave is within the range of the living species, although slightly more robust in the proximal and distal surfaces, but we cannot rule out the possibility that the specimen belongs to a large *Tetrameryx.*

A scaphoid (UCMP 154486; figure 21.4B) has a dorsal proximodistal thickness of 14.27 mm and a ventral proximodistal thickness of 15.60 mm; the greatest length (dorsoventral) is 21.52 mm. This specimen exhibits the same morphological pattern as, and is within the size range of, modern *Antilocapra americana.* It is smaller and less pronounced at the articulation with the proximal end of the magnum than in *Odocoileus* or *Ovis* (in which the articulation is much more cupped, with a deeper facet). The articular projection at the contact with the lunar is in the same position as in antilocaprids, closer to one-third of the dorsoventral length, whereas in *Odocoileus* this is approximately one-quarter of the dorsoventral length. This element is less robust than the scaphoid of *Ovis* or *Oreamnos.* In addition, the *Oreamnos* scaphoid is squarer in outline, to accommodate the greater width of the metacarpal. The proximal-ventral projection is pointed and narrow as in antilocaprids, not wide and square as in *Oreamnos.*

DISCUSSION A number of antilocaprids were found in North America during the Pleistocene, ranging in size from the small *Capromeryx* to the medium-sized *Stockoceros* to the larger forms of *Tetrameryx* and the living *Antilocapra.* Although certain skeletal elements of these various genera are identifiable to species, many of the postcrania have yet to be completely characterized. For this reason, many of the specimens from Porcupine Cave have not been identified to the generic level. The radius and humerus described previously appear to be from a large form of antilocaprid, presumably either *Antilocapra* or *Tetrameryx.* We were not able to make adequate comparisons of the Porcupine Cave specimens with large forms of *Tetrameryx.* Based on the size of the fossils (table 21.2), these specimens do not belong to the diminutive *Capromeryx* or the small *Stockoceros,* but we cannot determine at this time whether or not we have the living *Antilocapra* (as it would appear) or a large form of *Tetrameryx.* Although fossil pronghorns are rarely recovered (Chorn et al., 1988), select localities contain unusually complete records and large numbers of

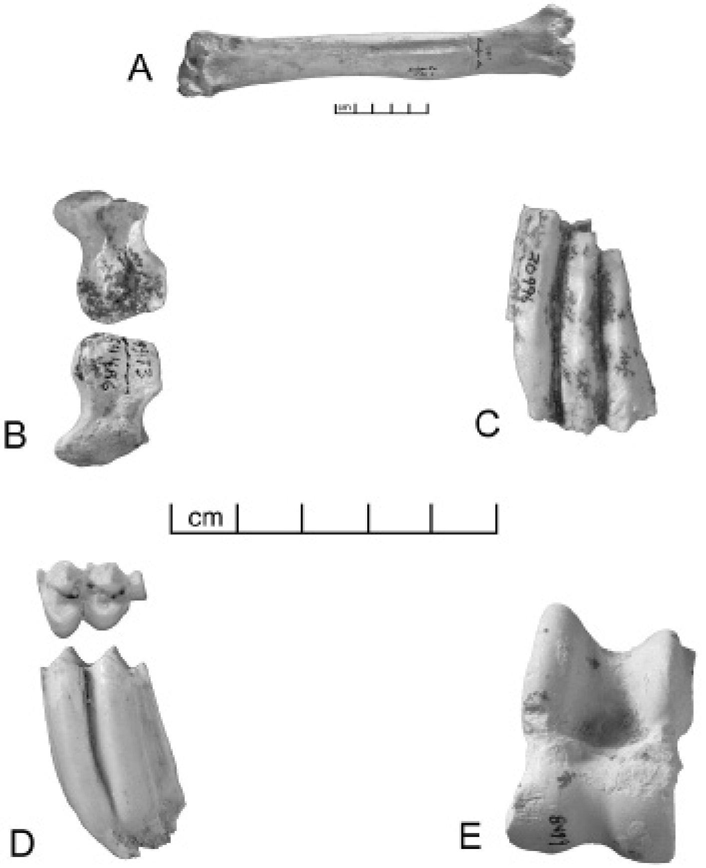

FIGURE 21.4 (A) L radius (UCMP 173746) of *Antilocapra* or *Tetrameryx*. (B) scaphoid (UCMP 154486) of *Antilocapra* or *Tetrameryx*. (C) Lm3 (DMNH 20996) of cf. *Stockoceros*. (D) Lm2 (UCMP 158678) of *Ovis*. (E) R astragalus (DMNH 8499) of Antilocapridae gen. et sp. indet.

specimens (Stock, 1930, 1932; Skinner, 1942). Antilocaprids are the dominant large mammals recovered from the various deposits within Porcupine Cave.

STOCKOCEROS *SP.*

IDENTIFICATION The Lm3 (DMNH 20996) is nearly complete (containing the three lobes and no evidence of a fourth; Skinner, 1942; figure 21.4C) and has an approximate occlusal length of 18.61 mm and a greatest width of 6.16 mm. This specimen is within the size range of *Stockoceros onusrosagris* from Papago Springs Cave, Arizona (Skinner, 1942; Czaplewski et al., 1999a) and is larger than those of the genus *Capromeryx* (Hibbard and Taylor, 1960). The protoconid and hypoconid are narrower and more rounded anteroposteriorly on DMNH 20996 than what is observed in *Antilocapra, Tetrameryx, Ovis,* or *Oreamnos.*

Antilocapridae gen. et sp. indet.

IDENTIFICATION Although we are confident in recognizing the skeletal elements listed in this section as antilocaprids, we are unable to unequivocally assign them to genus. The first phalanges recovered are all gracile and have the sharp edges characteristic of antilocaprids. The measurement Glpe ranges from 32.74 to 52.19 mm; SD ranges from 9.88 to 10.88 mm. The anterodorsal surface of an antilocaprid third phalanx lacks the angle present in *Ovis.* The facets are posterior to the highest point on the dorsal surface, unlike those observed in cervids. The third phalanx of the fossils and antilocaprids is narrower than that of *Ovis.*

A metapodial (DMNH 33766) exhibits the antilocaprid and *Ovis* character of having the shaft immediately proximal to the condyles extend no farther anteriorly than the edge of the condyle, but this specimen lacks the ridge on the anterolateral side of the condyles as seen in *Ovis.* The shaft extends farther than the condyle edge in *Odocoileus.*

All of the recovered astragali have the characteristic sharp edges found in antilocaprids (figure 21.4E). Antilocaprid astragali have a distal width less than the proximal width, contrary to that found in cervids. Antilocaprids have a more distinct medial salient than that found in cervids. The Porcupine Cave fossils and known taxa of antilocaprids have a less distinct lateral salient than that found in deer and *Ovis.* Table 21.3 provides the measurements made on astragali from Porcupine Cave identified as belonging to antilocaprids.

Antilocaprid distal humeri have a shallower external condylar groove than that found in cervids. The internal condylar groove is deeper than the external condylar groove on the fossils and antilocaprids in comparison to cervids. The sloping face of the external condyle in antilocaprids and the fossils is less steep than that found in cervids. The ectepicondylar ridge

TABLE 21.3

Measurements of Astragali Identified as Belonging to Antilocaprids from Porcupine Cave

Astragalus Specimen	*Proximal Width*	*Distal Width*	*GLl*	*Glm*
DMNH 8499	24.49	23.68	37.52	35.24
DMNH 20439	22.62	22.64	34.79	33.70
DMNH 20439	22.76	24.19	38.60	35.36
DMNH 42202	21.64	21.60	32.46	NA
UCMP 154470	24.82	NA	36.52	33.28
UCMP 155901	24.81	NA	NA	NA
UCMP 173752	21.42	NA	37.24	NA

NOTES: Measurements are in millimeters. NA, not available.

is better developed and extends well beyond the margin of the articular surface when viewed anteriorly in the fossils and antilocaprids. In cervids this ridge does not extend beyond the margin of the articular surface when the bone is viewed anteriorly. The condylar grooves are deeper, and the intercondylar ridges more distinct, in the fossils and antilocaprids than in *Ovis* and *Oreamnos.*

Superfamily Bovoidea

Family Bovidae

Subfamily Caprinae

Tribe Caprini

OVIS *SP.*

IDENTIFICATION The Lm2 (UCMP 158678) is mesohypsodont with rudimentary formation of the roots. There are two major lobes (typical of the m2), but the metastyle is somewhat enlarged posteriorly (figure 21.4D) and overlaps the anterior edge of the m3. The size of the tooth, degree of hypsodonty, formation of the rudimentary roots, and development of the enlarged metastyle are consistent with m2s of *Ovis.*

The juvenile horncore (DMNH 33767: anteroposterior width = 17.96 mm, lateral width = 12.03 mm; figure 21.5A) illustrates the mediolateral compression typical of *Ovis,* unlike the more rounded shape in "rupicaprines" such as *Oreamnos* and *Neotragocerus.* The horncore does not seem to have the extremely short or flattened shape of incipient horns belonging to the antilocaprids, such as *Antilocapra, Stockoceros,* or *Tetrameryx.* The specimen is extremely small even for juveniles of the living *O. canadensis.* We conclude that this juvenile belongs to a small species or form of *Ovis* not seen alive today in North America.

DISCUSSION *Ovis* is one of the most widely distributed genera of ungulates in the world today (Valdez, 1982). Based on body structure and habitat preferences, *Ovis* can be divided into three basic forms: (1) moufloniforms (European mouflon *[O. musimon]* and Asiatic mouflons and urials *[O. gmelinii* and *O. vignei]*); (2) argaliforms (argiles of central Asia *[O. ammon]*); and (3) pachyceriforms (Siberian snow sheep *[O. nivicola]* and North American mountain sheep *[O. dalli* and *O. canadensis]*). The pachyceriforms are stockiest in form, having shorter, more muscular bodies for the rockier, mountainous terrain that they typically inhabit (Valdez and Krausman, 1999). This pachyceriform group can be subdivided into two basic types: (1) bighorn (*O. canadensis;* Rocky Mountain and desert mountain sheep) and (2) thinhorn (*O. dalli;* Dall's and stone mountain sheep). Pachyceriforms could be classified as a single species, in which case *O. canadensis* Shaw, 1804, would have precedence over *O. dalli* Nelson, 1884. The two forms are distinct phenotypically, but they will interbreed in captivity and probably could in the wild if their distributional ranges overlapped (Valdez and Krausman, 1999).

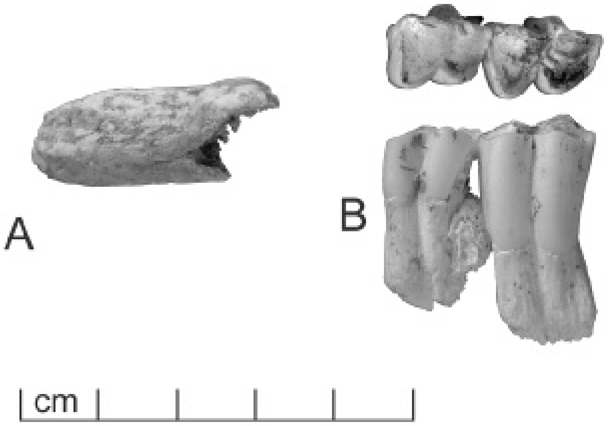

FIGURE 21.5 (A) juvenile horncore (DMNH 33767) of *Ovis.* (B) Lm1–2 of *Oreamnos harringtoni.*

Ovis first appeared in the Villafranchian (Pliocene) in Europe and Asia, along with other caprines such as *Sinocapra* in Asia in the late Pliocene (Kurtén and Anderson, 1980; Chen, 1991). The fossil history of *Ovis* in North America is not well known and is currently being studied by us in more depth. It is thought that *Ovis* dispersed into North America in the early Rancholabrean (Lundelius et al., 1987; McKenna and Bell, 1997), which is a reasonable conclusion given the published

TABLE 21.4
Measurements of the M1-2 of the Porcupine Cave Specimen CM 75510; *Oreamnos harringtoni* from Texas; *Oreamnos harringtoni* from the Grand Canyon, Arizona; *Oreamnos americanus;* and *Ovis canadensis*

	75510	*Or.h.Tx*	*Or.h.A*	*Or.h.B*	*Or.a.*	*Ovis can.*
L M1	11.3	13.7	15.8	12.7	12.5/13.4	17.2
W M1	9.2	12.8	13.6	12.5	10.9/12.5	11.7
L M2	14.5	16.1	19.7	17.1	16.3/18.2	18.9
W M2	9.6	14.2	13.6	15.4	11.4/12.3	12.7

NOTES: Measurements are in millimeters. Specimens other than that from Porcupine Cave are as follows: *Oreamnos harringtoni* from Texas (assumed male; USNM 244235; Jass et al., 2000; Or.h.Tx); *Oreamnos harringtoni* from the Grand Canyon, Arizona (Mead and Lawler, 1994; Or.h.A = GRCA55499; Or.h.B = GRCA 56441); *Oreamnos americanus* (female, modern NAU QSP 2797; male, modern NAU QSP 2796; Or.a.); and *Ovis canadensis* (*nelsoni* spp.; small species, modern; Ovis can.). *Abbreviations:* L, greatest length of tooth; W, greatest width at protocone.

data. Skeletal remains thought to represent *Ovis dalli* are reported from "Illinoian" glacial deposits near Fairbanks, Alaska (Guthrie, 1968). Such deposits, as currently understood, are suspected to lie along the transition of the Irvingtonian and Rancholabrean. The horncores and hornsheaths of *Ovis dalli* (as with the Siberian snow sheep *O. nivicola*) are slightly smaller in size and have a morphologically divergent configuration compared with those of *O. canadensis*. Based on the limited data at hand, it appears that a small sheep, approximating *Ovis dalli* in size, was the first bighorn to arrive in North America.

Shaw (1981) reported a mandible fragment of *Ovis* from the Irvingtonian deposits at El Golfo, Sonora, Mexico. This specimen is from an adult individual but of a small species. It is not known to which species these early remains belong, due to the small sample of specimens, and to the fact that one is a juvenile. The earliest unequivocal *Ovis* remains appear in North America by at least the Irvingtonian, based on the remains from El Golfo and Porcupine Cave.

Tribe Rupicaprini

OREAMNOS HARRINGTONI *STOCK, 1925*

IDENTIFICATION The single horncore (CM 49178) is nearly complete and is basically circular in cross section. It is relatively straight and lacks spiral torquing (=twisting), ridges, and grooves. These characters indicate that the specimen belongs to a "rupicaprine" and not to other bovids. This specimen is figured and discussed extensively in Mead and Taylor (1998).

The LM1-2 are from an old adult based on the amount of wear. The selenes are worn completely away on the M1, and partly on the M2. The crowns are relatively short and the roots are predominantly fused together (figure 21.5B). Although worn heavily (and thus shortened in anteroposterior length relative to the teeth of a young adult), these teeth are still from a relatively small individual. Although the data are very preliminary, the *Oreamnos harringtoni* of the Irvingtonian may have been smaller overall than any *Oreamnos* of the Rancholabrean or Recent.

The teeth are unlike those of *Ovis*. The teeth of the extinct *Oreamnos harringtoni* are typically as large or larger than those from the heavier living form, *O. americanus* (Mead and Lawler, 1994; table 21.4). The specimens of *O. harringtoni* used in table 21.4 include one apparent female (GRCA 56441) and two apparent males, as they are the largest of the known fossils for the species (one from Texas, USNM 244235, and one from the Grand Canyon, GRCA 55499). The *O. americanus* measurements are from adult female(s) and male(s). The adult teeth from Porcupine Cave appear to be from a female, or possibly from a smaller form, as they are smaller than the smallest known adult *Oreamnos harringtoni*. We assume they represent a female. These isolated teeth are not diagnostic to species, but are referred to *O. harringtoni* based on our identification of the horncore (CM 49178; Mead and Taylor, 1998). Horncore CM 49178 is from a small individual with nasal-nuchal and medial-lateral measurements well within the range of the small-horned *O. harringtoni* and not within the range of the much larger-horned *O. americanus* (Mead and Taylor, 1998).

DISCUSSION The specimen from the Pit locality represents the oldest identified *Oreamnos* specimen known. It extends the biostratigraphic range of *Oreamnos* by some 315,000–447,000 years. The ages of the teeth from the Crystal Room are not known, but they are assumed to be at least from the Irvingtonian. Together these specimens represent the earliest known fossil *Oreamnos* specimens. The Porcupine Cave specimens record *Oreamnos* in Colorado only during the Irvingtonian.

Tribe Ovibovini

GENUS AND SPECIES INDETERMINATE

IDENTIFICATION The horncore (DMNH 42621) from the undated deposits in the Badger Room is fragmented and slightly abraded (figure 21.6A). It appears to be a proximal portion, preserving some of the horncore at the burr and some of what appears to be the pedicle. The distal end and the

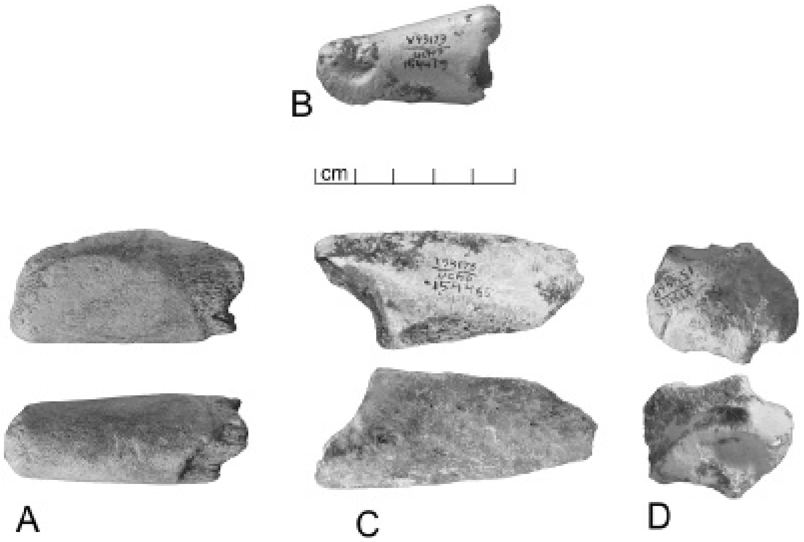

FIGURE 21.6 Remains of Ovibovini gen. et sp. indet.: (A) fragment of a horncore (DMNH 42621); (B) distal end of a first phalanx (UCMP 154479); (C) third phalanx (UCMP 154465); and (D) malleolus (UCMP 154468).

caudal edge show some rodent gnawing. Maximum length is 58.1 mm, with the greatest nasal-nuchal diameter of 28.9 mm and the greatest medial-lateral diameter of 22.6 mm. These measurements indicate that the horncore is mediolaterally flattened, completely unlike those of rupicaprines. The unabraded surface does not show any of the spiral torsion or deep grooves that are typical of horncores from the basal regions of adult ovibovines and selected other bovids. The width and cross-sectional shape for the preserved length would indicate that the horncore does not belong to young male or adult female Caprini such as *Ovis.* This same character would also remove antilocaprines from comparison.

The characters listed seem to indicate that the horncore belongs to a juvenile. This would explain why there is little torsion evident and why the shape and overall size do not fit any of the compared taxa. Adult *Bootherium, Euceratherium,* and *Soergelia* horncores all exhibit curvature and spiral torsion, along with obvious ridges and grooves on the surface. If the specimen is from a juvenile, it is all but impossible to identify the genus accurately, although it does appear to be some sort of ovibovine.

The proximal end of the first phalanx (UCMP 154479; figure 21.6B) is missing and the distal end is gnawed extensively. This phalanx is dorsovolarly thicker than that of *Ovis canadensis catclawensis* (large extinct form of bighorn), which has a straight rather than a slightly convex volar outline. The shape of the diaphysis of UCMP 154479 is distinct from that of cervids and presumably does not represent a small *Navahoceros* (the phalanges of which are unknown). UCMP 154479 is smaller (and less robust) than phalanges of *Euceratherium* and is much smaller than phalanges of *Cervus.* Although UCMP 154479 is a large phalanx, it is not the wide and robust form seen in both *Oreamnos americanus* and *O. harringtoni.* The phalanx seems to be from an animal with a mass greater than that of *Oreamnos* or *Ovis,* but not as great as that of a living *Bos* or any form of *Bison.* In form and size it appears most similar to smaller ovibovines, possibly *Euceratherium.*

UCMP 154465 is a third phalanx (figure 21.6C), slightly broken at the anterior end. The long and more slender shape of the phalanx, along with the shape and orientation of the articular facets, means that the specimen cannot belong to *Bison.* The third phalanx of *Ovibos* is typically much smaller than this specimen. The DLS is 69 mm, larger than that observed in the type specimen of *Euceratherium* from the Late Pleistocene of California (Furlong, 1905; 58 mm). A DLS of 69.68 mm is recorded for *Euceratherium* by Richards and McDonald (1991). The DLS of a *Bootherium* (=*Symbos*) from Indiana is 71.9 mm (Richards and McDonald, 1991). The dorsal surface is broken, precluding a DL measurement. We assume that the Porcupine Cave specimen could be from *Euceratherium, Praeovibos, Bootherium,* or *Soergelia,* and we agree with McDonald et al. (1991) that the postcranial elements of these musk oxen deserve detailed study. In fact, phalanges of all caprines and ovibovines are in need of comprehensive analysis.

A malleolus (UCMP 154468; figure 21.6D) has a GD of 38 mm. This is much smaller that that found in *Bison.* The configuration of the malleolus is not similar to those of the Bovini and appears more similar to those of the Ovibovini, but at this time we cannot provide a more detailed identification.

Discussion and Conclusions

Table 21.1 presents the list of artiodactyls and their locality associations in Porcupine Cave. Eleven different taxa are represented in the Porcupine Cave fauna, which appears to be rather diverse given the mountainous setting and altitude, albeit representing different periods of time and climatic environments within the Irvingtonian. Small, possibly vertical entrances appear to have imposed constraints on the accumulation of artiodactyl remains within the cave. Only the smaller skeletal elements have accumulated in the various deposits, with the sole exception being the skull of *Camelops* from the Tobacco Road locality (an inadequately studied area).

Phalanges were the most common artiodactyl skeletal elements recovered. The more scarce taxa in the cave record are typically the larger animals—those that tend to have larger skeletal elements and are less likely to have entered the cave owing to the size filter.

Tayassuids are represented by *Platygonus* sp. and are the second most abundant artiodactyl taxon from Porcupine Cave. This extinct pig may have been abundant in the local community, or, because of its smaller mass, its slighter skeletal elements may have been more likely to have entered the cave. Two genera of extinct peccaries are known from the Pleistocene of North America, *Platygonus* and *Mylohyus*. *Platygonus compressus* is probably the most common of all large Pleistocene mammals recovered from cave deposits in eastern and central North America. Many caves in the eastern United States contain abundant *Platygonus* remains, apparently representing herds (of all age classes) that made use of walk-in cave passages. Large collections of *Platygonus* are known to occur in such cave environments as Welsh Cave, Kentucky (Guilday et al., 1971); Cherokee Cave, Missouri (Simpson, 1949); and Laubach Cave, Texas (Slaughter, 1966b). There is no indication that entrances permitted walk-in or extensive use of Porcupine Cave as a *Platygonus* den.

Two camels were recovered, the large *Camelops* and the smaller *Hemiauchenia*. Neither camel is well represented in the fauna.

Cervids are represented by cf. *Cervus, Odocoileus,* cf. *Odocoileus,* and cf. *Navahoceros*. The recovery of *Cervus* and *Navahoceros* is intriguing and (although to be expected in mountainous terrain and habitat) demands further investigation, with the future discovery of additional skeletal remains. *Navahoceros* was once thought to be confined to the Rancholabrean, and its recovery in Porcupine Cave extends the known chronological range of this taxon into the Irvingtonian.

At least two antilocaprids are known from the cave, including the smaller *Stockoceros* and a larger form that is either *Antilocapra* or *Tetrameryx*. Antilocapridae represent the largest number of artiodactyl specimens. If the extinct diminutive pronghorn, *Capromeryx,* had occurred in the local community near Porcupine Cave, its remains should have been preserved; however, *Capromeryx* is as yet unknown from Porcupine Cave.

Bovids are represented by the extinct mountain goat *(Oreamnos harringtoni),* the bighorn sheep (*Ovis* sp.), and some form of ovibovine. The two known forms of *Oreamnos* include the extant, large species *(O. americanus)* and the smaller, extinct form (*O. harringtoni;* see Mead and Lawler [1994] for details). The earliest evidence of the mountain goat is now known from Porcupine Cave and includes only the small *O. harringtoni.* Previously *Oreamnos* was known only from the Rancholabrean (Mead and Taylor, 1998). *Ovis* was formerly thought to have entered North America during the Rancholabrean. The unpublished record from the Irvingtonian deposits at El Golfo, Mexico (Shaw, 1981), and the record from Porcupine Cave now demonstrate that *Ovis* entered North America by at least the mid-Irvingtonian. The few specimens known indicate that this early form was smaller than bighorn sheep today. Only a few fossils indicate that the Porcupine Cave local community contained some sort of ovibovine. Owing to the few and fragmentary elements preserved, even the genus is not differentiated in the remains, but the fossils presumably represent either *Euceratherium, Praeovibos, Bootherium,* or *Soergelia.*

The fossils from Porcupine Cave demonstrate that the artiodactyl community outside the cave was diverse during the Irvingtonian. Not all species were recovered from the same localities or equivalent stratigraphic levels; therefore it is unlikely that all would have been observed together outside the cave during any one time. Although the identifications are in some cases necessarily imprecise, Porcupine Cave provides a unique opportunity to examine some of the earliest bovids to enter North America. The oldest evidence of a North American caprine is *Neotragocerus* from the late Hemphillian of Nebraska (Matthew and Cook, 1909). Although this taxon has been placed within the Rupicaprini (Simpson, 1945), its assignment into this paraphyletic group (Gentry, 1992) and its association with *Ovis, Oreamnos,* and other bovids begs for further analysis. The accumulation of previously unknown Irvingtonian-age bovids probably is due to the high altitude and mountainous environment of the Rocky Mountains encircling Porcupine Cave. This rugged, montane setting may have been a north-south passageway for many forms of early Pleistocene bovids. Analysis of additional mountainous faunas dating to the Irvingtonian is needed to fully understand the evolving artiodactyl communities of the Quaternary.

Appendix 21.1. Artiodactyl Remains from Porcupine Cave

Institution/ Specimen No.	*Identification*	*Element*	*Location; Notes*
CM 49178	*Oreamnos harringtoni*	Horncore	Pt L2; as cf. Mead and Taylor (1988)
CM 49282	*Camelops*	R unciform	CR
CM 65595	Antilocapridae	LdP2	Pt G1L3
CM 65596	*Odocoileus*	R max dP2–4	Pt G1L3
CM 75503	*Platygonus*	Second phalanx	Pt G1L2
CM 75504	*Antilocapra/Tetrameryx*	R humerus	Bd
CM 75506	Antilocapridae	Second phalanx	Pt G1L3
CM 75507	Antilocapridae	Radius	Pt G5–6; fragment
CM 75508	Antilocapridae	R astragalus	CR
CM 75509	Antilocapridae	metapodial	FR; fragment
CM 75510	*Oreamnos harringtoni*	LM1–2	CR
CM 75512	*Camelops*	First phalanx	TS
CM 75513	*Hemiauchenia*	Metapodial	G
DMNH 8246	Antilocapridae	Second phalanx	G
DMNH 8498	*Odocoileus*	Rp2	VMX G1L10
DMNH 8499	Antilocapridae	R astragalus	VMX G1L10
DMNH 8933	Antilocapridae	RM1	VMX G7L2
DMNH 9896	*Platygonus*	Lc1	VMX G5L8
DMNH 10285	Antilocapridae	Third phalanx	VMX general
DMNH 10502	*Odocoileus*	M2	VMX G5L6
DMNH 10550	Antilocapridae	Second phalanx	VMX G6L1
DMNH 10640	*Platygonus*	R dp4	VMX G6L3
DMNH 10738	cf. *Navahoceros*	L naviculo-cuboid	VMX G6L1-4
DMNH 20437	Antilocapridae	R humerus	Bd; fragment
DMNH 20438	Antilocapridae	L humerus	Bd; fragment
DMNH 20439	Antilocapridae	L astragalus	Bd
DMNH 20440	*Platygonus*	First phalanx	Bd
DMNH 20996	*Stockoceros*	LM_3	VMX G20L7A
DMNH 21650	Antilocapridae	Metapodial	FR PC3
DMNH 22312	Antilocapridae	Third phalanx	CAR
DMNH 27055	cf. *Navahoceros*	L naviculo-cuboid	VMX G9L1
DMNH 28331	cf. *Cervus*	M3	VMX G2L3
DMNH 28333	Antilocapridae	Metapodial	Bd
DMNH 33766	Antilocapridae	Metatarsal	GDR; fragment
DMNH 33767	*Ovis*	Horncore	MS; juvenile
DMNH 38812	*Camelops*	Cranium	TR; fragment
DMNH 39805	cf. *Odocoileus*	First phalanx	WH PC11
DMNH 39811	Antilocapridae	Third phalanx	MS
DMNH 40673	*Platygonus*	First phalanx	MS
DMNH 42202	Antilocapridae	R astragalus	VMX G8-8AL2
DMNH 42203	*Platygonus*	First phalanx	Fe
DMNH 42205	Antilocapridae	L femur	MS; fragment
DMNH 42621	Ovibovini	Horncore	Bd; fragment
UCMP 154463	Antilocapridae	First phalanx	G
UCMP 154466	Antilocapridae	Humerus	Pt general; fragment
UCMP 154468	Ovibovini	L malleolus	Pt
UCMP 154470	Antilocapridae	L astragalus	Pt general
UCMP 154471	Antilocapridae	First phalanx	G

(continued)

Institution/ Specimen No.	*Identification*	*Element*	*Location; Notes*
UCMP 154477	*Platygonus*	Second phalanx	Pt
UCMP 154478	Antilocapridae	First phalanx	G
UCMP 154481	cf. *Odocoileus*	First phalanx	G
UCMP 154482	Antilocapridae	First phalanx	G
UCMP 154486	*Antilocapra*/*Tetram*eryx	L scaphoid	Pt
UCMP 155901	Antilocapridae	L astragalus	Pt surface
UCMP 155905	Antilocapridae	Second phalanx	Pt general
UCMP 155906	*Platygonus*	Third phalanx	G
UCMP 155923	Antilocapridae	Atlas	Pt general; fragment
UCMP 173745	cf. *Odocoileus*	First phalanx	Pt G5–6L2
UCMP 173746	*Antilocapra*/*Tetrameryx*	L radius	Bd
UCMP 173747	Antilocapridae	First phalanx	Pt G5–6L1
UCMP 173748	Antilocapridae	Lm2	Pt G5–6L1
UCMP 173749	Antilocapridae	dp2-4	Pt G5–6L1
UCMP 173750	Antilocapridae	First phalanx	Pt G5–6L2
UCMP 173751	*Antilocapra*/*Tetram*eryx	LM2	Pt G5–6L2
UCMP 173752	Antilocapridae	L astragalus	Pt general
UCMP 173753	Antilocapridae	Humerus	Bd; fragment
UCMP 173754	Antilocapridae	L humerus	Bd; fragment
UCMP 173755	Antilocapridae	RM2	Bd
UCMP 173756	Antilocapridae	Lm1	Bd
UCMP 173757	Antilocapridae	Second phalanx	G
UCMP 158678	*Ovis*	Lm2	Pt G5–6L1

NOTES: Locations are expressed as grid and level (G/L). *Abbreviations:* Bd, Badger Room; CAR, Come-A-Long Room; CR, Crystal Room; Fe, Ferret Room; G, General; GDM, Generator Dome; MS, Mark's Sink; Pt, the Pit; TR, Tobacco Road; TS, Trailside Entrance; VMX, Velvet Room Main Excavation, DMNH; WH, Will's Hole.

