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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

MAMMALIAN PALEONTOLOGY OF THE MONARCH MILL FORMATION AT EASTGATE, CHURCHILL COUNTY, NEVADA

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

By

Kent S. Smith

Norman, Oklahoma

2002

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MAMMALIAN PALEONTOLOGY OF THE MONARCH MILL FORMATION AT EASTGATE, CHURCHILL COUNTY, NEVADA

A Dissertation APPROVED FOR THE

DEPARTMENT OF ZOOLOGY

Richard L. Cifelli, chair

Nicholas J. Czaplewski

Gary D. Schnell

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Charles W. Harper

PREFACE

Presented herein is my dissertation as two separate chapters. Each chapter will be submitted to a peer-reviewed journal. Chapter 1 will be sent to the *University of California Publications in the Geological Sciences*. The second chapter will be submitted to the *Journal of Mammalogy*. The chapters of this dissertation are formatted as appropriate for the respective journals.

DEDICATION PAGE

This work is dedicated to the late Dr. Donald E. Savage for overseeing the loan of the Eastgate fossil material from the University of California at Berkeley, for his sustained interest in the Eastgate fossils and bringing the Eastgate fauna to my attention, for showing me the Eastgate localities, for his contributions to the Cenozoic of western North America, and for his guidance and friendship. He will be sorely missed by me and by the rest of the scientific community, colleagues, students, friends and family. Dr. Savage was a rare individual and the paleontological community will not be the same without his Texas charm, wit, and knowledge.

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I am grateful to R. L. Cifelli, for his unconditional support and guidance through all stages of this project and for sharing with me his vast knowledge of fossil mammals, recent mammals, geology, and field techniques. I thank N. J. Czaplewski for encouragement throughout the project, for his expertise and advice regarding Tertiary-age mammals, and for help with field work at the Eastgate localities. I extend my gratitude to G. D. Schnell for sharing his expertise in numerical taxonomy and statistical techniques. I appreciate B. M. Vestal, for his continued support and advice during my graduate career. I thank C. W. Harper for his continued support and advice during this project. For the loan of specimens, I am obliged to the following individuals: D. E. Savage, J. H. Lipps, J. H. Hutchinson, and P. A. Holroyd (UCMP); K. Seymour (ROM); L. Martin and M. Desui (UKVP). The following provided funding or support during this project: University of Oklahoma Department of Zoology; University of Oklahoma Graduate Student Senate; Oklahoma State Regents for Higher Education Doctoral Study Grant; Southern Regional Education Board Doctoral Scholars Program Dissertation Year Fellowship; the American Indian Graduate Center, Albuquerque, New Mexico; the Lt. William Johnson Scott Memorial Scholarship; and NSF grant DEB 9401094 to R. L. Cifelli. I thank L. F. Patterson for providing a vehicle for the field stage of this project. For providing permits to collect on BLM properties, I extend my gratitude to Prill Mecham of the United States Department of the Interior, Bureau of Land Management at the Carson

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ABSTRACT

The first Eastgate locality (UCMP V70138) was discovered by D. I. Axelrod in the late 1950s. Since the initial discovery of fossil vertebrates at Eastgate, researchers from the University of California at Berkeley (namely, D. E. Savage and J. H. Hutchison) and the University of Oklahoma have collected fossil remains from nearly 20 localities. Fossils were collected from within the volcanic tuffs that occur in the basalmost section of the Monarch Mill Formation. Screenwashing was limited to few localities.

The Eastgate local fauna, Churchill County, Nevada of Miocene (early Barstovian) age includes 25 families of mammals, as well as numerous fish, amphibians, reptiles, and birds. Sixty species of mammals including 18 insectivores, one chiropterian, seven lagomorphs, 33 rodents, five carnivores, three artiodactyls, and three perissodactyls are described for the Eastgate local fauna. A new species of insectivore, one genus, and nineteen species of rodents are described.

Three new species of *Leptodontomys* (*L. korthi* n. sp., *L. schnelli* n. sp., and *L. protistopikos* n. sp.) are described based on a large sample (249 specimens) of maxillae, mandibles, incisors, and isolated upper and lower cheekteeth. In addition to the descriptions, 18 quantitative dental characters of the p4 for *Leptodontomys* were examined using principal components analysis, correspondence analysis, and cluster analysis. These analyses provided a reliable separation of species.

Phylogenetic relationships for *Leptodontomys* were examined and a hypothetical phylogeny was constructed. This phylogeny is based on 74 characters of the maxillae, mandibles, and upper and lower cheekteeth of *Leptodontomys*. The phylogenetic analyses resulted in 14 most-parsimonious trees, indicating *Leptodontomys* as a monophyletic group. Results of the phylogenetic analyses, show two of the new species, *L. schnelli* n. sp. and *L. protistopikos* n. sp., form a tricotomy with *L. stirtoni*. The third new species, *L. korthi*, is a sister taxon to *L. quartzi*.

A Miocene (Barstovian) Mammalian Fauna from the Monarch Mill Formation, Churchill County, Nevada

Kent S. Smith

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Acknowledgment

I am grateful to R. L. Cifelli, for his unconditional support and guidance through all stages of this project and for sharing with me his vast knowledge of fossil mammals, recent mammals, geology, and field techniques. I thank N. J. Czaplewski for encouragement throughout the project, for his expertise and advice regarding Tertiary-age mammals, and for help with field work at the Eastgate localities. I extend my gratitude to G. D. Schnell for sharing his expertise in numerical taxonomy and statistical techniques. I appreciate B. M. Vestal, for his continued support and advice during my graduate career. I thank C. W. Harper for his continued support and advice during this project. For the loan of specimens, I am obliged to the following individuals: D. E. Savage, J. H. Lipps, J. H. Hutchinson, and P. A. Holroyd (UCMP); K. Seymour (ROM); L. Martin and M. Desui (UKVP). The following provided funding or support during this project: University of Oklahoma Department of Zoology; University of Oklahoma Graduate Student Senate; Oklahoma State Regents for Higher Education Doctoral Study Grant; Southern Regional Education Board Doctoral Scholars Program Dissertation Year Fellowship; the American Indian Graduate Center, Albuquerque, New Mexico; the Lt. William Johnson Scott Memorial Scholarship; and NSF grant DEB 94010194 to R. L. Cifelli. I thank L. F. Patterson for providing a vehicle for the field stage of this project. For providing permits to collect on BLM properties, I extend my gratitude to Prill Mecham of the

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Abstract

The first Eastgate locality (UCMP V70138) was discovered by D. I. Axelrod in the late 1950s. Since the initial discovery of fossil vertebrates at Eastgate, researchers from the University of California at Berkeley (namely, D. E. Savage and J. H. Hutchison) and the University of Oklahoma have collected fossil remains from nearly 20 localities. Fossils were collected from within the volcanic tuffs that occur in the basalmost section of the Monarch Mill Formation. Screenwashing was limited to few localities.

The Eastgate local fauna, Churchill County, Nevada of Miocene (early Barstovian) age includes 25 families of mammals, as well as numerous fish, amphibians, reptiles, and birds. Sixty species of mammals including 18 insectivores, one chiropterian, seven lagomorphs, 33 rodents, five carnivores, three artiodactyls, and three perissodactyls are described for the Eastgate local fauna. A new species of insectivore, one genus, and nineteen species of rodents are described.

Abbreviations

Abbreviations used herein including text, figures, captions, plates, and tables are as follows:

Institutional abbreviations

AC	Amherst College
CIT	California Institute of Technology
CNHM	Chicago Natural History Museum
LACM	Los Angeles County Museum of Natural History
KUVP	University of Kansas Museum of Natural History
OMNH	Oklahoma Museum of Natural History
SDSM	South Dakota School of Mines
UCMP	University of California Museum of Paleontology
UCR	University of California at Riverside
UO	University of Oregon Museum of Natural History

Dental characters

I	upper incisor
D	before the symbol for a tooth means deciduous upper tooth
P2-M3	represents teeth of maxilla
P2	upper second premolar
P3	upper third premolar
P4	upper fourth premolar
M1	upper first molar

M2	upper second molar
M3	upper third molar
i	lower incisor
d	before the symbol for a tooth means deciduous lower tooth
p2	lower second premolar
p3	lower third premolar
p4	lower fourth premolar
m1	lower first molar
m2	lower second molar
m3	lower third molar
p2-m3	represents teeth of mandible
AP	greatest anterorposterior length of tooth
T or TR	greatest transverse width of tooth
TA	greatest transverse width of anterior half of tooth
TP	greatest transverse width of posterior half of tooth

Other abbreviations

OMNH V	Oklahoma Museum of Natural History vertebrate paleontology locality number
RV	University of California, Riverside vertebrate paleontology locality number
UCMP V	University of California Museum of Paleontology, vertebrate paleontology locality number

m	meter
ma	mega-annum (millions of years)
mm	millimeter
P or PA	fossil plant localities for University of California at Berkeley

Introduction

The main focus of this investigation is fourfold, namely to: 1) review historic investigations of the vertebrate fossils of the Monarch Mill Formation; 2) determine the stratigraphic relationship of the Eastgate fauna within the Monarch Mill Formation; 3) examine the systematic paleontology of the mammalian taxa recovered from the Monarch Mill Formation; and 4) compare the temporal and spatial attributes of the Eastgate fauna to other known North American Barstovian-aged faunas.

This study provides stratigraphic information for the Eastgate localities and descriptions of 60 species of mammals from the Eastgate local fauna of the Monarch Mill Formation. These mammals include a single new species of insectivore, a new genus and species of a petauristine squirrel and 18 additional new species of rodents.

To date, there are 21 vertebrate fossil localities from the Monarch Mill Formation of the Middlegate basin. Three of the fossil mammal localities are Hemphillian in age, while 18 are considered to be Barstovian in age (Axelrod, 1985). Collectively, herein, the Barstovian-age mammal localities are termed the Eastgate fauna (Fig. 1). There are no known Clarendonian localities reported from the Monarch Mill Formation (D. E. Savage, personal communication).

Historical Overview

In the middle 1950s, Daniel Axelrod began to collect fossil plants from the Middlegate basin, Churchill County, Nevada. During his exploration of the Middlegate basin for additional fossil plant localities, scanty mammalian bone fragments were discovered at three separate localities. The fossil plants were discovered in the Middlegate Formation, while the fossil vertebrates came from the overlying Monarch Mill Formation (Axelrod, 1956). The first fossil mammal locality was discovered about 30 m above the principal plant locality (UCMP P 5101). The principal plant locality is located north of the town of Middlegate (north of State Highway 50). Curiously, Axelrod listed a tooth, jaw, and cervical vertebrae of a rhinocerotid (*Aphelops*?) from this locality. However, no additional comments (including locality designation) on these fossil remains were made. A second fossil mammal locality was discovered near U.S. Highway 50, southeast of the town of Middlegate. This locality produced the remains of a gomphotheriid and a camel. There is no locality number for these specimens. The third fossil mammal locality (UCMP V 5200) was discovered farther south and east of the second fossil mammal locality. This locality occurs in the basalmost part of the upper member of the Monarch Mill Formation and is considered to be Hemphillian in age (Axelrod, 1956). Axelrod (1956) referred to the assemblage from this locality (UCMP V 5200) as the Monarch Mill fauna. It was Tedford (Axelrod, 1956) who suggested a Hemphillian age for the Monarch Mill fauna

and identified the mammal material recovered from this locality. The fossils from this locality included the following groups of mammals: Felidae, Rhinocerotidae, Camelidae (small-and large-sized), and Gomphotheriidae.

Based on locality information at UCMP, a fourth fossil mammal locality from the Middlegate basin was discovered in 1967. This locality was not reported until Axelrod's (1985) description of a nearby fossil plant locality known as the Eastgate flora. This fourth fossil mammal locality is located about 0.8 km southwest of the Eastgate flora and is termed the Eastgate fauna.

Geology of the Middlegate Basin

The exposures in the middle and western parts of the Middlegate basin were originally described by Axelrod (1956) as the Middlegate Formation. He described the exposures that occur along the southeastern side of the Clan Alpine Mountains (Axelrod, 1956) and identified these rock exposures as the Middlegate Formation. The Clan Alpine Mountains stretch north and south along a line that incises the town of Middlegate, Churchill County, Nevada. The Middlegate Formation extends from the southeast side of the Clan Alpine Mountains south and east toward the town of Eastgate, Churchill County, Nevada (Axelrod, 1956). Axelrod (1956) reported a maximum thickness of 396 m for the Middlegate Formation.

Axelrod (1956) examined the geology of the region, in part, to determine

the stratigraphic relationship of the Middlegate flora within the Middlegate Formation. He reported the Middlegate Formation consists mainly of sedimentary rocks that rest unconformably on the Clan Alpine volcanics. For purposes of mapping, Axelrod (1956) divided the Middlegate Formation into three units (upper, middle, and lower members). The thickness and characterization of these units is as follows: the lower member ranges from about 1 m to 91 m thick and consists of sedimentary breccias, conglomerates, and sandstones (derived from the underlying volcanics); the middle member reaches a maximum thickness of 122 m and consists of a siliceous shale with alternating soft tuffaceous clay; and the upper member includes sandstone and rhyolite tuffs, interbedded with lake clays and thin shales (Axelrod, 1956). Axelrod (1956) placed the Middlegate flora within the middle member of the Middlegate Formation.

A second formation from the Middlegate basin was described by Axelrod (1956). He named this second formation the Monarch Mill Formation after a nearby stamp mill. Axelrod's (1956) original description of the Monarch Mill Formation was based on exposures in the middle and western parts of the Middlegate basin. From exposures in this region of the Middlegate basin, he mapped six rock units for the Monarch Mill Formation. Beginning at the bottom of the stratigraphic section, they are as follows: 1) tuffaceous claystone, conglomerate; 2) sandstone; 3) rhyolite tuff and pumice; 4) diatomite and tuffaceous siltstone; 5) conglomerate; and 6) rhyolitic claystone, pumice,

sandstone, and siltstone.

In 1985, Axelrod traced the Monarch Mill Formation into the eastern and southeast region of the Middlegate basin. In this region of the Middlegate basin, he suggested that the clastic sediments of the Monarch Mill Formation were much coarser than those from the middle and western parts of the Middlegate Basin. In addition, he suggested the basal part of the Monarch Mill Formation was a widespread sedimentary breccia that grades basinward into a conglomerate 4-7 m thick, containing cobble to small boulder-size particles (Figs. 2 and 3).

Excluding the brecciated basal member of the Monarch Mill Formation from the east and southeast region of the Middlegate basin, Axelrod (1985) provided additional characteristics for the Monarch Mill Formation. They are as follows: a conglomerate is scattered throughout the east and southeast region of the Middlegate basin, which is composed of a coarse, pebbly sandstone that is poorly indurated and poorly bedded, mudstone, shale, fine-grained tuffs; and slopes that are covered with rubble and vegetation. In addition to describing the lithology for this region of the Middlegate basin, Axelrod (1985) placed the Barstovian mammalian locality in the basal member of the Monarch Mill Formation.

Further study of the geology for the Middlegate basin was conducted by by Barrows (1971), who examined the geology of the nearby Desatoya Mountains, and Noble (1972), who described the Middlegate area as

representing a boundary for middle Miocene volcanism.

In the current study, three factors prompted a re-examination of the lithology from the eastern and southern region of the Monarch Mill Formation: 1) Axelrod's original description of the Monarch Mill Formation was based on the Monarch Mill Formation from the middle and western region of the Middlegate basin; 2) the Barstovian-age mammalian localities discovered in the eastern and southern region of the Middlegate basin were not precisely placed within the Monarch Mill Formation by Axelrod (1985); and 3) it would be useful to determine the stratigraphic relationships between selected Barstovian age mammalian localities within the Monarch Mill Formation.

Eighteen Eastgate localities occur within a 1.61 km^2 radius. Within this geographic area, four stratigraphic sections were measured and their lithology examined. Three factors essential for choosing stratigraphic sections for examination were: 1) the identification of a marker bed, consisting of a cream to white siliceous shale; 2) localities that provided large numbers of fossil vertebrates; and 3) extensive vertical and lateral exposures. The four sections measured from the Monarch Mill Formation included seven of the 18 fossil localities from the eastern and southern region of the Middlegate basin.

Most of the fossil mammal localities at Eastgate are separated by topographic features that prevent direct stratigraphic correlation among the fossil localities (Fig. 4). The measurements for the stratigraphic sections began at the top of a cream-to-white siliceous shale that is defined as the top of the upper

member of the Middlegate Formation (Axelrod, 1956). Axelrod (1956) suggested that the basalmost member of the Monarch Mill Formation directly overlies a paper-thin cream to white, siliceous shale. This cream-to-white siliceous shale is exposed throughout the eastern and southern region of the Middlegate basin.

The cream-to-white siliceous shale was selected as a marker bed for the following reasons: 1) it occurs at a contact zone above the breccia; 2) it is in the top of the upper member of the Middlegate Formation; 3) it lies below all of the fossil localities; 4) and it occurs frequently enough in the outcrops to be traced near seven of the Barstovian fossil localities. Stratigraphic continuity for all the measured sections was maintained by beginning all of the measurements and lithological descriptions at the cream-to-white siliceous shale.

The geographic locations of the four stratigraphic sections measured and described are as follows: 1) a stratigraphic section west of locality UCMP V70140, on a west facing slope; 2) a south-facing slope between localities UCMP V67245 and UCMP V70147; 3) a north-facing slope north of UCMP V67245; and 4) a west-facing slope at locality OMNH V974.

For the measured sections of the Monarch Mill Formation two units (unit 1 and unit 2) and six subunits (A-F) were identified (Table 1). At different outcrops in the eastern and southeastern part of the Middlegate basin, not all of the six subunits are found in units 1 and 2. However, they are exposed in all of the stratigraphic sections described and measured for this study. Thus, the descriptions of each unit and subunit, as they occur at Eastgate, are included in

each of the four measured sections. Below are the descriptions and measurements for the stratigraphic sections of the Monarch Mill Formation.

1) West of Locality UCMP V 70140

Only one subunit (subunit A) was identified in unit 1 (Fig. 3). subunit A is brecciated and contains concretions in the basal member. This subunit contains concretions of pebble to small boulder size that house small blocks of siliceous shale as their nuclei. Several of the boulders in the convoluted upper part of this section are 1.5 m in diameter, while other smaller boulders have apparently shattered in place. In contrast to the shattered smaller boulders, the volcanic clasts present in this section are not shattered. The brecciated/convoluted part of subunit A seems to be very localized and is limited to the area directly beneath the fossiliferous beds south of UCMP V70138 and west of UCMP V70140. Elsewhere, throughout the area subunit A appears to be represented by normally bedded cream-to-white, siliceous shales. Near the top of unit 1, the beds are brecciated and appear to have eroded in a planner fashion; hence, there is an unconformity with unit 2. With the exception of the top of subunit A, all other stratigraphic subunits examined in this section appear normally bedded.

Unit 2 consists of five subunits (B–F), of which the stratigraphically lowest is subunit B (Fig. 4). Here subunit B overlies, conformably, the top of subunit A (unit 1) and continues to the floor of the fossil localities UCMP V70140 and

V70142. This part of the section consists of gray-to-light-brown siltstones and claystones with occasional sandstones and ash fall tuff. Subunit B continues above the quarry floor (UCMP V70140) for about 10 m. Above subunit B is subunit C, which is a pebble/gravel conglomerate about 4 m thick with intermittent siltstones and sandstones. Subunits D and E are not apparent in this section. Subunit F is present above subunit C and continues to the top of the bench (Fig. 5). Subunit F is composed of loose gravels and vegetation; the soil is composed of gravels and siltstones that are probably Quaternary in age. Alternating beds of claystones, siltstones and sandstones are seen throughout subunits A, B, and C. It appears that only one tuff is present within this part of the Monarch Mill Formation and it occurs in subunit B. This is the stratigraphic layer where the Barstovian mammals were recovered.

2) South-facing Slope Between Localities UCMP V70147, UCMP 74103, UCMP 67245, AND OMNH V 976

The following stratigraphic units and subunits were measured south of the Barstovian localities UCMP V70147, UCMP 74103, UCMP 67245, and OMNH V 976. These four localities occur within a horseshoe-shaped slope that opens to the west (Fig. 6). On the south-facing slope, locality UCMP V 67245 occurs below and lateral to UCMP V 70147 and UCMP V 74103. The slopes north and south of V70147 were measured in order to correlate these four fossil localities

stratigraphically. As before, all measurements began at the white-to-cream, siliceous shale (unit 1, subunit A). Subunit E occurs only at these four localities. Subunit B is a 10-m-thick layer of grayish-brown siltstones, while subunit C consists of a pebble and gravel conglomerate intermixed with a lens-shaped channel fill that is cross-bedded and about 3 m thick. Subunit D is made up of gray-brown siltstones and claystones and is about 4 m thick. Subunit E is a lens-shaped conglomerate about 1 m thick, and subunit F consists of Quaternary sandstones and gravels that make up the top of the bench.

Locality UCMP V 70147 contains abundant root casts and charcoal, unlike the other sites. The fossils are from a grayish tuff about 11.5 m above subunit A. At 11 m above subunit A, in subunit B, is a thin layer of coarse grained yellowish gravely silts and pebbles that extends upward for about 0.5 m. A similar resistant bed occurs at UCMP V 70138. Subunits C, D, and E are not revealed at this locality but subunit F is present above subunit B.

These localities (UCMP V70147, UCMP 74103, UCMP 67245, AND OMNH V 976) occur at different stratigraphic levels. From the top of the white-to-cream, siliceous shale to the base level of each locality, the maximum, average, and minimum thicknesses are as follows: 22 m (UCMP V70147) 17.25 m, and 12 m (OMNH V976).

3) North-facing Slope South of OMNH V976 and UCMP V67245

The cream-to-white, siliceous shale of unit 1 (subunit A) protrudes from the floor of the canyon and is covered with dense vegetation. The next subunit above A is subunit B, which contains a tuff and claysstones. The fossils quarried at locality UCMP V 70147 were taken from a gray colored tuff 12 m above the cream-to-white, siliceous shale. Subunit C continues up section as pinkish-to-tan and pinkish-tan clays and siltstones with an associated pebble conglomerate (1 m or less in thickness) that occurs sporadically for about 25-30 m. Indistinguishable subunits D and E are likely masked by subunit F, which consists of Quaternary sandstones and gravels that make up the top bench.

4) West-facing Slope at Locality OMNH V974

Locality OMNH V974 occurs in subunit B of Unit 2 (Fig. 7). OMNH V974 is approximately 11 m above the top of subunit A in subunit B. Subunit B consists of a gray tuff. This locality has more hair-like gypsum crystals than any of the other quarry sites in this area. Subunit C is 16 m in thickness and contains pinkish-to-tan and pinkish-tan claystones and siltstones. Subunits D and E are not apparent at this locality. However, subunit F is present and about 0.1 m in thickness, consisting of pebbles and gravels before it disappears under the cover of modern vegetation.

Vertebrate Paleontology of the Middlegate Basin

In 1985, Axelrod reported an additional Middlegate Basin flora, the Eastgate Flora, near the town of Eastgate, Churchill County, Nevada. In addition to the flora, he found the remains of fossil mammals that occurred in the basal member of the Monarch Mill Formation. This was the fourth fossil mammal locality recorded for the Monarch Mill Formation. The four Miocene-age fossil localities for the Middlegate basin are as follows:

1) From near the original fossil plant locality, UCMP P 5101 north of the town of Middlegate, the remains of a rhinoceros were discovered about 30.5 m higher in the section than the fossil plants.

2) Southeast of the original plant locality and about 4.0 km across U.S. Highway 50, the remains of additional fossil mammal bones were discovered. These bones consisted of tooth fragments from a gomphothere and a calcaneum of a medium- to large-sized camel. D. E. Savage suggested a Barstovian through Clarendonian age for these fossils (Axelrod, 1956).

3) The Monarch Mill fauna was discovered in the middle of the Middlegate basin (about 5.5 km southeast of the Middlegate flora) and was placed stratigraphically in the basal part of the upper member of the Monarch Mill Formation. The following fossil taxa from the Monarch Mill fauna were identified by Tedford (see Axelrod, 1956): Carnivora (Felidae), Perissodactyla (Rhinocerotidae, *Teleoceras*), Artiodactyla (Camelidae, *Procamelus* or

Pliauchenia), and Proboscidea (Gomphotheriidae). The Monarch Mill fauna was considered to be Hemphillian in age by Tedford (Axelrod, 1956) and assigned to UCMP V 5200.

4) In 1985, Axelrod discussed an additional fossil mammal locality that was discovered about 0.8 km south of the Eastgate plant locality UCMP PA 533. Savage and Russell (1983) referred to this locality as Nevaxel in honor of the late D. I. Axelrod who discovered this locality in the late 1960s. I believe a more descriptive name for this fossil fauna would be the Eastgate fauna, named after the nearby town of Eastgate, Nevada. Therefore, this fossil fauna is referred herein as the Eastgate Fauna.

Axelrod (1985) provided a preliminary list of taxa for the Eastgate fauna, as identified by D. E. Savage: Insectivora (Soricidae, *Pseudotrimylus*; Plesiosoricidae, *Meterix*; Talpidae, *Mystipterus*), Lagomorpha (Leporidae, *Hypolagus*), Rodentia (Sciuridae; Castoridae, *Monosaulax*; Aplodontidae, *Liodontia*; Mylagaulidae, *Mylagaulus*; Cricetidae, *Copemys;* Heteromyidae), Carnivora (Canidae, *Tomarctus;* Mustelidae), Perissodactyla (Equidae, *Hypohippus*; Rhinocerotidae, *Teleoceras*; Chalicotheriidae, *Aphelops*), and Artiodactyla (Merycoidodontidae; Camelidae; Paleomerycidae, *Aletomeryx;* Antilocapridae).

Fossil remains that constitute the Eastgate fauna have been collected since the late 1960s by the University of California at Berkeley (D. E. Savage, personal communication). For the most part, fossil remains were collected from

the surface of the rock exposures in the eastern and southern region of the Middlegate basin. Little screenwashing of the rock matrix was implemented until the late 1980s. One University of California at Berkeley graduate student, Neil Burmister, screenwashed rock matrix from Eastgate in search of small mammals (D. E. Savage, personal communication). In 1995, I collected rock matrix for screenwashing. My efforts proved fruitful with the recovery of additional orders and families of mammals that were previously not known to the Eastgate fauna. They include Chiroptera, Felidae, Ochotonidae, Eomyidae, Geomyidae, and Zapodidae (Dipodidae). In addition to the mammalian taxa, the fauna also contains some fossil remains of fish, amphibians, reptilians, and birds. Only the mammals are evaluated in this study.

Numerous North American Barstovian localities have been reported by Savage and Russell (1983) and Tedford (1987). Savage (personal communication, 1999) suggested seven additional Barstovian localities for his published list (Savage and Russell, 1983). In addition, several of the Barstovian localities listed in Savage and Russell (1983) are not published faunal accounts; rather they are localities that have been collected by UCMP paleontologists and are housed at UCMP (D. E. Savage, personal communication), and to date are unstudied. Schiebout (1994) recorded the first Barstovian age vertebrate locality for Louisiana. Based on the literature there are more than 100 Barstovian localities in North America.

Methods and Materials

The locality information recorded for the Eastgate fauna by earlier workers is modified herein. For example, 11 of the 18 localities at Eastgate are based on isolated occurrences of single specimens (D. E. Savage, personal communication). In addition to isolated occurrences recorded for a single location, past workers provided locality numbers for each specimen collected side-by-side and from the same horizon. Thus, for this study, multiple UCMP V locality numbers may represent a single fossil locality as designated herein. For example, there are three UCMP V locality numbers (UCMP V70138, UCMP V70139, and UCMP V70141) for one immediate area (5 m^2) that I consider to be a single site. I collectively refer to them as UCMP V70138.

Twelve of the 18 fossil localities from the Monarch Mill Formation, in the eastern and southern region of the Middlegate basin, were examined. Stratigraphic sections were measured using a modification of the Hewett Method (see Prothero and Schwab, 1996). Measurements were made based on N. J. Czaplewski's eye height (1.6 m) multiplied by the cosine of the dip angle 10^0. While measuring these stratigraphic sections only major components of the lithology were noted. UCMP V depicts the University of California at Berkeley locality number; the OMNH V numbers represent the locality number for the Oklahoma Museum of Natural History as follows: UCMP V67245 = OMNH V966; UCMP V70138, V70139, and V70141= OMNH V967; UCMP V70140 = OMNH

V968; UCMP V70142 = OMNH V969; UCMP V70143 = OMNH V970; UCMP V70144, V70145, V70147 = OMNH V972; UCMP V74103 = OMNH V973; UCMP V74104, V87139, V88079, V88088, V92020; and OMNH V974-977. Of the 18 localities, 12 were examined during the summer of 1995. Four of the 12 are described herein as new for the Eastgate fauna. These additional localities (OMNH V974-977) were mapped, and rock samples were collected for screenwashing.

According to records at UCMP, two additional localities are recorded for the Eastgate area (UCMP V 70146 and V 70148). Unfortunately, these do not appear on the topographical map (1:24000; Eastgate, Nev.) on file at UCMP, and therefore, they could not be re-examined in the field. In contrast, the following localities (UCMP V 70148, V 87139, V 88079, V88080, and V 92020) are included on the topographic map (1:24000; Eastgate, Nev.); however, the current location of the fossil specimens are unsure. In any event, fossil mammal remains from 8 UCMP and 12 OMNH localities (UCMP V 70138, V 70140, V 70142-48, V 67245, V 74103 and OMNH V 966-77) are included in this study.

Processing of the rock matrix, in search of microvertebrates, follows the procedure outlined by Cifelli et al. (1996). In addition, the microvertebrates were prepared following the protocol outlined in Cifelli et al. (1996).

Key cranial (including teeth) and postcranial characters that aid in the identification of each mammal group at Eastgate are provided below for each group. Terminology, especially characters associated with tooth morphology,

used to described mammal teeth may differ from investigator to investigator. In addition, investigators may have coined new terms to identify characters for a particular group of mammals. Except for the abbreviations listed above, explanations of abbreviations used herein for the descriptions of teeth are included when encountered. Small mammal teeth were measured with a reflex microscope that is accurate to 0.001 mm (MacLarnon, 1989). Length and width measurements were taken from an occlusal view and are presented in mm (unless otherwise indicated, respectively). For select groups of mammals, additional measurements were taken. These groups include, but are not limited to, insectivores (Hutchison, 1966, 1968), lagomorphs (Voorhies and Timperely, 1997; White, 1987 and 1991), and geomyoids (Barnosky, 1986).

Catalogue numbers for the UCMP specimens were provided to me in lot numbers. Thus, the subunits affixed to the end of many UCMP catalogue numbers represent a different specimen in such a lot. For example, UCMP 141829 was assigned for a lot containing several hundred isolated jaws, maxilla, and teeth. Thus, each specimen in this lot received an individual variant of this number by placing numbers -01, -02, etc. If these secondary numbers were assigned and later more specimens from the same lot were encountered, they were assigned a letter rather than a number. For example, UCMP 141829-01a, 141829-01b, 141829-01aa, etc.

The systematics for higher categories follows that of Janis et al. (1998) and McKenna and Bell (1997). For systematics at and below the genus level, I

follow Hutchison (1966, 1968), Reppining (1967), Lindsay (1972), Barnosky (1986), Korth (1994), White (1987, 1991), and Voorhies and Timperley (1997). Other authorities are cited with each specific group. Herein, only the teeth, dentary and maxillae of the insectivores, lagomorphs, and rodents are described. The skulls and postcranial material of these small mammals will be the focus of future projects.

Systematic Paleontology

Order Soricomorpha Gregory, 1910

Family Plesiosoricidae Winge, 1917

Plesiosorex Pomel, 1848

Plesiosorex cf. *P. coloradensis* Wilson, 1960

Plate 1 (A-C)

Locality.— Eastgate, UCMP V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of species.— Hemingfordian: Pawnee Creek Formation, Logan County, Colorado (Wilson, 1960).

Referred specimen.— OMNH 54956, left m2 fragment.

Measurements.— AP = 2.12, TA = 1.68, TP = 1.60.

Description.— A fragment of a left m2 (OMNH 54956) is low crowned, slightly bulbous, and with moderate wear on the occlusal surface. This tooth is missing the anteromost part of the paraconid, the labialmost edge of the protoconid, and the entire entoconid. An anterior cingulid is present but other cingula are lacking. The trigonid is anteroposteriorly compressed. The talonid is longer than wide, while the trigonid appears wider than long. All three cusps on the trigonid are closely appressed. The trigonid basin is open lingually through a narrow valley formed between the metaconid and a lophid that begins at the posterolingual base of the paraconid, extending posteriorly and ending a small

distance anterior to the metaconid.

On the talonid, the hypoconid is heavily worn and joins the crista obliqua labially at the base of the protoconid. Because of breakage, it is unclear if the hypolophid joined the entoconid. There appears to be a low entoconid crest. The talonid basin does not open lingually or labially.

Comparison and discussion.— This tooth is slightly smaller in size but in other characteristics is similar to the m2 of *P. coloradensis* (KUVP 10004) studied by Wilson (1960), which measures AP = 2. 9, TR = 2.6. Therefore, until more complete material becomes available, this tooth is tentatively referred to this species.

Meterix Hall, 1929

Meterix sp. indet.

Plate 1 (D-F)

Locality.— Eastgate, UCMP V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the genus.— Barstovian: Esmeralda Formation, Esmeralda County, Nevada (Hall, 1929).

Referred specimens.— OMNH 54908, left dentary fragment with i1, p4-m2; OMNH 54909, left m2.

Measurements.— OMNH 54908, p4: AP = 2.49, T = 1.87; m1: AP = 4.50,

TA = 3.03, TP = 3.20; m2: AP = 3.16, TA = 2.78, TP = 2.46. OMNH 54909, m2: AP = 3.02, TA = 2.60, TP = 2.50.

Description.— A left dentary fragment (OMNH 54908) with the i1, p4–m2 preserved. The premolar and molars have little wear. The dentary appears to have been broken at an earlier time (prior to fossilization) between the incisor and the p4; however, the anterior and posterior pieces are fused together and the contact is partially filled with matrix. Because of the prior break in the dentary bone, it is unclear how many teeth may have been housed in this region of the jaw. No alveoli are apparent between the incisor and p4. The dentary is broken posterior to the anteromost alveoli of the m3.

Along the labial surface and midline of the dentary, two mental foramina occur in a depression below the middle of the m1. These foramina are placed side-by-side, and are directed toward each other; the anterormost mental foramen opens posteriorly while the posteromost mental foramen opens anteriorly.

The incisor is broken at the distal end; thus, about 90% of this tooth is preserved. The tooth is not strongly procumbent; instead, it projects anteriorly at approximately 45^0 to the dentary. This tooth is broad and stout.

The p4 has a low, small paraconid. The protoconid is the dominant cusp and is in close association with the metaconid. These two cusps are separated by a V-shaped protoloph. A posterior cingulid extends from below the metaconid labially below the posterolabial margin of the protoconid. A sulcus is present

between the lingualmost union of the protoconid and the posterior cingulum. Two roots are present on this tooth.

On the m1, the trigonid is longer but not wider than the talonid. The protoconid is the largest cusp but is equal in height to the metaconid. The paraconid is far forward and is separated from the protoconid by a deeply notched paracristid. The protoconid and metaconid are close to each other and separated by a shallow V-shaped notch in the protocristid. The trigonid basin opens low and lingually. There is no anterior cingulid, but a small posterior cingulid occurs below the hypolophid. The hypoconid joins the trigonid by the crista obliqua low and labially at the base of the protoconid. The hypolophid is straight and abuts the entoconid but does not join the entoconid. The entoconid is higher than the hypoconid and does not join the trigonid. Thus, an entoconid crest is not present on this tooth. There is a valley between the entoconid and the metastylid. The metastylid is small and attaches to the posterior base of the metaconid. The talonid basin is open low and lingually. Three roots are visible on the labial side. On the lingual side, the roots are obscured by the dentary bone and the bulbous crown of the tooth.

The m2 has a trigonid that is anteroposteriorly compressed and has a prominent anterior cingulid. The anterior cingulid begins at the labialmost extent of the paraconid and extends to the anterolabial base of the protoconid. The paraconid, protoconid, and metaconid are about equidistant to each other. The protoconid and metaconid are equal in height and taller than any of the other

cups on this tooth. A deep notch separates the paraconid and protoconid, while a shallow notch on the protolophid separates the protoconid and metaconid. The trigonid basin opens low and lingually. On the talonid, the hypoconid is the largest cusp with a crista obliqua joining the trigonid labially at the lingual base of the protoconid. The hypolophid abuts the entoconid. The entoconid is prominent and does not attach to the trigonid. No entoconid crest is present. A small metastylid is at the posterolabial base of the metaconid. A narrow valley is present between the entoconid and metastylid. The talonid basin is open lingually and low. Two roots are present.

Comparison.— A dentary of *M. latidens* (UCMP 29603) dentary with m2-m3 preserved from the deposits at Fish Lake (Esmeralda County, Nevada) is similar in size and shape to OMNH 54908. A few additional characters shared by OMNH 54908, OMNH 54909, and UCMP 29603 are the presence of a deep notch between the paraconid and protoconid, a cuspule at the base of the posterior side of the metaconid, and a small valley between this cuspule and the entoconid. However, specimens differ by the appearance of the cingulid and bulbousness of the m2. On the m2 of OMNH 54908, there is a strong anterior cingulid and the crown is bulbous, with the crown of the tooth overhanging the roots. UCMP 29603 has a very weak anterior cingulid and the crown is not bulbous; thus, the roots are not obscured. The mental foramen is not present on UCMP 29603 because the dentary anterior to the m2 is missing.

The m2 of *Metechinus nevadensis* (UCMP 29600) and OMNH 54908 are

similar in size; however, the other molars are shorter and wider with deep notches occurring in OMNH 54908. Furthermore, the p4 of OMNH 54908 and OMNH 54909 are much larger than the p4 of UCMP 29600.

Discussion.— Although the size of the m2 is similar between OMNH 54908 and UCMP 29600, they differ in other characteristics described above. In contrast, the similarity in tooth morphologies between UCMP 29603 and OMNH 54908 promotes the likelihood that they represent the same taxon. Until better material is recovered, the identification of this fossil is tentative.

Family Talpidae Vicq d' Azyr, 1792

Subfamily Uropsilinae Dobson, 1883

Mystipterus vespertilio Hall, 1930

Plate 1 (G-Q)

Localities.— Eastgate, UCMP V70147, UCMP V70140, and OMNH V974.

Age.— Barstovian.

Stratigraphic and biogeographic occurrences of the species.— Hemingfordian: Pawnee Creek Formation, Quarry A, Logan County, Colorado (Wilson, 1960); Barstovian: Quartz Basin fauna, Malheur County (Shotwell, 1963, 1967) and Clarendonian: Black Butte II fauna, Malheur County (Shotwell, 1963), Oregon; Fish Lake, Esmeralda Formation, Esmeralda County, Nevada (Hall, 1930).

Referred specimens.— OMNH 54931 left M2; OMNH 54932, left M2; OMNH 54933, left P4; OMNH 54935, left M2; OMNH 54937, left m3; OMNH 54939, left dentary fragment with m2; OMNH 54943, right m2.

Measurements.— See Tables 2 and 3.

Description.— The left P4 (OMNH 54933) has heavy wear on the occlusal surface. The paracone is the highest cusp on this tooth. The metacone and metacrista are indistinguishable because of the advanced stage of wear. The metastyle is preserved. A small parastyle is present at the anteromost corner of the tooth and occurs far below the paracone. The precingulum is present and joins a prominent protocone. A postcingulum extends from the protocone to below the metastyle. Two roots are present on this tooth. The anterior root occurs below the protocone and the posterior root occurs below the metastyle.

OMNH 54931 is a left M2 with little wear to the occlusal surface. The ectoloph is of medium height (for the talpids from Eastgate), W-shaped, and symmetrical. No ectocingula are present. The parastyle is absent. The paracone and metacone are equal in size. The mesostyle is the largest of the stylar cusps present. Both anterior and posterior cingulae are present. The anterior cingulum begins below the area of the parastyle and continues across the lingual surface of the protocone, then curves posteriorly as a posterior cingulum that terminates below the metastyle. A protoconule, preprotocrista, and protocone are present as are the postprotocrista and metaconule. The postmetaconule crista joins the posterior cingulum. No hypocone is present.

The posterior basil outline is concave.

The dentary fragment (OMNH 54939) with the m2 is broken through the anterior alveolus of the m1. Posteriorly, the dentary is incised through the anteromost alveolus of the m3.

The m2 (OMNH 54943) has little wear to the occlusal surface. A weak anterior cingulid is present and extends labially the length of the tooth before curving posteriorly, ending at the entostylid. A weak entocingulid is present (along the lingual side of the trigonid). The trigonid is much narrower and shorter than the talonid. The protoconid is the highest cusp on this tooth, with the metaconid and entoconid about equal in height (the hypoconid is too worn to compare), and the paraconid is the shortest. The protoconid and metaconid are closest to each other and are separated by a V-shaped notch. The ectocingulid closes the trigonid basin. The hypoconid connects to the labial side of the metaconid by a crista obliqua. The hypolophid ends at the base of the entoconid. The entoconid attaches to the trigonid by an entoconid crest that attaches about midway on the metaconid. No metastylid is present. The talonid basin is deep and closed lingually and labially. The hypoflexid opens at the level of the labial cingulid.

The m3 (OMNH 54937) has little wear to the occlusal surface and a strong anterior cingulid that begins at the anterolingual base of the paraconid and extends to the labialmost base of the protoconid, where it becomes much weaker but continues posteriorly to the posterolabial base of the hypoconid. At

this point, the cingulid is slightly stronger but becomes weak as it ascends toward the posterior end of the tooth. The trigonid and talonid are about equal in length but the trigonid is much wider. The protoconid is the highest cusp followed by the protoconid. The paraconid, hypoconid and entoconid are equal in height. On the trigonid, the protoconid and metaconid are closest to each other but are separated by a deep, V-shaped notch. The trigonid basin is open lingually and low on the tooth crown. On the talonid, the hypoconid joins the trigonid near the base of the metaconid. The hypolophid rests on, but does not join, the entoconid. A low entoconid crest is present and no metastylid is apparent. The talonid basin is closed and deep. The hypoflexid (reentrant valley) occurs at the level of the cingulid.

Comparison and discussion.— According to Hutchison (1968), two features characterize the uropsilin talpids (shrew-moles): the metastyle is absent and the cristid obliqua attaches directly to the protolophid.

These teeth closely resemble those of *M. vespertilio* (UCR 10048) described by Hutchinson (1968). OMNH 54933 is especially similar in sharing the following characteristics with *M. vespertilio* (UCR 10048): a P3 with three roots; a subtriangular, a low elongate protocone; a long paracone on labial edge; and a cingulum that encloses the entire tooth except for the lingual side of the protocone.

Mystipterus cf. *M. pacificus* Hutchison, 1968

Plate 2 (A-C)

Locality.— Eastgate, UCMP V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Quartz Basin, Malheur County, Oregon (Hutchison, 1968).

Referred specimen.— OMNH 54929, left M2.

Measurements.— M2: AP = 1.72, T = 1.93.

Description.— The left M2 (OMNH 54929) has little wear to the occlusal surface. The ectoloph is of moderate height, W-shaped, and slightly asymmetrical. No entocingula are present. The parastyle is hooked anterolingually. The mesostyle is the largest stylar cusp on this tooth and is twinned (with two peaks; see Hutchison, 1968). The paracone is slightly smaller than the metacone. No anterior or posterior cingula are present. A protoconule is present and is connected to a prominent protocone by the preprotocrista. A worn protocrista merges with the metaconule, and a discrete postmetaconule crista ends posteriorly between the base of the metacone and metastyle. The posterior margin of the tooth is straight.

Comparison and discussion.— OMNH 54929 is similar in size and shape to *M. pacificus* (UO 22510) described by Hutchison (1968). They share the following characteristics: rectangular outline (wider than long); twinned

mesostyle; metaconule slightly posterior to the level of the center of the metacone; and posterior margin of the tooth not concave. The later feature is one character that separates this species from *M. vespertilio*.

Although it is difficult to obtain specific identifications on isolated teeth, Hutchison (1968) described this species based on the morphology of an M2. The M2 (OMNH 54929) recovered from Eastgate is most similar to the M2 (UO 22510) described by Hutchison (1968). Therefore, until more complete material is present this tooth is placed within this species.

Mystipterus sp.

Plate 2 (D-I)

Localities.— Eastgate, UCMP V70147 and V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the genus.— Hemingfordian: Pawnee Formation (Wilson, 1960), Colorado and and Harrison Formation (Korth, 1992), Cherry County, Nebraska; Barstovian: Quartz Basin Fauna, Malheur County, Oregon (Shotwell, 1967); Clarendonian: Black Butte II fauna, Malheur County, Oregon and Esmeralda Formation, Fish Lake Valley fauna, Esmeralda County, Nevada (Hutchison, 1968).

Referred specimens.— OMNH 54916, isolated right m2; OMNH 54945, left dentary fragment with a fragment of the m1 and a complete m2; OMNH 54959,

right M3.

Measurements.— See Tables 2 and 3.

Description.— OMNH 54959 is a left M3 with little wear to the occlusal surface. The ectoloph is low, not W-shaped, and is asymmetrical. No ectocingula are present. The paracone is the prominent cusp on this tooth. The parastyle is anteroposteriorly elongate. The postparacrista and premetacrista unite labially at the mesostyle. The metacone is present. A prominent anterior cingulum is present, but there is no posterior cingulum present on this tooth. The protoconule is small and is not in close association with the protocone. The postprotocrista is long, narrow, and joins the metaconule. There is no postmetaconule crista present.

The m2 of OMNH 54916 is similar to OMNH 54945 except that the former has less wear to the occlusal surface; therefore, the following description is based on OMNH 54916. The tooth shows little wear to the occlusal surface and is pigmented on the upper one-half of the tooth crown. The tooth is high crowned and is not bulbous. A strong anterior cingulid becomes weaker along the labial side of the tooth but regains its strong appearance as it passes posterior to the hypoconid. The poster cingulid ends at the labial base of the entoconid and rests against a posterior accessory cusp. No lingual cingulid is present. The paraconid is the lowest cusp with all remaining cusps on this tooth of equal height. The metaconid and the paraconid are closer to each other than the protoconid is to the metaconid. The trigonid basin opens high on the tooth

crown. The hypoconid joins the trigonid on the lingual side of the protoconid. A postcristid joins the hypoconid to the base of the entoconid. The entoconid joins the trigonid by a low entoconid crest that is attached on the lingual margin of the metaconid rather than attaching more medially along the protoconid. This condition is similar to most shrews (not talpids). The entoconid is not cylindrical. Overall, the talonid basin is deep and does not open posteriorly between the hypoconid and the entoconid, or anteriorly between the entoconid and metaconid. The hypoflexid opens low but above the level of the cingulid.

Comparison and discussion.— Referral of these specimens to *Mystiptera* is based on the attachment of the crista obliqua directly to the protolophid and the lacking of a metastylid as described by Hutchison (1968) for this genus. OMNH 54916 differs morphologically from *M. vespertilio* in possessing a non-cylindrical entoconid on the m2, whereas in *M. vespertilio* the entoconid on the m2 is cylindrical.

Although these specimens are referable to *Mystipterus* as described by Hutchison (1968), they are dissimilar to the species *M. vespertilio*. The other moles from Eastgate strongly resemble *M. pacificus* that was described by Hutchison (1968). As lower molars have not yet been referred to *M. pacificus*, specific identification of the specimens from Eastgate is deferred until more complete material is available.

Domninoides sp.

Plate 2 (J-L)

Locality.— Eastgate, UCMP V70140 and V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the genus.— Arikareean: Harrison Formation, Cherry County, Nebraska (Korth, 1992). Barstovian: Guano Ranch fauna, Lake County and Quartz Basin fauna, Malheur County, Oregon (Hutchison, 1968).

Referred specimens.— OMNH 54938, right m3; OMNH 54940, left dentary fragment with m2; OMNH 54942, left dentary fragment m1-m3; and OMNH 54946, left dentary fragment with m1-m2.

Measurements.— See Table 3.

Description.— A left dentary fragment (OMNH 54942) with m1-m3 has little wear to the occlusal surface and the molars are high crowned. The dentary is broken anterior to the m1 and posteriorly at the base of the ascending ramus. There is no evidence of a mental foramen. No anterior cingulid or accessory cusps are present. However, on OMNH 54940 a strong anterior cingulid is present and extends from below the paraconid to the anteromost base of the protoconid. A weak labial cingulid begins below the posterolabial part of the protoconid and extends posteriorly to the anterolabial base of the hypoconid. A weak entostylid is present, but there is no posterior cingulid.

On the m1, the paraconid is the shortest cusp. The remaining cusps are about equal in height. The protoconid and metaconid are closely approximated but are separated by a deep notch. A lophid connects the metaconid to the paraconid preventing the trigonid basin from opening lingually. The hypoconid is connected to the metastylid by the crista obliqua. The metastylid is separate, but attached to the metaconid. The hypolophid attaches to the base of the entoconid. The entoconid is conical and does not have an entoconid crest. The talonid basin is deep and does not open lingually. The hypoflexid opens at the level of the cingulid. The trigonid is long and narrow compared to the wider, anteroposteriorly compressed talonid.

Unlike the m1, the m2 has a strong anterior cingulid that extends from anterior to the paraconid posteriorly, to the medial lingual base of the protoconid, where it joins a weak labial cingulid. The labial cingulid only spans the hypoflexid and ends at the anterolabial base of the hypoconid. A strong entostylid is present, but no posterior cingulid exists. The protoconid is the highest cusp on this tooth, and the paraconid is the shortest, while the hypoconid and entoconid are of intermediate height and are subequal. Although the trigonid and talonid are both compressed anteroposteriorly, the talonid is slightly wider than the trigonid. The paraconid and metaconid are closer to each other than they are to the protoconid. The trigonid basin is open low on the lingual side. The metaconid is heavily worn but remains separated from the protoconid by a V-shaped protolophid. The hypoconid joins the metastylid by the crista obliqua.

The metastylid is separate from the metaconid, but is attached to it by a small lophid. The hypolophid joins the entoconid. Similar to the preceding tooth, a deep V-shaped notch separates the entoconid from the metastylid but the depth of the talonid basin prevents it from being open lingually. The hypoflexid opens at the level of the labial cingulid.

On the m3, the anterior cingulid extends from the anteromost extent of the paraconid to the anterolingual base of the protoconid. A labial cingulid spans the hypoflexid. No entostylid is present; however, a weak posterior cingulid exists. The posterior cingulid begins below the apex of the entoconid but abruptly ends near the base of the entoconid. The trigonid does not appear as anteroposteriorly compressed as the talonid. The trigonid is wider than the talonid. The protocone is the highest of all the cusps on this tooth. The paraconid, protoconid, and metaconid are about equidistant from each other. The trigonid basin opens low and lingually. The hypoconid is prominent and connects to the metastylid by a cristid obliqua. It appears that two metastylids are present side-by-side. The cristid obliqua connects to the posterior of the two metastylids, which in turn joins the anterior metastylid. The anteromost metastylid joins the metaconid. No entoconid crest is present, but the depth of the talonid basin prevents it from opening lingually. The hypoflexid opens at the level of the labial cingulum.

Comparison.— Hutchison (1968) distinguished *Domninoides* from *Scalopoides* in that the latter lacks an entoconid crest on any of the molars, and

the cristid obliqua extends to the metastylid (thus, more labially placed) on the m2, while it occurs more lingually on the m1. The teeth listed here reflect the characters Hutchison (1968) outlined for *Domninoides* sp.

OMNH 54940 is very similar to Barstovian-age *Domninoides* described by Hutchison (1968) from Guano Ranch and the Quartz Basin in Oregon. A *Domninoides* reported by Dalquest et al. (1996) is very similar in size and morphology to these moles from Eastgate.

Discussion.— Hutchison (1968) described two basic patterns of the lower molars of talpids that are characteristic at the subtribe, tribe, or subfamily level. One pattern is depicted by the joining of the cristid obliqua of the m1 and m2 directly or labially to a well developed metastylid. This condition usually leaves the talonid basin open lingually. In the second pattern, the cristid obliqua attaches directly to the protolophid, as it does in shrews. In addition, the metastylid is usually absent or weak in this second pattern.

Subfamily Gailardiinae

Gaillardia cf. *G. thomsoni* Matthew, 1932

Plate 2 (M-O)

Locality.— Eastgate, UCMP V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Hemphillian:

McKay Reservoir (Shotwell, 1956), Oregon; upper Snake Creek beds (Matthew, 1932), Nebraska.

Referred specimen.— OMNH 54950, left dentary fragment with m2.

Measurements.— m2: AP = 2.31, TA = 1.60, TP = 1.60.

Description.— A left dentary fragment (OMNH 54950) with the m2 present and heavily worn. The dentary is robust and broken at the anterior alveolus on the m1. Posteriorly, the dentary is broken through the middle of the superior masseteric fossa and anterior to the mandibular condyle. A mental foramen occurs below the anterior alveolus of the missing m1. In addition to the alveolus of the m1, two alveoli occur posterior to the m2. A strong anterior cingulid is present but terminates before reaching the protoconid. No labial or posterior cingulids are present. A weak entostylid is present. The trigonid is not as long or wide as the talonid. On the trigonid, the paraconid and metaconid are closest to each other. The tooth is too worn to provide additional details regarding the trigonid. On the talonid, the entoconid and metastylid are closest to each other. The hypoconid connects to the metastylid by the cristid obliqua. The metastylid does not join the trigonid. The tooth is too worn to reveal more detail.

Comparison.— One of the most striking features of *G. thomsoni* is the crista obliqua, of the lower molars, that unites with the metastylid, which is separate from the metaconid. In all other talpids from Eastgate, the metastylid joins the metaconid and the crista obliqua unites with the metastylid that is united with the metaconid. Attachment of the crista obliqua is present in OMNH 54950.

Discussion.— Based on these unique features described by Hutchison (1968) this specimen is likely *G. thomsoni*.

Genus indet.

Locality.— Eastgate, UCMP V70140 and V70147.

Age.— Barstovian.

Referred specimens.— OMNH 54927, left M1; OMNH 54928, right M3; OMNH 54930, left M2; OMNH 54934, left M3; OMNH 54936, right M1; OMNH 54958, right p4.

Measurements.— See Table 2.

Description.— A right M1 (OMNH 54936) with moderate wear to the occlusal surface has an ectoloph that is low, not W-shaped (OMNH 54927 is W-shaped) and asymmetrical, and with a labial surface that is angulate. Ectocingula are lacking, but anterior and posterior cingula are present. The anterior cingulum extends from the parastyle lingually to the paraconule. The posterior cingulum begins below the metastyle and progresses lingually to the base of the metaconule. The parastyle is small and is detached from the paracone; thus, there is no preparacrista. The paracone is situated at the labial margin of the tooth and is smaller than the metacone. The postparacrista joins the weakly divided mesostyle. The metastyle projects posteriorly. The protocone and metaconule occur on the broad lingual cingulum. On the trigon,

the protocone is in close association with the protoconule; thus, the preprotocrista is short. However, the postprotocrista is long and broad. The metaconule and protoconule are about equal in size, but the protocone is slightly larger than either of these conules. No postmetaconule crista is present .

A left M2 (OMNH 54930) has moderate wear to the occlusal surface and most of the posterior cingulum is missing. The ectoloph is of medium height (for the Eastgate moles), W-shaped, and slightly asymmetrical. No ectocingula are present. The parastyle and mesostyle are equal in size. The paracone is slightly smaller than the metacone. No anterior cingulum is present; however, a posterior cingulum is present. The posterior cingulum begins below the metastyle and extends to the base of the metacone, where it is broken. The protocone is a prominent cusp on the trigon. The loph extending from the anterior base of the paracone is too worn to reveal any lophules or cristae. A metaloph joins the postprotocrista, but no metaconule is evident.

A right M3 (OMNH 54928) has little wear to the occlusal surface, has an ectoloph that is low, is not W-shaped, and is asymmetrical. No ectocingula are present. The paracone is the most prominent cusp on this tooth. The parastyle is large and is anteroposteriorly elongate. There is no separation between anterior and posterior mesostyles; thus, a single mesostyle is present. The postparacrista and premetacrista join labially at the mesostyle. The metacone is present. No anterior or posterior cingula are present. The protoconule is small and in close association with the protocone. The postprotocrista is long, narrow,

and joins the metaconule. No postmetaconule crista is present. There is a small notch on the labial side of the tooth between the protoconule and protocone. In OMNH 54934, this notch is not as deep as that on OMNH 54928.

A right p4 (OMNH 54958) with little wear to the occlusal surface has a protoconid that is the dominant cusp. A cingulid begins at the anterolingual part of the tooth and extends labially across the crown, terminating at the base of the entoconid. A small metaconid is present. The posteromost part of the entoconid is missing. Two prominent roots are present on this tooth.

Comparison and discussion.— These teeth closely resemble those described by Hutchison (1968) as Talpinae *incertae sedis* from Quartz Basin, Oregon. Until more complete material is available and the talpids from other localities are more accurately identified, these teeth remain unidentifiable at the genus level.

Family Heterosoricidae Viret and Zapfe, 1951

Genus *Trimylus* Roger, 1885 (=*Pseudotrimylus*, Gureev, 1971)

Pseudotrimylus cifellii, n. sp.

Plate 3 (A-C)

Holotype.— UCMP 141765-04, right dentary fragment with m1-m3.

Type locality.— Eastgate, UCMP V70138.

Etymology.— Named in honor of Richard L. Cifelli, whose contributions

and devotion toward the study of fossil mammals have enlightened many individuals.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimen.— Type only.

Measurements.— m1; AP= 2.06, TA= 1.53, TP=1.62: m2; AP=1.63, TA=1.69, TP=1.64: m3; AP= 1.52, TA= 1.38, TP=1.02.

Diagnosis.— A small heterosoricine that differs from *P. compressus*, *P. dakotensis*, and *P. mawbyi* in having a mental foramen below the trigonid of the m2. It also differs from these species in having an entoconid crest and a hypoconulid on the m1 and m2 (except *P. dakotensis*). Within the genus, *P. cifellii* is most similar to *P. roperi*, sharing the following characters: placement of the mental foramen below the trigonid of the m2; the m1 and m2 are low crowned, slightly bulbous, and have a slightly inflated labial cingulum extending from the paraconid posteriorly past the hypoconid; and the metalophid does not join the protolophid labially. However, the dentary and lower molars of *P. cifellii* and *P. roperi* differ by several characters: the mandibular foramen in *P. cifellii* occurs below the level of the tooth row, while in *P. roperi* this foramen occurs at the level of the tooth row; the m1 and m2 of *P. cifellii* do not exhibit a union between the hypoconid and entoconid as they do in *P. roperi*; instead, *P. cifellii* has a hypoconulid on the m1 and m2, with a low entoconid crest, lacking in *P.*

roperi on these teeth.

Description.— The dentary preserves a fragment of the lower incisor, three antemolar alveoli, the m1-3, and the anteromost part of the ascending ramus. The dentary of UCMP 141765-04 is massive and robust compared to the other species within this genus. The molars show little wear on the occlusal surface, and no pigmentation is present. The number of teeth that may have been housed by the three alveoli is difficult to determine because the dentary is broken. It is possible that as many as three additional teeth could have been present anterior to the m1. Wilson (1960) stated that no double-rooted premolars were known for any species of *Pseudotrimylus*. In addition, Repenning (1967) suggested one incisor, three antemolars, and three molars were usual for the lower teeth of this group.

For UCMP141765-04, there are several distinguishing features on the labial and lingual surfaces of the dentary. Excluding size, one of the most distinguishing features of this species is the placement of the mental foramen below the trigonid of the m2. Another notable feature of this species is a masseteric fossa that is deep, with only a superior fossa present. Therefore, unlike most shrews of this genus, UCMP 141765-04 lacks the bony ridge separating the superior fossa from the inferior fossa. On the lingual surface of the dentary, the mandibular foramen occurs below the level of the tooth row.

The lower molars are low crowned, slightly bulbous, display a slight inflation of the cingulid, and they decrease in size from first to last. On the m1-

m2, a low entoconid crest occurs between the entoconid and metaconid. The hypolophid and entoconid do not unite; thus, a hypoconulid is present, and the cristid obliqua and protolophid do not join labially. The talonid of the m3 appears as a crescent-like loph because the entoconid is reduced and not distinctly cuspate. The reduced entoconid promotes the appearance of a single cusp, the hypoconid.

Comparison.— Hutchison (1966), Repenning (1967), and Engesser (1979) listed distinguishing characteristics that included the dentary and the lower teeth for all North American genera of heterosoricinid shrews. Assignment to *Pseudotrimylus* is based on the following characteristics: the mental foramen is below the talonid of the m1 (except in *P. roperi*; it has a mental foramen that occurs below the trigonid of the m2); the m1 and m2 are low crowned, bulbous, have an inflated labial cingulid; and the m3 has a reduced talonid possessing a crescent-like loph (Repenning, 1967).

Four species of *Pseudotrimylus* have been described from Tertiary deposits in North America (Repenning, 1967). The oldest known taxon, *P. compressus*, is from the Oligocene of Colorado (Logan County) and Nebraska (Sioux County), described by Galbreath (1953) and Mawby (1960), respectively. Geologically younger species of this genus include *P. dakotensis* (discovered in Bennett County, South Dakota by R. A. Stirton in 1934), which is considered to be Arikareean in age (Repenning, 1967); *P. roperi* (discovered in Logan County, Colorado), described by Wilson (1960), who considered it to be Hemingfordian in

age; and *P. mawbyi* (collected in Lake County, Oregon by F. B. Van Houten in 1955), which is considered Barstovian in age (Repenning, 1967).

In *P. cifellii*, the mental foramen occurs below the trigonid of the m2, while in *P. compressus* it occurs below the talonid of the m1. The masseteric fossa in *P. cifellii* has only a single fossa (a superior fossa), a similarity to the condition found in *P. compressus*. *P. cifellii* has a mandibular foramen that occurs below the level of the tooth row, while in *P. compressus* the foramen occurs above or at the level of the tooth row. The m1 and m2 of *P. cifellii*, compared to those of *P. compressus*, are lower crowned, are more bulbous, have a greater inflation of the cingulid, and possess an entoconid crest. Unlike *P. cifellii*, *P. compressus* has a hypolophid and entoconid that unite. Neither species has a labial union of the cristid obliqua and protolophid. The m3 of both species has a crescent-like loph. The m1 and m2 of *P. cifellii* are similar in length to those of *P. compressus*, but the width in *P. cifellii* is greater; the m3 of *P. cifellii* is longer and wider than that of *P. compressus*.

In contrast to *P. cifellii*, the mental foramen occurs below the talonid of the m1 in *P. dakotensis*. Both species appear to have a single, superior masseteric fossa. *Pseudotrimylus cifellii* and *P. dakotensis* both have a mandibular foramen that occurs below the level of the tooth row. The m1 and m2 of *P. cifellii* differ from those of *P. dakotensis* in possessing a labial cingulid that begins at the protoconid and extends posteriorly past the hypoconid. On the m1 and m2 of *P. dakotensis*, the labial cingulum is restricted to the talonid of each tooth.

Pseudotrimylus dakotensis also differs from *P. cifellii* in that *P. dakotensis* does not have an entoconid crest on either the m1 or m2. However, *P. cifellii* and *P. dakotensis* share a unique character that is not apparent in any other species of this group, the presence of a hypoconulid on the m1 and m2. Neither species has a labial union of the cristid obliqua and protolophid. *Pseudotrimylus cifellii* and *P. dakotensis* have an m3 with a crescent-like loph on the talonid. However, the lower molar proportions differ between the species. The m1 of *P. cifellii* is slightly longer and much wider than that of *P. dakotensis*; the m2 of *P. cifellii* is similar in length, but much wider than *P. dakotensis*; and the m3 of *P. cifellii* is much longer and wider than that of *P. dakotensis*.

Unlike *P. cifellii*, the mental foramen of *P. mawbyi* occurs below the talonid of the m1. Both of these species have a single, superior, masseteric fossa. Similarly, *P. cifellii* and *P. mawbyi* posses a mandibular foramen that occurs below the level of the tooth row. Compared to *P. cifellii*, the lower molars of *P. mawbyi* are lower crowned, are more bulbous, and have a greater inflation of the labial cingulid. *Pseudotrimylus mawbyi* has no entoconid crest on the m1 or m2. In *P. cifellii*, the entoconid of the m1 and m2 do not merge with their respective hypolophid as seen in *P. mawbyi*. The cristid obliqua and protolophid on the m1 and m2 do not join labially in *P. cifellii* as they do in *P. mawbyi*. In both species, the m3 possesses a crescent-like loph on the talonid. All lower molars of *P. cifellii* and *P. mawbyi* differ in size. The m1 of *P. cifellii* is much smaller in length and width compared to that of *P. mawbyi* (see Repenning,

1967). In length, the m2 of *P. cifellii* is much smaller than *P. mawbyi*, while in width they are similar in size. *Pseudotrimylus cifellii* has an m3 that is similar in length to that of *P. mawbyi* but is slightly wider (see Repenning, 1967). Of the four species of *Pseudotrimylus*, previously known from North America, *P. cifellii* is most similar to *P. roperi*.