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PART THREE

EFFECT OF ENVIRONMENTAL CHANGE ON THE PORCUPINE CAVE FAUNA

TWENTY-TWO

Irvingtonian Mammals from the Badger Room in Porcupine Cave

Age, Taphonomy, Climate, and Ecology

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The Porcupine Cave locality that has received the most attention in previous publications is the Pit, a stratified sequence that provides temporally successive windows into the paleoenvironmental history of South Park (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996; Bell and Barnosky, 2000). This report synthesizes and analyzes information from the Badger Room, an unstratified, bulk-sampled deposit. Similar deposits are found throughout the cave, and each one is probably unique in its depositional history and geological age.

The Badger Room is a small chamber (2 × 3 m) in the Porcupine Cave system; it is located approximately 25 m from the modern entrance to the cave (figure 22.1; see also figure 2.3). The Badger Room may have communicated with the external environment via an ancient entrance located 3 m to the west (figure 22.1). In general, the fossils were obtained from a 2 × 2 × 1-m volume of sediment. Complex depositional history, bioturbation, and the techniques with which the fossils were collected make it impossible to attribute chronologic significance to the relative depth from which a fossil was recovered. Thus the assemblage is regarded as time averaged to an unknown degree.

One of the burdens on any faunal analysis is to estimate the scale of spatiotemporal averaging, but such estimation is difficult to do with certainty for the Badger Room. Recent investigations have demonstrated that fossil deposits like those of the Badger Room can accumulate rapidly in geological time. Stafford et al. (1999) used accelerator mass spectrometry ^{14}C dates of individual bones to show that non-analogue assemblages at sites in North America and Russia accumulated within less than 2000 years. Hadly (1999) reported that the fossiliferous sediments from Lamar Cave, Wyoming, accumulated within less than 3000 years, and within that interval the fossil assemblage faithfully sampled the local sagebrush grassland (extralocal taxa were not accumulated).

Our taphonomic objectives were to highlight the agents and pathways that produced the fossil accumulation and to assess how the organisms died. Previous work on the Badger Room had established that multiple taphonomic vectors were involved. Anderson (1996) reported that many of the carnivore fossils showed signs of rodent gnawing, but that none of the bones showed carnivore bite marks. Scott (chapter 20) notes possible evidence for carnivore activity on two equid fossils from the Badger Room (a distal metapodial, CM 49179, and a proximal scapula, CM 73356), and signs of rodent gnawing on two others (a phalanx, CM 49283, and a scaphoid, CM 49181). Mead and Taylor (chapter 21) note rodent gnawing on artiodactyl bones. Barnosky et al. and Finley (chapters 2, 8) have implicated wood rats as a primary agent of accumulation for many localities in Porcupine Cave.

The Badger Room mammal fauna is very diverse; it contains abundant lagomorph, rodent, and carnivore remains, providing a good opportunity for environmental and synecological reconstruction. Our studies analyzed the Pleistocene climate, vegetation, and local mammal fauna relative to the conditions known from recent historic times. Cooper (chapter 3) explains the modern setting in terms of its climate, geology, and flora, and we give additional descriptive information on

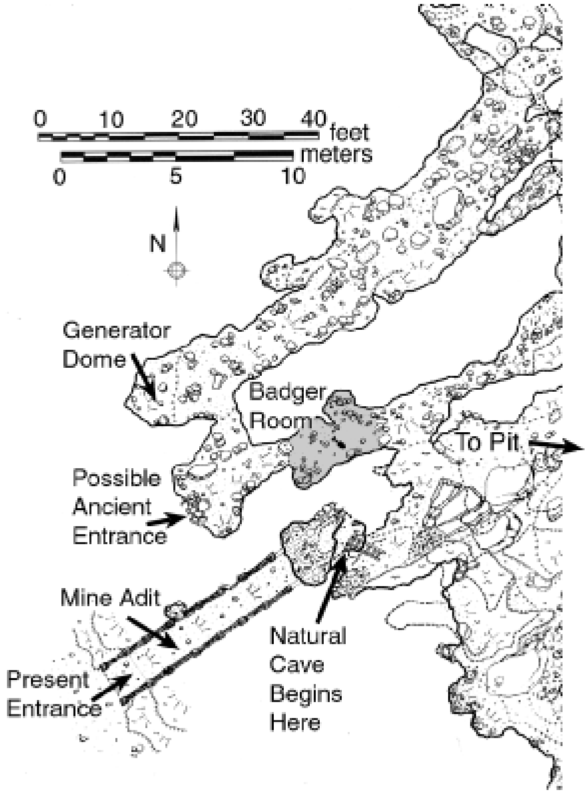

FIGURE 22.1 Location of the Badger Room (shaded area in middle corridor) within Porcupine Cave. Cartography by Hazel Barton, from a Silva/Sunto and tape survey done by Evan Anderson, Hazel Barton, Michael Barton, Beth Branson, Kirk Branson, Greg Glazner, Mike Grazi, Ted Lappin, Fred Luiszer, Emma Rainforth, Don Rasmussen, Vi Shweiker, and Ken Tiner.

the climate and vegetation in the "Modern Environment" section. Fitzgerald et al. (1994) provided detailed natural history data on Colorado mammals and vegetation zones, and the reader is directed to that work for further information. We compared the Pleistocene and modern South Park ecosystems in terms of temperature and precipitation patterns, the vegetation structure of the local landscape, the systematic diversity of the mammal fauna, and the ecological structure of the local mammal community (based on size, diet, and locomotor criteria). For native "modern" mammals, we used the ranges that existed before humans extirpated native species or introduced significant numbers of domestic stock, events that had occurred by the late nineteenth or early twentieth century.

Finally, the Badger Room fauna includes three pairs of taxa that today form complex biological associations, and we highlight these associations in order to draw attention to their coevolutionary history. The three associations are (1) the "horizontal" relationship between coyotes and badgers *(Canis latrans–Taxidea taxus),* (2) the predator-prey dynamic between fishers and porcupines *(Martes diluviana–Erethizon dorsatum),* and (3) the dependence of black-footed ferrets on prairie dogs *(Mustela nigripes–Cynomys).* Most investigations of these ecological relationships fail to reference their time depth. The black-footed ferret is one of the world's most endangered mammals, and a robust understanding of its natural history is critical for the formulation of sound recovery plans. Fishers have been introduced into many former habitats to provide a natural check on porcupine populations, and in this case also sound management depends on robust science. The "curious companionship" (Aughey, 1884:644) between the coyote and the badger provides insight into the nature of interspecific relationships.

Modern Environment

According to the Köppen-Trewartha system of climate classification (Trewartha and Horn, 1980), the macroclimate for this region of the Rocky Mountains is *temperate-boreal semiarid.* Climate influences the South Park landscape on two major scales: on a large scale across a wide region *(macroclimate)* and on a smaller scale determined by local landforms *(mesoclimate).* Mesoclimate parameters typically play the main role in determining the dominant vegetation.

Bailey (1976, 1983, 1996) drew upon climatological, geological, and ecological data to produce an ecoregional classification system. In this system, *ecoregions* are recognized at three main levels: domain, division, and province. For example, the polar domain (the area of the Earth's surface where frost action largely determines plant and soil development) is differentiated into the cold *tundra* division and the warmer *taiga* (boreal) division. In areas where effective moisture levels are low (such as on the basin floor at South Park), these divisions may grade into *semiarid steppe* (in the dry domain).

Steppe systems are open environments of grassland, shrubland, and patchily developed woodland. Steppe communities are hardy and able to tolerate wide fluctuations in temperature and low moisture levels. In an intermontane basin such as South Park, the most extreme climatic conditions often occur at the lowest elevations. Most precipitation falls on the encircling mountains, and effective moisture levels can be extremely low on the basin floor, especially in summer (effective moisture equals the net difference between precipitation and evapotranspiration). In addition, thermal inversions frequently lead to temperatures on the park floor that are substantially lower than the temperatures recorded at higher elevations. Thus the park floor often records the most extreme daily temperature minima and maxima, and the least moisture.

Trees are not prominent features of Rocky Mountain parks (early settlers referred to the vast open, rolling expanses as *parcs,* hence their modern designation as "parks" or "parklands"). Wide temperature fluctuations, severe moisture stress, and pedological factors in some combination exclude trees from the basin floor (Daubenmire, 1943). On warm, well-drained soils in Rocky Mountain parks, pinyon-juniper woodland *(Pinus-Juniperus)* may become established. However, the closed-canopy habitats—the mixed conifer forests and the needleleaf forests of pine-fir *(Pinus-Pseudotsuga)* and spruce-fir *(Picea-Abies)*—are characteristically restricted to a beltlike zone at intermediate to high elevations. Above treeline, alpine tundra and meadow systems occur among tracts of talus and rock outcrops. Across the landscape, spring-fed wetlands, ponds, streams, and small rivers form variable sources of water (bog and fen communities are typical).

Floristically South Park is diverse, and the many types of vegetation are correlated with the complex physical environment. In turn South Park supports a taxonomically rich mammal community—in recent times, as many as 49 species belonging to at least 16 families inhabited the region (Fitzgerald et al., 1994). The Rocky Mountains may have provided a biotic dispersal corridor between points as far distant as northeast Asia and the Mexican highlands, and South Park habitats may have provided refugia for a variety of organisms during glacial periods (Barnosky and Rasmussen, 1988; Bell and Barnosky, 2000). All these factors (habitat heterogeneity, corridor dispersal, refugium populations) may have contributed to the high biodiversity levels at South Park.

Materials and Methods

Fossil Collection, Excavation, and Specimens Analyzed

Three synonymous locality numbers designate the Badger Room (CM 1928, DMNH 942, UCMP V93176), reflecting the research efforts of the Carnegie Museum (CM), the Denver Museum of Nature and Science (DMNH), and the University of California Museum of Paleontology (UCMP). Surface collections of fossil material in the Badger Room were first carried out by A. D. Barnosky and D. L. Rasmussen in 1985. Preliminary excavations, under the auspices of the CM, began in 1986 and continued in 1987. The fossils from these early collections were loaned to the UCMP, where curatorial work and analysis proceeded. From 1987 to the late 1990s, crews from the DMNH have continued to excavate and collect in the Badger Room. The fossils recovered from these later excavations were assigned DMNH specimen numbers.

The CM excavation began with surface collections. These were followed by the use of trowels and trenching shovels, with fossils collected as they were sighted. Systematic screen washing was not employed. As a result, the early collections (generally specimens with CM and UCMP numbers) were biased toward bones larger than a few millimeters (i.e., bones that could be spotted easily with the naked eye in a dimly lit cave). In the later excavations by the DMNH, screen washing was employed, and as a result these excavations produced more micromammal remains.

We did not examine the specimens from the DMNH collections in detail. However, the DMNH collections database, and the data reported in other chapters of this book, were used to construct a comprehensive Badger Room faunal list (table 22.1). When possible, DMNH data were also used in our analyses. A complete list of the specimens included in this report is given in appendix 22.1.

Systematics and Faunal Lists

Barnosky and Rasmussen (1988) provided the first faunal list for the Badger Room, and Anderson (1996, chapter 13) published detailed inventories of the carnivores. Other well-studied fossil groups from the Badger Room include the birds (Emslie, chapter 12), equids (Scott, chapter 20), artiodactyls (Mead and Taylor, chapter 21), sciurids (Goodwin, 2002, chapter 17), and arvicoline rodents (Bell and Barnosky, 2000; Bell et al., chapter 19).

We followed identification criteria outlined in the publications listed in the preceding paragraph. Cranial and dental specimens of rodents and leporids in the CM and UCMP collections were identified by Bibi, Barnosky, Shabel, Kaplan, and Patrick Smith. Postcranial elements in the CM and UCMP collections were identified by Shabel and Van Leuvan. All of this work relied on the comparative collections at the UCMP and the University of California Museum of Vertebrate Zoology.

In general, Wilson and Reeder (1993) were considered the taxonomic standard for extant mammals, an exception being our use of *Lutra* (rather than *Lontra*) for the generic name of river otters, and *Mictomys* as a generic name for the bog lemmings. Wilson and Reeder regard *Mictomys* as a subgenus of *Synaptomys*. Our elevation of *Mictomys* to generic rank follows taxonomy used in chapter 19. It should be noted that recent work on the phylogenetics of placental mammals demonstrates that "Insectivora" is polyphyletic and that *Sorex* would be best classified in order "Eulipotyphla" (Springer et al., 1997; Stanhope et al., 1998; Waddell et al., 1999; Murphy et al., 2001). For ease of use, and in accordance with the other chapters in this volume, we follow the more familiar system. We use "Artiodactyla," although we recognize that it may not be ordinal per se.

Our data on recent South Park mammals were drawn from Fitzgerald et al. (1994). Presence versus absence was determined by simple inspection of the range maps in that volume, with a species recorded as present if its historic range fell within the boundaries of South Park. We included all taxa that were inhabitants of South Park in recent historical times, even if they are not present today (this includes, for example, *Canis lupus, Lynx lynx, Mustela nigripes, Ursus arctos,* and *Bison bison*). Borderline cases *(Martes americana, Microtus montanus, Ovis canadensis,* and *Lepus americanus)* were included in our tally, and thus our estimates of extant species richness are likely to be maxima.

Biochronology

The Badger Room assemblage of arvicoline rodents was compared to the assemblage occurring in the stratified Pit sequence, the ages of which have been approximated by

TABLE 22.1
Badger Room Faunal List

Taxon/Clade	*Common Name*
Gastropoda	
Species indeterminate	Gastropod
Aves	
Anseriformes	
Anatidae	
Species indeterminate	Anatid duck
Passeriformes	
Corvidae	
Corvus brachyrhynchos	American Crow
Corvus corax	Common Raven
Ciconiiformes	
Accipitridae	
Buteo sp.	Hawk
Amphibia	
Anura	Frog or toad
Mammalia	
Xenarthra	
Mylodontidae	
cf. *Paramylodon harlani*	Ground sloth
Insectivora	
Soricidae	
Sorex sp.	Shrew
Chiroptera	
?Vespertilionidae (uncertain identification)	?Vesper bat
Carnivora	
Canidae	
Canis edwardii	Edward's wolf
Canis latrans	Coyote
Canis sp.	Small coyote-like canid
Vulpes vulpes	Red fox
Felidae	
Miracinonyx cf. *M. inexpectatus*	Irvingtonian cheetah
Lynx rufus	Bobcat
Mustelidae	
cf. *Lutra*	River otter
Spilogale putorius	Eastern spotted skunk
Brachyprotoma obtusata	Short-faced skunk
Mephitis mephitis	Striped skunk
Martes diluviana	Extinct fisher
Mustela species A	New mustelid species
Mustela frenata	Long-tailed weasel
Mustela nigripes	Black-footed ferret
Taxidea taxus	American badger
Perissodactyla	
Equidae	
Equus sp. "small"	"Small" horse
Equus sp. "large"	"Large" horse
Artiodactyla	
Tayassuidae	
Platygonus sp.	Peccary
Cervidae	
Odocoileus sp.	White-tailed deer
Antilocapridae, species indeterminate	Pronghorn
Bovidae	
Ovibovini, genus and species indeterminate	Muskox
Ovis sp.	Bighorn sheep
Rodentia	
Sciuridae	
Marmota sp.	Marmot
?Cynomys andersoni, new species	Prairie dog
Cynomys sp.	Prairie dog
Spermophilus lateralis	Golden-mantled ground squirrel
Spermophilus cf. *S. elegans*	Wyoming ground squirrel
Spermophilus sp.	Ground squirrel
Geomyidae	
Thomomys sp.	Pocket gopher
Muridae	
Peromyscus sp.	Deer mouse
Neotoma sp.	Wood rat
Allophaiomys pliocaenicus	Vole
Mimomys virginianus	Virginia mimomys
Phenacomys gryci	Gryci's vole
Microtus 5T (five or six triangles)	Vole
Mictomys kansasensis/meltoni	Extinct bog lemming
Ondatra sp.	Muskrat
Erethizontidae	
Erethizon sp.	Porcupine
Lagomorpha	
Ochotonidae	
Ochotona cf. *O. princeps*	Pika
Leporidae	
Lepus sp.	Hare or jackrabbit
Sylvilagus sp.	Cottontail rabbit
Brachylagus sp. (cf. *B. coloradoensis*)	Pygmy cottontail
Aztlanolagus sp.	Aztlan rabbit
Unidentifiable leporid	Rabbit or hare

NOTES: The list includes taxa identified by the specialist contributors to this volume; taxa identified at the Denver Museum of Nature and Science (DMNH) and included in the DMNH collections database; and taxa identified by the authors at the University of California, Berkeley. See table 10.1 for the MNI and NISP of each taxon.

TABLE 22.2

Relative Abundance of Mammals in the Badger Room Assemblage

Taxon/Clade	NISP CM	 Other	 Total	Relative Abundance (%)
Lagomorpha	1076	387	1463	60
Rodentia	158	545	703	29
Carnivora	7	223	230	9.5
Artiodactyla	2	21	23	0.95
Perissodactyla	0	5	5	0.2
Chiroptera	2	3	5	0.2
Insectivora	—	1	1	0.04
Xenarthra	—	—	—	—

NOTES: Data are numbers of identifiable specimens (NISP) per taxon for all mandibles, maxillae, humeri, femora, and teeth in the Carnegie Museum collection (CM) and the DMNH/UCMP collections (Other). Total combines the NISP data for all collections. Relative abundance is the percentage abundance of each taxon relative to the total sample.

TABLE 22.3

Patterns of Representation among Skeletal Elements in the Carnegie Museum Badger Room Collection

Element	NISP	Left	Right	Unsided	Whole	Proximal	Distal	Fragment	Epiphysis
Humerus	180	87	90	3	23	28	101	25	3
Femur	229	99	117	13	39	64	81	41	4
Os coxa	174	87	86	1	3	—	—	—	—
Tibia	230	108	116	6	28	61	107	29	5
Radius	162	68	50	44	15	82	37	28	0
Ulna	124	64	54	6	0	112	11	1	0
Scapula	98	38	60	0	—	—	—	—	—
Mandible	121	58	60	3	—	—	—	—	—
Maxilla	96	50	44	2	—	—	—	—	—

correlation to the continentwide arvicoline rodent biochronology (Repenning, 1987; Bell and Barnosky, 2000). Other taxa were considered less reliable indicators of geological age, mainly because they have been less well studied than the arvicolines from a biochronologic perspective. However, none of the other taxa contradicts the conclusions reached on the basis of the arvicolines.

Taphonomy

CM specimens were used for all numerical analyses, and, where appropriate, we also included the published and unpublished DMNH data. Fossils in the CM collection were divided according to taxon and element, and each element was then subdivided into right and left sides and proximal and distal ends. Complete (whole) specimens were also noted. We focused on dentition, mandibles, maxillae, femora, humeri, os coxae, radii, scapulae, tibiae, and ulnae (referred to as focal elements). We did not include in the analysis other cranial fragments, metapodials, podials, phalanges, vertebrae, and other bones that were not readily identifiable to family, and we omitted unidentifiable long bone shafts.

Our interpretations of abundance relied on number of identifiable specimens (NISP) as the counting method (table 22.2). The DMNH database provided the details necessary to compute NISP but not minimum number of individuals (MNI). We calculated MNI for the CM collection. However, we did not utilize that data in our analysis because they result in relatively lower sample sizes and prevent comparison with the DMNH data. The MNI results for the CM collection do not contradict conclusions based on NISP. To calculate NISP per taxon and relative rank-order abundance percentages, we relied on humeri, femora, mandibles, maxillae, and teeth. (These elements tended to be numerous, well preserved, and identifiable to family.) MNI and NISP per taxon are shown in table 10.1.

TABLE 22.4

Patterns of Modification and Damage to Leporid Femora and Humeri in the Carnegie Museum Collection

	Left	*Right*	*Unsided*	*Total*	*Total Shafts Fractured*	*Irregular-Surface Fractures (No Biomodification)*	*Irregular-Surface Fractures + Biomodification*
Femora	43	66	0	109	84 (77%)	38 (35%)	16 (15%)
Humeri	59	64	2	125	91 (73%)	53 (43%)	12 (10%)

NOTES: Percentages are relative to the total number of specimens per element. Fifty-two femora sent for dating were not examined and are not included in these data.

We compared the numbers of focal elements to one another, as well as the numbers of specimens from left and right sides (table 22.3). All the focal elements were examined for (1) the paired grooves characteristic of rodent gnawing, (2) carnivore damage in the form of dental scrapes and punctures, and (3) patterns of breakage and corrosion indicative of biological processing (e.g., spiral fracture, cortical peeling, digestive acid etching).

We also examined the relative representation of proximal and distal components of the long bones, to assess whether the most nutritious parts of these bones were likely to have been consumed. We looked for fresh-break fracture surfaces and cortical peeling, to determine whether the bones were fresh at the time of breakage (table 22.4). To determine if articulated carcasses found their way into the cave, or if random elements were carried in by wood rats, we considered the relative percentage of whole bones and the general preservation of the fossils with regard to weathering. Because of the abundance of leporid fossils, the high quality of their preservation, and their potential role as prey items, we isolated the leporid specimens for a case study.

All data were managed in Microsoft Excel 5.0, and statistical tests were performed with StatView 5.0 (SAS Institute, Inc., Cary, North Carolina).

Paleoclimatology

Two of the Badger Room taxa were used to explore the paleoclimate of the region surrounding the cave. One of these taxa is extant: *Spermophilus* sp. cf. *S. elegans*. The second, *Mictomys (=Synaptomys) kansasensis* or *M. meltoni,* is extinct, but it can be considered an ecological equivalent of extant *Mictomys (=Synaptomys) borealis* for reasons given by Wood and Barnosky (1994). To estimate the climate spaces occupied by each of these species, their present geographic ranges (or, in the case of *Mictomys,* its modern equivalent, *Mictomys [=Synaptomys] borealis)* were superimposed on maps of mean monthly temperature and precipitation levels; range estimates and meteorological information were taken from Wilson and Ruff (1999) and Steinhauser (1979), respectively. The climate spaces were assumed to encompass the physiological tolerance limits of each taxon with regard to temperature and moisture. By overlaying the individual climate spaces, we defined a zone of overlap that estimates the climatic parameters within which both taxa could have coexisted (tables 22.5, 22.6). Because *Spermophilus* sp. cf. *S. elegans* cannot easily be distinguished from *S. richardsonii* by the morphological features on the Badger Room specimens, we repeated the analysis with *S. richardsonii* in place of *S. elegans.* Both sets of data are provided; however, for reasons outlined by Goodwin (2002, chapter 17), *S. elegans* is most likely the species represented.

Autecological Reconstruction

The autecological estimates used in the habitat reconstructions and in the analyses of community structure were based on natural history data provided in Nowak (1991, 1999) and Wilson and Ruff (1999) in addition to primary accounts for the following taxa: *Canis latrans* (Bekoff, 1977, 1978), *Vulpes vulpes* (Larivière and Pasitschniak-Arts, 1996), *Lynx rufus* (Larivière and Walton, 1997), *Spilogale putorius* (Kinlaw, 1995), *Mephitis mephitis* (Wade-Smith and Verts, 1982), *Martes pennanti* (Powell, 1981, 1993), *Mustela frenata* (Sheffield and Thomas, 1997), *Mustela nigripes* (Hillman and Clark, 1980), *Taxidea taxus* (Long, 1973), *Antilocapra americana* (O'Gara, 1978), *Cynomys gunnisoni* (Pizzimenti and Hoffmann, 1973), *Marmota flaviventris* (Frase and Hoffmann, 1980), *Spermophilus elegans* (Zegers, 1984), *Phenacomys intermedius* (McAllister and Hoffmann, 1988), *Erethizon dorsatum* (Woods, 1973), and *Ochotona princeps* (Smith and Weston, 1990).

Each mammal taxon was assigned to biomass, locomotor, and trophic categories. Taxa were categorized as *small* (S) if average adult biomass was estimated to be less than 0.5 kg, *medium* (M) if between 0.5 and 8.0 kg, or *large* (L) if greater than 8.0 kg. These size classes are based on empirically founded regularities (Legendre, 1986). In terms of locomotion, a taxon was classified as *terrestrial* (T) if most life history events were judged to have occurred on the ground, *fossorial* (F) if most activity occurred below ground, *natatorial* (N) if aquatic activity predominated, and *volant* (V) if the taxon flew. (There were no strictly *arboreal* taxa.) A taxon was considered *herbivorous* (H) if the majority of its annual diet consisted of vegetal material, *carnivorous* (C) if the diet consisted predominantly of vertebrate prey, or *insectivorous* (I) if the diet

TABLE 22.5

Estimates of the Minimum and Maximum Monthly Temperatures within the Geographic Ranges of Selected Indicator Taxa

	January	*February*	*March*	*April*	*May*	*June*	*July*	*August*	*September*	*October*	*November*	*December*
M. borealis minimum	–28.0	–26.0	–20.0	–10.0	–1.5	7.0	13.0	12.0	6.0	–2.0	–14.0	–23.0
M. borealis maximum	2.5	5.0	7.5	10.0	12.5	18.0	20.0	20.0	15.0	10.0	5.0	2.5
S. elegans minimum	–7.5	–5.0	–2.5	2.5	7.5	13.0	15.0	15.0	10.0	5.0	–2.5	–7.5
S. elegans maximum	0.0	0.0	2.5	7.5	12.5	20.0	23.0	21.0	16.0	10.0	5.0	0.0
Highest minimum	**–7.5**	**–5.0**	**–2.5**	2.5	**7.5**	**13.0**	**15.0**	**15.0**	**10.0**	**5.0**	–2.5	–7.5
Lowest maximum	**0.0**	**0.0**	**2.5**	7.5	12.5	18.0	20.0	20.0	15.0	10.0	**5.0**	**0.0**
Modern cave temperature	–2.5	–2.5	1.0	7.0	**13.5**	17.5	18.0	19.0	**17.0**	9.0	2.5	–1.0
S. richardsonii minimum	–15.0	–15.0	–7.5	2.5	10.0	15.0	18.0	18.0	13.0	7.5	–3.0	–13.0
S. richardsonii maximum	–5.0	–2.5	0.0	7.5	12.5	18.0	23.0	23.0	15.0	10.0	2.5	–2.5
Highest minimum	**–12.5**	**–7.5**	**–5.0**	2.5	**10.0**	**15.0**	**18.0**	**18.0**	**13.0**	**7.5**	–2.5	–7.5
Lowest maximum	**–5.0**	**–2.5**	**0.0**	7.5	12.5	18.0	20.0	20.0	15.0	10.0	**2.5**	**–2.5**
Modern cave temperature	**–2.5**	–2.5	**1.0**	7.0	**13.5**	17.5	18.0	19.0	**17.0**	9.0	2.5	**–1.0**

NOTES: Temperatures are in °C. Highest minima and lowest maxima define a zone of overlap for all taxa. Values in bold for modern cave temperatures fall outside the zone of overlap. Values in bold for highest minimum and lowest maximum indicate months in which estimates differ if *Spermophilus richardsonii* is substituted for *S. elegans.* The modern values for Porcupine Cave listed here differ from those in figure 3.7 because they are taken from contour maps that average weather data spatially, whereas figure 3.7 is compiled from a single local instrumental record.

TABLE 22.6

Estimates for the Highest Minimum and Lowest Maximum Monthly Precipitation Levels Based on Selected Indicator Taxa

	January	*February*	*March*	*April*	*May*	*June*	*July*	*August*	*September*	*October*	*November*	*December*
M. borealis minimum	10	0	0	0	0	10	25	25	25	25	25	25
M. borealis maximum	400	300	300	200	150	100	200	300	400	600	400	400
S. elegans minimum	0	0	25	25	25	25	0	0	0	25	0	0
S. elegans maximum	50	25	25	50	75	50	50	50	25	25	25	50
Highest minimum	10	0	25	25	25	25	25	25	25	25	25	25
Lowest maximum	50	25	25	50	75	50	50	50	25	25	25	50
Modern cave precipitation	15	15	25	40	40	25	50	50	25	25	**15**	**10**

NOTES: Measurements are in millimeters. Precipitation levels today fall within the hypothetical zone of overlap (see text) for all months except November and December (values in bold). The modern values for Porcupine Cave listed here differ from those in figure 3.5 because they are taken from contour maps that average weather data spatially, whereas figure 3.5 is compiled from a single local instrumental record.

consisted predominantly of nonvertebrate animal prey. If none of these food types formed a majority, the taxon was typed as *omnivorous* (O). (There were no *frugivorous* taxa.)

Although most clades can be unambiguously differentiated within this typology, exceptions occur among the Mephitinae (skunks). The diet of *Mephitis mephitis,* for example, may include up to 70% insects. However, the species is highly opportunistic and most populations utilize a shifting array of food types. *Mephitis mephitis* is usually described as an omnivore in the literature, and we have followed that classification here. *Spilogale putorius* is small and weasel-like, and it tends to be the most carnivorous skunk, feeding on small vertebrates and arthropods, although it will consume vegetal material when available (in summer). The proportionately long carnassial P4 of *Spilogale* is a presumed adaptation to meat eating (Kinlaw, 1995), and we have typed it as carnivorous. Finally, *Brachyprotoma obtusata,* an extinct mephitine well known from boreal faunas, was reconstructed by Kurtén and Anderson (1980) as a consumer of hard-shelled insects. In the absence of additional data, we have followed the literature and typed *Brachyprotoma* as insectivorous.

In terms of biomass, we classified *Erethizon dorsatum* as of medium size even though some adult individuals may exceed 8.0 kg. Other taxa straddle character states as a result of sexual dimorphism, seasonal fluctuation, or intraspecific variability. The size estimates of the purported new species of mustelid (*Mustela* sp. A) and the newly described sciurid (*?Cynomys andersoni* sp. nov.) were determined from the accounts provided in their formal descriptions (chapters 13 and 17, respectively). Finally, in terms of locomotion, some taxa combine a terrestrial lifestyle with activity in the trees *(Erethizon, Spilogale putorius),* whereas others combine fossoriality with terrestriality *(Spermophilus, Mustela nigripes, Cynomys).* In most cases, typing the taxa was straightforward. Borderline cases are recorded in the footnotes to table 22.7.

Comparative Synecology

The autecological data for the Badger Room fauna were combined to produce a synecological profile (table 22.7) that represents the spectrum of life history traits exhibited by the entire mammal community. The Badger Room community profile was juxtaposed with the profile for the recent historical South Park community (tables 22.7, 22.8) to examine ecological replacement patterns. “Deletions” refers to those taxa that were present in the Badger Room fauna but that were not present in the recent South Park community; “additions” refers to taxa that have not been identified from the Badger Room assemblage but that have been historically recorded from South Park.

As many as four species of *Sorex* and seven species of vespertilionid bat are known from the modern South Park region. The Badger Room fauna contains one soricid species (one specimen) and possibly one chiropteran species (two specimens that may be chiropteran but are too fragmentary to permit firm identification). Because the bones of these insectivorous clades are fragile and the teeth are small, their poor representation among the curated fossils is probably a result of taphonomy and collection technique; for this reason, soricids and chiropterans are not included in most analyses reported here.