The similarities and differences between *P. cifellii* and *P. roperi* are listed below. Both taxa are similar in having a mental foramen that occurs below the trigonid of the m2. They also share the following characters of the lower molars: low crowned, slightly bulbous, and slightly inflated cingulid. On the m1 and m2, the cingulid are continuous from paraconid posteriorly past the hypoconid. The cristid obliqua and protolophid of the m1 and m2 do not join labially, and the reduction of the entoconid on the m3 creates a crescent-like loph. However, *P. cifellii* differs from *P. roperi* in that the masseteric fossa of *P. cifellii* has only a single fossa, a superior fossa. In *P. roperi*, a masseteric fossa with an inferior and superior fossa is present. The mandibular foramen occurs below the level of the tooth row in *P. cifellii*; in *P. roperi* it occurs at the level of the tooth row. In *P. cifellii*, the entoconid crest is present on the m1 and m2, while in *P. roperi* there is no entoconid crest present on any of the lower molars. The hypolophid of the m1 and m2 in *P. cifellii* do not fuse with the entoconid on the m1 or m2 as they do in *P. roperi*. Thus, a hypoconulid is present on the m1 and m2 of *P. cifellii*, whereas it is lacking in *P. roperi*. *Pseudotrimylus cifellii* differs from the smallest specimen of *P. roperi* (KUVP 10027; m1 AP=2.1, TP=1.5; m2 AP=1.8, TP=1.3;

m3 AP=1.5, TP=1.2) in having shorter lengths of the m1 and m2, but the width is greater for both teeth. The lengths of the m3 of *P. cifellii* and *P. roperi* are similar, but the width is greater in *P. cifellii* (see Repenning, 1967).

Discussion.— Based on the characters of the dentary and cheekteeth, UCMP 141765-04 represents a new species that is most similar to *P. roperi*. However, it is curious that the geologically older *P. roperi* lacks purportedly primitive features that are present in the younger *P. cifellii*. A North American taxon, *Domnina gradata* (Cope), was recognized by Repenning (1967) as the oldest and most primitive heterosoricine shrew. *Domnina* and *P. cifellii* share some primitive features that are not present in *P. roperi*. For example, the m1 and m2 of *P. cifellii* has an entoconid crest and hypoconulid present, while both are absent on the m1 and m2 of *P. roperi*. In contrast, *P. cifellii* and *P. roperi* share a feature that is unique to them and an older European taxon, *Dinosorex*; the placement of the mental foramen below the trigonid of the m2 (Engesser, 1975). These features suggest the possibility that *P. cifellii* and *P. roperi* could merit placement in a distinct genus, when the dentition is more fully known.

Pseudotrimylus compressus (Galbreath), 1953

Plate 3 (D-F)

Locality.— Eastgate, UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Orellan: Cedar Creek (Repenning, 1967), Colorado; Oligocene: Pine Ridge (Repenning, 1967), Nebraska.

Referred specimens.— UCMP 112209, dentary fragment with m1-m3 present; UCMP 112210, left m2.

Measurements.— UCMP 112209, m1 AP= 2.49, TA= 1.81, TP= 1.84; m2 AP= 1.89, TA= 1.77, TP= 1.65; m3 AP= 1.52, TA= 1.45, TP= 1.03: UCMP 112210, m2 AP= 1.914, TA= 1.469, TP= 1.434.

Emended diagnosis.— This is a small heterosoricine that differs from *P. cifellii* and *P. dakotensis* in lacking a hypoconulid on the m1 and m2. Lower molars of *P. compressus* can easily be distinguished from *P. dakotensis*, *P. roperi*, *P. mawbyi*, and *P. cifellii* in having a greater crown height and no bulbousness. In contrast, the m1 and m2 of *P. compressus* are similar to those of *P. roperi*, *P. mawbyi*, and *P. cifellii* in having a labial cingulid that extends from the paraconid posteriorly past the hypoconid. Similar to all known species of this genus (except *P. cifellii* and *P. dakotensis*), *P. compressus* lacks an entoconid crest and a hypoconulid on the m1 and m2. The m1 and m2 are similar to those

of *P. roperi* and *P. mawbyi* in having the hypolophid and entoconid that unite; union of the cristid obliqua and protolophid united labially, as in *P. mawbyi*. In addition, the talonid of the m3 posseses a crescent-like loph as in other species of this genus. *Pseudotrimylus compressus* differs from *P. roperi* and *P. cifelli* in the placement of the mental foramen below the talonid of m1. The dentary of *P. compressus* is not as massive as those found in the other species of this group.

Description.— The dentary preserves three antemolar alveoli and the m1-m3; it is broken anterior to the ascending ramus. The dentary of UCMP 112209 is not as massive and robust as those of other species within this genus. The lower molars show little wear on the occlusal surface, and no pigmentation is present. The number of antemolar teeth that may have occurred in this specimen is unknown.

Since UCMP 112209 is an incomplete dentary fragment, it is impossible to distinguish whether several important mandibular features of the dentary were ever present. These features include the masseteric fossa and mandibular foramen. The only distinguishing feature that remains on the dentary is on the labial surface; the mental foramen. According to Repenning (1967), one of the most distinguishing features for this group is the placement of the mental foramen below the trigonid of the m1.

The lower molars are high crowned, not bulbous, display a slight inflation of the cingula, are distinctly longer than wide, and decrease in size from first to last. On the m1-m2, there is no entoconid crest between the entoconid and

metaconid. Rather, there is a deep valley that separates the prominent entoconid from the metaconid. The hypolophid and entoconid unite, and the crista obliqua and protolophid join labially. Although the m3 is not as reduced in size when compared to other species of this group, the talonid of the m3 possesses a crescent-like loph.

Comparison and discussion.— The mental foramen in *P. compressus* and *P. dakotensis* occurs below the talonid of the m1. The m1 and m2 of *P. compressus* differ from *P. dakotensis* in possessing a labial cingulid that begins at the paraconid and extends posteriorly past the hypoconid. On the m1 and m2 of *P. dakotensis*, the labial cingulid is restricted to the talonid of each tooth. Both species lack an entoconid crest on any of the lower molars. *Pseudotrimylus compressus* does not have a hypoconulid present on the m1 and m2, but *P. dakotensis* does possess a hypoconulid on both teeth. The cristid obliqua and protolophid do not join labially in *P. dakotensis* as they do in *P. compressus*. In both species the m3 has a crescent-like lophid on the talonid. The lower molar proportions differ between these species. The m1-m3 of *P. compressus* are slightly longer, but much wider than *P. dakotensis*.

Pseudotrimylus compressus and *P. mawbyi* have a mental foramen that occurs below the talonid of the m1. Compared to *P. compressus*, the lower molars of *P. mawbyi* are lower crowned, are more bulbous, and have a greater inflation of the labial cingulid. Neither species has an entoconid crest on the m1 or m2. In *P. compressus* and *P. mawbyi*, the entoconid of the m1 and m2 merge

with their respective hypolophids. The crista obliqua and protolophid on the m1 and m2 join labially in both species. Likewise, they both have an m3 with a crescent-like lophid on the talonid. Comparable lower molars of *P. compressus* and *P. mawbyi* differ in size. The m1 of *P. compressus* is much shorter in length and width compared to *P. mawbyi*. In length, the m2 of *P. compressus* is slightly shorter than that of *P. mawbyi*, while in width they are similar in size. *Pseudotrimylus compressus* has an m3 that is similar in length to *P. mawbyi* but is wider.

Pseudotrimylus compressus and *P. roperi* differ in that *P. roperi* has a mental foramen that occurs below the trigonid of the m2 and has lower molars that are low crowned and slightly bulbous. Both species have a slightly inflated cingulid on the m1 and m2. On the m1 and m2, the cingulids are continuous from paraconid posteriorly past the hypoconid. The cristid obliqua and protolophid of the m1 and m2 of *P. compressus* join labially; they do not do so in *P. roperi*. Both species possess the crescent-like lophid on the m3. Neither species has an entoconid crest on the lower molars. On the m1 and m2 of both *P. compressus* and *P. roperi*, the hypolophids fuse with the entoconid. Thus, no hypoconulid is present on the m1 or m2 of either species. *Pseudotrimylus compressus* differs from the smallest specimen of *P. roperi* (KUVP 10027; m1 AP=2.1, TP=1.5; m2 AP=1.8, TP=1.3; m3 AP=1.5, TP=1.2) in having a greater length and width of the m1 and m2. The length of the m3 of *P. compressus* and *P. roperi* are similar, but the width is greater in *P. compressus*.

The mental foramen in *P. compressus* occurs below the talonid of the m1, while in *P. cifellii* it occurs below the trigonid of the m2. The lower molars in *P. compressus* are much higher crowned, are less bulbous, and have a less inflated cingulid than those of *P. cifellii*. *Pseudotrimylus compressus* does not possess entoconid crests on the m1 and m2 like those of *P. cifellii*. In *P. compressus*, the entoconid of the m1 and m2 merge with their respective hypolophid. On the m1 and m2, the entoconid and hypolophid of *P. cifellii* do not join. The crista obliqua and protolophid on the m1 and m2 join labially in *P. compressus*, but not in *P. cifellii*. In contrast to these differences, they both have an m3 with a crescent-like lophid on the talonid. The lower molars of *P. compressus* and *P. cifellii* differ in size. The m1 of *P. compressus* is longer and wider compared to *P. cifellii*. In length, the m2 of *P. compressus* is longer than that of *P. cifellii*, while in width they are similar in size. *Pseudotrimylus compressus* has an m3 that is similar in length to *P. cifellii*, but is wider. Of the five species of *Pseudotrimylus*, UCMP 112209 is most similar to *P. compressus*.

Similarities between *P. compressus* and UCMP 112209 are presented below. Characters of the m1 and m2 shared between UCMP 112209 and *P. compressus* includes a high crown that is not bulbous, a labial cinulid that is slightly inflated, an entoconid crest lacking, an entoconid and metaconid separated by a narrow valley, a hypolophid united with an entoconid, an m3 with a crescent-like lophid, and a mental foramen below the talonid of the m1. The lower molars of UCMP 112209 are longer than those reported by Repenning

(1967) for *P. compressus*. Based on the characters of the lower molars and dentary, UCMP 112209 and UCMP 112210 can be confidently referred to *P. compressus*.

Pseudotrimylus sp.

Plate 3 (G-R)

Localities.— Eastgate, UCMP V70140, UCMP V70147, and OMNH V974.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the genus.— Orellan: Lawson Ranch (Engesser, 1979) Goshen County, Wyoming; Colorado, and Nebraska (see Galbreath, 1953 and Mawby, 1960). Hemingfordian: Pawnee Creek Formation (Wilson, 1960), Colorado; Flint Hill fauna (Repenning, 1967), South Dakota. Barstovian: Beatty Butte fauna, Guano Ranch, and Snyder Creek (Repenning, 1967), Oregon.

Referred specimens.— OMNH 54922, left M3; OMNH 54925, left P4; UCMP 112214, left maxilla fragment with P4-M2; UCMP 112216, left I2; UCMP 112217, right I2 fragment; UCMP 112218, right M2; UCMP 112227, right i3; UCMP 112228, left maxilla fragment with M2-M3.

Measurements.— See Table 4.

Description.— UCMP 112214 is a left maxilla fragment with the P4-M2 present. There is little wear to the occlusal surface of these teeth, and no

pigmentation is evident. The maxilla is broken anterior to the anteromost root of the P4. The infraorbital foramen opens anteriorly into a large, oval-shaped antorbital depression. The depression opens dorsal to the paracone of the P4 and extends dorsally past the roots of the P4 and posterodorsal to the paracone of the M1. At the anteromost dorsal part of the antorbital depression is a foramen that opens posteriorly. The lacrimal foramen opens ventrally at the base of the jugal part of the zygomatic arch and dorsal to the metacone of the M1. The jugal is broken at a point lateral to the M2. The maxilla ends posterior to the M2.

A left I1 (UCMP 112216) has a basal cuspule on its lateral side similar to that of other soricids (Galbreath, 1953). The incisor widens anteriorly where a medial cuspule forms, producing a bifid distal end. Galbreath (1953) described a groove on the root of the incisor of *Pseudotrimylus* and suggested that this may indicate the fusion of two roots. Most of the root of UMCP 112216 is missing; therefore, it is unclear if a deep groove was present on the root. This tooth is also similar in morphology to a specimen of *Pseudotrimylus* (KUVP 10010) figured by Wilson (1960: figs. 19a, b).

The P4 has an ectoloph that is higher on this tooth than on any of the molars of this specimen. There is no parastyle. The paracone is anteriorly placed, followed by a postparacrista that becomes concave immediately but straightens before reaching the metastyle. No parastyle is present. A precingulum joins the protocone on the anterolingual margin of this tooth. There

is no hypocone or metaconule. A strong postcingulum encloses the talon basin. The posterior basal outline is straight.

On the M1, the ectoloph is low, W-shaped, and asymmetrical, with no ectocingula present. The parastyle is equal in size to the mesostyle. The paracone is smaller than the metacone and does not extend as far lingually as the metacone. The metastyle is the smallest of the stylar cusps. No posterior or anterior cingula are present; however, a weak lingual cingulum is present. The protocone is small and occurs along the midlingual margin of the trigon shelf. The trigon shelf is placed slightly more dorsally and is slightly larger than the talon shelf. A low metaloph joins the postprotocrista and forms a minute metaconule. The hypocone is small. The posterior basal outline is straight.

On the M2, the ectoloph is low, W-shaped, and symmetrical; ectocingulae are lacking. The parastyle is hooked anteriorly and is smaller than the mesostyle. The paracone and metacone are about equal in length, but the metacone is slightly wider. The metastyle is the smallest stylar cusp on this tooth and is smaller than the metastyle of the M1. A weak posterior cingulum begins below the metastyle and continues anteriorly and lingually to the base of the protocone. At the base of the protocone on the M2, the M1 rests against the M2; thus, it is unclear whether this cingulum continues anteriorly past this point. The protocone is small and occurs along the midlingual margins of the trigon shelf. Although the trigon shelf is placed more dorsally than the talon shelf, the talon shelf is larger. A strong postcingulum encloses the talon shelf. The M1

can be distinguished from the M2 based on the following characters of the M1: asymmetry of the ectoloph, slightly larger length and width, parastyle rounded not hooked, and talon shelf is not as long.

The M3 (UCMP 112228) is moderately worn and pigmented. The ectoloph is broad, low, not W-shaped, and ends posteriorly with the premetacrista. The metacone is absent. Of the stylar cusps, the parastyle is dominant. Likewise, the paracone is prominent. The trigon shelf begins anteriorly at the base of the paracone. The protocone is present on the trigon. The trigon is separated from the talon by a deep sulcus; however, no hypocone is present. A strong postcingulum, extending from below the protocone to the postmetacrista, encloses the talon shelf. Like most shrews, the ectoloph has three commissures; however, the ectoloph is as long as it is wide, giving the appearance that it is W-shaped.

The right i3 (UCMP 112227) has little wear to the occlusal surface and is complete (includes the distal end of the tooth and a complete single root). A fragment of the premaxilla is preserved on the lingual side. In morphology, this tooth is similar to *P. roperi* (KUVP 10030) described by Wilson (1960).

Comparison and *discussion*.— The only species of *Pseudotrimylus* for which parts of the upper dentary have been described are *P. roperi* (Wilson, 1960) and *P. mawbyi* (Repenning, 1967). Wilson (1960) identified the following upper teeth as belonging to *P. roperi*: a maxilla with P3-P4 (KUVP 10015), a maxilla with M1-M2 (KUVP 10018), and an isolated P4 (KUVP 10019). A single

isolate M1 of *P. mawbyi* was identified by Repenning (1967). The only species of *Pseudotrimylus* recovered from Eastgate, based on lower teeth and dentary, are *P. cifellii* and *P. compressus*. Therefore, until more complete material is available for *P. cifellii* and *P. compressus*, the maxilla and upper teeth of *Pseudotrimylus* from the Eastgate fauna remain indeterminate at the species level.

Family Soricidae Fischer, 1817

Subfamily Limnoecinae Repenning, 1967

Genus *Sorex* Linnaeus, 1758

Angustidens vireti (Wilson), 1960

Plate 4 (A–C)

Locality.— Eastgate, OMNH V976.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— late Hemingfordian: Colorado, Pawnee Creek Formation (Wilson, 1960).

Referred specimen.— OMNH 54920, right dentary fragment with p3–m3.

Measurements.— p3: AP = 0.77, T = 0.59; p4: AP = 0.62, T = 0.64; m1: AP = 1.53, TA = 0.86, TP = -; m2: AP = 1.24, TA = 0.88, TP = 0.85; m3: AP = 1.07, TA = 0.70, TP = 0.48.

Description.— The dentary preserves the p3–m3 with little wear to the

occlusal surface and pigmentation on the upper one half of the crown of each tooth. The p3 has not previously been described for this species but Repenning (1967) suggested the p3 was vestigial based on the following characteristics of the type specimen (KUVP 10037): 1) a small alveolus on the anterior margin of the alveolus of the p4; and 2) a p3 that is longer, more narrow, and lower crowned than the p4.

The p4 (OMNH 54920) is similar to that of KUVP 10044 described by Repenning (1967). The tooth is triangular in occlusal outline and has a strong posterolabial crest that joins the cingulid medially on the posterior part of the tooth. The posterolingual crest is weaker than the posterolabial crest and does not join the primary cusp (protoconid).

The m1-m2 each possess a strong anterior cingulid that becomes weak labially until it reaches the posterior part of the tooth, where it becomes prominent and reaches the base of the hypoconid. A weak lingual cingulid extends the length of the tooth. The protoconid is the highest cusp followed by the metaconid. These cusps are situated medially close to each other. The trigonid basin opens low and lingually. On the talonid, the hypoconid and entoconid are about equal in height. The hypoconid is separate from the entoconid; thus, a valley is present between them. A hypoconulid is present. The crista obliqua joins the trigonid medially between the protoconid and metaconid. The hypoflexid opens superiorly to the labial cingulid of the m1. On the m2, the hypoflexid occurs slightly superior to the labial cingulid. The

entoconid is pillar-shaped and connects to the trigonid by a high entoconid crest.

The trigonid of the m3 has a similar morphology to that of the preceding molars. However, the talonid of the m3 differs from the preceding molars. On the talonid, the crista obliqua joins the trigonid more medially than the preceding molars. The entoconid is much reduced and appears to join the trigonid lingual to the metalophid. Thus, a long narrow trough forms lingual to the entoconid crest, and a trenchant heel is present. The talonid basin is closed off from both the lingual and labial sides.

Comparison and discussion.— OMNH 54920 is identical in morphology and tooth pigmentation to KUVP 87027 (a right dentary fragment with the m1-m3 present). Based on morphology, OMNH 54920 is most similar to *A. vireti*. According to Harris (1998), the only known occurrence for *Angustidens* is the Quarry A fauna in Colorado studied by Wilson (1960). Therefore, the occurrence of *Angustidens* at Eastgate extends the temporal range of this genus into the Barstovian and extends its biogeographic range further west.

Limnoecus tricupsis Stirton, 1930

Plate 4 (D-I)

Locality.— Eastgate, UCMP V70140 and V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: California, Rodent Hill (Stirton, 1930; Lindsay, 1972). Clarendonian: California, Big Cat Quarry (James, 1963). Hemphillian: Oregon, Rome (Repenning, 1967).

Referred specimens.— OMNH 54911, left dentary fragment with complete m2 and a fragment of the m3; UCMP 141768-01, left dentary fragment with m1; UCMP 141768-02, right dentary fragment with p4–m3; UCMP 141768-04, right dentary fragment with talonid of m2–m3; UCMP 141768-05, left dentary fragment with p4–m1 and m2 fragment; and UCMP141768-07, left dentary fragment with m1–m3.

Measurements.— See Table 5.

Description.— A long slender dentary (UCMP 141768-02) is broken anterior to the p4 and posteriorly at the base of the ascending ramus. It is not clear how many antemolar teeth or what type of incisor were present. The mental foramen is placed below the middle of the trigonid of the m1. It is unclear if the p4 had a labial or lingual cingulid because the base of this tooth is fragmentary. The p4 has a medially placed labial crest that is typical of the limnoecines (Repenning, 1967).

The p4 is triangular in occlusal outline and limnoecine in morphology as described by Hutchison (1967), Lindsay (1972), and Repenning (1968). For example, the protoconid and metaconid occur closer to each other than of the genera of Soricidae (see Repenning, 1967). On the lingual side of the p4, a cingulid is present, begining anterorlingual to the lingual cingulid and extending

the length of the tooth.

On the m1 of UCMP 141768-02, four cindulids (anterior, posterior, labial, and lingual) are present. The anterior and posterior cingulids are strong, while the labial and lingual cingula are weak. The labial cingulid is not visible from above because the tooth is bulbous; thus, the tooth crown overhangs a weak cingulid. The trigonid is longer than the talonid. The protoconid is the highest cusp and is closest to the metaconid. The paraconid is equal in height to the hypoconid and metaconid. The trigonid basin opens low and lingually. The trigonid is much higher than the talonid.

On the talonid of the m1, the hypoconid is the dominant cusp and attaches to the trigonid at the base of the protoconid. The hypolophid is straight until it terminates as a posteriorly oriented hypoconulid. The hypolophid does not join the entoconid; thus, there is a valley between the hypoconulid and entoconid. The entoconid is pillar-shaped and joins the trigonid by a low entoconid crest. The hypoflexid occurs well above the cingulid. Except for slightly smaller size and a lower hypoflexid, the m2 is similar to the m1.

A left dentary fragment (OMNH 54911) has an m2 with little wear to the occlusal surface. No pigmentation is present on the m2. An anterior cingulid begins as a prominent structure on the m2 but becomes weaker as it reaches the base of the protoconid and merges with the labial cingulid. The labial cingulid continues across the length of the tooth and merges with the posterior cingulid that becomes prominent across the posterormost margin of this tooth. A

weak lingual cingulid extends the length of the tooth. The protoconid is the highest cusp followed by the metaconid, with the paraconid being the shortest of the trigonid cusps. The trigonid basin opens lingually and low but above the lingual cingulid.

On the talonid, the hypoconid is much higher than the entoconid and is separated from it, so that a valley is present between these two cusps. A hypoconulid is present. The crista obliqua joins the trigonid midway on the protolophid and at the lingualmost margin of the protoconid. The hypoflexid opens above the level of the labial cingulid. The entoconid is low and connects to the trigonid by a low entoconid crest.

Compared to the preceding molars, the m3 (UCMP 141768-02) is much reduced in size. The m3 has a strong anterior cingulid that grades into a weaker labial cingulid. On the labial side of this tooth, the posterior part of the protoconid is absent, but the anterior, medial, and lateral sides are present. The labial cingulid continues posteriorly to the posterior base of the hypoconid. A weak lingual cingulid is present. The protoconid is broken, but appears to have been the highest cusp and is closest to the metaconid. The paraconid is low but higher than the hypoconid. The trigonid basin opens low and lingually.

The talonid is much reduced and appears to possess a single medial cusp that projects posteriorly, the hypoconid. The crista obliqua joins the trigonid low and medially between the protoconid and metaconid. The talonid basin is shallow and opens on the lingual side. The hypoflexid opens low and above the

level of the cingulid.

Comparison and discussion.— Except for stages of wear, all of the specimens listed here are morphologically similar to *L. tricupsis* (UCMP 78581) from Rodent Hill of the Barstow Formation studied by Lindsay (1972). Similar to the shrews of the Barstow Formation, San Bernardino County, California, *L. tricuspis* from Eastgate are among the smallest shrews of the Eastgate fauna.

Limnoecus niobrarensis Macdonald, 1947

Plate 4 (J-L)

Locality.— Eastgate, UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Nebraska, Niobrara River (Macdonald, 1947); South Dakota, Glenn Olson Quarry (Green and Holman, 1977).

Referred specimen.— OMNH 54918, right dentary fragment with i3, p2-m3.

Measurements.— See Table 5.

Description.— The i3, p2-m3 do not appear to be pigmented and show little wear on the occlusal surface. The dentary is long, slender, and broken posterior to the m3; no ascending ramus is preserved. The mental foramen

occurs below the p4. The m1-m3 are high crowned and bulbous. The m1 and m2 are similar in size and shape. In contrast, the m3 differs in size and shape from the preceding molars.

The incisor is procumbent and is broken near the proximal end; thus, it is not diagnostic. The p2 has labial and lingual cingula. It is noticeably longer than wide and is low crowned. There is a single medial blade on the p2 and a shallow sulcus on the posteromedial part of the tooth.

Three premolars are present in this specimen. The p3 is vestigial; it is not noticeable in occlusal or lingual views. Labially, this tooth is seen under the anteromost tip of the p4. The p4 is triangular in occlusal outline and is limnoecine in morphology. The labial cingulid begins posterior to where the p3 occludes with the p4. On the lingual side of the p4, a cingulid is present and begins anterolingual to the lingual cingulid and extends the length of the tooth.

On the m1, there are anterior, posterior, labial and lingual cingulids. The anterior and posterior cingula are strong, while the labial and lingual cingula are weak. The labial cingulid is not visible from above because the tooth is bulbous. In addition, the tooth crown overhangs this weak cingulid. The trigonid is longer than the talonid. The protoconid is the highest cusp and is closest to the metaconid. The paraconid is equal in height to the hypoconid and metaconid. The trigonid basin opens low and lingually. The trigonid is much higher than the talonid.

On the talonid of the m1, the hypoconid is the dominant cusp; the crsta

obliqua attaches to the trigonid at the base of the protoconid. The hypolophid is straight until it terminates as a posteriorly-oriented hypoconulid. The hypolophid does not join the entoconid so that a valley is present between the two cusps. The entoconid is pillar-shaped and joins the trigonid by a low entoconid crest. The crista obliqua joins the protolophid medially. The hypoflexid occurs well above the labial cingulid. Except for slightly smaller size and placement of the hypoflexid lower on the tooth crown, the m2 is similar to m1.

Compared to the preceding molars, the m3 is much reduced in size. The m3 has a strong anterior cingulid that grades into a weaker labial cingulid. On the labial side of this tooth, the protoconid is missing but provides enough detail to be diagnostic. The labial cingulid continues posteriorly to the posterior base of the hypoconid. A weak lingual cingulid is present. The protoconid is the highest cusp and is closest to the metaconid. The paraconid is low but higher than the hypoconid. The trigonid basin opens low and lingually.

The talonid of the m3 is much reduced and appears to possess a single medial cusp – the hypoconid- that projects posteriorly. The crista obliqua joins the trigonid low and medially between the protoconid and metaconid. The talonid basin is shallow and opens on the lingual side. The hypoflexid opens low but above the level of the cingulid.

Comparison and discussion.— The only dentary or tooth characteristic separating *L. tricuspis* and *L. niobrarensis* appears to be the presence of a vestigial p3 in the latter species. The m3 is one of the most diagnostic elements

for the genus but does not appear to provide any character that would aid in the separation of these taxa (see descriptions above for the cheekteeth of both species). At present, it is unclear if these two taxa merit taxonomic separation.

Lindsay (1972) suggested that *L. tricuspis* and *L. niobrarensis* may be synonomyzed. James (1963) synonymized them and suggested any differences reflect sexual dimorphism. However, Harris (1998) and Reumer (1998) considered the two to be different species. I have treated these taxa as separate species.

Limneocus sp. indet.

Plate 4 (M-T)

Localities.— Eastgate, UCMP V70138, V70140, V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the genus.—

Hemingfordian: Vedder (Hutchison and Lindsay, 1974), California.

Referred specimens.— OMNH 54910, left dentary fragment with talonid of m1 and complete m2-m3; OMNH 54919, right maxilla fragment with P4-M1; OMNH 54963, I1; UMCP 141764, palate with left P4-M3 and right M1-M3; UMCP 141765-02, left maxilla fragment with P4-M3; UCMP 141765-03, right maxilla fragment with P3-M3; UCMP 141768-06 left P4; UCMP141769-02, right maxilla fragment with M1-M2 present; UCMP 141769-05 left P4.

Measurements.— See Tables 4 and 5.

Description.— A left I1 (OMNH 54963) is very small compared to the I1 described earlier as belonging to *Pseudotrimylus* and is similar in size to that of *Limnoecus tricuspis* described by Lindsay (1972). OMNH 54963 is not buccolingually compressed; instead, it is broad. This tooth has a basal cuspule on the lateral side as in most soricids (Galbreath, 1953). The tooth widens anteriorly where a medial and lateral cuspules occur producing a trifid distal end to the tooth. The root is complete and has a groove along the midline that may represent the fusion of two roots. A similar groove was described for the much larger taxon, *Pseudotrimylus*, by Galbreath (1953).

A right maxilla fragment (UCMP 141765-03) has the P3–M3 with the occlusal surface of these teeth showing moderate wear and no pigmentation. OMNH 54919, UCMP 141768-06, and UCMP 141765-02 have pigmentation on their cusps, but it is not as prominent as the pigmentation of UCMP 1414769-02; UCMP141769-02, has pigmentation on the crowns of each tooth; UCMP 141765-02 and UCMP 141765-03 do not have any pigmentation.

The P3 (UCMP 141765-03) is very small with the anterior half of the tooth missing. The maxilla is broken where the anteromost roots of the P4 occur. The maxilla preserves the antorbital depression that opens dorsal to the middle of the M1 and extends posteriorly and dorsal to the posteromost edge of the M2. The maxilla is broken posteriorly through the middle of the M3.

The M1 has a high ectoloph that is W-shaped and asymmetrical. No

ectocingula are present. The parastyle is large and oval in shape. The paracone is similar in size to the parastyle and does not extend as far lingually as does the metacone. The mesostyle is similar in size to the parastyle. The metacone is slightly higher and larger than the paracone. The metastyle is small and projects posteriorly but does not appear hooked. A posterior cingulum is present. This cingulum begins at the metastyle and continues anteriorly past the talon shelf and ends below the protocone. The protocone is larger than the hypocone. The trigon shelf is much higher than the talon shelf. A low metaloph is present and connects to the postprotocrista. No metaconule is present. A small hypocone is present. The talon shelf is longer, broader, and set lower than the trigon shelf. The posterior cingulum encloses the talon shelf. The posterior basal outline is concave. Except for a slightly larger size, the M2 is similar in morphology to the M1.

The M3 shows moderate wear and is not pigmented. It possesses a low ectoloph with three commissures. The parastyle is the highest style and sets well above the paracone. The paracone is the largest cusp on this tooth. A mesostyle and a premetacrista are present. No metacone is present. Likewise, there is no posterior cingulum. A large protocone is present, but there is no hypocone.

A left dentary fragment (OMNH 54910) has only the talonid of the m1, but the m2-m3 are complete. The occlusal surface of all molar teeth show little wear and no pigmentation. The crowns of these teeth are bulbous with a weak labial

cinguluid on the m1 and m2. A labial cingulid is present on the talonid of the m3. However, a weak lingual cingulid is present on all three molars and extends the entire length of each tooth.

On the talonid of the m1, the hypoconid is much shorter than the entoconid. These cusps do not unite above their bases; thus, a valley is present between them. A hypoconulid is present. The cristid obliqua joins the trigonid low and midway between the protoconid and metaconid. The entoconid is pillar-shaped, is the highest cusp, and connects to the trigonid by a low entoconid crest. The hypoflexid opens low but above the level of the labial cingulid of the m1; on each of the succeeding teeth, the hypoflexid opens lower on the tooth crown. For example, on the m2 the hypoflexid opens near the level of the cingulid, while on the m3 the hypoflexid opens at the level of the cingulid.

The protoconid of the m2 is the highest cusp of this tooth. The protoconid and metaconid are close to each other, and the trigonid basin opens above the lingual cingulid. The talonid of this tooth is the same as for the preceding tooth. The trigonid of the m3, except for size, resembles the preceding tooth in form. However, the talonid differs from the preceding tooth and the known species for Eastgate. Thus, it may represent a different species than those listed for Eastgate, but no species identification was possible for the available material. The talonid of the m3 has a hypoconid and entoconid present. A long narrow talonid basin is present.

Comparison.— The m1 and m2 of OMNH 54910 are similar to those of *L.*

tricuspis, but the m3 is morphologically different from that of *L. tricuspis*. In the past, the upper dentition was ignored for species identifications for North American fossil shrews. For example, Wilson (1960), Hutchison (1966), and Repenning (1967) relied on the lower teeth for taxonomic identification of the shrews included in their studies. Lindsay (1972) was the first to describe the upper teeth of *L. tricuspis*. Unfortunately, his identifications were based on size, crown height, and relative abundance of this shrew from the Barstow Formation, and not morphology of the lower dentition. Lindsay (1972) indicated that the upper cheekteeth of *L. tricuspis* most closely resembled those of *Anetsorex* described by Wilson (1960). Following Lindsay (1972) and Wilson (1960), the lower dentition and dentary of both *Limnoecus* and *Antesorex* are represented at Eastgate. However, it is unclear if any *Antesorex* upper cheekteeth are present. Lindsay (1972) suggested when more complete material becomes available it may be appropriate to synonymize the two species.

Discussion.— Except for the described characters of the m3 for *L. tricupsis*, OMNH 54910 resembles *L. tricuspis* in morphology. The m3 of OMNH 54910 possesses a narrow talonid basin, a hypoconid, and an entoconid. A crescent-shape talonid on this same m3 is unlike the trenchant talonid of the m3 found in *L. tricuspis*. With the taxonomic emphasis placed on the m3 of soricid taxa by earlier workers (Repenning, 1967; Hutchison, 1966), OMNH 54910 may represent a new species of *Limnoecus*. Until better material becomes available, these specimens cannot be assigned to a given species.

Subfamily Soricinae Fischer, 1817

Tribe Blarinellini Reumer, 1998

Alluvisorex arcadentes Hutchison, 1966

Plate 5 (A-E)

Locality.— Eastgate, UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the genus.— Barstovian: Quartz Springs and Skull Springs (Hutchison, 1966), Oregon; Hemphillian: Lemoyne Quarry (Bown, 1980), Nebraska.

Referred specimens.— UMPC 141769-01, left dentary fragment with m2-m3; and UCMP 141769-03, left dentary fragment with the proximalmost of the i3 and p2 present.

Measurements.— UCMP 141769-01, m2: AP = 1.28, TA = 0.68, TP = 0.65. UCMP141769-03, i3: T = 0.64; p2: AP = 0.71, T = 0.77. UO 22307, i3: T = 0.51; p2: AP = 0.45 (broken), T = 0.75 (see Hutchison, 1966).

Description.— The dentary (UCMP 141769-03) fragment with the proximalmost part of the i3 and p2 is broken posterior to the p2. No mental foramina are present. The incisor is procumbent and has two ridges on the dorsal surface that are separated by two shallow troughs. The p2 is pigmented on the upper one-half of the tooth. No other diagnostic characters are present

for this specimen.

A left dentary fragment (UCMP 141769-01) with the m2 and m3 is broken anterior to the anterormost root of the m1 and posterior to the m3, at the base of the ascending ramus. Two alveoli are present anterior to the m2, and the mental foramen occurs below the alveolus that likely housed the anterior root of the m1. The teeth are heavily worn, but no pigmentation is present. The labialmost parts of the m2 and m3 are missing; therefore, it is unknown whether a labial cingulid was present in these teeth.

Although the cusps of the m2 are worn, it is clear that the protoconid is the highest cusp. The protoconid and metaconid are closest but not as close as in *Limnoecus*. The paraconid is lingually placed and is in line anteroposteriorly with the metaconid. The trigonid basin of the m2 opens low but above the lingual cingulid. Most of the hypoconid is missing, but it is apparent that it does not join the entoconid. Thus, a valley is present between these cusps. A weak hypoconulid is present. The entoconid is pillar-shaped and joins the trigonid by a low entoconid crest.

On the m3, the protoconid is the highest cusp and is in close association with the metaconid. The trigonid basin opens low, near the cingulid. The hypoconid joins the trigonid low and midway between the protoconid and metaconid. The entoconid is worn but appears to have joined the metaconid forming a lingual border for the talonid basin. Lingual to the entoconid is a sulcus that forms a small trough.

Comparison.— Only two species of *Alluvisorex* are known from North America, *A. arcadentes* and *A. chasseae*. According to Repenning (1967), only the number of teeth differ between the two species. He listed the following number of teeth for *A. arcadentes* (noupper teeth; lowers include one incisor, three antemolars, and three molars) and for *A. chasseae* (upper teeth; one incisor, six antemolars, and three molars; lower teeth, one incisor, two antemolars, and three molars). Unfortunately, none of the Eastgate specimens are complete enough to provide information regarding the total number of teeth in the mandible. However, he did list the following characters shared by both species: molars that are low crowned; the m1 with entoconid and metaconid close to each other, high entoconid crest, and labial cingulid; and the m3 with reduced talonid, low entoconid crest, no entoconid, and prominent hypoconid. On the dentary, the mental foramen occurs below the middle of the m1. The characters listed above as shared by the two species occur on the Eastgate specimens. However, for the Eastgate specimens, the mental foramen occurs below the anterior root of the m1, while for those described by Hutchison (1966) the mental foramen occurs below the middle of the m1.

Discussion.— UCMP 141769-01 and UCMP 141769-03 are larger than *Limnoecus*. The m3 of UCMP 141769-01 is morphologically very different from the m3 of *Limnoecus*. Based on the similar morphology of *A. aradentens* and the Eastgate specimens (UCMP 141769-01 and UCMP 141769-03), they likely represent *A. arcadentes* rather than *Limnoecus*. *Alluvisorex arcadentes* (Type,

UO 22307) described by Hutchison (1966) shares the following features with the *A. arcadentes* from Eastgate; the cheek teeth possess a high entoconid crest, the hypolophid does not attach to the entoconid, and the entoconid is cone-shaped.

Tribe Blarinini Kretzoi, 1965

Adeloblarina sp. indet.

Plate 5 (F- H)

Locality.— Eastgate, UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of genus.— Barstovian: Malhur County (Repenning, 1967), Oregon; Bijou Hills Quarry (Green, 1985), South Dakota; Eastgate Formation (present study), Nevada.

Referred specimen.— UCMP 141769-04, left dentary fragment with talonid of m1 and m2-m3 complete.

Measurements.— m2: AP = 1.29, TA = 0.77, TP = 0.78; m3: AP = 1.01, TA = 0.65, TP 0.43.

Description.— The left dentary fragment (UCMP 141769-04) is broken in two places: 1) anteriorly through the junction of the trigonid and the talonid of the m1; and 2) posteriorly at the base of the ascending ramus. The m2-m3 are complete and show little wear. No pigmentation is present on any of the teeth.

No foramina are preserved on the lingual or labial surfaces of the dentary.

On the talonid of the m1, a labial cingulid extends posteriorly past the hypoconid. The hypoconid is the highest cusp on the talonid and joins the trigonid labially. A hypolophid does not join the entoconid; instead, the hypolophid terminates at the hypoconulid. A valley occurs between the hypoconulid and the entoconid. The entoconid is pillar-shaped and does not join the trigonid; thus, there is no entoconid crest present and a valley lies between the entoconid and trigonid. The talonid basin opens low and lingually in two places -anterior and posterior to the entoconid.

On the trigonid of the m2, the protoconid is the highest cusp followed by the metaconid and paraconid, which are equal in height. The protoconid and metaconid are closest to each other. The paraconid is equidistant from the protoconid and the metaconid. The paraconid and metaconid are anteroposteriorly aligned. An anterior cingulid is present and is more prominent than the labial cingulid that ends at the posterolingual base of the hypoconid. The trigonid basin opens low and lingually. The talonid of the m2 is similar to that of the m1.

The m3 is smaller than the m2, but the characteristics of the trigonid are similar. However, the talonid of the m3 differs from that of the m2, most notably is the morphology of the hypoconid and entoconid. The following are characteristics of the m3: the hypoconid and entoconid are not prominent cusps; the hypoconulid joins the entoconid, but the entoconid does not join the trigonid;

there is a broad valley between the entoconid and the trigonid; the labial cingulid terminates at the anterior base of the hypoconid; and the cristid obliqua joins the protolophid midway between the protoconid and metaconid. The latter is a more lingual union than what occurs on the preceding molars.

Comparison and discussion.— UCMP 141769-04 is similar to *A. berklandi* described by Repenning (1967). UCMP 141769-04 and *A. berklandi* share the following characters: a prominent conical-shaped entoconid, no entoconid crest, hypolophid separate from the entoconid, entoconid close to the metaconid, labially placed cristid obliqua (one m1 and m2), and teeth not bulbous. In contrast, the m1 and m2 of UCMP 141769-04 differ from *A. berklandi* in possessing a hypoconulid and in lacking a lingual cingulid. The m1 and m2 of *A. berklandi* have a hypolophid that joins a lingual cingulid. Therefore, the latter species does not possess a hypoconulid on the m1 or the m2, unlike UCMP 141769-04.

Based on the above morphological characters described for the Eastgate shrew, UCMP 141764-04 differs from those examined by Repenning (1967). The Eastgate shrew is likely a new species of *Adeloblarina*, but I hesitate to name this shrew until more complete material is available.

Tribe Soricini (Fischer, 1817)

Genus *Antesorex* Repenning, 1967

Antesorex compressus (Wilson, 1960)

Plate 5 (I-K)

Locality.— Eastgate, UCMP V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Hemingfordian: Pawnee Creek Formation (Wilson, 1960), Colorado; Rosebud Formation (Martin and Green, 1984), South Dakota; Batesland Formation (Martin, 1976), South Dakota.

Referred specimen.— OMNH 54913, left dentary fragment with m2.

Measurements.— m2: AP = 1.28, TA = 0.80, TP = 0.78.

Description.— The m2 (OMNH 54913) has little wear on the occlusal surface, and no pigmentation is present. The anterior cingulid of this tooth is weak and becomes weaker along the labial margin of the tooth. In fact, the labial cingulid is difficult to detect. However, because this tooth is not bulbous, the entire length of the labial cingulid is visible from an occlusal view. There is a weak lingual cingulid that extends the length of the tooth. The protoconid and metaconid are not in close association with each other as they are in the genus *Limnoecus*. The trigonid basin opens low but above the lingual cingulid.

On the talonid, the hypoconid is slightly higher than the entoconid. The

hypoconid does not join the entoconid; thus, a valley forms between these two cusps, and a hypoconulid is present. The entoconid joins the trigonid by a low entoconid crest. The crista obliqua joins the trigonid labial to the metaconid. The hypoflexid opens labially and low but above the labial cingulid.

Comparison and discussion.— The m2 of OMNH 54913 is similar in size and morphology to the m2 of *Antesorex* from the Pawnee Creek Formation, Colorado described by Wilson (1960). Based on the Eastgate shrews, OMNH 54913 is larger than *Limnoecus* but smaller than *Angustidens*.

Although *Antesorex* and *Limnoecus* are similar, the Eastgate shrews display one feature that is unequivocally different, the shape of the entoconid. *Antesorex* has an entoconid that is pillar-shaped, whereas the entoconid of *Limnoecus* is not. Based on size and shape, OMNH 54913 most closely resembles *A. compressus* (KUVP 10056) from the Pawnee Creek Formation of Colorado (Wilson, 1960).

Antesorex sp. indet.

Plate 5 (L–N)

Locality.— Eastgate, UCMP V70140 and V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence for the genus.— Hemingfordian: Pawnee Creek Formation (Wilson, 1960), Colorado (Repenning,

1967); Batesland Formation, South Dakota (Martin, 1976).

Referred specimens.— OMNH 54917, left M2; UCMP 141768-03, right maxilla fragment with P4–M3.

Measurements.— See Table 4.

Description.— The maxilla that remains for UCMP 141768-03 is minimal; only the part that is directly associated with the tooth battery remains. The teeth present are pigmented on the occlusal surface, and moderate wear is evident on all of the teeth. The P4 has a high ectoloph that is straight. A small parastyle is present and occurs far inferior to the paracone. The paracone is the largest cusp on this tooth. A small metastyle is present. A posterior cingulum is present and extends from the metastyle along the posterior margin of the tooth, following the talon shelf anteriorly and reaching the anterorlingual cingulum and cingular cusps.

The M1 (UCMP 141768-03) has moderate wear, and pigmentation is present on the upper one-third of the cusps on the ectoloph. The ectoloph is high, W-shaped, and asymmetrical. No ectocingula are present. The parastyle is large and oval in shape. The paracone is similar in size to the parastyle and does not extend lingually as far as the metacone. The mesostyle is similar in size to the parastyle. The metacone is slightly higher and larger than the paracone. The metastyle is small and projects posteriorly but does not appear hooked. A posterior cingulum is present. This cingulum begins at the metastyle and continues anteriorly past the talon shelf, terminating below the protocone.

The protocone is larger than the hypocone. The trigon shelf is much higher than the talon shelf. A low metaloph is present and connects to the postprotocrista. No metaconule is present, but there is a small hypocone. The talon shelf is larger, is broader, and occurs lower than the trigon shelf. The posterior cingulum encloses the talon shelf. The posterior basal outline is concave. Except for the noticeably larger size of the M1, the M2 is similar to the M1.

A left M2 (OMNH 54917) has little wear to the occlusal surface, and no pigmentation present. The ectoloph is low, W-shaped, and slightly asymmetrical. Of the stylar cusps, the metastyle is the highest, while the parastyle has the largest diameter base. No ectocingula are present. A protocone is present, but the talon is missing. Thus, it is not possible to determine whether a hypocone was present. The trigon basin is deep and anteroposteriorly narrow. A metaloph and a posterior cingulum are present. The basal outline for this tooth is slightly concave on the lingual margin, while it is slightly convex on the labial margin.

The M3 (UCMP 141768-03) is moderately worn and is slightly pigmented. The ectoloph is low and contains only three commissures. The parastyle is the highest style and lies well above the paracone. The paracone is the largest cusp on this tooth. A mesostyle and premetacrista are present. No metacone or posterior cingulum is present. A large protocone is present, but there is no evidence of a hypocone. The talon basin is enclosed by the large protocone.

Comparison and discussion.— *Antesorex* has a less developed parastyle

on the P4 similar to UCMP 141768-03. On the M1 and M2, the hypocone and metacone are more pronounced than those present in *Limnoecus* (Wilson, 1960).

Lindsay (1972) suggested that the upper teeth of *Antesorex* and *Limnoecus* are more similar in size and characters than they are to those of other soricids. Both taxa have a posterior cingulum and lack an anterior cingulum, but the metaconule shelf is not as large or reach as high in *Antesorex* as in *Limnoecus*. Lindsay (1972) indicated the upper teeth of these taxa are similar in size. Unfortunately, he did not mention whether the lowers were different in size for these taxa. However, of these taxa, the lower teeth of *Limnoecus* and *Antesorex* identified from Eastgate (Nevada) and Quarry A (Colorado) differ in size, the latter being larger. Although a single species is currently known for *Antesorex*, no species identification is made for the specimen reported here; more complete material is needed. The Eastgate specimen may represent a new species.

Genus indet.

Locality.— Eastgate, UCMP V70140 and V70147.

Age.— Barstovian.

Referred specimens.— OMNH 54923, antemolar; OMNH 54924, antemolar; UCMP 112219, antemolar; UCMP 112220, antemolar; UCMP

112222, antemolar.

Measurements.— OMNH 54923, AP = 0.75, T = 1.04; OMNH 54924, AP 0.84, T = 0.74; UCMP 112219, AP = 1.11, T = 1.19; UCMP 112220, AP = 1.54, T = 1.23; UCMP 112222, AP = 1.60, T = 1.25.

Discussion.— All of these antemolar (teeth anterior to the molars, except the incisors) teeth surely belong to small insectivores but are unidentifiable. In size, they differ from one another, but all the teeth are too heavily worn, and do not reveal any diagnostic characters. However, they do possess pigmentation. Therefore, based on the size and pigmentation of these teeth, they are considered to be from soricids.

Order Chiroptera Blumenbach, 1779

Family indet.

Locality. Eastgate, UCMP V70140 and V70147.

Age. Barstovian.

Referred specimens.— OMNH 54955, right canine; UCMP 141619, loci unknown (specimen is lost).

Measurements.— c: AP = 1.62, T = 0.91.

Description.— The fragment of a right lower canine (OMNH 54955) with most of the crown missing is broken above the cingulid. The cingulid is the most striking character and is the basis for identifying this specimen as a

member of the Chiroptera (N. J. Czaplewski personal communication). The cingulid is prominent and circumscribes the base of the tooth crown. A single large root is present.

Discussion.— Two isolated, and fragmented, teeth from two sites (UCMP V 70140 and V 70147) at Eastgate are identified as Chiroptera. One of the two teeth (UCMP 141619) has been misplaced. The remaining specimen was collected in 1995 and is described above. Unfortunately, the only chiropteran tooth accounted for is too incomplete for identification beyond order. The size, shape, and characteristics mentioned above for OMNH 54955 separate this specimen from the other insectivores recovered from Eastgate.

Order Lagomorpha Brant, 1855

Family Ochotonidae Thomas, 1897

Genus *Desmatolagus* Matthew and Granger, 1923

Desmatolagus cf. *D. schizopetrus* Dawson, 1965

Plate 6 (A–I)

Localities.— Eastgate, UCMP V70140, V70142.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Hemingfordian: Split Rock local fauna, Split Rock Formation, Fremont County, Wyoming (Love, 1961; Dawson, 1965).

Referred specimens.— UCMP 141719, right maxilla fragment with P3–M1; UCMP 141736-05, right m3; UCMP 141736-03, right dp3; UCMP 141736-07, right upper molariform tooth; UCMP 141750-01, right maxilla fragment with P3–M1; UCMP 141750-02, left P3; UCMP 141763-05, M3; UCMP 141860, left upper molariform tooth.

Measurements.— See Tables 6 and 7.

Description.— The following is a list of terms associated with the descriptions of lagomorph teeth (see White, 1987,1991a, 1991b; Voorhies and Timperley, 1997): IAR (internal anterior reentrant), posterointernal reentrant (PIR), AER (anterior external reentrant), PER (posterior external reentrant), AIR (anterointernal reentrant), PIR (posterointernal reentrant), MAR (main anterior reentrant), and EAR (external anterior reentrant). The characters listed were identified and measured based on the work of previous researchers (Voorhies and Timperley, 1997; White, 1987). Details on these structures and points of measurements taken for the P2s and p3s are indicated in Fig. 8. A right maxilla fragment with the P3-M1 present (UCMP 141719) is broken through the anteromost alveoli of the P3 and posteriorly through the anteromost part of the alveoli of the M2. The palate that remains is minimal, but a single large lingual foramen is preserved below the P3. A second, maxilla fragment is similar to UCMP141719 except for the presence of two foramina rather than a single premolar foramen on the palate. These foramina occur along the lingual side of the trigon and talon. Labially, only the base of the zygomatic arch is preserved.

The P3 is short and wide, while the P4 is nearly as long as wide and the M1 is wider than long. The P3 and M1 are wider than the P4, but the P4 is longer than the P3 or the M1.

The P3 is not molariform but is unilaterally hypsodont with a strong lingual root and two weaker labial roots. It possesses a shallow hypostria (typically lost with advanced wear); no IAR (internal anterior reentrant) is present; an MAR (main anterior reentrant) that is cement-filled reaches more than one-half the length of the tooth, and is strongly deflected labially. The EAR (external anterior reentrant) is cement-filled, slightly deflected labially, and reaches about one-half the length of the tooth. On the anterolabial part of this tooth, a buccal cuspule is present and would remain through late stages of wear.

The P4 is molariform and is unilaterally hypsodont, with a single, strong lingual root and two labial roots that are much weaker. The talon is longer and wider than the trigon. A shallow, cement-filled hypostria occurs anterolingual to the lingualmost edge of the crescentic valley. The crescentic valley is V-shaped. The anterior arm of the valley closes before reaching the labialmost part of the trigon. The posterior arm of the crescentic valley narrows as it reaches the labial margin of the trigon but remains open to the labial margin of the talon. Two cuspules are present on the labial margin of the tooth; one is associated with the trigon and the other with the talon.

The M1 is molariform and is unilaterally hypsodont with one large lingual root and two labial roots that are much weaker. The trigon is longer and wider

than the talon. A narrow, cement-filled hypostria crosses one-third of the width of this tooth and terminates in a transverse line with a J-shaped crescentic valley. The anterior arm of the valley is closed. Two cuspules are present, one each on the labial margins of the trigon and talon. Wear stages seem to affect the cheekteeth in their occlusal morphology. For example, the M1 has a posterior arm of the crescentic valley that is J-shaped, but owing to wear on the labial margin of the tooth a transverse enamel lake almost connects with the posterior arm of the crescentic valley and the hypostria, and the M1 is very narrow and almost incised in half. If the anterior and posterior walls of the hypostria for the M1 were joined midway along its transverse path in a later stage of wear, an isolated enamal lake would be formed.

The dp3 has an anterior loph that has a single, strong anterolabial groove and is separate from the trigonid. The trigonid is as longer than wide. Two labial folds and three lingual folds are present. The posterior wall of the trigonid has a medial protrusion that projects posteriorly to join the talonid sublingual. The talonid is wider but anteroposteriorly narrower than the trigonid. The medial two-thirds of the anterior wall of the talonid is straight but is notched along the posterior labial groove. On the posterior wall of the talonid a posterior lophid is present (see Storer, 1975).

A right m3 (UCMP 141736-05) is hypsodont and possesses two strong roots. one root occurs below each loph of this tooth. The trigonid is wider than long, with an enamel lake that is centered and traverses three-quarters of the

width of the tooth. The posterior wall of the trigonid has a posteriorly directed medial protrusion. The talonid is nearly as long as wide and has an anterior protrusion on its anterior wall joining the trigonid medially. Cementum separates the trigonid and talonid, which do not join until reaching the base of the

crown.

Comparison and discussion.— Except for the dp3, all teeth listed above have been previously described for *Desmatolagus*. Therefore, the following comparisons include all but the dp3. Although these ochotonids from Eastgate are large, it is clear they belong to ochotonids rather than leporids based on a premolar foramen (Dawson, 1965) as seen in UCMP 141719. However, the other species of *Desmatolagus* (*D. robustus* and *D. vetustus*) do not posses this character. *Desmatolagus schizopetrus* described by Dawson (1965) was based on isolated teeth. The Eastgate specimens, being more complete, demonstrate the presence of a premolar foramen for this taxon. This character is a typical ochotonid character, but is absent in *D. robustus* and *D. vetustus*, while being present in *D. gobiensis*. However, *D.* cf. *D. schizopetrus* from Eastgate differs from the later in being larger than *D. gobiensis*.

Desmatolagus cf. *D. schizopetrus* from Eastgate is similar in size to *Russellagus vonhofi*, but differs from *R. vonhofi* in that *D.* cf. *D. schizopetrus* has the following characters (Storer, 1970; 1975): an isolated fossette (amphicone; see Storer, 1975) occurs closer to the buccal margin of the tooth in upper

molariform teeth; the lingual hypostria is relatively transversely longer; and the crescentic valley does not display anterior forking.

Dawson (1965) suggested a large ochotonid (*Desmatolagus*) from the Split Rock local fauna was more similar in size to leporids (*Hypolagus*) than to ochotonids (*Oreolagus*) and was less abundant. Likewise, the *Desmatolagus* from Eastgate are much larger than any of the rootless or rooted ochotonids from Eastgate and are less common. In contrast, Storer (1975) found two large taxa of ochotonids with rooted teeth more abundant than leporids (*Hypolagus*) at the Kleinfelder Farm locality, while the smaller rootless ochotonid (*Oreolagus*) was absent from the fauna.

The genus name *Desmatolagus* has been used for Asiatic and North American fossil ochotonids and with hesitation by Dawson (1965) for a new species of large, primitive, and very different ochotonids from the Split Rock fauna. Voorhies (1990) stated that *Russellagus vonhofi* may be a synonym of *D. schizopetrus*. However, herein I follow Dalquest et al. (1996) and accept both *D. schizopetrus* and *R. vonhofi* as valid taxa. Further investigation of this issue is beyond the scope of this paper; however, it is a topic that should be pursued.

Oreolagus nebrascensis McGrew, 1941

Plates 6 (J-O)

Locality.— Eastgate, OMNH V974, UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Arikeerean: Marsland Formation, Dawes County, Nebraska (McGrew, 1941). Hemingfordian: Split Rock local fauna, Split Rock Formation, Fremont County, Wyoming (Dawson, 1965). Barstovian: Virgin Valley, Esmeralda Formation, Esmeralda County, Nevada (Dawson, 1965).

Referred specimen.— OMNH 54970, right dentary fragment with dp3, dp4 m1; UCMP 141716-01, right dp3; UCMP 141716-05 is a left upper molariform; UCMP 141717-06, left upper molariform; UCMP 141720-01, right upper molariform; UCMP 141720-03, left dp3; UCMP 141720-14, right dp3; UCMP 141720-17, right P2; UCMP 141720-19, left lower molariform.

Measurements.— See Tables 6 and 7.

Description.— UCMP 141720-17, a right P2 has little wear to the occlusal surface. No roots are apparent. A shallow lingual hypostria is present and two reentrants occur on the anterior surface (EAR, MAR). A cement-filled MAR reaches more than one-half the length of the tooth and projects in a straight line posteriorly. The EAR is shallow and lacks cementum. The EAR would disappear with slight wear.

An upper left molariform tooth is hypsodont and rootless. The trigon is longer and wider than the talon. The hypostria transverses more than one-half the width of the tooth, and the anterior and posterior walls are straight. Two characters of the occlusal surface appear to vary with wear: 1) the crescentic valley varies from J-shaped to U-shaped; and 2) an enamel lake may be absent or present.

A right dentary fragment (OMNH 54970) with the dp3, dp4 m1 preserved is broken along the anterior lophid of the p3 and posteriorly through the alveolus of the m2. The labial side of the dentary is preserved but no foramina are visible. On the lingual side of the jaw, no dentary is preserved; thus, the roots of the cheek teeth are exposed. The teeth are unworn and appear to have barely erupted or, as for the m1, not erupted. The cheek teeth are longer than wide and decrease in size from front to back.

The dp3 has an anterior loph that has a strong anterolabial groove, has a weak anterolingual groove, and is separate from the trigonid. However, with additional wear to the occlusal surface, the anterior lophid and trigonid would join labially but remain separated from the labialmost part of the tooth to the lingual margin. The trigonid is as long as it is wide. The anterolabial wall of the trigonid protrudes anteriorly and would be the point of attachment for the anterior lophid. The posterior wall of the trigonid has a medial protrusion that projects posteriorly to join the talonid. The talonid is wider than long and more anteroposteriorly compressed than the trigonid. The medial two-thirds of the anterior wall of the

talonid is straight but has a deep labial groove on the anterolabial margin. The posterior wall of the talonid is interrupted medially by a groove on the posterolabial side of the tooth.

The dp4 has a trigonid that is as long as it is wide. The anterior wall of the trigonid is interrupted on the lingual side by a strong groove and on the labial side by a weak groove. These grooves promote the formation of a medial, anteriorly directed broad protrusion. The posterior wall of the trigonid has a medial, posteriorly directed, sharp protrusion that connects to the talonid to the trigonid. The shape of the talonid is similar to that of the dp3 except that the posterior wall has two grooves rather than one. These grooves form a medial, posteriorly directed protrusion.

The m1, for the most part, is obscured from view by the dentary bone. This tooth obviously was not erupted during the life of this pika. The trigonid appears similar to the trigonid of the preceding teeth but the lingual groove is not present. The posterior wall of the trigonid appears to be straight. The talonid is obscure from view.

Comparison and discussion.— The only genus of ochotonid without prominent roots is *Oreolagus* (Barnosky, 1986; Dalquest et al., 1996; Dawson, 1965). In size, *O. nebrascensis* differs from the Eastgate specimen in being larger than *O. colteri*, *O. nevadensis*, and *O. wallacei*. It is most similar in size to *O. nebrascensis* and *O. wilsoni*. The dp3 from Eastgate differs from *O. colteri* in possessing two grooves on anterior surface of tooth rather than a single groove.

According to Barnosky (1986), two species of *Oreolagus* (*O. nebrascensis* and *O. wilsoni*) possess two grooves on the anterior surface of the dp3. The hypastria of the upper molariform teeth are straight-walled for the Eastgate specimen, whereas in *O. wallacei* they are deep, nearly reaching the crescentic valley. Therefore, until more complete material from Eastgate is available for this species, these specimens are tentatively identified as *O. nebrascensis*.

Although there are numerous ochotonid specimens from Eastgate, most possess upper and lower cheekteeth that are rooted. The rootless ochotonids from Eastgate are few. This is in contrast Quarry A, Split Rock, and Beatty Buttes faunas that possessed ochotonids (Dawson,1965). In fact, Dawson (1965) suggested *Oreolagus* was the most abundant lagomorph from these fossil faunas. Storer (1975) reported lagomorphs from a Barstovian fauna, the Kleinfelder Farm locality of Saskatchewan. He suggested there were more ochotonids than leporids. Two species of rooted ochotonids (*Hesperolagomys* and *Russellagus*) were reported from Kleinfelder farm, while no species of *Oreolagus* were indicated from Kleinfelder farm (Storer, 1975).

Oreolagus colteri Barnosky, 1986

Locality.— Eastgate, UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian:

Colter Formation, Teton County, Wyoming (Barnosky, 1986).

Referred specimen.— UCMP 141737-16, right dp3.

Measurements.— See Tables 6 and 7.

Description.— A right dp3 (UCMP 141737-16) with moderate wear to the occlusal surface has an anterior loph with a strong medial groove that is separate from the trigonid. The anterior wall of the trigonid is straight, while the posterior wall has a labial posteriorly directed protrusion. This protrusion joins the talonid. The anterior wall of the talonid is concave posteriorly. The occlusal surface, of the talonid, is anteroposteriorly compressed on the labial and lingual ends. The labial side shows a stronger anteroposteriorly compression than is present on the lingual side. Thus, the medial two-thirds of the posterior wall of the talonid is the longest part of the talonid creating a convace posterior wall on the talonid.

Comparison.— The dp3 of *O. colteri* is similar in size to *O. nebrascensis* and *O. wilsoni*. *Oreolagus colteri* differs from these species in the morphology of the anterior loph. In *O. colteri*, a single, strong, medial groove is present, whereas two grooves separated by a median lobe are present in *O. nebrascensis* and *O. wilsoni* (Barnosky, 1986).

Russellagus cf *R. vonhofi* Storer, 1975

Plate 7 (A–E)

Locality.— Eastgate, OMNH V974; UCMP V70140, V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Wood Formation, Saskatchewan (Storer, 1975).

Referred specimens.— OMNH 54807, left dp3; OMNH 54808, right lower molariform; OMNH 54823, left upper molariform tooth; OMNH 54825, right upper molariform tooth; OMNH 54906, right lower molariform; OMNH 54907, left dp4; UCMP 141712-03, left molariform tooth; UCMP 141716-01, right dp3; UCMP 141717-07, right upper molariform tooth; UCMP 141717-08, left lower molariform; UCMP 141720-16, right DP2; UCMP 141720- 20h, right upper molariform; UCMP 141720-20k, right upper molariform; UCMP 141720-20l, right lower molariform; UCMP 141737-03, right molariform tooth; UCMP 141737-06, right upper molariform tooth; UCMP 141737-08, right upper molariform tooth; UCMP 141737-09, right upper molariform tooth; UCMP 141737-15, right DP2; UCMP 141737-18, right upper molariform tooth; UCMP 141737-02, left dp4; UCMP 141737-19, right molariform; UCMP 141737-20, left dp3; UCMP 141737-22, right upper molariform tooth; UCMP 141737-23b, right upper molariform tooth; UCMP 141737-23c, left P2; UCMP 141737-23g, left dp4; UCMP 141737-23i, right P2; UCMP 141737-23k, left upper molariform tooth;

UCMP 141737-23l, right maxilla fragment with a single molariform tooth; UCMP 141737-23t, left upper molariform tooth; UCMP 141737-23u, left upper molariform; UCMP 141737-23v, left lower molariform; UCMP 141737-23w, left molariform; UCMP 141737-23x, right p3; UCMP 141737-23z, right lower molariform; UCMP 141737-23bb, right lower molariform; UCMP 141737-23dd, right upper molariform tooth; UCMP 141748-04, right dp3.

Measurements.— See Tables 6 and 7.

Description.— A right DP2 with moderate wear to the occlusal surface contains two roots, one small labial root and one large lingual root. There is no IAR. Two anterior reentrants are present. The MAR is deep, cement-filled and reaches three-quarters of the length of the tooth and projects in a straight line posteriorly. The EAR is not as deep or transversely open as the MAR but is narrow transversely and runs about one-quarter the length of the tooth. The EAR is not cement-filled. Unlike in *Hypolagus*, the enamel circumscribes the entire occlusal outline of this tooth.

A left upper molariform tooth has three roots, and the trigon is wider but shorter than the talon. The hypostria is straight-walled and nearly reaches the crescentic valley. This valley is variable in its shape, but is usually V-shaped or U-shaped rather than J-shaped. Another variable character is the presence or absence of an enamel lake. These characters seem to vary with wear to the occlusal surface. For example, UCMP 141737-23l appears unworn and is only partially erupted. The hypostria is broad and nearly reaches the U-shaped

crescentic valley. A large labial isolated enamel lake is present. This tooth has a shallow labial groove that is straight-walled.

The dp3 is oblong-shaped, is large, does not have grooves, and is attached only medially where the posterior wall of the trigonid projects posteriorly to join the anterior projection of the anterior wall of the talonid. The trigonid is separated from the talonid by a thin band of cementum. The anterior wall of the trigonid is straight, while the posterior wall has a posteriorly directed protrusion that connects the trigonid to the talonid medially. The anterior wall of the trigonid has a small anterolabially directed protrusion. The anterior wall of the talonid is posteriorly concave except where the posteriorly directed protrusion opens into the talonid. Here the anterior wall of the talonid projects anteriorly to meet the posteriorly directed protrusion. The posterior wall of the talonid is slightly concave posteriorly with the labial side showing a stronger anteroposterior compression than is evident on the lingual side of this tooth. The lingual side of the talonid is much longer than the labial side.

The lower molariform teeth have a trigonid that is nearly as long as wide. The anterior wall of the trigonid is interrupted on the lingual and labial sides by shallow, but broad grooves. These grooves promote the formation of a medial anteriorly directed protrusion from the anterior wall of the talonid. The posterior wall of the trigonid has a labial, posteriorly directed protrusion. However, the trigonid and talonid are separated by a thin band of cementum. The talonid is longer than wide. The occlusal surface is pitted with a honeycomb pattern. The

anterior wall of the talonid follows the posterior wall of the trigonid from the lingual margin to the posterioly directed protrusion. The posterior wall of the trigonid is nearly straight rather than concave.

Comparison and discussion.— Storer (1975) suggested *R. vonhofi* from the Kleinfelder Farm fauna of Saskatchewan was similar in size to *Desmatolagus schizopetrus* but larger than *Hesperolagomys*. These size differences are shared by the former two taxa from Eastgate. In morphology of the occlusal surface, *R. vonhofi* differs from *D. schizopetrus* and *Hesperolagomys* as described by Storer (1975). For example, the upper premolars and molars of *R. vonhofi* differs from *D.* schizopetrus in having an amphicone that lies more labially, a crescentic valley lacking anterior forking, and a hypostria that is longer; and from *Hesperolagomys* in having a shorter crescentic valley and lacking a posterior loph (id).

Family Leporidae Gray, 1821

Subfamily Archaeolaginae Dice, 1929

Hypolagus Dice, 1917

Genus *Hypolagus* Dawson, 1958

Hypolagus parviplicatus Dawson, 1958

Plate 7 (F–J)

Locality.— Eastgate, UCMP V70138, V70140, V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Virgin Valley beds (Dawson, 1958; White, 1987), Nevada; Wood Mountain Formation (Storer, 1975; White, 1991), Saskatchewan; Trail Creek Quarry, Valentinian Ash Hollow Formation (White, 1991), Wyoming; Railway Quarries (West Valentine Quarry, Quarry A, Quarry B, Stewart Quarry, and Fischer Quarry) Valentine Formation (Voorhies and Timperley,1997), Nebraska.

Referred specimens.— OMNH 54809, right P2; UCMP 141716-03, left P2; UCMP 141720-05, left p3; UCMP 141720-20E, left or right P2; UCMP 141720-20G, left P2; UCMP 141737-23E, right P2; UCMP 141751-03, right maxilla fragment with P2–M1; UCMP 141751-02, right maxilla fragment with P3–M3; UCMP 141846, left dentary fragment with i1–m3.

Measurements. See Tables 8–10.

Description.— A right maxilla fragment (UCMP 141751-03) contains the P2-M3 and is broken along the anteromost edge of the alveolus of the P2. Posteriorly, the maxilla is broken through the posteromost margin of the alveolus of the M1. The palate has the proximalmost part of the zygomatic arch present but lacks any diagnostic characters because of incompleteness. The upper checkteeth are moderately worn and hypsodont. The P2 is the smallest of the cheekteeth, while the P3 and P4 are similar in size to each other and larger than the succeding molars. Other than size, the P3 and P4 are difficult to distinguish from the M1. The M1 is noticeably smaller than the P3 or P4.

The P2 is is noticeably wider than long, with the lingual margin much longer than the labial margin. There is no trace of an IAR, but a deep MAR is present. The MAR is cement-filled and extends posteriorly less than one-half the length of the tooth. Variation of the length of the MAR is apparent in the Eastgate rabbits as follows: a moderately worn right P2 (UCMP 141737-23E) has an MAR that extends three-quarters the length of the occlusal surface; on a left P2 (UCMP 141716-03) with moderate wear the MAR extends one-half the length of the tooth; and in UCMP 141720-20G, with heavy wear to the occlusal surface, the MAR extends about one-half the length of the tooth. The latter condition is likely because of the advanced stage of wear exhibited by the specimen. A shallow EAR without cement is present in UCMP 141751-03. However, in a more advanced stage of wear as seen in UCMP 141720-20G there is no EAR. In addition, the P2 of OMNH 54809 has a trace of an IAR and EAR present, but neither is cement-filled, while the MAR crosses more than one-half the length of the occlusal surface and is cement-filled.

On the P3, the trigon is noticeably narrower than the talon. In fact, the talon extends beyond the lingual and labial margins of the trigon, but the trigon and talon are about equal in length. The hypostria (internal reentrant) extends transversely about one-half way across the tooth. Crenulations on the anterior and posterior walls of the hypostria are present along their entire coarse. However, the crenulations on the labialmost anterior and posterior walls of the hypostria do not begin until they reach one-third across the width of the

hypostria. The walls of the lingual one-third of the hypostria are straight, not crenulated.

The P4 has a trigon and a talon that are about equal in width to each other. The hypostria extends transversely to about one-half way across the tooth. The anterior and posterior walls of the hypostria are straight-walled where they originate, before becoming crenulated as in the P3.

The characteristics of the M1 of UCMP 141751-03 are similar to the P4 of the same specimen except for size. However, the M1 of UCMP 141751-02 has a trigon and talon that are about equal in length and width. The hypostria extends transversely more than three-quarters of the occlusal surface. The lingual one-third of the hypostria are straight with the labial two-thirds of the hypostria crenulated.

The trigon of the M2 (UCMP 141751-02) is slightly wider and longer than the talon. The hypostria traverses about two-thirds the occlusal surface. The lingual one-third of the hypostria is straight, while the labial two-thirds are slightly crenulated.

The M3 (UCMP 141751-02) is longer than wide and shows heavy wear to the occlusal surface. The overall shape of this tooth is oblong with no distinction between the trigon and talon.

The dentary of UCMP 141846 is broken along its ventral surface; thus, exposing the entire ventral surface of the incisor. Posteriorly, the dentary is broken through the ascending ramus and the middle of the masseteric fossa.

The diastema is long, slender, and shallow. No pitting is present below the p3 on the lingual side, but pitting is present on the labial side of the dentary. The masseteric fossa terminates below the posterior wall of the talonid of the m2.

The incisor (UCMP 141846) is flat on the anterior surface and posteriorly rounded. The tooth is long but not strongly curved.

The p3 (UCMP 141846) is lacking the AR, IRs, AIR, and PIR but has two external reentrants (AER and PER). The AER is shallow and cement-filled, while the PER is deep and cement-filled. The anterior wall of the PER has thick enamel, while the posterior wall has thin enamel. Both walls are smooth with no crenulations present. The PER is slightly deflected anteriorly on its lingualmost end but on UCMP 141720-20J the PER is straight with no anterior or posterior deflections. The PER traverses 50% of the width of the tooth.

The p4–m2 of UCMP 141846 are noticeably longer than wide, with enamel lakes on the lingual margins of the trigonid and talonid of each of these cheekteeth. These teeth are similar in size and shape to each other. The m3 is the smallest tooth present on this specimen.

The p4 is similar to the other molariform teeth except that it has a slight V-shaped posterior wall of the trigonid. The posterior wall of the trigonids are straight in the m1 and m2. For the m1 and m2, the trigonids are much longer than that of the p4. However, the talonids of the p4 and m2 are longer than the talonid of the m1, while the widths of the talonids and trigonids of the molariform cheekteeth do not differ.

The m3 (UCMP 141846) is the smallest cheektooth present. The trigonid is much larger than the talonid. The trigonid is much wider than long, but the talonid is longer than wide.

Comparison.— White (1987) listed five genera of Archaeolaginae and their temporal ranges for North America as follows: *Archaeolagus*, Arikareean-Hemphillian; *Hypolagus*, Barstovian-Blancan; *Pewelagus*, Blancan; *Panolax*, Clarendonian and/or Hemphillian; and *Lepoides*, Hemphillian-Blancan. He stated that the best tooth loci for taxonomic diagnoses are the p3 and P2 if the latter are associated with the former. Most systematic work on Tertiary leporids is based on mandibles and especially the p3 (White, 1987).

For all archaeolagines, the internal reentrants (AIR, PIR) are lacking except for *Archaeolagus* and *Hypolagus fontinalis* (White, 1987). In contrast, the Leporinae are separated from the Archaeolaginae by the presence of an AIR and PIR in the p3 of adults (White, 1987). However, one of the archaeolagines, *H. fontinalis*, possesses a PIR, but it does not extend the full length of the tooth height (White, 1987). According to White (1987) and Dawson (1958), Archaeolaginae differs from the Palaeolaginea by the following characters: hypsodont cheekteeth; upper premolars more molariform; an anterior, single, shallow anterior reentrant on P2 (IAR); a hypostria with straight or crenulated walls; an posterointernal reentrant (PIR) present in early stages of wear; and the presence of two external reentrants (AER and PER) on the p3. The AER is usually shallower than the PER. Dawson (1958) implied difficulty in

differentiating between *Hypolagus* and *Archeaolagus* for incomplete specimens. Thus, for this study I have used only the p3 and P2 for identification of these specimens.

Although Dawson (1958) did not describe an upper P2 for this group, she did figure a P2 but provided length and width measurements (AP = 1.2, Tr = 2.8). She considered this tooth near *H. parviplicatus*, but hesitated to include it in the species until better material became available. Likewise, I tentatively place the upper maxillae and cheekteeth listed above in *H. parviplicatus* based on size and the following characters: a deep, cement-filled reentrant (MAR) that extends across 40–50% of the tooth width; a shallow EAR with or without cementum; and no IAR or PIR present.

Morphologically, the presence of a shallow AER that is cement-filled, the lack of internal reentrants (AIR and PIR), and the lack of an AR, are key characters in assigning the p3s to the genus *Hypolagus* rather than to *Pronotolagus* or *Alilepus*. The AER of the p3 in *Archaeolagus* is shallow, but is not cement-filled, which is the condition in *Hypolagus* (White, 1987).

For the lower cheekteeth, especially the p3s, the following species of *Hypolagus* are too large to be considered in the identification of the Eastgate leporids: *H. ringoldensis*, *H. gidleyi*, *H. regalis*, *H. oregonensis*, and *H. vetus*. In contrast, the following species of *Hypolagus* are too small *H. tedfordi*, *H. furlongi*, *H. edensis*, *H. voorhiesi*, and *H. arizonensis* (Tables 8 and 9) .

Other than size, the p3s from Eastgate listed above most closely

resemble *H. parviplicatus* by sharing the following characters: relative depth of the PER and AER (both are much shallower compared to *H. fontinalis*); PER slightly anteriorly deflected to straight; the thick enamel of the PER is usually straight not crenulated; the length and width are not noticeably different; and the lack of a PIR. Although the average size of the P2s and p3s for the *H. parviplicatus* specimens studied by Voorhies and Timperley (1997) are larger than those at from Eastgate, they are within the observed range for the species as provided by Voorhies and Timperley (1997).

Discussion.— In the sample of isolated P2s from the Valentine Railway Quarries, Voorhies and Timperely (1997) noted a slight overlap in length and width between the smallest P2s of *H. parviplicatus* and the largest P2s of *H. fontinalis*. However, they were able to discriminate between these taxa by plotting a measure of pattern complexity (depth of MAR) against a measure of overall size (width). In addition to this bivairate plot, Voorhies and Timperley (1997) found that *H. fontinalis* teeth are transversely narrower than those of *H. parviplicatus*, and have a deeper hypostria on the molariform cheekteeth and MARs that averages 57% in relative depth. In contrast, *H. parviplicatus* has a hypostria that averaged about one-fifth deeper than *H. fontinalis*, while the MARs averaged 46% in relative depth.

White (1987) considered the crenulations along the walls of the hypostria and the transverse length of the hypostria to be valid characters to separate the molariform cheekteeth (other than the p3s) of the different species of *Hypolagus*.

Based on the Eastgate leporids, I judge these characters alone to be insufficient for separating isolated molariform cheekteeth for the *Hypolagus* species because they appear to be highly variable. For example, the occurrence of crenulations along the anterior and posterior walls of the hypostria and transverse length of the hypostria varies among teeth of the same individual (UCMP 141751-02).

Hypolagus fontinalis Dawson, 1958

Plate 8 (A–E)

Locality.— Eastgate, UCMP V70138, V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Barstow (White, 1987), California; Railway Quarries (West Valentine Quarry, Quarry B, Stewart Quarry, and Fischer Quarry), Valentine Formation (Voorhies and Timperley,1997), Nebraska. Clarendonian: Ash Hollow Formation, Quinn Canyon (Dawson, 1958), Nebraska; Esmeralda Formation (Dawson, 1958; Clark et al., 1964), Nevada; Big Spring Canyon (Dawson, 1958; White, 1987), South Dakota.

Referred specimens.— UCMP 141509-03, left p3; UCMP 141550, right dentary fragment with p3–m2; UCMP 141716-04, left p3; UCMP 141720-20J, right p3; UCMP 141737-04, right P2; UCMP 141849-02, left p3.

Measurements.— See Tables 8–10.

Description.— The P2 is noticeably wider than long. The lingual margin is much longer than the labial margin. There is no trace of an IAR, but an MAR is present. The MAR is cement-filled and extends posteriorly less than one-half the length of the tooth. A slight EAR without cement is present.

A right dentary (UCMP 141550) containing the p3–m2 that is broken anteriorly through the middle of the alveolus of the p3 and posteriorly at the base of the ascending ramus. There are no foramina present on the lingual side of the dentary, but there is pitting (see Voorhies and Timperely, 1997; White, 1987).

On the labial side of the dentary, pitting exists in the middle of the dentary below the p4. The masseteric fossa ends below the posterior wall of the talonid. The p3 is broken dorsally below the level of the tooth row; however, the occlusal outline is preserved. The p4–m2 are much longer than wide and would be difficult to distinguish from each other if they were isolated teeth.

The p3 is lacking the AR and IRs but has two external reentrants. The AER is shallow and cement-filled, while the PER is deep and cement-filled. The anterior wall of the PER has thick enamel, while the posterior wall has thin enamel. Both walls are smooth with no crenulations present. The PER is strongly deflected posteriorly on the lingual one-third of the PER. However, UCMP 141720-0J and UCMP 141849-02 have straight rather than strongly deflected posteriorly PERs. The PER traverses an average of 53% (UCMP 141509-03, 52%; UCMP 141716-04, 51%) of the width of the tooth.

The p4–m2 have trigonids that are similar in size and shape and are much higher than the talonids. They each have an enamel lake on the lingual side of the occlusal surface of the trigonid and talonid. These teeth differ from each other in the following manner: the talonid of the p4 is oblong and larger than the talonid of the m1, but is not as long as the talonid of the m2; and the posterior wall of the p4 and m1 are broadly V-shaped, while the posterior wall of the m2 is slightly V-shaped.

Comparison.— For the P2s, the Eastgate specimens listed above most closely resemble *H. fontinalis* (in contrast with *H. parviplicatus*) by sharing the following characters: deep, cement-filled MAR; shallower, cement-filled EAR; no IAR; and transversely narrow tooth with deep reentrants (MAR and EAR).

The following species of *Hypolagus* are too large to be considered in the identification of this group of Eastgate leporids: *H. ringoldensis*, *H. gidleyi*, *H. regalis*, *H. oregonensis*, and *H. vetus*. In contrast, the following species of *Hypolagus* are too small: *H. tedfordi*, *H. furlongi*, *H. edensis*, *H. voorhiesi*, and *H. arizonensis* (Tables 8 and 9).

Other than size, the p3s from Eastgate listed above most closely resemble *H. fontinalis* by sharing the following characters: relative depth of the PER and AER are deep compared to those of *H. parviplicatus*; PER is strongly deflected posteriorly; thick enamel of PER is usually straight not crenulated; and noticeably greater length than width.

Discussion.— Previously, the few Miocene localities that produced upper

cheekteeth for *H. fontinalis* were from: the Barstovian of California and Nebraska (White, 1987); and the Clarendonian of Nebraska (Voorhies and Timperley, 1997), Nevada (Clark et al., 1964), and South Dakota (Dawson, 1958; White, 1987). Voorhies and Timperley (1997) listed characters that differed from those listed by Clark et al. (1964) for *H. fontinalis* as follows: the P2 has two anterior reentrants both filled with cementum; and the P3–M2 have hypostria that traverses more than one-half the distance of the occlusal surface with crenulations. However, the degree of crenulation on the anterior and posterior margins does not progressively decrease from P3 to M2 (Voorhies and Timperley, 1997).

Until maxillae and dentary are found in association, the identification of the upper cheekteeth to this group must be tentative. Therefore, I place the P2 listed above in this group cautiously until more complete material becomes available.

Subfamily Leporinae Trouessart, 1880

Genus *Pronotolagus* White, 1991

Pronotolagus sp. indet.

Plate 8 (F-J)

Locality.— Eastgate, UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Stewart Quarry (Voorhies and Timperley, 1997), Norden Bridge Quarry (White, 1991a, b), Nebraska. Clarendonian: Apache Canyon (Clark et al., 1964 and White, 1991a, b), California. Hemphillian: Lemoyne Quarry (White, 1991a, b), Nebraska.

Referred specimens.— UCMP 141720-11, right p3; UCMP 141751-01, right maxilla fragment with P2-P4.

Measurements.— See Tables 8 and 10.

Description.— A right maxilla fragment (UCMP 141751-01) containing the P2-P4 is broken anteriorly through the middle of the alveoli of the P4; however, the P4 is in place. Posteriorly, the maxilla is broken through the anteromost edge of the alveoli of the M1. On either side (laterally), the tooth row is too incomplete to provide any characters. The cheekteeth are moderately worn and hypsodont. The P2 is the smallest of the teeth, while the P3 and P4 are similar to each other in size.

The P2 is wider than long with a trace of an IAR, but the EAR is absent. The IAR is not cement-filled. This is the only Eastgate lagomorph to have an IAR present and an EAR absent on the P2. The MAR extends less than one-half the length of the tooth and is cement-filled.

The P3 is the largest tooth, has a trigon that is reduced in width, and is about the same length as the talon. On the labial side of the tooth, the talon is much wider than the trigon. In contrast, on the lingual side, the talon extends slightly more lateral than the trigon. The hypostria extends labially less than one-half the width of the tooth. Crenulations are present except for the lingual one-third of the anterior and posterior walls of the hypostria.

On the P4, the labial side of the trigon and talon are missing. The trigon is noticeably longer than the talon. The hypostria extends more than one-half the width of the tooth. Thus, relative to the P3, the hypostria is transversely longer on the P4. The lingual one-half of the anterior and posterior walls of the hypostria are straight but they become crenulated labially.

The p3 has a single IR (IAR), but no AR is present. The AIR is very shallow, is narrow, extends the entire height of the tooth crown, and has no cementum. There are two external reentrants present. The AER is shallow and cement-filled, while the PER is deep and cement-filled. The anterior wall of the PER has thick enamel, while the posterior wall has thin enamal. Both walls are smooth with no crenulations. The PER is strongly deflected anteriorly along the lingual one-third of this reentrant. The PER traverses 45% of the width

of the tooth.

Comparison.— The P2 is tentatively placed here because it belongs to a leporine not an archaeolagine. No archeolagines are known to possess an IAR on the P2 (Voorhies and Timperley, 1997). In contrast, the leporines possess an IAR on the P2 (Voorhies and Timperley, 1997). Unfortunately, there are no known P2s or any other upper tooth for *Pronotolagus*. However, I place (UCMP 141751-01) in this genus based on size and because it is the only leporine known from Eastgate (based on a p3). If this tooth belongs to *Pronotolagus*, it is the first to be described for the genus.

UCMP 141720-11 clearly belongs to a leporine rather than an archaeoligine because of the presence of an AIR on the p3. Of the leporines, the genus *Alilepus* is eliminated based on the lack of a PIR (on the Eastgate p3) that is as deep as the PER (Voorhies and Timperley, 1997). The genus *Pronotolagus*, however, does not possess a PIR but has a shallow IAR. *Pronotolagus albus* described by Voorhies and Timperley (1997) differs from the Eastgate *Pronotolagus* in that the former has a cement-filled IAR. Furthermore, *P. albus* has a p3 that is similar in length to width, while the Eastgate *Pronotolagus* has a p3 that is noticeably longer than wide.

Voorhies and Timperley (1997) described a new species of *Pronotolagus* (*P. albus*) from the Stewart Quarry near Valentine, Nebraska in the Valentine Formation. They suggested the p3 of this new species resembled the p3 of *Hypolagus* in character but was placed in the leporine group rather than

the archaeolagine group based on the presence of a prominent, cement-filled AIR. In addition, the only other tooth of this specimen was a p4 that they could not distinguish from that of *Hypolagus*.

Discussion.— The Eastgate *Pronotolagus* likely represents a new species. The size, greater length to width, and the lack of cementum in the IAR separate the Eastgate specimen from the only known species of *Pronotolagus*. Until additional material becomes available, however, I hesitate to name this taxon as a new species.

Order Rodentia Bowdich, 1821

Family Aplodontidae

Aplodontinae Trouessart, 1897

Genus *Tardontia* Shotwell, 1958

Tardontia nevadans Shotwell, 1958

Plate 9 (A–I)

Locality.—Eastgate, OMNH V974; UCMP V70140, V70142, V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Stewart Springs, Esmeralda Formation, County, Nevada (Shotwell, 1958).

Referred specimens.— OMNH 54803, right P4; OMNH 54805, right p4; OMNH 54806, right DP4; UCMP 130158, left dentary fragment with m1-m3;

UCMP 130159, right dentary fragment with m2-m3; UCMP 130160, left p4; UCMP 130161, left maxilla fragment with P3-M1; UCMP 130162, left dentary fragment with p4; UCMP 130163; right dentary fragment with p4-m3; UCMP 130164, left M1 or M2; UCMP 130166, right m1 or m2; UCMP 130167, right M1 or M2; UCMP 130168, left dP4; UCMP 130169, left dp4; UCMP 130171, left dp4; UCMP 130172, left M1 or M2; UCMP 130173, right m1 or m2; UCMP 130174, right dp4; UCMP 130175, right m3; UCMP 130176, right dp4.

Measurements.— See Tables 11 and 12.

Description.— A left maxillary fragment (UCMP 130161) with the P3-M1 present has the maxilla broken anterior to the P3, with only the base of the zygomatic arch preserved. Posteriorly, the maxilla is broken through the posteromost part of the alveoli of the M1. Lingual to the tooth row only the left side of a grooved palate remains. The P3 is the smallest tooth present and the P4 is the largest of the cheek teeth. The cheekteeth are rooted, high crowned, and show moderate wear to the occlusal surface.

The P3 is a small, peg-like tooth with a triangular outline shape. A groove is present along the anterolingual margin of the tooth and extends from the occlusal surface ventrally about one-third of the crown height. Thus, in later stages of wear the anterolingual groove would not be present.

The P4 has a prominent and well rounded anterocone. A shallow but broad groove occurs between the anterocone and the parastyle. The mesostyle is the most prominent of the styles on this tooth. The posterior border of the

tooth is essentially flat, with a thin layer of enamel present or absent (= enamel failure). The lingual border of the tooth is well rounded with thick enamel present. There are six fossettes visible from the occlusal view: anterofossette and parafossette (anterolabial); mesofossette and metafossette (posterolabial); and protofossette and hypofossette (posterolingual) (see Korth, 1994; 102). The parafossette is the largest of the fossettes, and from a dorsal view, appears to be L-shaped. The mesofossette is transversely oblong. The posterior fossettes (metafossette and hypofossette) are anteroposteriorly oblong. The protofossette is also anteroposteriorly oblong and joins a small oval-shaped anterofossette.

The M1 is much smaller than the P4. The anteromost and posteromost parts of the tooth are flat because of enamel failure. There is a prominent mesostyle. The lingual boarder of this tooth is well rounded and has very thick enamal. There are four fossettes as follows: parafossette, metafossette, protofossette, and hypofossette. All of the fosettes are oval-shaped and are longer than wide. The lingual two fossettes are the largest followed by the metafossette, while the parafossette is the smallest of the fossettes.

A right dentary fragment (UCMP 130163) with the p4–m3 is broken anterior to the mental foramen. Posteriorly, the dentary is broken along the anteromost part of the ascending ramus. There are no foramina present on the lingual side of the dentary; however, along an anteroposterior line the dentary is broken, exposing the incisive alveolus that housed the proximal part of the incisor. On the labial side, an anteriorly open mental foramen occurs in front of

the p4 and dorsoventrally low on the dentary. The massetteric scar is massive and V-shaped as it terminates below the anteromost edge of the m1. The p4 is the largest of the cheekteeth. The molars increase in length from front to back with the m3 being the largest of the molars. Unlike the upper cheekteeth, the widths of the cheekteeth are similar to each other. The cheekteeth are rooted, high crowned, and moderately worn on the occlusal surface; thus, the pulp cavity is closed.

The p4 has a V-shaped anteroflexid that extends the entire height of the tooth crown. The paraconid is not as large as the protoconid. A paraflexid is present but is almost completely closed lingually to form a parafossettid. A prominent entoconid is present. A protoflexid extending the entire height of the tooth crown is present. This later flexid almost reaches the medialmost edge of this tooth.

Across two-thirds of the anterior surface of the m1, enamel failure is evident. The lingual surface of this tooth is not straight, but rather slightly W-shaped. This W-shaped appearance is a result of the size and shape of the lingual cusps and stylids (metaconid, metastylid, mesostylid, and entoconid). The protoconid, metaconid, and hypoconid are similar in size, but much smaller than the entoconid. A shallow protoflexid is present and extends the entire height of the tooth crown. A mesafossettid is present lateral to the protoflexid; posterior to this fossettid is the larger metafossettid. Except for the length, the m2 shares those characters listed above for the m1.

The m3 is longer than the preceding molars and is lacking enamel failure. The protoconid and metaconid are similar to those of the preceding molars. The metaconid is more prominent than on the other molars. A deep metaflexid, rather than a metafossettid, occurs at the posteromost part of this tooth separating the entoconid from the hypoconid. A deep protoflexid is present and almost unites the mesofossettid.

A right dp4 (UCMP 130174) has little wear to the occlusal surface, is low crowned, and has five major cusps. The anteroconid is well rounded, grooved medially, and the lowest cusp on this tooth. The metaconid is the highest cusp on this tooth and joins the protoconid by a metalophid. The entoconid is lower than the hypoconid, and two fossettids (metafossettid and hypofossettid) occur between these cusps.

The m1-m3 of UCMP 130158 are unworn on the occlusal surface. On m1, a metaconid is the highest cusp followed by the entoconid, with the protoconid and hypoconid about equal in height. There are five fossettids present (anterofossettid, mesofossettid, metafossettid, entofossettid, and hypofossettid). The anterior and posterior fossettids are shallow and would disappear with only a little wear to the occlusal surface. In contrast, the two middle fossettids (metafossettid and mesofossettid) are deep and would remain visible through late stages of wear. The protoflexid is deep, almost reaching the mesofossettid, and continues for the entire height of the tooth crown.

Except for the protoflexid, the m2 is similar in morphology to the m1. The

protoflexid of the m2 is not as deep as on the m1. However, similar to the m1 and m3, the protoflexid spans the entire height of the tooth crown.

The morphology of the m3 varies from the m1 and m2. On the m3, a metaflexid is present rather than a metafossettid. Therefore, only four fossettids are present on the m3.

Comparison and discussion.— The type specimen of *Liodontia alexandrae* examined by Shotwell (1958) is a taxon that is very similar in character to *Tardontia nevadens*. A specimen of *L. alexandrae* (UCMP 11864, right dentary fragment with p4–m3 present) from Virgin Valley, Nevada is similar to *L. alexandrae* (CIT 327, 330, 331) from Thousand Creek, Nevada described by Shotwell (1958), except the former has hypsodont teeth and partially open pulp cavities. A universal characteristic of *L. furlongi* is that there is no partial or incipient closure of the pulp cavities, as seen in modern aplodontids (Shotwell, 1968).

All permanent cheekteeth of aplodontids from Easgate are rooted with the tooth pulp closed. Except for stages of wear and slight differences in size, all aplodontid (*T. nevadens*) teeth from Eastgate are similar in morphology. Aplodontid teeth recovered from Eastgate range from very worn to not yet erupted. The presence of aplodontids at Eastgate may infer an age no older than Barstovian (Korth, 1994).

Family Mylagaulidae Cope, 1881

Subfamily Mesogaulinae, Korth, 2000

Genus *Mesogaulus*, Riggs, 1889

Mesogaulus paniensis (Matthew, 1902)

Plate 10 (A-G)

Locality.— Eastgate, UCMP V70140, V70142.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Hemingfordian: Quarry A, Martin Canyon, Pawnee Creek Formation (Wilson, 1960), Logan County, Colorado; Marsland Formation, Sioux County, and Runningwater Formation, Cottonwood Creek, Dawes County, Nebraska (Cook and Gregory, 1941; Korth, 2000).

Referred specimens.— UCMP 130254, left p4; UCMP 130255, left P4; UCMP 130256, left p4; UCMP 141799-01, left M2; UCMP 141799-02, right M2; UCMP 141799-03, right M3; UCMP 141799-04, left M2; UCMP 141799-05, left M2; UCMP 141583, right dentary fragment with dp4.

Measurements.— See Tables 11 and 12.

Description.— The P4 has six fossettes on the occlusal surface. The anterofossette and parafossette are joined and form a Y-shaped fossette. The mesofossette lies posterolabial to the parafossette and is rectangular in shape. A small fossette occurs posterior to the mesofosette. This fossette was likely the

posterior border of the mesofossette but became separated from the other fossettes because of wear. The metafossette and hypofossette are long, are similar in size and shape, and run parallel to each other. The protofossette is narrow at the anterior end but widens posteriorly and is similar in size and shape to the parafossette, which it parallels.

Shotwell (1958) used the following terms; stria-struid to denote the grooves that occur along the lingual and labial column of the cheekteeth. Two grooves, the protostria and hypostria, occur on each side of the mesostyle. The protostria is more prominent. On the lingual side a single anterolingual groove, the parastria, is present. The tooth is concave lingually and is hypsodont with two rootlets.

The M2 is subquadrate in outline shape, possesses four fossettes, and is nearly straight along the labial side. The parafossette is slightly crescent-shaped and is small. The mesofossette is rectangular and runs transversely. The metafossette is oval in shape. On the lingual side, the protofossette and hypofossette are joined and form a single elongate fossette that extends nearly the entire length of the tooth. Variations of this tooth occur because of wear to the occlusal surface. For example, cheekteeth may possess five fossettes rather than four because of the union of the protofossette and hypofossette. The anterofossette may be absent. The anterofossette may join the parafossette forming an L-shaped or a Y-shaped parafossette. In addition, the orientation of the fossettes along the anteroposterior axis of the tooth may vary from

anteroposteriorly aligned to oblique.

The M3 has a labial side that is slightly concave. There are four fossettes. The anterofossette and mesofossette are similar in size, but the latter is oval-shaped. The anterofossette is narrower anteriorly and widens posteriorly. The smallest fossette is the metafossette, which is circular in shape and occurs on the posteromost edge of the tooth. The hypofossette is slightly crescent-shaped and slightly smaller in size relative to the anterofossette and parafossette.

A right dentary fragment (UCMP 141583) with the dp4 slightly above the alveoli of the dentary. The tooth is interpreted as being deciduous because there is no evidence of roots for this tooth, suggesting they had already been absorbed prior to death. The dentary is complete anteriorly but broken through the posteromost part of the alveoli of the dp4. Lingually, there are no noticeable foramina, but on the labial side the mental foramen is present. The mental foramen is slightly anterior to the dp4, occurs dorsoventrally about one-third the distance from the top of the dentary, and opens anterodorsally. The diastema is short and shallow. No dentary bone is covering the labial surface below the crown of the dp4. The anteroconid, protoconid, metaconid, and entoconid are well rounded, small cusps. The hypoconid is not as well rounded as the other cusps. Five fossettids are present and occur as follows: the anterofossettid and protofossettid are side-by-side, similar in size, and oval in shape; the hypofossettid and metafossettid are similar in size and oval in shape; and the mesofossettid is transversely elongate. The hypostriid is present, but barely

noticeable, while the protostriid is more noticeable than the former striid.

The p4 is oval in outline, narrows anteriorly, and widens posteriorly. The labial surface of the tooth is slightly concave lingually. Although the proximal end of the tooth is missing, the pulp cavity appears closed. A slight hypostriid is the only groove present. There are seven fossettids present; three are lingual (anterofossettid, mesofossettid, and metafossettid), two are labial (protofossettid and hypofossettid), one is anterior (anterofossettid), and one is posterior (metafossettid). The anterofossettid is long and bends lingually; the parafossettid and mesofossettid are shorter and hooked at the posterior end; the metafossettid is oval-shaped and is the smallest of the fossettids; the hypofossettid is slightly longer than the parafossettid and mesofossettid, and is straight-walled. The protofossettid is the longest of the fossettids and is slightly sigmoid-shaped, whereas the hypofossettid is slightly sigmoid-shaped, but less so than the protofossettid.

Comparison and discussion.— Korth (1999a, 2000b) recognized two genera of mylagaulids (*Hesperogaulus* and *Mesogaulus*) from the Great Basin during the Barstovian. Although these genera are similar in size and both have a P4 and a p4 that are twice (or more) the size of the molars, the genera are easily distinguished from one another. As wear increases in the Eastgate specimens, the fossettes change in size, shape, and number. The width and length of the occlusal surface increases until advance stages of wear. Korth (1999a, 2000b) indicated patterns and ranges in numbers of fossettes (ids) for the occlusal

surface of the P4s and the p4s of mylagaulids, and noted that variation and change with wear for these fossettes (ids) were specific for each group.

Mylagaulus paniensis and *Hesperogaulus* are similar in size and have similar temporal and zoogeographical occurrences. However, *M. paniensis* differs from *Hesperogaulus* in having fewer fossettes (ids). It also has a lingual and a labial forking of the anterofossette that remain attached to the parafossette. The fossettes of the P4 are anteroposteriorly oriented rather than oblique, and a mesostyle is present. The identification of the mylagaulid from Eastgate is tentative until more complete material becomes available.

Family Sciuridae Gray, 1821

Subfamily Sciurinae Gray, 1821

Tribe Marmotini Pocock, 1923

Protospermophilus Gazin, 1930

Protospermophilus dalquesti, n. sp.

Plate 11 (A–I)

Holotype.— UCMP 141630-01, right dentary fragment with p4–m3.

Type locality.— Eastgate, UCMP V70140.

Etymology.— Named in honor of the late Walter W. Dalquest, for his contributions to the study of Tertiary and Recent mammals of central and western North America and Central America.

Other localities.— Type only.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and UCMP 141631, left maxilla fragment with M2-M3; UCMP 141806-01, left maxilla fragment with a P4; UCMP 141806-02, right M1 or M2.

Measurements.— See Tables 18 and 19.

Diagnosis.— *Protospermophilus dalquesti* is a small marmotine that is most similar to *P. angusticeps*. *Protospermophilus dalquesti* shares the following characters with *P. angusticeps*: for the upper M1 and M2, small mesostyle occurring near the paracone, a constricted metaloph, absence of a protoconule, a complete protoloph, and a small parastyle; for the dentary, a long shallow diastema, a mental foramen near the dorsal edge of the diastema and anterior to the p4, and a masseteric scar that terminates below the m1 and is rounded on its distal end; for the p4, a weak anteroconid, absence of an anterior cingulid, the protoconid and metaconid appressed, a distinct mesoconid, a distinct entoconid, and a weak ectolophid; for the m1 and m2, absence of an anteroconid, a strongly bowed anterior cingulid, a distinct mesoconid, a distinct entoconid, a distinct ectolophid, and a small mesostylid.

Protospermophilus dalquesti differs from *P. kelloggi*, *P. malheurensis*, and *P. quatalensis* in having a small mesostyle that cccurs near the paracone on the

M1 and M2. *Protospermophilus dalquesti* differs from *P. kelloggi* in lacking a protoconule on the M1 and M2; in having a weak anteroconid, a protoconid and metaconid not closely appressed; and a m1 and a m2 with distinct entoconids. *Protospermophilus oregonensis* is the largest species of this genus and therefore is not considered in this diagnosis. However, the upper cheekteeth, dentary, and lower cheekteeth of *P. dalquesti* differ from those of *P. angusticeps* in several characteristics: the M1 and M2 of *P. dalquesti* possess a distinct metaconule and a small parastyle, whereas *P. angusticeps* have a small metaconule and a distinct parastyle; the p4 of *P. dalquesti* has a weak mesostylid, while *P. angusticeps* does not possess a mesostylid; the M1 and M2 of *P. dalquesti* posssesses a small mesostylid, whereas in *P. angusticeps* they have distinct mesostylids. In addition to the characters listed in Tables 13–17, *P. dalquesti* and *P. angusticeps* differ in size.

Descriptions.— A left maxillary fragment (UCMP 141806-01) has a P4 showing little wear to the occlusal surface. This tooth is the largest (2.57 X 2.00 mm) of the Eastgate sciurids. The straight anterior cingulum and a parastyle are well developed, contributing to the triangular occlusal outline of the tooth. The anterior cingulum makes an abrupt change in direction as it arises near the anterior base of the protocone, and extends labially to the parastyle. The anterior basin (anterior inner valley) is nearly as wide as it is long and is open labially. The protocone is the largest of the cusps, followed by the paracone and metacone in size. The protocone is anteroposteriorly elongate with the apex

anteriorly placed. The parastyle is well rounded and the paracone is transversely broad. The protoloph is not constricted, arises anterior to the apex of the protocone, and projects labially joining a small protoconule before continuing transversely in a sharp, posteriorly bent line that joins the paracone. The central basin is the widest of the basins and becomes broader posterolabially. The metaloph is constricted where it contacts the center of the apex of the protocone. However, a short, thin ridge occurs between the protocone and a prominent, well rounded metaconule. Labial to the metaconule, the metaloph forms a high ridge that diverges posteriorly. A small mesostyle lies medially between the paracone and metacone but does not close off the central basin labially. The posterior cingulum makes an abrupt change of direction as it arises from the posteromost part of the protocone (similar to the anterior cingulum arising from the anteromost of the protocone), forms a broad shelf posterior to the protocone, and narrows labially ending at the base of the metacone. A subquadrate occlusal outline is the result of an abrupt change in direction where the anterior and posterior cingula arise from the protocone. The posterior basin (posterior inner valley) is closed labially.

The M1 or M2 (UCMP 141806-02) shows no wear to the occlusal surface and is subquadrate in occlusal outline. The anterior cingulum makes an abrupt change of direction where it arises from the anteromost part of the protocone and is slightly bowed anteriorly; however, it is straight in UCMP 141631. Labially, the anterior cingulum is confluent with a small parastyle. The anterior basin is

widest lingually but converges labially; however, it remains open. The protocone is the largest of the cusps. The paracone is larger than the metacone. The protocone is anteroposteriorly elongate with its apex occurring anterior of center. The parastyle is small, low, and transversely elongate. The paracone is well rounded. The protoloph arises from the protocone anterior to the apex and in a sharp, straight line to join the paracone. A small protoconule is present near the protocone. The central basin is the widest of the basins and becomes progressively wider at the labial end. A mesostyle is present and closes the central basin. With additional wear the mesostyle would likely disappear. However, in UCMP 141631 there is no mesostyle. The metaloph is slightly constricted where it arises posterior to the apex of the protocone. The metaloph forms a high, thin ridge that diverges posterolabially until reaching a metaconule that lies lingual and near the protocone. Labially, the metaloph attaches to the metacone. The posterior cingulum (posteroloph) takes an abrupt change of direction and forms a broad shelf that narrows labially before terminating at the posterolingual base of the metacone. The abrupt change in direction, where the anterior and posterior cingula arise from the protocone, creates a subquadrate occlusal outline. In addition, the abrupt change of direction of the lingualmost part of the posterior cingulum results in formation of an incipient hypocone (see Hutchison and Lindsay, 1974). The posterior basin is open posterolabially.

The M3 is subtriangular in occlusal outline and is longer proportional to width than the preceding molars. The anterior cingulum arises lingually near the

anterior base of the protocone and terminates labially at the anterior base of the paracone. The anterior basin is long, narrow and open labially. The protocone is the largest of the cusps and is anteroposteriorly elongate. The protoloph arises from the protocone anterior to its apex and extends labially in a straight line, reaching the transversely elongate paracone. There is no metaloph or other structures in the large talon basin (posterior basin).

A dentary fragment (UCMP 141630-01) assigned to *P. dalquesti* preserves the p4–m3. The cheekteeth are bulbous, show moderate wear to the occlusal surface, and increase in size from front to back. The dentary is broken anterior to the mental foramen. Posteriorly, the dentary is almost complete, with only the proximalmost part of the ascending ramus and angular process missing. The mental foramen occurs high on the diastema, in front of the p4, and opens anteriorly. A smaller foramen occurs lower and posterior to the mental foramen. The masseteric scar ends below the middle of the m1. The ascending ramus arises lateral to the posteromost part of the m2. Lingually, the dentary is very fragmented, but a large, posteriorly open inferior dental foramen occurs at the base of the ascending ramus and at the level of the tooth row.

The p4 is longer than wide. A short anterior cingulid closes off the trigonid anteriorly. No anterior conid is present . A narrow V-shaped conid occurs between the protoconid and metaconid. A deep labial valley lies between the protoconid and hypoconid. A prominent mesoconid occurs on the ectolophid. The posterolophid is low and bends slightly posteriorly as it traverses the tooth to

join a prominent entoconid. There is no connection between the entoconid and a prominent mesostylid. Thus, the talonid basin is open lingually. A small groove occurs between the mesostylid and the protoconid, but they unite at their respective bases.

The m1 is longer than wide. An anteriorly bent anterior cingulid is present. No anteroconid is present. A wide, U-shaped notch occurs between the protoconid and the metaconid, but the trigonid remains closed to the talonid basin. A deep labial valley occurs between the protoconid and hypoconid. A prominent mesoconid occurs on a low, short ectolophid. The mesoconid lies closer to the protoconid than to the hypoconid. The protolophid is low and bends slightly posteriorly as it traverses lingually to join a prominent entoconid. There is a narrow valley that separates the entoconid and a prominent mesostylid. Therefore, the talonid basin is open lingually. A small groove occurs between the mesostylid and the protoconid, but they join at their respective bases.

The m2 differs from the m1 in being larger in size (length and width). The presence of a groove on the anterolabial side of the protoconid is present on the m2, not the m1. The m2 also differs from the m1 in having a protolophid that bends anterolingually as it reaches the entoconoid.

The m3 resembles the preceding molars except in being longer and having a more rounded talonid. The m3 also has a metalophid that joins the anterior cingulid low and labially at the base of the metaconid, not present on the preceding molars. In addition, the m3 differs from the other molars in having a

groove on the anterolabial surface of the protoconid that is more prominent (likely because this tooth has less wear to the occlusal surface); in having a groove between the metaconid and the mesostylid that reaches the talonid basin; and in having crenulations evident within the talonid basin along the bases of the protoconid, hypoconid, and entoconid. It is likely the m1 and m2 had similar crenulations, but they are worn away from the occlusal surface.

Comparison.— Six species of *Protospermophilus* have been described from the Tertiary deposits of North America (Korth, 1994). Two taxa occur in the Hemingfordian: *P. angusticeps* from Montana (near Fort Logan), described by Matthew and Mook (1963); and *P. kelloggi* from Wyoming (Fremont County), described by Black (1963). Geologically younger taxa of this genus include *P. vortmani* (discovered in the John Day Formation, Oregon and described by Cope, 1879), which is considered Arikareean in age (Black, 1963); *P. quatalensis* (discovered in Quatal Canyon, Ventura County, California and described by Gazin, 1930), which is considered Barstovian in age (Black, 1963); *P. malheurensis* (discovered at Skull Spring, Malheur County, and Beatty Butte local fauna, Oregon and described by Gazin, 1932), which is considered Barstovian in age (Korth, 1994); and *P. oregonensis* (discovered in Wheeler County, Oregon and described by Downs, 1956), which is considered Barstovian in age (Black, 1963).

The upper M1 and M2 of *P. dalquesti* differ from the known taxa of *Protospermophilus* in the following: from *P. kelloggi*, *P. malheurensis*, and *P.*

quatalensis in having a small mesostyle that occurs near the paracone; from *P. angusticeps*, *P. kelloggi*, *P. malheurensis*, and *P. quatalensis* in having a small parastyle; from *P. angusticeps* in having a distinct metaconule; and from *P. kelloggi* in the absence of a protoconule. In contrast, the M1 and M2 of *P. dalquesti* are most similar to *P. angusticeps* by possessing a mesostyle that occurs near the paracone and in the overall size of the upper cheekteeth.

The dentary of *P. dalquesti* differs from that of *P. quatalensis* in having a masseteric scar that is rounded and ends below the m1. It differs from *P. vortmani* in having a mental foramen that occurs near the dorsal edge of the diastema and anterior to the p4. The lower jaws of *P. kelloggi* and *P. malheurensis* are not known.

The lower cheekteeth of *P. dalquesti* differ from the other taxa of *Protospermophilus* in the following: the p4s (not known for *P. malheurensis*) of *P. kelloggi* and *P. quatalensis* do not possess an anterioconid; *P. kelloggi* has a protoconid and a metaconid that are very appressed (appear to be a single cusp), whereas in all other taxa (including *P. dalquesti*) the protoconid and metaconid are not as appressed; *P. vortmani* does not possess a mesoconid, which occurs in all other species of *Protospermophilus*; and *P. quatalensis* and *P. vortmani* possess an entoconid that is submerged within the posterolophid. *Protospermophilus dalquesti* shares a weak mesostylid with *P. kelloggi*, while a mesostylid is not found in any other *Protospermophilus*. For the p4s, *P. dalquesti* is most similar to *P. angusticeps* in sharing all characters examined,

except the absence of the mesostylid in *P. angusticeps*.

The lower molars of *P. dalquesti* differ from the other taxa of *Protospermophilus* as follows: *P. kelloggi* and *P. vortmani* have small mesoconids or none at all; *P. quatalensis* and *P. vortmani* possess a submerged to partially submerged entoconid and a weak ectolophid; *P. quatalensis* does not have a mesostylid. In contrast, the only features of the m1 and m2 that *P. dalquesti* shares with all known species of *Protospermophilus* are an anteroconid and a bowed anterior cingulid.

Discussion.— Although the size of *P. dalquesti* and *P. angusticeps* are similar, they differ in several characters of the upper cheekteeth, dentary, and lower cheekteeth as described above. Therefore, UCMP 141630-01 represents a new species that is most similar to *P. angusticeps*.

Miospermophilus Black, 1963

Miospermophilus cf. *M. bryanti* Black, 1963

Plates 11 and 12 (J-L; A-L)

Localities.— Eastgate, OMNH V974, V975, UCMP V70140, V70147, V74103.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Hemingfordian: Pawnee Creek Formation, Martin Canyon Quarry A, Colorado

(Black, 1963; Wilson, 1960).

Referred specimens.— OMNH 54540, left M1 or M2; OMNH 54548, left dentary fragment with i1–m3; OMNH 54569, left maxilla fragment with P3-P4; OMNH 54570, right M1 or M2; OMNH 54574, left maxilla fragment with M1–M3; OMNH 54578, right maxilla fragment with P3–M1; OMNH 54893, right P3; OMNH 54894, right P3; UCMP 141599-15, right p4; UCMP 141600-01, left M1 or M2; UCMP 141600-03, right M1 or M2; UCMP 141600-10, right M1 or M2; UCMP 141600-11, left M1 or M2; UCMP 141600-12, right M1 cr M2; UCMP 141600-13, right M1 or M2; UCMP 141600-15, left M1 or M2; UCMP 141600-20, left M1 or M2; UCMP 141600-23, right M1 or M2; UCMP 141600-25, right M1 or M2; UCMP 141600-27, left M1 or M2; UCMP 141600-28, left M1 or M2; UCMP 141600-29, right M1 or M2; UCMP 141601-09, left m1 or m2; UCMP 141601-14, left m1 or m2; UCMP 141606-01, right M1 or M2; UCMP 141606-03, right M1 or M2; UCMP 141608, right dentary fragment with m1; UCMP 141629-01, right dentary with p4–m1; UCMP 141629-06, right m1 or m2; UCMP 141629-08, left m1 or m2; UCMP 141629-09, right m1 or m2; UCMP 141632-02, right m1 or m2; UCMP 141800, right maxilla fragment with P4; UCMP 141802, left M1 or M2; UCMP 141820-01, right M3; UCMP 141824-06, left M1 or M2; UCMP 141824-09, left M1 or M2; UCMP 141829-01, right M1 or M2; UCMP 141829-04, left M1 or M2; UCMP 141829-10, left M1 or M2; UCMP 141829-13, right M1 or M2; UCMP 141829-14, right M1 or M2; UCMP 141829-17, right M1 or M2; UCMP 141830-21, right M3; UCMP 141830-22, right M3; UCMP 141830-23, right M3;

UCMP 141830-27, left M3; UCMP 141830-28, left M3; UCMP 141912, left maxilla fragment with P4–M3.

Measurements.— See Tables 18 and 19.

Description.— A maxilla fragment (UCMP 141912) having the P4–M3 with heavy wear to the occlusal surface. The P4 is the smallest of the cheekteeth, with the M1 and M2 being similar in size. The M3 is as wide but much longer than the preceding molars. The maxilla is broken anterior to the anteromost alveolus of the P3 and posteriorly through the posteromost part of the alveoli of the M3. Lingually, the left half of the palate remains but is broken along a transverse line extending anterior to the anteromost part of the M2. Labially, only the maxilla bone remains and the zygomatic process is broken at its proximal attachment.

The P3 has an oblong shape. The apex of the tooth occurs anterolabially and has a broad posterior cingulum that almost spans the entire width of the tooth. No other characters are apparent for this simple tooth.

The P4 is subquadrate in occlusal outline and has an anterior cingulum that is low, straight, and weakly developed, attaching to the anterolabial side of the protocone and extends to the lingual side of a well rounded parastyle. However, in OMNH 54578 the anterior cingulum arises at the anterior side of the protocone, extends shortly on the labial side, and terminates before reaching the base of the parastyle. Thus, the anterior cingulum does not traverse the entire width of the tooth in this specimen (OMNH 54578). In addition, OMNH 54678

has a large parastyle that is well rounded, and does not unite with the anterior cingulum or the paracone. The anterior basin is long, narrow, and closed labially, while in OMNH 54578 the anterior basin is open labially. The protocone is anteriorly placed and is the largest cusp with the paracone and metacone well rounded and similar in size. The protoloph arises from the anterolabial side of the protocone as a low, thin ridge joining a protoconule. The protoloph arises anterior to the center of the apex of the protocone and courses transversely in a straight line to join the paracone. The metaloph is very constricted between a large metaconule and the protocone, but becomes more prominent as it diverges slightly posteriorly to join the metaconule. Labial to the metaconule, the protoloph forms a high, rounded ridge that diverges strongly posteriorly until reaching the metacone. The central basin is the largest of the basins and is equally wide at its lingual origin (at the labial base of the protocone) and distal end (between the parcone and metacone). A large mesostyle is present but does not close the central basin labially, while in OMNH 54578 a small mesostyle is present and joins the anterior base of the metacone. Centered on the labial surface of the protocone, between the protoloph and metaloph, is a small transversely projecting lophule. The posterior cingulum forms a broad shelf posterior to the protocone but becomes narrower as it attaches to the posterolingual base of the metacone, thus, closing the posterior basin labially.

UCMP 141829-17 is the M1 or M2; it is subquadrate in occlusal outline and has little wear to the occlusal surface. The anterior cingulum is straight and

arises near the anterolabial base of the protocone. The anterior cingulum makes an abrupt change in direction as it arises near the anterior base of the protocone, and extends labially to join a small parastyle. The parastyle would likely disapear with additional wear to the occlusal surface. The anterior basin is long, narrow, and open labially. The protocone is the largest cusp followed by the paracone, with the metacone the smallest of the cusps. In UCMP 141829-13, the paracone and metacone are similar in size. The protocone is anteroposteriorly elongate with the apex of this cusp anteriorly positioned. No protoconule is present. In UCMP 141829-13, a small protoconule lies adjacent the protocone. On the labial side of the protoconule, the protoloph forms a high, thin ridge that extends labially in a straight line toward the paracone. The protoloph of UCMP 141829-17 arises anterior to the apex of the protocone as a thin, high ridge that diverges slightly posteriorly until reaching the well rounded paracone. The central basin is the widest of the basins, becomes broader posterolabially, and is open labially. A high, thin metaloph arises from the protocone and diverges strongly posteriorly until it reaches the lingual side of the metacone. A small, rounded metaconule is present but would likely become absent with additional wear to the occlusal surface. A small mesostyle occurs near the posterior base of the paracone. In UCMP 141829-13, a small mesostyle lies midway between the paracone and metacone. However, in UCMP 141829-10 there is no evidence of a mesostyle. At its contact with the protocone, the posterior cingulum takes an abrupt change of direction and forms a broad shelf, which narrows labially before terminating at

the posterolingual base of the metacone. Thus, the posterior basin is closed labially.

The M3 (UCMP 141830-27) is subquadrate in occlusal outline and has moderate wear to the occlusal surface. The anterior cingulum arises near the anterior base of the protocone and terminates labially at the anterolingual base of the paracone. The anterior basin is long and narrow, remaining open labially. The protocone is the largest of the cusps and is anteroposteriorly elongate. The protoloph arises from the protocone anterior to its apex and extends labially in a straight line to unite with a well rounded paracone. There is no metaloph or other structures in the large posterior basin.

A left dentary fragment (OMNH 54548) posseses the i1-m3, showing little wear to the occlusal surface. The cheekteeth increase in size from front to back. The dentary is very fragmented and broken anteriorly at the distalmost part of the diastema. The dentary is broken through the posteromost part of the alveolus of the m3. The mental foramen occurs high on the diastema, anteroposteriorly midway between the incisor and the p4, and opens anteriorly. The masseteric scar of OMNH 54548 is not preserved but on UCMP 141608 it ends below the posterior root of the p4.

The incisor is incomplete and laterally compressed, having no ornamentation on the mesal surface. The enamel is absent from the lingual side, but covers about one-quarter of the surface on the labial side.

The p4 is nearly as wide as long. A small anteroconid lies at the

anterolingual base of the protoconid. No metalophid is present. Rather, the protoconid and metaconid are side-by-side and separated by a narrow groove. This groove does not reach the talonid basin; thus, these cusps are united at their respective bases. A deep labial valley occurs between the protoconid and hypoconid. A small mesoconid occurs on a low, narrow ectolophid. With additional wear, the mesoconid would disappear. The mesoconid occurs midway between the protoconid and hypoconid. The posterolophid arises low (at the same level as the ectolophid joins the protoconid) on the posterolingual surface of the hypoconid. As the posterolophid traverses lingually, it ascends in a gradual fashion and bends slightly posteriorly before joining a prominent entoconid well above its base. Thus, the posterolophid occurs high above the floor of the talonid basin. There is a narrow valley that separates the entoconid from a small mesostylid or, as in UCMP 141629-01, a distinct mesostylid. A second small valley separates the mesostylid from the metaconid, but in UCMP 141629-01 the mesostylid joins the metaconid. Thus, the talonid basin in OMNH 54548 has two narrow valleys that open lingually.

The m1 is longer than wide. The anterior cingulid is strongly bowed anteriorly or, as in UCMP 141629-01, the anterior cingulid is slightly bowed anteriorly. No anteroconid is present. The metalophid arises low on the protoconid and quickly rises dorsally to attach high on the metaconid (at the same level as the anterior cingulid). Thus, the notch on the metalophid appears V-shaped and closes the trigonid basin from the talonid basin. A deep labial

valley occurs between the protoconid and hypoconid. A small mesoconid (distinct for UCMP 141608 and UCMP 141629-01) occurs on a low, short ectolophid. With additional wear to the occlursal surface, the mesoconid would disappear. The mesoconid occurs centrally between the protoconid and hypoconid. The posterolophid arises low, at the same level as the ectolophid on the anterior surface of the hypoconid, and at the posterolingual surface of the hypoconid. In addition, the posterolophid rises high dorsally and bends posteriorly before it joins a prominent entoconid (partially submerged entoconid for UCMP 141608) high above its base. Therefore, the posterolophid occurs well above the floor of the talonid basin. There is a wide valley that separates the entoconid from the small, cone-shaped mesostylid (no mesostylid for UCMP 141608). A narrow groove occurs between the mesostylid and the protoconid but they join at their respective bases. For UCMP 141629-01, a narrow valley separates the entoconid from a distinct mesostylid, which unites with the posterior base of the metaconid. Therefore, the talonid basin is open lingually at a single location, either posterior to the mesostylid or anterior to the mesostylid.

The m2 differs from the m1 in being larger in size and having a more prominent mesoconid. In addition, the m2 has a posterolophid that bends strongly anterolingually (greater than for the m1) as it reaches the entoconid.

The m3 resembles the preceding molars except in the following characters: longer than wide; more rounded talonid; no metalophid present (thus, the trigonid basin is open to the talonid basin); a lophid connecting the entoconid

to the mesostylid; a narrow valley separating the mesostylid from the metaconid; and crenulations being evident within the talonid basin at the bases of the protoconid and hypoconid. However, with wear to the occlusal surface these crenulations would disappear. The preceding molars available for study likely possessed similar crenulations at an earlier stage of wear.

Comparison.— The upper and lower cheekteeth of *M.* cf. *M. bryanti* from Eastgate are smaller than those of any known species of *Protospermophilus* but are larger than found in most species of *Tamias*. However, they do share a similar size with the following taxa of Miocene sciurids: *Spermophilus tephrus*, *S. primitivus*, *M. wyomingensis*, and *M. lavertyi*. Of these Miocene taxa, the Eastgate upper molars are most similar in size to *Miospermophilus wyomingensis*. However, in characters of the occlusal surface, the Eastgate upper molars most closely resemble those of *M. bryanti* (see Tables 19–23).

Three species of *Miospermophilus* have been recorded for the Tertiary of North America (Korth, 1994; Dalquest et al., 1996). Two taxa are known from the Hemingfordian and one from the Clarendonian. The two geologically older species are: *M. bryanti* (Pawnee Creek Formation, Martin Canyon Quarry A, Logan County, Colorado), described by Wilson (1960); and *M. wyomingensis* (Split Rock Formation, Fremont County, Wyoming), described by Black (1963). The geologically younger taxon *M. lavertyi* (Laverne Formation, Beaver County, Oklahoma), described by Dalquest et al. (1996) is considered Clarendonian in age .

The M1s and M2s from Eastgate differ from *M. lavertyi* in that *M. lavertyi* does not possess mesostyle, metaconule, protoconule, or constricted metaloph. The Eastgate M1s and M2s differ from *M. wyomingensis* in that *M. wyomingensis* has a distinct metaconule and a very constricted metaloph. *Miospermophilus bryanti* differs from the Eastgate upper molars in that *M. bryanti* is not known to possess a protoconule. Thus, in size the Eastgate M1s and M2s are most similar to those of *M. wyomingensis*, but in tooth characters they most closely resemble the M1s and M2s of *M. bryanti*.

The dentary and p4 for *M. wyomingensis* and *M. lavertyi* are not known. However, the p4 of *M. bryanti* is very similar in size and morphology to the p4s of *M.* cf. *M. bryanti* from Eastgate. Fortunately, all three recognized species of *Miospermophilus* are known from their m1s and m2s. The m1s and m2s of the Eastgate *M.* cf. *M. bryanti* share the following characters with the following species: for *M. lavertyi*, absence of an anteroconid, a strongly anteriorly bowed anterior cingulid, a submerged entoconid, a weak ectolophid, and a weak mesostylid: for *M. wyomingensis*, absence of an anteroconid, a variable mesoconid, and a variable entoconid: for *M. bryanti*; absence of an anteroconid, a stongly anteriorly bowed anterior cingulid, and a weak ectolophid and mesostylid.

In contrast, the m1s and m2s from Eastgate differ from *M. lavertyi* in that *M. lavertyi* does not have a mesoconid and has a submerged entoconid. The Eastgate m1s and m2s differ from *M. wyomingensis* in that *M. wyomingensis*

possesses a straight anterior cingulid, a distinct ectolophid, and a variable mesostylid. *Miospermophilus bryanti* differs from the Eastgate m1s and m2s in that *M. bryanti* does not possess a mesoconid, and the entoconid is partially submerged. In size, the Eastgate m1s and m2s are most similar to those of *M. wyomingensis*, but in tooth characters they most closely resemble the m1s and m2s of *M. bryanti.*

Discussion.— With character and size differences occurring between the left and right cheekteeth (P4/4, M1/1, and M2/2) and cheekteeth of the same tooth row on the same individual, variation among different species is difficult to evaluate. Thus, until more complete material becomes available, the extent of variation displayed by this group of sciurids in the western interior, including Eastgate, remains to be determined. For example, the metaloph of UCMP 141912 diverges posteriorly on the M1 and M2; however, it is more pronounced on the M2. Thus, the protoloph and metaloph appear to be more closely parallel on the M1 than they do on the M2. The posterior cingulum on the M1 is notched where it unites with the anterior cingulum of the M2, while the posterior cingulum of the M2 is straight.

Lindsay (1972) suggested that *Miospermophilus* possesses distinct entoconids on the lower molars, while Black (1963) stated that *Miospermophilus* has indistinct entoconids, an opinion followed by Dalquest et al. (1996). The lower molars of *Miospermophilus* from Eastgate are variable in this character. Therefore, all authors cited above may be correct. That is, several specimens

from Eastgate have submerged entoconids, whereas others display partially submerged or distinct entoconids. The Eastgate specimens may represent a new species of *Miospermophilus* but until more complete material becomes available, it cannot be adequately diagnosed at present.

Miospermophilus hutchisoni n. sp.

Plate 12 (M–O)

Holotype.— UCMP 131386, left dentary with il, dp4, p4–m2.

Type locality.— Eastgate, UCMP V70140.

Etymology.— Named after J. Howard Hutchison, for showing me the Eastgate localities and for helpful discussions concerning Eastgate.

Other localities.— OMNH V975, UCMP V70142, V74103.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54551, left dp4; OMNH 54566, right dentary with i1–m2; OMNH 54567, left dentary with m1–m3; OMNH 54577, left dentary with m1–m3; OMNH 54863, left dentary with m1–m2; UCMP 131386, left dentray with il, dp4, p4–m2; UCMP 141599-01, right dp4; UCMP 141599-03, right dp4; UCMP 141599-04, right dp4; UCMP 141599-05, right dp4; UCMP 141599-06, right dp4; UCMP 141599-09, left dp4; UCMP 141602-05, left m3;

UCMP 141602-07, left m3; UCMP 141602-08, right dp4; UCMP 141602-12, left m3; UCMP 141602-14, right m3; UCMP 141602-17, right m3; UCMP 141613-04, right dp4; UCMP 141801,left dp4; UCMP 141806-04, right dp4; UCMP 141826-02, right m1-m2; UCMP 141826-07, right m3; UCMP 141844, right dentary with i1-m3; UCMP 141909, left dentary with i1-m2.

Measurements.— See Table 19.

Diagnosis.— *Miospermophilus hutchisoni* is a small marmotine that differs from all species of *Protospermopilus* and most species of *Spermophilus* in possessing smaller sized lower cheekteeth, but larger than most species of *Tamias*. The dentary is similar to that of *S. primitivus* in having a masseteric scar that terminates in a point (rather than being rounded) below the anteromost part of the m1. The mental foramen of *M. hutchisoni* is similar to *S. primitivus*, *Protospermophilus vortmani*, and *Miospermophilus bryanti* in occurring near the dorsal edge of the diastema and centrally between the anteromost part of the anterior end of the diastema and the p4. The lower incisors of *M. hutchisoni* possesses numerous fine longitudinal striations on the mesal side. This condition has been reported for other species of *Miospermophilus* (e.g., Korth, 1994; Wilson, 1960).

The m1 and m2 of *M. hutchisoni* are most similar to *M. bryanti*, from which it differs in having a distinct mesoconid, and a partially distinct entoconid. *Miospermophilus hutchisoni* also differs from *M. bryanti* in having a distinct ectolophid, and a distinct mesostylid (see Tables 19-23).

Description.— The dentary fragment (UCMP 131386) possesses the i1, dp4, p4–m2. The cheekteeth have little wear to the occlusal surface and increase in size from front to back. Anteriorly, the dentary is broken along the anteromost margin of the incisor alveolus and posteriorly through the anteromost edge of the alveolus of the m3. The diastema is long and shallow. The mental foramen occurs high on the dorsal side of the diastema and centrally between the incisor and the p4. A robust masseteric scar ends below the anterior root of the m1. The ascending ramus arises lateral to the posteromost part of the m2. There are no unique features on the lingual surface of the dentary.

The incisor is incomplete. It is laterally compressed and has numerous fine striations on its mesial surface.

The dp4 is longer than wide, possesses two roots that increase in their separation distally (like a bipod stand), and an occlusal surface that is moderately worn. No anterior cingulid is present, but a small anteroconid occurs centrally between the protoconid and the metaconid. A very short metalophid unites the protoconid and metaconid (which are in close association with each other). A shallow labial groove occurs between the protoconid and hypoconid. A low but wide mesoconid occurs on a low, elongated ectolophid. The mesoconid lies closest to the hypoconid. The posterolophid arises low (at the same level as the ectolophid on the anterior surface of the protoconid) and at the posterolingual surface of the hypoconid. Furthermore, the posterolophid rises high dorsally and bends strongly anterolingually as it reaches the entoconid high above its base.

The posterolophid occurs well above the floor of the talonid basin.

The p4 is not fully erupted from the dentary, but the unworn occlusal surface is exposed, permitting the following description. The tooth is longer than wide and is lacking an anterior cingulid, an anteroconid, and a metalophid. The protoconid and metaconid are separated by a narrow groove but unite well above their respective bases. A deep labial valley occurs between the protoconid and hypoconid. The mesoconid is absent, but a low, short ectolophid is present. The posterolophid arises low on the posterolingual surface of the hypoconid and rises high dorsally as it bends strongly posteriorly before it joins a prominent entoconid high above its base. There is a small groove on each side of the entoconid. A small mesostylid occurs anterior to the entoconid and is not attached to the entoconid or metaconid. However, at the posterior base of the metaconid a lophid extends posteriorly but does not join the mesostylid.