Finally, we have not included the extant forest specialists *(Sciurus aberti, Tamiasciurus hudsonicus, Lepus americanus)* in our general comparative analysis. Forest specialists are notorious for their poor fossilization record, and no strictly forest-dwelling taxa have been identified from the Badger Room assemblage (whether the extinct fisher, *Martes diluviana,* should be reconstructed as a denizen of forests is debatable). The lack of such taxa in the Badger Room may be an artifact of taphonomy, or, in the case of *Lepus americanus,* it may result from the difficulty of specific identification owing to a lack of diagnostic dental characters. However, it is also possible that the absence of forest specialists indicates the absence of closed-canopy conditions on the local landscape, and we include this possible interpretation in the Discussion.

Results

Faunal Diversity

The Badger Room fauna includes gastropod snails, at least 4 species of birds, and a minimum of 42 species of mammals (table 22.1). Botanical remains have not been recovered.

Biochronology

The arvicoline rodents that have been identified in the Badger Room assemblage include *Allophaiomys pliocaenicus* (7 identifiable m1s), *Mimomys virginianus* (12 m1s), *Phenacomys gryci* (8 m1s), *Microtus* sp. (1 m1 with six triangles), and *Mictomys* sp. (cf. *kansasensis* or *meltoni*) (14 m1s) (chapter 19). The biostratigraphic ranges of these species were discussed in depth by Bell and Barnosky (2000) and in chapter 19. Those studies provide detailed justification for the following statements. The first three species bracket the probable age of the Badger Room to between 2.4 Ma and 820 Ka. *Microtus* is not known with certainty from faunas older than 840 Ka. The morphological stage of the *Mictomys* specimens is consistent with their occurrence within the age range bracketed by the other taxa.

The biochronologic data can be interpreted in two ways:

1. The age is somewhere between 800 and 900 Ka because it captures the overlapping ranges of ancient taxa *(Allophaiomys pliocaenicus, Mimomys virginianus, Phenacomys gryci)* and relatively recent taxa *(Microtus);* or
2. The assemblage is greatly time averaged, mixing taxa that lived as long as 2.4 Ma ago with those that lived more recently than about 820 Ka ago.

We favor interpretation (1) for three main reasons:

TABLE 22.7

Synecological Profiles for the Badger Room and Recent Historical South Park Taxa

Badger Room	*Diet*	*Size*	*Locomotion*	*Modern South Park*	*Diet*	*Size*
***Canis* sp. “small canid”** †	C	L[a]	T	***Lynx lynx*** *	C	L
Lynx rufus	C	L	T	*Lynx rufus*	C	L
Taxidea taxus	C	L	F	*Taxidea taxus*	C	L
Canis latrans	C	L	T	*Canis latrans*	C	L
Miracinonyx* cf. *M. inexpectatus †	C	L	T	***Felis concolor***	C	L
Canis edwardii †	C	L	T	***Canis lupus*** *	C	L
cf. *Lutra* †	C	L[b]	N	***Gulu gulo*** *	C	L
Mustela nigripes	C	M	F	*Mustela nigripes* *	C	M
***Mustela* species A** †	C	M[c]	T	***Mustela vison***	C	M
Martes diluviana †	C	M	T[d]	***Martes americana***	C	M
Vulpes vulpes	C	M	T	*Vulpes vulpes*	C	M
Spilogale putorius	C	S	T	***Mustela erminea***	C	S
Mustela frenata	C	S	T	*Mustela frenata*	C	S
Erethizon sp.	H	L[e]	T	*Erethizon dorsatum*	H	L
Antilocapra/Tetrameryx	H	L	T	*Antilocapra americana*	H	L
Antilocapridae, indeterminate	H	L	T	*Odocoileus hemionus*	H	L
Equus sp. “small” †	H	L	T	***Cervus elaphus***	H	L
Equus sp. “large” †	H	L	T	***Bison bison*** *	H	L
Ovibovini, indeterminate	H	L	T	*Ovis canadensis* *	H	L
Ovis sp. †	H	L	T	***Castor canadensis*** ¶	H	L
cf. *Paramylodon harlani* †	H	L	T			
Ondatra sp. †	H	M	N	***Ondatra zibethicus***	H	M
Marmota sp.	H	M	F	*Marmota flaviventris*	H	M
Lepus sp.	H	M	T	*Lepus townsendii*	H	M
Sylvilagus sp.	H	M	T	*Sylvilagus nuttallii*	H	M
Aztlanolagus sp.	H[f]	M	F	***Cynomys gunnisoni***	H	M
				Sciurus aberti Δ	H	M
				Lepus americanus Δ	H	M
				Spermophilus elegans	H	S
Allophaiomys pliocaenicus †	H	S	T	***Spermophilus tridecemlineatus***	H	S
Mictomys kansasensis /meltoni †	H	S	T	***Tamiasciurus hudsonicus*** Δ	H	S
?*Cynomys andersoni*, sp. nov. †	H	S[g]	F	***Tamias minimus***	H	S
Neotoma sp.	H	S	T	***Tamias quadrivittatus***	H	S
Spermophilus cf. *S. elegans*	H	S	T	*Thomomys talpoides*	H	S
Thomomys sp.	H	S	F	***Zapus princeps*** ¶	H	S
Microtus “5T form”	H	S	T	***Clethrionomys gapperi***	H	S
Phenacomys gryci †	H	S	T	*Neotoma cinerea*	H	S
Mimomys virginianus †	H	S	T	*Microtus longicaudus*	H	S
Ochotona cf. *O. princeps*	H	S	T	***Microtus pennsylvanicus***	H	S
Brachylagus sp. †	H	S	T	***Microtus montanus***	H	S
				Phenacomys intermedius	H	S
				Ochotona princeps	H	S
Spermophilus lateralis	O	S	T	*Spermophilus lateralis*	O	S
Peromyscus sp.	O[h]	S	T	*Peromyscus maniculatus*	O	S

TABLE 22.7 (continued)

Badger Room	*Diet*	*Size*	*Locomotion*	*Modern South Park*	*Diet*	*Size*
Mephitis mephitis	O	M	T	*Mephitis mephitis*	O	M
Brachyprotoma obtusata †	O[i]	M	T	***Bassariscus astutus*** ¶	O	M
				Procyon lotor ¶	O	M
***Platygonus* sp.** †	O	L	T	***Ursus americanus*** ¶	O	L
				Ursus arctos * ¶	O	L
				Homo sapiens	O	L
Sorex sp.	I	S	T	*Sorex* spp.	I	S
?*Chiroptera*	I	S	V	*Chiroptera* spp.	I	S

NOTES: "Modern South Park" denotes recent historical South Park taxa. Locomotor category is interpreted for the fossil forms from references listed in the text. Taxa in bold under Badger Room represent deletions with respect to the historic South Park fauna; taxa in bold under Modern South Park represent additions with respect to the Pleistocene fauna. *Abbreviations and symbols:* Diet: H, herbivore; C, carnivore; I, insectivore; O, omnivore. Locomotion: T, terrestrial; F, fossorial; N, natatorial; V, volant. Size: S, small (<0.5 kg); M, medium (0.5–8.0 kg); L, large (>8.0 kg). †, extinct. *, historically present in South Park but extirpated by the mid-20th century. Δ, forest specialist, possibly unlikely to be fossilized in Badger Room. ¶, possibly unlikely to be fossilized in Badger Room for taphonomic reasons.

[a] "Too small to be a coyote and too large to be a fox" (Anderson, chapter 13:147).

[b] "Large unknown lutrine" (Anderson, chapter 13:144).

[c] "All of the specimens are mink-ferret size" (Anderson, chapter 13:144).

[d] Descendants *(Martes pennanti)* have strong arboreal component to locomotor repertoire.

[e] High intraspecific variability and seasonal fluctuation; some individuals can be in medium size category (Nowak, 1999:1656).

[f] This taxon was "approximately the size of *Sylvilagus nuttallii*" (Baxter, chapter 15:167).

[g] "Distinguished from all extant and adequately known fossil *Cynomys* by smaller size" (Goodwin, chapter 17:180).

[h] The diets of *Peromyscus* species often include animal matter.

[i] "Its dental specializations indicate a probable diet of hard-shelled insects" (Kurtén and Anderson, 1980:163).

TABLE 22.8

Systematic Richness of the Badger Room Fossil Mammals Compared with the Recent Historical South Park Community

	Species		*Genera*		*Families*	
	Badger Room	*Extant*	*Badger Room*	*Extant*	*Badger Room*	*Extant*
Rodentia	14	21 [19]	13	16 [14]	4	6
Carnivora	15	19	11	12	3	5
Artidactyla	5	5	5	5	4	3
Lagomorpha	5	4 [3]	5	3	2	2
Perissodactyla	2	0	1	0	1	0
Xenarthra	1	0	1	0	1	0
Total	42	49 [46]	36	36 [34]	15	16

NOTES: "Extant" denotes recent historical South Park community. Comparisons are made per order at the ranks of species, genus, and family. Chiroptera and Insectivora are not included (see Materials and Methods). Data for the extant South Park fauna were taken from Fitzgerald et al. (1994). Brackets indicate counts if modern forest specialists are not included.

1. The deposit from which the fossils were recovered consisted of homogeneous, red-brown, poorly sorted, fine-grained, loosely consolidated sediments, indicating deposition during a period of uniform environmental conditions. This suggests that the deposits probably do not span more than 100,000 years, that is, the approximate length of one glacial-interglacial transition. In the Pit, different environmental episodes are clearly demarcated by sedimentological breaks coincident with changes in the relative abundance of environmentally sensitive taxa (Wood and Barnosky, 1994; Barnosky et al., 1996; Bell and Barnosky, 2000). In addition, other rooms in the cave have sediment types that differ from the Badger Room sediments; this observation suggests that the Badger Room would have combined different sediment types if it had accumulated material during different environmental episodes.
2. The Badger Room *Phenacomys gryci* specimens are among the most advanced morphotypes known for the species, and they are similar to the Pit specimens described by Bell and Barnosky (2000:120–21). This finding suggests that the age of these specimens approximates the younger limit of this taxon's known stratigraphic range. Unfortunately, the younger limit is not well dated, but it is at least as young as 1.5 Ma at Froman Ferry, Idaho (Repenning et al., 1995).
3. The Badger Room assemblage resembles the fauna from levels 4–8 in the well-stratified Pit locality, which Bell and Barnosky (2000) argued on biochronologic and paleomagnetic grounds dates to between 750 and 850 Ka; this estimate was revised to a slightly older figure, circa 800–900 Ka, in chapter 7.

A major difference in comparison to the Pit—and other well-sampled localities in the cave—is the absence of *Lemmiscus* in the Badger Room. The absence of this taxon might suggest for the Badger Room a slightly older age, as would the relatively abundant specimens of the "old" taxa *Mimomys virginianus* and *Phenacomys gryci.* However, *Lemmiscus* is found in low abundance in the purportedly correlative levels of the Pit, so its absence in the Badger Room may reflect a sampling issue. The presence of *Marmota* and five-triangled *Microtus* m1s argues against much greater antiquity of the Badger Room compared to the Pit. In the Pit, these taxa are not present below level 8. In view of all these considerations, it would be surprising if the age of the Badger Room was younger than about 800 Ka or much older than 900 Ka.

Taphonomy

In terms of the NISP of teeth, mandibles, maxillae, humeri, and femora, the most abundant taxa in the Badger Room collections were lagomorphs (60%), rodents (29%), and carnivores (9.5%) (table 22.2). When teeth were excluded from these analyses, the trend was the same, and the carnivores exhibited 8% relative abundance (75 specimens out of 910 total).

In decreasing order of relative abundance, the following taxa dominated the assemblage: *Lepus* (*n* = 632), *Marmota* (*n* = 96), *Neotoma* (*n* = 90), *Spermophilus* (*n* = 79), *Spilogale putorius* (*n* = 75), *Taxidea taxus* (*n* = 69), *Sylvilagus* (*n* = 58), *Canis latrans* (*n* = 43), and *Cynomys* (*n* = 39, including ?*Cynomys andersoni*). Also well represented were *Thomomys* (*n* = 20), *Mimomys* (*n* = 20), *Ochotona* (*n* = 18), *Mictomys* (*n* = 17), *Peromyscus* (*n* = 16), *Canis edwardii* (*n* = 14), *Allophaiomys* (*n* = 11), *Phenacomys* (*n* = 9), *Martes diluviana* (*n* = 5), *Mustela frenata* (*n* = 5), and *Lynx rufus* (*n* = 4). The remaining taxa were represented by only one or a few specimens each.

When humeri and femora of all taxa were examined, it was found that 16% and 22%, respectively, exhibited evidence of biological processing by carnivores or rodents (see Materials and Methods for an explanation of the evidence used to infer biological processing). For 86% of the processed humeri, and for 78% of the processed femora, the agents of modification—based on the appearance of dental scrapes, pits, and puncture marks—were mammalian carnivores. Dental markings on the leporid bones are attributable to small to medium-sized carnivores such as foxes, skunks, badgers, and coyotes. Modification of bone or tooth enamel by digestive corrosion was not observed under a light microscope (up to 40× magnification) on any specimens from the CM/UCMP Badger Room collection. However, Ware and Anderson (see figure 9.6) illustrate acid etching on a Badger Room leporid specimen (DMNH 20052).

Of 175 leporid humeral and femoral shaft fractures, 87% (*n* = 153) were ancient (i.e., could not be attributed to excavation technique). Of these ancient fractures, 59% (*n* = 91) possessed an irregular, angular fracture surface (table 22.4). Of 109 leporid femora, 84 (77%) were fractured at the shaft, 38 (35%) displayed irregular-surface spiral breakage, and 16 (15%) displayed irregular-surface breakage *and* showed evidence of carnivore or rodent modification (figures 22.2, 22.3, 22.4). Of 25 nonleporid humeral and femoral shaft fractures, 76% (*n* = 19) were ancient. Of these ancient fractures, 56% (*n* = 14) were spiral fractures that possessed a rough fracture surface.

Of 122 leporid humeri, 91 (75%) were fractured at the shaft, 53 (43%) displayed irregular-surface breakage, and 12 (10%) showed irregular-surface breakage and evidence of carnivore or rodent modification. Of 36 prairie dog–size or larger rodent femora and humeri, 22 (61%) showed ancient shaft fractures. Irregular-surface fractures were visible on 64% of the bones with ancient fractures and 39% of all prairie dog–size or larger rodent femora and humeri (*n* = 14).

Cortical peeling was observed at a number of breakage points (figure 22.5). Of the leporid humeri and femora, 14% and 7%, respectively, exhibited peeling.

Of all humeri and femora (*n* = 409), 15% were complete specimens. None of the leporid or rodent bones in the analyzed collection displayed weathering beyond the earliest

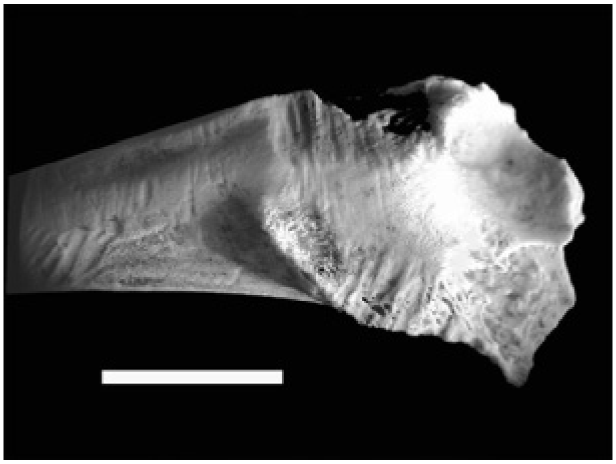

FIGURE 22.2 Paired grooves indicative of rodent gnawing on a left femur, CM 74771. Scale bar = 1.0 cm.

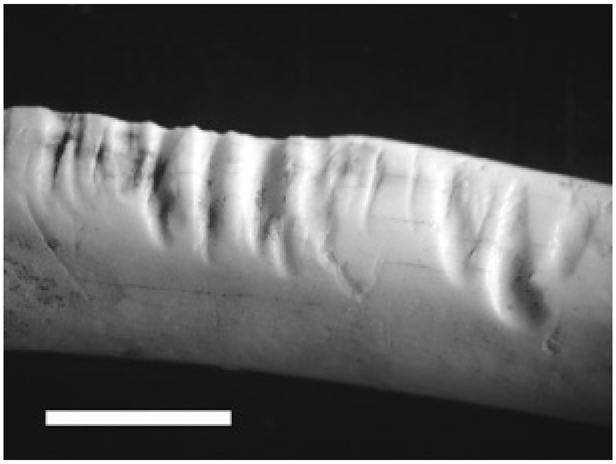

FIGURE 22.3 Damage to CM 74511, a left humerus, indicative of nonrodent dental scraping and pitting, lateral view. Scale bar = 1.0 cm.

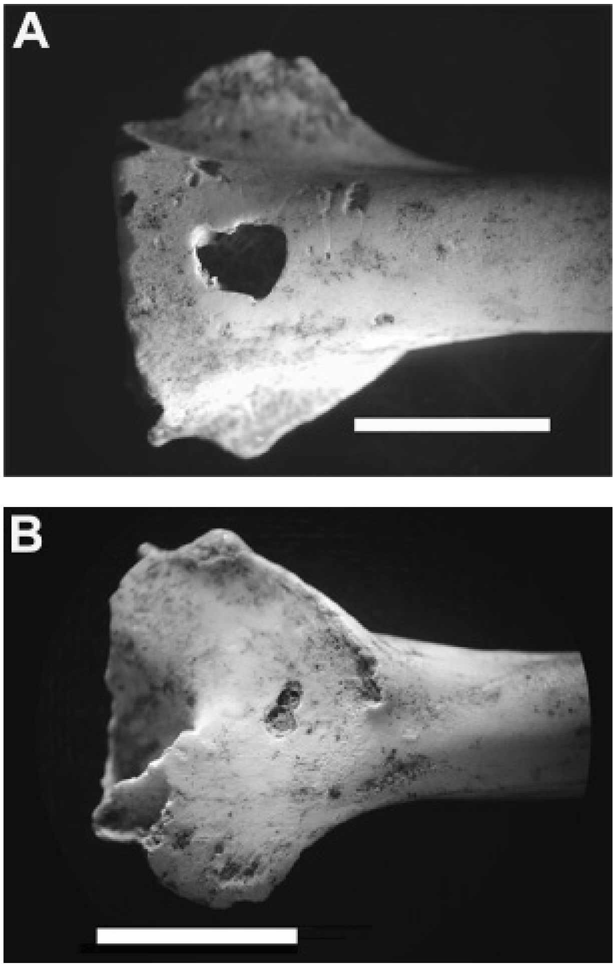

FIGURE 22.4 Tooth puncture mark and pitting on a left proximal femur, CM 74742, anterior (A) and posterior (B) views. Scale bar = 1.0 cm.

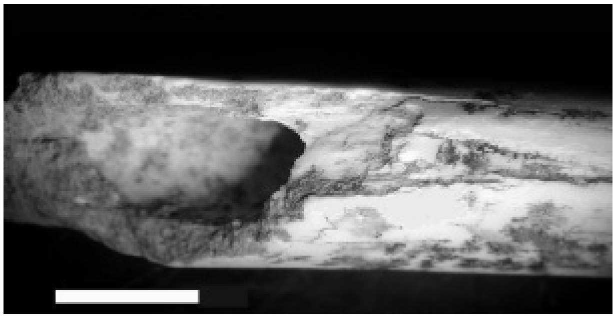

FIGURE 22.5 Cortical peeling at an ancient fracture surface. Specimen is a left humerus, CM 74525. Scale bar = 0.5 cm.

phases of stage 1, which is characterized by the longitudinal splitting of the bone cortex parallel to fiber structure (Behrensmeyer, 1978; Andrews, 1990).

Paleoclimatology

The present geographic ranges of the species used in our analysis *(Spermophilus elegans* or *S. richardsonii* and *Mictomys [=Synaptomys] borealis)* differ from one another considerably (figure 22.6), as do their preferred habitats. *Spermophilus elegans* is found in a variety of habitats, including prairie, steppe, tundra, woodland, rocky landscapes, and desert mountain ranges, from southeastern Montana and northern Nevada to northern Colorado (Nowak, 1991, 1999). The annual activity cycle of this ground squirrel (dormant in winter, active in summer) resembles that of marmots, except that it goes underground earlier (usually in August) in response to moisture stress. Thus late summer moisture is probably an influence on the geographic range of *S. elegans*. *Spermophilus richardsonii* exhibits a natural history similar to that of *S. elegans,* but it is restricted to areas farther north (figure 22.6).

Mictomys (=Synaptomys) borealis is patchily distributed in cold, mesic systems in the extreme northern United States

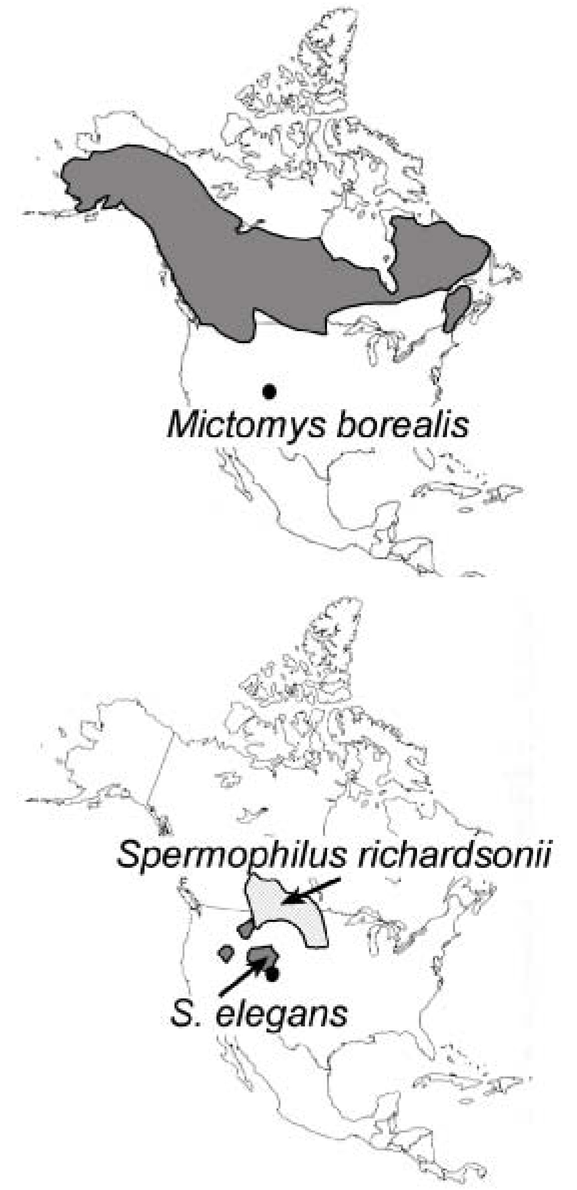

FIGURE 22.6 Range maps for the indicator species used in the quantitative climate analysis. Black dot identifies location of Porcupine Cave.

and Canada south of the tundra (Hall, 1981; Nowak, 1991, 1999). This taxon typically inhabits wetlands, where it feeds on plant tissues, and the existence of suitable habitat types often depends on summer precipitation (spring-fed systems are an exception). The northern boundary of *Mictomys (=Synaptomys) borealis* matches treeline at the taiga-tundra boundary, suggesting at least an indirect link with the same climatic parameters that determine the presence or absence of trees (i.e., winter temperature, frost action, and length of the growing season). Bog lemmings are active in burrows during winter, and snow must fall during critical months if they are to be insulated against extreme low temperatures.

We determined the range of temperature and precipitation values that encompass the geographic ranges of each of these species (tables 22.5 and 22.6, respectively). For the analysis of temperature, we first assumed that *S. elegans* was the ground squirrel represented in the Badger Room; then we addressed how the scenario would be modified if *S. richardsonii* was substituted for *S. elegans*. For the analysis of precipitation, the substitution of *S. richardsonii* did not alter the results, and thus *S. richardsonii* was not used for the precipitation estimates (table 22.6).

When *S. elegans* was used in the analysis, the coldest temperatures in which both species could have coexisted was –2.5°C to –7.5°C for most of the winter (November through February). *S. elegans* defines the –7.5°C cold limit for sympatry. *M. borealis* exists in localities that are much colder in the winter (–28°C). The warmest winter temperatures in which these species coexist are around 0°C. The warmest summer temperatures, found in July, are 23°C for *S. elegans* and 20°C for *M. borealis*. The coolest summer temperatures are in June, at 13°C for *S. elegans* and 7°C for *M. borealis*.

These values bound the coexistence of the two species to areas with mean winter temperatures (e.g., between November and February) between 0°C and –7.5°C, and mean summer temperatures (July) between 13°C and 20°C. Modern monthly means at Porcupine Cave generally fell within these ranges, but modern May and September may be slightly warmer than the temperatures suggested by the Pleistocene species associations (table 22.5, figure 22.7A). If *S. richardsonii* is substituted for *S. elegans,* December, January, and March, in addition to May and September, appear to be warmer today (table 22.5, figure 22.7B). We recognize, however, that the modern climate values fall so slightly outside the inferred paleoclimate envelope that the observed differences may simply be an artifact of uncertainties in the data. Therefore we also offer the alternative, more conservative, interpretation that the two fossil species may have been able to coexist within the modern temperature regime at the cave.

Limits defined by mean annual precipitation vary considerably between *S. elegans* and *M. borealis,* mainly at the upper boundary. Both species are found today in areas with as little as a few hundred millimeters of annual precipitation (table 22.6). However, *S. elegans* is confined to the relatively arid zones, whereas *M. borealis* can occur in areas where annual precipitation may be very high.

The difference between winter precipitation and spring-summer precipitation is important. *Mictomys (=Synaptomys) borealis* occurs in areas that may be dry throughout the spring but that receive a minimum of 25 mm of precipitation during each month from July through December. Thus the presence of rain during late summer and early fall, and the development of at least some snowpack during the early winter months and through the winter, seems critical. *Spermophilus elegans* experiences distinct fall and spring precipitation seasons, with at least 25 mm of precipitation each month from April through June and 25 mm during October. This pattern translates to rainfall in the spring with snow developing in areas of higher elevation during April and October. In sum, a comparison of the monthly range of precipitation inferred from sympatry

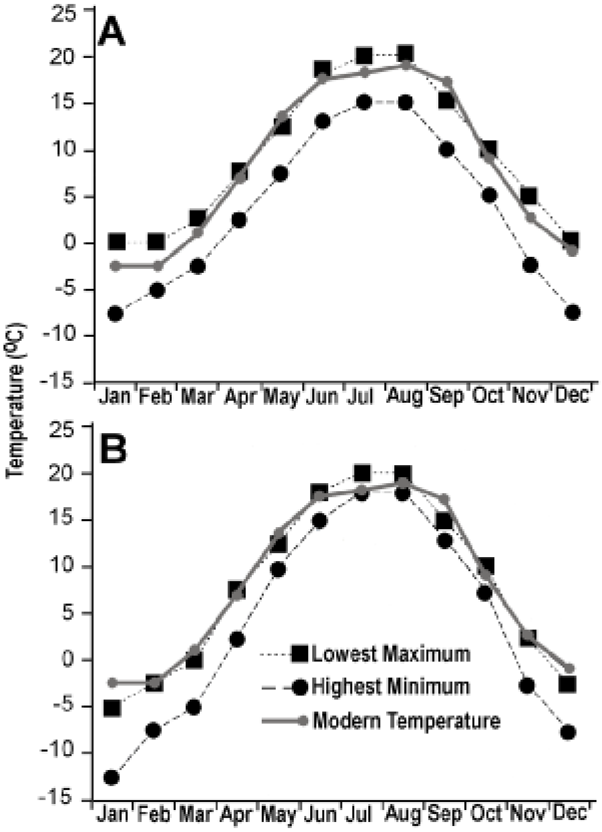

FIGURE 22.7 Highest temperature (summer) minima and lowest temperature (winter) maxima on the climate space shared by the indicator taxa, using *Spermophilus elegans* (A) and *S. richardsonii* (B). Note that modern cave temperatures (gray line and dots) fall within the range of the reconstructed climate space except for very slight excursions in the months of May and September when *S. elegans* is used and in the months of January, March, May, September, and December when *S. richardsonii* is used.

of the fossil species with modern means suggests more precipitation in November and December during the middle Pleistocene (table 22.6).

Landscape and Vegetation

Based on a review of the literature for autecological information (see Materials and Methods), several of the Badger Room mammal clades appear to be good indicators of particular habitat types (see Discussion for caveats). The presence of Anatidae, Lutrinae, and *Ondatra* indicates a perennial source of water. *Mictomys* suggests subarctic, boreal conditions and mesic, grassy microhabitats near water. A cold and moist, tundralike environment is indicated by *Ochotona* and, perhaps, Ovibovini. Cool to cold conditions are indicated by *Phenacomys*. Although many authors link *Cynomys* and *Spermophilus* species to warm and xeric habitats, these genera are speciose and well differentiated with regard to their tolerance limits. Open environments (grassland, steppe) are inferred for the antilocaprid, the equids, and *Miracinonyx*. *Ochotona* and *Marmota* in mountainous environments show strong preference for rocky outcrops, and *Ovis* species depend on rocky escape terrain to avoid predators. *Erethizon* and *Martes diluviana* may indicate forest conditions, but this conclusion is ambiguous (see Discussion).

Comparative Synecology

In terms of systematic diversity, the Badger Room assemblage and the extant fauna show similar total numbers of species (table 22.8), especially when it is taken into account that sampling issues mean that the modern species counts represent the maximum and the fossil counts the minimum number of species that could have coexisted in the community. The biggest difference within orders is the presence of fewer species of Pleistocene rodents; this may be in part because (1) the South Park counts include species whose range today does not extend into the 18-km radius around the cave, which is the probable maximum sampling radius for the fossil fauna (see Spatiotemporal Averaging), and (2) because the small mammal fossils may be underrepresented in the Badger Room fauna for taphonomic reasons. The "missing" Pleistocene rodents are *Zapus,* castorids, *Tamiasciurus,* and *Sciurus,* all of which in the living fauna generally occur in low densities and would have low potential for preservation in Porcupine Cave. However, these sampling issues would not explain the observation that there were more lagomorph species and genera in the Pleistocene; in fact, the sampling issues make that observation even more robust. Carnivoran diversity also seems higher in the modern historic fauna, but this observation also is hard to interpret in view of sampling issues. The "missing" Pleistocene carnivorans are bears (two species), which are known elsewhere in the cave deposits, although they were not preserved in the Badger Room, and procyonids (two species), which are seldom fossilized because their habits do not usually place them in areas where fossilization is likely, especially given the taphonomic situation at Porcupine Cave. Note that ordinal diversity was higher in the Badger Room fauna (eight orders) than it has been in recent history (six orders) as a consequence of the loss of xenarthrans and perissodactyls from the region. Among taxa that have disappeared from the fauna are mylodontid ground sloths, equids (horses), and tayassuids (pecarries).

The same was done for the recent South Park community, and the two data sets were compared (table 22.7). The total number of herbivorous and carnivorous clades identified from the Badger Room (when obligate forest-dwelling taxa were omitted) was very similar to the total number for the recent South Park community (one less fossil herbivore but an identical number of carnivores) (table 22.9). This similarity exists in spite of the potential sampling problems noted previously, and the fact that the turnover of species approximated 43%, with 20 herbivore and carnivore clades from the Badger Room not represented at South Park today.