The m1 is longer than wide and the anterior roots are fused. It is unclear if the posterior roots are fused because they are housed in their alveolus (i). An anteriorly bowed anterior cingulid is present. No anteroconid is present. The metalophid has a narrow, U-shaped groove between the protoconid and the metaconid, but the trigonid remains closed to the talonid basin. A deep labial valley occurs between the protoconid and the hypoconid. A distinct mesoconid occurs on a low, short ectolophid. The mesoconid lies midway between the protoconid and hypoconid. The posterolophid arises low (at the same level as the ectolophid on the anterior surface of the hypoconid) at the posterolingual

surface of the hypoconid. In addition, the posterolophid rises high dorsally and bends slightly posteriorly before it connects with the entoconid. The posterolophid occurs well above the floor of the talonid basin. There is a narrow groove between the posterolophid and the entoconid. A deep, narrow valley lies between the entoconid and the mesostylid. Thus, the talonid basin opens lingually. The mesostylid unites with the posterior base of the metaconid.

The m2 differs from the m1 in being larger in size. It also has a posterolophid that bends strongly anterolingually (more so than in the m1) as it arises from the hypoconid.

The m3 resembles the preceding molars except being longer than wide, and having a more rounded hypoconid. It also has a metalophid that joins the anterior cingulid low near the protoconid, and lacks a mesostylid. The talonid basin has crenulations near the bases of the protoconid and hypoconid. The preceding cheekteeth likely possessed similar crenulations at an earlier stage of wear.

Comparison.— For the dentary, *M. hutchisoni* is distinguished from *Protospermophilus* by the following: a mental foramen that occurs near the dorsal edge of the diastema and centrally between the anteromost part of the diastema and the p4 (except *P. vortmani*); and a masseteric scar that terminates below the anterior root of the m1 with a rounded distal end. The m1 and m2 of *M. hutchisoni* differ from most species of *Protospermophilus* in having a distinct mesoconid (except *P. angusticeps* and *P. quatalensis*), a distinct ectolophid

(except *P. angusticeps* and *P. kelloggi*), and a partially submerged entoconid (except *P. quatalensis*).

Miospermophilus hutchisoni is most similar to *M. wyomingensis* in size but, in characters of the lower cheekteeth it is most similar to *M. bryanti*. The following characters are similar for the p4s of all known species of *Miospermophilus* (except *M. lavertyi* for which no lower cheekteeth have been reported): absence of an anteroconid or anterior cingulid, an appressed protoconid and metaconid (very appressed in *M. bryanti*), and a weak ectolophid. In contrast, the characteristics found in *M. hutchisoni* that differ from *M. bryanti* and *M. wyomingensis* include having a mesoconid, a variable entoconid (except *M. wyomingensis*), a weak mesostylid, and grooves on each side of the entoconid.

Excluding size, the p4 of *M. hutchisoni* are similar to the known p4s of *Protospermophilus* in the absence of a mesoconid (except *P. vortmani*), a weak mesostylid (except *P. kelloggi*), a weak ectolophid, and a partially submerged entoconid. However, *M. hutchisoni* differs from most species of *Protospermophilus* in having the protoconid and metaconid so closely appressed that they appear to be a single cusp (except in *P. kelloggi*). The latter condition also occurs in *M. bryanti* and *Spermophilus primitivus*. However, the p4 of *M. hutchisoni* differs from most p4s of *Protospermophilus*, *Spermophilus*, and *Miospermophilus* in the following: absence of an anteroconid (except *P. angusticeps* and *P. quatalensis*), a protoconid and metaconid that are very

appressed (except *P. kelloggi* and *S. primitivus*), and a small mesostylid (except *P. kelloggi* and *S. primitivus*) (see Tables 19–23).

The dentary of *M. hutchisoni* is similar to that of *M. bryanti*, *Protospermophilus*, and *S. primitivus* in having a long and shallow diastema. They also share a mental foramen that occurs dorsoventrally centered between the dorsal and ventral surfaces of the diastema, and anterior to the p4 (except *P. angusticeps*); a masseteric fossa that terminates anteriorly below the m1 (except *P. quatalensis* and *M. bryanti*); and a rounded anterior end of the masseteric fossa (except *P. quatalensis* and *S. primitivus*).

The incisor of *M. hutchisoni* differs from all known species of *Protospermophilus* and *Miospermophilus* in having few distinct longitudinal striations on the mesial surface of this tooth. The incisor for *S. primitivus* is unknown.

The m1 and m2 of *M. hutchisoni* differs from known species of *Protospermophilus*, *S. primitivus*, and most species of *Miospermophilus* in having a variable entoconid (except *M. wyomingensis*), and a distinct ectolohid (except *P. angusticeps*, *P. kelloggi*, and *M. wyomingensis*). In addition, *M. hutchisoni* differs from *Protospermophilus*, *S. primitivus*, and most species of *Miospermophilus* in having a distinct mesostylid (except *P. angusticeps* and *M. wyomingensis*), and the presence of two gooves on each side of the entoconid.

Discussion.— Until more complete material is recovered for all species of *Miospermophilus*, their taxonomic relationships will remain difficult to determine.

However, based on the available material, *M. hutchisoni* appears to have a few characters that Black (1963) listed as primitive and that do not occur in geologically older forms like *M. bryanti*. These characters include: a masseteric scar that terminates below the m1; few distinct longitudinal striations on the mesal surface of the lower incisor; and on the p4, weak mesostylids and mesoconids. The molars of *M. wyomingensis* share more characters with *M. hutchisoni* than *M. bryanti* or *M. lavertyi*.

Tamiini Black, 1963

Tamias Illiger, 1811

Tamias sp. indet.

Plates 13 and 14 (A–L; A–G)

Localities.— Eastgate, OMNH V976, UCMP V70140, V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the genus.— Hemingfordian: Pawnee Creek Formation, Martin Canyon Quarry A, Colorado (Black, 1963; Wilson, 1960). Barstovian: Barstow Formation, Barstow fauna, San Bernardino County, California (Lindsay, 1972); Esmeralda Formation, Tonapah fauna, Nye County, Nevada (Black, 1963; Henshaw, 1942). Clarendonian: Matthews Ranch fauna and Nettle Springs fauna, Ventura County, California (James, 1963).

Referred specimens.— OMNH 54531, right p4; OMNH 54532, right m1 or m2; OMNH 54534, left DP4; OMNH 54536, left M1 or M2; OMNH 54535, left m1 or m2; OMNH 54536, left M1 or M2; OMNH 54541, left M1 or M2; OMNH 54555, right p4; OMNH 54559, right M1 or M2; OMNH 54560, right m1 or m2; OMNH 54561, right P4; OMNH 54565, left dentary fragment with i1-p4; OMNH 54576, right p4; UCMP 141599-02, left dp4; UCMP 141599-07, right dp4; UCMP 141599-08, right p4; UCMP 141599-10, left p4; UCMP 141599-14, right p4; UCMP 141599-19, left p4; UCMP 141599-20, left p4; UCMP 141599-21, right p4; UCMP 141600-02, right M1 or M2; UCMP 141600-04, left M1 or M2; UCMP 141600-07, left M1 or M2; UCMP 141600-08, right M1 or M2; UCMP 141600-14, left M1 or M2; UCMP 141600-16, left M1 or M2; UCMP 141600-17, left M1 or M2; UCMP 141600-18, right M1 or M2; UCMP 141600-19, left M1 or M2; UCMP 141600-21, left M1 or M2; UCMP 141600-22, left M1 or M2; UCMP 141600-24, left M1 or M2; UCMP 141600-26, left M1 or M2; UCMP 141601-03, right m1 or m2; UCMP 141601-07, right m1 or m2; UCMP 141601-10, left m1 or m2; UCMP 141601-17, left m1 or m2; UCMP 141601-19, left m1 or m2; UCMP 141601-20, right m1 or m2; UCMP 141601-21, right m1 or m2; UCMP 141601-22, right m1 or m2; UCMP 141601-26, left m1 or m2; UCMP 141601-28, left m1 or m2; UCMP 141601-32 right m1 or m2; UCMP 141602-11, right m3; UCMP 141602-15, left m3; UCMP 141602-21, right m1 or m2; UCMP 141606-04, right M1 or M2; UCMP 141607, right dentary fragment with m2; UCMP 141613-01, left p4; UCMP 141628, left dentary i1-m2; UCMP 141632-01, right m1 or m2; UCMP

141632-04, right m3; UCMP 141635, left dentary fragment with i1,m1; UCMP 141691, right dentary with i1-m3; UCMP 141824-07, left M1 or M2; UCMP 141826-01, left M1 or M2; UCMP 141826-03, left M1 or M2; UCMP 141826-05, right m1 or m2; UCMP 141826-10, right p4; UCMP 141826-11, left m1 or m2; UCMP 141829-02, left M1 or M2; UCMP 141829-03, right M1 or M2; UCMP 141829-08, left M1 or M2; UCMP 141829-09, left M1 or M2; UCMP 141829-12, right M1 or M2; UCMP 141829-16, right M1 or M2; UCMP 141829-18, right M1 or M2; UCMP 141829-75, left M1 or M2; UCMP 141830-03, right P4; UCMP 141830-07, right P4; UCMP 141830-08, left DP4; UCMP 141830-09, right DP4; UCMP 141830-11, left DP4; UCMP 141830-12, left DP4; UCMP 141830-13, right P4; UCMP 141830-17, right M3; UCMP 141830-19, left P4; UCMP 141830-01, left DP4.

Measurements.— See Tables 18 and 19.

Description.— The DP4 (UCMP 141830-11) is triangular in occlusal outline and has little wear to the occlusal surface. The anterior cingulum is greatly expanded anteriorly, lies well below the central basin, and attaches to a prominent parastyle. In addition, the anterior cingulum spans less than one-half the width of the tooth. Thus, it does not attach to the protocone. The anterior basin is much wider than long. The protocone is the largest cusp followed in size by the metacone and protocone, respectively. The protocone is anteroposteriorly elongated with a centered apex. The protoloph arises from the anterolabial side of the protocone and forms a high, thin ridge that projects

labially in a straight line to join the paracone. The central basin becomes broader posteriolabially and remains open labially. No mesostyle is present. The metaloph is constricted at its contact with the protocone. A large metaconule occurs adjacent to the protocone. Labial to the metaconule, the metaloph forms a low, thin ridge that diverges strongly posterolabially. The posterior cingulum forms a broad shelf posterior to the protocone and narrows labially, terminating at the posterolingual base of the metacone.

The P4 (OMNH 54561) is subquadrate in occlusal outline with little wear to the occlusal surface. The anterior cingulum bows strongly anteriorly, arises low on the anterolabial base of the protocone, and attaches to a small parastyle (large in UCMP 141830-11). The anterior basin is very short and narrow but remains open labially. The protocone is the largest of the cusps followed in size by the metacone and paracone, respectively. The protocone is anteroposteriorly elongate with the apex anteriorly placed but in UCMP 141830-11 it is centered. The protoloph arises anterior to the apex of the protocone and extends labially in a straight line to join with the paracone. No protoconule is present. The central basin is the widest of the basins and becomes broader posterolabially. The metaloph is constricted at its contact with the protocone. However, a short, thin ridge occurs between the protocone and a metaconule. Labial to the metaconule, the metaloph forms a high, thin ridge that diverges strongly posterolabially. No mesostyle is evident and the central basin is open labially. The posterior cingulum forms a broad shelf posterior to the protocone and

narrows labially, terminating at the posterolingual surface of the metacone. Thus, the posterior basin is closed labailly.

The M1 or M2 (UCMP 141829-08) is subquadrate in occlusal outline and possesses little wear to the occlusal surface. The anterior cingulum arises at the anterior base of the protocone where it takes an abrupt change of direction labially. It then continues in a straight line joining a small parastyle (for other Eastgate sciurid upper molars, these structures are closer to each other). The anterior cingulum is strongly bowed anteriorly. The anterior basin is fusiform in shape with the widest end labial and the narrowest end lingual. The anterior basin is open labially. The protocone is the largest cusp followed in size by the paracone and metacone, respectively. For UCMP 141600-24 and UCMP 141600-21, the paracone and metacone are about equal in size to each other. The protoloph arises anterior to the apex of the protocone and diverges slightly posteriorly toward the paracone. In UCMP 141600-24 and UCMP 141600-21, the protoloph is straight rather than bent posteriorly. No protoconule is evident. The central basin is the widest of the basins; it becomes broader posterolabially and remains open labially. The metaloph is slightly constricted between a small metaconule and the protocone. Labial to the metaconule, the metaloph forms a low, thin ridge that diverges strongly (or slightly as in OMNH 54541) posteriorly until reaching the metacone. A strong, anteroposteriorly oriented mesostyle is present and attaches to the base of the paracone. In UCMP 141600-24, the mesostyle is small, rounded, and occurs near the base of the paracone. The

posterior cingulum makes an abrupt change in direction where it joins the protocone. After the direction change, the posterior cingulum forms a broad shelf that narrows labially until joining the posterior base of the metacone. Thus, the posterior basin is closed labially.

The M3 (UCMP 141830-17) is triangular in occlusal. The anterior cingulum arises lingually near the anterior base of the protocone and terminates labially at the anterior base of the paracone. The anterior basin is long, narrow, and open labially. The protocone is the largest cusp and is anteroposteriorly elongate. The protoloph arises from the anterolabial surface of the apex of the protocone and extends labially in a straight line to join the paracone. The paracone is prominent and well rounded. There is no metaloph or any other structure in the large posterior basin.

The dentary (UCMP 141691) has cheekteeth that increase in size from front to back. The diastema is shallow and long. The mental foramen occurs high dorsally and well in front of the p4. However, the mental foramen occurs closer to the p4 than to the incisor. The masseteric scar ends below the anterior root of the m1. The ascending ramus arises lateral to the posteromost part of the m3. Lingually there is a large, posteriorly open inferior dental foramen. This foramen occurs below the level of the tooth row.

The incisor is laterally compressed and extends well above the tooth row. It has six distinct longitudinal striated lines on the mesial surface.

The p4 is wider than long. No anterior cingulid is present, but a small

anteroconid occurs low and between the protoconid and metaconid. There is no metalophid. A narrow, shallow groove occurs between the protoconid and metaconid. A deep, labial valley occurs between the protoconid and hypoconid. A small mesoconid occurs on a low, short ectolophid. The mesoconid is centrally placed between the protoconid and hypoconid. The posterolophid arises low (at the same level as does the ectolophid on the anterior surface of the hypoconid) at the posterolingual surface of the hypoconid. In addition, the posterolophid arises high dorsally and forms a well rounded posterolingual corner. An entoconid emerges above the posterolophid. A small mesostylid is submerged within a lophid that extends from the entoconid to the posterior base of the metaconid.

An m1 or m2 (UCMP 141601-22) is subquadrate in occlusal outline and has little wear to the occlusal surface. The anterior cingulid is strongly bowed anteriorly. The metalophid arises high on the protoconid, descends rapidly, and quickly ascends to join the anterior cingulid midway between the protoconid and metaconid. A deep labial valley occurs between the protoconid and hypoconid. A distinct (small on UCMP 141691), centrally located mesoconid occurs on a low, short ectolophid. The posterolophid arises low on the hypoconid and descends quickly as it traverses the tooth then quickly ascends to unite with the entoconid. The posterolophid occurs well above the floor of the talonid basin. The entoconid is submerged within the posterolophid. However, in UCMP 141691 a distinct entoconid rises well above the posterolingual corner of the

posterolophid. The posterolophid forms a well rounded corner at the entoconid. A lophid continues from the entoconid to join at the posterior base of a distinct metaconid. In UCMP 141691, a lophid rises low on the anterior side of the entoconid but becomes constricted at the posterior base of the metaconid. No mesostylid is present, and the talonid basin is closed lingually and labially.

The m3 (UCMP 141691) is heavily worn on the occlusal surface. This tooth is similar to the preceding molars except for the following: much longer than wide, larger overall size, and more rounded hypoconid. Because of the late stage of wear, no other characters are evident.

Comparison.— Dalquest et al. (1996) stated that *Tamias* possess mesoconids on their lower cheekteeth, while Black (1963) noted that *T. ateles* from Tonopah (Nevada), *T.* sp. from Thomas Farm (Florida), and *Tamias* sp. from Martin Canyon Quarry A (Colorado) do not possess mesoconids on the lower m1 or m2. However, Black (1963) indicated that *Tamias* sp. from Wounded Knee (South Dakota) has a distint mesoconid. Lindsay (1972) also noticed the lack of mesoconids for *Tamias ateles* from Barstow, California.

The DP4s listed above are smaller than those of *Protospermophilus*, *Spermophilus*, and *Miospermophilus* but are similar in size to the larger *Tamias* sp. reported from the Wounded Knee local fauna by Black (1963). In addition to size, the *Tamias* sp. from Eastgate resembles *Tamias* sp. from the Wounded Knee local fauna in sharing the following characters: a triangular occlusal outline, a complete metaloph and protoloph, a metaconule and protoconule, a distinct

mesostyle, and a reduced posterior cingulum.

The P4s of *Tamias* sp from Eastgate are smaller than those of *Protospermophilus*, *Spermophilus*, and *Miospermophilus* but are similar in size to the larger *Tamias* sp. reported from the Wounded Knee local fauna by Black (1963). The *Tamias* sp. from Eastgate are most similar to *Tamias* sp. from the Wounded Knee local fauna and share the following: a complete protoloph without a protoconule, and a constricted metaloph with a distinct metaconule. However, the Eastgate *Tamias* sp. differs from the Wounded Knee *Tamias* sp in having a mesostyle, which is not found in the *Tamias* sp. from the Wounded Knee local.

The M1 and M2 listed above are smaller than *Protospermophilus*, *Spermophilus*, and *Miospermophilus* but are similar in size to the larger *Tamias* reported from Martin Canyon Quarry A by Wilson (1960). In addition to size, the *Tamias* sp. from Eastgate share the following characters with the *Tamias* sp. from Martin Canyon Quarry A in possessing a metaconule and a distinct mesostyle. In contrast, one specimen (SDSM 58100) from Martin Canyon Quarry A described by Black (1963) has both a metaconule and a protoconule, a condition not displayed by any of the Eastgate *Tamias* sp.

The M3s of *Tamias* sp. from Eastgate are smaller than *Protospermophilus*, *Spermophilus*, and *Miospermophilus* but are similar in size to the larger *Tamias* sp. reported from Martin Canyon Quarry A by Wilson (1960). In addition, the *Tamias* sp. from Eastgate are most similar to *Tamias* sp. from the

Wounded Knee local fauna and shares the following characters: triangular shape, long narrow anterior basin open labially, large protocone, distinct well rounded paracone, and mesostyle. However, the M3 of *Tamias* sp. from Eastgate differs from the *Tamias* sp from the Wounded Knee local fauna in lacking a metaloph, which is present in the Wounded Knee specimen.

Unfortunately, complete dentaries of *Tamias* sp. are rare from the Miocene of North America. Most reports of *Tamias* sp. are based on isolated teeth or incomplete dentary fragments. Therefore, the characters of the dentary listed for *Tamias* sp. from Eastgate can only be compared to a single specimen of *Tamias* sp. from Thomas Farm, Gilchrist County, Florida (Black, 1963). The *Tamias* sp. from Eastgate and *Tamias* sp. from Thomas Farm share a single character of the dentary, a long and shallow diastema.

In contrast, they differ in the following: *Tamias* sp. from Eastgate has a mental foramen that is dorsoventrally centered between the dorsal and ventral surfaces of the diastema and lies anterior to the p4, whereas in *Tamias* sp. from Thomas Farm a mental foramen occurs near the dorsal edge of the diastema and central to the p4 and incisor; the distal end of the masseteric scar of *Tamias* sp. from Eastgate ends below the m1 and is rounded, whereas in *Tamias* sp. from Thomas Farm it occurs below the p4 and is pointed distally.

The incisors of *Tamias* sp. from Eastgate differ from *Spermophilus* in having six, distinct, longitudinal striations on the mesial surface of the incisor (Dalquest et al., 1996).

The p4 of *Tamias* sp. from Eastgate differ in size from other described *Tamias* sp. (from the Miocene of North America), *Spermophilus primitivus*, and *Miospermophilus bryanti* as follows: slightly smaller compared to *Tamias* sp. from the Wounded Knee local fauna, Pennington County, South Dakota; much smaller than *S. primitivus* from the Madison Valley Formation, Gallatin County, Montana; and smaller than *M. bryanti* from the Martin Canyon Quarry A, Logan County, Colorado.

The p4 of *Tamias* sp. from Eastgate shares the following characters with other Miocene-age sciurids: with *Tamias* sp., an appressed protoconid and metaconid, a small mesoconid, and a small entoconid; with *M. bryanti* and *M. wyomingensis*, absence of an anterocingulid, an appressed protoconid and metaconid, and a weak ectolophid; with *S. primitivus*, a small mesostylid. In contrast, the p4 of *Tamias* sp. from Eastgate differs from other Miocene-age sciurids as follows: from *Tamias* sp., presence of a weak anteroconid, a weak ectolophid, and a weak mesostylid; from *M. bryanti* and *M. wyomingensis*, a weak anteroconid, a small mesoconid, a small entoconid, and a small mesostylid; from *S. primitivus*, a weak anteroconid, a protoconid and metaconid that are not tightly appressed, a small mesoconid, and a small ectolophid (see Tables 29–33).

The m1 and m2 of *Tamias* sp. from Eastgate are similar in size to those of *M. wyomingensis*, whereas they are slightly larger than *Tamias* sp. from Martin Canyon Quarry A (prior to this study, it was the largest *Tamias* sp. reported), but

much smaller than *S. primitivus*. The *Tamias* sp. from Eastgate shares more characters with *Tamias* sp. from Martin Canyon Quarry A than with any other *Tamias* sp. reported. For example, they lack an anteroconid and share a strongly anteriorly bowed anterior cingulid, a variable mesoconid, a variable entoconid, a variable ectolophid, and a variable mesostylid. Most species of *Miospermophilus* possess several characters (listed below) that distinguish them from *Tamias* sp.: a straight anterior or bowed cingulid, absence of a mesoconid, a partially submerged entoconid, a weak ectolophid, and a small mesostylid. From *S. primitivus*, *Tamias* sp. from Eastgate differs in having a distinct mesoconid, a partially submerged entoconid, a low posterolophid, a distinct ectolophid, and a distinct mesostylid (the last two characters are variable for *Tamias* sp. from Eastgate).

The m3 of *Tamias* sp. from Eastgate were not compared to the other known sciurids from the Miocene of North America because of their rare occurrence and lack of distinguishing characters for *Tamias*. For example, Pratt and Morgan (1989) listed the reduction of the metalophid on the m3 as a dental synapomorphy for *Nototamias*, *Tamias*, and *Eutamias*. Dalquest et al. (1996) suggested this character was also present in *Miospermophilus* and other genera within the family Sciuridae. This is evident by the sample of sciurids from Eastgate. In addition, when an m3 was included in published reports, these teeth usually were isolated occurrences and not associated with the preceding teeth. The m3s provided little aid in the identification of *Tamias* sp. from

Eastgate. Therefore, placement of the m3s listed above are based on size and direct association (i.e., occurring in the same tooth row) with other lower cheekteeth for this group.

Discussion.— The Eastgate upper premolars listed above for *Tamias* sp. are the smallest sciurid cheekteeth (except for the petauristines) from Eastgate. In size, they are very similar to the upper P4 of *Tamias* sp. from the Wounded Knee fauna studied by Black (1963). The upper molars of *Tamias* sp. from the Wounded Knee fauna are similar in size to the *Tamias* sp. from Barstow described by Lindsay (1972), but they are much smaller than *Tamias* sp. from Martin Canyon Quarry A described by Wilson (1960). Thus, based on size these upper P4s from Eastgate are too small to be considered anything other than *Tamias* sp. and may represent a new species of *Tamias*.

In size, the upper cheekteeth of the Eastgate sciuirds listed above are similar to *Tamias* sp. from the Martin Canyon Quarry A. The *Tamias* sp. specimens from Quarry A are the largest specimens of *Tamias* described from the Miocene of North America. Except for a mesostyle placed near the metacone, these Eastgate specimens are very similar in character to *Tamias* sp. (MWSU 12847) from the Clarendonian of Oklahoma studied by Dalquest et al. (1996). In contrast, these Eastgate specimens are smaller than *S. tephrus* (LACM 334) figured in Black (1963). However, an Eastgate specimen (OMNH 54541) and LACM 334 share a unique character, a large mesostyle (not small) that lies adjacent the metacone. Until more complete material becomes

available for this group of sciurids from Eastgate, the identification to *Tamias* sp. to species is not possible.

Although Black's (1963) review of the Tertiary squirrels of North America was comprehensive, additional specimens collected from North America's Tertiary deposits are proving difficult to identify with any degree of certainty. This is certainly the case for the Eastgate sciurids. The literature is laden with inconsistencies for characters that occur within the same species. Based on the Eastgate sciurids, greater variation of characters for upper and lower cheekteeth may exist. For example, OMNH 54548 exhibits no mesoconid on the p4 or m1 but possesses a weak mesoconid on the m2. If the m1 and m2 were isolated teeth, their differences for this character, their size, and their shape could lead an investigator to place each tooth in a different species.

After reviewing the literature and examining the Eastgate sciurids, I agree with W. W. Dalquest (W. W. Dalquest, personal communication), who stated that the Tertiary sciurids should be re-examined. A good starting point might be to evaluate the characters that authors list for separating the different genera and species, and to develop a common nomenclature for the characters examined. In addition, one should try to determine how much variation that occurs for these characters both intraspecifically and interspecifically. By quantifying characters and evaluating intraspecific and interspecific variation, a baseline could be established to allow future investigators to use a reliable set of data to make comparisons and help identify taxa collected from Tertiary deposits in North

America.

Subfamily Petauristinae Miller, 1912

Micropetauristodon vestali new genus and species

Plate 14 (H-J)

Holotype.— OMNH 54564, left M1 or M2.

Type locality.— Eastgate, UCMP V70140.

Etymology.— Named in honor of Bedford M. Vestal, for his guidance and support during my graduate career at the University of Oklahoma.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimen.— Type only.

Measurements.— Ap=0.68, Tr=0.63.

Diagnosis.— *Micropetauristodon vestali* is an exceedingly small petauristine that is more than 70% smaller in size than any known taxa. The M1 or M2 differ from other known petauristines in the following: lacking a metaloph, presence of an isolated metaconule that lies in the middle of the central basin, and presence of two lophs that arise from the posterior cingulum and are directed anteriorly toward the protoloph. These lophs have additional lophules projecting lingually and labially along their entire length.

Description.— OMNH 54564, a left M1 or M2, is subquadrate in occlusal outline, possesses three roots (one large lingual and two smaller labial), and has little wear to the occlusal surface. The anterior cingulum arises near the anterolabial base of the protocone (anterior to where the protoloph arises) and projects anterolabially to insert on the lingual side of a small parastyle. The anterior basin is long, narrow, and open labially. The protocone is the largest cusp, followed in size by the paracone. The protocone is anteroposteriorly elongate with its apex centered anteroposteriorly. The parastyle is small, low, and transversely elongate. The paracone is a small conical-shaped cusp on the terminal end of the protoloph. The protoloph arises from the anterolabial side of the base of the protocone at the point where anterior cingulum arises. The protoloph is constricted at its origin but becomes much wider labially to a small protoconule as it courses in a straight line to join the paracone. The anterior cingulum and protoloph are both low. The central basin is the largest basin on this tooth and remains closed labially. Near the base of the protocone is a metaconule that projects labially and towards the protoloph. The metaloph is absent. The posterior cingulum is short and does not close the small posterior basin. Along the anterior surface of the posterior cingulum two low, thin lophs arise and project anteriorly, reaching the anterior side of the protoloph.

Comparison and discussion.— It is not possible to directly compare *M. vestali* to any previously described petauristines from the Tertiary of North America because there are no M1 or M2 of similar-sized petauristines to

compare to the Eastgate specimen.

Lindsay (1972) described the smallest known Nearctic sciurid (*Petauristodon minimus*) from the Barstow Formation, San Bernardino, California. Unfortunately, the cheekteeth Lindsay (1972) described did not include an M1 or M2. However, he did describe a P4 and M3 for *P. minimus*. Their measurment are as follows: P4, Ap=0.95, Tr=1.14; M3, Ap=0.96, Tr=1.16.

Typically for the upper cheekteeth of sciurids they increase in size from front to back as follows: the P4 is smaller than the molars; whereas the M3 may be slightly longer, it is usually not wider than the preceding molars. The petauristine described by Lindsay (1972) does not follow this trend in decreasing size from front to back. However, the M1 or M2 of *M. vestali* from Eastgate is nearly 70% smaller than the P4 or M3 described by Lindsay (1972) (Figs. 9 and 10). Based on size alone, the Eastgate specimen is easily distinguished from other petauristines.

This taxon is the smallest petauristine reported from the Miocene of North America and is among the smallest of all known squirrels. The M1 or M2 represented by *M. vestali* is much smaller than either tooth reported by Lindsay (1972). Thus, the tooth reported herein for *M.* vestali would be much smaller than an M1 or M2 from *P.* minimus from the Barstow Formation. For the Miocene, and perhaps the Neogene, *M. vestali* may represent the world's smallest petauristine. However, this is a topic that will be evaluated in a separate paper.

Petauristodon Engesser, 1978

Petauristodon axelrodi n. sp.

Plates 14 and 15 (K–M; A–I)

Holotype.— UCMP 141805, right dentary fragment with p4, m2–m3.

Type locality.— Eastgate, UCMP V70140.

Etymology.— Named in honor of the late Daniel I Axelrod, who discovered the first Eastgate locality (UCMP V70138).

Other localities.— OMNH V975; UCMP V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54545, left M3; OMNH 54546, left P4; OMNH 54549, left M1 or M2; OMNH 54550, right M1 or M2; OMNH 54552, left M1 or M2; OMNH 54553, right p4; OMNH 54554, left M3; OMNH 54556, left p4; OMNH 54558, right p4; OMNH 54563, left M1 or M2; OMNH 54568, left M3; OMNH 54571, right m1 or m2; OMNH 54575, left M1 or M2; UCMP 141823-01, left m3; UCMP 141823-03, M1 or M2; UCMP 141823-04, left P4; UCMP 141823-05, left M1 o M2; UCMP 141823-06, left M1 or M2; UCMP 141823-07, left M1 or M2; UCMP 141823-08, left M1 or M2; UCMP 141823-09, left M1 or M2; UCMP 141823-10, right M3; UCMP 141823-11, right p4; UCMP

141823-12, left p4; UCMP 141823-13, right m1 or m2; UCMP 141823-14, right p4; UCMP 141823-15, right p4.

Measurements.— See Tables 33 and 34.

Diagnosis.— This is a small petauristine squirrel most similar in size to *Petauristodon minimus* and in possessing a large paracone, as well as a protoloph and metaloph that are deeply crenulated. *Petauristodon axelrodi* differs from *P. minimus* in having a triangular-shaped P4, a prominent mesostyle, a protoconule, a distinct metaconule, and a continuous posterior cingulum,

Description.— The P4 (UCMP 141823-04) is triangular in occlusal outline but is equally wide as it is long, and has little wear to the occlusal surface. The anterior cingulum and paracone are well developed and contribute, anteriorly, to the triangular occlusal outline of this tooth. The anterior cingulum makes an abrupt change of direction where it arises low at the anterior base of the protocone and attaches to the lingual side of the paracone. The anterior basin is nearly as wide as it is long, and is open labially. The protocone is the largest cusp, with the paracone being slightly larger than the metacone. The protocone is anteroposteriorly elongate with the apex placed anteriorly. The parastyle is transversely elongate, while the paracone is conical in shape. The protoloph is constricted where it arises low and anterior to the apex of the protocone. A low, worn protoconule lies between the protocone and paracone. The protoloph continues in a straight line ending at the lingual side of the paracone. A mesoloph, a loph that occurs between the protoloph and metaloph and attaches

near the center of the labial side of the protocone (Pratt and Morgan, 1989), is present. The central basin is the largest of the basins and filled with robust but shallow crenulations. The central basin is similar in width on both lingual and labial ends. The metaloph arises high on the protocone and posterior to its apex. This loph continues posterolabially as a high, rounded ridge. A distinct metaconule is present. A prominent mesostyle occurs at the posterolabial base of the paracone. A small labial shelf extends from the anteromost part of the anterior cingulum to the anterolabial base of the metacone. The central basin is open labially between the mesostyle and the metacone. The posterior cingulum makes an abrupt change of direction where it arises on the posterolabial side of the protocone to form a hypocone. In addition, the posterior cingulum forms a broad shelf that narrows labially before ending at the posterolingual base of the metacone. Thus, the posterior basin is closed labially.

The M1 or M2 (OMNH 54549) is subquadrate in occlusal outline. The anterior cingulum makes an abrupt change as it arises low on the anterior surface of the protocone and bends slightly anteriorly, with the parastyle submerged. Posterior to the parastyle, the anterior cingulum bends sharply posteriorly and inserts on the anterior surface of the paracone. The anterior basin is broad, deep, and closed labially. The protocone is the largest cusp and is anteroposteriorly elongate, with the paracone larger than the metacone. The protoloph arises low and anterior to the apex of the protocone. The protoloph is constricted at its contact with the protocone but quickly forms a low, thin ridge

that projects in a straight line to join the paracone. No protoconule is evident. The central basin is narrow lingually but becomes broader labially and is the largest basin on this tooth. The metaloph arises posterior and low with respect to the apex of the protocone and forms a low, thin ridge that continues posterolabially until it reaches the metacone. No metaconule is evident. A mesostyle arises near the posterolabial base of the paracone and extends posteriorly to join the anterior base of the metacone. Thus, the central basin is closed labially. The posterior cingulum forms a broad shelf posterior to the protocone and narrows labially before ending at the posterolingual base of the metacone, making the posterior basin closed labially.

In addition to the above characters for the M1 or M2, two variations are present for this group. UCMP 141823-03 is similar but has a strong labial shelf, while the posterior basin is reduced and a very low posterior cingulum is present on UCMP 141823-07.

The M3 (OMNH 54545) is subtriangular in occlusal outline. The anterior cingulum arises at the anterolabial base of the protocone and attaches to the anterolingual base of the paracone. The anterior basin is long, narrow, and closed labially. The protocone is the largest of the cusps and is anteroposteriorly elongate. The protoloph arises low and anterior to the apex of the protocone, extending in a straight line to reach the conical-shaped paracone. The talonid basin contains shallow, small crenulations. No other diagnostic structures are present.

The dentary fragment (UCMP 141805) has an incisor, as well as the p4, m2, and m3. The cheekteeth show little wear to the occlusal surface and increase in size from front to back. In addition, all cheekteeth possess numerous, shallow crenulations within their talonid basins. The dentary is complete anteriorly, but posteriorly the dentary is broken midway through the ascending ramus. The diastema is short and deep. An anteriorly open mental foramen occurs in the middle of the diastema and in front of the p4. The masseteric scar is well rounded and terminates below and between the anterior and posterior alveoli of the m1. On the lingual side of the dentary, a posteriorly oriented inferior dental foramen occurs at the posterior base of the ascending ramus. This foramen occurs below the level of the tooth row.

The incisor, which is broken distally, bears no ornamentation. It is buccolingually compressed, flat on the lingual side, and well rounded or convex on the labial side. Enamel covers almost one-half of the labial side but is absent on the lingual side.

The p4 is longer than wide. A small anteroconid is present. The larger metaconid is separated from the smaller protoconid by a short metalophid that attaches higher on the metaconid than on the protoconid. The trigonid basin is closed to the talonid basin. A deep valley parallels the labial side of the ectolophid. A small mesoconid occurs on a low, short ectolophid. The mesoconid is centrally located with respect to the protoconid and hypoconid. The posterolophid arises low (at the same level as the ectolophid joins the

anterior surface of the hypoconid) at the posterolingual surface of the hypoconid. Furthermore, the posterolophid rises and bends slightly posterolingually as it unites with a small entoconid high above its base. There is a narrow, shallow valley that separates the entoconid from a small mesostylid. Thus, the talonid basin is closed lingually.

The m1 or m2 is longer than wide. The anterior cingulum is strongly bowed anteriorly and attaches low on the anterolabial side of the protoconid. At the point where the anterior cingulum bows anteriorly, the metalophid attaches and arises on the anterolingual side high on the protoconid. Thus, the trigonid basin appears as a narrow, shallow groove running parallel to the labial end of the anterior cingulum. The trigonid basin is closed from the talonid basin. A deep labial valley occurs between the protoconid and hypoconid. A distinct, centrally placed mesoconid occurs on a low, short ectolophid. The posterolophid arises low on the hypoconid and descends quickly as it traverses the tooth, then quickly ascends to unite with the entoconid. The entoconid is partially submerged within the posterolophid (posterior cingulid). The posterolophid forms a well rounded corner at the entoconid. A narrow, shallow groove separates the entoconid from the mesostylid that joins the metaconid on the posterior base, the talonid basin is closed.

The m3 is similar to the preceding molars. However, it differs in being much longer than wide, and has a more rounded hypoconid. It also lacks a mesostylid.

Comparison and discussion.— The P4s of all known species of *Petauristodon*, except *P. minimus*, are much larger than those of *P. axelrodi*, although the P4 of *P. axelrodi* is slightly larger than *P. minimus* described by Lindsay (1972) (Figs. 9–14). The P4 of *P. axelrodi* differs from that of *P. minimus* in being equally long as wide. It also differs from *P. minimus* in having a protoconule, a mesoloph, a prominent metaconule, a distinct mesostyle, and a hypocone located where the posterior cingulum takes an abrupt change in direction. In addition, in *P. axelrodi* the posterior cingulum that reaches the metacone, whereas it does not do so in *P. minimus*.

The only other cheektooth of *P. minimus* that has been described is the M3. The M3 of *P. axelrodi* is much longer than wide, and its overall size is larger than that of *P. minimus*, which is more square in occlusal outline. In addition, the M3 of *P. axelrodi* differs from that of *P. minimus* in possessing a distinct anterior cingulum that reaches the paracone, a complete protoloph that reaches a distinct paracone, and an enlarged talonid basin.

Petauristodon axelrodi has a P4 that is similar in size to that of *P. minimus*; however, these two species differ in the characters listed above for this tooth. In addition, the M3 of *P. axelrodi* is much larger and differs in several characters from that of *P. minimus*. Except for *P. minimus*, all previously described species of this genus are much larger than *P. axelrodi*. Evaluation of relationships among these species must await recovery of additional, more complete material.

Petauristodon savagei n. sp.

Plates 15 and 16 (J–L; A–L)

Holotype.— OMNH 54537, left dentary with i1, m1–m2.

Type locality.— Eastgate, OMNH V972.

Etymology.— Named in honor of the late Donald E. Savage, who presented this project to me, aided in obtaining the UCMP specimens for this study, and introduced me to the Eastgate localities.

Other localities.— Type and OMNH V975.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54542, left m1 or m2; OMNH 54573, right p4; UCMP 141599-12, right p4; UCMP 141599-13, right p4; UCMP 141599-16, left p4; UCMP 141613-02, right dp4; UCMP 141629-02, right p4; UCMP 141629-04, right m3; UCMP 141629-05, left m1 or m2; UCMP 141824-02, right P4; UCMP 141824-10, right M3; UCMP 141826-04, right M3.

Measurements.— See Tables 33 and 34.

Diagnosis.— *Petauristodon savagei* is a medium sized petauristine squirrel that is much smaller than *P. pattersoni*, *P. jamesi*, *P. uphami*, and *P. matthewsi*, but much larger than *P. axerodi* or *P. minimus*. In size, *P. savagei* is

intermediate in size between the previously described species (see Figs. 9, 11-14). Excluding its much smaller size, *P. savagei* is most similar to *P. pattersoni* in sharing the following characters: for the P4, distinct parastyles, a parastylar cusp, presence of protoconules and metaconules, and a complete metaloph that is not parallel to protoloph. For the M3, they both possess a complete protoloph and metacone. The p4 of each of these two species has a reduced anterior cingulid (= protolophid; see Pratt and Morgan, 1989), a metaconid and protoconid that are closely appressed, and a distinct mesostylid. In addition, they both possess an anterior cingulid and complete metalophid for the m1-m2.

The P4 of *Petauristodon savagei* differs from *P. jamesi*, *P. matthewsi*, and *P. axelrodi* in having a distinct protoconule, a complete protoloph (not composed of several small cusps), two enamel spurs that join the metaconule to the posterior cingulum (no P4 is known for *P. uphami*). For the M3, *P. savagei* differs from that of *P. axelrodi* in having an anterior cingulum that does not reach the paracone, a groove that occurs between the paracone and the anterior cingulum, a trigon basin that is open labially, and a small mesostyle that separated from the paracone by a groove (no M3s are known for *P. jamesi* or *P. matthewsi*). It differs from that of *P. uphami* in having a metacone (both species share the presence of a mesostyle and lack of a hypocone). The p4 of *P. savagei* differs from that of *P. matthewsi* in lacking an anteroconid, and the mesoconid is not labially placed (p4s are not known for *P. uphami* or *P. jamesi*).

The m1-m2 of *P. savagei* differ from all species (except *P. pattersoni*) in being longer than wide, and in lacking a complete anterior cingulid. In addition, P. savagei differs from all species of *Petauristodon* in having a complete metalophid (except *P. matthewsi*), and in having a mesostylid that occurs midway between the protoconid and hypoconid.

Most similarities of the upper cheekteeth shared by *P. savagei* and *P. pattersoni* help to differentiate them from other species of *Petauristodon*. However, the upper and lower cheekteeth of *P. savagei* differ from those of *P. pattersoni* by several characters. The P4 of *P. savagei* differs from *P. pattersoni* in lacking a small cuspule that lies near the anterior edge of the parastyle, a double metaconule. The P4 of *P. savagei* differs from *P. pattersoni* in having two enamel spurs that join a single metaconule to the posterior cingulum, and a mesostyle that adjoins the paracone. The M3 of *P. savagei* differs from *P. pattersoni* in having a reduced anterior region, a protoloph is not complete, and a metaloph is lacking. The p4 of *P. savagei* differs from *P. pattersoni* in: lacking a double mesoconid (the mesoconid does not occur along the labial edge of the tooth); lacking a labial shelf; having a talonid basin narrow and deep between the hypoconid and entoconid. The m1-m2 of *P. savagei* differ from *P. pattersoni* in having an anterior cingulid that does not join the metaconid, and a mesostylid that is not appressed to the metaconid.

Description.— The P4 (UCMP 141824-02) is subquadrate in occlusal outline with heavy wear to the occlusal surface. The anterior cingulum arises low

on the anterior side of the protocone and projects anterolabially to join a distinct parastyle and a smaller parastylar cusp. There is no connection between the parastyle and the paracone. The parastyle is free. A parastylar cusp lies on the posterior side adjacent to the parastyle. The anterior basin is triangular in shape, is narrow lingually, broadens anteroposterioriy, and is open labially. The protocone is the largest cusp, is anteroposteriorly elongate, and has an anteriorly placed apex. The protoloph arises high and anterior to the apex of the protocone and takes an abrupt change of direction as it joins the protocone. There is a small protoconule at the point of abrupt change. Posterior to the small protoconule, the protoloph diverges strongly posterolabially to join with the posterior base of the metacone.

A small protoconule occurs near the protocone. The central basin is the widest of the basins being equally wide at the lingual and labial ends. The metaloph arises high and posterior to the apex of the protocone and diverges posterolabially for three-quarters of the transverse width of the tooth; it bends posterolabially, then bends again anteriorly to join the posterolingual side of the metacone. A large metaconule lies near the base of the protocone and has two enamel spurs that join the posterior cingulum. A mesoloph occurs along the labial side of the protocone closest to the metaloph. A narrow but deep groove separates the metacone from a distinct mesostyle, which joins the anterior base of the paracone. The central basin is open labially. The posterior cingulum forms a broad shelf posterior to the protocone and narrows labially before

terminating at the posterolingual base of the metacone. The posterior basin is closed labially.

To date, no M1s or M2s have been recovered for *P. savagei*. The M3 (UCMP 141826-04) is subtriangular in occlusal outline and has moderate wear to the occlusal surface. The anterior cingulum arises lingually near the anterior base of the protocone and terminates labially before reaching the paracone. The anterior basin is open labially by a narrow, deep groove that separates the anterior cingulum from the paracone. The protocone is the largest cusp and is anteroposteriorly elongate. The protoloph arises high and anterior to the apex of the protocone and extends labially in a straight line ending at a conical-shaped paracone. A small mesostyle is separated from the paracone anteriorly by a narrow groove. The entocone is submerged within the posterior cingulum and separated from the mesostyle by a deep, narrow groove.

The dentary fragment with i1, m1-m3 (OMNH 54537) has little wear to the occlusal surface of the cheekteeth. The three molars are similar in width but increase in length from front to back. Each cheektooth is low crowned and bulbous with robust, shallow crenulations within their deep talonid basins. The dentary is very fragmented and held together on the labial side by the rock matrix. On the lingual side of the dentary, only the incisor and distalmost part of the dentary are present, though very fragmented. Except for the size and shape of the diastema (short and deep), no other structures of the dentary are clearly visible.

The incisor is laterally flattened and has no ornamentation on the mesal surface. It is flat with no enamel on the lingual side, but is slightly convex with enamel on the labial side. The enamel covers one-third of the labial surface of this tooth.

The dp4 (UCMP 141613-02) has two roots that are widely separated anteroposteriorly. The tooth is much longer than wide and has heavy wear to the occlusal surface. A short, anteriorly bent anterior cingulid arises high on the labial side of the metaconid and inserts low on the anterolabial surface of the protoconid. No anteroconid is present. The metalophid is narrow and has a V-shaped notch halfway between the protoconid and metaconid. The trigonid basin is closed to the labial basin. A deep labial valley occurs between the protoconid and hypoconid. A distinct mesoconid occurs centrally on a low ectolophid between the protoconid and hypoconid. The posterolophid arises low (at the same level as the ectolophid joins the anterior surface of the hypoconid) on the posterolingual surface of the hypoconid. In addition, the posterolophid gains height and bends strongly posteriorly prior to joining the entoconid high above its base. There is a narrow valley that separates a distinct entoconid from a distinct mesostylid. The mesostylid is posteroadjacent to the base of the metaconid. The talonid basin is open lingually.

The p4 (UCMP 141629-02) is slightly longer than wide, and the occlusal surface is heavily worn. No anterior cingulid or anteroconid is evident. The protoconid and metaconid are tightly appressed to each other (similar to

Spermophilus primitivus and *Protospermophilus kelloggi*). The metalophid is narrow and has a V-shaped notch midway between the protoconid and metaconid. The trigonid basin is closed to the talonid basin. A deep labial valley occurs between the protoconid and hypoconid. A distinct mesoconid lies on a low, thin ectolophid between the protoconid and hypoconid. The posterolophid arises low (higher than the ectolopohid on the anterior surface of the hypoconid). In addition, the posterolophid gains height and bends slightly posteriorly before it reaches a distinct entoconid high above its base. There is a narrow valley that separates the entoconid from a distinct mesostylid. The mesostylid lies posteroadjacent to the base of the metaconid. The talonid basin is open lingually.

The m1 is longer than wide. A short, high, straight anterior cingulid arises midway on the labial side of the metaconid but terminates before reaching the protoconid. Thus, a narrow, deep groove separates the anterior cingulid from the protoconid. No metalophid is present. A deep labial valley occurs between the protoconid and the hypoconid. A distinct mesoconid with deep, narrow grooves occurs midway between the protoconid and hypoconid on the low, thin ectolophid. The posterolophid arises low (at the same level as the ectolophid to join the anterior surface of the hypoconid) at the posterior lingual surface of the hypoconid. In addition, the posterolophid gains height and bends anterolingually until reaching a distinct entoconid high above its base. There is a narrow valley that separates the entoconid from the mesostylid. The mesostylid is transversely

elongate and unites with the posterolingual surface of the base of the metaconid. Thus, the talonid basin is open lingually.

Except for two characters, the m2 is similar to the m1. The m2 is longer and wider, and the posterolophid bends more anterolingually than the m1.

The m3 resembles the preceding molars except in having a longer, more rounded hypoconid. It also has a mesostylid that is anteroposteriorly elongate rather than transversely elongate. In addition, it has an entoconid and mesoconid that are united rather than separated by a narrow groove.

Comparison and discussion.— There are no M1s or M2s known for *P. savagei*, but the other upper and all lower cheekteeth are described above for this taxon. In general, the known upper cheekteeth and all lower cheekteeth of *P. savagei* are much smaller than previously described species for *Petauristodon* (except *P. minimus* and *P. axelrodi*) (see Figs. 9, 11-14).

The P4 of *P. savagei* is similar to that of *P. jamesi* in sharing a distinct parastyle, a protoconule, and a complete protoloph. *Petauristodon savagei* has a P4 that is similar to that of *P. matthewsi* in sharing a distinct parastyle, mesostyle, a parastylar cusp, and a large metaconule. The P4 of *P. savagei* is similar to that of *P. jamesi P. pattersoni* in sharing a parastylar cusp, a complete protoloph, and a small protoconule. *Petauristodon savagei* has a P4 that is similar to that of *P. axelrodi* in sharing a small protoconule and mesoloph.

The P4 of *P. savagei* differs from that of *P. jamesi* in having a parastylar cusp, a small protoconule, and a large metaconule. It differs from that of *P.*

matthewsi in possessing a small hypocone, a protoloph and metaloph that are not parallel to each other, and a small mesostyle. From *P. pattersoni*, it differs in having a hypocone and, a single distinct metaconule, as well as in not having an enamel spur associated with the metaconule. The P4 of *P. savagei* differs from *P. axelrodi* in having a parastylar cusp, a free distinct parastyle, an anterior basin that is triangular in shape, a complete protoloph, a large metaconule, and a small mesostyle that occurs near the paracone.

The M3 of *P. savagei* is similar to that of *P. pattersoni* and *P. axelrodi* in lacking a parastylar cusp and mesoloph. The M3 of *P. savagei* differs from that of *P. pattersoni* and *P. axelrodi* in having an anterior cingulum that does not reach the parcone, a distinct mesostyle, and a deep anterolabial groove.

The m1 and m2 of *P. savagei* are similar to all known species of this genus in possessing the following characters: a distinct, centrally placed mesoconid that is separated from the protoconid and hypoconid by deep, vertical grooves; and a distinct mesostyle that occurs near the posterobase of the metaconid (except *P. jamesi*). In contrast, the m1 and m2 of *P. savagei* differ from other species of the genus in the following: a distinct mesostylid separated from the metaconid by a narrow, deep groove and the entoconid by a wide, deep groove; a strongly anteriorly bowed anterior cingulid; absence of a metalophid (except *P. jamesi* and *P. axelrodi*); and a distinct, transversely elongated mesostylid.

The m3 of *P. savagii* is similar to all known species of this genus in

sharing the following characters: presence of a mesostylid; absence of a metalophid (except *P. pattersoni*); and a distinct mesoconid (except *P. axelrodi*). The m3 of *P. savagii* differs in having an anterior cingulid that is separated from the metaconid by a deep and narrow groove, lacking a metalophid, and in possessing a distinct and transversely elongated mesostylid.

Petauristodon czaplewskii n. sp.

Plate 17 (A–I)

Holotype.— UCMP 141630-02, left dentary fragment with m1–m2.

Type locality.— Eastgate, UCMP V70140.

Etymology.— Named in honor of Nicholas J. Czaplewski, for his guidance and support, and for his contributions to knowledge of Neogene insectivores and rodents.

Other localities.— Type only.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens. — Type and OMNH 54562, right m1 or m2; UCMP 141601-02; right m1 or m2; UCMP 141601-01, left m1 or m2; UCMP 141601-04, right m1 or m2; UCMP 1414601-06, right m1 or m2; UCMP 141601-12, left m1 or m2; UCMP 141601-13, left m1 or m2; UCMP 141601-15, left m1 or m2; UCMP

141601-18, left m1 or m2; UCMP 141601-24, right m1 or m2; UCMP 141601-25, left m1 or m2; UCMP 141601-27, right m1 or m2; UCMP 141601-29, right m1 or m2; UCMP 141601-30, left m1 or m2; UCMP 141601-31, right m1 or m2; UCMP 141601-33, right m1 or m2; UCMP 141602-01, right m3; UCMP 141602-02, left m3; UCMP 141602-06, right m3; UCMP 141602-10, right m3; UCMP 141602-13, left m3; UCMP 141602-19, right m1 or m2; UCMP 141602-22, right m1 or m2; UCMP 141602-23, right m1 or m2; UCMP 141613-03, left m1 or m2; UCMP 141826-08, right m1 or m2; UCMP 141826-09, left m1 or m2; UCMP 141830-14, right M3; UCMP 141830-20, right M3; UCMP 141830-26, right M3.

Measurements.—See Table 33 and 34.

Diagnosis.— *Petauristodon czaplewskii* is a medium sized petauristine squirrel that is much smaller than *P. pattersoni*, *P. jamesi*, *P. matthewsi*, and *P. uphami*. However, *P. czaplewskii* is larger than *P. savagei*, *P. axelrodi*, and *P. minimus* (see Figs. 11 and 13).

The M3 of *P. czaplewskii* is most similar to *P. savagei* in lacking the following: greatly expanded anterior region, parastylar cusp, complete protoloph, protoconule, accessory loph, metacone, and hypocone. The m1 of *P. czaplewskii* is similar to *P. savagei* in having a greater length than width, a distinct mesoconid and mesostylid, and a mesoconid that lies midway between the protoconid and hypoconid.

The M3 of P. *czaplewskii* differs from *P. savagei* in having a metaloph and lacking a mesostyle. The p4 of *P. czaplewskii* differs from *P. savagei* in having

an anteroconid, and lacking a complete anterior cingulid and metalophid. In *P. czaplewskii*, the m1 differs from *P. savagei* in having a distinct anteroconid, a wide trigonid basin, an anterior cingulid that joins the metaconid, a complete metalophid, and a metastylid that is closely appressed to the metaconid.

Description.— There are no upper teeth present for *P. czaplewskii* except for the M3 (UCMP 141830-26). The M3 is much longer than wide. The anterior cingulum arises near the anterior base of the protocone and terminates labially prior to reaching the paracone. The anterior basin is long and narrow, opening labially. The protocone is the largest cusp and is anteroposteriorly elongate. The protoloph arises from the anterolabial side of the protocone and extends labially in a straight line to reach the conical-shaped paracone. A mesostyle is absent. The talonid basin is long and narrow, housing several worn but robust crenulations. There is a weak metaloph present, but no additional diagnostic features are present on the occlusal surface of the talonid basin.

The dentary fragment (UCMP 141630-02) with the m1-m2 has little wear to the occlusal surfaces. Shallow, robust crenulations occur in the talonid basin of the lower cheekteeth. The dentary is broken anterior to the m1 and posteriorly through a large posterior alveolus of the m3 and does not possess any diagnostic characters.

The m1 is longer than wide. An anteroconid is present and joins the anterior cingulid. The anterior cingulid arises at the same height as the metaloph and midway between the protoconid and metaconid to insert low on the anterior

base of the protoconid. An incomplete metalophid forms a narrow, deep, V-shaped notch between the junction of the anterior cingulid and the metaconid that courses along the lingual side of the protoconid. The trigonid basin is open anterolabially. A deep labial valley occurs between the protoconid and hypoconid. A distinct mesoconid lies on a short, high, narrow ectolophid. The mesoconid occurs midway between the protoconid and hypoconid. On the anterior and posterior sides of the mesoconid are deep, narrow grooves that separate the mesoconid from the protoconid and hypoconid. The posterolophid arises on the posterolingual side of the hypoconid and bends strongly anterolabially to form a well rounded posterolingual corner where the entoconid is submerged within the posterolophid. The posterolophid continues anteriorly toward the metaconid but terminates at the mesostylid. A wide, deep groove separates the mesostylid from the metaconid. The talonid basin is open lingually and houses a few robust, deep crenulations.

The m2 differs from the m1 in being longer and wider. In addition, it also has a posterolophid that bends more anterolingually.

The m3 (UCMP 141602-01) differs from the other lower molars in being larger and havng a more rounded hypoconid. It also has a reduced metalophid that occurs lower on the anterior cingulid and protoconid.

Comparison and discussion.— *Petauristodon czaplewksii* is much larger than *P. axelrodi*, and they are easily distinguished on size alone (Figs. 11 and 13). The M3 of *P. czaplewskii* is similar in size to *P. savagei* but has

distinguishing differences as referenced in the diagnosis. Differences between *P. czaplewskii* and other species of *Petauristodon* are listed below.

The M3 of *P. czaplewskii* differs from *P. pattersoni* in lacking an expanded anterior region, a complete protoloph, a protoconule, a metacone, lacking a complete metaloph, and a mesostyle. The p4 of *P. czaplewskii* differs from *P. matthewsi*, and *P. pattersoni* in having a distinct anteroconid. It differs from *P. savagei* and *P. pattersoni* in having a reduced anterior cingulid. It differs from *P. pattersoni* in having a single mesoconid that occurs on the labial edge of the tooth, lacking both a labial shelf and a wide shallow talonid basin. The m1 of *P. czaplewskii* differs from *P. pattersoni* in having an anterior cingulid that does not join the protoconid. It differs from *P. matthewsi* and *P. jamesi* in lacking a complete anteiror cingulid, and having a complete metalophid.

As for the m1 or m2, the only described species of this genus that is similar in size to *P. czaplewskii* is *P. savagei*. However, the m1 or m2 of *P. czaplewski* differs from *P. savagei* in lacking several structures that occur in the latter species. These structures include a strongly anteriorly bowed anterior cingulid, an incomplete metalophid, and a submerged entoconid.

Family Castoridae Gray, 1821

Subfamily Castoroidinae Trouessart, 1880

Genus *Monosaulax* Stirton, 1935

Monosaulax lotseei n. sp.

Plate 18 (A-G)

Holotype.— OMNH 54800, right dentary fragment with p4-m3.

Type locality.— Eastgate, OMNH V968.

Etymology.— Named in honor of Lotsee F. Patterson, for her financial support of this project, and for her continued support of my education.

Other localities.— Type and UCMP V70138, V74103.

Age.—Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54801, left P4; UCMP 141491, left P4; UCMP 141542, RP4; UCMP 141544, right dentary fragment with m1-m2; UCMP 141545, left dentary fragment with p4; UCMP 141547, left maxilla fragment with P4; UCMP 141555, left P4; UCMP 141556, palate with left P4-M1 and right M2; UCMP 141725, left dentary fragment with i1-m2; UCMP 141741, right dentary fragment with i1-m3; UCMP 141754, rigth m3; UCMP 141755, left P4; UCMP 141759-01, right dentary fragment with dp4; UCMP 141759-03, left P4; UCMP 141759-04, left P4; UCMP141759-06, left DP4; UCMP 141759-07,

left DP4; UCMP 141759-08, right DP4; UCMP 141759-09, left DP4; UCMP 141759-10, left P4; UCMP 141759-12, left dp4; UCMP 141759-13, right m1 or m2; UCMP 141759-14, right DP4; UCMP 141759-15, left dp4; UCMP 141759-17, left P4; UCMP 141759-18, left P4; UCMP 141759-19, right P4; UCMP 141759-20, right p4; UCMP 141759-22, left P4; UCMP 141759-24, left dp4; UCMP 141759-25, left P4; UCMP 141759-26, left p4; UCMP 141759-31, right P4; UCMP 141762, left dentary fragment with i1-m3; UCMP 141763, right dentary fragment with i1-m2; UCMP 141913, right dentary fragment with p4.

Measurements.— See Tables 35 and 36.

Diagnosis.— *Monosaulax lotseei* is a small castoroidine typically smaller than *M. pansus*, *M. curtus*, and *M. tedi*. *Monosaulax lotseei* differs from all species of this genus, except *M. curtus* and *M. tedi*, in having both the parafossettid and metafossettid present when the mesofossettid forms. If the parafosssettid and metafossettid are absent when the mesofossettid forms, a sigmoid pattern occurs on the occlusal surface (see Korth, 1999b). This S-shaped pattern is not evident on *M. lotseei*. *Monosaulax lotseei* is similar to all species of this genus in having an anteriorly concave parafossettid on p4 (except *M. curtus* which has a straight parafossettid). *Monosaulax lotseei* differs from all species of this genus in having an accessory fossettid always present on p4 (present in 12% of p4s for *M. tedi*). *Monosaulax lotseei* is similar to all species of this genus in having a long mesostriid that spans greater than 50% of the total crown height (except *M. tedi*).

Description.— The P4 is the largest of the upper cheekteeth followed in size by the M3. The M1 and M2 are much smaller than the other cheekteeth but are similar to each other in size. The posterior palatine foramen occurs along the palatine-maxillary suture, as is typical for castorids (Korth, 1994; Olson, 1964).

The P4 is longer than wide, and has a parafossette that is sigmoid-shaped and does not open externally. The hypoflexus is L-shaped, extending anterolingually across nearly one-third of the occlusal surface of the tooth or, as in UCMP 141542, the hypoflexus is rectangular-shaped and crosses about one-half the width of the occlusal surface. The hypofossette is closed lingually, thus suggesting a very late stage of wear for this tooth. The parafossette and hypofossette show a definite crossing at the midline of the occlusal surface, whereas in UCMP 141542 (with heavy wear to the occlusal surface) the parafossette and hypofossette lie adjacent to each other at the midline of the tooth and do not cross each other, unite, or touch at the midline of this tooth. The mesofossette is crescent-shaped, bending anteriorly (anteriorly concave), and is closed externally. The metafossette is oval-shaped and closed externally. The metafossette is the smallest of the fossettes on this tooth. The hypostria and mesostria are lacking because of the advanced stage of wear or, as in UCMP 141542, a short hypostria is present, but the mesostria is lacking on this tooth.

The M1 is much wider than long and possesses two fossettes. The

anteromost fossette, the hypofossette, stretches from the posterolingual part of the tooth to the anterolabial part, forming a hook or J-shaped end on the anterolabial side. The parafossette and metafossette are not present because of the advanced stage of wear to the occlusal surface of this specimen. The second fossette on this tooth is the mesoffossette, which is weakly crescent-shaped.

The M2 is similar to the M1 except that it is slightly less worn. Thus, several features are present on the M2 that do not occur on the M1. These features and their characteristics are as follows: the hypofossette is open lingually on the M2; the parafossette is a small, oval-shaped fossette that lies on the labial end of the hypofossette; and a second oval-shaped fossette, the metafossette, occurs on the posterolabial part of the occlusal surface.

The p4 is the largest of the lower cheekteeth followed in size by the m3. The m1 and m2 are smaller than the other cheekteeth but are similar to each other in size. The dentary is very stout and robust. The diastema is deep and short. The mental foramen lies low on the diastema, below the anteromost part of the p4, and opens anteriorly. The masseteric scar is triangular-shaped on the distal end and occurs below the posterior root of the p4. The ascending ramus arises lateral to the posteromost part of the m1. Lingually, the dentary possesses no diagnostic characters.

The distal tip of the lower incisor occurs below the level of the occlusal surface of the lower cheekteeth. The incisor is large, has a rounded anterior

surface, and possesses no ornamentation on the mesal surface.

The p4 is longer than wide. An accessory fossettid occurs anterolingually to the parafossettid. At present, these two fossettids are contiguous with each other, but would form separate fossettids with additional wear to the occlusal surface. The parafossettid is strongly anteriorly bent (anteriorly concave). The hypoflexid extends medially about one-third of the transverse width of the tooth. At the midline of the tooth, the hypoflexid lies adjacent to the mesofossettid. The hypostriid ascends more than one-half the height of the tooth crown. The mesostriid is much longer than the hypostriid and spans nearly the entire height of the tooth crown. A small oval-shaped fossettid occurs on the posterolingual corner of the tooth and joins the more prominent metafosettid. With additonal wear to the occlusal surface, the metafossettid and the smaller posterolingual fossettid would become separate fossettids.

The m1 is longer than wide and shows moderate wear, based on the short mesostriid, to the occlusal surface. The parafossettid is closed and an anterior fossettid is lacking. The hypoflexid extends medially more than one-half the width of the occlusal surface and slightly overlaps the metafossettid along the midline of the tooth. The mesostriid ascends the entire height of the tooth crown. The hypostriid is much shorter than the mesostriid and terminates below the occlusal surface.

The m2 is similar in size and morphology to the preceding molar. However, with less wear to the occlusal surface of the m2, several characters are

evident on this tooth that are not present on the m1. These differences include a mesostriid that descends lower on the tooth crown and a metafossettid that is nearly open lingually. A thin layer of enamel closes the lingual end of the metafossettid.

The m3 resembles the anterior molars except in having a trigonid that is much higher than the talonid. Its occlusal surface has less wear. A small fossettid lies anterior to the parafossettid. The metafossettid is open lingually by a narrow groove.

Comparison and discussion.— Korth (1994) recognized seven species of *Monosaulax* (*M. pansus*, *M. complexus*, *M. hesperus*, *M. curtis*, *M. senrudi*, *M. typicus*, and M. *progressus*) from the Tertiary of North America. I compared the lower cheekteeth of the Eastgate castoroidine directly with two specimens of *M. pansus* on loan from UCMP (UCMP 31426 and UCMP 19802; both are figured and discussed in Stirton, 1935). All lower castoroidine cheekteeth from Eastgate agree in morphology to those described by Stirton (1935) for *Monosaulax*.

Stirton (1935) and Stefen (2001) both noted variation in tooth morphology for *Monosaulax*. The latter considered wear stages as a major factor for variation in size and occlusal morphology. The Eastgate castoroidines provides an excellent opportunity to examine variation that can occur in a sample of castoroidine teeth from a single fauna. The Eastgate castroidines are similar in general size of the cheekteeth and in patterns of the hypoflexus and paraflexus of the P4. At Eastgate, the variations exhibited by these two flexi are as follows:

each flexus lies adjacent to the other at the midline of the tooth but does not cross or join; or each flexus overlap the others slightly at the midline of the tooth; or each flexus overlaps the other strongly at the midline of the tooth.