Table 22.10 differentiates the deletion and addition data across biomass and trophic groups. In contrast to the relative

TABLE 22.9

Species Richness of the South Park Mammal Community Broken Down by Size Class and Trophic Group

	Small	*Medium*	*Large*	*Total*
Herbivores	11/14 [13]	5/7 [5]	8/7	24/28 [25]
Carnivores	2/2	4/4	7/7	13/13
Omnivores	2/2	2/3	1/3	5/8
Total	15/18 [17]	11/14 [12]	16/17	42/49 [46]

NOTES: Datum preceding each slash is the total number of species for the Badger Room. Datum following the slash is the total number of mammal species recorded in South Park in recent historical times. Insectivores are not included. Brackets indicate counts if modern forest specialists are excluded.

TABLE 22.10

Species Deletion and Addition Information Broken Down by Size Class and Trophic Group

	Small	*Medium*	*Large*	*Total*
Herbivores	6/8	2/2	4/3	12/13
Carnivores	1/1	2/2	4/4	7/7
Omnivores	0/0	1/2	1/3	2/5
Total	7/9	5/6	9/10	21/25

NOTES: Datum preceding each slash is the total number of species "deletions" (i.e., the number of taxa present in the Badger Room but not known from South Park in recent historical times). Datum following the slash is the total number of species "additions" (i.e., the number of taxa known from recent historical times but not identified among the Badger Room fossils). Forest specialists and insectivores are not included.

parity that exists in the herbivore and carnivore groups, note that larger omnivores were added to the historic South Park fauna relative to what was found in the fossil deposits. These additions involve ursids, procyonids, and humans. As noted earlier, we cannot discount taphonomic issues as an explanation for the absence of ursids and procyonids in the Badger Room; if sampling issues do apply, and we remove humans from the counts, parity would exist between the fossil and modern omnivores as in the other size-sorted trophic categories. Among the large omnivores recorded in the fossil deposits, peccaries *(Platygonus)* probably played a functional role analogous to that of raccoons and bears in the modern ecosystem. As a gregarious taxon, *Platygonus* may have filled a wide trophic niche as a consumer of seeds, seedlings, tubers, and small vertebrates. Omnivorous humans immigrated into the region in two waves (circa 10 Ka ago and then again beginning in the nineteenth century).

There were fewer medium-sized mammal taxa than large and small taxa in the Badger Room fauna (table 22.9), similar to the structure of the modern community. Various studies have suggested that open habitats support relatively fewer medium-sized mammals than closed habitats (Valverde, 1964; Legendre, 1986). The fact that the Badger Room fauna includes a lower percentage of medium-sized taxa supports a reconstruction of the local environment as generally unforested. (The correlation between mammal size and habitat openness is further addressed in the Discussion.)

In South Park, at least two large terrestrial herbivore (LTH) genera underwent extinctions between Pleistocene and recent times: *Equus* and *Paramylodon.* An additional LTH extinction may be indicated by the ovibovine that has been identified from the Badger Room, but its generic affinities are indeterminate. *Bison* and *Cervus* are two LTHs that were added to the local fauna since the middle Pleistocene, resulting in a net loss of one species in the LTH category.

Finally, carnivores deleted from the Badger Room were replaced by roughly "equivalent" ecomorphs (table 22.7). A niche similar to that of *Miracinonyx* is probably occupied today by *Felis concolor* (see Discussion). A small canid intermediate in size between a coyote and a fox has been identified from the Badger Room, and the niche of this carnivore can be considered roughly analogous to that of *Lynx lynx,* which weighs 9–11 kg (Nowak, 1999). It is easy to imagine that *Canis edwardii* played a role analogous to that of extant wolves *(Canis lupus)* in ecosystems today. *Spilogale putorius* and *Mustela vison* can be considered rough analogues in that both are small predators (under 1000 g) that prefer vegetative cover and climb well; these taxa have largely allopatric distributions today, an observation consistent with the argument that they are functionally similar. Finally, *Martes diluviana* and the *Mustela* species A from the Badger Room were replaced by congeneric taxa. Hypothetically, the extinct *Martes* and *Mustela* clades occupied niches similar to those occupied by the extant marten and mink *(Martes americana* and *Mustela vison).*

Discussion

Agents of Fossil Accumulation

In general, several features indicative of processing of bones by mammalian carnivores are evident in the Badger Room assemblage. However, some commonly recognized features of mammalian carnivore processing were absent. Andrews (1990: 88) noted that postcranial bones subjected to digestion by mammalian carnivores typically have damaged ends that show "rounding." Tooth enamel that has been subjected to digestion is typically cracked, exposing the underlying dentine, which itself may show etching. We did not observe any such damage on the CM specimens.

Fractures that possess a jagged, irregular fracture surface may indicate that breakage occurred on fresh bone (Shipman, 1981; Johnson, 1985). Likewise, peeling of cortical bone at fracture points indicates that the bone was probably fresh at the time of breakage (White, 1992). That more than half of the ancient shaft fractures showed irregular-surface breakage, along with the presence of cortical peeling on some specimens, suggests that most of the bones in the assemblage were broken while still fresh, presumably around the time of the death of the organism. That 10% of all long bones were still whole, and that no specimens displayed weathering beyond the early phases of stage 1, suggests that most bones made it into the cave while still fresh, without prolonged exposure to external environmental factors such as sunlight and trampling.

Transporting whole carcasses to denning sites is not uncommon for carnivores. It would not be unreasonable to expect that predators also occasionally cached prey in the Badger Room, which may have been located within a few meters of an ancient cave entrance (figure 22.1). In this context, the anecdote of a freshly killed rabbit carcass in the Gypsum Room of Porcupine Cave (chapter 2) is relevant. Anderson (1996:279) concluded that *Taxidea* probably "denned and died" in the Badger Room, based on the abundance of their fossil remains; *Canis latrans* may have denned there too, based on the presence of two juvenile maxillae. Badgers feed primarily on fossorial rodents and only occasionally prey on leporids (Nowak, 1999), and it is unlikely that the badger was a primary vector of accumulation.

The high proportion of leporids is consistent with coyote prey ratios (Windberg and Mitchell, 1990). The patterns of breakage of the leporid radii, ulnae, femora, and scapulae are similar to those reported by Andrews and Nesbit Evans (1983) and Schmitt and Juell (1994) in analyses of leporid and similarly sized bones from coyote scat. Both of these studies documented very few or no whole femora, tibiae, humeri, and radii. The presence of significant numbers of complete bones among the Badger Room leporids is consistent with the hypothesis that the Badger Room served as a den, and that the assemblage represents not just scatological remains, but also the remains of undevoured carcasses (table 22.3). Schmitt and Juell (1994) note that the degree of fragmentation of coyote prey is inversely related to the availability of prey. MacCracken and Hansen (1987) noted an inverse relation between the diversity of coyote diets and the abundance of black-tailed jackrabbits *(Lepus americanus)* in Idaho. The high frequency of leporids, especially *Lepus;* the presence of carnivore dental markings and a characteristic pattern of breakage; and the presence of juvenile and adult coyote remains (chapter 26) all serve to implicate *Canis latrans* as the primary vector of accumulation for the Badger Room assemblage.

According to Andrews (1990) and Schmitt and Juell (1994), the effects of digestive corrosion on bones ingested and deposited by coyotes and other carnivores are typically severe and marked. In this light the very low frequency of acid etching in the Badger Room assemblage (three etched bones are reported in appendix 9.1) contradicts the carnivore-accumulation hypothesis or indicates that a substantial number of the bones were from carcasses that were collected but not eaten. However, Rensberger and Krentz (1988) found only subtle digestion effects (i.e., fine fissures that resemble cracks unless examined at 1000×) on bones consumed and deposited by coyotes, and they noted that specimens must often be subjected to scanning electron microscopy (SEM) before one is able to observe the effects of digestive modification. Therefore the Badger Room assemblage (and others like it) should be subjected to SEM analysis before any conclusive verdict is made about the presence of acid etching.

Raptors are major contributors to fossil assemblages through the preservation of their bone-laden regurgitation pellets. Ravens too have recently been recognized as important predators and likely contributors to fossil faunas (McEneaney, 1995; E. A. Hadly, pers. comm.). Raptor pellet accumulation probably contributed to the Badger Room assemblage, but definitive differentiation of raptor versus mammalian carnivore activity is difficult. Most of the observable evidence points to mammalian carnivores as a more important vector than raptors in the Badger Room.

Assemblages created by raptors can exhibit beak puncture marks, bone and enamel corrosion by digestive acids, a high ratio of humeri and femora to mandibles and maxillae, and a high ratio of whole to broken bones (Andrews, 1990). Not all these features typically characterize a raptor-accumulated assemblage, however, and some mammalian carnivore assemblages exhibit similar features. In the Badger Room, none of the puncture marks evident on the fossils could be attributed to birds, but instead were characteristic of mammalian carnivory based on one or more of the following features: corresponding puncture marks on the side opposite to the puncture (Andrews, 1990; Hockett, 1991; Schmitt and Juell, 1994), association with other tooth markings (i.e., tooth scraping), severe long bone fragmentation (Andrews and Nesbit Evans, 1983), and epiphyseal destruction. However, beak puncture marks would not be expected to be abundant if prey had been swallowed whole.

Mayhew (1977:25) makes a distinction between owls, which generally swallow their prey whole, and diurnal raptors, which tend to "divide" their prey before swallowing. According to Dodson and Wexlar (1979:282), leporids and other large prey tend to be "flensed with minimal skeletal disarticulation or destruction" by owls. In contrast, Hockett (1991) stated that diurnal raptors often break the long bones of leporids and other prey whose bones are too large to be swallowed whole. Therefore it is reasonable to expect a positive correlation between the size of the prey (in relation to the raptor) and the degree of long bone fragmentation. Hockett (1991) also observed that analyses of bone fragmentation by raptors (i.e., Dodson and Wexlar, 1979; most of Andrews, 1990) have concentrated on assemblages in which mice were the principal prey, and that such studies may have little applicability to taphonomic analyses of leporid bones that are both larger and more gracile. In light of these observations, the ratio of whole to fragmented long bones in the Badger Room does little to support or exclude raptors as the primary vector of accumulation (table 22.3).

Hockett (1991) developed a set of criteria that may help identify raptor involvement in modification of leporid bones: the presence of tibial "diaphysis cylinders," beak or talon punctures, damage to the greater trochanter, pellet matter adhering to bones, a high ratio of juveniles to adults, and a higher frequency of forelimb bones over hindlimb bones (vice versa for kill sites). Twenty-three (16 left, 7 right) tibial "diaphysis cylinders" are present in the Badger Room assemblage among leporid and leporid-sized tibiae. No punctures that may be attributed to raptor beak or talon action were observed. Damage to the greater trochanter is present on many leporid femora; however, this feature (like the puncture marks described earlier) is most often associated with dental gnaw marks indicative of processing by mammals. No pellet matter adheres to any bones in the assemblage, though this would almost certainly be a result of preservation bias. Of 79 femoral specimens identifiable as to age class, 37 are adult and 42 (45 including epiphyses) are immature; of 103 humeral specimens identifiable as to age class, 97 are adult whereas only 6 (8 including epiphyses) are immature. Thus we find a low overall frequency of juvenile to adult leporids in the Badger Room, though this may also be an effect of preservation bias against immature bone. The roughly equal frequencies of leporid humeri and femora (table 22.4) dispute the hypothesis that the Badger Room was primarily a raptor roost or kill site. Thus the data do not support avian accumulation as a primary vector for the leporids, although raptors probably contributed some remains.

Wood rats often gather carnivore scats and avian pellets, as well as isolated bones, and transport them back to their nests (in caves). *Neotoma* fossils are well represented in the Badger Room assemblage, and rodent gnaw marks in the size range of those produced by *Neotoma* are evident on several elements (e.g., CM 74844, CM 74852, CM 74854, CM 75125, CM 75954). *Neotoma* can be implicated as a taphonomic agent in most Porcupine Cave localities, and the Badger Room is no exception.

Hockett (1989) found that up to 51% of nonrodent bones in assemblages created by *Neotoma* may display evidence of carnivore gnawing, with few displaying rodent gnawing. That the majority of the biomodifications on the bones in the Badger Room were created by mammalian carnivores does not discount the possibility that *Neotoma* was an important vector of accumulation.

Scott (chapter 20) catalogued several equid elements from the Badger Room assemblage that exhibited stage 1 weathering (sensu Behrensmeyer, 1978). However, the degree of weathering described by Scott for these specimens is more advanced than that observed for the Badger Room leporids and rodents (although both have been broadly classified as "stage 1"). The implication of *Neotoma* as the primary agent of accumulation for the Badger Room equids is probably fair.

It is possible that some of the fauna were simply trapped in the cave. However, natural traps (without strong attraction factors) tend to show less sample bias than other depositional settings (Behrensmeyer and Hook, 1992). If the Badger Room acted as a natural trap, one would expect a more even distribution of abundance among the fossils (with fewer lagomorphs and carnivores, for example). One might further expect less incidence of carnivore damage to fresh bone (Wang and Martin, 1993).

Spatiotemporal Averaging

Time averaging and space averaging are the bugbears of paleoecology. Spatiotemporal averaging can mix organisms that lived far from one another in time or distant from one another on the landscape. However, some degree of averaging is critical if uncommon taxa are to be accumulated and the local community is to be sampled with fidelity (Behrensmeyer and Kidwell, 1985; Barnosky, 1992; Hadly, 1999). Fossil deposits such as those that characterize Porcupine Cave may resolve between 100 and 10,000 years, and the fossil organisms in such cave deposits are typically sampled from proximal habitats (Vrba, 1980; Brain, 1981; Behrensmeyer, 1991; Barnosky, 1994; Hadly, 1999; Porder et al., 2003). We have no reason to suspect that Porcupine Cave is exceptional in this regard. We suspect the Badger Room deposits accumulated over at least a few hundred years and at most within a few thousand years. Ten thousand years seems a reasonable upper limit. Given that mammalian carnivores such as coyotes and badgers were apparently the most important collectors of the assemblage, spatial sampling probably was confined within the hunting ranges of such predators, which usually would be within a 5- to 18-km radius of the cave (Hadly, 1999; Porder et al., 2003).

Habitat Reconstruction

The presence of duck, muskrat, and otter provides unambiguous evidence for standing water in the sampling range of the cave. Otters are historically rare in Colorado and have not been recorded for South Park. Pioneer Colorado mammalogist E. R. Warren (1910) attributed the statewide rarity of otters to high variability in water levels, and the presence of otters in South Park during the Irvingtonian probably indicates large, stable, productive water bodies (this finding reinforces the other lines of evidence that suggest more moisture in general). These water bodies were possibly associated with riparian forest conditions; however, none of the Badger Room taxa is a conclusive indicator of such conditions.

The signal for forested habitats in general is weak. The New World porcupines (Erethizontidae) are distinguished by postcranial adaptations for arboreality (Nowak, 1999), and today *Erethizon dorsatum* favors wooded areas, although it ranges widely through nonforested sites as well. *Martes diluviana* (the species of fisher known from the Badger Room) is thought to be ancestral to *M. pennanti,* the extant fisher (Anderson, 1994). The historical range of the living fisher basically corresponds to the distribution of boreal, north temperate, and montane forests in North America (Wilson and Ruff, 1999), suggesting a close link between this taxon and closed environments. Conceivably the fisher and porcupine inhabited forested environments in the past, as many of their descendants do today, but the link is tenuous. The lack of arboreal sciurids (e.g., *Tamiasciurus*) in the Badger Room assemblage reinforces the impression that forest was not a prominent part of the local landscape. At the same time, forest-dwelling organisms are rare as fossils, and their absence in the Badger Room could be an artifact of taphonomy.

Since Legendre (1986), paleoecologists have interpreted a relative paucity of medium-sized mammals as an indication of open habitats. On open landscapes, small mammals can avoid predation by quickly securing shelter, whereas large mammals rely on a variety of defense and escape mechanisms, including, for example, enormous size, herding behavior, rapid and sustainable flight, or horns and antlers. Valverde (1964) noted that medium-sized mammals in open environments often rely on specialized means for predator avoidance. Among the medium-sized Badger Room taxa, such specializations are certainly evident: *Erethizon* (quills), *Ondatra* (aquatic escape), *Lepus* (rapid, erratic flight), *Marmota* and *Cynomys* (colonial lifestyle in burrow complexes), *Mephitis mephitis* (noxious scent). In a stringent review of cenogrammatic techniques in paleoecology, Rodríguez (1999) supported the inverse correlation between open environments and medium-sized mammals, at least in some environments.

At the autecological level, open environments (probably including shrub-steppe and grassland) are indicated by the presence of antelopes, horses, prairie dogs, ground squirrels, and "cheetahs" *(Miracinonyx).* The presence of the extinct North American cheetah *(Miracinonyx)* is usually considered a good indicator of open environments based on an analogy with the extant African cheetah. Adams (1979) initially argued that the skeleton of *Miracinonyx* was as specialized for cursoriality as that of the living cheetah *(Acinonyx).* Later Van Valkenburgh et al. (1990:453) wrote that "the New World genus *(Miracinonyx)* never achieved the extent of muscle and dental reduction seen in the extant Old World cheetah. Whether this reflects adaptation to slightly different environments or the consequence of ancestry is difficult to know."

Miracinonyx is associated with two other large felids (a jaguar and a sabretooth) at several Plio-Pleistocene sites in eastern North America (Van Valkenburgh et al., 1990; Morgan and Seymour, 1997). In sympatry with the other two big cats, *Miracinonyx,* like the extant cheetah, probably specialized in the pursuit of fast prey on open landscapes. In the absence of strong intrafamilial competition, however, *Miracinonyx* would have been flexible in its use of the landscape, foraging opportunistically in multiple habitat types like a puma (this reconstruction agrees with that of Turner and Antón [1997]). In any event, it is clear that some type of open ecosystem was present near Porcupine Cave in the Pleistocene. The evidence suggests two options: a mosaic model and a shrub-tundra model.

The mosaic model reconstructs the landscape as dominated by xeric steppe, mesic grasslands, some woodland or forest, and alpine tundra. This model assumes that the habitat preferences of living taxa provide a strict indication of the autecology of fossil forms. It also assumes that the vegetation types that exist today (steppe, woodland, forest, grassland, tundra) were present on the landscape in the past, and that these vegetation types have simply shifted in relative abundance and distribution. Finally, the mosaic model requires that the scale of spatial averaging was sufficiently great that the Badger Room sampled fauna from each of these very different habitats. If 5 km is taken to be the typical maximum distance over which carnivoran and avian predators would transport bones to a depositional site (Hadly, 1999), then these habitats would have occurred within an area of less than 80 km^2.

The second model reconstructs the ancient landscape as a grassy shrub-tundra system, with or without forest. There is an extensive literature on the subject of steppe-tundra ecosystems for the Late Pleistocene (Hibbert, 1982; Delcourt and Delcourt, 1991:187–91). The evidence for a once extensive steppe-tundra biome ("tundra-steppe" in the Russian literature, "arctic steppe" elsewhere) derives from independent lines of research pursued in Russia, Beringia, the Canadian Yukon, and the Brooks Range Mountains (Livingstone, 1955; Guthrie, 1966, 1968; Matthews, 1976; Hopkins et al., 1982). Because South Park is so high in elevation, it climatically approximates these more northerly areas to some degree, and Cooper (chapter 3) has clearly demonstrated the floristic connection along the wide arc from Colorado to Russia.

The signal that emerges from the paleoclimatological and habitat reconstructions is that the middle Pleistocene landscape was primarily open, and the environment was on average cooler and wetter than that seen today, with the exception of some very dry and warm interglacials (as represented by Pit levels 1–3). Steppe systems are characterized by dry conditions with extreme temperatures. At higher effective moisture levels, semiarid shrub-steppe systems become more grassy. With higher moisture levels and colder temperatures, frost action becomes limiting (particularly where temperature inversions are common), and tundra vegetation is best equipped to withstand heavy frost and low temperature minima. In this way, South Park may have been characterized by a grassy shrub-tundra system, with or without trees.

Climate Reconstruction

The South Park regional climate was likely to have been wetter and possibly colder during the time the Badger Room deposits accumulated than it is today. The analysis of overlapping climate spaces for the two mammal taxa discussed previously suggests that November-December precipitation values would have been higher; temperatures in late spring and early fall may not have differed much from those today or may have been a little lower. This observation implies that insulative snow cover may have been present earlier in the fall and later in the spring, and the late summer-fall dry season would have been shorter relative to that today. The key difference if *S. richardsonii* is substituted for *S. elegans* is that paleowinters appear even cooler. Thus our estimates with *S. elegans* are conservative.

However, our technique does not ascribe significance levels to these inferred differences between the modern climate and the paleoclimate, and, for temperature, the observed differences between the climate space inferred from fossils and the modern climate space are slight. Therefore the results should be regarded as a hypothesis to be tested against future work. A factor that complicates our approach, and one that must be further examined, is that "climate space" provides but one parameterization of an organism's fundamental niche. However, factors other than temperature and precipitation influence biogeographic distribution, and the organism's realized niche may be determined by other biological imperatives, such as food availability and the presence of competitors. Theoretically such biological factors operate on a local scale, whereas the direct and indirect effects of climate determine overall range.

A final caveat pertains generally to environmental reconstructions that are based on autecology. The evolution of physiological tolerance limits is not well understood, and we have very little evidence concerning the rapidity with which a clade's habitat preferences may change. The assumption is usually made that if an organism does not change morphologically, then it has probably not changed much physiologically or behaviorally. In other words, it is assumed that the form-function correlation is strong. Several of our results rest on this assumption.

Our climate reconstruction for the Badger Room generally agrees with that of Wood and Barnosky (1994) and Barnosky et al. (1996) for the Pit fauna, but the Badger Room analysis indicates even cooler, moister winters. This finding mainly reflects the absence in the Badger Room assemblage of *Lemmiscus curtatus,* a species present in both glacial and interglacial deposits throughout the stratified Pit sequence (Bell and Barnosky, 2000). If the absence of *Lemmiscus* from the Badger Room is due to sampling bias, the climate space defined in Wood and Barnosky (1994) would apply to the Badger Room fossils as well.

Species and Higher Taxon Richness Patterns

As research continues on the paleontology of Colorado and the Rocky Mountains, the diversity of mammals known from high-elevation Irvingtonian sites will no doubt increase. Indeed, further work by specialists on the Badger Room collections would almost certainly increase the number of identified taxa (e.g., lagomorph and rodent species diversity would be likely to increase). As an example, if the Badger Room sample were to be combined with the small-mammal sample from level 4 of the Pit (perhaps roughly contemporaneous; chapter 23 and table 10.9), the species diversity of rodents would rise from the 14 species now known from the Badger Room to 24 species. In contrast, further work on recent historical South Park mammals probably will not substantially increase the counts of native species. At the present stage of research and in view of the likely underrepresentation of rodent species in the paleosample, the Badger Room mammals can be considered to show biodiversity comparable to that of the recent fauna at the species level (42 species versus 49 species, not including shrews and bats).

Community Structure: Stability and Change

The systematic and functional structures of the Badger Room and historic South Park mammal communities seem similar in terms of species richness and trophic structure. However, considerable faunal turnover (>40% of identified species) has occurred since the middle Pleistocene, and ordinal diversity has decreased. This suggests a certain amount of stability in community structure, with fluid replacement patterns at the level of individual taxa. Humans have recently influenced community structure. For example, by the early twentieth century European immigrants had caused carnivorans to decline in richness and abundance (*Canis lupus* and *Lynx lynx,* as well as *Ursus arctos,* had been extirpated from the region). Pressure on the large herbivores, which probably began after the late Pleistocene–early Holocene wave of immigration by *Homo sapiens,* became heightened in recent historical times, resulting in reduced abundance of native large herbivores, local extinction of *Bison bison,* and introduction of herbivores such as domestic horses, cattle, and sheep. It is not clear how such impacts will affect long-term community structure. Some of their implications are discussed in chapter 26.

Interspecific Relationships

As native North Americans well knew (Dobie, 1950), and as early scientists and natural historians quickly learned (Aughey, 1884; Seton, 1929; Cahalane, 1950; Young and Jackson, 1951), the coyote and badger form a complex intraguild relationship. Coyotes and badgers are large opportunistic predators that inhabit grasslands, shrub-steppe, and broken woodland. Both clades prey primarily on small mammals, especially rodents and rabbits (together referred to as the group glires); however, the badger is primarily fossorial while coyotes hunt above ground. The two often form a partnership that is, by turns, commensalistic, mutualistic, and "parasitic."

Most accounts of coyote-badger social relations are anecdotal. One study was conducted at the National Elk Refuge in Wyoming on coyote and badger populations that preyed primarily on semicolonial ground squirrels *(Spermophilus armatus)* (Minta et al., 1992). The dominant vegetation was relatively open grassland or shrubland. Solitary coyotes hunted these squirrels above ground with a search-and-ambush sequence, whereas badgers dug after their prey, trapping them in their burrows. A hunting association began when one of the species initiated predatory behavior in the other (Minta et al., 1992). A coordinated hunting effort then began that lasted anywhere from a few minutes to several hours. The badger tended to flush the squirrels out of their burrows and into the open for the coyote, and the coyote's presence may have caused many squirrels to remain below ground, where they became prey for the badger.

It is relatively costly for both predators to hunt solitarily in the brushy areas: above ground plant structure inhibits the coyote in its search and pursuit, while below ground root systems inhibit the digging badger. However, Minta (1990) found that *Spermophilus armatus* occurs at higher densities in brushy areas, and thus shrublands apparently offer high potential energetic returns. The association between coyotes and badgers probably makes shrubland hunting more efficient for both taxa, but certainly for the coyote (Minta et al., 1992).

Canis latrans and *Taxidea taxus* (coyote and badger) are the two most abundant carnivores in Porcupine Cave. They are most common in the Badger Room, and they have been found together in at least a half-dozen other Porcupine Cave localities. It is impossible to demonstrate strict continuity in an interspecific pair bond with fossil evidence, because there are too many gaps in the paleontological record. However, if fossils of taxa are commonly discovered in association, and if it is assumed that lineages have some degree of phylogenetic memory for interactions that strongly influence fitness, then a succession of sites with associated taxa is suggestive of an enduring coevolutionary history.

Fishers and porcupines also have a rich fossil history together. As of 1993, all five sites with fossils of *Martes diluviana* had also produced fossils of *Erethizon* (Anderson, 1994). The living fisher *(Martes pennanti),* a fascination for naturalists (Brander and Books, 1973; Powell, 1993), is the North American carnivore best equipped to prey routinely on porcupines. Canids and felids, by virtue of their height, are forced to attack porcupines from above, where the porcupine is well protected. Fishers, in contrast, have a low-slung body plan that allows them access to the porcupine's face. What is more, fishers are agile climbers, and they effectively pursue porcupines in and among trees.

Fishers are thought to provide a natural check on porcupine populations, and they have been (re)introduced in many states to prevent porcupines from decimating forests and croplands. Research at a reintroduction site on Michigan's Upper Peninsula suggested to Powell and Brander (1975) that fisher and porcupine populations interact in a manner that leads to dynamic stability in numbers of individuals. The Badger Room documents the first appearance of the fisher-porcupine association, extending its occurrence back to circa 800 Ka ago. Many of the reintroduction sites offer data that could be used to test predator-prey models and related problems in population ecology, and all sites at which fishers coexist with porcupines offer insight into the nature of their relationship.

Another well-known biological association exists between black-footed ferrets *(Mustela nigripes)* and prairie dogs *(Cynomys).* Historically, the range of the black-footed ferret overlapped the range of the prairie dog, and most ferret study populations inhabited the colonial prairie dog's burrow systems and utilized prairie dogs as prey. Over the past twenty years, a vigorous recovery program has sought to reintroduce the endangered ferret into its former range; workers generally assume that "the ultimate fate of black-footed ferrets in the wild still depends on the fate of prairie dogs" (Dobson and Lyles, 2000:987). Owen et al. (2000) challenged the common notion that the black-footed ferret is an obligate predator of prairie dogs and noted that 42% of the fossil sites with *M. nigripes* lack *Cynomys.* However, as these authors also noted, the earliest fossil evidence for *M. nigripes* is indeed associated with *Cynomys.* If the biochronologic estimates in this chapter are accurate, the Badger Room provides the earliest appearance date for *Mustela nigripes,* and in this case also the black-footed ferret is found in association with prairie dogs (as well as other fossorial, semicolonial rodents).

Conclusions

The Badger Room locality in Porcupine Cave is a time-averaged deposit that spans at least a few hundred years and at most about 10,000 years. Biochronologically the fossil assemblage appears to date to between 800 and 950 Ka based on the temporal overlap of arvicoline rodent species. Taphonomically, the primary vectors of accumulation were probably mammalian carnivores in addition to wood rats. Many bones show evidence for rodent gnawing and processing by carnivores. Based on a definition of the climate space common to two species *(Spermophilus* cf. *elegans* and *Mictomys kansasensis/ meltoni)* that appear to have been sympatric in the middle Pleistocene at Porcupine Cave, we infer somewhat longer, cooler, moister winters relative to the modern climate system. This interpretation rests mainly on the presence of *Mictomys* in the assemblage; the geographic range of *S.* cf. *S. elegans* defines a climate space that encompasses that of Porcupine Cave today. The lack of *Lemmiscus curtatus* in the Badger Room assemblage makes winters appear even cooler and moister than is suggested by a similar paleoclimatic analysis on the Pit deposits; it is unclear whether this absence is biological reality or sample bias. In terms of local landscape structure, we have two working hypotheses. The first reconstructs the local environment as a well-differentiated mosaic of habitats not unlike the modern South Park system, and the second recognizes the possibility that "extinct" ecosystem types were formerly present in the Rocky Mountain intermontane valleys.

For the mammal community, there appears to be evidence of stability through time in parameters of taxonomic richness and ecological structure. This stability was maintained in spite of a high number of deletions and additions of individual taxa. The Badger Room provides the first appearance date for the black-footed ferret *(Mustela nigripes),* and it is found in association with prairie dogs *(Cynomys)* and ground squirrels *(Spermophilus).* The Badger Room assemblage also contains two other pairs of taxa that are functionally closely related today: the fisher and porcupine *(Martes diluviana–Erethizon dorsatum)* and coyote and badger *(Canis latrans–Taxidea taxus).* Clearly these associations have had a long coevolutionary history.

An explanation of the generally high level of biodiversity at South Park has several components. First, the region's topographic and geological heterogeneity sustained a diversity of floral and vegetation types and this, in turn, supported a rich mammal fauna. Second, the region may have acted as a refugium for plants and animals during the glacial-interglacial cycles of the Pleistocene. And third, South Park may have formed part of a complex dispersal corridor between Asia and Mexico.

The Badger Room assemblage represents a sample very different from that of the Pit, the Porcupine Cave locality that has received the most attention in the published literature. The Badger Room sediments were unstratified and generally homogeneous, whereas those of the Pit were stratified and sedimentologically heterogeneous. The Pit was excavated with tight stratigraphic control and uniform screening techniques by similar crews from season to season. The Badger Room fossils were gathered by a variety of workers over a number of years and, initially, screening techniques were not employed. The Pit deposit clearly records glacial-interglacial transitions; the Badger Room most likely records only a single cool, moist episode. The contrasts between the Badger Room and the Pit highlight the fact that Porcupine Cave is a collection of many fossil localities. Each assemblage must be analyzed independently if we are to paint a comprehensive picture of life in South Park during the middle Pleistocene.

Appendix 22.1. Repository Numbers of All Specimens Used in the Badger Room Analyses

CM 45400, 45401
CM 49108
CM 49289
CM 49291
CM 74000–74862
CM 74864–75024
CM 75026–75029
CM 75031–75037
CM 75040
CM 75093–75199
CM 75205
CM 75207
CM 75210
CM 75216–75233
CM 75650–75849
CM 75950–75957
CM 75959–75963
DMNH 5666, 5667
DMNH 5717–5719
DMNH 10950–10974
DMNH 11015, 11016
DMNH 11569–11571
DMNH 11917
DMNH 13799
DMNH 13851–13888
DMNH 13906–13942
DMNH 13944–13946
DMNH 13951–13954
DMNH 14300–14317
DMNH 14647–14652
DMNH 14725–14728
DMNH 14959–14965
DMNH 15073–15081
DMNH 15175, 15176
DMNH 15185
DMNH 16001–16017
DMNH 16093
DMNH 17435–17449
DMNH 17475–17490
DMNH 17550–17563
DMNH 17679–17682
DMNH 18151
DMNH 18353
DMNH 19869–19871
DMNH 20050–20074
DMNH 20100–20124
DMNH 20130–20209
DMNH 20425–20454
DMNH 21238–21240
DMNH 22084, 22085
DMNH 22648–22665
DMNH 22768, 22769
DMNH 22823–22858
DMNH 23070–23076
DMNH 23078–23084
DMNH 23296–23309
DMNH 23457, 23458
DMNH 26646, 26647
DMNH 27010–27019
DMNH 27024–27031
DMNH 27046–27054
DMNH 27056–27065
DMNH 27402
DMNH 27765
DMNH 27862
DMNH 27926
DMNH 27934
DMNH 28332, 28333
DMNH 28928
DMNH 28932
DMNH 28934–28936
DMNH 29143–29149
DMNH 29309–29312
DMNH 29314
DMNH 29316
DMNH 29702, 29703
DMNH 30019–30024
DMNH 30074
DMNH 30076
DMNH 30194
DMNH 30197–30200
DMNH 33454, 33455
DMNH 33461
DMNH 33463
DMNH 33479–33481
DMNH 33492–33494
DMNH 33503, 33504
DMNH 33509
DMNH 33573
DMNH 33650–33657
DMNH 33779
DMNH 33901, 33902
DMNH 33910
DMNH 34200, 34201
DMNH 34250
DMNH 35370
DMNH 35386–35388
DMNH 35449
DMNH 36153
DMNH 36538–36541
DMNH 36547
DMNH 36565
DMNH 36588–36593
DMNH 36675–36679
DMNH 37003, 37004
DMNH 38273–38309
DMNH 38358–38360
DMNH 38400
DMNH 38548
DMNH 38894–38899
DMNH 39514
DMNH 39516
DMNH 39522–39524
DMNH 39526, 39527
DMNH 39533, 39534
DMNH 39536, 39537
DMNH 40204, 40205
DMNH 40212, 40213
DMNH 40216
DMNH 40222–40224
DMNH 40226
DMNH 40396
DMNH 40650
DMNH 40891
DMNH 40896
DMNH 41006–41018
DMNH 41032, 41033
DMNH 41401
DMNH 41414–41417
DMNH 41430–41433
DMNH 41441–41443
DMNH 41448
DMNH 42560
UCMP 147067
UCMP 164632–16466

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TWENTY-THREE

Faunal Dynamics of Small Mammals through the Pit Sequence

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The Pit locality, located about 35 m inside Porcupine Cave (see figure 2.3), contains a stratified, circa-2-m-thick sequence of sediment that has yielded more than 7200 identified fossils representing more than 1500 individual animals. A minimum of 1 amphibian species, 2 reptile species, 1 bird species, and 57 mammal species have been recognized (see tables 10.9, 10.10). The fossils are spread through the top 13 of the Pit's 15 discrete stratigraphic intervals, which are numbered 1–14, with level 8 separated into 8 and 8a (figure 23.1).

Characteristics of the sediments in the Pit have been used to divide the sequence into interglacial (levels 1–3, 6–9, probably 11) and glacial (levels 4–5, 10) deposits (Barnosky and Rasmussen, 1988; Barnosky and Bell, 2000; chapter 7). Previous studies (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996; Bell and Barnosky, 2000) pointed out the dramatic faunal change that accompanied the transition from the uppermost glacial (levels 5 and 4) to the uppermost interglacial (levels 3–1). The earlier work also recognized that, within each of these major climatic intervals, relative abundance of taxa fluctuated, and that species composition changed somewhat from lower to upper levels. With the more complete data set now available, it is possible to describe and interpret the faunal dynamics through the entire sequence and for most taxa, and that is the focus of this chapter. Tracing the taxa through the sequence leads to inferences about how the South Park mammal community assembled through the middle Pleistocene, how the fauna of interglacials differed from that of glacials, and how environments may have subtly fluctuated within the major climatic intervals defined by sedimentary criteria.

Materials and Methods

Details of the Pit excavation were provided by Barnosky and Rasmussen (1988) and Bell and Barnosky (2000), and in chapter 2. This analysis focuses on the mammal taxa, especially small mammals, because they are more adequately sampled than the other vertebrate groups. A total of 6981 identified specimens (numbers of identified specimens [NISP]) representing at least 1402 individuals (minimum numbers of individuals [MNI]) were included. Raw data are presented in tables 10.9 and 10.10.

Relative abundances of mammals were calculated using MNI. Relative abundance results based on NISP are not substantially different, although the MNI technique slightly overestimates the abundance of rare taxa. Percentages for relative abundances were calculated in Microsoft Excel 9.0.

To assess the minimum sample size at which rare taxa might be expected to appear in a given level, NISP at each level was plotted against species richness for the following groups of taxa: all Pit taxa (including reptiles, amphibians, and birds), mammals only, carnivores, rodents, lagomorphs, arvicolines, *Neotoma, Spermophilus,* and *Cynomys.* Rarefaction curves were computed by considering each stratigraphic level a single sample and using the Coleman rarefaction algorithm in EstimateS 5.01 (R. Colwell, Storrs, Connecticut) (Colwell, 1997; Colwell and Coddington, 1994). One rarefaction curve included all mammal taxa; a second one was computed for only rodents and lagomorphs. Various problems arise in applying the EstimateS algorithms to paleontological samples (Barnosky and Carrasco, 2002), but the results are nevertheless useful in comparing taphonomically similar fossil deposits, as are the Pit levels.

To assess how well each level represented the expected species diversity based on the total Pit sample, the number of species expected for a given NISP based on the rarefaction analysis was plotted against the observed number of species at each stratigraphic level. If samples are perfectly homogenous (all levels equal in species diversity), the correlation approaches 1.0. Levels with anomalously high or low diversity

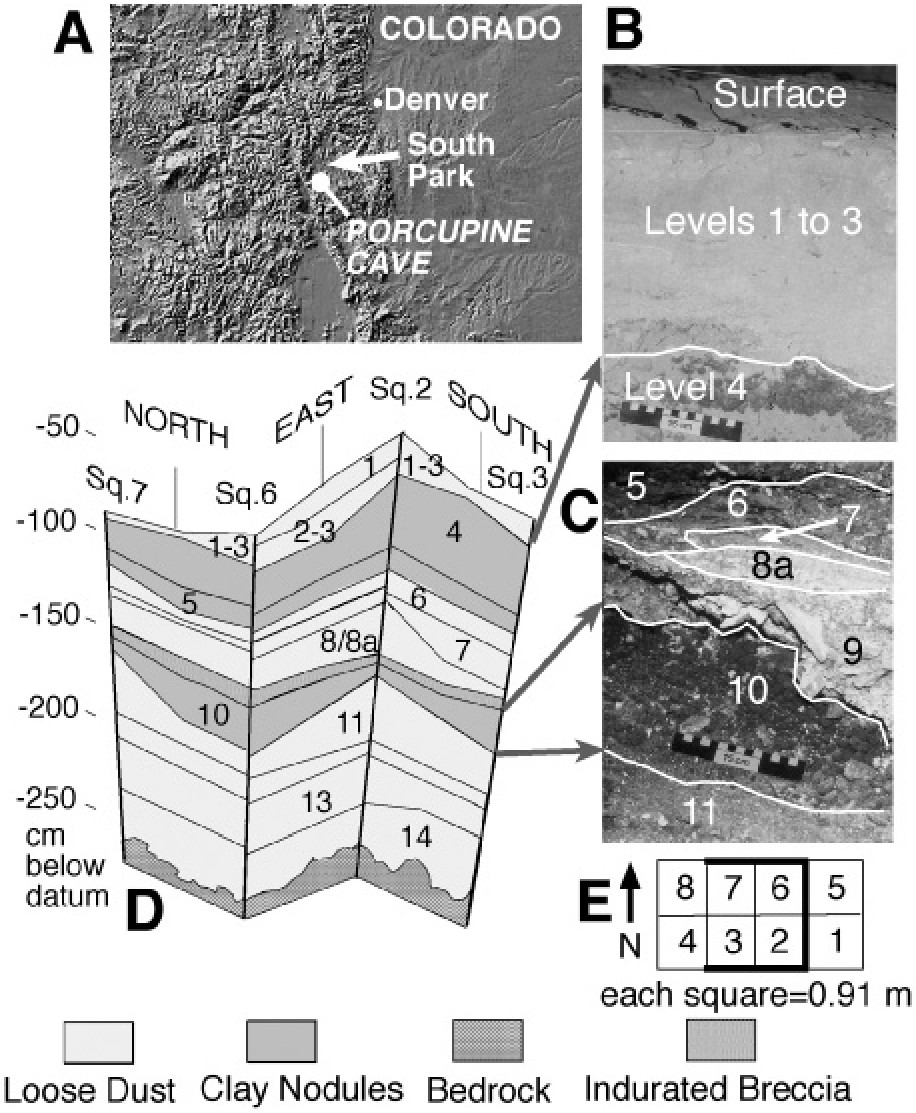

FIGURE 23.1 General location of Porcupine Cave (A) and stratigraphy in the Pit locality (B–D). The grid (E) is a plan view of how the excavated squares 1, 2, 3, 5, 6, and 7 relate to one another. The fence diagram (D) shows schematic stratigraphy for the three walls of the excavation indicated by bold lines in the plan view; numbers on the fence label stratigraphic levels. Stratigraphy of levels 6–9 is more complex than can be shown at the scale at which the fence diagram is drawn. Some of the complex relationships of these beds are illustrated in the photos at right. Panel B shows sediments representative of levels 1–4 in the west wall of square 1 (south is at left, north at right). Panel C exemplifies sediments characteristic of levels 5–11 in the south wall of square 3 (east is at left, west at right). Scale bars in the photos = 15 cm. See Bell and Barnosky (2000) and Wood and Barnosky (1994) for additional relevant information on stratigraphy and location of the Pit within Porcupine Cave.

plot as exceptionally high or low outliers, respectively. Correlation statistics were derived in StatView 5.0 (SAS Institute, Inc., Cary, North Carolina).

Results and Discussion

Sampling Considerations

The fossil small mammals from the Pit very probably provide a reasonable representation of the animals that constituted the middle Pleistocene community around Porcupine Cave, given the taphonomic pathways detailed in chapter 2. Essentially, the taphonomic pathways resembled those analyzed by Hadly (1999) for Lamar Cave, Wyoming, which demonstrated remarkable fidelity to the sampling universe from which the fossils were taken. Thus the primary sampling concern, as in most paleontological samples, is whether adequate numbers of specimens exist to compare relative abundance and diversity patterns from one stratigraphic level to another.

When the Pit sample is considered as a whole, the rarefaction curve suggests that, even with nearly 7000 specimens, additional sampling can be expected to yield more species

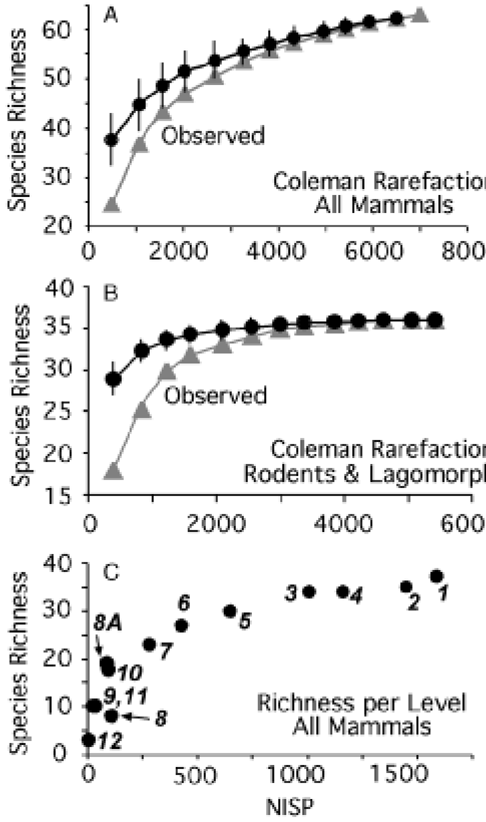

FIGURE 23.2 Rarefaction curves (A, B) and species-richness-per-level plotted against NISP (C) for the Porcupine Cave Pit data set. (See tables 10.9 and 10.10 for raw data.) In the rarefaction curves, the upper curve (black dots) shows the Coleman rarefaction curve, with black bars representing two standard deviations. The lower gray curves show the observed species accumulation curve. In the species-richness-per-level curve, each black dot represents the observed species richness at one stratigraphic level; levels are labeled by their numbers.

(figure 23.2). The continual rise in the curve probably reflects two factors. First, the entire sequence spans 200,000–300,000 years, each level is of slightly different geological age, and therefore some new species are added through time. This temporal effect is removed in the richness-per-level curve, which indicates that stratigraphic levels that contain more than 500 specimens gain few new species with additional sampling. The second factor contributing to the consistent rise in the rarefaction curve is that the artiodactyls, perissodactyls, and carnivorans are poorly sampled relative to the rodents and lagomorphs because of taphonomic considerations. The rarefaction curve for rodents and lagomorphs alone rises more steeply than that for all taxa, consistent with the poorer sampling of large mammals. The fact that it does not level off until more than 1000 specimens (versus 100–300 specimens for the richness-per-level-curve for rodents and lagomorphs) reflects the addition of species through time.

The richness-per-level curves for subgroups of mammals verify that the large mammals are inadequately sampled (figure 23.3). However, for rodents and lagomorphs there is no correlation between sample size and species richness above a total NISP of about 100 for rodents and 300 for lagomorphs. This also holds true at the generic level for rodents. Therefore the sample for these groups is adequate in levels 1–6 (NISP = 1580, 1442, 1020, 1154, 656, 434, respectively); marginally adequate but less than desirable in levels 7, 8, 8A, and 10 (NISP = 283, 104, 125, 119, respectively); and clearly inadequate in levels 9, 11, and 12 (NISP = 25, 36, 3, respectively).

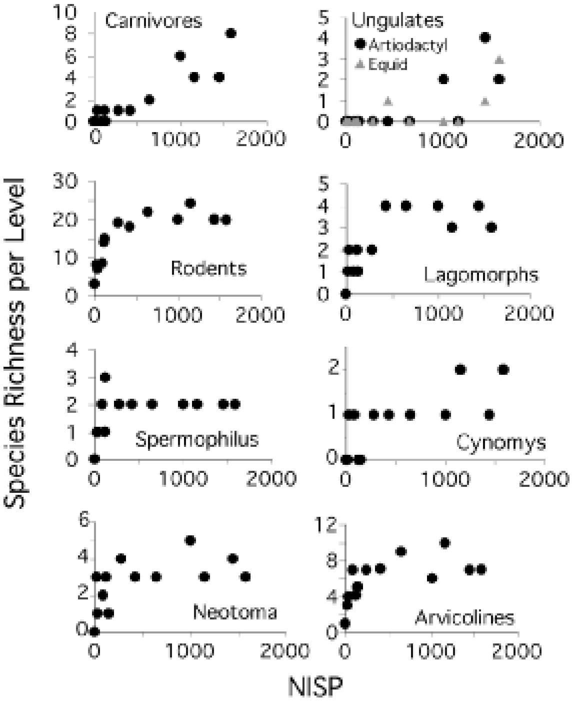

FIGURE 23.3 Species-richness-per-level curves for Porcupine Cave Pit taxa broken out by subgroups. Each black dot represents the observed species richness and NISP at one stratigraphic level.

Small-Mammal Community Composition

Taxa present in most levels of the Pit include *Ochotona* (pika), leporids (rabbits), *Marmota* (marmot or woodchuck), *Spermophilus* (ground squirrel), *Cynomys* (prairie dog), *Thomomys* (pocket gopher), *Neotoma* (wood rat), *Peromyscus* (deer mouse), and arvicolines (voles, lemmings, and muskrats). Species within each genus are united by generally similar ecological preferences. *Ochotona* lives in rocky alpine environments, which are in the vicinity of Porcupine Cave today and presumably were there throughout the Quaternary. Leporids and *Peromyscus* are ecological generalists, occupying a variety of habitats in grasslands, forests, and semiarid regions. *Spermophilus* and *Cynomys* are typically found in grasslands and semiarid shrublands. *Marmota,* although similar to ground squirrels and prairie dogs in aspects of life history (burrowing and long periods of hibernation or aestivation), generally occurs in more mesic areas. Most arvicoline rodents inhabit relatively moister microhabitats than *Spermophilus* or *Cynomys;* an exception is *Lemmiscus curtatus,* characteristic of semiarid regions where sagebrush is abundant. *Neotoma* species typically build nests in caves when they are available, but spend most of their life foraging outside the cave as ecological generalists.

Many of these same genera dominate in numbers of species and numbers of individuals in the fauna around Porcupine Cave today (Fitzgerald et al., 1994). The fact that a similar assemblage of genera (or numbers of genera within a subfamily, in the case of arvicolines) has persisted largely unchanged in the Porcupine Cave region for more than 800,000 years suggests remarkable stability in montane communities at the generic level, even in the face of the major climate changes that have taken place during the Pleistocene. However, two of the most abundant taxa in the Porcupine Cave record, *Mictomys* (bog lemming) and *Lemmiscus curtatus,* do not occur in the region today, and many of the species are extinct, demonstrating that a modicum of fluidity operates within the basic community stability.

Relative Abundance of Small Mammals and Its Climatic Implications

The taxa that occur in the highest relative abundances, in order of abundance in most levels, are as follows: arvicolines, *Neotoma, Spermophilus* and *Marmota,* leporids, and *Thomomys* (figures 23.4, 23.5). The high relative abundance of *Neotoma* may reflect a taphonomic bias relative to the modern landscape, in that the fossil accumulation is basically a stacked series of wood rat nests in which the residents occasionally died. However, because this bias was constant throughout the deposit, it is still valid to compare relative abundances between levels. The high number of arvicolines in the fossil deposits parallels the situation on the landscape today at Porcupine Cave, as do the high numbers of *Spermophilus* and *Marmota.* This suggests that the same kinds of species that are most often sighted (or found in modern owl pellets and carnivore scat) on the landscape today were also most abundant on the landscape during the middle Pleistocene.

Despite the stability in the presence and rank-order abundance of genera, some clear changes in relative abundances of individuals within each genus occurred. *Marmota* first appears coincident with a slight decrease in *Spermophilus* and *Cynomys* at level 8 (figure 23.4). This probably represents an immigration of *Marmota* into the Porcupine Cave region, which took place during a climatic interval that the sediments suggest was an interglacial. Interestingly, this immigration coincides with a time that the arvicoline fauna suggests was among the wettest intervals represented in the entire record. It seems unlikely that *Marmota*'s first appearance in the Pit sequence is solely the result of sampling bias, given the reasonably large sample in level 10, the abundance of *Marmota* in levels 8 and above, and the coeval dip in *Spermophilus* and *Cynomys.* The temporary depression of those two xeric taxa would be consistent with expansion of the mesic microhabitats that favored *Marmota* and may even indicate competition for burrow habitat, given that all species share similar life history traits that focus on hibernating from fall to spring. *Marmota* continued to be abundant throughout this interglacial and the ensuing glacial, then decreased dramatically as *Spermophilus* and *Cynomys* increased with the onset of what was probably the warmest, driest interglacial.

Arvicolines demonstrate an inverse relationship with *Spermophilus* (figure 23.6). Hadly (1996) suggested that a similar inverse relationship at Lamar Cave reflected the shifting abundance of xeric *(Spermophilus)* and mesic (arvicolines) microhabitats. This hypothesis has been confirmed by subsequent trapping and statistical analyses of bones found in raptor pellets from xeric versus mesic environments in and around Yellowstone National Park (Hadly, 1999; E. A. Hadly, pers. comm.). The peak of arvicolines in the uppermost glacial (at level 5) represented at Porcupine Cave thus suggests more mesic microhabitats relative to the upper part of the preceding or the entire subsequent interglacial. Interestingly, arvicolines peak during level 8, in the midst of an interglacial according to the sedimentary record. This peak coincides with the arrival of *Marmota,* substantiating a relatively wet time during the interglacial. However, it is noteworthy that one of the arvicolines that peak during this time is *Lemmiscus curtatus,* the sagebrush vole, today confined to the arid Great Basin and adjoining areas, where sagebrush abounds (Carroll and Genoways, 1980). The other arvicoline that contributes to the high abundance is *Mictomys,* the bog lemming, indicating an increase in very wet areas around the cave.

Arvicolines also show an inverse relationship with *Neotoma* (figure 23.5). The *Neotoma* peak in level 9 may not be meaningful, given the small sample size. However, both of the *Neotoma* peaks occur immediately after the transition from a glacial into an interglacial. Today only *N. cinerea* occurs around the cave, and at both *Neotoma* peaks that species is most abundant. Also present are *N. floridana* and *N. micropus* in level 8A, and *N. floridana* and *N. stephensi* in level 3. The species other than *N. cinerea* are all found at lower elevations and warmer effective temperatures than characterize the Porcupine Cave region today (Repenning, chapter 18). All except *N. stephensi* occur within 80 km of the cave. Thus their increased numbers at the beginning of interglacials would be consistent with climatic warming. Repenning (chapter 18) speculated that tectonic changes might explain *Neotoma* distributions, but little geological evidence exists to support that suggestion.

The arvicoline rodent fauna of Porcupine Cave Pit contains 10 species and abundant specimens; thus it is diverse enough to meaningfully examine relative abundance changes at the species level (figure 23.7). All the arvicoline species except *Lemmiscus curtatus* and probably the *Microtus* specimens designated 5T are extinct. For reasons given by Wood and Barnosky (1994), *Mictomys* is probably an ecological analogue for the living bog lemming, *Mictomys borealis.* For most of the record, *Lemmiscus curtatus* and *Mictomys* dominate in abundance. Given the contrasting environmental preferences of these two species—*Lemmiscus* indicating relatively xeric microhabitats and *Mictomys* indicating relatively mesic microhabitats—they provide a guide to environmental fluctuations within the glacial and interglacial episodes demarcated by the sediments. Below level 10 sample sizes are too small for meaningful discussion.

The basic pattern that appears above level 10 is as follows: high abundance of *Mictomys* in the lower interglacial (levels 9–6) coupled with fluctuating abundances of *Lemmiscus;* in the ensuing glacial (level 5–4), intermediate but declining values for *Mictomys* with the inverse for *Lemmiscus;* and finally, in the upper interglacial (levels 3–1), very low percentages of *Mictomys* with high, then low, then high abundances of *Lemmiscus* (figure 23.7). The general climatic inference from *Mictomys* is that mesic microhabitats were most abundant during the lower interglacial, slightly less widespread during the glacial, and sparse during the uppermost interglacial. The climatic inference from *Lemmiscus* is that sagebrush grasslands were at first abundant during the lower interglacial (level 9), then fluctuated until they were less abundant during the upper part of that interglacial (levels 8A–6). The addition of morphologically modern *Microtus* (with five triangles) in level 6 may suggest that the decline in sagebrush-dominated areas was accompanied by an increase in mesic grassy areas, but not as mesic as those preferred by *Mictomys,* because *Mictomys* declines beginning in level 6. During the glacial (levels 5 and 4), the relatively high percentage of *Lemmiscus* suggests increasing coverage by sagebrush grassland, which in turn implies a drier climate than prevailed during much of the preceding interglacial. In the uppermost interglacial (levels 3–1), the fluctuation between *Lemmiscus, Microtus meadensis,* and *Microtus* 5T (these are possibly extant species characterized by ml with 5 or 6 alternating triangles, but they cannot be identified to species) and the decline in *Mictomys* both suggest the driest times in the record, with levels 3 and 1 dominated by sagebrush grassland, and level 2 slightly more mesic, with grassland spreading at the expense of sagebrush.

Taken in concert, the arvicoline fluctuations imply that the lower interglacial (levels 6–9) was generally moist relative to the subsequent glacial (levels 4 and 5) and interglacial (levels 1–3). Temperatures were cooler in the lower interglacial than in the uppermost glacial, fluctuating from warm (level 9), to cool (level 8A), to warm again (levels 8–6). The level 4–5 glacial appears dry relative to the preceding interglacial, but wet relative to the subsequent interglacial. It was perhaps nearly as warm as the preceding interglacial but cooler than the uppermost interglacial (levels 1–3). The high abundance of *Mictomys* in level 10, combined with the relatively low abundance of *Lemmiscus,* suggests a cool, relatively moist glacial in the lowest level that produced reasonably abundant fossils.

Information from sciurids is in agreement (Goodwin, chapter 17). The perennially low abundance of *Tamiasciurus* (red squirrel or chickaree), a woodland indicator, drops after level 6, and it all but disappears by level 1.

These data agree with climatic interpretations derived from pollen, isotope, and invertebrate fossil data recovered about 200 km south of Porcupine Cave at the Hansen Bluff site at 2300 m, an elevation somewhat lower than that of Porcupine Cave but still reasonably high (Rogers et al., 1992). Assuming the correlation presented in figure 7.5, the uppermost interglacial sediments at Porcupine Cave were probably deposited during oxygen isotope stage 21; the middle glacial, during stage 22; the preceding interglacial, during a slight warming excursion that lasted from about 900 to 910 Ka ago; and the lower glacial, coincident with a cold spell between about 910 and 960 Ka ago. The Hansen Bluff climatic reconstruction suggests that stage 21 was marked by the warmest, driest conditions, but that fluctuations toward cooler, wetter conditions took place within it; this is very similar to the pattern indicated by the arvicolines in levels 1–3 at Porcupine Cave. Glacial stage 22 is interpreted as somewhat cooler and wetter than interglacial stage 21 at Hansen Bluff but was still characterized as warm and dry. The warm, dry overall character parallels the arvicoline interpretation for levels 5 and 6 in Porcupine Cave, but the high abundance of *Mictomys* and the sediments of those levels (Bell and Barnosky, 2000) are consistent with generally wetter conditions relative to the overlying levels. The preceding interglacial at Hansen Bluff was characterized as cold and wet; this is consistent with the arvicoline interpretation at Porcupine Cave of an interglacial that was relatively cool and moist compared to levels 1–3, with some intervals that may have been as cool as the subsequent glacial.

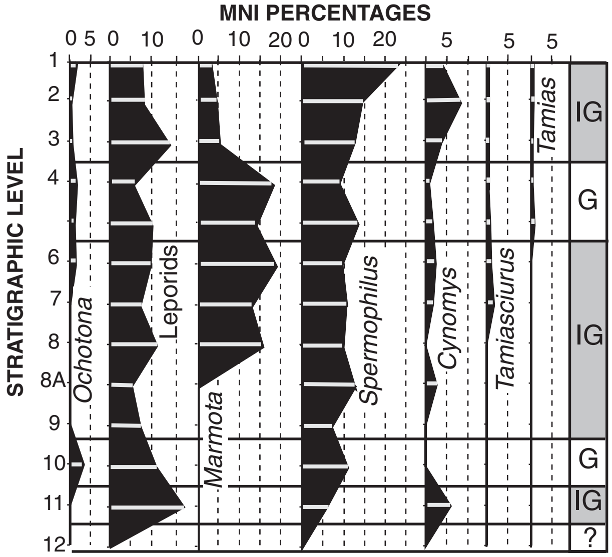

FIGURE 23.4 Relative percentages of small-mammal taxa through time in the Porcupine Cave Pit sequence, based on MNI. The total of 100% includes the taxa shown in figure 23.5. The climatic intervals at right are determined by independent sedimentary criteria. *Abbreviations:* G, glacial; IG, interglacial.

Striking similarities are evident between the arvicoline relative percentages at Porcupine Cave and a pollen diagram from Hansen Bluff. The sagebrush *(Artemisia)* pollen percentages through stage 21 at Hansen Bluff (Rogers et al., 1992:figure 10) start out high, drop to a low in the middle, and then increase

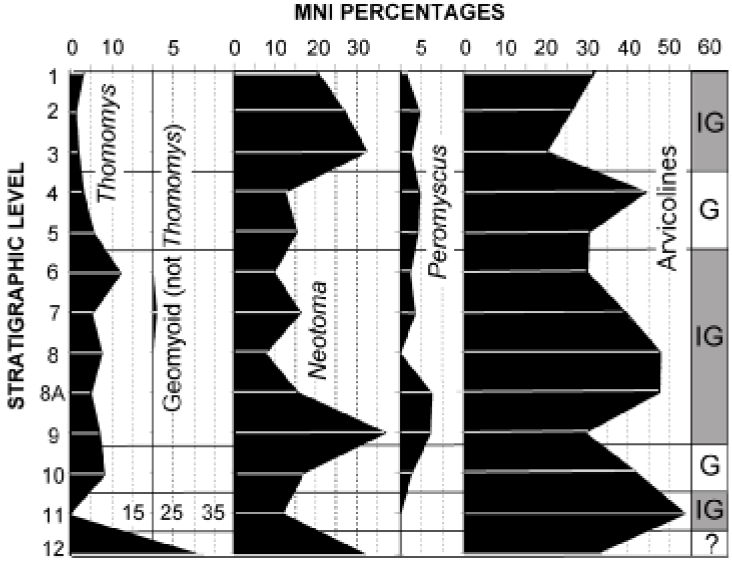

FIGURE 23.5 Relative percentages of small-mammal taxa through time in the Porcupine Cave Pit sequence, based on MNI. The total of 100% includes the taxa shown in figure 23.4; see the caption to that figure for further explanation.

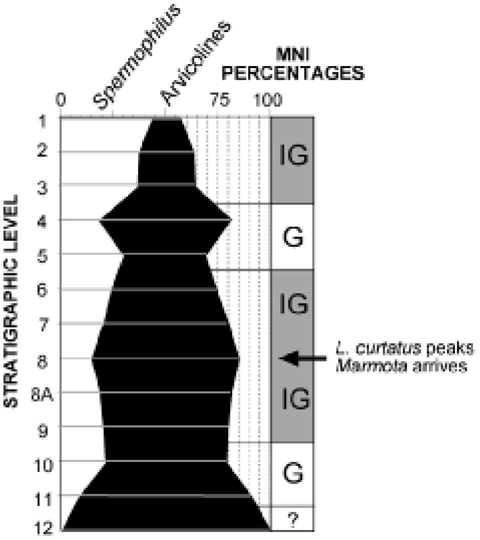

FIGURE 23.6 Relative percentage of *Spermophilus* and arvicolines. Climatic intervals are explained in figure 23.4.

again, just as the sagebrush vole *(Lemmiscus)* percentages do in levels 3–1 at Porcupine Cave. During stage 22 at Hansen Bluff, *Artemisia* percentages fluctuate with a peak in the middle, as do the *Lemmiscus* percentages at Porcupine Cave. Poaece (grass) and *Pinus* (pine) pollen percentages, which correlate with more mesic times, dip at the stage 22–stage 21 boundary and at the top of stage 21, consistent with the decline in *Mictomys* percentages at the corresponding parts of the Porcupine Cave record (levels 4–1).