Several authors (Barnosky, 1986; Lindsay, 1972; Stirton, 1935) have suggested that the association of the hypoflexus to that of the paraflexus on the P4 represented an important specific difference among the species of *Monosaulax*. However, more recent papers on tooth morphology and systematics of *Monosaulax* (including a description of a new species) failed to consider these structures as being important in species identification (Korth, 1999b, 2000a; Stefen, 2001).

Recently, Korth (1999) described a new species of *Monosaulax* (*M. tedi*) from the Barstovian of Nebraska. *Monosaulax lotseei* represents a new Barstovian species that most closely resembles *M. tedi*.

Family Eomyidae Depéret and Douxami, 1902

Subfamily Eomyinae Depéret and Douxami, 1902

Tribe Eomyini Depéret and Douxami, 1902

Genus *Pseudotheridomys* Schlosser, 1926

Pseudotheridomys woodburnei n. sp.

Plate 19 (A–I)

Holotype.— UCMP 109300, dentary with p4–m3.

Type locality.— Eastgate, UCMP V70140.

Etymology.— Named in honor of Michael O. Woodburne, for his contributions to the study of Tertiary mammals and for the loan of important eomyid material.

Other localities.— UCMP V70139 and V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Eastgate fauna, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54618, right p4; OMNH 54619, left m1 or m2; OMNH 54620, left m3; OMNH 54621, right dentary fragment with p4–m2; OMNH 54746, left m1 or m2; OMNH 54747, left m1 or m2; UCMP 109301, right maxilla fragment with P4; UCMP 141564, left dentary fragment with p4–m2; UCMP 141774-01, left M1 or M2; UCMP 141774-02, left M1 or M2; UCMP 141774-03, left m1 or m2; UCMP 141774-04, right p4; UCMP 141774-06,

right m1 or m2; UCMP 141774-07, left p4; UCMP 141774-08, left P4; UCMP 141818-02, left p4; UCMP 141818-03, right m1 or m2.

Measurements.— See Tables 37 and 38.

Diagnosis.— *Pseudotheridomys woodburnei* is a large species of *Pseudotheridomys* that differs from all know species in that the upper and lower cheekteeth possess four lophs (ids) rather than five. For this species, the mesoloph (id) is absent.

Description.— The P4 bears four principal cusps (paracone, protocone, metacone, and hypocone) that are not joined by the four lophs (anterior cingulum = anteroloph, protoloph, metaloph, and posterior cingulum = posteroloph); three transverse valleys or basins (synclines; 1, 2, 4) occur between the lophs. The P4 is low crowned and bulbous, and has three roots (a single large root along the center of the lingual margin and two smaller roots along its anterolabial and posterlabial margins). The anterior cingulum extends from the anterolabial margin of the protocone and extends labially ending at the labial margin of the tooth; it does not join the paracone. The protocone and paracone are not joined to each other by the protoloph. The protoloph joins the anterior cingulum to the paracone. The anterior arm of the ectoloph is low and weak, arising along the lingual end of the protoloph. The posterior arm is low and weak, joining the middle of the metaloph. A mesoloph, mesocone, and mesostyle are absent. A metaloph joins the hypocone and metacone. A posterior cingulum arises along the posterolabial margin of the hypocone and ends along the posteromedial

margin of the metacone. The posterior cingulum is anteroposteriorly narrow and closed labially.

The M1 or M2 is quadrate, low crowned and bulbous, having four major cusps like the preceding cheektooth. The anterior cingulum arises high on the anterolabial margin of the protocone and traverses the anteromost edge of the tooth but does not join the paracone; the anterior valley is thus open labially. The protocone and paracone are not joined by the protoloph, which instead joins the anterior cingulum, labial to the protocone, to the middle of the paracone. The anterior arm of the ectoloph is absent, whereas the posterior arm is distinct and arises from the lingualmost part of the metaloph. The mesoloph, mesocone, and mesostyle are absent. A metaloph joins the hypocone and metacone. A posterior cingulum arises along the posterolabial margin of the hypocone and does not reach the metacone. The posterior valley is narrow and open labially.

The p4–m3 are low crowned and bulbous, possessing four cusps (metaconid, protoconid, entoconid, and hypoconid) that are united by lophids. The four lophids for the p4–m3 are as follows: anterior cingulid (anterolophid), metalophid, hypolophid, and posterior cingulid (posterolophid). In addition, the p4–m3 each have three transverse valleys or basins (synclines; 1, 2, 4) that occur between the lophids. In fact, the lophids of p4–m3 make it very difficult to distinguish the individual cusps through all stages of wear. The p4–m2 are equal in size, whereas the m3 is noticeably smaller. There are three roots on all lower cheekteeth except the p4. The p4 has two large roots, one anterior and the

other posterior. The m1–m3 have two small anterior roots (one anterolabial and the other anterolingual) and a single, large, posteromedial root that occurs along the posteromost part of the tooth crown.

The dentary has a diastema that is long and deep. A very small, anteriorly open mental foramen occurs along the dorsoventral midline of the diastema, anterior to the p4, and near the level of the ventral shelf of the masseteric scar. The masseteric scar is rounded anteriorly, ends below the anteromost margin of m1, and has weak ventral and dorsal shelves. A fossa occurs anterior to the distal end of the masseteric scar, below the p4, and may house a foramen. On the lingual surface of the dentary there are many foramina below the cheekteeth.

The p4 is oblong and molariform, having an anterior cingulid that courses from the anteromedial margin of the protoconid and extends lingually to join the anterolingual margin of the metaconid. The protoconid and metaconid are joined centrally by a metalophid. The anterior and posterior arms of the ectolophid are absent. A mesolophid, mesoconid, and mesostylid are absent. A hypolophid arises along the labial margin of the entoconid and joins the posterior cingulid posterior to the hypoconid. A posterior cingulid arises along the posterolingual margin of the hypoconid and ends along the posteromedial margin of the entoconid. The posterior cingulid is anteroposteriorly narrow and closed labially.

The m1 is oblong; on the anterolingual surface of this tooth, the anterior cingulid arises high on the anterolabial margin of the protoconid and traverses

the anteromost margin of the tooth to join the anteromedial margin of the metaconid. The protoconid and metaconid are joined centrally to each other by a metalophid (the metalophid may be complete or incomplete). The anterior and posterior arms of the ectolophid are absent. A mesolophid, mesoconid, and mesostylid are absent. The hypolophid is incomplete (it is incised vertically along its midline) and, therefore, does not join the hypoconid and entoconid. The posterior cingulid arises along the posterolingual margin of the hypoconid and ends along the posteromedial margin of the entoconid. The posterior cingulid is anteroposteriorly narrow and closed laterally. The m2 does not differ significantly in any characters or size from that of the m1. The m3 is distinguished from the preceding molars only by its smaller size and a more rounded posterior margin.

Comparison and discussion.— *Pseudotheridomys woodburnei* is the largest species of *Pseudotheridomys* known (Figs. 15–18). In addition to size, it is unlike any other species of this genus in that it lacks a mesoloph (id) and ectoloph (id), and has three valleys and four lophs (ids). All other known species of *Pseudotheridomys* possess a mesoloph (id), ectoloph (id), and have four valleys separated by five lophs (ids). These characters clearly separate this species from other known species of this genus and may represent a generic difference. However, until additional material is available for study, it is unclear if a new genus is warranted.

Pseudotheridomys tedfordi n. sp.

Plates 19, 20 (J-L; A-C)

Holotype.— UCR 15412, skull and mandible.

Type locality.— RV 7043.

Etymology.— Named in honor of Richard H. Tedford, for his contributions to our knowledge of Tertiary mammals.

Age.— Hemingfordian.

Stratigraphic and biogeographic occurrence of the species.— Hemingfordian: High Rock Sequence, Massacre Lake local fauna, Washoe County, Nevada (Morea, 1981).

Referred specimens.— Type and UCR 18708, skull fragment with right P4 and left DP4; UCR 18709, palate fragment with left P4.

Measurements.— See table 36, 37.

Diagnosis.— *Pseudotheridomys tedfordi* is the Largest species of *Pseudotheridomys* differing from all other species except *P. woodburnei* in having four lophs (ids) on the cheekteeth. Its P4 differs from that of *P. wooburnei* in having a protoloph that does not join the anterior cingulum, the anterior arm of the ectoloph is absent, the posterior arm of the ectoloph is strong and joins the lingual end of the metaloph, and the posterior cingulum is open labially. For the M1 or M2, *P. tedfordi* differs from *P. woodburnei* in having the protoloph that joins the anterior cingulum labial to the protocone and to the

middle of the paracone, the anterior arm of the ectoloph is distinct, the posterior arm arises from the labialmost part of the hypocone, and a mesostyle is present. For the m1, *P. tedfordi* differs from *P. woodburnei* in having a distinct anterior and posterior arms of the ectolophid, and the hypolophid joins the hypoconid and entoconid.

Description.— The P4 possesses four cusps united by four lophs separated by three transverse valleys; it is low crowned, bulbous, and has three roots. The anterior cingulum extends labially from the anterolabial margin of the protocone, ending at the labial margin of the tooth. It does not join the paracone. The protocone and paracone are not joined by a protoloph. In addition, the protoloph does not join the anterior cingulum to the paracone. The anterior arm of the ectoloph is absent. The posterior arm is strong and joins the lingual end of the metaloph. A mesoloph, mesocone and mesostyle are absent. The metaloph is incised centrally and does not join the hypocone to the metacone. A posterior cingulum arises along the posteromedial margin of the hypocone and ends before reaching the metacone. The posterior cingulum is anteroposteriorly narrow and open labially.

The M1 is quadrate, low crowned and bulbous; it has four major cusps like the preceding cheektooth and has little wear to the occlusal surface. The anterior cingulum arises high on the anterolabial margin of the protocone and traverses the anteromost part of the tooth but does not join the paracone; and thus the anterior valley is open labially. The protocone and paracone are not

joined by the protoloph, which instead are joined by the anterior cingulum on the labial margin of the protocone and middle margin of the paracone. The anterior arm of the ectoloph is distinct and arises along the center of the protoloph; the posterior arm, also distinct, arises from the labialmost part of the hypocone. The mesoloph and mesocone are absent. A mesostyle is present. A metaloph joins the hypocone and metacone. A posterior cingulum arises along the posterolabial margin of the hypocone and does not reach the metacone; thus, the posterior valley is narrow and open labially. The M2 is similar to the M1 except that it lacks a mesostyle. The M3 also lacks a mesostyle; it is similar to the preceding molars except for its noticeably smaller size.

The m1-m3, like the upper cheekteeth, are low crowned, bulbous, and have four cusps and four lophids (anterior cingulid, metalophid, hypolophid, and posterior cingulid); the lophids are separated from each other by transverse valleys. The high lophids of the lower cheekteeth make it difficult to distinguish the individual cusps through all stages of wear. The m1-m2 are equal in size, while the m3 is noticeably smaller. The m1-m3 have two small anterior roots and a single, large, posteromedial root.

No complete dentary is available for this species, and thus the diastema, mental foramen, and masseteric scar are unknown. The lingual surface of the preserved dentary does not indicate any foramen below the cheekteeth.

The m1 is oblong. On its anterolingual surface, an anterior cingulid arises high on the anterolabial margin of the protoconid and traverses the anteromost

part of the tooth, to join the anteromedial margin of the metaconid. The protoconid and metaconid are joined centrally by a metalophid. A distinct anterior arm of the ectolophid is present but the posterior arm is absent. A mesolophid, mesoconid, and mesostylid are absent. A hypolophid joins the hypoconid and entoconid. The posterior cingulid arises along the posterolingual margin of the hypoconid and ends along the posteromedial margin of the entoconid. The posterior cingulid is anteroposteriorly narrow and closed laterally.

The m2 differs from the m1 in the following: the anterior arm of the ectolophid is absent, and the hypolophid is not complete. The m3 is distinguished from the preceding molars only by its smaller size and a more rounded posterior margin.

Comparison and discussion.—In size, *P. tedfordi* is the largest of the known species of *Pseudotheridomys* (Figs. 15–18). It is most similar to *P. woodburnei* in that they share the following characters: absence of a mesoloph (id) and posterior arm of the ectoloph (id); and presence of only three transverse valleys and four lophs (ids). However, they differ in that *P. tedfordi* possesses the following characters of the P4: the protoloph does not join the anterior cingulum; the anterior arm of the ectoloph is absent, whereas the posterior arm is strong and joins the lingual end of the metaloph; and the posterior cingulum is open labially.

The M1–M2 of *P. tedfordi* differ from that of *P. woodburnei* in that *P. tedfordi* possesses the following: the protoloph joins the anterior cingulum along

the labial margin of the protocone, and along the middle margin of the paracone; the anterior arm of the ectoloph is distinct; a mesostyle is present (except M2 of for *P. tedfordi*); and the posterior transverse valley is narrow and open labially. The m1-m2 of *P. tedfordi* differ from that of *P. woodburnei* in that in *P. tedfordi* the ectolophid has a distinct anterior arm, and the hypolophid joins the hypoconid and entoconid.

The holotype of *Pseudotheridomys tedfordi* was collected by M. O. Woodburne and studied by M. F. Morea. At the time, Morea (1981) suggested a new genus and species "*Bobwilsonomys tedfordi*" based on a detailed description of the skull, mandible, and upper and lower cheekteeth. However, according to ICZN (2000) Articles 8 and 9, Morea's genus and species names are not available.

A direct comparison of P. tedfordi with *P. woodburnei* from Eastgate clearly indicates that these species are closely related and belong within the same genus. These taxa may merit placement within a new genus, but until additional material becomes available, I hesitate to name a new genus.

Pseudotheridomys cuyamensis Lindsay, 1974

Plate 20 (D–L)

Localities.— Eastgate, OMNH V974 and V976; UCMP V70140, V70142, and V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Hemingfordian: Branch Canyon Formation, Vedder local fauna, Santa Barbara County, California (Lindsay, 1974).

Referred specimens.— OMNH 54579, left dentary fragment with p4–m1; OMNH 54580, left dentary fragment with i1–m2; OMNH 54581, left dentary fragment with p4–m3; OMNH 54582, left dp4; OMNH 54583, right dp4; OMNH 54585, left p4; OMNH 54586, left p4; OMNH 54587, right dp4; OMNH 54588, right dp4; OMNH 54590, left dp4; OMNH 54594, right m1 or m2; OMNH 54596, left m1 or m2; OMNH 54597, right m1 or m2; OMNH 54599, left m1 or m2; OMNH 54600, right m1 or m2; OMNH 54601, right m1 or m2; OMNH 54603, right m1 or m2; OMNH 54605, right m1 or m2; OMNH 54606, right m1 or m2; OMNH 54607, left m1 or m2; OMNH 54608, right m1 or m2; OMNH 54609, right m1 or m2; OMNH 54610, right m1 or m2; OMNH 54611, left m1 or m2; OMNH 54612, left m1 or m2; OMNH 54614, left m1 or m2; OMNH 54615, right m1 or m2; OMNH 54616, left m1 or m2; OMNH 54617, right m1 or m2; OMNH 54622, left maxilla with P4–M1; OMNH 54623, left m3; OMNH 54624, left DP4; OMNH

54625, left DP4; OMNH 54626, left DP4; OMNH 54627, right m1 or m2; OMNH 54628, left P4; OMNH 54629, right m3; OMNH 54630, left M1 or M2; OMNH 54631, left P4; OMNH 54632, left P4; OMNH 54633, left P4; OMNH 54634, left m1 or m2; OMNH 54635, left M1 or M2; OMNH 54636, right DP4; OMNH 54637, right m3; OMNH 54637, right m3; OMNH 54638, right DP4; OMNH 54639, right m3; OMNH 54640, right m1 or m2; OMNH 54641, right m3; OMNH 54642, right m1 or m2; OMNH 54643, right m1 or m2; OMNH 54644, right m3; OMNH 54645, right m3; OMNH 54646, left P4; OMNH 54647, left M1 or M2; OMNH 54648, right M1 or M2; OMNH 54649, right M1 or M2; OMNH 54650, left m1 or m2; OMNH 54651, left m1 or m2; OMNH 54652, left m1 or m2; OMNH 54653, right m3; OMNH 54654, right P4; OMNH 54655, right M1 or M2; OMNH 54656, left P4; OMNH 54657, left m3; OMNH 54658, left P4; OMNH 54659, left M1 or M2; OMNH 54660, left M1 or M2; OMNH 54661, right P4; OMNH 54663, right P4; OMNH 54664, right M1 or M2; OMNH 54665, left M1 or M2; OMNH 54666, left P4; OMNH 54668, left m1 or m2; OMNH 54671, left M1 or M2; OMNH 54672, right M1 or M2; OMNH 54673, right DP4; OMNH 54675, left M1 or M2; OMNH 54676, left M1 or M2; OMNH 54677, right M3; OMNH 54678, left M3; OMNH 54680, left M3; OMNH 54681, left P4; OMNH 54682, right P4; OMNH 54683, right M1 or M2; OMNH 54684, right M1 or M2; OMNH 54685, left M1 or M2; OMNH 54686, right M1 or M2; OMNH 54687, left M3; OMNH 54688, right M3; OMNH 54689, right M1 or M2; OMNH 54690, left dentary fragment with m1-m3; OMNH 54691, right dp4; OMNH 54692, right dp4; OMNH 54693, left dp4; OMNH

54694, left m1 or m2; OMNH 54745, left m3; OMNH 54972, right P4; UCMP 141672-01, left maxilla fragment with P4; UCMP 141672-02, right maxilla fragment with P4; UCMP 141672-03, right maxilla fragment with P4–M1; UCMP 141673-01, left maxilla fragment with P4; UCMP 141673-02, right dentary fragment with dp4; UCMP 141673-03, left dentary fragment with p4; UCMP 141673-04, left maxilla fragment with P4; UCMP 141675-14, left dentary fragment with dp4; UCMP 141678-09, left maxilla fragment with P4–M1; UCMP 141679-01, right dp4; UCMP 141682, left dentary fragment with p4; UCMP 141683-01, left dentary fragment with p4–m3; UCMP 141683-02, left maxilla fragment with M1–M2; UCMP 141683-03, right dentary fragment with i1–p4; UCMP 141683-04, left maxilla fragment with P4–M1; UCMP 141683-05, left dentary fragment with m2; UCMP141684-01, left dentary fragment with p4–m1; UCMP 141684-02, right dentary fragment with dp4; UCMP 141685-01, left maxilla fragment with P4–M1; UCMP 141685-02, right dentary fragment with i1, m1; UCMP 141772, right dentary fragment with i1, p4, m3; UCMP 141778, left dentary fragment with i1–p4; UCMP 141779-05, left dentary fragment with p4–m3; UCMP 141780-01, left P4; UCMP 141780-02, right P4; UCMP 141780-03, right m1 or m2; UCMP 141780-04, left P4; UCMP 141780-05, left dp4; UCMP 141780-07, right P4; UCMP 141780-08, left m1 or m2; UCMP 141780-09, right dp4; UCMP 141780-10, right p4; UCMP 141780-11, left m3; UCMP 141780-14, left M1 or M2; UCMP 141780-15, right m1 or m2; UCMP 141780-16, right dp4; UCMP 141780-17, right m1 or m2; UCMP 141780-18, left

dp4; UCMP 141780-19, left m1 or m2; UCMP 141780-20, right M1 or M2; UCMP 141780-21, right dp4; UCMP 141780-23, right dp4; UCMP 141780-24, right M1 or M2; UCMP 141780-25, left DP4; UCMP 141780-26, left DP4; UCMP 141780-28, right dp4; UCMP 141780-29, right dp4; UCMP 141780-30, right m1 or m2; UCMP 141780-31, right m1 or m2; UCMP 141780-32, right m1 or m2; UCMP 141780-34, right m3; UCMP 141780-35, right M1 or M2; UCMP 141780-36, left DP4; UCMP 141780-37, right M1 or M2; UCMP 141780-38, left M3; UCMP 141780-39, left m1 or m2; UCMP 141780-42, right dp4; UCMP 141780-45, left m1 or m2; UCMP 141780-46, left DP4; UCMP 141780-47, left m3; UCMP 141780-48, right DP4; UCMP 141780-49, left m1 or m2; UCMP 141780-50, left p4; UCMP 141780-53, left M1 or M2; UCMP 141780-54, left m1 or m2; UCMP 141780-57, left M1 or M2; UCMP 141780-59, right m1 or m2; UCMP 141780-63, right dp4; UCMP 141780-65, right M1 or M2; UCMP 141780-66, left m1 or m2; UCMP 141780-67, left P4; UCMP 141780-69, right M1 or M2; UCMP 141780-70, left M1 or M2; UCMP 141780-72, left M1 or M2; UCMP 141780-73, right p4; UCMP 141780-74, right p4; UCMP 141780-75, right m1 or m2; UCMP 141780-77, right m1 or m2; UCMP 141780-78, right DP4; UCMP 141780-79, right m1 or m2; UCMP 141780-80, right dp4; UCMP 141780-84, right P4; UCMP 141780-86, left M3; UCMP 141780-87, left P4; UCMP 141780-90, left M1 or M2; UCMP 141780-92, left m1 or m2; UCMP 141780-94, right m1 or m2; UCMP 141780-100, right M1 or M2; UCMP 141780-102, left DP4; UCMP 141780-103, left maxilla fragment with P4; UCMP

141780-104, right dentary fragment with m2–m3; UCMP 141780-105, right M1 or M2; UCMP 141780-106, right dentary fragment with m2–m3; UCMP 141780-109, left m1 or m2; UCMP 141780-112, right P4; UCMP 141780-113, right m1 or m2; UCMP 141780-114, left p4; UCMP 141780-116, right m3; UCMP 141780-117, right dp4; UCMP 141780-119, right M1 or M2; UCMP 141780-120, left M1 or M2; UCMP 141780-121, left P4; UCMP 141780-123, left maxilla fragment with P4–M3; UCMP 141780-125, left p4; UCMP 141780-128, left M1 or M2; UCMP 141780-129, left M1 or M2; UCMP 141780-130, right M1 or M2; UCMP 141780-132, left M1 or M2; UCMP 141780-134, right dp4; UCMP 141780-138, left P4; UCMP 141780-139, right M1 or M2; UCMP 141780-140, left p4; UCMP 141780-141, left p4; UCMP 141780-144, left m3; UCMP 141780-146, left P4; UCMP 141780-148, left m1 or m2; UCMP 141780-151, right m1 or m2; UCMP 141780-152, right dp4; UCMP 141780-156, right M1 or M2; UCMP 141780-157, right m1 or m2; UCMP 141780-158, right m1 or m2; UCMP 141780-161, left m1 or m2; UCMP 141780-162, right m3; UCMP 141780-164, left M1 or M2; UCMP 141780-166, left m1 or m2; UCMP 141780-169, right m3; UCMP 141780-170, left m1 or m2; UCMP 141780-174, left m1 or m2; UCMP 141780-175, right m1 or m2; UCMP 141780-176, left m1 or m2; UCMP 141780-178, left M1 or M2; UCMP 141780-181, right M3; UCMP 141780-184, right M3; UCMP 141780-185, right M1 or M2; UCMP 141780-187, right m1 or m2; UCMP 141780-190, left p4; UCMP 141780-191, left M1 or M2; UCMP 141780-192, right M1 or M2; UCMP 141780-193, left P4; UCMP 141780-194, right m1 or m2; UCMP 141780-195,

right M1 or M2; UCMP 141780-198, left M1 or M2; UCMP 141780-199, left P4; UCMP 141780-200, left dp4; UCMP 141780-201, left DP4; UCMP 141780-202, right M1 or M2; UCMP 141780-203, left m1 or m2; UCMP 141780-204, left P4; UCMP 141780-205, right m1 or m2; UCMP 141780-207, left M1 or M2; UCMP 141780-208, right M1 or M2; UCMP 141780-212, left P4; UCMP 141780-213, left M1 or M2; UCMP 141780-214, right M1 or M2; UCMP 141780-216, left dp4; UCMP 141780-217, right m1 or m2; UCMP 141780-220, right M1 or M2; UCMP 141780-221, left m1 or m2; UCMP 141780-223, right DP4; UCMP 141780-227, right M1 or M2; UCMP 141780-228, left M1 or M2; UCMP 141780-229, left DP4; UCMP 141780-230, right maxilla fragment with P4–M1; UCMP 141780-231, left P4; UCMP 141780-232, right M1 or M2; UCMP 141780-233, left dentary fragment with m1 or m2; UCMP 141780-234,left m1 or m2; UCMP 141780-235, right DP4; UCMP 141780-239, left maxilla fragment with P4–M2; UCMP 141780-240, left maxilla fragment with P4–M2; UCMP 141780-249, left dentary fragment with i1–m3; UCMP 141780-251, right dentary fragment with i1–m3; UCMP 141780-258, right maxilla fragment with P4–M3; UCMP 141780-269, right maxilla fragment with P4-M1; UCMP 141780-271, left maxilla fragment with P4-M1; UCMP 141780-272, left dentary fragment with i1–m2; UCMP 141780-280, right dentary fragment with m2–m3; UCMP 141780-281, left dentary fragment with p4–m2; UCMP 141796-01, right m1 or m2; UCMP 141796-02, left P4; UCMP 141796-03, left dentary fragment with p4; UCMP 141796-04, left p4; UCMP 141796-05, left DP4; UCMP 141796-06, left m3;

UCMP 141843-42, right P4; UCMP 141882, left dentary fragment with dp4-m1.

Measurements.— See Tables 37-40.

Description.— The P4-M3 possses four cusps, five lophs and four transverse valleys. The lophs include an anterior cingulum, a protoloph, a mesoloph, a metaloph, and a posterior cingulum. As for other species of *Pseudotheridomys*, the lophs of the cheekteeth make it very difficult to distinguish the individual cusps through all stages of wear. The cheekteeth decrease in size from anterior to posterior and are low crowned and bulbous. There are three roots on all upper cheekteeth. The P4 has a single, large root along the anterolingual margin and two smaller roots along the anterolabial and posterolingual margins of the tooth. The M1 and M2 have a single, large lingual root that occurs along the midline, and two smaller roots that occur along the anterolabial and posterolingual margins of the tooth. The roots of the M3 are similar to those of the preceding molars except that the posterolabial root flares more posterolabially.

The DP4, like deciduous teeth of other rodents, has variable characters of the occlusal surface. In general, the tooth is triangular in occlusal outline and is not molariform. The labial cusps are better defined prior to wear than those of the P4, the lophs form low but sharp ridges, the valleys may be open or closed, a mesostyle may be present, the roots are sprawled apart from each other, all three roots are similar in size, and the tooth is low crowned. Other than the characters mentioned herein, the DP4 is similar to the P4s (see below) of this

species.

The P4 is subquadrate, molariform, low crowned and bulbous. The anterior cingulum extends from the anterolabial margin of the protocone (or is free of the protocone) to join the anteromedial margin of the paracone (or, as in UCMP 141780-240, it may be free of the paracone). The protocone and paracone are not joined directly by the protoloph; instead, the protoloph attaches anterior to the protocone to join the lingualmost part of the anterior cingulum. The anterior arm of the ectoloph, if present, arises along the posterolingual end of the protoloph. The posterior arm, if present, joins the anteromedial margin of the hypocone. No mesocone is present. A mesoloph arises along the center of the ectoloph. The mesoloph of this species has three basic variations: it may or may not reach the labial margin of the tooth, or it may join the paracone along its posteromedial margin. A mesostyle is usually absent, but a few specimens appear to have a weak mesostyle. If present, the mesostyle occurs between the paracone and metacone, closing the labial margin of the valley. A metaloph joins the hypocone and metacone (or it may be incomplete along its midline, in which case these cusps are not united). A posterior cingulum arises along the posterolabial margin of the hypocone and ends along the posterolingual margin of the metacone. The posterior cingulum is anteroposteriorly narrow and may be open labially during early stages of wear or it may be closed during the entire duration of the tooth.

The M1 is subquadrate, low crowned and bulbous, having four major

cusps like the preceding cheektooth. The anterior cingulum arises high on the anterolabial margin of the protocone and traverses the anteromost part of the tooth to join the anteromedial margin of the paracone (or it is free and does not join the paracone, resulting in the anterior valley opening labially). The protocone and paracone are not joined centrally by a protoloph. Instead, the protoloph arises along the lingualmost part of the anterior cingulum and extends labially to the center of the paracone. The anterior arm of the ectoloph, if present, arises along the posterolingual margin of the anterior cingulum (or is free), and the posterior arm joins the anterolabial margin of the hypocone. No mesocone is present. A mesoloph arises along the center of the ectoloph, or if the ectoloph is absent, from the posterolabial margin of the protocone. The mesoloph always reaches the labial margin of the tooth; however, it may be free labially or it may attach to the protoloph or the paracone. A mesostyle is usually absent. The mesostyle may occur between the paracone and metacone closing, the labial margin of the valley that occurs between these cusps. A metaloph joins the hypocone and metacone (or may be incomplete and not unite these cusps). A posterior cingulum arises along the posterolabial margin of the hypocone and ends along the posteromedial margin of the metacone. The posterior cingulum is anteroposteriorly narrow and open labially during early stages of wear but is usually closed during advanced stages of wear (few specimens have an open posterior valley in early-to-middle stages of wear).

The M2 differs from the M1 in that: the M2 is wider than long (almost

rectangular in few specimens); the protoloph may not be attached to the protocone; both anterior and posterior arms of the ectoloph may be absent; the metaloph may be incomplete.

The M3 is distinguished from the preceding molars by the following: it is noticeably smaller in size; the anterior cingulum may not attach (or does so weakly) to the protocone; the metalophid does not reach the ectolophid, and thus the ectolophid appears to have a single arm that joins the protoloph and metaloph; and the posterior half of the tooth is greatly reduced.

The dentary has a ventral surface that is slightly convex ventrally. The diastema is deep and short. A distinct mental foramen occurs high on the diastema. The ventralmost part of the foramen occurs above the dorsalmost part of the distal end of the masseteric scar. In addition, it occurs anteroposteriorly midway between the p4 and the anterior end of the diastema. This foramen is open anterodorsally. The masseteric scar terminates below the anterior root of the p4. Posterior to its distal end, the masseteric scar forms moderately strong ventral and dorsal shelves. No shallow fossa occurs between the p4 and the masseteric scar. The ascending ramus arises lateral to the posterior part of the m2. Numerous foramina occur on the lingual surface of the diastema.

The incisor possesses the following characters: the tip occurs above the level of the tooth row; the tooth is flat mesially and rounded labially with little enamel present on the lingual surface, while about one-half of the labial side of

the tooth is covered with enamel; and, in cross section, the tooth is oblong.

The dp4 usually possesses all of the characters as described below for the p4. However, it differs from the p4 in being much longer than wide; in having roots that are sprawled apart. In addition, the all lophids of the dp4 are usually open lingually until advanced stages of wear; and have stylids that often occur along the lingual margins of the valleys between the lophids.

The p4–m3, like most other species of this genus, have four cusps, five lophids, and four transverse valleys. The m1 is larger than the m2 and slightly larger than the p4. The m3 is the smallest cheektooth of the lower dental battery.

The p4 is oblong, molariform, low crowned, and bulbous. The anterior cingulid arises from the anterolingual margin of the protoconid and extends lingually to join the anterolabial margin of the metaconid. However, it is incised vertically along the midline part of the tooth; thus, the anterior valley opens anteromedially. The anterior cingulid is variably short, not reaching the lingualmost margin of the tooth. Therefore, the protoconid and metaconid are not joined by the anterior cingulid. However, in other specimens, the anterior cingulum is complete and joins the protoconid and metaconid. This union closes the anterior valley. This character appears to vary with different stages of wear. The protoconid and metaconid are joined centrally by a second lophid (metalophid). The anterior arm of the ectolophid usually arises along the posteromedial margin of the protoconid, while the posterior arm joins the

anterolingual margin of the hypolophid (this connection can be strong or weak depending on the stage of wear). No mesoconid is present. A mesolophid arises along the center of the ectolophid (or directly off of the posterolingual margin of the protoconid). The mesolophid may reach the lingual margin of the tooth or join the metaconid along its posteromedial margin. A mesostylid is usually absent. However, if present, the mesostylid occurs between the mesolophid and entoconid, closing the lingual margin of the valley that occurs between the mesolophid and hypolophid. A hypolophid usually joins the hypoconid and entoconid, but it may be incised vertically near the midline part of the tooth; thus, the cusps are not joined by this lophid. A posterior cingulid arises along the posterolingual margin of the hypoconid and ends along the posterolabial margin of the entoconid. The posterior cingulid is anteroposteriorly narrow and usually open labially; however, this character varies according to wear and the cingulid may become closed in advanced stages of wear.

The m1 is subquadrate and the anterior cingulid arises high on the anterolingual margin of the protoconid to traverse the anteromost part of the tooth. It usually does not join the anteromedial margin of the metaconid (in several specimens from Eastgate were it does, the anterior valley is open). The protoconid and metaconid are joined centrally (or anteriorly) by a metalophid. The anterior arm of the ectolophid arises along the labial end of the metalophid (or posterolingual margin of the protoconid), whereas the posterior arm usually joins the the labial end of the hypolophid (varies with wear). No mesoconid is

present. A mesolophid arises along the center of the ectolophid (or if the ectolophid is absent, directly from the posterolingual margin of the protoconid). The mesolophid reaches the lingual margin of the tooth, or it may join the metaconid along its posteromedial margin. A mesostylid is usually absent. If present, the mesostylid may arise at the end of the mesolophid, or it may occur between the mesolophid and entoconid, closing the lingual margin of the valley that occurs between the mesolophid and hypolophid. A hypolophid may join the hypoconid and entoconid, or the hypolophid may be incompete and not unite on these cusps. A posterior cingulid arises along the posterolingual margin of the hypoconid and ends along the posterolabial margin of the entoconid. The posterior cingulid is anteroposteriorly narrow and open labially (this valley is always closed in advanced stages of wear). The m2 resembles the m1 in all characters described above for this species except that it is slightly smaller.

The m3 is distinguished from the preceding molars by reduced size. In addition, the posteromost part of the tooth is well rounded and laterally narrower than the trigonid. A reduced posterior valley is also present.

Comparison and discussion.— Korth (1994) listed three species of *Pseudotheridomys* (*P. hesperus*, *P. cuyamensis*, and *P. pagei*), all of which possess five lophs (ids). In size, the cheekteeth (uppers and lowers) of *P. hesperus* and *P. pagei* are similar but smaller than those of *P. cuyamensis* (Figs. 15–18). A fourth species identified by Korth (1992) as *Pseudotheridomys* sp. also has five lophs (ids) and is much larger than those belonging to *P. hesperus*,

P. cuyamensis, and *P. pagei*. It may represent a new species, but additional material is needed to make a definite determination.

Compared to *P. woodburnei* from Eastgate, *P. cuyamensis* is much smaller and has the typical pattern of five lophs separated by four synclines present for most species of this genus. Based on the Eastgate sample of five-lophed *Pseudotheridomys* (*P. cuyamensis*), the cheekteeth are variable in their occlusal characters. This corroberates Engesser's (1999) statement that the three species of *Pseudotheridomys* (*P. hesperus*, *P. pagei*, and *P. cuyamensis*) are highly variable. Diversity displayed in other groups of rodents is not uncommon. It not is surprising to have a single species of the five-lophed group represented at Eastgate.

Initially, all cheekteeth of *Pseudotheridomys* from Eastgate were grouped by locus (e.g., P4, M1, M2, M3, p4, m1, m2, and m3) and the coefficients of variation (CVs) were examined. The CV values were very high (30.0 for the length and 20.0 for the width) for all locus samples. However, when the cheekteeth with four lophs (ids) were removed from their respective samples, the CVs were much lower (6.0 for the length and 8.0 for the width). Carrasco (1998) indicated a value of 10.0 or greater for a sample of fossil heteromyid cheekteeth indicated more than a single species was present in the sample. This trend held true for all upper and lower teeth at each loci. For additional explanation for the use of CVs, see Smith (2001).

As indicated above, the cheekteeth vary in their occlusal characters with

wear. When additional material becomes available for the five lophed species from Eastgate and elsewhere, a better understanding of their relationships may become apparent, and new taxa may be described.

Pseudotheridomys sp.

Plate 20 (M-O)

Locality.— Eastgate, UCMP V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the genus.— Arikareean: Harrison Formation, McCann Canyon local fauna, Cherry County, Nebraska (Korth, 1992); Hemingfordian: Pawnee Creek Formation, Martin Canyon Quarry A, Logan County, Colorado (Wilson, 1960); Branch Canyon Formation, Vedder local fauna, Santa Barbara County, California (Lindsay, 1974); Barstovian: Quartz Basin fauna, Malheur County, Oregon (Shotwell, 1967).

Referred specimens.— OMNH 54591, left dp4; OMNH 54592, right dp4; OMNH 54593, right dp4.

Measurements.— OMNH 54591: AP = 2.38, T = 1.62; OMNH 54592: AP = 2.35, T = 1.66; OMNH 54593: AP = 2.17, T = 1.44.

Description.— The dp4 is typical of dp4s for this genus. The anterior cingulid courses from the anterolingual margin of the protoconid and extends lingually to join the anterolabial margin of the metaconid. The protoconid and

metaconid are joined by the metalophid as follows: the metalophid arises at the posterolingual margin of the protoconid and traverses in a straight line to join the anterolabial margin of the metaconid. The anterior and posterior arms of the ectolophid are absent. A submerged mesoconid occurs along the middle part of the mesolophid. The mesolophid reaches the lingual margin of the tooth but does not join the metaconid. A mesostylid is absent. A hypolophid joins the posterior cingulid posterior to the hypoconid and joins the entoconid along its labial margin. The hypolophid is not complete (a narrow anteroposteriorly directed valley occurs near the attachment to the posterior cingulid). A posterior cingulid arises along the union of the hypolophid and the hypoconid, while lingually it ends along the posterolabial margin of the entoconid. The posterior cingulid is anteroposteriorly narrow and open at the narrow anteroposteriorly directed valley, but closed laterally. Of the four valleys present on this tooth, the anterior and posterior valleys are laterally closed, while the two middle valleys (syncline 2 and 3; see Engesser, 1999) are open on both lateral ends.

Comparison and discussion.— The dp4s included in this group are much larger than any of the dp4s from any of the five-lophed group recovered from Eastgate and smaller than the p4s of the four-lophed group, *P. woodburnei* (Figs. 15–18). If size differences observed between the dp4s and p4s of the five-lophed smaller species of *Pseudotheridomys* from Eastgate are a good indication of size differences between dp4s and p4s of the same species, then these dp4s are too large to be from the five-lophed species from Eastgate.

Thus, it is likely that these dp4s represent a new species, but more adult cheekteeth are needed in order to make such determination.

Genus *Leptodontomys* Shotwell, 1956

Leptodontomys sp. indet.

Locality.— Eastgate, UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the genus.— Orellan: Cedar Ridge local fauna, Tepee Trail Formation, Natrona County, Wyoming (Setoguchi, 1978); Arikareean: Killdeer Formation, Slope County, North Dakota (Burke, 1934; Korth and Bailey, 1992); Gering Formation, Dawes County, Nebraska (Korth and Bailey, 1992); Harrison Ranch local fauna, South Dakota (Simpson, 1985; Korth, 1989) and Vedder fauna, Branch Canyon Formation, Santa Barbara County, California (Lindsay, 1974): Barstovian: Quartz Basin and Red Basin faunas, Malheur County, Oregon (Shotwell, 1967); Barstow Formation, Barstow fauna, San Bernardino County, California (Lindsay, 1972); Kleinfelder Farm locality, Wood Mountain Formation, Saskatchewan (Storer, 1975); and Monarch Mill Formation, Easgate fauna, Churchill County, Nevada (present study); Clarendonian: Black Butte, Malheur County, Oregon (Shotwell, 1956, 1967); Whisenhunt Quary local fauna, Laverne Formation, Beaver County, Oklahoma (Smith, unpublished data); Hemphillian: Bartlett Mountain fauna,

Harney County, Oregon (Shotwell, 1967); and McKay Reservoir fauna, Umatilla County, Oregon (Shotwell, 1956).

Referred specimens.— See separate report (Smith, 2002).

Measurements.— See separate report (Smith, 2002).

Discussion.— The taxonomy of *Leptodontomys* from Eastgate is treated in a separate report (Smith, 2002).

Family Heteromyidae Gray, 1868

Subfamily Harrymyinae Wahlert, 1991

Genus *Lignimus* Storer, 1970

Lignimus cf. *L. transversus* Barnosky, 1986

Plate 21 (A–I)

Locality.— Eastgate, UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Cunningham fauna, Colter Formation, Teton County, Wyoming (Barnosky, 1986).

Referred specimens.— OMNH 54758, right p4; OMNH 54769, left m3; UCMP 141787-02, right p4; UCMP 141787-03, left m1 or m2; UCMP 141792-01, right dentary fragment with m2; UCMP 141792-02, left dentary fragment with p4; UCMP 141819-02, right m3; UCMP 141807-03, right m3; UCMP 141820-40, left

m3.

Measurements.— See Table 41.

Description.— A left dentary fragment (UCMP 141792-02) possesses a p4 with no wear to the occlusal surface. Barnosky (1986b) quantified crown height by dividing labial enamel height by the greatest transverse width (=LEH/T). Based on these measurements, these specimens are moderately high crowned and may be described as mesolophodont.

The diastema is long and shallow with a mental foramen that possesses the following characters: occurs high dorsoventrally on the diastema at the level of the dorsalmost margin of the masseteric scar, well in front of the p4; and opens anteriorly. The masseteric scar consists of a single, lower shelf; a dorsal shelf is absent. The ventral shelf arises high on the diastema and is placed well in front of the p4. It forms a broad shelf anterodorsally but terminates below the alveolus of the posterior root of the m1 near the ventral surface of the dentary. There are numerous foramina on the lingual side of the dentary below the alveoli of the cheekteeth.

The incisor is broken at its proximal association with the dentary. Thus, it is unclear if the distal end of the incisor occurred above the level of the tooth row, at the level, or below the level. However, the shape and coverage of enamel on the lateral and medial sides are evident. From a medial view, the tooth is flat lingually but laterally the tooth is slightly convex. The tooth is long mesodistally and narrow laterally. On the lingual side, the enamel covers less

than 25% of the surface area, whereas on the labial side it covers almost 50%. There is no ornamentation on the mesial surface.

The p4 is longer than wide, is not bulbous at the base of the tooth crown, is high crowned (LEH/T=0.75), has two roots, and does not have labial chevrons. There are two cusps (protoconid [= protoconid-metaconid complex; see Barnosky, 1986] and a protostylid) and an accessory cusp on the metalophid. The protoconid is D-shaped, larger than the D-shaped protostylid, and the anterolingual part of the cusp is anterior to that of the protostylid. The accessory cusp occurs on the anterolingual side of the protostylid and does not unite the protostylid and protoconid. A deep, wide valley separates the protoconid from the protostylid. The lophids unite labially below the occlusal surface but well above the enamel-dentine junction. The metalophid may possess two or three cusps (entoconid, hypoconid, and hypostylid). A hypostylid occurs on 33% of the specimens from Eastgate. When present, the hypostylid is much smaller than the other cusps of the hypolophid and its apex occurs below that of the hypoconid. With additional wear to the occlusal surface, the hypostylid would merge with the hypoconid. In addition, the width of the hypolophids varies little between the teeth that possess or do not possess a hypostylid. Thus, the width of the p4, in this case, does not reveal the presence or absence of an additional cusp (the hypostylid). The entoconid and hypoconid are subequal in size and are anteroposteriorly compressed. Note: a narrow V-shaped transverse valley indicates that the lophids are in close association with each other at their

respective bases and remain in close association at the occlusal surface, while a broad V-shaped valley indicates the lophids are in close association at their respective bases but become distant from each other distally. A narrow U-shaped valley indicates that the lophids are not in close association at their respective bases but remain at a similar distance from each other distally. A broad U-shaped valley indicates that the lophids are not in close association at their respective bases and remain distant from each other distally. A V-shaped notch occurs along the anteromedial margin of these cusps. In addition, these cusps are separated by a shallow, narrow valley. However, posteriorly these cusps unite below the occlusal surface. No posterior cingulid is present. The floor of the transverse valley is deep, wide, and open lingually.

For most Miocene-age heteromyids, the size and occlusal characters of the m1s are similar to those of the m2s for the same species. For example, the m2 (UCMP 141792-01) has has an occlusal surface showing moderate wear. It has thick enamel and roots fused almost to their distal ends. In addition, it has a crown that is not bulbous at its base, but is low crowned (LEH/T=0.38). The m2 is also noticeably wider than long with an anterior cingulid that appears to have run from the protoconid to the anterior surface of the protostylid. It also is lacking a posterior. The metalophid and hypolophid unite centrally first, then labially. A large metaconid projects posterolabially toward the hypoconid. The hypoconid occurs more anteriorly than the other two cusps of the hypolophid, while the metalophid and hypolophid form a posterior and an anteriorly directed

V-shaped metalophid and hypolophid, respectively. No chevrons are evident and, from a lateral view the lophids are straight with three cusps on each lophid.

The m3 (UCMP 141820-40) is distinguished from the preceding molars by its smaller size, oval-shaped occlusal surface (noticeably longer than wide), and reduction in size of the hypolophid (reduction in size and height of hypostylid). This tooth has no wear to the occlusal surface, and thus the enamel thickness on the lophids is not distinguishable. The tooth is not bulbous at the base of the tooth crown and possesses two roots (UCMP 141807-03) that are nearly as wide as the lophids and are fused along their entire distance. Chevrons are lacking.

Comparison.— The size and characters of the cheekteeth, incisors, and dentaries of *L.* cf. *L. transversus* from Eastgate were compared to numerous taxa of heteromyids that occurred during the Miocene in North America. Based on size, the m1s and m2s show similarities to those of the following taxa: *Mojavemys magnimarcus*, *Lignimus transversus*, *Balantiomys oregonensis*, *B. borealis*, and *Mioheteromys amplissimus* (=*Diprionomys agrarius*; see Korth, 1997). The characteristics of the m1s or m2s for the Eastgate heteromyids listed above share more similarities with *L. transversus* then with any of the other taxa of similar size.

Characters of the lower cheekteeth examined and utilized to separate the Eastgate heteromyids into each taxon group included size (width vs. length), tooth crown height (LEH/T=0.38, mean value for group), fusion of roots (roots fused except at their distal end), enamel thickness, presence or absence of

chevrons, presence or absence of an anterior cingulid, presence or absence of a posterior cingulid, point of attachment of the metalophid and hypolophid, and size and orientation of the cusps on each lophid. The *L.* cf. *L. transversus* from Eastgate share several characters with *Mojavemys magnimarcus*; these include size and low crowned cheekteeth. The major ways in which *L.* cf. *L. transversus* differs from *M. magnimarcus* are possession of a central union of the lophids, V-shaped lophids, and roots that are fused distally from the base of the tooth crown. *Lignimus* cf. *L. transversus* from Eastgate shares with *Balantiomys oregonensis* the following characters: lophids on the m1s and m2s unite centrally first, then labially; V-shaped lophids (however, these lophids unite between the protoconid and hypoconid in *B. oregonensis*, unlike in *L.* cf. *L. transversus* where they join between the metaconid and hypoconid); and low crowned cheekteeth. *Lignimus* cf. *L. transversus* differs from *B. oregonensis* in that the former is larger in size, and has thin enamel, and the lophids join centrally between different metalophid and hypolophid cusps (see above). The hypolophids of *B. borealis* are straight, whereas they are V-shaped in *L.* cf. *L. transversus*. *Lignimus* cf. *L. transversus* differs from all species of *Peridiomys* in having nonbulbous teeth, a straight transverse valley on the labial end (rather than deflected posteriorly), fused but not heavily rooted cheekteeth, lophids that unite at their stylids, and subequal hypoconid and entoconid. *Lignimus* cf. *L. transversus* from Eastgate is similar to *Mioheteromys amplissimus* in sharing a V-shaped hypolophid that unites with the metalophid centrally and labially. These lophids join labially first.

The roots are fused. An anterior cingulid is present, and a posterior cingulid is lacking. In contrast, they differ in the following: teeth of *L.* cf. *L. transversus* are lower crowned; have thick enamel; have a posterior wall of the hypolophid that is straight rather than posteriorly bowed as in *M. amplissimus*; have a hypolophid and metalophid that join centrally first then labially; have a metaconid that forms a V-shape and unites with a V-shaped hypolophid; have an anterolabial cingulid that is not as angular (thus, creating a straighter anterior wall for the metalophid); and have a hypolophid that is anteroposteriorly compressed.

The Eastgate specimens differ from other species of *Lignimus* in being larger in overall size and having a higher crown height (LEH/T=0.38). However, in morphology UCMP 141792-01 is very similar to *Lignimus transversus* (compare Plate 21 (A–I) with Bamosky, 1986b: plate V, figs. D, G, and H; Storer, 1975: fig. 74D).

Discussion.— Based on size and morphology of the occlusal surface, *L.* cf. *L. transversus* from Eastgate may represent a new species for this genus; however, until more complete material is recovered, I hesitate to name a new species. In addition to size and characters of the cheekteeth, there are no grooved upper incisors recovered from Eastgate (except for those of lagomorphs and zapodids). According to Korth (1997), the lack of grooved upper incisors would aid in eliminating the following heteromyid taxa that possess grooved upper incisors: *Mioheteromys*, *Perognathus*, and *Mookomys*.

Subfamily Mioheteromyinae Korth, 1997

Genus *Balantiomys* Korth, 1997

Balantiomys cf. *B. borealis* (=*Peridiomys borealis* Storer, 1975)

Plate 21 (J-N)

Localities.— Eastgate, OMNH V974; UCMP V70140, V710147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Kleinfelder fauna, Wood Mountain Formation, Saskatchewan, Canada (Storer, 1975). Nenzel Quarry, Valentine Formation, Cherry County, Nebraska (Korth, 1997).

Referred specimens.— OMNH 54751, left dentary fragment with p4-m2; OMNH 54760, left maxilla with P4-M2; OMNH 54768, left m1 or m2; OMNH 54769, left m3; OMNH 54778, left m1 or m2; OMNH 54781, left m1 or m2; OMNH 54782, left m1 or m2; OMNH 54788, left M1 or M2; OMNH 54789, right M1 or M2; OMNH 54790, left M1 or M2; OMNH 54797, left M3; OMNH 54798, right M3; OMNH 54799, right M3; UCMP 141610-01, left dentary fragment with m3; UCMP 141773, right m1 or m2; UCMP 141782-01, left p4; UCMP 141790, right dentary fragment with p4-m1; UCMP 141786-01, left maxilla fragment with P4-M1; UCMP 141788-01, right maxilla fragment with P4-M1; UCMP 141791, right dentary fragment with p4, m2-m3; UCMP 141807-01, right m3; UCMP 141807-02, right m3; UCMP 141807-04, right m3; UCMP 141807-05, right

m3;UCMP 141808, skull with left P4–M3 and right P4–M2; UCMP 141819-01, left m3; UCMP 141819-05, right m3; UCMP 141820-03, left M1 or M2; UCMP 141820-04, right M3; UCMP 141820-06, left M1 or M2; UCMP 141820-08, right M1 or M2; UCMP 141820-10, left P4; UCMP 141820-12, right M1 or M2; UCMP 141820-13, left M1 or M2; UCMP 141820-14, left M3; UCMP 141820-16, right M3; UCMP 141820-17, right M3; UCMP 141820-18, right M1 or M2; UCMP 141820-22, left M1 or M2; UCMP 141820-23, right M3; UCMP 141820-25, left M1 or M2; UCMP 141820-26, right M1 or M2; UCMP 141820-32, left M1 or M2; UCMP 141820-33, right P4; UCMP 141820-38, right M1 or M2; UCMP 141820-39, left M3; UCMP 141820-44, right M3; UCMP 141820-46, right M1 or M2; UCMP 141821-03, left P4; UCMP 141821-05, right P4; UCMP 141821-07, left maxilla with P4–M1; UCMP 141822-08, left M1 or M2; UCMP 141822-09, left m1 or m2; UCMP 141822-11, left M3; UCMP 141822-17, left m3; UCMP 141822-30, left m1 or m2; UCMP 141822-31, right P4; UCMP 141822-32, right M1 or M2; UCMP 141825-04, left M3; UCMP 141825-05, left m1 or m2; UCMP 141825-09, left M1 or M2; UCMP 141825-17, right M1 or M2; UCMP 141825-18, left M1 or M2; UCMP 141825-21, right m1 or m2; UCMP 141825-22, left m1 or m2; UCMP 141825-26, right dentary fragment with p4-m1; UCMP 141825-28, left M3; UCMP 141827-02, right m1 or m2; UCMP 141827-10, right m1 or m2; UCMP 141827-18, right m1 or m2; UCMP 141828-06, left m1 or m2; UCMP 141828-08, left m1 or m2; UCMP 141828-09, left m3; UCMP 141828-13, left m1 or m2; UCMP 141843-130, right M1 or M2.

Measurements.— See Tables 41 and 42.

Description.— A maxilla with cheekteeth that decrease in size from front to back, are moderately high-crowned, and are slightly bulbous at the crown bases.

The P4 is slightly longer than wide. The protoloph contains a single, large, oval-shaped cusp (protocone) that is attached to the metaloph lingually at the entostyle. No accessory cusps are present on the protoloph or metaloph (except UCMP 141822-31, which possesses a single accessory cusp that occurs on the anterolabial side of the protocone but below the occlusal surface). The floor of the transverse valley is open labially but closed lingually. The metaloph has three cusps (metacone, hypocone, and entostyle). The metacone and entostyle are transversely aligned with each other, but the hypocone occurs posterior to the former two cusps. The posterior cingulum arises on the posterolingual surface of the hypocone and extends lingually to join the entostyle.

The M1 or M2 is wider than long. The anterior cingulum arises from the anterolingual side of the paracone and terminates at the anterolabial base of the protocone. Thus, the anterior cingulum unites the paracone and protocone anteriorly. The protoloph has three cusps. The paracone and protostyle are transversely aligned with each other, while the protocone occurs posterior to the former two cusps. The floor of the transverse valley is deep, narrow, open labially, and closed lingually. The lingual union of the two lophs occurs below the occlusal surface but well above the base of the tooth crown. The metaloph has

three cusps; the metacone and entostyle are transversely aligned, but the hypocone occurs posterior to the former two cusps. The posterior cingulum extends from the protostyle to the posterolingual base of the metacone. Thus, on the posterior side the three cusps of the metaloph are united below the occlusal surface.

The M2 differs from that of the M1 in being smaller and more anteroposteriorly compressed. M2 is also differs from the M1 in being noticeably wider than long.

The M3 differs from the preceding molars in the following: reduced size, C-shaped occlusal outline, and reduced size and morphology of the metaloph. The protoloph is much wider transversely than the metaloph and possesses three cusps. The cusps of the protoloph are transversely aligned. The paracone and the protocone are subequal and anteroposteriorly compressed. The protostyle is similar in size to the other cusps of the protoloph but is anteroposteriorly elongated. The floor of the transverse valley is deep, wide, and closed lingually but open labially. The lophs unite lingually. The metaloph has three cusps. The metacone and hypocone are circular-shaped, but the entostyle is anteroposteriorly elongated. The hypocone occurs posterior to the other cusps of the metaloph.

The lower cheekteeth are low crowned and not bulbous at the crown bases (except for the p4 which is slightly bulbous). The p4 is smaller than the m2 but larger than the m3. The entire ventral surface is slightly convex. The

diastema is long and shallow. The mental foramen opens anteriorly, occurs high dorsoventrally on the diastema, and lies below the distalmost margin of the masseteric scar. The masseteric scar arises high on the diastema and anterior to the p4. It forms a broad, single, anterodorsal shelf that terminates below the posterior alveolus of the m1 near the ventral margin of the dentary. There are numerous foramina on the lingual side of the dentary, below the alveoli of the cheekteeth.

The lower incisor (UCMP 141791) is broken inside its alveolus, limiting the information that can be obtained about this particular tooth. Unfortuately, this is the only incisor present for this species. However, the part of the incisor that remains in the dentary provides the following characters: from a mesial view, the tooth is flat lingually but convex labially; on the lingual surface, the enamel covers approximately 25% of the surface; on the labial surface, the percent of enamel cannot be determined because of the presence of the dentary bone. No ornamentation is present.

The p4 is longer than wide, is slightly bulbous at the base of the tooth crown, is low crowned, has two roots nearly as wide as their respective lophids, and has a labial chevron. There are two cusps (protoconid and protostylid) and an accessory cusp (see Barnosky, 1986b) on the metalophid. The protoconid is D-shaped, is slightly larger than the D-shaped protostylid, and has an anterolingual part of this cusp that is anterior to the protostylid. The anteroconid unites the protoconid and protostylid anteriorly. Otherwise, a deep, narrow valley

separates the protoconid and protostylid. The lophids unite labially below the occlusal surface but well above the enamel-dentine junction. The metalophid possesses two cusps (entoconid and hypoconid), and no hypostylid or accessory cusps are present. The entoconid and hypoconid are subequal, with the former being more anteroposteriorly compressed. A V-shaped indentation occurs along the anteromedial margin of these cusps. In addition, these cusps are separated by a very narrow, shallow transverse valley. However, these cusps are united posteriorly. No posterior cingulid is present. The floor of the transverse valley opens lingually.

The m1 or m2 is wider than long (with thin enamel on both the anterior and posterior walls of each lophid), is slightly bulbous at the crown base, is low crowned, has two roots that are nearly as wide as their respective lophids and fused near the crown base, and has a small labial chevron present. The anterolabial cingulid arises from the anteromedial surface of the protostylid and projects about 45° anteriorly until it reaches a point anterior to a transverse line anterior to the anteromost part of the protoconid, where it bends posterolingually to join the anterolingual surface of the protoconid at the occlusal surface. The lophids join labially and centrally at about the same level on the tooth crown. Thus, the labial and central union of the lophids would occur at about the same stage of wear. The union of lophids occurs well below the occlusal surface near the floor of the transverse valley. In more advance stages of wear, an enamel lake would form between these points of union of the lophids (labial enamel

lake). Three cusps occur on the metalophid and join at their respective bases low on the tooth crown near the floor of the transverse valley. The protoconid and metaconid are transversely aligned and the protostylid occurs more posterior than the former two cusps. The floor of the transverse valley is deep, narrow, open lingually, and closed labially. For the lophids in lingual view, the anterior wall of the metalophid and posterior wall of the hypolophid are straight, while the posterior wall of the metalophid projects slightly anteriorly; the anterior wall of the hypolohid projects slightly posteriorly. Therefore, a narrow, V-shaped transverse valley is apparent. The hypolophid has three cusps (entoconid, hypoconid, and hypostylid). The entoconid and hypostylid are transversely aligned, but the hypoconid occurs anterior to the entoconid and hypoconid. With additional wear to the occlusal surface of this tooth, the entoconid and hypoconid would merge. The hypostylid would merge with the hypoconid with heavy wear to the occlusal surface. No posterior cingulid is present.

The m2 differs from the m1 in the m2 being slightly smaller in size and having a central connection of the lophids that occurs higher on the tooth crown. Therefore, the central union of the lophids occurs at an earlier stage of wear than it would on the m1.

The m3 is similar to the preceding molars except in being smaller in size and much longer than wide. It also has a posterior root that is much reduced and strongly bent posteriorly, and a labial or central union between the lophids is lacking. The lophids join only at the floor of the transverse valley.

Comparison.— Korth (1997) described a new genus (*Balantiomys*) of heteromyid based, in part, on *Diprionomys* and *Peridiomys*. For this new genus, he recognized four species (*B. oregonensis*, *B. borealis*, *B. nebraskensis*, and *B. meridionalis*). He distinguished *Balantiomys* from perognathines and dipodomyines by the following characters: a non-central union of lophs on p4s, a lingual union on P4s, and cheekteeth not hypsodont as in the latter subfamily. In addition, p4s of *Balantiomys* possess a protostylid and a metaconid are large, subequal in size, and D-shaped (Korth, 1997). Korth (1997) noted other heteromyines possessed a metaconid that is twice as large as the protostylid, and one or both of these cusps are circular in shape. The cheekteeth of *B. borealis* have been described in detail by Storer (1975) and Korth (1997).

The P4s of *B.* cf. *B. borealis* from Eastgate differ from those of *B. oregonensis* in that *B.* cf. *B. borealis* is smaller in size and possesses an accessory cusp. There are no known P4s of *B. nebraskensis* The Eastgate specimens differ from the P4 of *B. meridionalis* in that *B.* cf. *B. borealis* is much smaller in size, possesses an accessory cusp, and has an oval-shaped protocone.

The upper molars of *B.* cf. *B. borealis* from Eastgate differ from those of *B. oregonensis* in that *B.* cf. *B. borealis* is smaller in size; however, additional comparisons are not easily made because the available upper molars of *B. oregonensis* are worn. There are no known upper molars for *B. nebraskensis*. The Eastgate specimens differ from upper molars of *B. meridionalis* in that *B.* cf

B. borealis is much smaller than the M1 discussed by Korth (1997) but is similar in size to the M2 discussed by Korth (1997), who noted the morphology is the same for the M1 and M2 for *B. meridionalis*. In addition to size, *B.* cf. *B. borealis* differs from *B. meridionalis* in that the former possesses anterior and posterior cingula. It is possible, however, that cingula may be present on unworn teeth of *B. meridionalis*.

The p4s of *B.* cf. *B. borealis* from Eastgate differ from those of *B. oregonensis* in that *B.* cf. *B. borealis* is smaller in size, possesses two cusps on the hypolophid (Wood, 1935 indicated that the p4s he studied were worn, but the hypolophid appeared to possess three cusps), and on the anterior one-half of the hypolophid the entoconid and hypoconid are separated by a narrow valley. They differ from those of *B. nebraskensis* in that *B.* cf. *B. borealis* is larger in size; its cusps on the metalophid are strongly D-shaped, and they do not meet near the midline of the tooth. Currently, there are no known lower teeth for *B. meridionalis*.

The lower molars of *B.* cf. *B. borealis* from Eastgate differ from those of *B. oregonensis* in that *B.* cf. *B. borealis* is smaller and the lophids unite labially and centrally at about the same stage of wear rather than uniting centrally first. Unfortunately, the lower molars of *B. nebraskensis* are too worn for a primary comparison with the Eastgate material.

Based on the cheekteeth, especially the P4s and p4s, *B.* cf. *B. borealis* from Eastgate are most similar to *B. borealis* sharing the following

characteristics: size (length and width) of the cheekteeth; P4s possessing an accessory cusp and havng a single, oval-shaped protocone; and metalophids of the p4s having two cusps that are subequal in size and strongly D-shaped.

Discussion.— According to Korth (1997) the first species of *Balantiomys* that occurred outside the northern Great Plains is *B. oregonensis*. The presence of *B.* cf. *B. borealis* at Eastgate marks the second occurrence of this genus outside this region and the first for this species. Carrasco (1998, 2000a, b) examined cheekteeth of recent heteromyids, in particular *Dipodomys*, in order to determine the utility of quantitative characters for species determination for fossil heteromyids. He found tooth size, in particular length of p4, often (>70%) provided a correct species classification for *Dipodomys*. When examining cheekteeth of fossil heteromyids, he suggested limiting comparisons to specific age groups. Carrasco (2000a) examined 18 dental characters and determined the lengths of the p4s were among the most diagnostic character because of species-specific wear patterns on this tooth. Additional researchers (Bamosky, 1986b; Korth, 1996; and Storer, 1975) have separated heteromyids based on similar quantitative characters of the lower premolar.

Balantiomys nevadensis n. sp.

Plate 22 (A–I)

Holotype.— OMNH 54754, left dentary fragment with i1–m1.

Type locality.— Eastgate, OMNH V974.

Etymology.— Named after the state of Nevada, from where it was collected.

Other localities.— UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54762, left P4; OMNH 54764, right P4; OMNH 54773, right m3; OMNH 54774, right m1 or m2; OMNH 54777, left m3; OMNH 54787, right M1 or M2; UCMP 141788-03, right p4; UCMP 141789-02, right p4; UCMP 141789-03, right p4; UCMP 141795, left dentary with p4–m3; UCMP 141798, left maxilla with M1–M3; UCMP 141809-03, left p4; UCMP 141819-04, left m3; UCMP 141820-02, left M1 or M2; UCMP 141820-05, right M1 or M2; UCMP 141820-07, right M1 or M2; UCMP 141820-19, left M1 or M2; UCMP 141820-24, left P4; UCMP 141820-29, left M1 or M2; UCMP 141820-30, left M1 or M2; UCMP 141820-31, right maxilla with P4; UCMP 141820-34, left M1 or M2; UCMP 141820-35, right M1 or M2; UCMP 141820-36, right P4; UCMP 141820-37, right M2; UCMP 141820-41, left M1 or M2; UCMP 141820-

43, right P4; UCMP 141820-45, right M1 or M2; UCMP 141821-01, left dentary fragment with p4–m1; UCMP 141821-10, right P4; UCMP 141822-01, right M1 or M2; UCMP 141822-02, left m1 or m2; UCMP 141822-10, left m1 or m2; UCMP 141822-21, right maxilla with P4–M1; UCMP 141822-24, left m1 or m2; UCMP 141822-25, left p4; UCMP 141822-34, left M1 or M2; UCMP 141825-02, left M1 or M2; UCMP 141825-08, right M1 or M2; UCMP 141825-12, right m1 or m2; UCMP 141825-13, left M1 or M2; UCMP 141825-14, left M1 or M2; UCMP 141825-15, left m1 or m2; UCMP 141825-20, right M1 or M2; UCMP 141825-25, right M1 or M2; UCMP 141827-06, right m1 or m2; UCMP 141827-07, right m3; UCMP 141827-08, right m3; UCMP 141827-14, right m1 or m2; UCMP 141827-19, right m3; UCMP 141828-02, left m1 or m2; UCMP 141828-10, left m1 or m2; UCMP 141828-11, left m1 or m2; UCMP 141828-17, left m1 or m2; UCMP 141828-18, left m1 or m2.