Assembly of Species: Immigration, Extinction, and Evolution

The species composition was not static through the Porcupine Cave record. Immigration events include *Microtus meadensis* at level 8A, *Marmota* at level 8, *Microtus paroperarius* at level 7, and *Microtus* 5T at level 6. All these immigration events took place within the interglacial represented by levels 9–6, but they were staggered through the climatic interval, rather than clustered at its beginning or end.

In addition to these clear-cut first appearances, *Brachylagus coloradoensis* is first identified in level 7, and *Sylvilagus* and *Lepus* first appear in level 6. Prior to these levels all identifiable leporid specimens are either *Hypolagus* or *Aztlanolagus*. But there are many leporid specimens in lower levels that are not diagnostic at the generic level and could represent one of the later-appearing lagomorphs. Within the sciurids, *Cynomys* cf. *C. leucurus* first appears in level 5, along with *Tamias* cf. *T. minimus*. *Tamiasciurus hudsonicus* is first found in level 7 (Goodwin, chapter 17). The latter two species are difficult to substantiate as true immigrants, given their rarity, and their absence in lower levels could simply reflect small sample sizes.

Extinction, in contrast to immigration, does seem to cluster at the major climatic boundaries. *Allophaiomys pliocaenicus, Mimomys virginianus,* and *Phenacomys gryci* make their last appearance at the level 4/3 boundary. All three of these disappearances cluster at the transition from the middle glacial into the uppermost interglacial. *Hypolagus* appears last in level 10, as does the extinct morphotype of *Spermophilus* (?*Otospermophilus*) sp. (Goodwin, chapter 17). The transition from level 10 to level 9 also represents a glacial-interglacial transition. Extinctions at the glacial-interglacial boundaries are of interest in the context of the end-Pleistocene extinction debate, which pits human-caused extinction against environmentally caused extinction (Martin and Klein, 1984; Barnosky, 1989; Alroy, 2001). These middle Pleistocene examples from Porcupine Cave demonstrate that extinctions are a common feature at glacial-interglacial transitions, even in the absence of humans, though the only extinctions documented at Porcupine Cave are of small mammals.

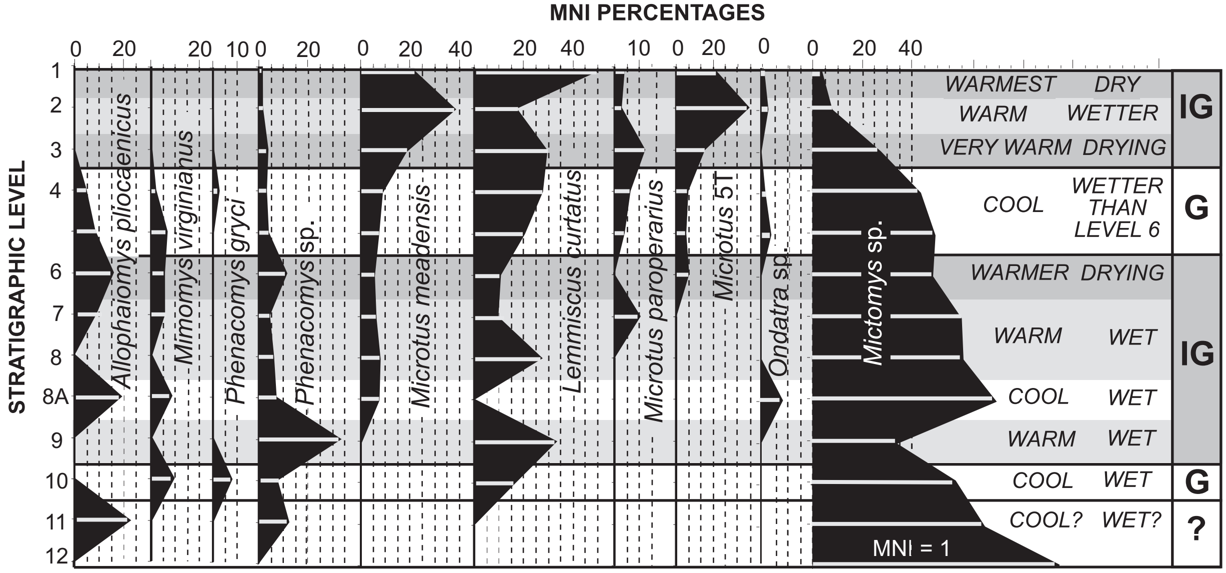

FIGURE 23.7 Relative percentages of species of arvicolines. *Phenacomys* sp. represents a species other than *P. gryci* in levels 1–6, but below level 6 specimens could belong to *P. gryci* or another species. The warm/dry interpretations within glacials and interglacials are based primarily on the relative percentages of the various species, especially *Lemmiscus* and *Mictomys.* Climatic intervals are explained in figure 23.4.

Even with the immigrations, faunal turnover, and extinctions, the breakup of so-called disharmonious or non-analogue assemblages—that is, the sympatric occurrence of taxa that are presently allopatric—is not observed in the Porcupine Cave Pit sequence. This is in contrast to the situation at the latest Pleistocene-to-Holocene transition, where the breakup of non-analogue assemblages has been observed in mammals (Graham and Grimm, 1990). The only non-analogue association that characterizes the assemblage is the co-occurrence of *Mictomys* and *Lemmiscus* (Wood and Barnosky, 1994), and the association persists across all the major climatic boundaries.

Evolutionary patterns have been studied in marmots (Barnosky et al., chapter 25; Polly, 2003), other sciurids (Goodwin, chapter 17), and *Lemmiscus curtatus* (Barnosky and Bell, 2003). Marmots demonstrate no statistically significant morphological changes through the Porcupine Cave sequence. Goodwin (chapter 17) suggested that *Cynomys* cf. *C. leucurus* exhibited changes in the third lower molar, and *Spermophilus* cf. *S. elegans* in the fourth lower premolar, that potentially correlated with increased aridity. Barnosky and Bell (2003) observed that a shift in the frequency of *Lemmiscus* specimens with four triangles on their lower first molar versus those with five triangles became statistically significant only in the uppermost interglacial, suggesting a correlation with increasing aridity (figure 23.8). Thus it appears that climate change may have contributed to evolutionary change in some species, but only when it was most extreme—that is, during the increased aridity in the uppermost interglacial, which was apparently warmer than any of the climatic fluctuations that occurred lower in the sequence.

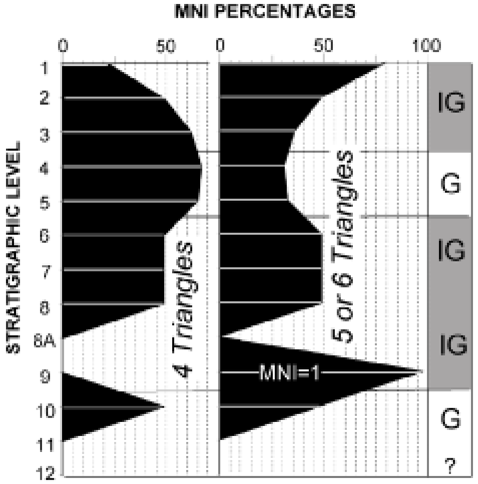

FIGURE 23.8 Relative percentage of *Lemmiscus* lower first molars with four triangles versus those with five or more triangles. Climatic intervals are explained in figure 23.4.

Species Richness Patterns

Analysis of species richness patterns was confined to taxa and stratigraphic levels that the rarefaction analysis (figure 23.2) and species-richness-per-level plots (figure 23.3) indicated were adequately sampled: rodents and lagomorphs from levels 1–6. These levels contain the following numbers of rodent and lagomorph species: level 1, 24; level 2, 25; level 3, 25; level 4, 29; level 5, 27; level 6, 23. A plot of these observed richness

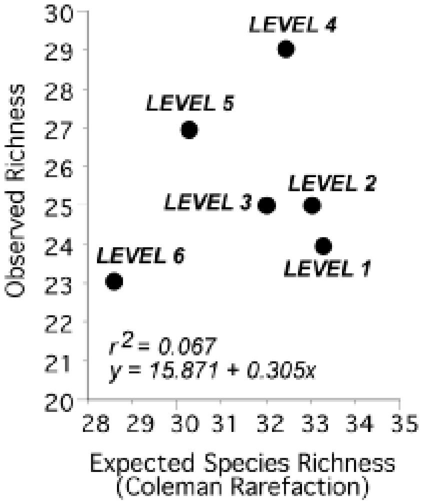

FIGURE 23.9 Plot of the rodent and lagomorph species richness expected from the Coleman rarefaction analysis against the observed richness for stratigraphic levels with sufficiently high NISP. Each point represents one stratigraphic level.

values against the values expected from Coleman rarefaction analysis suggests that the interglacial levels 1–3 are less species rich than glacial levels 4 and 5, and interglacial level 6 (figure 23.9). The r^2 value for the lower three levels is 0.932, indicating very close agreement for expected and observed values when only the glacial and immediately preceding levels are considered. The upper interglacial has observed values so far below the expected values that r^2 drops to 0.067 when they are included in the regression. Moreover, observed richness drops more and more in the progression from level 3 to level 1, suggesting that richness declines successively as the interglacial progresses.

The species that disappeared at the glacial-interglacial boundary or within the interglacial included the arvicolines *Allophaiomys pliocaenicus, Mimomys virginianus,* and *Phenacomys gryci,* the pocket gopher *Thomomys* aff. *T. bottae,* and the wood rats *Neotoma micropus* and *N. mexicana* (see figures 7.1–7.3). Species diversity within the sciurids *Spermophilus* and *Cynomys* remained constant throughout all the environmental changes indicated in the Porcupine Cave record (figure 23.3), even though the species within those genera changed through time (Goodwin, chapter 17). Likewise, lagomorph diversity remained constant, even though the species and even the genera changed, from *Hypolagus* and *Aztlanolagus* in the lower levels to *Lepus, Sylvilagus,* and *Brachylagus* in the upper levels.

Conclusions

Rodents and lagomorphs from the Porcupine Cave Pit sequence are adequately sampled and provide the basis for assessing how faunal dynamics correlate with independently assessed glacial-interglacial cycles; they also fill in details of climatic conditions within each glacial and interglacial episode. On the generic and subfamilial levels, remarkable stability through glacial-interglacial cycles is apparent. The same genera (or, in the case of arvicolines, subfamilies) that are abundant on the landscape today were abundant in each of the glacial-interglacial cycles represented over 780,000 years ago. However, the population densities of species within those genera fluctuated in response to environmental changes, both within each glacial-interglacial episode and across glacial-interglacial transitions.

Ecological interpretations of those fluctuating relative abundances suggest that the uppermost interglacial in the Pit sequence was by far the warmest and driest climatic episode; the preceding glacial was dry and warm in general character but cooler and wetter than the uppermost interglacial; and the middle interglacial was relatively cool and moist compared to the uppermost interglacial. Within at least the glacial (levels 4 and 5) and uppermost interglacial (levels 1–3), climatic fluctuations altered the abundance of sagebrush grassland relative to more mesic grassland and boggy areas, resulting in fluctuations in the relative abundance of the species that prefer the respective microhabitats: *Lemmiscus curtatus* as a sagebrush-grassland inhabitant, *Microtus* spp. as grassland specialists, and *Mictomys* as a wet grassland occupant. These interpretations parallel those based on the sediments of the Pit sequence in Porcupine Cave, and those of Hansen Bluff, which covers the same time period as the Porcupine Cave Pit sequence but yields climatic interpretations from fossil pollen, invertebrates, and isotopic data.

Species composition was not static through the 200,000 years or more represented by the Porcupine Cave Pit sequence. Immigration of at least 4 and possibly 10 species occurred during the middle interglacial interval. These first appearances were staggered through the interval, rather than clustered at any one stratigraphic level, suggesting gradual assembly of the species rather than a single community moving en masse.

In contrast, extinctions clustered at glacial-interglacial transitions: at least two species at the lower transition, and three species at or near the upper glacial-interglacial transition. Added to three species that went extinct at the upper transition are at least three more that were extirpated either at the transition or within the uppermost interglacial.

This loss of species significantly decreased species richness in the uppermost interglacial relative to the preceding glacial. Taxa whose species seemed most affected by diversity fluctuations include *Thomomys, Neotoma,* and arvicoline rodents. Taxa whose species richness remained constant through the numerous climate changes indicated in the Pit sequence include *Spermophilus* and lagomorphs.

In the taxa that have been studied, evolutionary changes correlating with climate change either are not apparent or are confined to the most pronounced climate change, the increasing warmth and aridity in the uppermost interglacial interval.

In sum, the faunal dynamics indicate both stability and change in montane communities over the past million years or so. The stability is evident in the general structure of the community at the generic level: most of the genera that are found as fossils in the Porcupine Cave Pit sequence still have representatives in the fauna today. The taxa that are abundant on the landscape today are also the ones that were most abundant some 800,000 years ago at the generic and subfamilial levels. And the rank-order abundance of genera and subfamilies (in the case of arvicolines) was not much affected even by major climatic transitions. Within this overall context of higher-level stability, however, are important changes indicating that the players change through time at the species level. Most evident in this regard is the long co-occurrence of two taxa, *Lemmiscus* and *Mictomys,* that today do not live around Porcupine Cave but that, during the time of the Pit deposits, were among the most abundant small mammals on the landscape. Further stamps of faunal change on the basic pattern of stability are various minor fluctuations in the relative abundance of taxa, probably in response to changes at the microhabitat level, immigrations, extinctions, and, in some taxa, probable evolutionary changes. Of particular importance in view of current global warming is the question of whether the basic stability of communities or the overprints of faunal change are more likely to prevail. That issue is the subject of chapter 26.

Acknowledgments

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TWENTY-FOUR

Stable Carbon and Oxygen Isotope Analysis of Marmot Cheek Teeth from the Pit Locality

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The Pit locality within Porcupine Cave, Park County, Colorado, spans at least two glacial-interglacial cycles, the upper of which dates to somewhere between 780 and 900 Ka (Bell and Barnosky, 2000). The deposits probably correlate with parts of oxygen isotope stages 21 and 22, or, less likely, 19 and 20 (see figure 7.5). Recent work has demonstrated that carbon and oxygen isotope values found in the tooth enamel of large mammals (*Equus* and *Cuvieronius;* MacFadden, 2000) and small mammals (*Thomomys* and *Geomys;* Rogers and Wang, 2002) correlate well with the marine isotope record. This chapter reports isotopic signatures of marmot tooth enamel from stratigraphically superposed levels in the Pit in hopes of refining correlations and assessing vegetational change as indicated by diet.

The carbon isotope values in the enamel of fossil teeth are useful in determining paleodiet because different photosynthetic pathways impart different $^{13}C/^{12}C$ ratios to different plants, and these ratios are ultimately reflected in the animals that eat the plants (DeNiro and Epstein, 1978; O'Leary, 1988; Ehleringer et al., 1991; Quade et al., 1992; Ehleringer and Monson, 1993; Cerling et al., 1999; Feranec and MacFadden, 2000). Although postdepositional diagenesis can overprint carbon isotope values in bone (Schoeninger and DeNiro, 1982), tooth enamel is not prone to diagenetic alteration, and thus it reliably reflects isotope values derived from feeding (Quade et al., 1992; Wang and Cerling, 1994; Koch et al., 1997). As a general guide, grazers are predominantly C_4 feeders, browsers are predominantly C_3 foragers, and intermediate and crassulacean acid metabolism (CAM) feeders utilize both C_3 and C_4 in modern ecosystems. In addition to their use in determining paleodiet, carbon isotope values fluctuate during glacial-interglacial cycles and so can be used for correlating the terrestrial and marine isotope records (Raymo et al., 1997; MacFadden, 2000).

Oxygen isotope ratios in mammalian tooth enamel have been shown to reflect the isotopic ratio of ingested waters (Land et al., 1980; Longinelli, 1984; Luz et al., 1984; Koch et al., 1989). Luz et al. (1984) and Koch et al. (1989) suggested that the oxygen isotope composition of teeth is dependent on the isotopic composition of the water ingested, the consistent fractionation of oxygen isotopes between the body water and the enamel, and the metabolism of the particular animal. If comparisons are made using the same species over time, the fractionation and metabolism effects should be the same for all samples. Therefore the tooth enamel oxygen isotope values should represent changes in the isotopic composition of the water, which is temperature dependent, and not changes in the metabolism or fractionation of the animals being sampled (Rozanski et al., 1992, 1993). Because oxygen isotope values of meteoric waters should be temperature dependent, this method should allow for discrimination between glacial stages (cold periods) and interglacial stages (warm periods).

Body size of various taxa has been a significant concern when studying the oxygen isotope composition of tooth enamel. Bryant and Froelich (1995) suggested that the largest animals in a fauna are likely to be the best markers of paleoclimate. Similarly, Luz et al. (1984) suggested that the mammals best suited for this type of analysis are those that are obligate drinkers and have a low metabolism. Marmots are not the largest animals in the fauna within the Pit, nor do they continually drink or have a constant low metabolism throughout the year. However, they are among the larger animals that occur abundantly in all levels, and with sufficient frequency for reliable statistical analysis to be performed. Marmot life histories include birth of most animals in early spring and hibernation from early fall through winter, generally about eight months per year (Frase and Hoffmann, 1980). (Additional information on the life history of marmots is given in chapter 25.) Because of this life history, the possibility for erroneous isotopic interpretation owing to seasonal differences among individuals in diet and water intake is minimal. Additionally, Lindars et al. (2001) and Rogers and Wang

(2002) have demonstrated good paleoclimate signals in tooth enamel from rodents much smaller than marmots.

Materials and Methods

Within the Pit sequence, level 1 is the youngest and level 7 is the oldest of the levels analyzed here. *Marmota* teeth were analyzed from each of these levels (figure 24.1). See Barnosky et al. (1996), Wood and Barnosky (1994), Bell and Barnosky (2000), and Chapters 7 and 23 for details of the stratigraphy. The method for stable isotope sampling and preparation followed that of MacFadden and Cerling (1996) and Koch et al. (1997). Sampling focused on, but was not confined to, the fourth premolar and third molar because these teeth are among the last to mineralize and erupt (Munson, 1984), thereby maximizing the probability that the metabolic pathways that ultimately determine isotopic signatures were those of adult animals. Sampling involved removing all nonenamel portions of the tooth so that only pristine enamel remained. The enamel was then crushed into a fine powder using a mortar and pestle. The pristine enamel powder was first treated with 35% hydrogen peroxide for 24 hours to remove organics. It was then decanted and washed with distilled water, and soaked in 0.1 N acetic acid for 24 hours to remove any diagenetic carbonate. The sample was again decanted and washed with distilled water, rinsed with 100% ethyl alcohol, and dried overnight.

Following the treatment, the samples were analyzed using an Isocarb automated carbonate preparation system attached to a Micromass Optima gas source mass spectrometer (GV Instruments, Manchester, United Kingdom, for both instruments) at the Department of Earth and Ocean Sciences, University of California, Santa Cruz. During analysis the samples were dissolved in 100% phosphoric acid at 90°C to create CO_2. The results were compared using the following equation:

$$X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000,$$

where X is the $\delta^{13}C$ or $\delta^{18}O$ value and $R = {}^{13}C/{}^{12}C$ or ${}^{18}O/{}^{16}O$. All isotope values are reported relative to the V-PDB. The precision for the analysis was ± 0.1‰. A total of 20 samples were collected, prepared, and analyzed. For the analysis of diet, values more negative than –8.0‰ were interpreted to indicate dominantly C_3 feeders, values more positive than –2.0‰ were interpreted to signal dominantly C_4 feeders, and values between –2.0‰ and –8.0‰ were assumed to reflect intermediate feeding strategies.

Mean differences in carbon and oxygen isotope values of *Marmota* tooth enamel between levels and from glacial and interglacial stages in the Pit were compared using single-factor analysis of variance (ANOVA) and Tukey honest significant difference (HSD) tests. (Tukey HSD tests are similar to *t*-tests but take into account multiple comparisons and are generally more conservative.) Because the requirements of ANOVAs (normal distribution, homogeneity of variances) may have been violated by such small sample sizes, a nonparametric Kruskal-Wallis test was also performed. The results from this nonparametric test were the same as those from the ANOVA; therefore only the results from the parametric ANOVA are reported. Statistical analyses were performed in Microsoft Excel 2000 and JMP IN 4.0 (SAS Institute, Inc., Cary, North Carolina), with significance set at $p < 0.05$.

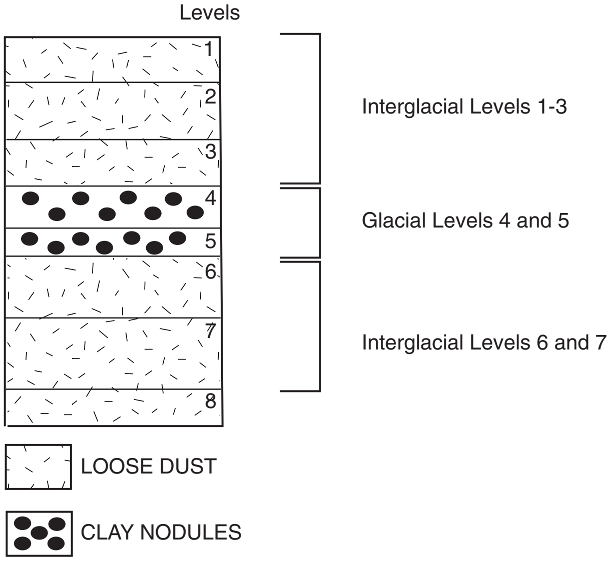

FIGURE 24.1 Schematic stratigraphic column within the Pit sequence showing sediment type. Marmot teeth were obtained from levels 1–7. Glacial and interglacial groupings of levels are indicated. For a more complete description of the stratigraphy within the Pit, see Barnosky and Rasmussen (1988), Wood and Barnosky (1994), Bell and Barnosky (2000), and chapters 2, 7, and 23. (Modified from Wood and Barnosky [1994] and Bell and Barnosky [2000].)

Results

The statistical analysis of isotopic values was conducted on two different scales. The first compared isotopic values between all sampled stratigraphic levels within the Pit, irrespective of whether the level had been assigned to a glacial or an interglacial by evidence independent of isotopes (Wood and Barnosky, 1994; Barnosky et al., 1996; Bell and Barnosky, 2000; Barnosky et al., chapter 23). The other comparison lumped samples into interglacial levels 1–3, glacial levels 4 and 5, and interglacial levels 6 and 7. The expectation was that more differences might be evident between major climatic episodes than within them.

Statistical Analysis by Stratigraphic Level

The carbon and oxygen isotope values for each specimen sampled are presented in table 24.1. Mean stable oxygen isotope values for each level are as follows: level 1, –0.4‰; level 2, 2.2‰; level 3, 1.4‰; level 4, 0.9‰; level 5, 0.4‰; level 6, 4.3‰; level 7, –0.3‰ (figure 24.2). The ANOVA and Tukey

TABLE 24.1

Oxygen and Carbon Isotope Values for *Marmota* Tooth Enamel

Sample Number	*UCMP Specimen Number*	*Level*	*Tooth Sampled*	$\delta^{18}O$	$\delta^{13}C$
RSF 001	181095	1	LM1 or LM2	–0.1‰	–11.8‰
RSF 002	181120	1	Rm1 or Rm2	–0.1‰	–11.7‰
RSF 003	181117	1	Rm1 or Rm2	–0.1‰	–12.5‰
RSF 004	181180	2	Lm1 or Lm2	1.5‰	–11.8‰
RSF 005	181176	2	Rp4	5.0‰	–10.3‰
RSF 006	181194	2	LM3	0.1‰	–11.4‰
RSF 007	181216	3	LP4	1.6‰	–10.6‰
RSF 008	93173	3	Lm3	2.1‰	–12.3‰
RSF 009	181304	3	RP4	0.7‰	–10.4‰
RSF 010	181476	4	RP4	–0.6‰	–10.4‰
RSF 011	181403	4	Lm1 or Lm2	0.1‰	–12.0‰
RSF 012	181357	4	LP4	3.3‰	–9.4‰
RSF 013	181764	5	Lp4	2.8‰	–9.8‰
RSF 014	181723	5	LP4	–0.5‰	–10.0‰
RSF 015	181866	5	LP4	–1.1‰	–11.2‰
RSF 017	182040	6	RP4	6.3‰	–10.5‰
RSF 018	182058	6	RP4	2.3‰	–10.3‰
RSF 019	182088	7	Lp4	3.2‰	–10.3‰
RSF 020	182086	7	LP4	–1.1‰	–9.3‰
RSF 021	182159	7	Rp4	–3.1‰	–8.1%

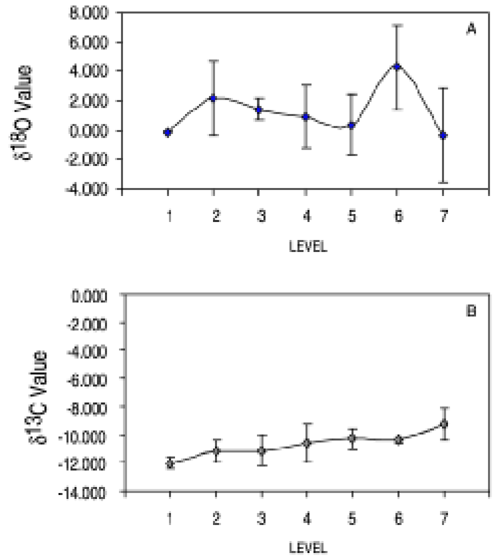

FIGURE 24.2 Oxygen (A) and carbon (B) isotope values obtained from the different levels within the Pit. Error bars represent one standard deviation from the mean.

HSD tests showed no significant differences in mean oxygen isotope values between levels.

The means for stable carbon isotope values for each level are as follows: level 1, –12.0‰; level 2, –11.2‰; level 3, –11.1‰; level 4, –10.6‰; level 5, –10.3‰; level 6, –10.4‰; level 7, –9.2‰ (figure 24.2). ANOVA suggested no significant differences between levels, but the Tukey HSD test showed a significant difference in the carbon isotope values between level 1 and level 7.

Statistical Analysis between Glacial Stages and Interglacial Stages

Mean stable oxygen isotope values for the glacial and interglacial stages are as follows: interglacial levels 1–3, 1.1‰; glacial levels 4 and 5, 0.7‰; interglacial levels 6 and 7, 1.5‰ (figure 24.3). ANOVA and Tukey HSD tests showed no significant differences in the oxygen isotope values between the glacial and interglacial stages.

Mean stable carbon isotope values for the glacial and interglacial stages are as follows: interglacial levels 1–3, –11.5‰; glacial levels 4 and 5, –10.5‰; interglacial levels 6 and 7, –9.7‰ (figure 24.3). ANOVA suggested a significant difference in carbon isotope values between the glacial and interglacial stages ($p < 0.01$). The Tukey HSD test showed a significant

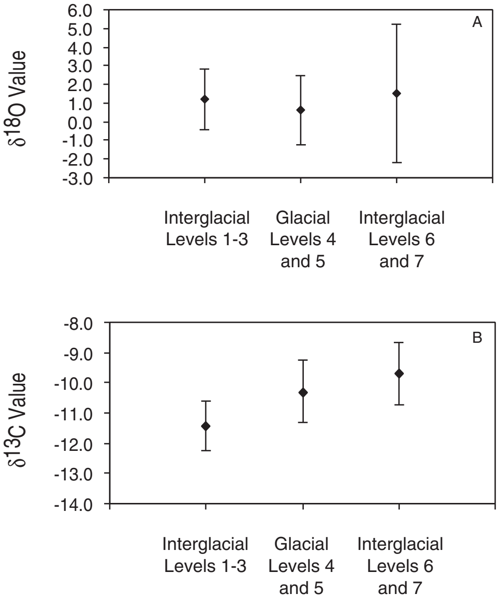

FIGURE 24.3 Oxygen (A) and carbon (B) isotope values from glacial or interglacial strata within the Pit. Error bars represent one standard deviation from the mean.

difference in carbon isotope values between interglacial levels 1–3 and interglacial levels 6 and 7.

Discussion

Possible influences on the isotopic value of marmot tooth enamel might include changes in the isotopic value of source waters, individual metabolic differences, and percentage of water obtained from plant material. Changes in the isotopic value of precipitation have been noted to occur in the Rocky Mountain region, and this observation suggests that the dominant source of precipitation for this area arises from either the Pacific Ocean or the Gulf of Mexico, depending on atmospheric circulation, which changed between glacials and interglacials (Amundson et al., 1996).

It is impossible to correlate the *Marmota* enamel δ^{18}O values with the marine oxygen isotope record because no significant differences were observed in the oxygen isotope values between either stratigraphic levels or glacial-interglacial stages. Rogers and Wang (2002) used isotopic data from *Thomomys* and *Geomys* (pocket gophers) incisors to examine the correlation of similarly aged deposits at Hansen Bluff, Colorado and SAM Cave, northern New Mexico, with the marine oxygen isotope record. Although direct correlation with the marine record was not possible with the Porcupine Cave *Marmota* data, it is of interest that the general trends shown in figure 24.2—highest δ^{18}O values in level 6, little change in levels 5–2, and a slight drop in level 1—would not contradict the pattern noted for the pocket gopher teeth from Hansen Bluff–SAM Cave for the interval 780–900 Ka ago.

Assuming small sample size is not the issue, a possible reason for the constancy of oxygen isotope values through all levels and glacial-interglacial stages might be that there was no significant shift in the meteoric water isotope values during the time sampled. Another possibility is that marmots' life history, specifically hibernation, may influence the isotopic value of their tooth enamel. Munson (1984) has shown that the eruption of the fully formed fourth premolar and third molar of marmots from eastern North America occurs in May, soon after the animals emerge from hibernation. This finding would suggest that these teeth were forming and mineralizing late in the hibernation period. The isotopic values displayed by the teeth may not therefore represent values related to differences in the isotopic value of meteoric water, since body water probably equilibrated to a different value from that of meteoric water ingested before hibernation. The isotopic signal may therefore be overprinted by differences in metabolism, body temperature, or both among individuals during hibernation.

Using adult teeth, as described in the Materials and Methods section, avoided the problems that would be introduced by comparing juveniles and adults. However, given the small sample sizes, it is impossible to know whether the apparent isotopic values vary between levels as a result of comparing males to females, large individuals to smaller ones, or pregnant females to nonpregnant individuals. Such gender and size differences could conceivably have an effect on the metabolism and ultimately the isotopic value of tooth enamel. If an individual marmot obtained a significant amount of water from plant leaves, seeds, or fruits, it might display different enamel isotope values than an individual that drank a significant amount (Sponheimer and Lee-Thorp, 1999, 2001; Helliker and Ehleringer, 2000).