Measurements.— See Tables 41 and 42.

Diagnosis.— *Balantiomys nevadensis* is a medium sized mioheteromine differing from *Balantiomys oregonensis*, *B. borealis*, *B. nebraskensis*, and *B. meridionalis* in having a much smaller P4 with numerous accessory cusps. For the upper molars, *B. nevadensis* is similar to related taxa in occlusal morphology but differs in length and width proportions. It is wider than *B. borealis*, narrower than *B. oregonensis*, and smaller in both dimensions than *B. meridionalis*. There are no known upper molars for *B. nebraskensis*. The p4 of *B. nevadensis* differs from most other species of *Balantiomys* in having accessory cusps and a lower

crown height (except *B. oregonensis* and *B. nebrascensis*). Proportions of the p4 of *B. nevadensis* differ in being wider than *B. borealis* and *B. nebrascensis*, and shorter in length than *B. oregonensis*. No p4s are known for *B. meridionalis*. The lower molars of *B. nevadensis* differ from all species of *Balantiomys* in being smaller and having lophids that unite centrally.

Description.— The P4 is wider than long. The protoloph contains a single cusp (protocone) that is small, oval-shaped, and lingually attached to the metaloph, with numerous accessory cusps. The lingual attachment of the lophs occurs at the entostyle (=hypostyle; see Korth, 1997) by a low ridge extending from the lingual side of the protocone, uniting with the entostyle high on its anteromost surface. Three accessory cusps are present on the protoloph. One accessory cusp occurs anterior to and below the protocone, and one accessory cusp occurs on the labial and lingual sides of the protocone. The accessory cusp on the labial side extends posteriorly, closing the anterior one-half of the transverse valley. The transverse valley is open labially but closed lingually. The metaloph has three cusps (metacone, hypocone, and entostyle). The metacone and entostyle are transversely aligned, whereas the hypocone occurs more posteriorly. A small, low ridge arises well above the anterior side of the base of the metacone and projects anteriorly in a straight line that terminates at the center of the floor of the transverse valley. The posterior cingulum arises on the posterolabial corner of the entostyle and extends labially to the posterolingual corner of the hypocone.

The M1 is much wider than long. The anterior cingulum arises from the anterolingual side of the paracone and terminates along the anterior surface of the protocone. The protoloph has three cusps (paracone, protocone, and protostyle). The paracone and protostyle are transversely aligned, but the protocone occurs more posteriorly than the former two cusps. The floor of the transverse valley is deep, narrow, open labially, and closed lingually. The protoloph and metaloph are united lingually by the protostyle and the entostyle. The lingual union of these two lophs occurs below the occlusal surface but well above the base of the tooth crown. The metaloph has three cusps (metacone, hypocone, and entostyle). The metacone and entostyle are transversely aligned, but the hypocone is situated more posteriorly than the former two cusps. The M2 differs from the M1 in lacking anterior and posterior cingula and being smaller in size.

The M3 is distinguished from the preceding molars by its smaller size, C-shaped occlusal surface, and reduction in size of the metaloph. The protoloph is the widest of the lophs and possesses three cusps (paracone, protocone, and protostyle). The paracone and protostyle are transversely aligned, whereas the protocone occurs slightly posterior to the transverse line extending from the paracone to the protostyle. The floor of the transverse valley is open labially but closed lingually by the union of the protostyle and entostyle. The lingual union of the protoloph to the metaloph occurs at the occlusal surface. The metaloph contains three cusps (metacone, hypocone, and entostyle). The metacone is

situated anterolabial, but adjacent to the hypocone. The hypocone is posteriorly placed compared to the metacone or the entostyle. The entostyle occurs anterolingual to the hypocone and projects anterolingually to join the protostyle. The entostyle projects anteriorly perpendicular to the metaloph.

The ventral surface of the dentary is slightly convex. The diastema is long and shallow with a mental foramen that occurs high but below the level of the distal edge of the masseteric scar and well in front of the p4. The mental foramen opens anteriorly. The ventral shelf of the masseteric scar is strong anteriorly but diverges posteroventrally and terminates near the ventral margin of the dentary below the m2. The dorsal shelf of the masseteric scar is lacking. Numerous foramina occur on the lingual side of the dentary below the alveoli of the cheekteeth.

The distal end of the incisor occurs near the level of the tooth row. Medially the tooth is flattened, but laterally it is slightly convex. Mesodistally the tooth is long and narrow. On the lingual side, the enamel covers less than 25% of the surface area, whereas on the labial side it covers 33%. There is no evidence of ornamentation on the mesial surface.

The p4 is longer than wide. It is low crowned (LEH/T=0.31), smaller than the m1, and slightly bulbous at the crown base. The metalophid contains two subequal-sized cusps (protoconid and protostylid), both of which are D-shaped. An anteroposteriorly elongate valley separates these two cusps, but is closed anteriorly by an accessory cusp. The protoconid is anterior to the protostylid.

The tooth has the following characteristics: is slightly bulbous at the crown base, is low crowned, has two roots narrower than their respective lophid, has anterior and posterior cingulids, and has another accessory cusp. The second accessory cusp occurs on the lingual side of the entoconid, well below the occlusal surface. At a later stage of wear, the second accessory cusp would disappear. The lophids (metalophid and hypolophid) join labially well below the occlusal surface but above the enamel-dentine junction. On the hypolophid, there are three transversely aligned cusps. The entoconid and hypoconid are subequal and similar in morphology, but the hypostylid is much reduced in size and would disappear with additional wear to the occlusal surface. A shallow, anteroposteriorly directed valley separates the entoconid and hypoconid. This valley would disappear during early stages of wear but could be detected in later stages of wear by a shallow indentation occurring on the anterior surface of the hypolophid posterior and in line with the valley that separates the protoconid and protostylid on the metalophid.

The m1 is wider than long. The following are characters of the m1 for this species: thin enamel on each lophid; slightly bulbous crown base; low crowned; two roots nearly as wide as their respective lophid; roots fused proximally below tooth crown; and small labial chevrons present. The anterolabial cingulid arises from the anteromedial surface of the protostylid, projecting lingually at about 45° until it reaches a point anterior to a transverse line anterior to the anteromost margin of the protoconid, where it bends more than 90° posterolingually to join

the anterior surface of the protoconid at the occlusal surface. The lophids join centrally. The transverse valley floor opens lingually and labially. The lophids unite well below the occlusal surface. Three cusps are present on the metalophid and join, at their respective bases, near the tranverse valley floor. Of the cusps of the metalophid, the metaconid is anteroposteriorly compressed and slightly larger than the oval-shaped protoconid and the L-shaped protostylid. The metaconid and protoconid are transversely aligned, but the protostylid lies posterior to them. The floor of the transverse valley is deep, narrow, and open laterally (labial and lingual). In lingual view, the anterior wall of the metalophid is straight, and the posterior wall of this lophid projects anteriorly; the anterior wall of the hypolophid projects posteriorly, while the posterior wall of this lophid is straight. Thus, a narrow, U-shaped valley is present.

The hypolophid has three cusps (entoconid, hypoconid, and hypostylid) that are transversely aligned but unite at different heights on the tooth crown. The protostylid and protoconid unite about midway along the tooth crown, but the base of the labial cusp unites with the base of the hypoconid near the base of the transverse valley floor. Thus, with moderate wear to the occlusal surface the entoconid and hypoconid would merge, but the hypostylid would remain as a distinguishable cusp. However, at a very late stage of wear the hypostylid would merge with the hypoconid. No posterior cingulid is present on this tooth. The m2 is very similar in morphology to the m1.

The m3 is longer than wide, has thin enamel, and is not bulbous at the

crown base. The anterolabial cingulid arises from the anteromedial surface of the protostylid and becomes strongly, labially convex before terminating along the anterolabial surface of the protoconid well below the apex of the cusp. The lophids join centrally but not labially or lingually. The lophids unite well below the occlusal surface near the floor of the transverse valley. Three cusps occur on the metalophid and join at their respective bases about midway between the occlusal surface and the transverse valley floor. The largest cusp of the metalophid is the anteroposteriorly compressed protoconid followed in size by the anteroposteriorly compressed metaconid and the anteroposteriorly elongated protostylid. The protoconid and metaconid are transversely aligned, but the protostylid occurs posterior to the other cusps on this lophid. The floor of the transverse valley is deep, narrow, and open laterally. From a lingual view, the anterior and posterior walls of the metalophid are straight, the anterior wall of the hypolophid projects slightly posteriorly, and the posterior wall of the hypolophid is straight. A narrow, V-shaped transverse valley is apparent. The hypolophid has three cusps that are transversely aligned but unite at different heights. The entoconid and hypoconid unite high and with little wear to the occlusal surface would merge. The apex of the hypostylid occurs well below the occlusal surface and unites with the hypoconid near the floor of the transverse valley. A posterior cingulid is lacking.

Comparison and *discussion*.— The P4s of *B. nevadensis* differ from those of *B.* cf. *B. borealis* and *B. oregonensis* in that *B. nevadensis* is much smaller in

size and has numerous accessory cusps. There are no known P4s of *B. nebraskensis*. The P4 of *B. nevadensis* differs from that of *B. meridionalis* in being much smaller, having accessory cusps and an oval-shaped protocone.

Excluding size, the upper molars of *B. nevadensis* are difficult to distinguish from those of other species of *Balantiomys*. In proportions, upper molars of *B. nevadensis* differ from those of *B. borealis* (from Eastgate) in having teeth that are wider; however, lengths are similar. They differ from the M2 of *B. oregonensis* in being narrower but similar in length, and from the M1 of *B. oregonensis* in being smaller in overall size. There are no known upper molars of *B. nebraskensis*. The M1 of *B. nevadensis* differs from that of *B. meridionalis* in being smaller and from the M2 of *B. meridionalis* in being noticeably wider than long.

The p4s of *B. nevadensis* differ from those of *B. borealis* in being lower crowned (LEHT/=0.31), having similar length and being wider, having an anteroposterioly directed valley on the metalophid closed anteriorly by an accessory cusp, having an accessory cusp on the lingual surface of entoconid, and having shallow anteroposteriorly directed valley on hypolophid. It differs form *B. oregonensis* in being higher crowned, being similar in width but much shorter anteroposteriorly, having D-shaped protoconid, and having accessory cusp on the lingual surface of entoconid. The p4 of *B. nevadensis* differs from *B. nebraskensis* in being lower crowned, similar in length but much wider, having anteroposterioly directed valley on the metalophid that is closed anteriorly by an

accessory cusp, having accessory cusp on the lingual surface of the entoconid, and having shallow anteroposteriorly directed valley on the hypolophid. There are no known p4s of *B. meridionalis*.

The lower molars of *B. nevadensis* differ from all known species of *Balantiomys* in being smaller and having lophids that unite centrally. There are no known lower molars known for *B. meridionalis*.

Although the P4s and p4s of *B. nevadensis* are smaller than those belonging to other species of this genus, *B. nevadensis* is most similar to *B. borealis* in sharing the following characteristics: for the P4, an oval-shaped protocone and the presence of accessory cusps; for the p4, a subequal, D-shaped protoconid and protostylid, and a deep anteroposteriorly directed valley between the protoconid and protostylid on the metalophid.

Subfamily Dipodomyinae Coues, 1875

Cupidinimus Wood, 1935

Cupidinimus eastgatensis n. sp.

Plate 22 (J-L)

Holotype.— UCMP 141856, left dentary fragment with p4–m2.

Type locality.— Eastgate, UCMP V70142.

Etymology.— Named after the nearby town of Eastgate, Churchill County, Nevada.

Other localities.—Eastgate, OMNH V974; UCMP V70140, V70142, V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54755, left p4; OMNH 54757, left p4; OMNH 54768, left m1 or m2; OMNH 54769, left m3; OMNH 54771, left m1 or m2; OMNH 54779, left m1 or m2; OMNH 54784, left m1 or m2; OMNH 54785, left m1 or m2; OMNH 54786, left m1 or m2; OMNH 54794, right m3; UCMP 141781, left dentary fragment with p4, m2; UCMP 141782-02, left p4; UCMP 141782-03, left p4; UCMP 141789-01, right p4; UCMP 141809-01, left p4; UCMP 141809-02, left p4; UCMP 141816, left p4; UCMP 141819-03, left m3; UCMP 141821-06, right m1 or m2; UCMP 141822-07, right p4; UCMP 141825-32, right m3; UCMP 141827-04, right m1 or m2; UCMP 141827-09, right m1 or m2; UCMP 141827-11, right m1 or m2; UCMP 141827-12, right m1 or m2; UCMP 141827-13, right m1 or m2; UCMP 141827-15, left m1 or m2; UCMP 141827-16, right m1 or m2; UCMP 141827-17, right m1 or m2; UCMP 141828-03, left m1 or m2; UCMP 141828-05, left m3; UCMP 141828-14, left m1 or m2.

Measurements.— See Table 43.

Diagnosis.— *Cupidinimus eastgatensis* is a large species of *Cupidinimus* differing from most known species in having a much larger p4 (except *C. avawatzensis*) with an accessory cusp (except *C. avawatzensis*, *C. kleinfelderi*,

and *C. saskatchewanensis*), and lophids that unite labially (except *C. avawatzensis*, *C. madisonensis*, *C. kleinfelderi*, and *C. saskatchewanensis*). The p4 of *C. eastgatensis* differs from *C. kleinfelderi* and *C. saskatchewanensis* in lacking a central enamel ridge. The lower molars of *C. eastgatensis* are larger than those of all known species of *Cupidinimus* and differ in having a labial union of lophids followed by a central union and a small posterior cingulid.

Description.— The diastema is long and shallow. The mental foramen occurs high on the diastema, below the level of the anteromost part of the masseteric scar, in front of the p4. The mental foramen is large and opens anteriorly. The masseteric scar arises high on the distalmost part of the diastema anterior to the p4. It forms a broad ventral shelf anterodorsally but terminates below the posterior alveolus of the m1 and near the ventral surface of the dentary; no dorsal shelf is indicated. There are numerous foramina that occur on the lingual surface below the alveoli of the cheekteeth. The cheekteeth are low crowned and slightly bulbous at the crown base.

From a mesial view the incisor is flat lingually and convex labially. Mesodistally the tooth is short, whereas it is wide laterally. On the lingual side, the enamel covers about 25% of the surface area, whereas on the labial side it covers about 33%. No ornamentation is present on the mesial surface.

The p4 is shorter than wide. The crown base is not bulbous, possesses two roots, is of medium crown height (LEH/T=0.44), and has a small labial chevron. Another p4 (UCMP 141856) that is fully erupted has two cusps and an

accessory cusp on the metalophid; the protoconid is oval-shaped, while the protostylid is circular-shaped; and both cusps are transversely aligned. The protoconid and protostylid are separated by a deep, narrow valley. These cusps are not united anteriorly by the accessory cusp. The lophids unite labially well below the occlusal surface. The hypolophid possesses three cusps (entoconid, hypoconid, and hypostylid) and a posterior cingulid. The entoconid is slightly larger and more anteroposteriorly compressed than the hypoconid. The hypostylid is small and occurs well below the apex of the hypoconid. A deep, wide valley separates the entoconid and the hypoconid. However, well below the occlusal surface the entoconid and hypoconid are joined posteriorly by the posterior cingulid. The floor of the transverse valley is deep, narrow, and open lingually.

The m1 is wider than long, possesses thin enamel, is not bulbous at the crown base, is low crowned (LEH/T=0.35), possesses two roots that are nearly as wide as the lophids and fused near the base of the tooth crown, and have a short labial chevron. The anterolabial cingulid arises from the anteromedial surface of the protostylid, projects straight anteriorly past the protoconid where it bows strongly to connect with the anterolingual surface of the protoconid and inferior to the apex. The lophids join labially first and then centrally. The union of lophids occurs well below the occlusal surface of the unworn cheekteeth. In a late stage of wear, an enamel lake would form between the labial and central union of the lophids. Three cusps occur on the metalophid (metaconid,

protoconid, and protostylid) and join at their respective bases low on the tooth crown (near the floor of the transverse valley). The transversely elongated metaconid is the largest cusp of the metalophid, followed by an oval-shaped protoconid and a small, L-shaped protostylid. The metaconid and protoconid are transversely aligned, but the protostylid is placed slightly posterior to the other two cusps on the metalophid. The floor of the transverse valley is deep, narrow, and closed labially. In lingual view, the anterior and posterior walls of the metalophid project slightly anteriorly, whereas the anterior wall of the hypolophid projects slightly posteriorly; the posterior wall of the hypolophid is straight. Thus, a narrow, U-shaped transverse valley is apparent. The hypolophid has three cusps (entoconid, hypoconid, and hypostylid) that are transversely aligned and tunite at their bases midway between the occlusal surface and the floor of the transverse valley. A small posterior cingulid is present between the entoconid and hypoconid on the posterior side of the hypolophid. The m2 is similar to the m1.

The m3 is wider than long, has thin enamel; and has a crown base that is not bulbous. Only the tooth crown is present. So it is not possible to determine if this species possessed a labial chevron for this tooth. The anterolabial cingulid arises on the anterolingual surface of the protostylid and bows weakly around the protoconid to join between the protoconid and metaconid below the occlusal surface where the bases of the protoconid and metaconid unite medially. The lophids join labially but not centrally. The union of the lophids occurs well below

the occlusal surface near the floor of the transverse valley. Three cusps are present on the metalophid and join well above their respective bases. The transversely elongated metaconid is the largest cusp on the metalophid. It is followed in size by an oval-shaped protoconid and a very small, anteroposteriorly elongated protostylid. All three cusps are transversely aligned. The floor of the transverse valley is deep, narrow, open lingually, and closed labially.

In lingual view, the anterior wall of the metalophid and the anterior and posterior walls of the hypolophid are straight, while the posterior wall of the metalophid projects anteriorly. The narrow transverse valley floor is V-shaped. The hypolophid has three cusps (entoconid, hypoconid, and hypostylid). The entoconid and hypostylid are transversely aligned, but the hypoconid lies more anterior to the former two cusps. The entoconid and hypoconid unite high on the tooth crown and would merge with little wear to the occlusal surface. Although the apex of the hypostylid is missing, it is clear that this cusp would remain distinguishable from the other two cusps through a very late stage of wear. No cingulids are present.

Comparison and discussion.— The lower p4s of *C. eastgatensis* are much larger than those of all known species of *Cupidinimus* except *C. avawatzensis* (Figs. 19, 20). Other than size, the p4s of *C. eastgatensis* differ from those of *C. boronensis* in having an accessory cusp on the metalophid, lophids that unite labially, and a posterior cingulid. The p4 of *C. eastgatensis* differ from those of *C. halli* in having an accessory cusp, a hypostylid, and protoconid and protostylid

that are not united posteriorly. It differs from those of *C. eurekensis* in having an accessory cusp, a hypostylid, and lophids that unite labially. The p4 of *C. eastgatensis* differs from those of *C. lindsayi* in having an accessory cusp and the lophids unite labially. It differs from those of *C. whitlocki* in having an accessory cusp, protoconid and hypoconid well developed, in lacking a central enamel ridge, and lophids that unite labially. The p4 of *C. eastgatensis* differs from that of *C. madisonensis* in being shorter than wide and possessing an accessory cusp and a posterior cingulid. It differs from *C. nebraskensis* in having an accessory cusp and a posterior cingulid, lacking a central enamel ridge, and having lophids that unite labially. The p4 of *C. eastagensis* differs from that of *C. kleinfelderi* in having a weak hypostylid. It differs from those of *C. saskatchewanensis* in lacking a central enamel ridge. The p4 of *C. eastgatensis* differs from that of *C. avawatzensis* in being much lower crowned (p4, LEH/T=0.44; m1 or m2, LEH/T=0.35), an oval-shaped protoconid and protostylid, a protoconid that is anterior to the protostylid, and a protoconid and protostylid that are subequal.

The lower molars of *C. eastgatensis* are larger than those of all known species of *Cupidinimus*. Other than size, the lower molars of *C. eastgatensis* differ from those of *C. boronensis* in having a protostylid that is smaller than the protoconid, a first union of lophids occuring labially, and a small posterior cingulid. They differ from those of *C. halli* in being low crowned and having a distinct hypostylid, a weak posterior cingulid, and lophids that unite labially and then centrally with wear. The lower molars of *C. eastgatensis* differ from those of *C. eurekensis* in being wider than the p4; other characters are impossible to compare to those of *C. eurekensis* because of the wear to the occlusal surface of all cheekteeth. The lower molars of *C. eastgatensis* differ from those of *C. lindsayi* in having a labial union of lophids followed by a second union (centrally) that occurs with additional wear to the occlusal surface. In addition, *C. eastgatensis* has a small posterior cingulid, while *C. lindsayi* does not possess a small posterior cingulid. The lower molars of *C. eastgatensis* differ from those of *C. whitlocki* in being lower crowned and possessing a small posterior cingulid. Except for size, the lower molars of the holotype (CM 8770) for *C. madisonensis* are too worn to allow a direct comparison to that *C. eastgatensis*. The lower molars of *C. eastgatensis* differ from those of *C. nebraskensis* in having: a metaconid that is circular-shaped; a hypostylid that is not separate from the hypoconid; a labial union of the lophids that occurs higher on the tooth crown and is followed by a central union that will create an enamel lake in advance stages of wear; and a small posterior cingulid. There are no known lower molars

for *C. kleinfelderi* or *C. saskatchewanensis*. The lower molars of *C. eastgatensis* differ from those of *C. avawatzensis* in possessing a small posterior cingulid.

The p4s of *C. eastgatensis* are among the largest of the *Cupidinimus* species that have p4s that are shorter than wide (see Barnosky, 1986b). In addition, they possess the following characters: an anterior cingulid; an accessory cusp low on the lingual side of the protoconid; a protoconid and protostylid that are subequal; a protostylid that is circular-shaped; a protoconid that is oval-shaped; and lophids that connect labially first. Three cusps are present on the hypolophid; a large accessory cusp occurs on the lingual side of the entoconid; a V-shaped valley partially separates the entoconid and hypoconid; and a posterior cingulid occurs between the entoconid and hypoconid. The protostylid is not anterior to the protoconid.

Compared to those for other heteromyids from Eastgate, the lower molars of *C. eastgatensis* are most similar in size to those of *B.* cf. *B. borealis*. However, the two taxa have very distinct p4s and lower molars.

Cupidinimus barnoskyi n. sp.

Plate 22 (M-O)

Holotype.— OMNH 54750, left dentary fragment with p4-m1.

Type Locality.— Eastgate, UCMP V70147.

Etymology.— Named after Anthony D. Barnosky, for his contributions to

knowledge of the genus *Cupidinimus*.

Other localities.— UCMP V70140.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and UCMP 141797, left dentary fragment with i1-p4; UCMP 141821-04, left m3; UCMP 141825-07, left m3; UCMP 141828-01, left m1 or m2.

Measurements.— See Table 43.

Diagnosis.— *Cupidinimus barnoskyi* is a small-sized species of *Cupidinimus*. It is smaller than most known species of *Cupidinimus* except *C. eurekensis*. The p4 of *C. barnoskyi* differs from all other species of *Cupidinimus* in being much shorter than wide (except *C. whitlocki*). It differs from *C. whitlocki* in being higher crowned, having an accessory cusp on the metalophid, and having the lophids that join labially first. The lower molars of *C. barnoskyi* differ from all known species of *Cupidinimus* in having a labial union of the lophids followed by the central union of lophids, and having a posterior cingulid (except *C. eastgatensis*). From *C. whitlocki*, the lower molars of *C. barnoskyi* differ in having a distinct anterolabial cingulid. The lower molars of *C. barnoskyi* differ from those of *C. nebraskensis* in being higher crowned, having a deeper and narrower transverse valley, and having a posterior cingulid. *Cupidinimus barnoskyi* is most similar to *C. eastgatensis*, from which it differs in being higher

crowned and lacking a labial chevron.

Description.— The holotype (OMNH 54750) has moderate wear to the occlusal surface. The cheekteeth are high crowned (LEH/T=0.63) and are the highest of all the *Cupidinimus* from Eastgate. The cheekteeth increase in size from front to back and are not bulbous at the crown bases. The dentary is incomplete with only the proximalmost part of the diastema present anteriorly; posteriorly, it is broken through the posterior alveolus of the m1. The ventral surface of the dentary is straight. Although the distalmost part of the diastema is missing, the diastema appears to have been long and shallow. The mental foramen occurs high on the diastema at the level of the anteromost margin of the masseteric scar, well in front of the p4, and opens anteriorly. The masseteric scar arises high on the diastema and occurs in front of the p4. It forms a broad shelf that terminates below the posterior alveolus of the p4 about midway between the tooth row and the ventral surface of the dentary.

The incisor tip occurs at the level of the tooth row. From a mesial view the tooth is flat lingually but slightly convex labially. The tooth is long mesodistally but narrow laterally. On the lingual side, the enamel covers about 25% of the surface area, while on the labial side the enamel covers 33%. No ornamentation is present on the mesial surface of this tooth.

The p4 is wider than long, is high crowned, is not bulbous at the crown base, has two roots that are nearly as wide as their respective lophids, and has a labial chevron. There are two cusps and an accessory cusp on the metalophid.

The protoconid is anteroposteriorly compressed and subequal in size to the circular-shaped protostylid, with its anterolingual part lying anterior to that of the protostylid. The accessory cusp unites the protoconid and protostylid anteriorly. A deep, wide, anteroposteriorly directed valley lies between the protoconid and protostylid but is closed anteriorly by the accessory cusp. The lophids unite labially below the occlusal surface but well above the base of the tooth crown. The hypolophid has two cusps. The hypostylid is absent. The entoconid and hypoconid are subequal in size and are anteroposteriorly compressed. A shallow, wide valley separates the entoconid and hypoconid, but these cusps unite posteriorly at the occlusal surface by a posterior cingulid. The floor of the transverse valley is deep, wide, and open lingually.

The m1 is wider than long. The enamel is equally thin on the anterior and posterior walls of each lophid, the crown base is not bulbous, and the tooth is high crowned (LEH/T ranges from 0.59-0.67). Two roots are present on this tooth, each of which is nearly as wide as its respective lophid. No chevrons are present. The anterolabial cingulid arises from the anteromedial surface of the protostylid, projects straight anteriorly past the metalophid, and then bends sharply at a right-angle to join the anterolingual surface of the protoconid at the occlusal surface. The lophids join labially and then centrally. The union of the lophids occurs below the occlusal surface but well above the dentine-enamel junction. In a later stage of wear, an enamel lake would form between the labial and central union of the lophids. Three cusps occur on the metalophid and join,

at their respective bases, low on the tooth crown. The transversely elongated metaconid is the largest cusp of the metalophid followed in size by the transversely elongated protoconid and the anteroposteriorly elongated protostylid. The protoconid and metaconid are transversely aligned, but the protostylid occurs more posteriorly than the former two cusps. The floor of the transverse valley is deep, narrow, open lingually, and closed labially. From a lingual view, the anterior and posterior walls of the metalophid bend anteriorly, while both walls of the hypolophid are straight dorsoventrally. Thus, a narrow, V-shaped transverse valley is apparent. The hypolophid has three cusps that are transversely aligned and united high on the tooth crown. With moderate wear to the occlusal surface all cusps would merge. A posterior cingulid is present between the entoconid and the hypoconid. There are no teeth in this group that can be positively identified as an m2.

The m3 is similar in morphology to the m1 except that the m3 has no accessory cusps, and the roots are fused lingually along their entire height. However, on the labial side the roots are only fused near the crown base. The anterior and posterior walls of the metalophid are straight, as is the anterior wall of the hypolohid, but the posterior wall of the hypolophid is bent posteriorly.

Comparison.— The p4 of *C. barnoskyi* is among the smallest of the species of *Cupidinimus*. The smallest species of this genus (*C. eurekensis*) has a p4 that is similar in length to that of *C. barnoskyi*, but it is narrower. *Cupidinimus barnoskyi* has a p4 that is similar in length and width to that of *C.*

whitlocki. All other known species of *Cupidinimus* except *C. halli*, *C. eastgatensis*, and *C. boronensis* have a p4 that are much longer than wide; in these three species it is equally long and wide.

In addition to size, the p4s of *C. barnoskyi* differ from those of *C. boronensis* in that C. *barnoskyi* is higher crowned, is shorter than wide, possesses an accessory cusp, has a labial union of lophids, and has a posterior cingulid. It differs from those of *C. halli* and *C. lindsayi* in that the p4 of *C. barnoskyi* is higher crowned, possesses an accessory cusp, has lophids that unite labially, and it has a posterior cingulid. Known p4s of *C. eurekensis* are too worn to provide comparison to those of *C. barnoskyi*. The p4 of *C. barnoskyi* differs from that of *C. whitlocki* in being higher crowned, possessing an accessory cusp on the metalophid, having lophids that unite labially, having a distinct protoconid and hypoconid, and having a posterior cingulid. It differs from *C. madisonensis* in being higher crowned and having an accessory cusp, having lophids that unite labially, and having a posterior cingulid. The p4 of *C. barnoskyi* differs from that of *C. nebraskensis* in being higher crowned, having an accessory cusp, having lophids that unite labially, and having a posterior cingulid. It differs from *C. kleinfelderi* and *C. saskatchewanensis* in that *C. barnoskyi* has a labial union of lophids, lacks a hypostylid, and has a posterior cinglulid. *Cupidinimus barnoskyi* differs from that of *C. eastgatensis* in having a p4 that is higher crowned, having a central enamel ridge, and lacking a hypostylid. The p4 of *C. barnoskyi* differs from that of *C. avawatzensis* in having

a prominent accessory cusp but lacking a prominent labial chevron.

In addition to size, the lower molars of *C. barnoskyi* differ from *C. boronensis* in being higher crowned with lophids that join labially, then centrally, and having a posterior cingulid. It differs from those of *C. halli* in having lophids that unite labially, then centrally, and having a posterior cingulid. The lower molars of *C. eurekensis* are too worn to provide comparison to those of *C. barnoskyi*. They differ from those of *C. lindsayi* in having a labial union of the lophids that is preceded by a central union, and having a posterior cingulid. From *C. whitlocki*, the lower molars of *C. barnoskyi* differ in being higher crowned and possessing a prominent anterolabial cingulid, having a labial union of lophids that join first followed by a central union, and having a posterior cingulid. Except for size, the lower molars of the holotype (CMNH 8770) for *C. madisonensis* are too worn to allow a direct comparison to that *C. barnoskyi*. Lower molars of *C. barnoskyi* differ from those of *C. nebraskensis* in being higher crowned with a deeper and narrower transverse valley; a posterior cingulid is present. The lower molars for *C. kleinfelderi* or *C. saskatchewanensis* are unknown. For the lower molars, *C. barnoskyi* differs from those of *C. eastgatensis* in being higher crowned and lacking a labial chevron. *Cupidinimus barnoskyi* has lower molars that differ from those of *C. avawatzensis* in possessing a posterior cingulid. The most similar species to that of *C. barnoskyi* is *C. eastgatensis* from which it differs in having a much greater crown height and lacking a labial chevron.

Cupidinimus boronensis Whistler, 1984

Plates 22 and 23 (P–R; A–F)

Localities.— Eastgate, UCMP V70140, V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Hemingfordian: Boron local fauna, Arkose Member of the Cramer Beds, Kern County, California (Whistler, 1984).

Referred specimens.— OMNH 54761, right M1 or M2; OMNH 54763, left maxilla with P4–M1; OMNH 54765, right P4; OMNH 54766, left P4; OMNH 54772, left m3; OMNH 54792, right M1 or M2; OMNH 54796, right M1; UCMP 141624, left dentary fragment with p4–m2; UCMP 141783, right M1 or M2; UCMP 141797-02, left dentary fragment with p4–m2; UCMP 141820-09, right M1 or M2; UCMP 141821-02, right P4; UCMP 141821-08, left P4; UCMP 141820-21, right M1 or M2; UCMP 141820-28, left P4; UCMP 141820-42, left P4; UCMP 141821-09, left P4; UCMP 141821-11, right P4; UCMP 141822-18, left m3; UCMP 141822-20, right P4; UCMP 141822-33, left P4; UCMP 141825-03, right m3; UCMP 141825-16, left M1 or M2; UCMP 141825-23, right M1 or M2; UCMP 141825-29, right M1 or M2; UCMP 141827-01, right m3; UCMP 141828-16, left m3; UCMP 141828-19, left m1 or m2.

Measurements.— See Table 43.

Description.— For the upper cheekteeth the P4 is longer than the M1, but

both teeth are similar in width. The P4 is wider than long. The protoloph has a single cusp that is small and circular-shaped. The lophs join lingual of center and well below the occlusal surface. Neither accessory cusps nor anteroconid are present on the protoloph. The transverse valley is deep, narrow, and open labially. The metaloph has three cusps subequal in size. The metacone and hypocone are oval-shaped, whereas the entostyle is anteroposteriorly elongated. A posterior cingulum arises from the posteriolabial surface of the entostyle and courses labially, terminating along the posteromedial surface of the hypocone below the occlusal surface.

The M1 is wider than long, high crowned, and has straight-walled lophs. Because of the heavy wear to the occlusal surface, the anterior cingulum is not clearly defined. The protoloph appears to have three cusps. The paracone and protostyle are transversely aligned but the protocone occurs posterior to the former two cusps. The floor of the transverse valley is shallow, narrow, and open labially but closed lingually. The protoloph and metaloph are united lingually at the protostyle and entostyle. The union of the lophs occurs below the occlusal surface but well above the base of the tooth crown. The floor of the transverse valley opens on the labial side about one-half of the way between the occlusal surface and the base of the tooth crown. The metaloph has three cusps. The metacone and entostyle are transversely aligned but the hypocone occurs posterior to the former two cusps. The metaloph is not as wide as the protoloph. Because of the late stage of wear to the occlusal surface, the

posterior cingulum is not evident.

The lower cheekteeth are of medium crown height (LEH/T=0.49-0.56); with the m1 being the largest, followed in size by the p4 and m2; they are not bulbous at the crown bases. The dentary is broken anterior to the mental foramen and posteriorly through the posterior alveolus of the m2. Based on the proximal half of the diastema, it was likely long and shallow. The mental foramen occurs high on the diastema, below the level of the anteromost edge of the masseteric scar, and well in front of the p4; the foramen opens anteriorly. The masseteric scar arises high on the diastema and occurs anterior to the p4. It forms a broad shelf that extends anterodorsally but terminates below the posteromost part of the p4. There is no dorsal shelf of the masseteric scar. There are few foramina on the lingual side of the dentary that occur below the alveoli of the cheekteeth. There is no incisor known for this species from Eastgate.

The p4 is nearly as long as it is wide, has little wear to the occlusal surface, is slightly bulbous at the crown base, is of medium crown height, has two roots that are nearly as wide as their respective lophids, and has a labial chevron. There are two cusps and no accessory cusps on the metalophid; thus, the cusps are not united anteriorly. The protoconid is oval-shaped and subequal to the circular-shaped protostylid. The anteromost part of the protoconid is anterior to that of the protostylid. A low, central enamel ridge (see Bamosky, 1986b) occurs between the posterior surface of the protoconid and protostylid.

This central enamel ridge unites the metalophid with the hypolophid posteriorly. A narrow and deep anteroposteriorly directed valley separates the anterior two-thirds of the protoconid and protostylid. The central union of the lophids occurs near the occlusal surface, well above the crown base. The hypolophid has two cusps. The entoconid and hypoconid are subequal; the former cusp is more anteroposteriorly compressed than the latter. There is no anteroposteriorly directed valley between the entoconid and hypoconid. No posterior cingulid is present. The floor of the transverse valley is deep, narrow, and open laterally (labial and lingual).

The m1 is nearly as long as it is wide. It has enamel on the anterior and posterior walls of both lophids that is equally thin. The tooth is slightly bulbous at the crown base, is of medium crown height (LEH/T= 0.49-0.56), possesses two roots that are nearly as wide as its lophids, and lacks chevrons. On the lateral sides of this tooth at the enamel-dentine junction, undulations are present at the crown base but above each root. In addition, this tooth has a shallow lingual re-entrant. The anterolabial cingulid has merged with the anterior cusps because of wear. However, it appears to have arisen from the anteromedial surface of the protostylid where it projectes about 45° anterolingually until reaching a location anterior to a tranverse line anterior to the anteromost part of the protoconid. Here it bends more than 90° posterolingually to join the anterior surface of the protoconid at the occlusal surface. The lophids join labially and centrally along the same height of the tooth crown. Thus, the labial and central union of the

lophids occur at the same stage of wear. At more advanced stages of wear, an enamel lake would form between the labial and central unions. Although all cuspids on the metalophid are merged because of the stage of wear on this specimen, it likely possessed three cusps at an earlier stage of wear. Based on the enamel pattern, the cusps join low on the tooth crown. The transversely elongated protoconid is the largest cusps on the metalophid followed by the transversely elongated metaconid; the anteroposteriorly elongated protostylid is the smallest. The metaconid and protoconid are transversely aligned, but the protostylid occurs more posteriorly than the former two cusps. The floor of the transverse valley is deep, narrow, open lingually, and closed labially. From a laterial view, the anterior wall of the metalophid is straight, the posterior wall is slightly bent anteriorly; and the anterior and posterior walls of the hypolophid are straight. This allows for a narrow, V-shaped transverse valley. The hypolophid appears to have three cusps. These cusps are transversely aligned and at an earlier stage of wear were likely united high on the tooth crown. At the current stage of wear, all three cusps are merged forming a continuous transverse lophid. No posterior cingulid is present.

The m2 is similar in morphology to the m1. Except it is much smaller, has no re-entrants present on the lingual side, and has no undulations on the labial side of the enamel-dentine junction. The m3 is similar to the preceding molars except that it is smaller in size, and the anterolabial cingulid bends lingually, attaching to the middle of the hypoconid well below the occlusal surface.

Comparison and discussion.— The P4s of *C. boronensis* from Eastgate are much smaller than those of *C. kleinfelderi*, *C. saskatchewanensis*, and *C. avawatzensis*, while they are larger than *C. madisonensis*, *C. lindsayi*, and *C. nebraskenis*. There are no known P4s for *C. eastgatensis* or *C. barnoskyi*. In addition to size, the P4s of *C. boronensis* from Eastgate differ from those of *C. halli*, *C. lindsayi*, and *C. whitlocki* in possessing a circular-shaped protocone, lacking an accessory cusp (except *C. lindsayi* and *C. whitlocki*), and having a protoloph that unites lingual of center. The P4s of *C. boronensis* differ from those of *C. nebraskensis*, *C. kleinfelderi*, *C. saskatchewanensis*, and *C. avawatzensis* in having a circlular-shaped protocone. In addition, the P4s of *C. boronensis* differ from the latter two species in lacking an accessry cusp. The P4s of *C. eurekensis*, *C. madisonensis*, *C. eastgatensis*, and *C. barnoskyi* are unknown.

The upper molars of *C. boronensis* are smaller than those of *C. avawatzensis*, whereas they are larger than *C. halli*, *C. madisonensis*, *C. nebraskensis*, and *C. lindsayi*. The occlusal surface of the upper molars are too worn for additional comparisons with the other species of *Cupidinimus*. There are no known upper molars for *C. kleinfelderi* and *C. saskatchewanensis*

The p4s of *C. boronensis* from Eastgate are smaller than those of *C. halli*, *C. kleinfelderi*, *C. saskatchewanensis*, *C. eastgatensis*, and *C. avawatzensis*. In contrast, *C. boronensis* from Eastgate has p4s that are larger than those of *C. lindsayi*, *C. nebraskensis*, *C. eurekensis*, *C. whitlocki*, and *C. barnoskyi*.

In addition to size, the p4s of *C. boronensis* differ from those of *C. halli* and *C. lindsayi* in lacking a hypostylid. The p4s of *C. boronensis* differ from those of *C. halli* in being higher crowned. The p4s of *C. boronensis* differ from those of *C. eurekensis* and *C. whitlocki* in having a central enamel ridge. Additional characters of *C. eurekensis* are not evident because of the heavy wear to the occlusal surface. The p4s of *C. boronensis* differ from those of: *C. madisonensis* in possessing a posterior union of the protoconid and protostylid; *C. nebraskensis* in being lower crowned and having a low central enamel ridge that unites the protoconid and protostylid posteriorly, and in having the protoconid and protostylid not closely appressed; *C. kleinfelderi* and *C. saskatchewanensis* in lacking an accessory cusp and a hypostylid; *C. eastgatensis* in being higher crowned, lacking an accessory cusp, possessing a low enamel ridge, having a protoconid that is anterior to the protostylid; *C. barnoskyi* in being lower crowned, nearly as long as wide, lacking an accessory cusp, and possessing a central enamel ridge; and *C. avawatzensis* in being lower crowned, lacking a hypostylid, and having an anteroposteriorly directed valley between the entoconid and hypoconid.

The lower molars of *C. boronensis* from Eastgate are smaller than those of *C. whitlocki*, *C. eastgatensis*, and *C. avawatzensis*. In contrast, the lower molars of *C. boronensis* are larger than *C. halli*, *C. madisonenis*, *C. lindsayi*, *C. nebraskensis*, and *C. eurekensis*.

In addition to size, the lower m1s or m2s of *C. boronensis* differ from: *C.*

halli in being lower crowned and in lacking a prominent protolophule and a labial chevron; *C. lindsayi*, *C. whitlocki*, and *C. nebraskensis* in lacking labial chevrons and the lophids unite labially and centrally at the same stage of wear; *C. eastgatensis* in being higher crowned and lacking a labial chevron; and *C. avawatzensis* in being lower crowned and lacking a labial chevron. The lower molars of *C. eurekensis* and the holotype (CM 8770) for *C. madisonensis* are too worn to provide comparison to those of *C. boronensis*. There are no known lower molars for *C. kleinfelderi* or *C. saskatchewanensis*.

Heteromyidae subfamily indet.

genus and species indet.

Locality.— Eastgate, UCMP V70140, V70147.

Age.— Barstovian.

Referred specimens.— OMNH 54752, left dp4; OMNH 54753, right dp4; OMNH 54756, right dentary fragment with dp4, m3; OMNH 54759, right dp4; OMNH 54770, right m3; UCMP 141760-08, right dp4, p4; UCMP 141788-02, left dp4; UCMP 141793, right dentary fragment with dp4, m3; UCMP 141803-01, right dp4; UCMP 141803-02, left dp4; UCMP 141804, left dp4; UCMP 141825-01, right dp4; UCMP 141825-06, right dp4; UCMP 141825-11, left dp4; UCMP 141825-19, left dp4; UCMP 141828-07, left m3.

Measurements.— See Table 44.

Description.— A right dentary fragment (UCMP 141793) possesses a dp4 and an m3 with little wear to the occlusal surface of either tooth; the dp4 is fully erupted, whereas the m3 is not. Thus, it is not possible to determine the crown height of a permanent tooth for this specimen or whether the crown base was bulbous. The dentary is nearly complete anteriorly but is broken posterior to m3. The diastema is short and deep. The mental foramen occurs high on the diastema, below the level of the anteromost edge of the masseteric scar and well in front of the p4. The masseteric scar arises high on the diastema and below the anterior root of the dp4. It forms a broad shelf anterodorsally but terminates below the anterior alveolus of the m1 near the ventral surface of the dentary. There are numerous foramina on the lingual side of the dentary below the alveoli of the cheekteeth.

The incisor is flat lingually but convex labially. The distal end of the incisor occurs at the level of the tooth row. Enamel covers about 25% of the lingual surface, while on the labial side the enamel covers less than 50%. There is no ornamentation on the mesial surface. The following cheekteeth are not represented in this group: p4, m1, or m2.

The m3 possesses enamel that is thickest on the posterior wall of each lophid and thinner on the anterior wall. The presence of chevrons, crown height, and bulbousness are not evident for this tooth because it is not fully erupted. The anterolabial cingulid arises from the anteromedial surface of the protostylid and bends anterolingually, terminating along the anterolabial surface of the

protoconid well below its apex. The lophids join labially and centrally. Both unions of the lophids occur well below the occlusal surface at about the same dorsoventral height. Three cusps are present on the metalophid (metaconid, protoconid, and protostylid). The metaconid and protoconid join low on their respective bases, but the protostylid joins the protoconid high on the tooth crown. Of the cusps on the metalophid, the transversely elongated (anteroposteriorly compressed) metaconid and the oval-shaped protoconid are subequal in size, but the anteroposteriorly elongated protostylid is smaller than the former two cusps. The floor of the transverse valley is deep, narrow, open lingually, and closed labially.

In lingual view, the anterior and posterior walls of the metalophid projects anteriorly, but the anterior and posterior walls of the hypolophid are dorsoventrally straight. The transverse valley is narrow and V-shaped. The hypolophid has three cusps (entoconid, hypoconid, and hypostylid). The entoconid and hypocoonid are transversly aligned, but the hypostylid is more posteriorly placed. In addition, the apex of the hypostylid occurs well below the apex of the adjacent hypoconid. No cingulids are present on this tooth. The following cheekteeth are not represented in this group: p4, m1, and m2.

Comparison and *discussion* .— These teeth are not identifiable to the genus level because they are: isolated and incomplete; having worn occlusal surfaces; in being deciduous; or not associated with a p4 (the most diagnostic tooth for geomyoids; see Carrosco, 2000a, 2000b). Thus, there is insufficient

information on any of the above specimens to merit a taxonomic placement below the level of family.

The dp4s are triangular in shape and have a variable occlusal pattern. For example, the posterior cingulid may: occur across the entire posterior width of the tooth; or continue anteriorly around the base of the entoconid to join the posterior base of the metaconid; or be reduced such that it resembles an accessory cuspid. Typically, there are three principal cuspids (protoconid, entoconid, and hypoconid), a protostylid, and numerous accessory cuspids.

Family Geomyidae Bonaparte, 1845

Geomyinae Bonaparte, 1845

Genus *Mojavemys* Lindsay, 1972

Mojavemys cf. *M. magnumarcus* Barnosky, 1986

Plate 22 (G-L)

Locality.— Eastgate, UCMP V70140.

Age.—Barstovian.

Stratigraphic and biogeographic occurrence of the species.— late Barstovian: North Pilgrim 2, Colter Formation, Teton County, Wyoming (Barnosky, 1986a, b).

Referred specimens.— OMNH 54775, right m1 or m2; OMNH 54776, left m1 or m2; OMNH 54791, right M1 or M2; UCMP 141784, left maxilla fragment

with P4-M1; UCMP 141787-01, right P4.

Measurements.— See Table 44.

Description.— The P4 has a large oval-shaped protocone that is attached to the metaloph lingually. A small accessory cusp is present on the labial side of the protocone. With additional wear, the accessory cusp would be incorporated into the protocone and would not be identifiable. However, the anterolingual increase in the occlusal surface of the protocone with wear is identifiable because of the presence of the accessory cusp. The floor of the transverse valley is shallow, open labially, and closed lingually. The metaloph has three cusps: the metacone is anteroposteriorly compressed and transversely aligned with the anteroposteriorly elongated entostyle; and the circular-shaped hypocone occurs posterior to the former two cusps of the metaloph. A weak posterior cingulum arises on the posterolabial corner of the entostyle and extends labially to join the hypocone.

The M1 is wider than long, high crowned, and has straight-walled lophs. The anterior cingulum is distinct and arises on the anterolabial side of the paracone, extending to the anterolingual surface of the protostyle. The protoloph has three cusps. The paracone and protostyle are transversely aligned, but the protocone lies more posteriorly. The floor of the transverse valley is shallow, narrow, and open labially and lingually. The protoloph and metaloph are united low between the bases of the paracone and metacone, between the bases of the protocone and hypocone, and between the bases of the protostyle and entostyle.

The union of these two lophs occurs well below the occlusal surface and near the base of the tooth crown on the labial side. On the lingual side, the union of these two lophs occurs below the occlusal surface but about two-thirds of the way above the crown base. The metaloph has three cusps. The metacone and entostyle are transversely aligned, but the hypocone is placed slightly posterior to the other two cusps. The metaloph is noticeably narrower than the protoloph.

The m1 or m2 is much wider than long. In addition, it possesses the following characters: has enamel on the anterior wall is thinner than that of the posterior wall of each lophid; is not bulbous at the crown base (from a lingual view); is high crowned; possesses two roots that are as wide as the lophids and fused near the base of the tooth crown (fused high); and lacks chevrons. However, in OMNH 54776 the enamel-dentine junction lies above each root and forms an enamel arch at the crown base on both the lingual and labial sides of this tooth. Since the enamel arches occur above each root rather than centrally between the roots, I do not consider these attributes to be chevrons.

The anterolabial cingulid arises from the anteromedial surface of the protostylid and projects lingually at about 45° in an anterior direction until reaching a point anterior to a line transverse with the anteromost part of the protoconid, where it bends greater than 90° posterolingually to join the anterior surface of the protoconid below the occlusal surface. The lophids join labially and centrally at about the same point. Therefore, the labial and central union of the lophids would occur at the occlusal surface at about the same stage of wear.

The union of lophids occurs well below the occlusal surface. In late stages of wear, an enamel lake would form between all points where the lophids unite. Three cusps (metaconid, protoconid, and protostylid) occur on the metalophid and join, at their respective bases, well above the floor of the transverse valley.

Of the cusps on the metalophid, the transversely elongated metaconid is the largest, followed by a transversely elongated protoconid and an anteroposteriorly (or L-shaped) elongated protostylid. The metaconid and protoconid are transversely aligned, but the protostylid is placed more posteriorly than the former two cusps. The floor of the transverse valley is shallow, narrow, open lingually, and closed labially.

From a lingual view, the anterior and posterior walls of the metalophid project anteriorly, the anterior wall of the hypolophid projects posteriorly, and the posterior wall is straight. Thus, a narrow, V-shaped transverse valley is apparent. Another character that is revealed from the lingual view is that of a small re-entrant valley (OMNH 54776). This is the only Eastgate geomyoid with this character.

The hypolophid has three cusps (entoconid, hypoconid, and hypostylid). These cusps are transversly aligned and unite high on the tooth crown. Thus, with little additional wear to the occlusal surface these three cusps would merge into a single hypolophid leaving no trace of their morphological characteristics. No posterior cingulid is present on this tooth. There are no definite m2s or m3s known for this species from Eastgate.

Comparison.— Barnosky (1986a) recognized four species of *Mojavemys* (*M. lophatus*, *M. alexandrae*, *M. mascallensis*, and *M. magnumarcus*), whereas Korth (1994) considered *M. mascallensis* to be a heteromyid (*?Prodipodomys mascallensis*) as originally desribed by Downs (1956). The correct taxonomic placement of *?Prodipodomys mascallensis* is beyond the scope of this study; I follow Korth (1994) in recognizing three species of *Mojavemys*.

The *M.* cf. *M. magnumarcus* from Eastgate are the largest cheekteeth of geomyoids from the Eastgate localities. The identification of the Eastgate specimens to *M.* cf. *M. magnumarcus* is, in part, based on size, the occurrence of a short anterolabial cingulid on the lower molars, and a shallow transverse valley floor on the upper and lower molars. In addition, I have followed Lindsay (1972) and Barnosky (1986a) in differentiating *M.* cf. *M. magnumarcus* from the other species of *Mojavemys*. They differ in size, the P4s of *M.* cf. *M. magnumarcus* differ from those of *M. lophatus* in that the former is wider than long and smaller in overall size; the other characters (including the presence of an accessory cusp on the protocone) of the lophs are similar (see Lindsay, 1972; fig. 35b).

Mojavemys cf. *M. magnumarcus* differs in the following ways from other taxa: *M. alexandrae* in upper molars being smaller and not equally wide as long; *M. lophatus* in the M1 and M2 being much larger; *M. alexandrae* in the M1 being wider and upper molars being much larger; upper molars of *M. lophatus* and *M. alexandrae* in size and the M1 and M2 of in having a transversely narrower and

less lophate metaconid and the lophs being less anteroposteriorly compressed; , as well as in lower molars having a less distinct anterior cingulid (it traverses less than one-half the metalophid; see Barnosky, 1986a). There are no known p4s of *M.* cf. *M. magnumarcus* from Eastgate.

Discussion.— Until the current study, no accessory cusp had been reported on the protoloph for *Mojavemys*. The Eastgate specimens (UCMP 141784 and UCMP 141787-01) possess an accessory cusp on the labial side of the protocone. Based on *M. lophatus* (UCMP 78863) and *M. alexandrae* (UCMP 78155) figured in Lindsay (1972: fig. 35b), the anteroposteriorly elongated shape of the unworn and worn protocone, respectively, may provide evidence for the presence of an accessory cusp for *M. lophatus* and *M. alexandrae* (see Lindsay, 1972; Fig. 35b). Lindsay (1972) described these species as being typical for the genus, with no accessory cusps present on the protoloph. This now appears incorrect. *Mojavemys lophatus* (UCMP 78863) appears to have an accessory cusp, while *M. alexandrae* (UCMP 78155) has an anteroposteriorly protocone that is very elongated (i.e., more than one cusp present) but has heavy wear on the occlusal surface of the protocone, which may mask the earlier presence of an accessory cusp.

Based on the size and morphological characters described above of the Eastgate specimens, *M.* cf. *M. magnumarcus* may represent a new species. However, more complete material is needed to make a definative assessment.

Family Zapodidae Coues, 1875

Subfamily Sicistinae Allen, 1901

Genus *Macrognathomys* Hall, 1930

Macrognathomys shotwelli n. sp.

Plate 23 (M–Q)

Holotype.— UCMP, 141623, left dentary fragment with i1–m3.

Type locality.— UCMP V70140.

Etymology.— Named in honor of the late J. A. Shotwell, for his contributions on the Tertiary mammals of the Great Basin.

Localities.— Type and UCMP V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54730, right M2; OMNH 54885, left M2; OMNH 54900, left M2; OMNH 54901, right M2; OMNH 54902, left M2; OMNH 54903, left M2; OMNH 54904, right m2; UCMP 141602-12, right m2; UCMP 141603-01, right dentary fragment with i1–m1; UCMP 141603-02, left M1; UCMP 141603-03, left m1; UCMP 141603-04, right M2; UCMP 141603-05, left dentary fragment with m3; UCMP 141603-06, left dentary fragment with m3; UCMP 141603-7, left maxilla fragment with M1–M2; UCMP 141603-09, left dentary fragment with m1–m2; UCMP 141603-10, right M3; UCMP 141603-11,

right maxilla fragment with P4; UCMP 141603-13, right dentary fragment with m1; UCMP 141603-14, left dentary fragment with m1; UCMP 141603-15, left M1; UCMP 141603-16, left dentary fragment with m3; UCMP 141603-18, left m2; UCMP 141603-26, left m1; UCMP 141603-27, left m1; UCMP 141603-28, left m1; UCMP 141603-29, right M2; UCMP 141603-30, left M1; UCMP 141678-01, left M2; UCMP 141678-02, left m1; UCMP 141678-04, left M1.

Measurements.— See Tables 45 and 46.

Diagnosis.— *Macrognathomys shotwelli* is a small species of *Macrognathomys* that differs from all other small species (*M. gemmacollis* and *M.* sp.) in lacking a small accessory spur between the entoconid and posterior cingulid, and in having an accessory crest. *Macrognathomys shotwelli* is similar to *M. nanus* in having accessory cusps but is much smaller, but is most similar in size to *Macrognathomys*. sp. described by Shotwell (1968).

Description.— The upper cheekteeth increase in size from front to back. These teeth are low crowned and bulbous, and possessing three roots.

The P4 is a simple peg with a cingulum that circumscribes all but the anteromost part of the occlusal surface. The anterior margin is rounded, while the posterior margin is V-shaped. A high, conical-shaped cusp occurs at the center of the tooth. On the posterolingual margin of the cusp, a loph joins the cingulum posterolingually. Along the posterolabial margin of the cusp, a second loph joins the cingulum posterolabially. A deep, closed valley occurs between the lophs, cingulum, and cusp.

The M1 is longer than wide and the trigon is wider than the talon. The anterior, central, and posterior basins are deep. Four major cusps (protocone, paracone, hypocone, and metacone) are all anteroposteriorly compressed. The anterolabial basin is closed. The anterocone is small and occurs at the junction of the anterior cingulum and anterolophule. The labial arm of the anterior cingulum is distinct and reaches the anterolabial margin of the paracone. An anterolophule joins the lingualmost part of the protoloph (protolophule II; see Green, 1977a) lingual to the midline part of the tooth. The protoloph joins the paracone and protocone medially. The endoloph has anterior and posterior arms that are slightly bent and attached to the posterolabial and anterolabial margins of the protocone and hypocone, respectively. A small cone with two lophs is present along the endoloph (Green, 1977a) between the protoloph and the mesocone. One loph is directed labially and the other lingually, but neither reaches the lateral margins of the tooth. Midway between the un-named cone and the metalophule I (Green, 1977a) is a distinct mesocone. A distinct mesoloph arises from the mesocone and joins an anteroposteriorly elongated mesostyle at the labial margin of the tooth. The labial basin of the central basin is closed labially by the mesostyle; it opens lingually. The metaloph (metalophule II; Green, 1977) arises at the posterolingual margin of the hypocone and extends in a straight line posteriorly to join the hypoconule. The posterior cingulum arises from the labialmost part of the metaloph and at the hypoconule to form labial and lingual arms. The lingual arm is weak and does

not reach the lingual margin of the tooth, but the labial arm reaches the posteromedial margin of the metacone. The lingual posterior basin is open, while the posterior labial basin is closed. Two anteroposteriorly directed lophs occur on both the anterior and posterior surfaces of both the protocone and hypocone.

The M2 differs from the M1 in having a weak anterocone, having a short anterolophule, and lacking a lingual arm of the anterior cingulum, lacking a lingual loph between the protolophule II and the mesocone, and lacking a mesostyle. The posterior basin is anteroposteriorly elongated and divided by an anteroposteriorly directed loph midway along the posterior cingulum (this loph is present on M1 but does not join the posterior cingulum). There is an additional loph on the anterior and posterior surfaces of the protocone (the anterior loph joins the protocone and the labial arm of the anterior cingulum).

The M3 differs from the preceding molars in being anteroposteriorly longer. The mesoloph, mesostyle, and accessory lophs are lacking. The posterior cingulum is reduced.

The ventral surface of the dentary is convex. The diastema is long and deep. A distinct mental foramen occurs high on the diastema, with the dorsalmost part of the foramen below the anteromost part of the masseteric scar and anteroventral to the m1. The mental foramen opens anterodorsally. The masseteric scar terminates below the posterior root of the m1. A weak ventral shelf is present on the masseteric scar and grades ventrally, while the dorsal

shelf is lacking. Although all but the ascending ramus is missing, the proximalmost part of the ascending ramus appears to arise lateral to the posterior part of the m2.

The lower cheekteeth are low crowned and slightly bulbous at the crown bases; each possess two large roots (anterior and posterior). The m2 is the largest tooth followed in size by the m1; the m3 is the smallest.

The incisor is flat lingually and has little enamel present. Labially the tooth is V-shaped and enamel covers about one-half of the surface. In cross section the tooth is subtriangular.

The m1 is longer than wide, and the trigonid is equal in width to the talonid. The anterior, middle, and posterior basins are deep. The anterior and central basins are open labially, whereas the central and posterior basins are closed lingually. The anterior basin is open lingually. The anteroconid occurs along the midline of the tooth. The anterior cingulid is absent. A distinct anterolophulid (anterior extension of the ectolophid; Green, 1977a) joins the anteroconid to the middle of the metalophulid II (Green, 1977a). The metalophulid II arises at the proximalmost part of the anterolophulid and joins the labial margin of the metaconid. The anterior and posterior arms of the ectolophid are bent and attached to the posterolingual and anterolingual margins of the protoconid and hypoconid, respectively. A mesoconid is present; it gives risealong the lingual margin to a distinct mesolophid that extends lingually to join a mesostylid at the lingual margin of the tooth. An unnamed lophid joins the

posterolabial margin of the metaconid to the mesostylid. A hypolophulid I joins the hypoconid and entoconid anteriorly. A hypoconulid is present. The posterior cingulid attaches to the posterolingual margin of the hypoconid and bows slightly posteriorly as it extends lingually; it ends at the posteromedial margin of the entoconid. The posterior basin is closed lingually.

The m2 is anteroposteriorly longer than the m1. The former has a reduced anteroconid. The labial arm of the anterior cingulid is present. Two unnamed lophids join the hypolophulid I and the posterior cingulid. The posterolingual corner of the tooth is rounded.

Unlike the m2, the m3 differs in having a distinct anteroconid, and having labial and lingual arms of the anterior cingulid. An unnamed lophid lies between the protocone and the mesolophid, not reaching the mesostylid. The mesostylid is reduced, and the hypoconid is absent.

Comparison and discussion.— Green (1972) synonomyzed *Schaubeumys* with *Plesiosminthus*, an action questioned by Engesser (1979). Korth (1980) provided six characteristics of the upper and lower cheekteeth that aid in separating *Schaubeumys* from *Plesiosminthus*. In 1987, Korth described a new species of *Schaubeumys*. However, Green (1992) again indicated he did not believe *Schaubeumys* and *Plesiosminthus* warranted separation. Later, Korth (1994) established a strong argument to retain the separation of *Schaubeumys* from *Plesiosminthus*.

Korth (1994) listed four species of zapodids that occurred in North

America during the Barstovian: *S. cartomylos* from the Valentine Formation, Nebraska, South Dakota, and the Wood Mountain Formation, Saskatchewan (Korth, 1987); *M. gemacollis* from the Valentine Formation, Bijou Hill, Glenn Olson Quarry (Green, 1977b); and *M. tiheni* and *M. gladiofex* from the Valentine Formation, Norden Bridge Quarry, Nebraska and the Valentine Formation, Feyereisen Gap, Springer local fauna, South Dakota (Klingener, 1966; Green, 1977a). Another Barstovian species of zapodid from the Quartz Basin fauna in Malheur County, Oregon was described by Shotwell (1968) as *Macrognathomys* sp.

The Eastgate specimens are much smaller than most species belonging to *Megasminthus* or *Schaubeumys*, and they differ in morphological characters as well. Although the only species of *Plesiosminthus* (*P. clivosus*) listed by Korth (1994) occurred at an earlier time (Arikareean), it is similar in size to the Eastgate zapodids but differs in several characters; namely, the ectolophid of the m1 do not join the metalophulid II, and the lack of accessory lophids.

Based on size and characters of the occlusal surface, *M.shotwelli* is similar in size to *M. gemmacollis* and *Macrognathomys*. sp. from the Quartz Basin fauna. The m1 of *M. shotwelli* differs from the m1 of *M. gemmacollis* and *Macrognthomys* sp. in that *M. shotwelli* lacks a small accessory spur between the entoconid and posterior cingulid, and in having accessory crests. It also differs in size from *M.nanus* (the largest species) from the Clarendonian of Nevada (Hall, 1930). However, they are similar in having accessory crests. The

m2 of *M. shotwelli* differs from *M.* nanus, in having a trigonid and talonid that are similar in width to each other.

The only other cheekteeth that can be compared are the P4 and M1 of *Macrognathomys* sp. The P4 and M1 of *M. shotwelli* differ from those of *Macrognathomys* sp. in having: a distinct but small anterocone; a short anterolophule; an accessory loph that extends lingually and labially and between the protolophule II and the mesocone; accessory lophs on the anterior and posterior surfaces of the protocone and hypocone; and a metalophule I that joins the metacone to the hypocone. These cheekteeth of *M. shotwelli* differ from those of *Macrognathomys* sp. in lacking a short cingulum that unites the mesostyle and paracone, a bifurcated metaloph that joins the metacone, and a pair of short accessory lophs that join the metacone.

Family Cricetidae Rochebrune, 1883

Subfamily Sigmodontinae Wagner, 1843

Tribe Peromyscini Hershkovitz (1966)

Genus *Copemys* Wood, 1936

Copemys tenuis Lindsay, 1972

Plate 24 (A–F)

Localities.— Eastgate, OMNH V974, V976; UCMP V70138, V70140, V70142, V70147, and V74103.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Barstow Formation, San Bernardino County, California (Lindsay, 1972).

Referred specimens.— OMNH 54372, left m2; OMNH 54375, left M3; OMNH 54378, left M3; OMNH 54382, right m2; OMNH 54385, right M1; OMNH 54389, right maxilla fragment with M1-M3; OMNH 54392, left maxilla fragment with M1; OMNH 54395, left m3; OMNH 54397, left M3; OMNH 54398, left m3; OMNH 54401, left m3; OMNH 54404, left m3; OMNH 54409, right m1; OMNH 54415, left m1; OMNH 54417, right M2; OMNH 54420, left m2; OMNH 54422, left m2; OMNH 54423, left m1; OMNH 54424, right m3; OMNH 54426, left m2; OMNH 54427, left dentary fragment with m1; OMNH 54430, right m3; OMNH 54431, left m2; OMNH 54433, left m2; OMNH 54435, left dentary fragment with m1-m2; OMNH 54436, right maxilla fragment with M1-M2; OMNH 54439, right dentary fragment with i1, m1; OMNH 54442, right M2; OMNH 54443, left M1; OMNH 54445, right M1; OMNH 54446, right m3; OMNH 54448, left M1; OMNH 54449, left m2; OMNH 54450, right m2; OMNH 54451, left m2; OMNH 54460, left dentary fragment with m1-m2; OMNH 54461, left M3; OMNH 54465, right m2; OMNH 54467, left m3; OMNH 54468, left M2; OMNH 54476, left M2; OMNH 54480, left m2; OMNH 54492, right M1; OMNH 54493, left m1; OMNH 54498, right m2; OMNH 54500, left M1; OMNH 54503, left m2; OMNH 54506, right m2; OMNH 54510, left m1; OMNH 54511, right m1; OMNH 54512, left m1; OMNH 54513, right maxilla M2; OMNH 54516, left M3; OMNH 54517, left M1;

OMNH 54519, left m2; OMNH 54520, right M2; OMNH 54529, right dentary fragment with i1, m1; UCMP 141605-14, right maxilla fragment with M1-M2; UCMP 141609-07, right maxilla fragment with M1; UCMP 141609-09, left M3; UCMP 141675-02, right maxilla fragment with M1-M2; UCMP 141675-003, right M1; UCMP 141675-04, left M1; UCMP 141678-03, left m3; UCMP 141721, right dentary fragment with m1; UCMP 141724, right dentary fragment with m3; UCMP 141728, right dentary fragment with i1, m1-m2; UCMP 141730, left maxilla fragment with M1-M3; UCMP 141731, right maxilla fragment with M1-M3; UCMP 141733-01, left dentary fragment with m1-m3; UCMP 141738-01, left dentary fragment with i1, m1-m3; UCMP 141739, left dentary fragment with m1-m3; UCMP 141742-03, left m1; UCMP 141742-04, left m1; UCMP 141746-01, right dentary fragment with i1, m1-m3; UCMP 141748-01, left maxilla fragment with M1; UCMP 141748-02, right dentary fragment with m1; UCMP 141748-03, left dentary fragment with i1, m1-m3; UCMP 141760-04, left m1; UCMP 141760-05, left m2; UCMP 141760-07, left m3; UCMP 141760-10, left M1; UCMP 141760-12, right M1; UCMP 141765-01, right dentary fragment with m1; UCMP 141766-02, right dentary fragment with m1-m2; UCMP 141767-02, left dentary fragment with m1; UCMP 141767-05, left dentary fragment with m1-m2; UCMP 141767-06, right dentary fragment with m1-m2; UCMP 141767-07, right dentary fragment with m3; UCMP 141767-08, m2; UCMP 141767-12, right dentary fragment with m1-m3; UCMP 141767-13, right dentary fragment with m1-m2; UCMP 141767-15, left dentary fragment with

m1-m3; UCMP 141767-17, right dentary fragment with i1, m1, m3; UCMP 141767-21, left dentary fragment with i1, m1-m3; UCMP 141767-22, left dentary fragment with m2-m3; UCMP 141767-24, right dentary fragment with m1-m3; UCMP 141767-25 , left dentary fragment with m2-m3; UCMP 141767-28, right dentary fragment with m2; UCMP 141767-030, left dentary fragment with m1, m3; UCMP 141775-04, left dentary fragment with m1, m3; UCMP 141777-03, right maxilla fragment with M1, M3; UCMP 141777-04, right maxilla fragment with M1-M2; UCMP 141777-05, right maxilla fragment with M2; UCMP 141777-15, right maxilla fragment with M1-M3; UCMP 141777-16, right M1; UCMP 141777-19, left maxilla fragment with M1-M2; UCMP 141777-20, left maxilla fragment with M1-M3; UCMP 141777-25, right maxilla fragment with M1-M2; UCMP 141777-34, left maxilla fragment with M1-M3; UCMP 141843-01, left M1; UCMP 141843-02, right M1; UCMP 141843-04, right M1; UCMP 141843-08, right M1; UCMP 141843-10, right M1; UCMP 141843-13, left M1; UCMP 141843-16, left M1; UCMP 141843-21, left M1; UCMP 141843-22, right M1; UCMP 141843-29, left m2; UCMP 141843-32, left m2; UCMP 141843-33, left m2; UCMP 141843-34, left m2; UCMP 141843-38, right m2; UCMP 141843-39, left m1; UCMP 141843-41, left m3; UCMP 141843-43, left m1; UCMP 141843-45, left M2; UCMP 141843-46, right m3; UCMP 141843-47, right m3; UCMP 141843-49, right m1; UCMP 141843-52, left m2; UCMP 141843-53, left M3; UCMP 141843-57, right M3; UCMP 141843-58, left m2; UCMP 141843-59, right m2; UCMP 141843-61, left m2; UCMP 141843-63, right m2;

UCMP 141843-65, left m2; UCMP 141843-67, right m2; UCMP 141843-72, right m3; UCMP 141843-73, right M1; UCMP 141843-74, left M1; UCMP 141843-80, left M3; UCMP 141843-81, left m3; UCMP 141843-83, left left m3; UCMP 141843-84, right m2; UCMP 141843-89, left m1; UCMP 141843-90, left m3; UCMP 141843-96, left m3; UCMP 141843-98, right m2; UCMP 141843-102, right m2; UCMP 141843-105, left m2; UCMP 141843-109, right m2; UCMP 141843-110, right m2; UCMP 141843-111, right m2; UCMP 141843-116, left m3; UCMP 141843-119, left m1; UCMP 141843-121, right m2; UCMP 141843-122, right m1; UCMP 141843-124, right m2; UCMP 141843-126, left M3; UCMP 141843-127, left m2; UCMP 141843-128, left m2; UCMP 141843-132, right m1; UCMP 141843-133, right m2; UCMP 141843-139, left m3; UCMP 141843-142, right M1; UCMP 141843-144, right m3; UCMP 141843-145, right m2; UCMP 141843-154, right m2; UCMP 141843-162, left m3; UCMP 141843-165, left m2; UCMP 141843-166, right m2; UCMP 141843-167, right M3; UCMP 141843-178, left M2; UCMP 141843-180, left m3; UCMP 141895-002, right m1; UCMP 141895-04, right m1; UCMP 141895-05, left m1; UCMP 141895-07, right m1; UCMP 141895-09, right m1; UCMP 141895-10, right m1; UCMP 141895-11, left m1; UCMP 141895-12, right m1; UCMP 141895-13, right m1; UCMP 141895-15, right m1; UCMP 141895-16, left m1; UCMP 141895-18, left m1; UCMP 141895-19, right m1; UCMP 141895-20, left m1; UCMP 141895-21, left m1; UCMP 141895-22, left m1; UCMP 141895-23, left m1; UCMP 141895-24, left m1; UCMP 141895-25, left m1; UCMP 141895-32, right m1; UCMP 141914, right

dentary fragment with i1, m1-m2.

Measurements.— See Tables 47-50.

Description.— The upper cheekteeth decrease in size from front to back. They are low crowned and bulbous, possessing three roots.

The M1 is longer than wide, and the trigon is slightly wider than the talon. The four principal cusps are subequal in size; the anterior, central, and posterior basins are deep. The anterolabial basin is closed. The anterocone is asymmetrical and appears weakly bilobed where the anterolophule joins the anterocone. A labially bent anterolophule joins the protocone high and along the central part of the anterocone. A distinct paralophule is present, but a parastyle is lacking. The protolophule I is variable (absent to distinct). If present, it joins the anterolingual margin of the paracone with the proximalmost part of the anterolophule. In addtion, the protolophule II is present and arises at the posterolingual margin of the paracone, attaching near the center of the ectoloph. The ectoloph has anterior and posterior arms that are bent and attach to the posterolabial and anterolabial margins of the protocone and hypocone, respectively. A distinct mesoloph is present and usually reaches the lingual margin of the tooth. A mesostyle is usually absent. The labial part of the central basin is open. An enterostyle is usually absent, and thus the lingual part of the central basin is typically open. The metalophule I is absent, but the metalophule II is distinct. The posterior cingulum attaches to the posterolabial margin of the hypocone and is anteroposteriorly narrow as it extends labially and attaches to

the posteromedial margin of the metacone. The posterior basin is open lingually.

The M2 differs from the M1 in that the M2 has an anterocone that is greatly reduced. It also differs from that of the M1 in having a short anterolophule and enterostyle always present.

The M3 differs from the M2 in that the M3 is reduced in overall size and triangular in occlusal outline. In addition, the M3 differs from the M2 in having the metacone and hypocone that are greatly reduced.

The ventral surface of the dentary is slightly convex ventrally and the diastema is long and shallow. A distinct mental foramen occurs high on the diastema, with the dorsalmost part of the foramen level with the anteromost part of the masseteric scar. The mental foramen lies anteroventrally below the m1 and opens anterodorsally. The masseteric scar terminates below the anterior root of m1. Posterior to its distal end, the masseteric scar forms a strong ventral shelf that grades ventrally with the ramus; the dorsal shelf is weak. The ascending ramus arises lateral to the posterior part of m2. On the lingual surface of the dentary, several small foramina are present.

The lower cheekteeth decrease in size from front to back. They are high crowned and slightly bulbous at the base of the tooth crown; each has two large roots (anterior and posterior).

The tip of the incisor lies above the level of the tooth row. It is rounded labially with little enamel present on the medial surface. On the laterial side of the incisor, about one-third of the surface area is covered with enamel. In cross

section, the tooth is oblong.

The m1 is longer than wide, and the trigonid is slighlty narrower than the talonid. The four principal cusps are subequal in size; the anterior, middle, and posterior basins are deep. The anterior and central basins are open laterally, while the posterior basin is closed. The anteroconid occurs centrally (central along the midline of the anteromost part of the tooth) with a strong anterior cingulid present on the labial side of the anteroconid, as is a weak metalophulid (name assigned herein to the lingual shelf that extends from the lingualmost part of the anteroconid and joins the anterior margin of the metaconid). The presence of the anterior cingulid and metalophulid provides for a symmetrical appearance of the anteroconid. The anterior cingulid attaches low to the anteromedial base of the protoconid, but the anterolabial valley is open labially. The metalophulid is submerged within the anteroconid and does not reach the metaconid. A deep, narrow valley separates the anteroconid and metaconid; and thus this basin is open lingually. A distinct, high anterolophulid (= anterior mure; James, 1963) attaches to the middle of the metalophid (= metalophule I; Lindsay, 1972). The metalophid arises at the proximalmost part of the anterolophid and joins the labial margin of the metaconid. The anterior arm (= posterior arm of protoconid; Sutton and Korth, 1995) and posterior arm (= anterior arm of hypoconid; Sutton and Korth, 1995) of the ectolophulid (= central mure; James, 1963) are bent and attached to the posterolingual and anterolingual margins of the protoconid and hypoconid, respectively. A

mesoconid is absent, whereas a mesolophid lies at the center of the ectolophulid and extends in a straight line to the lingual margin of the tooth. The mesostylid is lacking. Along the labial margin of the central basin, an ectostylid is present and closes this basin labially. An ectolophid is absent. A hypolophid joins the hypoconid and entoconid anteriorly. A hypoconulid is lacking. The posterior cingulid attaches to the posterolingual margin of the hypoconid, bows strongly posteriorly as it extends lingually, and ends before reaching the posteromedial margin of the entoconid. The posterior basin is open lingually.

The m2 differs from the m1 in that the m2 has a trigonid and talonid that are equal in width; being wider but shorter; lacking an anteroconid; lacking a distinct lingual arm of the anterior cingulid. The mesolophid attaches near the posterolingual margin of the metaconid and is weak. The ectostylid of the central basin is weak and does not close the central basin on the labial margin. A lophid attaches to the posterolabial margin of the entoconid and extends posteriorly, where it attaches to the labialmost part of the posterior cingulid.

The m3 differs from the m2 in having a trigonid that is much wider than the talonid. The lingual arm of the anterior cingulid is more distinct. The mesolophid is weak and does not reach the lingual margin of the tooth; the central basin is closed lingually by a mesostylid. The entoconid is greatly reduced. The posterior cingulid attaches high on the posteromedial margin of the entoconid, and the posterior basin is closed lingually.

Comparison.— Korth (1994) lists seven species of *Copemys* that occurred

in North America during the Barstovian: *C. loxodon*, *C. longidens*, *C. niobrariensis*, *C. russelli*, *C. pagei*, *C. tenuis*, and *C. barstowensis*. Most of the species of *Copemys* overlap in the sizes of the upper and lower cheekteeth; specimens of *Copemys* from Eastgate are no exception. However, the lengths of the M1/1 differ between the species (see Figs. 19 and 20). Therefore, characters of the occlusal surface, and length rather than width, form the main basis for species identifications.

The M1 and m1 are the most frequently used tooth loci for species identifications of *Copemys* and other cricetid rodents. These are known for all species of *Copemys* from Eastgate. Lindsay (1972) indicated that *C. niobrariensis* is very similar to *C. longidens* and that the two are likely synonymous. *Copemys pagei* is smaller than any of the Eastgate specimens, and thus is not represented at Eastgate.

Copemys tenuis is similar in size to *C. longidens*, *C. russelli*, and *C. barstowensis*. *Copemys tenuis* differs from *C. longidens* in having: an M1 that is asymmetrical and bilobed anterocone; a labially bent anterolophule that joins the anterocone centrally; a distinct paralophule; a distinct mesoloph that reaches the lingual margin of the tooth. It also differs in that a mesostyle that is usually absent; it lacks a metalophule I, but a metalophule II is present. For the m1, *C. tenuis* differs from *C. longidens* in having an anteroconid that occurs centrally, a deep, narrow valley that separates the anteroconid from the metaconid, a weak metalophulid, a metalophid, and a mesolophid that reaches the lingual margin of

the tooth. It lacks a mesostylid and an ectostylid.

The M1 of *C. tenuis* differs from that of *C. russelli* in having an anterocone that occurs centrally, a protocone and paracone that are subequal, a distinct paralophule, and a distinct protolophule I usually present, in contrast, it lacks a protolophule II or a mesostyle (usually). For the m1, *C. tenuis* differs from *C. russelli* in having: an anteroconid and anteropholulid that occur centrally; a metalophulid; and a deep, narrow valley that separates the anteroconid from the metaconid. It lacks an ectolophid.

The M1 of *C. tenuis* differs from that of *C. barstowensis* in having an asymmetrical anterocone that appears to be bilobed, an anterolophule that joins the anterocone along the midline part of the tooth, a distinct paralophule, a protolophule I, and a distinct mesoloph that reaches the lingual margin of the tooth; it usually lacks a mesostyle. For the m1, *C. tenuis* differs from *C. barstowensis* in having: an anterolophulid that joins the middle of a distinct metalophid; and a deep, narrow valley that separates the anteroconid from the metaconid. It lacks an ectolophid or ectostylid. as well as a labial arm of the posterior cingulid.

Copemys tenuis from Eastgate possess a bilobed anterioconid on the m1 and is the only Barstovian species of *Copemys* to have this character. One species of *Copemys* (*C. esmeraldensis*) from the Clarendonian does have a bilobed anteroconid on the m1 (Lindsay, 1972).

Discussion.— In addition to size, Shotwell (1967b) examined variation of

the occlusal morphology for the upper and lower cheekteeth of *Copemys*. He found that for the upper cheekteeth, the paralophule-parastyle was limited in its complexity relative to the mesoloph-mesostyle. In contrast to the upper cheekteeth, the ectolopihd-ectostylid showed limited complexity on the lower cheekteeth. Therefore, the paralophule-parastyle of the upper cheekteeth and the ectolophid-ectostylid of the lower cheekteeth may prove more useful for species identifications than the more variable mesoloph (id)-mesostyle (id) complex of the upper and lower cheekteeth. These and other characters were used to identify the species of *Copemys* at Eastgate. A re-examination of interspecific and intraspecific variation of tooth morphology for this genus using multivariant techniques (Smith, 2002) would likely be informative, but is beyond the scope of the present study.

Copemys russelli James, 1963

Plate 24 (G-L)

Localities.— Eastgate, OMNH V974, V976; UCMP V70138, V70140, V70142, and V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Barstow Formation, San Bernardino County, California (Lindsay, 1972); Clarendonian: Matthews Ranch and Nettle Spring faunas, Caliente Formation,

Ventura County, California (James, 1963).

Referred specimens.— OMNH 54374, right m1; OMNH 54376, left m3; OMNH 54377, left M1; OMNH 54379, left M3; OMNH 54380, left m1; OMNH 54394, left M3; OMNH 54414, right dentary fragment with i1, m1–m3; OMNH 54428, right M3; OMNH 54429, right M3; OMNH 54441, left m1; OMNH 54453, left M3; OMNH 54455, left M1; OMNH 54462, right M2; OMNH 54466, left M2; OMNH 54469, right m3; OMNH 54479, left M3; OMNH 54481, left m1; OMNH 54491, right m1; OMNH 54497, right m1; OMNH 54507, right m1; OMNH 54518, right M3; OMNH 54522, left maxilla fragment with M3; UCMP 141541, right M2; UCMP 141605-12, left maxilla fragment with M2–M3; UCMP 141605-22, left dentary fragment with i1, m1–m3; UCMP 141609-10, left M2; UCMP 141675-01, right dentary fragment with m1–m2; UCMP 141675-10, left M1; UCMP 141675-12, right M3; UCMP 141678-07, left M3; UCMP 141727, right dentary fragment with m1, m3; UCMP 141729, left M2; UCMP 141738-02, right m2; UCMP 141742-02, left M2; UCMP 141744, right dentary fragment with i1, m1–m3; UCMP 141745, left dentary fragment with i1, m1–m3; UCMP 141760-09, right M2; UCMP 141767-09, right dentary fragment with m1–m3; UCMP 141767-11, left dentary fragment with m2–m3; UCMP 141767-29, left dentary fragment with m3; UCMP 141777-07, left maxilla fragment with M1–M2; UCMP 141777-26, right maxilla fragment with M1–M2; UCMP 141777-31, right maxilla fragment with M2–M3; UCMP 141777-33, left maxilla fragment with M2–M3; UCMP 141783-176, left maxilla fragment with M2–M3; UCMP

141843-06, left M1; UCMP 141843-07, right M1; UCMP 141843-09, right M1; UCMP 141843-11, left M1; UCMP 141843-12, left M1; UCMP 141843-14, right M1; UCMP 141843-15, right M1; UCMP 141843-20, right M1; UCMP 141843-24, right M1; UCMP 141843-31, right M2; UCMP 141843-51, right m3; UCMP 141843-71, left m2; UCMP 141843-76, right M1; UCMP 141843-77, right M1; UCMP 141843-79, right M1; UCMP 141843-82, left M2; UCMP 141843-94, left m3; UCMP 141843-97, right m2; UCMP 141843-99, left m2; UCMP 141843-101, left m2; UCMP 141843-103, left M2; UCMP 141843-108, ritght M2; UCMP 141843-114, right M3; UCMP 141843-124, left M2; UCMP 141843-125, left m2; UCMP 141843-140, left m2; UCMP 141843-146, right m2; UCMP 141843-170, right m3; UCMP 141843-172, right M2; UCMP 141843-37, left m2; UCMP 141851, right dentary fragment with m1; UCMP 141854-01, right dentary fragment with m1, m3; UCMP 141895-08, left m1; UCMP 141895-27, right m1; UCMP 141895-30, left m1; UCMP 141895-33, right m1; UCMP 141910, left dentary fragment with m1-m3.

Measurements.— See Tables 47-50.

Description.— The upper cheekteeth decrease in size from front to back, being low crowned and bulbous. The M1 is longer than wide, the trigon is equal in width to the talon, and the protocone is the largest of the four principal cusps. The anterior, central, and posterior basins are deep. The anterocone is symmetrical and is weakly bilobed. An anterolophule joins the protocone high and lingual to the center (=subcentral; Lindsay, 1972) of the anterocone between

the two cusps of the anterocone. A paralophule is absent, but an anteroposteriorly elongated parastyle is present, partially closing the anterolabial part of the anterior basin. The protolophule I is absent, while the protolophule II is present and joins the paracone and protocone medially and posteriorly, respectively. The ectoloph has anterior and posterior arms that are bent and attached to the posterolabial and anterolabial margins of the protocone and hypocone, respectively. A weak mesoloph is present but does not reach the lingual margin of the tooth. The mesostyle is absent. The labial side of the central basin is open labially. An enterostyle is usually absent, thus, the lingual side of the central basin is usually open lingually. The metalophule I is absent, whereas a weak metalophule II is present. The posterior cingulum attaches to the posterolabial margin of the hypocone and is anteroposteriorly narrow as it extends labially and attaches to the posteromedial margin of the metacone. The posterior basin is closed lingually.

The M2 differs from the M1 in having an anterocone that is greatly reduced. It also differs from the M1 in having an anterolophule that is short, having a distinct protolophule I, and having a distinct metalophule II. In addition, the M2 differs from the M1 in lacking an enterostyle.

The M3 differs from the M2 in that the M3 is reduced in overall size and is triangular in occlusal outline. It also differs from the M2 in having a mesostyle. In addition, the M3 differs from the M2 in lacking a paralophule, lacking a parastyle, and lacking a mesoloph.

The ventral surface of the dentary is slightly convex. The diastema is long and shallow. A distinct mental foramen occurs high on the diastema with the dorsalmost part of the foramen occurring above the anteromost part of the masseteric scar and anteroventrally below the m1; it opens anterodorsally. The masseteric scar terminates below the middle part of the m1. Posterior to its distal end the masseteric scar forms a weak ventral shelf that grades ventrally with the ramus, but the dorsal shelf is lacking. The ascending ramus arises lateral to the posterior part of the m2. Several small foramina are present on the lingual surface of the dentary.

In general, the lower cheekteeth are high crowned and slightly bulbous at the base of the tooth crown, and has two large roots (anterior and posterior roots). The lower cheekteeth decrease in size from front to back.

The incisor has a rounded labial surface and a flattened lingual surface. Enamel is present on the medial surface, but only about one-half of the labial side of the tooth is covered with enamel; in cross section, the tooth is oblong.

The m1 is longer than wide, and the trigonid is slightly narrower than the talonid. The anterior, middle, and posterior basins are deep. The anterior and central basins are open lingually and labially, whereas the posterior basin is only open lingually. The anteroconid occurs subcentral and is symmetrical. It has a distinct anterior cingulid and no metalophulid, and thus the anterolingual basin opens lingually. The anterior cingulid attaches low to the anterolabial base of the protoconid, but the anterolabial valley is open labially. A deep, narrow valley

separates the anteroconid and metaconid, and such that this basin opens lingually. A weak, low anterolophulid attaches to the middle part of the metalophid. The metalophid arises at the proximalmost part of the anterolophulid and joins the labial margin of the metaconid. The anterior and posterior arms of the ectolophulid are bent and attached to the posterolingual and anterolingual margins of the protoconid and hypoconid, respectively. A mesoconid is absent, while a distinct mesolophid lies at the center of the ectolophulid extending in a transverse line to the lingual margin of the tooth. The mesostylid is absent. An ectolophid is present (few specimens have a distinct ectolophid, while others of this species have a weak ectolophid); an ectostylid is lacking. A hypolophid joins the hypoconid and entoconid anteriorly. A hypoconulid is absent. The posterior cingulid attaches to the posterolingual margin of the hypoconid and bows slightly posteriorly as it extends lingually; it ends before reaching the posteromedial margin of the entoconid. The posterior basin is open lingually.

The m2 differs from the m1 in the following: being wider but shorter, and having a trigonid and talonid that are equal in width. It differs from the m1 in having a weak metalophulid and a mesolophid that attaches near the posterolingual margin of the metaconid, having a hypoconulid, and having a weak labial arm of the posterior cingulid. The m2 also differs from the m1 in lacking an anteroconid.

The m3 differs from the m2 in having: a trigonid that is wider than the

talonid, and a more distinct metalophulid, a central basin that is closed lingually by a distinct mesostylid, and having a greatly reduced entoconid. Unlike the m2, the posterior cingulid of the m3 attaches high on the posteromedial margin of the entoconid and the posterior basin is closed lingually. The m3 differs from the m2 in lacking the labial arm of the metalophid.

Comparison and discussion.— *Copemys russelli* is similar in size to *C. longidens*, *C. tenuis*, and *C. barstowensis* (Figs. 19 and 20). However, *C. russelli* differs in several characters of the upper and lower cheekteeth from other Barstovian-age species of *Copemys*: differs from *C. longidens* in having a symmetrical and a weakly bilobed anterocone, and a weak mesoloph, whereas lacking a protolophule I, a mesostyle, an enterostyle, and a metalophule I; differs from *C. longidens* in having a deep, narrow valley that separates the anteroconid from the metaconid, a metalophid, a distinct mesolophid that reaches the lingual margin of the tooth, and an ectolophid, while lacking a mesostylid and an ectostylid.

The M1 of *C. russelli* differs from that of *C. barstowensis* in having a symmetrical and weakly bilobed anterocone, an anterolophule that joins the anterocone subcentrally, a parastyle, and a distinct mesoloph that reaches the lingual margin of the tooth. It lacks a protolophule I and a mesostyle. Also for the m1, *C. russelli* has an anteroconid that lies lingual to the midline of the tooth (rather than centrally); an anterolophulid that joins the center of the metalophid; a deep, narrow valley that separates the anteroconid from the metaconid; and a

weak metalophid that joins along the anterior margins of the metaconid and protoconid.

Copemys tyleri n. sp.

Plate 25 (A-F)

Holotype.— OMNH 54371, right dentary fragment with m1-m3.

Type locality.— OMNH V974.

Etymology.— Named in honor of Jack D. Tyler, who introduced me to the study of vertebrates and encouraged me to pursue my graduate degrees.

Other localities.— Eastgate: UCMP V67245, V70138, V70140, V70142, and V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54370, left dentary fragment with m2; OMNH 54373, left m2; OMNH 54383, right m2; OMNH 54386, right maxilla fragment with M2; OMNH 54391, right dentary fragment with m3; OMNH 54399, left M3; OMNH 54403, left m3; OMNH 54405, left M2; OMNH 54411, right dentary fragment with m1; OMNH 54412, right dentary fragment with i1, m3; OMNH 54413, right dentary fragment with i1, m1, m3; OMNH 54419, left M2; OMNH 54432, right m3; OMNH 54437, right dentary fragment with i1-m2; OMNH

54452, left M2; OMNH 54454, left m1; OMNH 54464, right M1; OMNH 54472, right M2; OMNH 54490, right M2; OMNH 54495, left M2; OMNH 54496, left M1; OMNH 54499, right M2; OMNH 54502, left maxilla fragment with M2-M3; OMNH 54505, left M2; OMNH 54508, left maxilla fragment with M2; OMNH 54509, right M2; OMNH 54521, left M2; OMNH 54526, left M3; OMNH 54530, right maxilla fragment with M2-M3; OMNH 54889, left m2; OMNH 54905, right maxilla fragment with M1-M3; UCMP 141605-02, right dentary fragment with m3; UCMP 141605-15, left maxilla fragment with M1-M2; UCMP 141605-21, right maxilla fragment with M2-M3; UCMP 141609-02, left m1; UCMP 141609-03, left maxilla fragment with M2; UCMP 141609-11, right M2; UCMP 141675-07, right M3; UCMP 141726, left maxilla fragment with M2-M3; UCMP 141746-03, left dentary fragment with m1-m3; UCMP 141746-05, right maxilla fragment with M1-M2; UCMP 141757-02, right maxilla fragment with M1-M2; UCMP 141766-01, right dentary fragment with m2-m3; UCMP 141766-03, left maxilla fragment with M1-M2; UCMP 141766-04, right dentary fragment with m1; UCMP 141767-04, dentary fragment with m2; UCMP 141767-14, right dentary fragment with m1-m3; UCMP 141767-16, left dentary fragment with i1, m1-m3; UCMP 141767-19, right dentary fragment with i1, m1-m2; UCMP 141767-20, right dentary fragment with i1, m1; UCMP 141767-23, right dentary fragment with m1-m3; UCMP 141767-26, right dentary fragment with i1, m1; UCMP 141767-27, left dentary fragment with i1, m1-m3 UCMP 141775-01, left maxilla fragment with M2; UCMP 141775-05, right M1; UCMP 141776, skull with right

and left maxillae with M1–M3; UCMP 141777-09, right maxilla fragment with M1–M3; UCMP 141777-10, right M1; UCMP 141777-11, right maxilla fragment with M2; UCMP 141777-14, right maxilla fragment with M1–M2; UCMP 141777-21, right maxilla fragment with M1–M2; UCMP 141777-23, right maxilla fragment with M1–M3; UCMP 141777-24, right maxilla fragment with M3; UCMP 141777-27, left maxilla fragment with M1–M2; UCMP 141777-28, right maxilla fragment with M1–M2; UCMP 141843-19, right M1; UCMP 141843-25, right M1; UCMP 141843-26, right M1; UCMP 141843-30, left M2; UCMP 141843-44, left M2; UCMP 141843-48, left M2; UCMP 141843-50, left M2; UCMP 141843-56, right M2; UCMP 141843-60, right M2; UCMP 141843-62, right M3; UCMP 141843-64, right m3; UCMP 141843-66, right m1; UCMP 141843-68, left M2; UCMP 141843-70, right m2; UCMP 141843-75, left M1; UCMP 141843-85, left M2; UCMP 141843-87, right M2; UCMP 141843-88, right m3; UCMP 141843-92, right m2; UCMP 141843-104, left M2; UCMP 141843-112, left M2; UCMP 141843-115, right m2; UCMP 141843-117, right m3; UCMP 141843-123, right m3; UCMP 141843-134, left m3; UCMP 141843-135, right M2; UCMP 141843-137, left M2; UCMP 141843-141, left m2; UCMP 141843-147, left maxilla fragment with M2; UCMP 141843-149, left m2; UCMP 141843-150, right m2; UCMP 141843-151, right m3; UCMP 141843-152, left M2; UCMP 141843-153, left m1; UCMP 141843-159, right m3; UCMP 141843-160, left m2; UCMP 141843-163, left m1; UCMP 141843-171, right m3; UCMP 141843-177, left m3; UCMP 141845, right dentary fragment with m1–m2; UCMP 141895-01,

left m1; UCMP 141895-03, right m1; UCMP 141895-06, right m3; UCMP 141895-17, right m1; UCMP 141895-28, left m1; UCMP 141895-29, right m1; UCMP 141895-31, left m1.

Measurements.— See Tables 47-50.

Diagnosis.— *Copemys tyleri* is a medium-sized species of *Copemys* with an M1 differing from those of *C. tenuis*, *C. russelli*, *C. barstowensis*, and *C. longidens* in having a symmetrical, having a strongly bilobed anterocone, having a distinct mesostyle (except *C. russelli* and *C. longidens*), having an enterostyle (except *C. russelli*), having a submerged parastyle, having a distinct mesoloph (except *C. tenuis* and *C. barstowensis*); and in lacking a paralophule (except *C. tenuis*), lacking a protolophule I (except *C. russelli*) and lacking a protolophule II. For the m1, *C. tyleri* differs from *C. tenuis*, *C. russelli*, *C. barstowensis*, and *C. longidens* in having an elongate mesostyle. It lacks an anterolophulid, metalophid, and metalophulid, which is different than *C. tenuis*.

Description.— The cheekteeth decrease in size from front to back, are low crowned, and are bulbous. The M1 is longer than wide, the trigon is equal in width to the talon, and the four principal cusps are subequal in size. The anterolabial basin is closed by the presence of a distinct paralophule. The anterocone is symmetrical and strongly bilobed. An anterolophule joins the protocone low and on the center part of the anterocone. A parastyle is submerged within a distinct paralophule. The protolophule I is absent, whereas the protolophule II is present and joins the posterolingual part of the paracone to

the center of the ectoloph. The ectoloph has anterior and posterior arms that are bent and attached to the posterolabial and anterolabial margins of the protocone and hypocone, respectively. A distinct mesoloph is present, but it does not reach the lingual margin of the tooth. An anteroposteriorly elongated mesostyle is present and closes the central basin labially. Along the lingual margin of the central basin, an enterostyle is present, but it does not close this basin lingually. The metalophule I and II are both absent. The posterior cingulum attaches to the posterolabial margin of the hypocone and is anteroposteriorly narrow as it extends labially and attaches to the posteromedial margin of the metacone. The posterior basin is closed lingually and does not possess a lingual arm.

The M2 differs from the M1 in having an anterocone that is greatly reduced, having a short anterolophule, and having a distinct protolophule I. It differs from the M1 in lacking a parastyle. In addition, the M2 differs from the M1 in having a mesoloph that reaches the lingual margin of the tooth, and the enterostyle is anteroposteriorly elongated, and closing the central basin lingually. The metalophule I is present.

The M3 differs from the M2 in being reduced in overall size and triangular in occlusal outline. In addition, the metacone and hypocone are greatly reduced.

The ventral surface of the dentary is slightly convex. The diastema is long and shallow. A distinct mental foramen occurs high on the diastema near the dorsal margin, with the dorsalmost part of the foramen below the anteromost part of the masseteric scar and anteroventrally below the m1; it opens anterodorsally.

The masseteric scar terminates below the anterior root of the m1. Posterior to its distal end, the massteric scar forms a weak ventral shelf that grades ventrally with the ramus; the dorsal shelf is absent. The ascending ramus arises lateral to the posterior part of the m2. Several small foramina are present on the lingual surface of the dentary.

The distal end of the incisor lies below the level of the tooth row. It is rounded labially with little enamel present on the medial surface. On the lateral surface of the incisor, nearly one-third of tooth is covered with enamel. In cross section, the tooth is oblong.

The m1 is longer than wide, and the trigonid is slightly narrower than the talonid; the anterior, middle, and posterior basins are deep. The anterior and central basins are open laterally but the posterior basin is closed. The anteroconid occurs subcentral with a distinct anterior cingulid; the metalophulid is lacking. The anterior cingulid attaches low to the anterolabial base of the protoconid, but the anterolabial valley is open. A deep, narrow valley separates the anteroconid and metaconid; this basin opens lingually. An anterolophulid is absent, thus the anteroconid is free from the metaconid, protoconid, or metalophid. The metalophid is absent. The anterior arm of the ectolophulid is bent, while the posterior arm is straight. They attach to the posterolingual and anterolingual margins of the protoconid and hypoconid, respectively. No mesoconid is present, but a weak mesolophid occurs at the center of the ectolophulid and extends in a straight line to the lingual margin of the tooth,

joining an anteroposteriorly elongated mesostylid. There is no ectostylid along the labial margin of the central basin; this basin opens labially. The ectolophulid is absent. A hypolophid joins the hypoconid and entoconid anteriorly. A hypoconulid is lacking. The posterior cingulid attaches to the posterolingual margin of the hypoconid and bows slightly posteriorly as it extends lingually and joins the posteromedial margin of the entoconid. The posterior basin closes lingually.

The m2 differs from the m1 in being wider, but shorter and possessing a trigonid and talonid that are equal in width. It differs from the m1 in lacking an anteroconid and metalophulid. The metalophid is present and joins the labial arm of the anterior cingulid. The mesolophid attaches to a mesostyid which, in turn, attaches to the posteromedial margin of the metaconid. A distinct hypoconulid is present.

The m3 differs from the m2 in having: a trigonid that is wider than the talonid; an anterior cingulid that is more distinct; a mesolophid that is weak; and a central basin that is closed lingually by a mesostylid. The posterior arm of the ectolophid is very weak and the entoconid greatly reduced. A posterior cingulid attaches high on the posteromedial margin of the entoconid and the posterior basin closes lingually.

Comparison and discussion.— *Copemys tyleri* is similar in size to *C. longidens*, *C. russelli*, *C. tenuis*, and *C. barstowensis*, but is most similar in morphology to *C. longidens* (Figs. 19 and 20). The M1 of *C. tyleri* differs from

that of *C. tenuis* in having: a symmetrical and strongly bilobed anterocone; a distinct mesostyle; an enterostyle; a parastyle; and a distinct mesoloph that does not reach the lingual margin of the tooth. It lacks a protolophule I and metalophule II. The m1 of *C. tyleri* differs from *C. tenuis* in possessing an anteroconid that lies subcentral, a distinct mesostylid, a metalophid weak, an anteroposteriorly elongated mesostylid, whereas lacking an anterolophulid, an ectostylid, and a metalophulid.

Copemys tyleri differs in its M1 compared to *C. russelli* in having subequal cusps, a distinct paralophule, a symmetrical and strongly bilobed anterocone, mesostyle. It also differs in having a parastyle, and enterostyle, as well as an anterocone that lies centrally, while lacking a protolophule I and a metalophule II. For the m1, *C. tyleri* differs from *C. russelli* in having: a deep, narrow valley that separates the anteroconid from the metaconid; an anteroposteriorly elongated mesostylid; and a weak mesolophid; while lacking an anterolophulid, a metalophid, an ectolophulid, and an ectostylid.

The M1 of *C. tyleri* differs from that of *C. barstowensis* in having: a symmetrical and strongly bilobed anterocone; a paralophule and parastyle; a distinct mesoloph and mesostyle; and an enterostyle. In contrast, it lacks a protolophule I and metalophule II. For the m1, *C. tyleri* differs from *C. barstowensis* in having: an anteroconid that occurs lingual to the midline of the tooth (subcentral); a deep, narrow valley that separates the anteroconid from the metaconid; a labial arm of anterior cingulid; an anteroposterior elongated

mesostylid; and a weak mesolophid. It lacks an anterolophulid and metalohid, which is also different from *C. barstowensis*.

The M1 of *C. tyleri* differs from *C. longidens* in possessing: a strongly bilobed anterocone; an anterolophule that joins the center of the anterocone; a mesostyle and enterostyle; and a distinct paralophule and mesoloph. In contrast, it lacks a protolophule and a distinct parastyle. For the m1, *C. tyleri* differs from that of *C. longidens* in having: an anteroconid that does not join the metaconid directly and occurs lingual to the midline of the tooth; an anteroposteriorly elongated mesostylid; and a mesolophid that reaches lingual margin of tooth. It also differs in lacking a metalophulid, a metalophid, and an anterolophulid.

Copemys harperi n. sp.

Plate 25 (G-L)

Holotype.— UCMP 141767-10, left dentary fragment with m1-m3.

Type locality.— UCMP V70140.

Etymology.— Named in honor of Charles W. Harper, for his continued support during this project.

Other localities.— Eastgate: Type and OMNH, V974; UCMP V70142 and V70147.

Age.— Barstovian.

Stratigraphic and biogeographic occurrence of the species.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimens.— Type and OMNH 54381, left M2; OMNH 54384, left m2; OMNH 54387, right maxilla fragment with M1; OMNH 54388, left maxilla fragment with M1; OMNH 54396, right m2; OMNH 54406, left M1; OMNH 54408, left M1; OMNH 54418, left m1; OMNH 54425, left M3; OMNH 54444, left M3; OMNH 54458, left m1; OMNH 54472, right M3; OMNH 54475, left M2; OMNH 54478, left M1; OMNH 54485, right m2; OMNH 54486, right M3; OMNH 54501, right m1; OMNH 54523, right M3; OMNH 54973, right M3; UCMP 141609-01, right maxilla fragment with M2; UCMP 141675-05, left M1; UCMP 141675-08, left M1; UCMP 141678-06, right M3; UCMP 141678-10, right M1; UCMP 141722, left maxilla fragment with M2; UCMP 141742-01, right m2; UCMP 141743, right m1; UCMP 141746-04, left maxilla fragment with M1-M2; UCMP 141747, right dentary fragment with m1-m3; UCMP 141760-01, left m2; UCMP 141760-02, right m2; UCMP 141760-03, right M3; UCMP 141760-13, right m2; UCMP 141767-04, right dentary fragment with m1-m3; UCMP 141767-18, right dentary fragment with i1, m1-m3; UCMP 141775-02, right dentary fragment with m2; UCMP 141777-02, left maxilla fragment with M1-M2; UCMP 141777-08, right maxilla fragment with M1-M2; UCMP 141777-13, left maxilla fragment with M2-M3; UCMP 141777-17, left maxilla fragment with M1-M2; UCMP 141777-18, right maxilla fragment with M2-M3; UCMP 141777-35, left maxilla fragment with M1-M3; UCMP 141777-36, left maxilla fragment with M1-M3; UCMP 141843-03,

left M1; UCMP 141843-17, left M1; UCMP 141843-18, left M1; UCMP 141843-23, left M1; UCMP 141843-54, right M3; UCMP 141843-55, left M1; UCMP 141843-78, left M1; UCMP 141843-95, right m1; UCMP 141843-100, left M3; UCMP 141843-107, left M2; UCMP 141843-129, left M2; UCMP 141843-138, right m1; UCMP 141843-157, right maxilla fragment with M2-M3; UCMP 141843-164, right M2; UCMP 141843-169, left M2; UCMP 141843-179, right M2; UCMP 141895-14, right M1.

Measurements.— See Tables 47-50.

Diagnosis.— *Copemys harperi* is a medium-sized species of *Copemys* with an M1 differing from those of *C. russelli*, *C. longidens*, and *C. tyleri* in having an asymmetrical anterocone. From *C. tenuis*, *C. russelli*, and *C. tyleri*, the M1 of *C. harperi* differs in lacking a bilobed anterocone. It differs from the M1 of *C. tenuis*, *C. russelli*, *C. tyleri*, *C. barstowensis*, *C. longidens* in having a weak paralophule, and from those of *C. russelli*, *C. tyleri*, and *C. longidens* in lacking a parastyle. From *C. tenuis*, *C. tyleri*, *C. barstowensis*, and *C. longidens*, the M1 of *C. harperi* differs in having a weak mesoloph that does not reach the lingual margin of the tooth. For the m1, *C. harperi* differs from *C. tenuis*, *C. barstowensis* and *C. longidens* in having an anteroconid that lies lingual to the midline of the tooth. The m1 of *C. harperi* differs from those of *C. tenuis*, *C. barstowensis* and *C. longidens* in having a metalophulid. In contrast, *C. tenuis*, *C. russelli*, and *C. barstowensis*, the m1 of *C. harperi* differs lacks an anterolophulid. The m1 of *C. harperi* differs from that of *C. tyleri* in having a

metalophulid.

Description.— The M1 is longer than wide, and the trigon is equal in width to the talon. The four principal cusps are subequal in size. The anterior, central, and posterior basins are deep. A weak paralophule is present, resulting in the anterolabial basin being closed. The anterocone is asymmetrical and not bilobed. A straight anterolophule joins the protocone low and subcentrally on the anterocone. A parastyle is lacking. The protolophule I is absent, but the protolophule II is present and joins the posterolingual part of the paracone to the anterior arm of the ectoloph. The mesoloph is weak and does not reach the lingual margin of the tooth. A weak mesostyle is present but does not close the central basin labially. Along the lingual margin of the central basin an enterostyle occurs along the anteromedial margin of the hypocone; it does not close the central basin lingually. The metalophule I is absent, but the metalophule II is present. The posterior cingulum attaches to the posterolabial margin of the hypocone and is anteroposteriorly narrow as it extends labially and attaches to the posteromedial margin of the metacone. The posterior basin opens lingually.

The M2 differs from the M1 in having a greatly reduced anterocone, a short anterolophule, a weak protolophule I, a distinct enterostyle, and a metalophule I. In contrast it lacks a parastyle.

The M3 differs from the M2 in being reduced in overall size and triangular in occlusal outline, and in having greatly reduced metacone and hypocone. It also differs from the M2 in lacking an enterostyle and metalophule I.

The ventral surface of the dentary is slightly convex. The diastema is long and shallow. A distinct mental foramen occurs high on the diastema, with the dorsalmost part of the foramen occurring below the level of the anteromost part of the masseteric scar and anteroventrally below the m1; it opens anterodorsally. The masseteric scar terminates below the middle of the m1. Posterior to its distal end, the masseteric scar forms a strong ventral shelf that grades ventrally with the ramus; the dorsal shelf is usually weak. The ascending ramus arises lateral to the posterior part of the m2. Several small foramina are present on the lingual surface.

The lower cheekteeth are high crowned and slightly bulbous at the crown bases. The also decrease in size from front to back.

The distal end of the incisor lies above the level of the tooth row. It is rounded labially with little enamel present on the medial surface, but nearly one-quarter of the lateral side of the tooth is covered with enamel. In cross section, the tooth is oblong.

The m1 is longer than wide, and the trigonid is slightly narrower than the talonid. The anterior basin is closed labially and lingually, whereas the central basin opens laterally and the posterior basin opens lingually. All basins are deep. The anteroconid occurs lingual to the midline of the tooth (subcentral) with a distinct anterior cingulid and a weak metalophulid. The anterior cingulid attaches to the anteromedial base of the protoconid. The metalophid is weak and reaches the metaconid. The anteroconid and metaconid are joined. An

anterolophulid is absent. The metalophid is present, so that the protoconid and metaconid are joined. A mesoconid is absent, but a distinct mesolophid occurs at the center of the ectolophulid and extends in a straight line to the lingual margin of the tooth, where it joins a mesostylid (or, as in UCMP 141767-10, the mesostylid is absent, allowing the distal end of the mesolophid to reach the lingualmost margin of the tooth). An ectostylid is absent, resulting in the central basin being open labially. The ectolophulid is absent, but the ectostylid is usually present (or absent as in UCMP 141767-10). If present, the ectostylid closes the labial part of the central basin. A hypolophid joins the hypoconid and entoconid anteriorly. A hypoconulid is absent. The posterior cingulid attaches to the posterolingual margin of the hypoconid and bows slightly posteriorly as it extends lingually but ends before reaching the posteromedial margin of the entoconid. The posterior basin is open lingually.

The m2 differs from the m1 in possessing a trigonid and talonid that are equal in width. It also differs from the m1 in having a greater width than length, a weak anterior cingulid, and a mesoconid. The m2 differs from the m1 in lacking a mesolophid and an anteroconid.

The m3 differs from the m2 in having a trigonid that is much wider than the talonid, having a distinct anterior cingulid, having a central basin that is closed lingually by a lophid, having a greatly reduced entoconid , having a posterior cingulid attached high on the posteromedial margin of the entoconid, and having a posterior basin that closes lingually. In addition, the m3 differs

from the m2 in lacking a mesolophid (different from m1).

Comparison and discussion.— *Copemys harperi* is similar in size to *C. longidens*, *C. russelli*, *C. tenuis*, *C. barstowensis*, and *C. tyleri* (Figs. 19 and 20). However, *C. harperi* differs from these species in several characters of the upper and lower cheekteeth.

The M1 of *C. harperi* differs from that of *C. longidens* in having: an asymmetrical anterocone that does not join the metacone; a weak mesoloph; a mesostyle and enterostyle; and a metalophule II. In contrast, it lacks a protolophule I, a parastyle, and a metalophule I. The m1 of *C. harperi* differs from that of *C. longidens* in having: a subcentral anteroconid; a metalophid; and a mesolophid that joins a distinct mesostyle. *Copemys harperi* lacks an anterolophulid and ectostylid that are present in *C. longidens*.

The M1 of *C. harperi* differs from that of *C. russelli* in having: an asymmetrical; a single lobed anterocone; a mesoloph that does not reach the lingual margin of the tooth; and a mesostyle and enterostyle. The M1 of *C. harperi* lacks a paralophule, parastyle, protolophule I, and metalophule I that are present in *C. russelli*. For the m1, *C. harperi* differs from that of *C. russelli* in having: a metalophulid and mesostylid. In contrast, it lacks a valley that separates the anteroconid from the metaconid, which is present in *C. russelli*. In addition, it lacks an anterolophulid, lacks an ectolophulid, and lacks mesostylid and ectostylid, which are present in *C. russelli*.

The M1 of *C. harperi* differs from that of *C. tenuis* in having an anterocone

that is not bicusped, a mesoloph that does not reach the lingual margin of the tooth, a mesostyle, an enterostyle, and a weak paralophule. The M1 of *C. haperi* also differs from *C. tenuis* in lacking a protolophule I and metalophule II. For the m1, *C. harperi* differs from that of *C. tenuis* in having an asymmetrical and subcentral anteroconid, a distinct metalophulid, and a mesolophid that joins a distinct mesostylid. In contrast, the m1 of *C. harperi* differs from the m1 of *C. tenuis* in lacking a deep, narrow valley between the anteroconid and metaconid. The anterolophulid and ectostylid are also absent on the m1 of *C. harperi* but present on the m1 of *C. tenuis*.

The M1 of *C. harperi* differs from that of *C. barstowensis* in having an anterolophule that joins the anterocone to the metaloph subcentrally, a paralophule and parastyle, a weak mesoloph, and a mesostyle and enterostyle. In contrast, the M1 of *C. harperi* differs from that of *C. barstowensis* in lacking a protolophule I and metalophule I. Distinquishing characters on the m1 include having an asymmertrical anteroconid that is subcentral, a distinct labial arm of the anterior cingulid, a mesolophid that joins a distinct mesostylid, and a metalophulid; it also differs in lacking a deep, narrow valley between the anteroconid and metaconid. Other characters lacking on the m1 of *C. harperi* include an anterolophulid, a parastyle, an ectolophid, and an ectostylid; all are present in *C. barstowensis*.

M1 of *C. harperi* differs from that of *C. tyleri* in having an asymmetrical anterocone that is not bicusped, an anterolophule that joins the anterocone

subcentrally, a weak paralophule, a weak mesoloph and mesostyle, a metalophule II, and a posterior basin that opens lingually. The M1 of *C. harperi* differs from that of *C. tyleri* in lacking a parastyle. For the m1, *C. harperi* differs from that of *C. tyleri* in having a metalophid and a distinct mesolophid, a metalophulid, an anterior basin that is closed labially and lingually, an anteroconid and metaconid that are joined lingually, and a posterior basin that opens lingually. In addition, *C. harperi* differs from that of *C. tyleri* in lacking an elongated mesostyle.

Copemys harperi is most similar in size and morphology to *C. tyleri*. They share the following characters: the M1 has a greater length than width, four subequal principal cusps, haing a protolophule II and an enterostyle, while lacking a protolophule I, and lacking a metalophule I. The m1 has the following: a greater length than width, an anteroconid that is subcentral, a distinct anterior cingulid, and a anterolophulid. In contrast, the following are lacking: mesoconid, ectostylid, and ectolophulid. With the addition of new species of *Copemys* discovered at Eastgate and large samples of other species of *Copemys* from Eastgate (including a skull), the systematics of *Copemys* needs to be examined. This is a topic I hope to pursue, but is beyond the scope of the present paper.

Order Carnivora Bowdich, 1821

Family Canidae Fischer, 1817

Subfamily Borophaginae Simpson, 1945

Genus *Tomarctus* Cope, 1873

Tomarctus cf. *T. brevirostris* (Cope, 1873)

Plate 26 (A-F)

Locality.— Eastgate, UCMP V70147.

Age.— Barstovian.

Additional ages.— early Barstovian of Colorado, Nebraska, New Mexico, and California; and early late Barstovian of Colorado; late Barstovian of Texas (see Wang, et al., 1999).

Referred specimens.— OMNH 54975, left edentulous dentary fragment; UCMP 141836, left dentary fragment with m1 and m2 fragments; UCMP 141908, left dentary fragment with p2, p4, and m1 fragment; UCMP 141920, right dentary fragment with m1 fragment; UCMP 141916, left m2.

Measurements.— See below.

Comparison and discussion.— *Tomarctus* cf. *T. brevirostris* is represented at Eastgate by dentary fragments with teeth, an edentulous dentary, and an isolated lower molar. No cranial elements, upper teeth, or postcranial elements are known from this region. Of the borophagine material from Eastgate, the most diagnostic is a fragmented dentary with a complete p2 and p4, a

fragmented m1, and a complete m2 (UCMP 141908). This specimen has primitive characters that indicate it belongs to *Tomarctus* not *Aelurodon* (Wang et al., 1999): the talonid of the m1 is not narrowed; the m2 is less reduced than in *Aelurodon*; and on the m2, the metaconid and protoconid are equal in height to each other. In addition to these characters, the length and width of the p2, p4, and m2 of UCMP 141908 are smaller than those for any species of *Aelurodon* listed by Wang et al. (1999).

Two species of *Tomarctus* (*T. hippoghaga* and *T. brevirostris*) are listed by Wang et al. (1999). Based on the characters and size of the p2 (8.27 x 4.69 mm), p4 (11.48 x 7.07 mm), and the m2 (10.14 x 6.21 mm) of UCMP 141908 and them2 (13.27 x 8.65) of UCMP 141916, the Eastgate material is most similar to *T. brevirostris*. However, until more complete material becomes available this species identification is tentative.

Subfamily Caninae Fischer, 1817

Genus *Leptocyon* Matthew, 1918

Leptocyon sp. indet.

Plate 27 (A-C)

Locality.— Eastgate, UCMP V70138.

Age.— Barstovian.

Additional ages.— late Oligocene through late Hemphilian (see Munthe,

1998).

Referred specimen.— UCMP 141482, right m1.

Measurements.— m1: AP = 8.45, T = 4.66.

Comparison and discussion.— This small, isolated m1 missing the paraconid is tentatively identified as *Leptocyon* sp. based on its size and the fact that the entoconid is reduced. This character is among those listed by Munthe (1998) for this genus. Unfortunately, no additional comment or further identification is possible without more complete material.

Subfamily indet.

Plate 27 (D–F)

Locality.— Eastgate, UCMP V70147.

Age.— Barstovian.

Additional ages.— Barstovian: Monarch Mill Formation, Churchill County, Nevada.

Referred specimen.— UCMP 141911, left maxilla fragment with P2.

Measurements.— P2: AP = 8.31, T = 5.11.

Comparison and discussion.— The P4 is little worn; it has a subtriangular outline shape, and two roots. An anterior cingulum is present uniting an incipient parastyle to a reduced protocone; these are transversely parallel to each other. The lingual cingulum is strong, and it has a carnassial blade formed by a

posteriorly directed paracone and a reduced metacone.

Family Procyonidae Bonapart, 1850

Subfamily Procyoninae Gill, 1872

Genus *Bassariscus* Coues, 1887

Bassariscus cf. *B. parvus*

Plate 27 (G-I)

Localities.— Eastgate, UCMP V74103 and V70147.

Age.— Barstovian.

Additional ages.— early Barstovian through late Pliocene (Baskin, 1998b).

Referred specimens.— OMNH 54974, right dentary with p3-m1; UCMP 141928, right and left dentaries with p2-m2.

Measurements.— OMNH 54974, p3: AP = 5.59, T = 3.26; p4: AP = 5.86, T = 4.04; m1: AP = 9.45, T = 4.65. UCMP 141928, left p2: AP = 4.67, T = 2.43; p3: AP = 4.99, T = 2.48; p4: AP = 5.91, T = 3.03; m1: AP = 9.86, T = 4.51; m2: AP = 6.72, T = 3.62. UCMP 141928, right p2: AP = 4.54, T = 2.46; p3: AP = 4.53, T = 2.51; p4: AP = 5.85, T = 3.58; m1: AP = 9.75, T = 4.33; m2: AP = 6.52, T = 3.56.

Comaparison and discussion.— These specimens are referred to Procyonidae rather than Mustelidae on the basis of the unreduced M2, among other features (Baskin, 1998b). Within Procyonidae, the specimens are

assigned to *B.* cf. *B. parvus* based on the following characters: the m1 has an entoconulid that merges with the entoconid and the hypoconulid is distinct; and the m2 is elongate, with a narrow talonid and a hypoconulid that occurs along the posteromedial margin of the talonid. The trenchant talonid of the m2 is very rugose, which is common among procyonids and would support an omnivorous lifestyle.

Family Mustelidae Fischer, 1817

Genus *Promartes* Riggs, 1942

cf. *Promartes* sp.

Plate 27 (J-L)

Locality.— Eastgate, UCMP V70140.

Age.— Barstovian.

Additional ages.— late Arikareean through late Hemingfordian (see Baskin, 1998a).

Referred specimen.— UCMP 113319, left dentary fragment with p3-m1.

Measurements.— place here p3: AP = 2.89, T = 1.50; p4: AP = 3.22, T = 1.51; m1: AP = 5.43, T = 2.43.

Comparison and discussion.— Mustelids are represented at Eastgate by a single dentary with the p3-m1. Although the m2 is missing from this specimen, a single alveolus for it is present, indicating that m2 was reduced. The premolars

increase in size from front to back and have a single high cusp. The m1 is more complex in morphology than the preceding cheekteeth and possesses the following characters: the trigonid is open; the paraconid is lower than and anterior to the protoconid; the protoconid is the highest cusp and forms a carnassial blade with the paraconid; the metaconid is small and occurs lingual to the protoconid; the talonid is semitrenchant with a low internal rim; the entoconid is absent; and the hypoconid is separated from the protoconid by a narrow valley.

Based on the characters of the Eastgate specimen, including the size of the m1, it is most similar to the mustelid *Promartes*. The characters listed by Baskin (1998a) for the m1 of *Promartes*, seen in this specimen, are: open trigonid; semitrenchant talonid; low internal rim along talonid basin; protoconid and hypoconid separated by a valley; protoconid and metaconid opposite each other, and metaconid small and much lower than the paraconid.

Baskin (1998a) indicated that *Promartes* had a geologic range from the late Arikareean to the Hemingfordian. If the Eastgate specimen belongs to *Promartes*, it would extend this geologic range into the Barstovian.

Family Felidae Fischer, 1817

Subfamily indet.

Plate 27 (M-O)

Locality.— Eastgate, UCMP V70138.

Age.— Barstovian.

Referred specimen.— UCMP 141531, left dentary fragment with a partial p4.

Measurements.— p4: AP = 7.26, T = 2.96.

Discussion.— This specimen is a dentary fragment with a partial p4 is the only specimen of a felid from Eastgate. Unfortunately, the specimen is too incomplete for identification below the family level.

Order Artiodactyla Owen, 1848

Family Merycoidodontidae Thorpe, 1923

Subfamily Ticholeptinae Cope, 1878

Genus *Ticholeptus* Cope, 1878

Ticholeptus sp. indet.

Plate 28 (A-D)

Locality.— Eastgate, UCMP V70142.

Age.— Barstovian.

Additional ages.— early Hemingfordian through late Barstovian (see Lander, 1998).

Referred specimens.— UCMP 141873, left dentary fragment with a complete m1 and an incomplete m2.

Measurements.— See below.

Comparison and discussion.— This dentary fragment has cheekteeth that are similar to *T.* cf. *T. obliquidens*, based on a complete dentary with p2-m3 (UO 22798) from the Red Basin fauna, Oregon (Shotwell, 1968). In addition, Morae (1981) identified 11 dentaries of *T.* cf. *T. zygomaticus* from the Massacre Lake local fauna, Washoe County, Nevada; these specimens also are similar to the Eastgate fossil. No measurements of m1 of UO 22798 were available, but the m1 from Eastgate (UCMP 141873) has an anteroposterior length of 14.88 mm and width of 10.01 mm. The measurements of the Eastgate material are similar to those listed by Morae (1981) for the m1s of *T.* cf. *T. zygomaticus* (m1 AP = 12.70–14.60, T = 8.30–10.10 mm). In addition to size, the specimen from Eastgate is similar in characteristics to those listed by Shotwell (1968) for *T.* cf. *T. obliquidens*. No additional specimens of *Ticholeptus* sp. are known from Eastgate. The identification of this material is limited to genus until additional material is discovered.

Family Dromomerycidae Frick, 1937

Subfamily Aletomerycinae Frick, 1937

Genus *Aletomeryx* Lull, 1920

Aletomeryx sp. indet.

Plate 28 (D-L)

Localities.— Eastgate, OMNH V974; UCMP V70138, V70142, V70140.

Age.— Barstovian.

Additional ages.— late Arikareean through early Barstovian (see Janis and Manning, 1998).

Referred specimens.— OMNH 54976, left dentary fragment with p2-m3; OMNH 54977, right dentary with p4, m3; UCMP 141499, right dentary fragment with m1; UCMP 141518, right dentary fragment with m1 fragment and m2-m3; UCMP 141524, seven isolated cheekteeth and a maxilla fragment with M1-M2; UCMP 141527, median phalanx; UCMP 141650, right dentary fragment with p3-p4; UCMP 141654, right dentary fragment with p3-p4; UCMP 141655, left maxilla fragment with P2-M1; UCMP 141669, left dentary fragment with p3-m3; UCMP 141702, right dentary fragment with p2-m3; UCMP 141863, left maxilla fragment with M2-M3; UCMP 141664, right dp4; UCMP 141667, left DP3; UCMP 141693, left m2 fragment.

Measurements.— See below.

Comparison and discussion.— Six mandible fragments with cheekteeth

three maxillae fragments with cheekteeth, three isolated cheekteeth, and a median phalanx represent *Aletomeryx* sp. at Eastgate. These elements were identified as *Aletomeryx* sp. based on size and morphology of the upper and lower cheekteeth.

The range of the length and width measurements for the m2s from Eastgate are as follows: AP = 11.84–12.35 mm, T = 6.85–7.69 mm. The range for the length of the m2 for *Aletomeryx* is 10.0–14.6 mm (Janis and Manning, 1998). In addition to size, Eastgate specimens referred to *Aletomeryx* sp. possesses the following characters: the M3 is larger than M2; upper molars have an anterior cingulum, a mesostyle, a metastyle, and external ribs; the p4 has an anterior fossettid that is open; the palaeomeryx folds are present on the lower molars, but are reduced; the lower molars have anterior and posterior cingulids; and the m3 has a double posterior lobe that is closed posteriorly. These characters agree with those listed by Janis and Manning (1998) for the cheekteeth of *Aletomeryx*.

Tedford et al. (1987) suggested that *Aletomeryx* was limited to the early Hemingfordian, but Janis and Manning (1998) extended its range into the late Hemingfordian based on a specimen from the Frick collection. The occurrence of this *Aletomeryx* at Eastgate extends its known geologic age from the late Hemingfordian into the early Barstovian of North America.

Family indet.

Localities.— Eastgate, OMNH V974; UCMP V70141, V70142, V70145, V70147, V74103.

Age.— Barstovian.

Referred specimens.— OMNH 54895, astragulus; OMNH 54978, astragalus fragment; OMNH 54979, cervical vertebrae fragment; OMNH 54981, sesmoid bone; OMNH 54982, cuboid; OMNH 54983, calcaneus; OMNH 54984, astragulus; UCMP 141701-01, metapodial; UCMP 141701-02, metapodial; UCMP 141839, proximal part of a scapula; UCMP 141961, vertebral fragments; UCMP 141980, head of a femur.

Comaparison and discussion.— Several postcranial bones and tooth fragments have been collected by OMNH and UCMP researchers at Eastgate. These elements are similar in size to artiodactyls identified from Eastgate. Based on the diversity of the other mammals from Eastgate, it is plausible that the postcranial bones represent additional species of artiodactyls. However, the bones and teeth are too fragmented for confident allocation at even the family level, and thus these specimens warrant only passing mention.

Order Perissodactyla Owen, 1848

Family Equidae Gray, 1821

Subfamily Equinae Gray, 1821

Genus Merychippus Leidy, 1857

Merychippus sp. indet.

Plate 29 (A-E)

Localities.— Eastgate, UCMP V70138, V70142, V70143, V70145, V70148

Age.— Barstovian.

Additional ages.— late Hemingfordian through early Clarendonian (see MacFadden, 1998).

Referred specimens.— UCMP 141537, middle phalanx; UCMP 141698, astragulus; UCMP 141837-01, astragulus; UCMP 141837-02, isolated tooth fragments; UCMP 141899-01, proximal humerus; metatarsal; UCMP 141899-02, magnum; UCMP 141899-03 2nd or 4th; UCMP 141921, distal tibia.

Discussion.— These elements were identified by the late Donald E. Savage. Of the elements identified as *Merychippus* sp., none are helpful for species idendification.

Family Chalicotheriidae Gill, 1872

Subfamily Schizotheriinae Holland and Peterson, 1914

Genus *Moropus* Marsh, 1877

Moropus sp. indet.

Plates 29 and 30 (F; A-B)

Localities.— Eastgate, UCMP V67245, V70141, V70146, V70147, V74103.

Age.— Barstovian.

Additional ages.— late Arikareean through early Clarendonian (see Coombs, 1998).

Referred specimens.— UCMP 80398, proximal radius and ulna, and a distal end of a tibia; UCMP 141896, phalange; UCMP 141917, proximalmost phalanx 1; UCMP 141945, distal tibia; UCMP 141946, humerus fragment; UCMP 141954-01, ungual phalanx; UCMP 141954-02, phalanx 1; UCMP 141960, metapodial; UCMP 141972, calcaneus; UCMP 141978-01, complete tibia; UCMP 141978-02, radial fragment; UCMP 141978-03, ulna fragment; UCMP 141978-04, distal fused radius and ulna; UCMP 141981, partial femur.

Comparison and discussion.— Chalicotheres are represented at Eastgate by numerous postcranial specimens. Unfortunately, the material from Eastgate is not useful for species identification.

Family Rhinocerotidae Gray, 1821

Subfamily Aceratheriinae Dollo, 1885

Genus *Teleoceras* Hatcher, 1894

Teleoceras sp. indet.

Plate 30 (C–E)

Localities.— Eastgate, UCMP V67245, V70140, V70141, V70142, V74103.

Age.— Barstovian.

Additional ages.— late Hemingfordian through early Blancan (see Prothero, 1998).

Referred specimens.— OMNH 54978, astragalus fragment; OMNH 54986, ulna fragment; UCMP 83779, right P3 or P4 fragment; UCMP 120127, palate with left and right P1–M3, symphysis of dentary with left and right i2s; UCMP 141947-03, three phalanges; UCMP 141948-03, three phalanges; UCMP 141961, cervical vertebra fragment; UCMP 141962, thoracic vertebra fragment; UCMP 141839, proximal part of scapula; UCMP 141841, dentary fragment with fragmented cheekteeth; UCMP 141979, humerus; UCMP 141981, femur fragment.

Comparison and discussion.— At Eastgate, a rhinoceros is represented by a palate with a complete set of upper cheekteeth. Postcranial specimens are present as well. The upper molars have a diagnostic π-shaped pattern formed by the union of several lophs (protoloph, metaloph, and ectoloph) (Prothero, 1998). These specimens were identified as belonging to *Teleoceras* sp. based on the presence of the i2 on the symphysis of the dentary (UCMP 120127) and other characters listed by Prothero (1998). The upper cheekteeth are too worn and postcranial material does not allow a specific identification.

Concluding Remarks

Fossil vertebrates have been collected from the Eastgate localities for more than 30 years by researchers at the University of California Museum of Paleontology (UCMP) and a single field season by the Sam Noble Oklahoma Museum of Natural History (OMNH) researchers. Most of the fossils obtained by UCMP were recovered by surface collecting, whereas OMNH emphasized collecting rock matrix for screenwashing. Collectively, the screenwashed rock matrix (a total of about 820 kg) yielded several thousand specimens, of which about 1800 identifiable skulls, palates, maxillae, mandibles, and isolated teeth were examined.