The δ^{13}C values displayed by *Marmota* teeth at all stratigraphic levels suggest a C_3-dominated diet because mean values at all levels were more negative than –8.0‰. This result is consistent with the modern flora around Porcupine Cave, with a flora growing at 2900 m elevation elsewhere (Sage et al., 1999), and with expected conditions in the Pleistocene. The significant differences observed between levels 1 and 7, or between interglacial levels 1–3 and interglacial levels 6 and 7, may indicate a gradual shift to a flora with a more positive C_3 photosynthetic pathway, a shift to a more open habitat where CO_2 was not recycled, or inconsistent local CO_2 levels in the atmosphere, which would cause photosynthetic changes in the flora. Without further knowledge of the flora over the time period studied, through study of either macro- or microbotanical data, an unambiguous choice between these alternative explanations is impossible. Other possibilities that would cause a significant shift in δ^{13}C values are summarized by Ehleringer et al. (1991), Ehleringer and Monson (1993), Heaton (1999), Sage and Monson (1999), and references therein. The carbon isotope values in *Marmota* tooth enamel, similar to the oxygen isotope values, show no correlation with glacial-interglacial cycles per se. However, the carbon shift does parallel the overall climatic drying trend in the sequence and is compatible with the Hansen Bluff–SAM Cave data for the time between 780 and 900 Ka ago.

Conclusions

Oxygen isotope analysis of tooth enamel in *Marmota* showed no significant difference between levels within the Pit, or between glacial strata and interglacial strata. Therefore it was impossible to correlate the δ^{18}O values from fossil marmot enamel with the marine oxygen isotope record. Hibernation characterized by a lower metabolism and little ingestion of water for most of the year may introduce metabolic effects that mask any isotopic differences that in other taxa might hold a climate signal.

Analysis of δ^{13}C values suggests that the marmots from Porcupine Cave were feeding on a C_3 diet. This is consistent with the modern flora growing around Porcupine cave, and generally with flora expected at the cave's current elevation. The δ^{13}C values do not appear to correlate with any glacial-interglacial cycling. Significant differences between levels 1 and 7, and between interglacial levels 1–3 and interglacial levels 6 and 7, suggest a change in the dominant flora over the time period studied. At the same time, other evidence indicates an overall drying trend (Barnosky et al., chapter 23). The δ^{13}C values show no cycling or apparent correlation with the marine carbon isotope record.

Although it was impossible to correlate strata within the Pit with the marine isotope record using *Marmota* tooth enamel isotope values, the technique may still have potential for this site. The significance of the isotopic stability at the site requires further analysis focusing on animals that are obligate drinkers and do not hibernate, or perhaps by microsampling marmot incisors, in which a hibernation line is visible and would facilitate sampling parts of the tooth that were growing when the animal was not hibernating (Goodwin and Gonzalez, 2001).

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TWENTY-FIVE

Assessing the Effect of Middle Pleistocene Climate Change on *Marmota* Populations from the Pit Locality

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This chapter uses fossil dental remains of marmots (genus *Marmota*) to examine the effects of climate changes on populations of a taxon whose modern ecology, demography, physiology, and systematics have been extensively studied (e.g., Armitage and Downhower, 1974; Svendsen, 1974; Kilgore and Armitage, 1978; Frase and Hoffmann, 1980; Schwartz and Armitage, 1980; Webb, 1981; Barash, 1989; Melcher et al., 1990; Ferron, 1996; Kwiecinski, 1998; Schwartz et al., 1998; Steppan et al., 1999; Inouye et al., 2000; Polly, 2003). The fossil sample comes from the top seven levels of the Pit sequence (UCMP V93173). Marmot specimens from level 8 were not available for inclusion in this study and are unknown from lower levels. Information about the climatic intervals represented in the Pit sequence is presented in chapters 7 and 23. Level 7 is interpreted as a moist time within an interglacial and level 6 as a drier time within the same interglacial. Levels 5 and 4 are thought to represent a cool glacial period that was on average drier than the preceding interglacial. Levels 3–1 represent an interglacial that was the driest, warmest interval of the entire record. The whole sequence represents successive slices of time from around 780 Ka ago at the top to around 900 Ka ago at the bottom (see figure 7.5).

It is unclear which species of marmot is fossilized at Porcupine Cave. Polly (2003) subjected the lower third molars of the Porcupine Cave specimens, *Marmota flaviventris, M. monax, M. caligata, M. vancouverensis,* and *M. broweri,* to morphometric analyses and used the results to interpret systematic and phylogeographic patterns. He found that the Porcupine Cave fossils nested within the *M. monax* clade. On that basis the Porcupine Cave specimens seem more closely related to *M. monax* than to *M. flaviventris.* However, the Porcupine Cave specimens differed morphologically from crown-group *M. monax* to the extent that referral to the extant species is not certain. Until further work can be done to resolve the species assignment, in this book the marmots are conservatively referred to as *Marmota* sp. For the purposes of analyzing the population-level variation through the Porcupine Cave sequence, it does not make much difference which species is represented. Both *M. monax* and *M. flaviventris* (and other marmot species) share similar life history traits, namely hibernating from early September to late spring (in colder climates) or early spring (in warmer climates) (Barash, 1989).

Relevant Life History Traits

Most work on marmot ecology has been carried out on *M. flaviventris,* the yellow-bellied marmot, which is the species inhabiting the Porcupine Cave region today. Its geographic range is confined mainly to mountainous regions of the western United States. *Marmota flaviventris* inhabits rocky meadows and vegetated talus slopes, typically in subalpine or alpine regions, though members of the species range into low and middle elevations and even semidesert areas (Svendsen, 1974; Frase and Hoffmann, 1980). Yellow-bellied marmots have a semifossorial lifestyle. They spend most of the year hibernating because winter temperatures through their range are very cold, with monthly means in the Porcupine Cave area between 0° and –2°C in September and May, respectively, down to about –16°C in January (Cooper, chapter 3). Extreme winter temperatures are even colder, down to about –48°C. Near Gothic, Colorado (approximately 100 km west of Porcupine Cave and at a similar elevation), yellow-bellied marmots spend about 80% of their lives in burrows, with about 60% of that time concentrated in hibernation from early September to May (Svendsen, 1974; Frase and Hoffmann, 1980). Burrows are characterized by a relatively constant temperature, which deviates little from 10°C from June to October (Kilgore and Armitage, 1978), and probably little from that value during the rest of the year (Svendsen, 1974). Kilgore and Armitage (1978) reported burrow temperatures as low as 8.6°C, with mean temperatures of 9.3°C in late September and 9.1°C in early October. Availability of this thermally constant environment is apparently critical to marmots in both summer and winter; individuals of *M. flaviventris* have not been documented above ground when the temperature near ground level was less than 1.2°C or greater than 26.4°C. Near Gothic, Colorado, where these data were compiled, air temperatures rarely reach 25°C (Kilgore and Armitage, 1978).

The burrow temperatures in hibernacula are substantially lower than body temperature in an active marmot, which is minimally around 36°C (Kilgore and Armitage, 1978), and slightly below hibernating body temperature, which is about 11°C (Svendsen, 1974). Therefore, survival during winter reflects an interplay among fat reserves built up during the feeding season, metabolic rate, and burrow temperature. In *M. flaviventris,* metabolic rate lowers significantly during hibernation, dropping from 0.54 ml O_2/g per hour at 30°C to 0.03 ml O_2/g per hour when hibernating (Frase and Hoffmann, 1980). Thus the main variables for survival are fat reserves and burrow temperature. Falling on the wrong side of this balance during hibernation is suspected to be the leading cause of death in *M. flaviventris* (Armitage and Downhower, 1974; Frase and Hoffmann, 1980; Arnold and Psenner, 1990). Most studies suggest that winter kill in hibernacula affects all age classes equally (Armitage and Downhower, 1974; Frase and Hoffmann, 1980; Schwartz et al., 1998).

The amount of food per se seems not to be a limiting resource for yellow-bellied marmots (Kilgore and Armitage, 1978). They eat a wide variety of grasses, forbes, and succulents. Near Gothic, Colorado, marmot populations utilize only about 2–6.4% of the food energy available to them (Svendsen, 1974; Armitage and Downhower, 1974; Kilgore and Armitage, 1978). More critical to building up adequate fat reserves is the length of the season during which nutritious food is available, and to some extent when food becomes available in relation to emergence from hibernation. In general, the earlier the spring of the natal year, the greater the number of young that survive to become yearlings (Frase and Hoffmann, 1980). The feeding season maximally lasts from the time marmots emerge from hibernation in May, when they have lost about 50% of their body weight (Armitage et al., 1976), to the time they commence hibernation again in early September.

Functionally the feeding season is somewhat shorter, and dependent on a complex set of variables, including the amount of snow cover at emergence, spring and summer effective precipitation, and the timing of the first snow cover in fall. Inouye et al. (2000) predicted that warm spring air temperatures combined with high winter snowfalls would adversely affect marmot survival because animals emerge earlier in the spring (responding to warm temperatures) but before snow cover has disappeared to the extent that adequate vegetation is available to eat. They found that, in the Colorado Rocky Mountains, marmots are emerging from hibernation 38 days earlier than they were 23 years ago, presumably in response to warmer April air temperatures. At emergence time now there is 57 cm more snow on the ground than was the case 23 years ago. Armitage and Downhower (1974) suggested that the availability of food could be critical in the early part of the growing season not only because it affects the fat reserve balance, but also because limited food availability could result in fewer females becoming pregnant or carrying a litter to term. They noted that more young per female and more litters were produced when winters were short, began late, and ended early.

Burrow temperature is controlled by lodge construction, outside air temperatures, and amount of snow cover. Even when marmots have adequate fat, they still can fall prey to winter cold if their lodge is not properly built. Just before they initiate hibernation, marmots plug the access holes to their lodge. The plug insulates the lodge and keeps potential predators out, but it also limits the depth of the nesting chambers because an adequate supply of oxygen and the exhaust of exhaled carbon dioxide must be assured (Arnold and Psenner, 1990). If a plug collapses or is too porous, the temperature within the lodge will drop precipitously to a level that can freeze even the fattest of marmots; however, if it restricts air flow too much the entire colony can suffocate. During the snow-free months, changes in mean burrow temperature lag changes in air temperature by about one month. Burrow temperatures increase from about 9.0°C in June to 11.3°C in late August, then drop to 9.3°C in late September and to 9.1°C in early October (Kilgore and Armitage, 1978). Adequate snow cover is apparently required to insulate the burrows from extremely cold air temperatures during winter. Svendsen (1974) reported that, despite extremely cold winter temperatures near Gothic, Colorado (which fall to –40°C), where the snow pack was undisturbed the ground never froze. Hibernation burrows in that area were situated where snow accumulation was greatest, not where snow melted earliest. Greatest winter mortality occurred where snow accumulation was least and where snow melted earliest (Svendsen, 1974). Thus the link between winter precipitation and marmot survival is tight.

Because of the thermal constancy provided by burrows, adequate burrow sites have been cited as a limiting resource for marmot distribution (Anderson et al., 1976; Frase and Hoffmann, 1980). However, in areas occupied by marmot colonies, burrows outnumber residents. Either burrow sites do not limit population sizes in such colonies, or subtle aspects of burrow quality, rather than number of burrows, are the limiting factor (Armitage and Downhower, 1974). Lack of adequate burrow sites may limit sizes of populations in satellite sites.

Dispersal characteristics of *Marmota flaviventris* result in high gene flow. Yellow-bellied marmots live in colonies (polygynous groups composed of one or more males and their harems), or in satellite sites (containing "peripheral animal[s that] live near a colony, probably [have] sensory contact with members of the colony, but may have no direct social contacts") (Armitage and Downhower, 1974:1233; Svendsen, 1974). Transient animals can pass through colonies or satellite sites but do not remain for more than a few days. In the Gothic, Colorado, study sites, all adult colonial males and 41% of colonial females were recruited from outside the colony (Armitage and Downhower, 1974). Schwartz and Armitage

(1980:666) used such data to conclude that "the patchiness of suitable marmot habitat in the Rocky Mountains and the degree of temporal stability of colonies are conditions that favor genetic drift. However, the high rate of gene flow into colonies, the dispersal of most young, and the de facto avoidance of inbreeding indicate that this system actively retards the fixation of genetic variants."

Marmota monax is more widely distributed than *M. flaviventris,* ranging from as far southeast as Alabama and Georgia to as far northwest as Alaska; however, the range does not overlap with that of *M. flaviventris. M. monax* is not found in Colorado today, but Polly (2003) provided a plausible phylogeographic scenario that could put the species there during Porcupine Cave Pit time. The ecology of *Marmota monax* very much resembles that of *M. flaviventris,* but it differs in a few respects (Kwiecinski, 1998). Ferron (1996) noted that *M. monax* tends to hibernate singly, unlike most other species, and that, in the northern part of their range, they are less specialized than montane species of marmots. They lose more weight during hibernation than the montane species *M. marmota* (the alpine marmot of Europe). The hibernacula of *M. monax* typically provide better insulation than hibernacula of species such as *M. flaviventris* that live in mountainous areas. Body temperatures of *M. monax* (32–36°C) during active periods resemble those of *M. flaviventris,* but hibernating body temperatures may be lower in *M. monax* (3–8°C versus up to 11°C). *M. monax* typically emerges from hibernation in March or April, which is slightly earlier than is typical for *M. flaviventris.* In warmer parts of their range, emergence for both species is earlier than in colder parts of the range. As in *M. flaviventris,* emergence can occur before abundant vegetation is available to eat (Kwiecinski, 1998), and the length of the growing season and its timing relative to emergence are critical for building adequate fat reserves.

Expected Climatic Effects on Marmot Evolution

Given these considerations, climatic fluctuations manifested as changes in growing season and in amount and timing of snow cover would be expected to affect marmot survival and reproductive success, and therefore population-level evolution. This chapter accordingly examines whether the shifts in climate hypothesized in chapter 23 and by Rogers et al. (1985, 1992) and Wood and Barnosky (1994)—a probable transition from a relatively moist interglacial to a cool-dry glacial to a very warm-dry interglacial—were of sufficient magnitude to cause detectable change in marmot populations. In the absence of fossil preservation adequate to allow recovery of ancient DNA (Hadly et al., 1998; Hadly et al., 2003), interpretation of population-level evolution through long time spans must rely on morphologic criteria. For marmots (as for small mammals in general), the morphologic criteria are further restricted to dental traits, because teeth are the only fossils that provide adequate statistical samples. It is important to understand how the examined dental traits may or may not be affected by specific climatic parameters.

We examined traits that manifest at two different morphologic levels, which we recognize as discrete traits and integrated traits. Discrete traits are individual characters that may not have a clear functional significance unless combined with other characters. For example, tooth width might be expected to vary independently (within limits) of all other tooth measurements, as long as its variation did not critically affect the overall function of the tooth. In contrast, integrated traits are those that are built of two or more interacting discrete traits. For example, the overall shape of a tooth is defined by the interaction of length versus width, and it might be expected to have functional significance relating to jaw mechanics and the ability to process certain kinds of foods. In effect, discrete characters are those that theoretically should show broad variation within the "selective rubber band" discussed by Barnosky (1993), whereas integrated traits define how far the rubber band can stretch without breaking. Natural selection is the force that stretches the rubber band. Whether the rubber band stretches or not, therefore, depends on whether a specific selective force is available to pull on it. Put another way, the integrated trait is selectively significant if there is a selective force available to affect it, but is otherwise selectively neutral.

The discrete traits we focus on in this study include length and width of three different teeth: fourth upper premolar (P4), fourth lower premolar (p4), and third lower molar (m3). The integrated characters are tooth shape as defined by the ratio of length to width, and body size as reflected by log(area) of P4. We also regard Polly's (2003) morphometric measure of tooth shape as an integrated trait. Given that the discrete characters should vary randomly within a given selective rubber band, we expect to see no relationship between their morphologic change through time and climate change, because climatically induced natural selection should not affect them. Likewise, we expect no relationship to climate change in the integrated character of tooth shape in either our study or Polly's (2003). We regard tooth shape as selectively neutral for our purposes because the main selective force that would act upon it is related to food availability. Food is not a limiting resource for marmots, nor is it necessarily affected by climate, since the range of plants that marmots eat exists in a broad range of climatic zones. Discrete dental traits and tooth shape do vary somewhat between different populations of marmots, presumably because of random genetic variation. However, the random variation in these traits would be expected to be homogenized through time, given the high gene flow and the evolutionary model proposed for marmots by Schwartz and Armitage (1980).

On the other hand, a very clear selection potential exists for traits that allow more efficient retention of heat during hibernation. One such trait is body size; larger-bodied animals more efficiently retain heat because of the relationship between surface area and volume. Thus during climatic intervals when mean hibernaculum temperature decreased even slightly during critical parts of the year (most likely because of the depth of snow, the timing of snowfall, or both), larger mean body sizes might be favored. Alternatively, changes in body size might reflect a phenotypic response to changes in the length or timing of the growing season. In either case, we expect body size to be selectively significant, and to see a response in the integrated trait log(area) of P4, since that trait is highly correlated with body size (see Materials and Methods).

Selection is not the only way that climate changes can affect population-level evolution. Theoretically climate change may enhance or limit chances of immigration from other populations and thereby increase gene flow in some cases, and lead to isolation and genetic drift in others (Vrba, 1995). Thus clustering of morphologic change at climatic events might be expected even in discrete traits, in our case the suite of dental traits previously noted. Given the normal high rates of gene flow among marmot colonies, we do not expect this effect for discrete characters in marmots, but we nevertheless interpreted our results with the possibility in mind.

Materials and Methods

To test these theoretical expectations with the Porcupine Cave data, we examined such features as mean, variance, and shapes of frequency distributions of the analyzed morphologic traits in the temporally superposed samples. We utilized museum collections from three institutions: the Carnegie Museum (CM), the University of California Museum of Paleontology (UCMP), and the University of California Museum of Vertebrate Zoology (MVZ). In an attempt to determine the species represented at Porcupine Cave, the fossil marmot teeth listed in appendix 25.1 were compared to representative MVZ collections of modern species: *M. monax,* including *M. monax bunkeri* (MVZ 7964)*, M. monax canadensis* (MVZ 77810, 77811)*, M. monax petrensis* (MVZ 32759, 32965, 32966, 47776), *M. monax monax* (MVZ 6349, 81418), *M. monax preblorum* (MVZ 81988, 81989), and *M. monax rufescens* (MVZ 96793); *M. olympus* (MVZ 84153); *M. vancouverensis* (MVZ 12091, 12092); *M. caligata* (MVZ 961, 27518, 27526, 114117); and *M. flaviventris* (MVZ 27517–27520, 27522–27526, 25533, 27551).

The Porcupine Cave specimens in all levels could be distinguished from most of the species based primarily on the size and morphology of the m3s, but could not be confidently differentiated from either *M. monax* or *M. flaviventris* using qualitative criteria. Dental specimens of the modern *Marmota flaviventris* could not be reliably separated from those of modern *M. monax.* Polly (2003) used a different set of comparative material and suggested that qualitatively as well as quantitatively the Porcupine Cave specimens resembled modern *M. monax* more than *M. flaviventris* in two traits: (1) a less pronounced curve on the mesial margin of the crown just buccal to the protocone, and (2) a relatively larger distal than medial lobe on the buccal side of the crown.

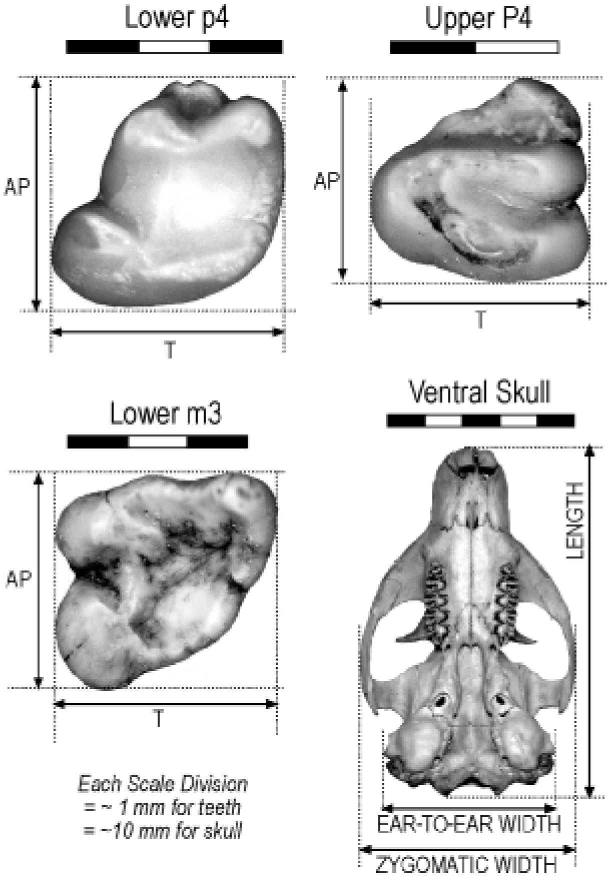

FIGURE 25.1 Tooth terminology and measurements discussed in text and tables 25.1–25.3. Teeth from the left side are illustrated. Lower p4: UCMP 181108 from square 1, level 1. Upper P4: UCMP 173077 from square 1, level 2. Lower m3: UCMP 181183, from square 1, level 2. Ventral skull: MVZ 86954, *Marmota flaviventris avara,* from Idaho County, Idaho.

Lengths and widths of m3s, p4s, and P4s of the fossil specimens of *Marmota* were determined by measuring the distances illustrated in figure 25.1 at 10× magnification through a Wild M8 binocular microscope. In addition to these six measurements, four other quantitative features were calculated: the ratio of length to width in m3, p4, and P4, and the log(area) of P4. Henceforth in this chapter, width or transverse measurements are abbreviated T, and length or anterior-posterior measurements as AP. Table 25.1 presents summary statistics.

Differences among stratigraphic levels for each tooth dimension were evaluated using both qualitative and quantitative methodologies. The qualitative features assessed were the position of cusps, gross size of cusps, and degree of hypsodonty. Because these features were found to be indistinguishable between levels, further analyses concentrated on the quantitative aspects of the teeth.

Each dental measurement was statistically analyzed using a single-factor analysis of variance (ANOVA). Because ANOVAs require the data to be normally distributed, the distribution of each variable was evaluated using normal probability plots. Deviations from normality were generally small, and those

TABLE 25.1

Summary Statistics for Tooth Measurements in *Marmota*

Tooth and Measurement	Level						
	1	*2*	*3*	*4*	*5*	*6*	*7*
Upper P4 T	3.10 ± 0.257 ($N = 9$)	3.08 ± 0.373 ($N = 8$)	3.21 ± 0.145 ($N = 10$)	3.13 ± 0.243 ($N = 37$)	2.96 ± 0.274 ($N = 20$)	3.08 ± 0.122 ($N = 8$)	3.04 ± 0.152 ($N = 5$)
Upper P4 AP	2.71 ± 0.270 ($N = 9$)	2.90 ± 0.281 ($N = 8$)	2.98 ± 0.253 ($N = 10$)	2.80 ± 0.221 ($N = 37$)	2.83 ± 0.239 ($N = 20$)	2.89 ± 0.195 ($N = 8$)	2.86 ± 0.152 ($N = 5$)
Upper P4 AP/T	0.88 ± 0.004 ($N = 9$)	0.95 ± 0.003 ($N = 8$)	0.93 ± 0.004 ($N = 10$)	0.90 ± 0.003 ($N = 37$)	0.96 ± 0.015 ($N = 20$)	0.94 ± 0.002 ($N = 8$)	0.94 ± 0.002 ($N = 5$)
Lower p4 T	3.18 ± 0.341 ($N = 4$)	3.39 ± 0.167 ($N = 7$)	3.35 ± 0.472 ($N = 6$)	3.13 ± 0.285 ($N = 37$)	3.13 ± 0.310 ($N = 16$)	2.92 ± 0.508 ($N = 6$)	3.30 ± 0.100 ($N = 6$)
Lower p4 AP	3.13 ± 0.330 ($N = 4$)	3.29 ± 0.134 ($N = 7$)	3.10 ± 0.352 ($N = 6$)	3.05 ± 0.264 ($N = 37$)	3.08 ± 0.228 ($N = 16$)	2.83 ± 0.476 ($N = 6$)	3.13 ± 0.055 ($N = 6$)
Lower p4 AP/T	0.98 ± 0.001 ($N = 4$)	0.97 ± 0.002 ($N = 7$)	0.93 ± 0.008 ($N = 6$)	0.98 ± 0.006 ($N = 37$)	0.99 ± 0.004 ($N = 16$)	0.97 ± 0.000 ($N = 6$)	0.95 ± 0.001 ($N = 6$)
Lower m3 T	—	3.74 ± 0.224 ($N = 11$)	3.64 ± 0.378 ($N = 8$)	3.74 ± 0.217 ($N = 54$)	3.70 ± 0.276 ($N = 31$)	3.71 ± 0.311 ($N = 13$)	3.54 ± 0.239 ($N = 10$)
Lower m3 AP	—	3.06 ± 0.138 ($N = 11$)	2.99 ± 0.155 ($N = 8$)	3.01 ± 0.221 ($N = 52$)	3.01 ± 0.130 ($N = 29$)	2.97 ± 0.167 ($N = 11$)	2.89 ± 0.241 ($N = 8$)
Lower m3 AP/T	—	0.82 ± 0.004 ($N = 11$)	0.83 ± 0.011 ($N = 8$)	0.81 ± 0.004 ($N = 52$)	0.82 ± 0.0021 ($N = 29$)	0.80 ± 0.003 ($N = 11$)	0.82 ± 0.001 ($N = 8$)

NOTES: Measurements are in millimeters. Measurements are mean ± standard deviation.

specimens (one M3 and one P4) that were identified as extreme outliers were reevaluated. In addition, ANOVAs require the homogeneity of variances, which was examined using Levene's tests. Because of a large number of violations of this assumption, nonparametric Kruskal-Wallis ANOVAs by ranks were also performed. Because the results of these nonparametric tests were identical to those of the parametric ANOVAs, only the parametric ANOVA results are reported (table 25.2). After the ANOVAs had been carried out, post-hoc comparisons of each stratigraphic level for each measurement were completed to identify which levels were significantly different from each other. Because a large number of comparisons were made for each dental dimension (21 for a seven-level comparison), Tukey honest significant difference (HSD) tests (instead of t-tests or Fisher's least significant difference tests) were performed. All statistical analyses were carried out using Statistica 5.1h (StatSoft, Tulsa, Oklahoma).

The log(area) of P4 was used as a gauge for body size. Log(area) of m1 is generally used to predict body size in mammals, but m1 is not distinguishable from m2 in sciurids. P4 can be reliably identified and made up the largest sample of an individual tooth in our data set. Area was calculated as T × AP. To verify that the P4 area is a reliable predictor of body size for our purposes, we regressed measurements of P4 against skull length for 11 specimens of modern *M. flaviventris,* which yielded r values of 0.66, 0.70, and 0.84 for T, AP, and log(area), respectively (figures 25.1, 25.2; table 25.3). In turn, skull length in rodents is typically correlated with body size.

TABLE 25.2

ANOVA p-Values for Each
Dental Dimension in Marmot Teeth

Tooth	*Measurement*	p-*Value*
P4	T	0.180
	AP	0.265
	AP/T	0.010*
	log(area)	0.389
p4	T	0.093
	AP	0.153
	AP/T	0.657
m3	T	0.376
	AP	0.502
	AP/T	0.850

NOTE: See text for dental abbreviations.

* $p < 0.05$.

In addition to the statistical analyses, frequency distributions and graphs of the mean and variance of each measurement for each stratigraphic level were evaluated to identify any patterns in tooth size through time. We looked for patterns consistent with directional, stabilizing, or disruptive

TABLE 25.3

Measurements of Modern Marmot Teeth and Skulls from MVZ Collections

MVZ Specimen Number	*AP*	*T*	*log(area)*	*Ear-to-Ear Width*	*Zygomatic Width*	*Skull Length*	*Sex*
27518	2.1	2.0	0.623249	30.7	40.0	59.4	M
27526	2.1	1.9	0.600973	40.7	31.4	60.6	F
27525	2.2	2.1	0.664642	31.2	40.5	63.2	M
25533	2.8	3.0	0.924279	37.4	49.0	71.5	F
27517	2	2.0	0.60206	29.5	37.2	54.9	F
27519	2.3	2.1	0.683947	30.9	39.0	57.6	F
27520	2.6	3.0	0.892095	39.0	52.1	74.8	F
27551	2.5	2.6	0.812913	36.7	48.9	71.3	F
27522	2.6	2.6	0.829947	42.5	53.0	82.5	M
27523	2.6	2.6	0.829947	35.7	48.8	71.0	F
27524	2.4	2.5	0.778151	34.8	45.2	70.0	F

NOTES: See figure 25.2 for illustration of measurements. Area = AP × T.

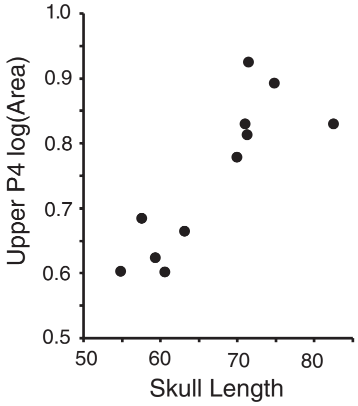

FIGURE 25.2 Log of the area (AP × T) of the upper P4 plotted as a function of skull length. See table 25.3 for measurements.

selection (Skelton, 1993; Starr, 1999), or evidence for immigration events, that coincided with independent evidence for climate change as inferred from the sediments. We also tried to determine whether changes in various dental traits were linked to or independent of one another. All graphs were drawn using Microsoft Excel 2001 and Statview 5.0 (SAS Institute, Inc., Cary, North Carolina).

Results and Discussion

Measurements are summarized in table 25.1 and graphed in figures 25.3–25.6. Results of the ANOVAs (table 25.2) and analysis of the graphs (figures 25.3–25.6) indicate that the size of marmot teeth has changed little through time. Only one variable (the ratio AP/T for the P4) displayed a significant *p*-value ($p < 0.010$). However, post-hoc comparisons for this dimension, as well as all others, revealed no significant differences

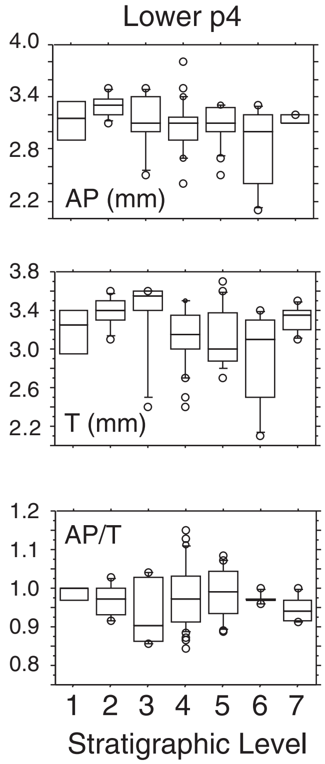

FIGURE 25.3 Box plots comparing the measurements of lower p4 across the seven stratigraphic levels. The bar inside the box shows the median; the lower boundary of the box shows the 25th percentile (i.e., 25% of the measurements are smaller than this value); the upper boundary shows the 75th percentile of the variable (i.e., 75% of the measurements are smaller). The lower extension shows the 10th percentile and the upper extension shows the 90th percentile. Values below the 10th and above the 90th percentile are plotted as points. The youngest stratigraphic level (1) is at the left, the oldest (7) at the right. *Abbreviations:* AP, anterior-posterior measurement; T, transverse width measurement.

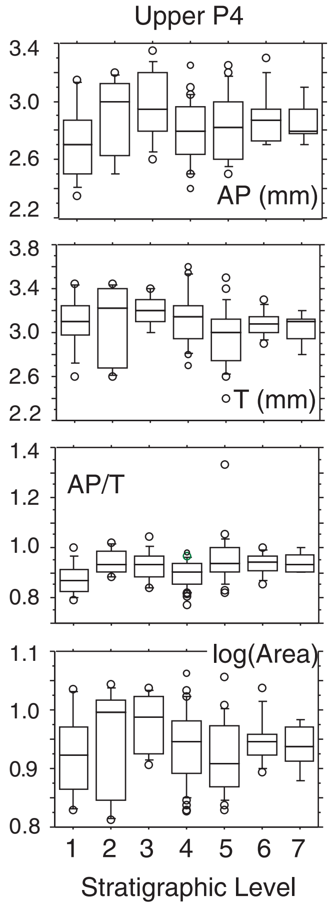

FIGURE 25.4 Box plots comparing the measurements of upper P4 across the seven stratigraphic levels. The log(area) is the log of the AP × T measurements. See figure 25.3 caption for additional explanation.

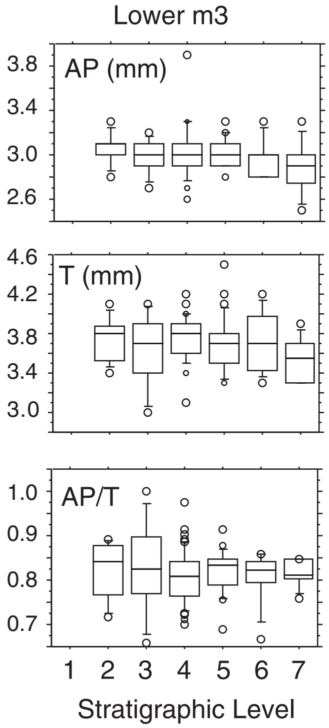

FIGURE 25.5 Box plots comparing the measurements of lower m3 across the seven stratigraphic levels. See figure 25.3 caption for additional explanation.

between any two stratigraphic levels. The lack of significant differences in dimensions of P4 suggests lack of significant differences in body size as well (figures 25.4, 25.6).

Correspondence between changes in analyzed traits, teeth, and independent indicators of climate change is not obvious. These results do not support a morphologic response to climate change. However, it is interesting that some bimodality begins to characterize the frequency distribution of P4 log(area) at the most pronounced climatic transition in the sequence, from level 4 (glacial) to level 3 (dry interglacial) (figure 25.6). This also corresponds to decreasing abundance of marmot specimens relative to those of other ground-dwelling squirrels *(Cynomys* and *Spermophilus)* (figure 25.6). Because P4 log(area) is correlated with body size (figure 25.2), and the relative abundance of marmot fossil specimens probably correlates with the relative abundance of marmots on the landscape (Hadly, 1999), it is tempting to speculate that the glacial-interglacial transition decreased marmot population density and affected body size. However, there are no statistically significant differences between the levels involved. Whether this in part reflects the small sample sizes remains to be seen. The differences in shapes of frequency distributions from level to level illustrated in figure 25.6 are among the most pronounced observed in this study. Therefore the analysis does not provide robust support for these population-level traits responding to disruptive, directional, or stabilizing selection. The very slight changes in mean, none of which is statistically significant, are consistent with a model of random fluctuation of traits in local populations being swamped by gene flow through time.

Polly (2003) also found little correlation between the shape of the m3 and climatic events, despite morphologic differences between levels that were greater than would be expected by chance alone. He concluded that the morphologic changes he observed were consistent more with in situ evolution operating independent of climate change than with immigration events.

Conclusions

Detailed analysis of dental traits of marmots suggests very little, if any, net change at the population level in the examined dental traits through the time represented by the Porcupine Cave Pit sequence. Polly's (2003) morphometric analysis of m3 shape yielded the same conclusion. Our data hint that a decrease in marmot population density may have accompa-

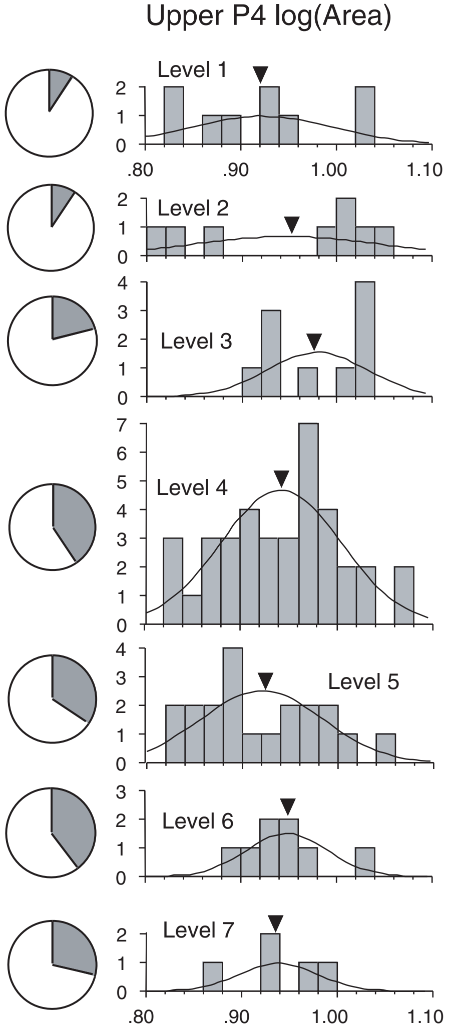

FIGURE 25.6 Frequency distributions by level for log(area) of upper P4. The theoretical normal distribution that would fit the observations is shown by a line. Arrows show mean at each level. None of the differences in mean or variance is statistically significant. Pie diagrams at left show the percentage of marmot specimens (shaded) compared to those of other ground-dwelling squirrels *(Cynomys* and *Spermophilus).* The percentages of marmot specimens in levels 1–7 are 9, 9, 21, 41, 34, 40, and 29%, respectively.

nied a transition from a glacial to an interglacial and had some effect on body size, but the evidence for even this morphologic change is not compelling. The data suggest that climate changes on the order of those that characterize the Porcupine Cave record do not perturb evolution of marmots outside the bounds inferred from studies of modern populations. Clearly aspects of marmot life history are influenced by climate change, as has been demonstrated by Inouye et al. (2000), but the morphologic results of these influences seem masked or counteracted by changes that are random with respect to climate and that may or may not have a selective basis elsewhere.

The general decoupling we observed between population-level evolution and climate over more than 100,000 years probably arose because marmots are confined to certain microhabitats; in the case of *M. flaviventris,* the microhabitats are meadows with large rocks and hibernation chambers characterized by a restricted thermal environment (Melcher et al., 1990). These sorts of habitats would have been moderately abundant throughout the time represented by the Porcupine Cave Pit sequence, as they are in the area today, and were also presumably utilized by the extinct populations, whatever their species may have been. Moreover, the life history strategy of marmots leads to dispersal and high gene flow no matter what the climate. Thus, even in the face of climate change, the populations existed within an effectively stable environment, and dispersal rates were little affected because the base level of dispersal is so high. Climatically critical aspects of marmot habitats include hibernaculum temperatures; fall, winter, and spring snow cover versus temperature regimes; length of growing season; and feeding season (spring-summer) temperature and precipitation. Should these vary beyond critical limits, local extinction rather than evolution would be the likely result.

The fact that marmots have persisted in the South Park ecosystem since Porcupine Cave time (more than 780 Ka ago), with only minor, statistically insignificant within-population morphologic changes at glacial-interglacial transitions, indicates a remarkable persistence of their habitat and stability of their niche in the ecosystem. Therefore any evidence of their decline or increasing morphologic change could be a reliable indicator of human-induced global change.

Appendix 25.1. Listing of Analyzed *Marmota* Specimens

All are from Porcupine Cave Pit locality, UCMP V93173. The following specimens from level 8 were examined in 1991 at UCMP and reliably recorded in notes of A. D. Barnosky but have since been lost: five p4, seven P4, two m3, five M3. *Abbreviations:* G, grid (= square in figure 23.1, and refers to the square within the excavation grid from which the specimen came); L, level.

P4

G1L1—CM 65237–65239, 65241; UCMP 181089–181093. *G1L2*—CM 65776, 65778, 65797, 65799; UCMP 173077, 181138–181140, 181152. *G1L3*—UCMP 181215, 181217–181220, 181222, 181223. *G5/6L3*—UCMP 181302, 181303, 181305. *G1L4*—UCMP 181328, 181331. *G2L4*—UCMP 181354–181356, 181360–181363. *G3L4*—UCMP 181442–181447, 181449, 181456, 181458–181461, 181463–181475, 181477–181480. *G2L5*—UCMP 181724–181735. *G3L5*—UCMP 181795–181797. *G6L5*—UCMP 181825–181828. *G7L5*—UCMP 181864, 181865, 181867, 181868, 181870, 181871. *G2L6*—UCMP 181924, 181927, 181928. *G3L6*—UCMP 181957, 181958. *G6L6*—UCMP 182038. *G7L6*—UCMP 182055–182057. *G2L7*—UCMP 182091. *G3L7*—UCMP 182119. *G6L7*—UCMP 182135. *G7L6*—UCMP 182059.

Acknowledgments

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p4

G1L1—UCMP 65774, 65795, 181088, 181107–181109. *G7L2*—UCMP 181199–181202. *G1L2*—UCMP 181175. *G1L3*—UCMP 181270–181273. *G1L4*—UCMP 181339. *G2L4*—UCMP 181049, 181353, 181359, 181395–181397. *G3L4*—UCMP 181615–181643. *G2L5*—UCMP 181765–181767, 181770. *G3L5*—UCMP 181810–181812, 181814–181816. *G6L5*—UCMP 181848, 181849. *G7L5*—UCMP 181902, 181903. *G2L6*—UCMP 181901, 181939, 181941–181944. *G6L6*—UCMP 182037. *G7L6*—UCMP 182073. *G6L7*—UCMP 173078. *G7L7*—UCMP 182158, 182160.

m3

G1L1—CM 65250, 65251, 65789, 66368. *G1L2*—CM 66473, 65021, 65790, 65810, 65811; UCMP 180985–180989, 181183, 181184, 181186. *G1L3*—UCMP 180990–180994, 181292, 181293, 181295. *G1L4*—UCMP 180995, 180996. *G2L4*—UCMP 180997–181009. *G3L4*—UCMP 181010–181037, 181705–181717. *G1L5*—UCMP 181793. *G2L5*—UCMP 181038–181042, 181781–181783. *G3L5*—UCMP 181043–181048. *G6L5*—UCMP 181049, 181050. *G7L5*—UCMP 181051–181057. *G2L6*—UCMP 181952. *G3L6*—UCMP 181058–181063. *G6L6*—UCMP 181064–181067. *G2L7*—UCMP 181102. *G3L7*—UCMP 181068–181070. *G7L7*—UCMP 181072, 181073, 182161.

TWENTY-SIX

Effect of Climate Change on Terrestrial Vertebrate Biodiversity

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Biodiversity means different things to different people, because measures of diversity can be applied at all levels of the biological hierarchy, ranging from genes to individuals, populations, species, genera, higher taxa, trophic and size levels, landscapes, ecosystems, and globally (Norton, 1987; Erlich, 1988; Wilson, 1988; Huston, 1994; Hughes et al., 1997; Lovejoy, 1997). The Porcupine Cave data are amenable to biodiversity analyses at several of these levels: populations, species, genera, families, orders, and trophic and size structure.

There are many reasons to expect that climate should influence biodiversity (MacDonald and Brown, 1992; Harte and Shaw, 1995; Brown et al., 1997; Kerr and Packer, 1998; Schneider and Root, 1998; Pounds et al., 1999; Brown et al., 2001; McCarty, 2001). For example, one of the clearest macroecological patterns on Earth is the increase in species richness with decreasing latitude (Brown, 1995). The underlying cause of the latitudinal gradient is not latitude itself. Rather the drivers are more likely the myriad of climatic differences that also correlate with latitude, as Huston (1994:29) specifies: sun angle, day length, seasonality, temperature means and extremes, rainfall amount and timing, frequency and timing of storms, and so on. Lending credence to the link between climate and patterns of species richness is the elevational gradient, whereby more species are found at lower elevations. Of course, factors other than climate are important in influencing species richness, among them ecological interactions, geological history, phylogenetic history, and geographic area considerations (Schluter and Riklefs, 1993; Rosenzweig, 1995; Brown and Lomolino, 1998; Barnosky et al., 2001). But few would argue that climate does not play a dominant role in determining which species can live where.

Correlations between characteristics of species geographic ranges, population density and distribution, and genetic structuring of populations (Brown and Maurer, 1989; Brown, 1995; Maurer, 1999; Hadly and Maurer, 2001) suggest that, just as climate influences the geographic range of a species, it also influences these lower levels of the biological hierarchy. Especially in the case of small mammals, species with the largest geographic ranges also tend to have the highest population densities and the most gene flow between populations (Maurer, 1999). Therefore a species whose geographic range contracts substantially owing to a change in climate might also be expected to decrease population densities and gene flow between populations (Sæther et al., 2000). Small, isolated populations in turn have lower genetic diversity than large, connected populations, and the smaller, less genetically diverse the population, the higher the chance of extinction.

Because population structure theoretically influences speciation potential, and climatic controls on species ranges feed back on population structure, climate-induced changes to species ranges may also play a part in controlling biodiversity at higher taxonomic levels. However, at the species level and higher, immigration, extirpation (leaving an area but remaining extant), and extinction of species become important in the diversity equation (Brown, 1995; Rosenzweig, 1995; Maurer, 1999). These processes too are heavily influenced by climate, a connection that led Vrba (1995) to develop models of faunal turnover in which climate is the main driver.

The many links between climate and distribution of modern species, plus the links between size of species ranges and population density and gene flow, suggest that through time changing climatic patterns should exert an influence on ecosystem structure and evolutionary patterns. Three research methodologies have dominated in examining the role of climate change on past ecosystems.

One methodology relies on compiling large databases and analyzing how such features as species diversity or trophic and size structure change through time. The faunal changes are then compared with independent climatic proxies (often the global oxygen isotope curve) to assess correlations with global climate change (Janis, 1993; Webb et al., 1995; FAUNMAP Working Group, 1996; Alroy, 1998; Alroy et al., 2000; Barnosky, 2001; Barnosky and Carrasco, 2002).

The second methodology emphasizes tracking changes through time in certain lineages and comparing those changes with either global or local proxies for climate (Janis, 1989; Van Valkenburgh and Janis, 1993; Vrba, 1993, 1995). These methods are extremely useful in assessing regional trends, but the scales are so broad-brush that the effect of a specific climate change at a specific place on a specific community or ecosystem can be obscured (Barnosky, 2001). Further complications arise when the global climate signal is used to assess a local or regional faunal response (Barnosky and Carrasco, 2002).

A third approach is to utilize stacked samples of fossils from a single geographic region, track the community changes indicated by the fossils through time, and compare those changes with independent local, regional, and global climate proxies. This approach has been used primarily with palynological data (Webb, 1992; Jackson and Overpeck, 2000 and references therein) and fossil mammal data from the late Pleistocene–Holocene transition (Graham, 1992; FAUNMAP Working Group, 1994 and references therein, 1996) and late Holocene (Hadly, 1996, 1997; Hadly et al., 1998). It allows a more refined view of how climate changes affect biota at one place through time.

The ideal study, of course, would use many such local sequences distributed widely over geographic space coupled with climate models to understand both regional and local biotic response. This ideal has been most closely realized with palynological data (COHMAP Members, 1988; Webb, 1992; Jackson and Overpeck, 2000) and to a lesser extent with mammal data (FAUNMAP Working Group, 1994, 1996) from the last 40,000 years or so. The geologically short temporal extent of the data has been an advantage in that modern ecosystems have in essence been traced backward in time, and most species are still extant, leading to more robust conclusions about ecosystem structure and function. The disadvantage is that the time scale is still short geologically, and it has therefore been difficult to assess whether the observed changes are signal or noise in the context of how ecosystems persist on the landscape over even a single glacial-interglacial cycle. The Porcupine Cave data allow the local-site approach to climate-ecosystem dynamics to be applied in deeper time, yet still with genera and in some cases with species that are extant. What do the data tell us about the effect of climate change, and especially global warming, on terrestrial mountain ecosystems?

Population-Level Diversity

Information on diversity of populations at Porcupine Cave is available for arvicoline (Barnosky, chapter 23; Barnosky and Bell, 2003) and sciurid (Goodwin, chapter 17; Barnosky et al., chapter 25; Goodwin, 2002; Polly, 2003) rodents, with most data available for *Lemmiscus curtatus, Marmota* sp., and *Spermophilus* cf. *S. elegans.*

In the case of *Lemmiscus curtatus,* populations can be characterized by the frequency of three different morphotypes of lower first molars: those with four triangles, five triangles, and six triangles. Only five- and six-triangle morphotypes are found in populations today. Barnosky and Bell (2003) demonstrated that the frequency of four- and five-triangle forms did not differ statistically between levels below level 2 in the Pit, but levels 2 and 1 showed highly significant differences as compared with lower levels. At level 2, the middle level of the uppermost interglacial, the frequency of five-triangle morphotypes increased significantly, and above that, in level 1, the first six-triangle forms appear (see figure 23.8). This pattern suggests a population-level response to the most extreme climate change indicated by the Pit sediments—increasing aridity in the uppermost interglacial—but not to the lesser-magnitude climatic fluctuations that took place earlier. Only during that interval were all three morphotypes present; the four-triangle morphotype subsequently became extinct. Thus, coincident with the most extreme global warming event recorded in the sediments, population-level diversity reached a maximum within this species. This maximum came at the same time population densities of *Lemmiscus* were highest, as indicated by the relative abundance diagrams (see figure 23.7).

Morphometric analyses of taxonomically significant dental characters in *Marmota* (Barnosky et al., chapter 25; Polly, 2003) suggests random variation of populations through the more than 100,000 years over which they occur as abundant fossils in the Pit sequence. The crash in population density (relative abundance) at the uppermost glacial-interglacial transition produced no statistically significant change in mean or variance of phenotypic attributes that characterized the respective populations, although a statistically insignificant shift toward larger body size was noted (Barnosky et al., chapter 25). Neither did molar shape change in a way that could be distinguished from random changes in lower levels (Polly, 2003).

Spermophilus cf. *S. elegans* (Goodwin, 2002) may have increased width in its lower fourth premolar coincident with the uppermost glacial-interglacial transition in the Pit, and in general the measurement is wider in interglacial levels than in glacial ones (see figure 17.3). Statistically significant differences in mean or variance were not detected, however, and population densities remained more or less constant throughout the record.

The life history strategy of *Lemmiscus* differs from that of *Marmota* and *Spermophilus.* The latter two species are active only during the late spring and summer months, spending the rest of the year hibernating in burrows that shelter them at mean temperatures considerably more hospitable than the outside temperature. *Lemmiscus,* in contrast, is active all year, in winter utilizing snow tunnels in which members of the species scatter vegetation cuttings (Fitzgerald et al., 1994). The lifestyles of the two sciurids buffer them somewhat from climate changes, whereas *Lemmiscus* is more directly exposed to the surface environments. It therefore is not surprising that the effects of climate on population-level diversity manifest differently in *Lemmiscus* (an increase in variability during the uppermost interglacial) than in the two sciurids (no change). All three taxa have in common the lack of statistically significant population-level change associated with the lower transition from a glacial (level 10) to an interglacial (levels 9–6). Likewise no changes characterize the shift from an interglacial (level 6) to a glacial (level 5), or the more minor environmental changes that apparently took place within each glacial and interglacial interval. This finding suggests that, even in species such as *Lemmiscus,* only climate changes that are out of the ordinary stimulate population-level responses. In other words, population-level changes in diversity are not to be expected at all glacial-interglacial transitions, but only at those that are aberrant. This hypothesis is consistent with arguments presented by Bennett (1990, 1997), Dynesius and Jansson (2000), Barnosky (2001), Jansson and Dynesius (2002), and Barnosky and Bell (2003) that, in general, climate changes on the scale of those caused by orbital variations (so-called Milankovitch cycles) should not produce significant evolutionary change.

Three arvicoline species *(Allophaiomys pliocaenicus, Mimomys virginianus,* and *Phenacomys gryci)* reach their highest abundance in the lower interglacial (Pit levels 9–6); then abundance gradually decreases through the subsequent glacial (levels 5 and 4), ending in extinction by the beginning of the uppermost interglacial (see figure 23.7). This pattern is consistent with moister environmental conditions of the lower interglacial favoring the three species, and less favorable (drier) conditions during the glacial causing population densities to gradually dwindle until the species became extinct as the most arid phase ensued. In these cases, climate change appeared to decrease population density, and by inference genetic diversity, to the point of extinction.

Species-Level Diversity

Salient data on species-level diversity were presented in chapter 23 and indicate that species richness of small mammals decreased in the uppermost interglacial. A wide spectrum of species were involved in this reduction, including voles, pocket gophers, and wood rats. The three voles *(Mimomys virginianus, Allophaiomys pliocaenicus,* and *Phenacomys gryci)* are extinct, but, as noted previously, their relatively high abundance during moist times suggests that their demise was linked to increasing aridity. Likewise, the ecological requirements of the pocket gophers that dropped out of the record *(Thomomys* aff. *T. bottae* and an unidentifiable species possibly related to *Geomys)* are unknown, but their living relatives prefer moist, well-drained soils (Fitzgerald et al., 1994). The two wood rats that disappeared *(Neotoma mexicana* and *N. micropus),* in contrast, are not linked to relatively high moisture; in fact, they are found only in areas effectively warmer and drier than those around Porcupine Cave today. All the affected species, however, are characterized by relatively low abundance throughout the time they are present, consistent with theoretical work that suggests such species are most prone to disappear during times of environmental disruptions (Maurer and Nott, 1998; Maurer, 1999).

The coincidence of reductions in species richness with the warmest interglacial suggests that similar reductions might also characterize other higher than usual warming events, at least in ecological settings resembling South Park. Interestingly, a decrease in mammalian species diversity seemed to characterize the late Pleistocene-Holocene transition, as nonanalogue species assemblages separated (Graham and Grimm, 1990; Graham, 1992) and late Pleistocene megafauna became extinct (Martin and Klein, 1984). However, the role of global warming in that case is difficult to tease out, because by the late Pleistocene human activities may already have been altering the landscape (Martin, 1984; Barnosky, 1989; Alroy, 2001).

Higher Taxonomic Levels

Chapter 23 pointed out that some taxa of small mammals consistently appear in high abundance throughout the Porcupine Cave record, and that the high numbers of arvicoline rodents, *Spermophilus,* and *Marmota* resemble the modern situation around Porcupine Cave. Hadly and Maurer (2001), through analyses of temporally long (circa 3000 years) and geographically widespread (Great Basin and Northern Rocky Mountains) data sets that included many of the same genera of small mammals that occur at Porcupine Cave, demonstrated that genera that are abundant on the landscape today are also most likely to be abundant as the record extends back through time. They used a preliminary data set from Porcupine Cave to verify that the Porcupine Cave genera characterized by high relative abundances were in fact the same ones that are abundant today in communities throughout much of the western United States (Hadly and Maurer, 2001) (they are currently analyzing the now more complete Porcupine Cave data set). Thus diversity at the generic levels might be expected to remain stable even in the face of environmental fluctuations.

The lists compiled by Shabel et al. (chapter 22) for the Badger Room analysis indicate that such stability is indeed the case. As noted in chapter 7, the Badger Room assemblage of fossils probably correlates with the upper glacial (levels 5 or 4) or middle interglacial (levels 8, 7, or 6) in the Pit sequence. It has the advantage of a taphonomic pathway that sampled more large mammals and carnivores than the Pit, as well as rodents and lagomorphs, which makes the presence-absence data more complete. The Badger Room assemblage includes 42 species; the count for the historic fauna around Porcupine Cave is 49. As noted in chapter 22, taphonomic biases probably depress the species count somewhat for the fossils, especially for Rodentia and Carnivora. At the generic level, the counts are 36 for the fossil fauna and 36 for the historic. At the family level, the counts are 15 for the fossil fauna and 16 for the historic (see table 22.8). But, as Shabel et al. point out in chapter 22, the number of orders is lower today—6 Pleistocene orders versus 4 modern ones.

Trophic and Size Structure

Shabel et al. also used their data to examine the similarities in trophic structure between the Badger Room assemblage and the modern Porcupine Cave fauna (see table 22.9). After taking taphonomic considerations and biases in data compilation into account, they found that the number of small-bodied, medium-sized, and large herbivores, carnivores, and omnivores was very similar more than 800,000 years ago as compared to today. This finding indicates overall stability in trophic and size structure, even in the face of the more than six glacial-interglacial cycles that temporally separate the two samples, and the high turnover of the involved species.

What Does It All Mean?

Can we generalize from the Porcupine Cave data? To some extent, yes. The stability in trophic and size structure, overall species and higher-level diversity, and relative abundance patterns is striking. Glacial-interglacial transitions from the middle Pleistocene to now do not seem to have had much effect on these measures of diversity. Brown et al. (2001) found the same pattern of stability in species richness but variance in taxonomic composition through climate changes on the decadal and ten-thousand-year time scales. Such patterns suggest that, over the long term (hundreds of thousands of years), ecosystems have an inherent stability and are resilient even in the face of climate changes at the scale of glacial-interglacial transitions. The stability is at the level of functional relationships between species, not the species themselves, as evidenced by the high species turnover (>40%) in South Park since the middle Pleistocene. In other words, species come and go, but the ecological niches they fill remain the same.

Within this overall stability, however, extraordinary perturbations can be expected to affect diversity at the population and species levels. In the case of the Porcupine Cave data, the aberrant perturbation was the transition into the uppermost interglacial, which represents the warmest time in the record and possibly signals the shift from dominance of the 41,000-year periodicity for glacial-interglacial cycles to the 100,000-year rhythm. Which species are affected at the population level depends on the life history traits of the particular species. In the Porcupine Cave data set, species buffered from the environmental changes (*Spermophilus* cf. *S. elegans* and *Marmota* sp.) showed no changes in population variance, whereas another (*Lemmiscus,* a species that is active year round), demonstrated increased population-level variance. Population densities of species that are ecological specialists *(Mictomys, Lemmiscus)* can be expected to fluctuate in abundance as environmental changes expand and shrink the distributions of necessary microhabitats. These kinds of population-level effects percolate upward to influence which species persist through environmental changes and which ones survive.

The data at Porcupine Cave are consistent with theories that predict that taxa with low population densities are least likely to survive extreme environmental perturbations. It was these taxa that disappeared in the uppermost interglacial, leading to the reduction in species diversity at that time. Taxa with high previous population densities survived the onset of the especially xeric time (with lowered densities), even though they were specialists for relatively moist environments *(Mictomys* and *Marmota).* In contrast, species with previous low abundance disappeared, even though they were apparently well adapted to the xeric conditions of the uppermost interglacial *(Neotoma mexicana* and *N. micropus).*

Predictions for the Future

Returning to the analogy presented in chapter 1, we have now identified the canary in the coal mine. It is the functional stability of natural ecosystems, which is reflected in long-term stability of diversity at the species level, higher taxonomic levels, and trophic structure. We can expect species to come and go. But if many more go than come, the canary dies.

What should we expect in ecosystems as global warming continues over the coming decades? One model was proposed by Barnosky et al. (2003), in part based on the Porcupine Cave data but also integrating information from the mammalian response to global warming on hundred-year, thousand-year, and million-year time scales. The response to "natural" global warming events—those with rates within the bounds of what has characterized the past 65 million years (see figure 1.1)—is for ecological specialists to alter their relative abundance, which in turn affects population densities. If warming rates are at the high end of normal, population densities may change to the extent that population-level genetic and morphological diversity are affected for some species. Some extinctions and pronounced changes in geographic ranges are inevitable and normal. Such responses, in fact, are already occurring with the current global warming crisis (e.g., Brown et al., 1997; Sæther et al., 2000; Wuethrich, 2000; Etterson and Shaw, 2001; McCarty, 2001).

However, within "normal" global warming events, functional stability of ecosystems seems to have been maintained. The exact process by which functional stability maintains itself is as yet poorly understood, but it almost certainly involves open dispersal corridors that allow nearby ecological equivalents to replace species that disappear locally. Probably another important part of the equation is maintenance of evolutionary potential within species and higher taxa, in the form of high diversity within and between populations. In the natural scheme of things, over time (hundreds to thousands of years) these two processes (immigration and evolution) apparently act to keep functional ecological niches filled. To put it another way, when one species is excluded from the ecosystem by a specific climatic parameter, there seems to be another waiting in the wings that does the same thing for a living but has slightly different and appropriate climatic tolerances.

In the context of the current global warming crisis, ecosystems face two major problems:

1. If rates of warming continue as predicted, the warming event will so far exceed what is normal for ecosystems that the species waiting in the wings simply will not be able to get on stage fast enough, in part because they may face their own climate change–induced troubles, and in part because natural immigration rates may be outpaced by an accelerated rate of population decline.
2. As pointed out in chapter 1 and references therein, habitat fragmentation by humans has so dissected the natural landscape that even species with the potential to colonize vacant ecological niches will not be able to do so on their own.

The predicted result is that species diversity will dramatically decrease at the local level, to the point that the functional stability of the ecosystems that have persisted on Earth for at least hundreds of thousands of years will break down. The net effect may well be the catastrophic shifts in ecosystem states that Sheffer et al. (2001) recognized as a possibility.

Human activities have brought about this state of ecological affairs. Is there anything we can do about them? The encouraging news is that the canary is not yet dead. The South Park ecosystem, for example, still seems to have the functional integrity that characterized it some 800,000 years ago. The Greater Yellowstone Ecosystem is still functionally intact (Hadly, 1996), as are vast swaths of Canada, Alaska, and other parts of the world. Therefore, one necessary action is to keep ecologically similar areas as connected as possible, to allow the natural migrations of biota that keep species diversity stable (but see Barnosky et al. [2001] for cautions about establishing the proper geographic context for this). That is, habitat fragmentation must be minimized. Second, effective climate mitigation policies are essential to minimize the magnitude and extent of human-caused global warming. Either habitat fragmentation or the predicted global warming has the potential to drastically alter the functional stability of Earth's ecosystems; together, they can supply a potentially fatal one-two punch.

Practically speaking, humans already have tinkered extensively with Earth's ecosystems, and it is naïve to think that we will not continue to do so. To do so responsibly, however, the goal of tinkering should be to maintain the functional—not necessarily the precise taxonomic—stability that has apparently been in place for hundreds of thousands of years. In that context, it is essential that we continue to monitor diversity in natural systems through the coming century, and to compare the emerging diversity patterns with those evident from studying museum collections and paleontological data. In this way, problems that lead to potential ecosystem collapse can be recognized before it is too late to do something about them, for example, by repopulating the area with related taxa that serve similar ecological functions. It is also critical to integrate these field-based observations with theory and laboratory work designed to unravel the complexities of ecosystem function. Through these activities we can help the Earth maintain the ecological properties that have been natural through the time during which *Homo sapiens* evolved, and which therefore are natural (some would argue essential) to us. In short, there is still a chance, but it is probably the last chance. We should not squander it.

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INDEX

Page numbers followed by *f* and *t* indicate figures and tables, respectively. *Italicized* page numbers occur within chapter appendixes.

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