The Eastgate fauna occurs within the basal part of the Monarch Mill Formation, Churchill County, Nevada. Seven orders, 25 families, and 60 species of mammals were identified from the Eastgate fauna. Another species, *Pseudotheridomys tedfordi*, from the Massacre Lake fauna was named and described herein because of its close affinity to *Pseudotheridomys woodburnei*.

This study emphasized the descriptions and alpha taxonomy of the mammalian fauna at Eastgate. Detailed comparisons to other well known Hemingfordian-Barstovian faunas as well as an examination of the biogreography, paleoecology, and paleoenvironment are beyond the scope of this project, though such studies are planned for the near future. Although study of the fauna at higher levels of interpretation is beyond the purview of the

present work, a few remarks on the biochronology and faunal composition are appropriate.

Relative Age.— Neither absolute nor relative age is well established for the Eastgate fauna. No radiometric dates have been obtained from the Monarch Mill Formation. However, the Middlegate Formation, which underlies the Monarch Mill Formation, was radiometrically dated by Swisher (1992). He provided a radiometric determination of 15.96 ma for the uppermost part of the Middlegate Formation, which provides a maximum possible age for Eastgate. Woodburne and Swisher (1995) placed the Hemignfordian Barstovian boundary at about 15.9 ma. They divided the Barstovian into early and late intervals. Earlier work by Tedford et al. (1987) divided the Barstovian into early and late intervals and further divided the late into early late and late late Barstovian intervals.

Tedford et al. (1987) defined the onset of late Hemingfordian time based on the first occurrence of petauristine squirrels and *Teleoceras*. Both taxa occur at Eastgate and the former are abundant and diverse (four species). These occurrences constrain the Eastgate fauna as no older than late Hemingfordian. None of the taxa listed by Tedford et al. (1987) as having a last occurrence in the late Hemingfordian is present at Eastgate. Tedford et al. (1987) defined onset of Barstovian time as based on the first occurrences of *Hemicyon* and *Copemys*. *Hemicyon* is not known from Eastgate; however, *Copemys* is both abundant (25% of all specimens recovered) and diverse (four species) at Eastgate. Of the four genera cited by Tedford et al. (1987) as having a last occurrence in the early

Barstovian, *Ticholeptus* is present at Eastgate. Further age assessment based on formal characterization is limited to constraints imposed by the range of a single family, Chalicotheriidae, also present at Eastgate. The last occurrence of Chalicotheriidae is late Barstovian (Tedford et al., 1987). These occurrences constrain the age of Eastgate as probably Barstovian, with some indication that it lies within the early part of that land mammal age.

Further refinement of age will depend, in large part, on the revised interpretation of Barstovian biochronology, currently in progress (M. O. Woodburne, personal communication). For example, Woodburne and Swisher (1995) suggested that the appearance of probscideans in North America, which was taken as a first appearance for late Barstovian, was diachronous. In addition to the proboscidean, Woodburne and Swisher (1995) stated that *Copemys* is known from the Alvord Mountains of southern California, from strata associated with a late Hemingfordian fauna; thus occurrence of *Copemys* is also diachronous.

However, specimens collected from Eastgate suggest that such a refined interpretation may well be feasible. For example, *Plesiosorex*, *Angustidens*, *Antesorex*, *Desmatolagus* and *Ticholeptus* present at Eastgate, are otherwise only known from Hemingfordian and older faunas. Several other taxa from Eastgate, are otherwise restricted to Barstovian and Hemingfordian assemblages: *Tardontia*, *Mesogaulus*, *Protospermophilus*, *Miospermophilus*, *Petauristodon*, *Monosaulax*, *Pseudotheridomys*, *Lignimus*, *Balantiomys*,

Cupidinimus, *Mojavemys*, and *Macrognathomys*. A working hypothesis, therefore, is that Eastgate will fall near the Hemingfordian-Barstovian boundary.

Faunal sampling and composition.— More than 100 Barstovian localities are known from North America (Savage and Russell, 1983). Of these, Barstovian faunas less than 13 contain greater than six taxa. The well sampled early Barstovian localities include the *Cupidinimus nebrascensis* zone of the Barstovian fauna (Mojave Desert, California); the Mascall and Virgin Valley faunas (Great Basin, Nevada); Eubanks fauna (Rocky Mountains, Colorado); and Fort Polk fauna (Southern North America, Louisiana). The well sampled late Barstovian faunas include *Leptodontomys stirtoni* zone, *Copemys longidens* zone, and *Copemys russelli* zone of the Barstow fauna; Dome Springs fauna (West Coast, California); Tonapah fauna (Great Basin, Nevada), Quartz Basin and Red Basin faunas (Great Basin, Oregon); Anceney fauna (Rocky Mountains, Montana); Colter Formation (Rocky Mountains, Wyoming); Norden Bridge fauna (Great Plains, Nebraska); and Kleinfelder Farm fauna (Great Plains, Saskatchewan) (see Tables 51-60).

Eastgate clearly provides a wealth of new information for examining mammalian history, especially for the insectivores, lagomorphs, and rodents, during this time interval; this is particularly true for the heterosoricids, ochotonids, sciurids, eomyids, heteromyids, and cricetids. The Eastgate fauna includes 60 species of which 50 are insectivore, lagomorph, and rodent taxa making it the most diverse known Barstovian local fauna. By comparison, the next most diverse local faunas are the Barstow local fauna with 48 species (30 insectivore,

lagomorph, and rodent taxa) and the Kleinfelder Farm fauna with 57 species (25 insectivore, lagomorph, and rodent taxa). Other Barstovian local faunas, mentioned above are not as well sampled as Eastgate, Barstow or Kleinfelder faunas (e.g., Mascall fauna, 16 taxa; Virgin Valley fauna, 6 taxa; Eubanks fauna, 7 taxa; and Ft. Polk fauna, 23 taxa; Dome Springs fauna, 20 taxa; Tonapah fauna, 20 taxa; Quartz Basin fauna, 26 taxa; Red Basin fauna, 29 taxa; Anceney fauna, Colter Formation, 21 taxa; and 24 taxa; Norden Bridge fauna, 14 taxa). Eastgate differs from other Barstovian local faunas not only in greater taxonomic diversity but taxonomic composition. This raises intriguing new questions concerning paleogeography and paleoecology for this time interval. For example, 19 of 60 taxa (31.6%) are only known from Eastgate. This compares to four endemic taxa (12%) for the Barstow fauna and five endemic taxa (11.4%) for the Kleinfelder Farm fauna. The unique nature of many taxa suggests a higher-level of endemicity for the Eastate fauna. The reasons for this are not presently clear.

A noteworthy aspect of faunal composition at Eastgate is the relatively great diversity of insectivores, lagomorphs, and rodents, in particular, eomyids, petauristine and tamiine squirrels. This compositional pattern presumably reflects complex interactions of biogeographic, environmental, and paleoecological factors, the relative importance of which remains to be determined. For example, the eomyids *Leptodontomys* and *Pseudotheridomys* are present at Eastgate and are great in numbers and diversity. Elsewhere, these eomyids are rare and do not occur sympatrically outside of the Great

Basin. Other patterns seem more clearly to reflect paleoenvironment. Woodland vegetation is suggested by the great abundance of petauristine and tamiine squirrels. The high number and great diversity of the insectivores further suggest that this woodland habitat was high in primary productivity, such as that seen in a temperate forest.

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TABLE 1

Measurements of seven fossil localities at Eastgate and their relative height above Unit 1 (subunit A)

Fossil locality	Meters above subunit A
UCMP V70140	9 m
UCMP V70138	10 m
OMNH V974	11 m
OMNH V976	12 m
UCMP V67245	16 m
UCMP V74103	19 m
UCMP V70147	22 m

TABLE 2

Measurements (mean, range, and n) of upper cheekteeth of talpids from Eastgate

Tooth and character		*Mystipterus vespertillio*	*Mystipterus* sp.	Genus indeterminate
P4	AP	1.32, 1		
	T	1.40, 1		
M1	AP			2.50, 2.36-2.63, 2
	T			1.77, 1.65-1.88, 2
M2	AP	1.28, 1.22-1.32, 3		0.94, 1
	T	1.37, 1.35-1.40, 3		1.03, 1
M3	AP		1.12, 1	1.43, 1.11-1.74, 2
	T		0.99, 1	1.27, 1.04-1.50, 2

TABLE 3

Measurements (mean, range, and n) of lower cheekteeth of talpids from Eastgate

Tooth and character		*Mystipterus vespertillio*	*Mystipterus* sp.	*Dominoides* sp.
m1	AP			1.63, 1.55-1.70, 2,
	TA			0.93, 0.91-0.95, 2
	TP			1.08, 0.99-1.16, 2
m2	AP	1.34, 1.27-1.41, 2	1.43, 1.41-1.44, 2	1.42, 1.21-1.62, 2
	TA	0.77, 0.71-0.82, 2	0.93, 0.92-0.94, 2	1.07, 1.16-1.21, 2
	TP	0.86, 0.84-0.88, 2	0.99, 0.97-1.00, 2	1.24, 1
m3	AP	1.10, 1		1.52, 1.51-1.53, 2
	TA	0.74, 1		0.92, 0.86-0.97, 2
	TP	0.62, 1		0.74, 0.67-0.80, 2

TABLE 4

Measurements (mean, range, and n) of upper cheekteeth of shrews from Eastgate.

Tooth and character		*Pseudotrimylus* sp.	[a] *Limneocus* sp.	*Antesorex* sp.
P4	AP	1.60, 1	1.32, 1.05-1.45, 6	0.90, 9
	T	1.80, 1	1.17, 0.92-1.32, 6	1.01, 1
M1	AP	1.90, 1	1.41, 1.31-1.52, 5	0.99, 1
	T	20.1, 1	1.40, 1.20-1.59, 5	1.12, 1
M2	AP	1.59, 1.30-1.77, 3	1.27, 1.22-1.32, 4	0.88, 0.85-0.90, 2
	T	1.71, 1.40-1.94, 3	1.44, 1.38-1.50, 4	1.08, 1.07-1.09, 2
M3	AP	1.43, 1.40-1.45, 2	0.62, 0.60-0.64, 3	0.48, 1
	T	1.39, 1.13-1.65, 2	1.29, 1.22-1.33, 3	1.11, 1

[a] P3: AP = 0.41, T = 0.57

TABLE 5

Measurements (mean, range, and n) of lower cheekteeth of shrews from Eastgate.

Tooth and Character		*Limnoecus tricupsis*	*Limnoecus niobrarensis* [a]	*Limnoecus* sp.
p4	AP	0.53, 0.53-0.53, 2	0.61, 1	
	T	0.40, 0.30-0.50, 2	0.52, 1	
m1	AP	1.02, 0.90-1.09, 4	1.06, 1	
	TA	0.59, 0.56-0.61, 4	0.54, 1	
	TP	0.61, 0.56-0.66, 4	0.58, 1	
m2	AP	0.96, 0.90-1.02, 2	1.00, 1	0.98, 1
	TA	0.64, 0.61-0.67, 2	0.66, 1	0.63, 1
	TP	0.60, 0.56-0.63, 2	0.60, 1	0.52, 1

TABLE 5 CONTINUED

Tooth and character		*Limnoecus tricupsis*	*Limnoecus niobrarensis* [a]	*Limnoecus* sp.
m3	AP	0.72, 0.66-0.78, 3	0.82, 1	0.89, 1
	TA	0.52, 0.50-0.57, 3	0.55, 1	0.53, 1
	TP	0.33, 0.31-0.36, 3	0.41, 1	0.34, 1

[a] p3: AP = 0.52, T = 0.50.

TABLE 6

Measurements (mean, range, and n) of upper cheekteeth of ochotonids from Eastgate.

Tooth and character		*Desmatolagus schizopetrus*	*Oreolagus nebrascensis*	*Russellagus vonhofi*
DP2	AP			1.05, 0.99-1.11, 2
	T			2.02, 1.93-2.10, 2
P2	AP			0.99, 0.98-1.00, 2
	T			1.74, 1.63-1.85, 2
P3	AP	1.85, 1.64-2.10, 3		
	T	4.60, 3.30-6.20, 3		
P4	AP	2.44, 2.34-2.53, 2		
	T	4.60, 4.26-4.85, 2		
M*	AP	2.40, 2.00-2.50, 4	1.51, 1.44-1.56, 3	1.48, 1.36-1.61, 15
	T	5.30, 4.34-6.20, 4	2.46, 2.30-2.66, 3	2.25, 1.87-2.65, 15

* molariform tooth

TABLE 7

Measurements (mean, range, and n) of lower cheekteeth of ochotonids from Eastgate.

Tooth and character		*Desmatolagus schizopetrus*	*Russellagus vonhofi*
dp3	AP	3.18, 1	2.31, 2.25-2.41, 5
	T	1.75., 1	1.77, 1.70-1.92, 5
dp4	AP		1.94, 1.85-2.11, 3
	T		1.76, 1.60-1.85, 3
m1	AP		
	T		
m*	AP		1.89. 1.66-2.10., 8
	T		1.78, 1.40-1.99, 8
m3	AP	2.73, 1	
	T	2.88, 1	

TABLE 7 CONTINUED

Tooth and character		*Oreolagus nebrascensis*	*Oreolagus colteri*
dp3	AP	2.27, 2.22-2.30, 4	2.19, 1
	T	1.75, 1.45-1.82, 4	1.75, 1
dp4	AP	1.90, 1	
	T	1.70, 1	
m1	AP	1.76, 1	
	T	1.58, 1	
m*	AP	2.10, 1	
	T	1.81, 1	

* molariform tooth

TABLE 8

Measurements (mean, range, and n) of lower p3s of *Hypolagus* and *Pronotolagus* taxa.

	Hypolagus			
Character	*H. vetus**	*H. parviplicatus***	*H. gidleyi**	*H. fontinalis***
AP	3.10, 2.30-3.60, 94	3.20, 2.80-3.70, 53	3.30, 3.00-3.60, 38	2.80, 2.30-3.30, 30
T	2.80, 2.30-3.30, 91	2.80, 2.50-3.40, 53	3.00, 2.60-3.60, 38	2.30, 2.00-2.60, 30
Depth of posterior external reentrant	0.52, 0.40-0.62, 55	0.48, 0.38-0.55, 53	0.60, 0.49-0.58, 40	0.51, 0.46-0.57, 30
Depth of anterior external reentrant	0.18, 0.09-0.28, 55	0.15, 0.10-0.19, 53	0.19, 0.09-0.30, 39	0.24, 0.19-0.35, 30

TABLE 8 CONTINUED

	Hypolagus			
Character	*H. tedfordi**	*H. fulongi**	*H. edensis**	*H. oregonensis**
AP	2.60, 2.20-2.80, 39	2.60, 2.40-2.80, 18	2.60, 2.00-2.90, 39	3.20, 3.00-4.00, 14
T	2.30, 1.90-2.50, 39	2.30, 2.10-2.50, 18	2.30, 1.90-2.60, 39	3.00, 2.60-3.10, 14
Depth of posterior external reentrant	0.45, 0.34-0.55, 42	0.55, 0.50-0.61, 20	0.51, 0.45-0.59, 35	0.51, 0.45-0.56, 18
Depth of anterior external reentrant	0.25, 0.19-0.31, 42	0.22, 0.15-0.30, 26	0.34, 0.25-0.46, 36	0.21, 0.18-0.25, 18

TABLE 8 CONTINUED

Character	*Hypolagus*			
	*H. ringoldensis**	*H. regalis**	*H. voorhiesi**	*H. parviplicatus****
AP	3.50, 3.00-4.00, 60	3.30, 2.70-3.60, 43	2.60, 2.20-2.90, 24	2.75, 2.67-2.82, 2
T	3.20, 2.70-3.70, 60	2.90, 2.40-3.70, 43	2.30, 2.00-2.60, 24	2.42, 2.42, 2
Depth of posterior external reentrant	0.55, 0.42-0.65, 59	0.60, 0.53-0.70, 40	0.57, 0.43-0.66, 23	0.53, 0.50-0.55, 2
Depth of anterior external reentrant	0.22, 0.14-0.35, 59	0.26, 0.16-0.40, 39	0.25, 0.16-0.28, 23	0.15, 0.14-0.16, 2

TABLE 8 CONTINUED

	Hypolagus	*Pronotolagus*	
Character	*H. fontinalis****	*Pronotolagus***	*Pronotolagus* sp. ***
AP	2.97, 2.83-3.12, 5	3.10, 2.60-3.50, 19	2.70, 1
T	2.30, 2.20-2.35, 5	2.70, 2.40-3.30, 19	2.13, 1
Depth of posterior external reentrant	0.54, 0.49-0.61, 5	0.50, 0.43-0.58, 19	0.45, 1
Depth of anterior external reentrant	0.23, 0.21-0.26, 5	0.19, 0.12-0.26, 19	0.19, 1

* Data from White (1987). ** Data from Voorhies and Timperley (1997). *** Data from Eastgate specimens.

TABLE 9

Measurements of lower p3s of *Hypolagus*.

Taxon	Number of specimens	PER divided by T times 100
*H. vetus**	91	52.00
*H. parviplicatus**	1	47.00
*H. gidleyi**	38	54.00
*H. fontinalis**	17	48.50
*H. tedfordi**	39	47.50
*H. fulongi**	18	55.50
*H. edensis**	39	51.00
*H. oregonensis**	14	50.80
*H. ringoldensis**	60	56.50
*H. regalis**	43	60.00
*H. voorhiesi**	24	57.00
*H. parviplicatus***	2	53.00
*H. fontinalis****	5	54.00

* Data from White (1987). ** Data from Eastgate specimens of *Hypolagus*.

TABLE 10

Measurements (mean, range, and n) of upper P2s of leporids.

Character	*Hypolagus parviplicatus**	*Hypolagus fontinalis**	*Pronotolagus albus**
AP	1.50, 1.30-1.80, 19	1.30, 1.10-1.40, 15	1.50, 1.20-1.70, 4
T	3.10, 2.90-3.40, 19	2.60, 2.40-3.00, 15	2.80, 2.30-3.20, 4
Depth of external anterior reentrant	0.14, 0.0-0.22, 19	0.21, 0.16-0.28, 15	0.20, 0.18-0.23, 4
Depth of main anterior reentrant	0.46, 0.40-0.52, 19	0.57, 0.49-0.65, 15	0.53, 0.48-0.54, 4

TABLE 10 CONTINUED

Character	*Hypolagus parviplicatus***	*Hypolagus fontinalis***	*Pronotolagus* sp. **
AP	1.35, 1.27-1.44, 6	1.46, 1	1.64, 1
T	2.76, 2.23-3.26, 6	2.42, 1	3.26, 1
Depth of posterior external reentrant	0.70, 0.03-0.10, 6	0.41, 1	
Depth of main anterior reentrant	0.26, 0.18-0.36, 6	0.46, 1	0.24, 1

* Data from Voorhies and Timperley (1997). ** Data from Eastgate specimens.

TABLE 11

Measurements (mean, range, and n) of upper cheekteeth of aplodontids and mesogaulids from Eastgate.

Tooth	Character	*Tardontia nevadens*	*Mesogaulus paniensis*
P3	AP	1.90, 1	
	T	1.60. 1	
DP4	AP	3.54, 3.42-3.76, 3	
	T	3.04, 2.12-3.51, 3	
P4	AP	4.29, 4.20-4.39, 2	8.26, 1
	T	3.45, 2.64-4.27, 2	5.40, 1
M1	AP	3.06, 2.68-3.50, 4	
	T	3.26, 2.77-3.57, 3	
M2	AP	2.68, 1	3.91, 3.41-4.37, 4
	T	2.25, 1	3.40, 2.61-3.99, 4
M3	AP	2.96, 1	4.24, 1
	T	1.81, 1	2.36, 1

TABLE 12

Measurements (mean, range, and n) of lower cheekteeth of aplodontids and mesogaulids from Eastgate.

Tooth	Character	*Tardontia nevadens*	*Mesogaulus paniensis*
dp4	AP	3.28, 3.20-3.37, 3	5.62, 1
	T	2.09, 1.98-2.30, 3	4.10, 1
p4	AP	3.81, 3.26-4.34, 5	8.17, 8.08-8.26, 2
	T	2.78, 2.30-3.35, 4	5.27, 5.13-5.40, 2
m1	AP	3.01, 2.82-3.19, 4	
	T	2.15, 1.83-2.45, 4	
m2	AP	2.91, 2.68-3.07, 3	
	T	2.40, 2.15-2.79, 3	
m3	AP	3.21, 2.96-3.50, 4	
	T	2.09, 1.81-2.44, 4	

TABLE 13

Characters that separate P4s for *Protospermophilus dalquesti* from North American Miocene tamiines and marmotines.

	Taxon[a]											
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12
Size (L X W)	MI	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	LA
Mesostyle	S	-	A	S	S	-	S	S	S	S	S	S
Metaconule	D	-	S	S	A	-	S	S	D	D	D	D
Metaloph	CO	-	C	VC	C	-	CO	CO	CO	CO	CO	CO
Protoconule	A	-	A	A	S	-	A	A	A	A	A	S

TABLE 13 CONTINUED

	Taxon[a]											
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12
Protoloph	C	-	C	C	C	-	C	C	C	C	C	C
Parastyle	S	-	S	S	D	-	S	S	S	A	S	D

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. dalquesti*.

[b] A=absent, C=complete, CO=constricted, D=distinct, LA=large size (range), MI=middle size (range), S=small, SC=slightly constricted, SM=small size (range), VC=very constricted.

TABLE 14

Characters that separate M1 or M2s for *Protospermophilus dalquesti* from North American Miocene tamiines and marmotines.

	Taxon[a]											
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	LA
Mesostyle	A	A,T	T	T	A	D	D,M	D	T	T	T	T,P
Metaconule	A,P	T	T	D	A	W	W	T	D	D	D	D
Metaloph	CO	C	SC	VC	C	SC	C	CO	CO	CO	CO	CO
Protoconule	A	A	A	A	A	A	A	A	W	A	A	A

TABLE 14 CONTINUED

	Taxon[a]											
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12
Protoloph	C	C	C	C	C	C	C	C	C	C	C	C
Parastyle	T	T	D	D	T	D	A	D	D	D	D	T

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P.dalquesti*.

[b] A=absent, C=complete, CO=constricted, LA=large size (2.14-2.70, 2.70-3.30), M=near metacone, MI=middle size (1.66-1.97, 1.97-2.40), P=near paracone, SC=slightly constricted, SM=small size (1.26-1.70, 1.50-1.90), T=tiny, VC=very constricted, W=weak.

TABLE 15

Characters that separate dentary and incisors for *Protospermophilus dalquesti* from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Diastema	LS	-	LS	-	-	LS	-	LS	-	-	LS	LS	LS
Mental Foramen	DC	-	DVC	-	-	DVC	-	DA	-	-	DA	DVC	DA
Masseteric Scar	p4,P	-	p4,R	-	-	m1,P	-	m1,R	-	-	p4,P	m1,R	m1,R
Incisor Striated	-	-	MF	-	-	-	-	N	-	-	MF	N	-

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) S. *trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *P. dalquesti*.

TABLE 15 CONTINUED

[b] Characters: DA=near the dorsal edge of the diastema and anterior to the p4, DC=near the dorsal edge of the diastema and central to the p4 and incisor, DVA=dorsoventrally centered between the dorsal and ventral surfaces of the diastema and anterior to the p4, DVC=dorsoventrally centered between the dorsal and ventral surfaces of the diastema and centrally between the incisor and p4, FS=few striations, LS=long and shallow, MF=many fine striations, m1=masseteric scar ends below m1, N=no, P=pointed, p4=masseteric scar ends below p4, R=rounded, SD=short and deep, SP=superior position, SS=short and shallow, W=weakly, WB=well below the level of the diastema.

TABLE 16

Characters that separate p4s for *Protospermophilus dalquesti* from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	10	11	12	13	E_1
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	LA	LA
Anterioconid	A	A	A	A	-	A	-	W	A	-	A	W	W
Anterocinguid	SR-B	SR-B	A	A	-	A	-	A	A	-	A	A	A
P/M	Y	Y	Y	Y	-	V	-	Y	V	-	Y	Y	Y
Mesoconid	A-W	A	A	A	-	D	-	D	D	-	D	A	D
Entoconid	SU-W	SU	SU	SU	-	SU	-	D	D	-	SU	SU	D
Ectolophid	D	W	W	W	-	D	-	W	W	-	W	W	W
Mesostylid	D	A	A	A	-	W	-	A	W	-	A	A	W

TABLE 16 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *P. dalquesti*.

[b] Characters: A=absent, B=anteriorly bowed, D=distinct, LA=large size, MI=middle size, PS=partially submerged, P/M=Protoconid/Metaconid appressed (N=no, Y=yes, V=very appressed), SM=small size, SR=straight, SU=submerged,V=variable, W=weak.

TABLE 17

Characters that separate m1 and m2s for *Protospermophilus dalquesti* from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	LA	LA
Anterioconid	A	A	A	A	A	A	-	A	A	-	A	A	A
Anterocinguid	SR-B	B	SR-B	SR	B	B	-	B	B	-	B	SR	B
Mesoconid	A-S	A	A	V	A	D	-	D	S-A	-	D	A	D
Entoconid	SU-D	SU	PS	SU-D	SU	PS	-	D	D	-	PS	S	D
Ectolophid	D-W	D	W	D	W	D	-	D	D	-	W	W	D
Mesostylid	D-W	A	S	V	S	D	-	D	S	-	A	S	S

TABLE 17 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*,12) *P. vortmani*, 13) *P.* dalquesti.

[b] Characters: A=absent, B=anteriorly bowed, D=distinct, LA=large size, MI=middle size, PS=partially submerged, S=small, SM=small size, SR=straight, SU=submerged, W=weak, V=variable.

TABLE 18

Measurements (*mean, range, and n*) of upper cheekteeth of tamiine and marmotine squirrels from Eastgate.

Tooth and character		*Protospermophilus dalquesti*	*Miospermophilus cf. M. bryanti*	*Tamias sp.*
P3	AP		0.75, 0.68–0.88, 4	
	T		0.82, 0.76–0.91, 4	
DP4	AP			1.52, 1.40–1.71, 4
	T			1.39, 1.29–1.46, 4
P4	AP	2.47, 1	1.64, 1.60–1.67, 2	1.35, 1.20–1.54, 6
	T	2.64, 1	1.94, 1.80–2.10, 2	1.50, 1.38–1.59, 6
M1 or M2	AP		1.85, 1.72–1.97, 26	1.64, 1.52–1.75, 29
	T		2.23, 2.01–2.42, 26	1.95, 1.80–2.13, 29

TABLE 18 CONTINUED

Tooth and character			*Protospermophilus dalquesti*	*Miospermophilus cf. M. bryanti*	*Tamias sp.*
M1		AP	2.14, 1	1.77, 1.69–188, 3	
		T	2.96, 1	2.14, 2.10–2.20, 3	
M2		AP	2.37, 1	1.80, 1.80–1.81, 3	
		T	3.11, 1	2.24, 2.14–2.34, 3	
M3	AP		2.46, 1	2.06, 1.86–2.28, 7	1.95, 1
	T		2.70, 1	2.18, 2.10–2.34, 7	1.97, 1

TABLE 19

Measurements (mean, range, and n) of lower cheekteeth of tamiine and marmotine squirrels from Eastgate.

Tooth and character		*Protospermophilus. dalquesti*	*Miospermophilus.* cf. *M. bryanti*
dp4	AP		
	T		
p4	AP	2.22, 1	1.67, 1.55–1.78, 3
	T	2.12, 1	1.74, 1.54–1.93, 3
m1 or m2	AP		1.72, 1.61–1.91, 6
	T		1.88, 1.70–2.15, 6
m1	AP	2.12, 1	1.81, 1.72–1.90, 3
	T	2.42, 1	2.01, 1.94–2.10, 3
m2	AP	2.24, 1	2.15, 1
	T	2.41, 1	1.90, 1
m3	AP	2.93, 1	2.52, 1
	T	2.73, 1	1.72, 1

TABLE 19 CONTINUED

Measurements (mean, range, and n) of lower cheekteeth of tamiine and marmotine squirrels from Eastgate.

Tooth and character		*Miospermophilus hutchisoni*	*Tamias sp.*
dp4	AP	1.41, 1.11–1.71, 4	1.51, 1.26–1.65, 8
	T	1.30, 0.94–1.63, 4	1.34, 1.21–1.45, 8
p4	AP		1.41, 1.19–1.67, 14
	T		1.29, 1.07–1.80, 14
m1 or m2	AP		1.83, 1.63–2.00, 18
	T		1.97, 1.75–2.20, 18
m1	AP	1.89, 1.62–2.05, 8	1.71, 1.61–1.83, 4
	T	1.92, 1.40–2.14, 8	1.82, 1.76–1.89, 4
m2	AP	2.14, 1.94–2.35, 8	1.91, 1.60–2.10, 4
	T	2.10, 1.98–2.22, 8	2.06, 1.95–2.16, 4
m3	AP	2.47, 1.98–2.74, 9	2.20, 2.04–2.33, 4
	T	2.06, 1.82–2.19, 9	1.87, 1.80–1.92, 4

TABLE 20

Characters that separate P4s for *Miospermophilus* cf. *M. bryanti* from North American Miocene tamiines and marmotines.

	Taxon[a]											
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12
Size (L X W)	MI	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	MI
Mesostyle	S	-	A	S	S	-	S	S	S	S	S	D
Metaconule	D	-	S	S	A	-	S	S	D	D	D	D
Metaloph	CO	-	C	VC	C	-	CO	CO	CO	CO	CO	CO
Protoconule	A	-	A	A	S	-	A	A	A	A	A	S
Protoloph	C	-	C	C	C	-	C	C	C	C	C	CO
Parastyle	S	-	S	S	D	-	S	S	S	A	S	D

TABLE 20 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi, 6) Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *M.* cf. *M. bryanti*.

[b] Characters: A=absent, C=complete, CO=constricted, D=distinct, LA=large size, MI=middle size, S=small, SC=slightly constricted, SM=small size, VC=very constricted.

TABLE 21

Characters that separate M1 or M2s for *Miospermophilus* cf. *M. bryanti* from North American Miocene tamiines and marmotines.

	Taxon[a]											
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	MI
Mesostyle	A	A,T	T	T	A	D	D,M	D	T	T	T	S
Metaconule	A,P	T	T	D	A	W	W	T	D	D	D	S
Metaloph	CO	C	CO	VC	C	CO	C	CO	CO	CO	CO	CO
Protoconule	A	A	A	A	A	A	A	A	W	A	A	A,S
Protoloph	C	C	C	C	C	C	C	C	C	C	C	C
Parastyle	T	T	T	T	T	D	A	D	D	D	D	S

TABLE 21 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *M.* cf. *M. bryanti*.

[b] Characters: A=absent, C=complete, CO=constricted, LA=large size (2.14-2.70, 2.70-3.30), M=near metacone, MI=middle size (1.66-1.97, 1.97-2.40), P=near paracone, SM=small size (1.26-1.70, 1.50-1.90), T=tiny, VC=very constricted, W=weak.

TABLE 22

Characters that separate dentary and incisors for *Miospermophilus* cf. *M. bryanti* from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Diastema	LS	-	LS	-	-	LS	-	LS	-	-	LS	LS	LS
Mental Foramen	DC	-	DVC	-	-	DVC	-	DA	-	-	DA	DVC	DVC
Masseteric Scar	p4,P	-	p4,R	-	-	m1,P	-	m1,R	-	-	p4,P	m1,R	p4,R
Incisor Striated	-	-	MF	-	-	-	-	N	-	-	MF	N	-

TABLE 22 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *M.* cf. *M. bryanti*.

[b] Characters: DA=near the dorsal edge of the diastema and anterior to the p4, DC=near the dorsal edge of the diastema and central to the p4 and incisor, DVA=dorsoventrally centered between the dorsal and ventral surfaces of the diastema and anterior to the p4, DVC=dorsoventrally centered between the dorsal and ventral surfaces of the diastema and centrally between the incisor and p4, FS=few striations, LS=long and shallow, MF=many fine striations, m1=masseteric scar ends below m1, N=no, P=pointed, p4=masseteric scar ends below p4, R=rounded, SD=short and deep, SP=superior position, SS=short and shallow, W=weakly, WB=well below the level of the diastema.

TABLE 23

Characters that separate p4s for *Miospermophilus* cf. *M. bryanti* from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	LA	MI
Anterioconid	A	A	A	A	-	A	-	W	A	-	A	W	S
Anterocinguid	SR-B	SR-B	A	A	-	A	-	A	A	-	A	A	A
P/M	Y	Y	Y	Y	-	V	-	Y	V	-	Y	Y	Y
Mesoconid	A-W	A	A	A	-	D	-	D	D	-	D	A	A-S
Entoconid	SU-W	SU	SU	SU	-	SU	-	D	D	-	SU	SU	D
Ectolophid	D	W	W	W	-	D	-	W	W	-	W	W	W
Mesostylid	D	A	A	A	-	W	-	A	W	-	A	A	S

TABLE 23 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *M.* cf. *M. bryanti*.

[b] Characters: A=absent, B=anteriorly bowed, D=distinct, LA=large size, MI=middle size, PS=partially submerged, P/M=Protoconid/Metaconid appressed (N=no, Y=yes, V=very as to appears as a single cusp), SM=small size, SR=straight, SU=submerged,V=variable, W=weak.

TABLE 24

Characters that separate m1 or m2s for *Miospermophilus* cf. *M. bryanti* from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	LA	LA
Anterioconid	A	A	A	A	A	A	-	A	A	-	A	A	A
Anterocinguid	SR-B	B	SR-B	SR	B	B	-	B	B	-	B	SR	B
Mesoconid	A-S	A	A	V	A	D	-	D	S-A	-	D	A	V
Entoconid	SU-D	SU	PS	SU-D	SU	PS	-	D	D	-	PS	S	V
Ectolophid	D-W	D	W	D	W	D	-	D	D	-	W	W	W
Mesostylid	D-W	A	S	V	S	D	-	D	S	-	A	S	S

TABLE 24 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *M.* cf. *M. bryanti*.

[b] Characters: A=absent, B=anteriorly bowed, D=distinct, LA=large size, MI=middle size, PS=partially submerged, S=small, SM=small size, SR=straight, SU=submerged, W=weak, V=variable.

TABLE 25

Characters that separate M1 or M2s for *Miospermophilus hutchisoni* from North American Miocene tamiines and marmotines.

	Taxon[a]											
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	MI
Mesostyle	A	A,T	T	T	A	D	D,M	D	T	T	T	T,M
Metaconule	A,P	T	T	D	A	W	W	T	D	D	D	D
Metaloph	CO	C	CO	VC	C	CO	C	CO	CO	CO	CO	CO
Protoconule	A	A	A	A	A	A	A	A	W	A	A	A
Protoloph	C	C	C	C	C	C	C	C	C	C	C	C
Parastyle	T	T	T	T	T	D	A	D	D	D	D	T

TABLE 25 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *M. hutchisoni*.

[b] Characters: A=absent, C=complete, CO=constricted, D=distinct, LA=large size (2.14-2.70, 2.70-3.30), M=near metacone, MI=middle size (1.66-1.97, 1.97-2.40), P=near paracone, SM=small size (1.26-1.70, 1.50-1.90), T=tiny, VC=very constricted, W=weak.

TABLE 26

Characters that separate dentary and incisors for *Miospermophilus hutchisoni* from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Diastema	LS	-	LS	-	-	LS	-	LS	-	-	LS	LS	LS
Mental Foramen	DC	-	DVC	-	-	DVC	-	DA	-	-	DA	DVC	DVC
Masseteric Scar	p4,P	-	p4,R	-	-	m1,P	-	m1,R	-	-	p4,P	m1,R	m1,P
Incisor Striated	-	-	MF	-	-	-	-	N	-	-	MF	N	MF

TABLE 26 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *M. hutchersoni*.

[b] Characters: DA=near the dorsal edge of the diastema and anterior to the p4, DC=near the dorsal edge of the diastema and central to the p4 and incisor, DVA=dorsoventrally centered between the dorsal and ventral surfaces of the diastema and anterior to the p4, DVC=dorsoventrally centered between the dorsal and ventral surfaces of the diastema and centrally between the incisor and p4, FS=few striations, LS=long and shallow, MF=many fine striations, m1=masseteric scar ends below m1, N=no, P=pointed, p4=masseteric scar ends below p4, R=rounded, SD=short and deep, SP=superior position, SS=short and shallow, W=weakly, WB=well below the level of the diastema.

TABLE 27

Characters that separate m1 or m2s for *Miospermophilus hutchisoni* from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	LA	LA
Anterioconid	A	A	A	A	A	A	-	A	A	-	A	A	A
Anterocinguid	SR-B	B	SR-B	SR	B	B	-	B	B	-	B	SR	B
Mesoconid	A-S	A	A	V	A	D	-	D	S-A	-	D	A	D
Entoconid	SU-D	SU	PS	SU-D	SU	PS	-	D	D	-	PS	S	SU
Ectolophid	D-W	D	W	D	W	D	-	D	D	-	W	W	W
Mesostylid	D-W	A	S	V	S	D	-	D	S	-	A	S	A

TABLE 27 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *M. hutchisoni*.

[b] Characters: A=absent, B=anteriorly bowed, D=distinct, LA=large size, MI=middle size, PS=partially submerged, S=small, SM=small size, SR=straight, SU=submerged, W=weak, V=variable.

TABLE 28

Characters that separate P4s for *Tamias*. sp. from North American Miocene tamiines and marmotines.

	Taxon[a]											
Characters[b]	1	2	3	4	5	6	7	8	9	10	11	12
Size (L X W)	MI	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	MI
Mesostyle	S	-	A	S	S	-	S	S	S	S	S	A
Metaconule	D	-	S	S	A	-	S	S	D	D	D	D
Metaloph	CO	-	C	VC	C	-	CO	CO	CO	CO	CO	CO
Protoconule	A	-	A	A	S	-	A	A	A	A	A	A
Protoloph	C	-	C	C	C	-	C	C	C	C	C	C
Parastyle	S	-	S	S	D	-	S	S	S	A	S	S

TABLE 28 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi, 6) Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *T.* sp.

[b] Characters: A=absent, C=complete, CO=constricted, D=distinct, LA=large size, MI=middle size, S=small, SC=slightly constricted, SM=small size, VC=very constricted.

TABLE 29

Characters that separate M1 or M2s for *Tamias*. sp. from North American Miocene tamiines and marmotines.

	Taxon[a]										
Character[b]	1	2	3	4	5	6	7	9	10	11	12
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	MI
Mesostyle	A	A,T	T	T	A	D	D,M	D	T	T	S, D, M
Metaconule	A,P	T	T	D	A	W	W	T	D	D	A–S
Metaloph	CO	C	CO	VC	C	CO	C	CO	CO	CO	C,CS
Protoconule	A	A	A	A	A	A	A	A	W	A	A
Protoloph	C	C	C	C	C	C	C	C	C	C	C
Parastyle	T	T	T	T	T	D	A	D	D	D	S

TABLE 29 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *Tamias* sp.

[b] Characters: A=absent, C=complete, CO=constricted, LA=large size (2.14-2.70, 2.70-3.30), M=near metacone, MI=middle size (1.66-1.97, 1.97-2.40), P=near paracone, SM=small size (1.26-1.70, 1.50-1.90), T=tiny, VC=very constricted, W=weak.

TABLE 30

Characters that separate dentary and incisors for *Tamias*. sp. from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Diastema	LS	-	LS	-	-	LS	-	LS	-	-	LS	LS	LS
Mental Foramen	DC	-	DVC	-	-	DVC	-	DA	-	-	DA	DVC	DVC
Masseteric Scar	p4,P	-	p4,R	-	-	m1,P	-	m1,R	-	-	p4,P	m1,R	m1,R
Incisor Striated	-	-	MF	-	-	-	-	N	-	-	MF	N	FS

TABLE 30 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *Tamias* sp.

[b] Characters: DA=near the dorsal edge of the diastema and anterior to the p4, DC=near the dorsal edge of the diastema and central to the p4 and incisor, DVA=dorsoventrally centered between the dorsal and ventral surfaces of the diastema and anterior to the p4, DVC=dorsoventrally centered between the dorsal and ventral surfaces of the diastema and centrally between the incisor and p4, FS=few striations, LS=long and shallow, MF=many fine striations, m1=masseteric scar ends below m1, N=no, P=pointed, p4=masseteric scar ends below p4, R=rounded, SD=short and deep, SP=superior position, SS=short and shallow, W=weakly, WB=well below the level of the diastema.

TABLE 31

Characters that separate p4s for *Tamias*. sp. from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	LA	MI
Anterioconid	A	A	A	A	-	A	-	W	A	-	A	W	S
Anterocinguid	SR-B	SR-B	A	A	-	A	-	A	A	-	A	A	A
P/M	Y	Y	Y	Y	-	V	-	Y	V	-	Y	Y	Y
Mesoconid	A-W	A	A	A	-	D	-	D	D	-	D	A	S
Entoconid	SU-W	SU	SU	SU	-	SU	-	D	D	-	SU	SU	S
Ectolophid	D	W	W	W	-	D	-	W	W	-	W	W	W
Mesostylid	D	A	A	A	-	W	-	A	W	-	A	A	S

TABLE 31 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *Tamias* sp.

[b] Characters: A=absent, B=anteriorly bowed, D=distinct, LA=large size, MI=middle size, PS=partially submerged, P/M=Protoconid/Metaconid appressed (N=no, Y=yes, V=very appressed), SM=small size, SR=straight, SU=submerged, V=variable, W=weak.

TABLE 32

Characters that separate m1 or m2s for *Tamias*. sp. from North American Miocene tamiines and marmotines.

	Taxon[a]												
Character[b]	1	2	3	4	5	6	7	8	9	10	11	12	13
Size (L X W)	SM	SM	MI	MI	MI	MI	MI	LA	LA	LA	LA	LA	MI
Anterioconid	A	A	A	A	A	A	-	A	A	-	A	A	A
Anterocinguid	SR-B	B	SR-B	SR	B	B	-	B	B	-	B	SR	B
Mesoconid	A-S	A	A	V	A	D	-	D	S-A	-	D	A	V
Entoconid	SU-D	SU	PS	SU-D	SU	PS	-	D	D	-	PS	S	V
Ectolophid	D-W	D	W	D	W	D	-	D	D	-	W	W	V
Mesostylid	D-W	A	S	V	S	D	-	D	S	-	A	S	V

TABLE 32 CONTINUED

[a] 1) *Tamias* sp., 2) *T. ateles*, 3) *Miospermophilus bryanti*, 4) *M. wyomingensis*, 5) *M. lavertyi*, 6) *Spermophilus primitivus*, 7) *S. trephrus*, 8) *Protospermophilus angusticeps*, 9) *P. kelloggi*, 10) *P. malheurensis*, 11) *P. quatalensis*, 12) *P. vortmani*, 13) *Tamias* sp.

[b] Characters: A=absent, B=anteriorly bowed, D=distinct, LA=large size, MI=middle size, PS=partially submerged, S=small, SM=small size, SR=straight, SU=submerged, W=weak, V=variable.

TABLE 33

Measurements (mean, range, and n) of upper cheekteeth of petauristine squirrels from Eastgate.

Tooth and character		*Petauristodon axelrodi*	*Petauristodon savagei*	*Petauristodon czaplewskii*
P4	AP	1.01, 0.74–1.04, 2	1.70, 1	
	T	1.02, 1.00–2.04, 2	1.88, 1	
M1 or M2	AP	1.24, 1.17–1.30, 11		
	T	1.40, 1.32–1.45, 11		
M3	AP	1.52, 1	1.90, 1.77–2.02, 2	2.15, 2.01–2.31, 3
	T	1.26, 1	1.97, 1.85–2.10, 2	2.06, 1.91–2.19, 3

TABLE 34

Measurements (mean, range, and n) of lower cheekteeth of petauristine squirrels from Eastgate.

Tooth and character		*Petauristodon axelrodi*	*Petauristodon savagei*	*Petauristodon czaplewskii*
p4	AP	1.17, 0.94–1.30, 6	1.66, 1.53–1.80, 6	
	T	0.94, 0.78–1.05, 6	1.56, 1.36–1.69, 6	
m1 or m2	AP	1.38, 1.33–1.47, 3	2.00, 1.81–2.00, 4	2.00, 1.72–2.23, 21
	T	1.29, 1.21–1.37, 3	2.14, 1.98–2.33, 4	2.02, 1.74–2.21, 21
m1	AP			1.96, 1
	T			1.93, 1
m2	AP			2.30, 1
	T			2.14, 1
m3	AP	1.47, 1	2.37, 1	
	T	1.25, 1	1.99, 1	

TABLE 35

Measurements (mean, range, and N) of upper cheekteeth of *Monosaulax* species from literature (Stefen, 2001) and Eastgate.

Tooth and character		*Monosaulax lotseei*	*Monosaulax pansus*
DP4	AP	3.31, 3.06–3.94, 5	
	T	3.83, 3.23–4.80, 5	
P4	AP	3.60, 2.73–5.28, 15	4.85, 4.70–5.00, 6
	T	3.83, 3.22–5.11, 14	5.20, 4.90–5.70, 6
M1	AP	3.18, 2.84–3.56, 5	*3.10, 2.90–3.30, 20
	T	4.05, 2.73–5.38, 5	*3.50, 3.00–4.00, 20
M2	AP	3.46, 1	
	T	4.95, 1	
M3	AP	3.69, 1	3.10, 3.00–4.70, 11
	T	4.83, 1	3.33, 3.10–4.10, 11

* Indicates M1 or M2.

TABLE 36

Measurements (mean, range, and N) of lower cheekteeth of *Monosaulax* species from literature (Korth, 1999; Lindsay, 1972; Stefen, 2001) and Eastgate.

Tooth and character		*Monosaulax lotseei*	*Monosaulax tedi*	*Monosaulax curtus*	*Monosaulax pansus*
dp4	AP	4.24, 3.97–4.50, 4			
	T	3.27, 3.00–3.58, 4			
p4	AP	4.61, 3.00–6.12, 16	5.12, 4.40–5.80. 20	4.85, 4.40–5.30, 6	4.70, 3.20–6.00, 43
	T	4.10, 3.22–5.21, 15	3.31, 2.70–4.00, 20	3.75, 3.00–4.00, 6	3.90, 2.95–4.90, 43
m1	AP	3.51, 2.86–3.75, 7		3.40, 1	*3.40, 3.00–3.90, 34
	T	4.17, 3.73–4.57, 7		3.72, 1	*3.50, 2.90–4.00, 34
m2	AP	3.41, 2.76–3.70, 7			
	T	4.26, 4.02–4.50, 7			

TABLE 36 CONTINUED

Tooth and character		*Monosaulax lotseei*	*Monosaulax tedi*	*Monosaulax curtus*	*Monosaulax pansus*
m3	AP	4.00, 3.41–4.53, 4			
	T	3.56, 3.24–3.75, 4			

* = indicates m1 or m2.

TABLE 37

Measurements (mean, range, and n) of upper cheekteeth of *Pseudotheridomys* taxa from Eastgate (excluding *Pseudotheridomys* sp.).

Tooth and character		*Pseudotheridomys*		
		P. cuyamensis	*P. woodburnei*	*P. tedfordi*
DP4	AP	1.14, 1.04-1.28, 11		
	T	1.09, 0.99-1.21, 11		
P4	AP	1.13, 0.91-1.28, 53	2.00, 1.88-2.03, 2	2.88, 2.85-2.91, 2
	T	1.16, 0.83-1.34, 53	1.79, 1.79-1.80, 2	3.10, 3.00-3.20, 2
M1/2	AP	1.02, 0.77-1.18, 63	2.00, 1.92-2.07, 2	2.61, 2.49-2.69, 4
	T	1.20, 1.00-1.42, 63	2.22, 2.12-2.33, 2	2.85, 2.66-3.09, 4

TABLE 37 CONTINUED

Tooth and character		*Pseudotheridomys*		
		P. cuyamensis	*P. woodburnei*	*P. tedfordi*
M3	AP	0.74, 0.65-0.85, 8		2.12, 2.07-2.17, 2
	T	1.00, 0.95-1.10, 8		2.45, 2.28-2.61, 2

TABLE 38

Measurements (mean, range, and n) of lower cheekteeth of *Pseudotheridomys* taxa from Eastgate (excluding *Pseudotheridomys* sp.).

Tooth and character		*Pseudotheridomys*		
		P. cuyamensis	*P. woodburnei*	*P. tedfordi*
dp4	AP	1.27, 0.93-1.40, 28		
	T	0.85, 0.76-0.97, 28		
p4	AP	1.13, 0.93-1.29, 28	2.35, 2.27-2.43, 7	
	T	1.00, 0.70-1.20, 28	2.17, 2.09, 2.29, 7	
m1/2	AP	1.07, 0.80-1.26, 87	2.00, 1.74-2.58, 11	2.65, 2.50-2.91, 3
	T	1.08, 0.83-1.28, 87	2.23, 2.08-2.33, 11	2.91, 2.79-3.11, 3

TABLE 38 CONTINUED

Tooth and character		*Pseudotheridomys*		
		P. cuyamensis	*P. woodburnei*	*P. tedfordi*
m3	AP	0.92, 0.80-1.15, 26	1.86, 1.56-2.19, 3	2.39, 2.29-2.49, 2
	T	0.95, 0.78-1.09, 26	1.92, 1.82-2.02, 3	2.38, 2.32-2.43, 2

TABLE 39

Measurements (mean, range, and n) of known upper cheekteeth of *Pseudotheridomys*.

Tooth and character		*Pseudotheridomys*			
		P. cuyamensis	*P. hesperus*	*P. pagei*	* *P.* sp.
P4	AP	1.14, 1.02-1.22, 7	0.95, 0.90-1.00, 3	1.00, 0.98-1.06, 5	1.50, - , 1
	T	1.18, 1.08-1.29, 7	0.80, 0.7-0.90, 3	0.85, 0.78-0.89, 5	1.50, - , 1
M1	AP	0.99, 0.90-1.06, 12	1.12, - , 1	0.99, 0.95-1.02, 3	
	T	1.19, 1.09-1.24, 12	1.10, - , 1	0.99, 0.98-1.00, 3	
M2	AP		1.00, - , 1	0.76, - , 1	1.53, - , 1
	T		1.10, - , 1	0.93, - , 1	1.75, - , 1
M3	AP	0.85, 0.78-0.92, 5		0.65, - , 1	
	T	0.95, 0.89-1.09, 5		0.92, - , 1	

TABLE 39 CONTINUED

* Measurements reported by Korth (1992a, b) from the Harrison Formation, Cherry County Nebraska.

Other measuremnts are from the literature (Wilson, 1960; Shotwell, 1967; Lindsay, 1974a, b).

TABLE 40

Measurements (mean, range, and N) of known lower cheekteeth of *Pseudotheridomys*.

Tooth and character		*Pseudotheridomys*			
		P. cuyamensis	*P. hesperus*	*P. pagei*	* *P.* sp.
p4	AP	1.22, 1.17-1.26, 7	- , 0.90-1.00, 3	1.00, 0.98-1.06, 5	1.71, - , 1
	T	0.95, 0.85-0.99, 7	- , 0.70-0.90, 3	0.85, 0.78-0.89, 5	1.49, - , 1
m1	AP	1.11, 1.09-1.17, 4	1.15, 1.00-1.10, 2	1.00, 0.97-1.02, 5	
	T	1.10, 1.05-1.14, 4	1.15, 1.00-1.10, 2	0.96, 0.94-1.01, 5	
m2	AP	1.04, 0.90-1.12, 4	0.95, 0.90-1.00, 2	0.91, 0.89-0.95, 4	
	T	0.98, 0.92-1.03, 4	1.00, - , 1	0.94, 0.93-0.98, 4	
m3	AP	1.01, 0.86-1.12, 2		0.94, - , 1	
	T	0.90, 0.82-0.98, 2		0.84, - , 1	

TABLE 40 CONTINUED

* Measurements reported by Korth (1992a, b) from the Harrison Formation, Cherry County Nebraska.

Other measuremnts are from the literature (Wilson, 1960; Shotwell, 1967; Lindsay, 1974a,b).

TABLE 41

Measurements (mean, range, and n) of lower cheekteeth for heteromyid taxa (*Lignimus* and *Balantiomys*) from Eastgate.

Tooth and character		*Lignimus* cf. *L. transversus*	*Balantiomys borealis*	*Balantiomys nevadensis*
p4	AP	1.63, 1.58-1.69, 2	1.25, 1.08-1.35, 3	1.20, 1.17-1.23, 6
	T	1.52, 1.50-1.53, 2	1.34, 1.18-1.46, 3	1.39, 1.26-1.47, 6
m1 or m2	AP	1.32, 1.18-1.46, 2	1.22, 0.97-1.40, 17	1.20, 1.13-1.25, 15
	T	1.79, 1.71-1.87 2	1.42, 1.24-1.55, 17	1.46, 1.31-1.59, 15
m3	AP	1.12, 1.09-1.14, 3	1.14, 0.96-1.27, 9	1.17, 1.10-1.24, 5
	T	1.35, 1.29-1.38 3	1.34, 1.25-1.42, 9	1.30, 1.24-1.34, 5

TABLE 42

Measurements (mean, range, and n) of upper cheekteeth of *Balantiomys* taxa from Eastgate.

		Balantiomys	
Tooth and character		*B. borealis*	*B. nevadensis*
P4	AP	1.41, 1.12-1.59, 11	1.22, 1.08-1.46, 8
	T	1.57, 1.40-1.64, 11	1.30, 1.12-1.38, 8
M1 or M2	AP	1.15, 1.00-1.32, 29	1.15, 0.99-1.41, 22
	T	1.50, 1.35-1.71, 29	1.50, 1.36-1.60, 22
M3	AP	1.04, 0.90-1.17, 14	
	T	1.28, 1.20-1.41, 14	

TABLE 43

Measurements (mean, range, and n) of cheekteeth of *Cupidinimus* taxa from Eastgate.

Tooth and character		*Cupidinimus*		
		C. eastgatensis	*C. barnoskyi*	*C. boronensis*
p4	AP	1.23, 1.10-1.33, 13	0.89, 1	1.04, 0.92-1.16, 2
	T	1.30, 1.22-1.44, 13	0.97, 1	0.96, 0.88-1.04, 2
m1 or m2	AP	1.24, 0.97-1.37, 21	0.98, 2	0.99, 0.91-1.14, 3
	T	1.46, 1.19-1.57, 21	1.26, 1.25-1.28, 2	1.24, 1.20-1.27, 3
m3	AP	1.12, 1.09-1.14, 3	0.90, 0.85-0.95, 2	0.84, 0.72-0.91, 5
	T	1.35, 1.29-1.38, 3	1.22, 1.20-1.23, 2	1.10, 0.87-1.26, 5
P4	AP			1.28, 1.13-1.64, 12
	T			1.44, 1.32-1.55, 12

TABLE 43 CONTINUED

Tooth and character		*Cupidinimus*		
		C. eastgatensis	*C. barnoskyi*	*C. boronensis*
M1 or M2	AP			1.00, 0.85-1.21, 7
	T			1.23, 1.11-1.44, 7

TABLE 44

Measurements (mean, range, and n) of cheekteeth of geomoid taxa from Eastgate.

Tooth and character		Heteromyidae species indeterminate	*Mojavemys* cf. *M. magnumarcus*
p4	AP	0.89, 1	1.60, 1
	T	0.97, 1	1.71, 1
m1 or m2	AP	0.98, 2	1.58, 1.51-1.64, 2
	T	1.26, 1.25-1.28, 2	1.91, 1.84-1.97, 2
m3	AP	0.90, 0.85-0.95, 2	
	T	1.22, 1.23-1.43, 2	
P4	AP		1.66, 1.51-1.80, 2
	T		2.01, 2

TABLE 44 CONTINUED

Tooth and character		Heteromyidae species indeterminate	*Mojavemys* cf. *M. magnumarcus*
M1 or M2	AP		1.55, 1.38-1.72, 2
	T		2.05, 1.84-2.26, 2

TABLE 45

Measurements (mean, range, and n) of upper cheekteeth of *Macrognathomys* taxa from Eastgate and literature.

Tooth and character		*Macrognathomys shotwelli*	[a]*Macrognathomys* sp.
P4	AP	0.48, 0-0, 1	0.46, 0-0, 1
	T	0.51, 0-0, 1	0.57, 0-0, 1
M1	AP	1.00, 0.89-1.03, 5	0.94, 0-0, 1
	T	0.97, 0.81-1.03, 5	0.86, 0-0, 1
M2	AP	0.97, 0.87-1.08, 10	
	T	0.86, 0.78-0.98, 10	
M3	AP	1.16, 0-0, 1	
	T	0.91, 0-0, 1	

[a] Shotwell, 1968

TABLE 46

Measurements (mean, range, and n) of lower cheekteeth of *Macrognathomys* species from Eastgate and literature.

Tooth and character		*Macrognathomys*			
		M. shotwelli	[a]*M. gemmacollis*	[a]*M. nannus*	[b]M. sp.
m1	AP	1.00, 0.93-1.16, 10	1.09, 1	1.21, 1	1.00, 1
	T	0.74, 0.65-0.81, 10	0.80, 1	0.91, 1	0.66, 1
m2	AP	1.06, 0.94-1.15, 5	1.10, 1	1.20, 1	
	T	0.81, 0.75-0.87, 5	0.80, 1	0.91, 1	
m3	AP	0.89, 0.81-0.96, 4	1.09, 1	0.99, 1	
	T	0.69, 0.64-0.75, 4	0.81, 1	0.80, 1	

[a] Green, 1977. [b] Shotwell, 1968.

TABLE 47

Measurements (mean, range, and n) of upper cheekteeth of *Copemys* species from Eastgate.

Tooth and character		*Copemys*			
		C. tenuis	*C. russelli*	*C. tyleri*	*C. harperi*
M1	AP	1.96, 1.74-2.26, 41	1.93, 1.80-2.05, 17	1.94, 1.73-2.14, 21	1.91, 1.79-2.07, 21
	T	1.31, 1.11-1.48, 41	1.28, 1.18-1.40, 17	1.28, 1.18-1.41, 21	1.28, 1.17-1.40, 21
M2	AP	1.50, 1.40-1.70, 21	1.48, 1.32-1.62, 19	1.51, 1.24-1.71, 47	1.53, 1.41-1.67, 18
	T	1.33, 1.23-1.51, 21	1.30, 1.05-1.42, 19	1.32, 1.12-1.51, 47	1.34, 1.15-1.45, 18
M3	AP	1.07, 0.90-1.22, 18	1.08, 0.94-1.20, 15	1.08, 1.00-1.25, 16	1.11, 0.98-1.21, 15
	T	1.14, 0.98-1.31, 18	1.15, 1.04-1.22, 15	1.15, 1.06-1.25, 16	1.14, 1.00-1.33, 15

TABLE 48

Measurements (mean, range, and n) of lower cheekteeth of *Copemys* species from Eastgate.

Tooth and character		*Copemys*			
		C. tenuis	*C. russelli*	*C. tyleri*	*C. harperi*
m1	AP	1.67, 1.51-1.92, 63	1.64, 1.53-1.78, 20	1.66, 1.57-1.78, 24	1.57, 1.49-1.65, 10
	T	1.18, 1.10-1.34, 63	1.18, 1.09-1.37, 20	1.18, 1.02-1.37, 24	1.17, 1.07-1.35, 10
m2	AP	1.50, 1.28-1.65, 58	1.48, 1.40-1.65, 16	1.49, 1.34-1.66, 20	1.52, 1.41-1.69, 11
	T	1.24, 1.00-1.38, 58	1.22, 1.12-1.35, 16	1.23, 1.13-1.36, 20	1.23, 1.13-1.42, 11
m3	AP	1.37, 1.24-1.61, 26	1.38, 1.22-1.50, 13	1.38, 1.11-1.57, 20	1.38, 1.34-1.44, 4
	T	1.07, 0.86-1.21, 26	1.07, 0.98-1.23, 13	1.08, 0.93-1.23, 20	1.10, 1.07-1.14, 4

TABLE 49

Measurements (mean, range, and N) of upper cheekteeth of *Copemys* species from the literature.

Tooth and character		*Copemys*			
		[a]*C. tenuis*	[a]*C. russelli*	[a]*C. longidens*	[a]*C. niobraniensis*
M1	AP	1.74, 1.51-1.90, 15	1.73, 1.60-1.85, 10	1.90, 1.55-2.05, 54	1.89, 1
	T	1.13, 0.98-1.30, 17	1.13, 1.10-1.20, 12	1.27, 1.15-1.39, 53	1.26, 1
M2	AP	1.36, 1.22-1.50, 12	1.30, 1.15-1.40, 13	1.47, 1.35-1.70, 63	
	T	1.20, 1.05-1.30, 11	1.14, 1.05-1.25, 11	1.25, 1.07-1.45, 57	
M3	AP	0.96, 0.90-1.03, 9	0.95, 1	1.04, 0.75-1.15, 25	
	T	1.05, 0.97-1.10, 10	1.00, 1	1.05, 0.98-1.10, 25-	

TABLE 49 CONTINUED

Tooth and character		*Copemys*		
		[a]*C. barstowensis*	[a]*C. pagei*	[b]*C. pagei*
M1	AP	2.05, 2.05-2.06, 3	1.52, 1.48-1.55, 2	1.63, 1.51-1.74, 23
	T	1.33, 1.30-1.35, 3	0.99, 0.92-1.05, 2	1.03, 0.93-1.15, 23
M2	AP			1.22, 1.10-1.22, 12
	T			1.04, 0.98-1.13, 12
M3	AP	1.25, 1		0.96, 0.96-0.97, 5
	T	1.15, 1		0.95, 0.92-0.98, 5

[a] Lindsay (1972). [b] Shotwell (1967b).

•TABLE 50

Measurements (mean, range, and n) of lower cheekteeth of *Copemys* species from the literature.

Tooth and character		*Copemys*		
		[a]*C. tenuis*	[a]*C. russelli*	[a]*C. longidens*
m1	AP	1.63, 1.55-1.75, 10	1.48, 1.37-1.71, 6	1.72, 1.55-1.90, 52
	T	1.07, 1.03-1.11, 10	1.04, 1.00-1.12, 6	1.15, 1.00-1.30, 55
m2	AP	1.36, 1.28-1.45, 12	1.28, 1.20-1.35, 12	1.47, 1.35-1.60, 35
	T	1.15, 1.02-1.15, 12	1.01, 0.91-1.10, 13	1.17, 1.03-1.30, 36
m3	AP	1.23, 1.20-1.25, 3	1.21, 1.10-1.30, 9	1.33, 1.20-1.45, 23
	T	0.98, 0.90-1.05, 2	0.92, 0.80-1.00, 10	1.02, 0.95-1.10, 24

TABLE 50 CONTINUED

Tooth and character		*Copemys*		
		[a]*C. barstowensis*	[a]*C. pagei*	[b]*C. pagei*
m1	AP	1.77, 1.70-1.85, 8	1.49, - , 1	1.39, 1.26-1.53, 11
	T	1.18, 1.15-1.20, 8	1.10, - , 1	0.98, 0.92-1.07, 11
m2	AP	1.55, 1.50-1.60, 4	1.26, 1.20-1.32, 4	1.25, 1.23-1.28, 6
	T	1.19, 1.15-1.23, 4	0.98, 0.95-1.00, 3	1.02, 0.99-1.04, 6
m3	AP	1.54, 1.42-1.65, 2	1.01, 0.90-1.12, 2	1.17, 1.14-1.23, 5
	T	1.01, 1.00-1.02, 2	0.89, 0.77-1.00, 2	0.89, 0.85-0.93, 5

[a] Lindsay (1972). [b] Shotwell (1967b).

TABLE 51

Insectivores from Eastgate and comparisons to other known early Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian					
	Early					
Locality / Taxon	*C. neb.* AZ. Barstow	Mascall	Virgin Valley	Eubanks	Olcott	Ft. Polk
Plesiosorex cf. *coloradensis*						
Meterix sp.						
Mystipterus vespertilio						
Mystipterus cf. *M. pacificus*						
Domninoides sp.						
Gaillardia cf. *G. thomsoni*						
Pseudotrimylus cifellii, n. sp.						
Pseudotrimylus compressus						
Angustidens vireti						
Limnoecus tricupsis	S					

TABLE 51 CONTINUED

	Barstovian					
	Early					
Locality / Taxon	*C. neb.* AZ. Barstow	Mascall	Virgin Valley	Eubanks	Olcott	Ft. Polk
Limnoecus niobrarensis						S
Alluvisorex arcadentes						
Adeloblarina sp. indet.						
Antesorex compressus						

TABLE 52

Insectivores from Eastgate and comparisons to other known late Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian										
	Late										
Locality / Taxon	L. strirt. AZ Barstow	C. long. AZ Barstow	C. russ. AZ Barstow	Dome Springs	Tonapah	Quartz Basin	Anceney	Norden Bridge	Red Basin	Kleinfelder Fm.	Colter Formation
Plesiosorex cf. *coloradensi*											
Meterix sp.						G			G		
Mystipterus vespertilio						G			G		
Mystipterus cf. *M. pacificus*						S			G		
Domninoides sp.			G			G				G	G
Gaillardia cf. *G. thomsoni*											
Pseudotrimylus cifellii, n. sp.											
Pseudotrimylus compressus									G	G	

TABLE 52 CONTINUED

Taxon \ Locality	Barstovian: Late: L. strirt. AZ Barstow	C. long. AZ Barstow	C. russ. AZ Barstow	Dome Springs	Tonapah	Quartz Basin	Anceney	Norden Bridge	Red Basin	Kleinfelder Fm.	Colter Formation
Angustidens vireti											
Limnoecus tricupsis	S	S	S		S				G		
Limnoecus niobrarensis											
Alluvisorex arcadentes						S			S		
Adeloblarina sp. indet.											
Antesorex compressus											

TABLE 53

Lagomorphs from Eastgate and comparisons to other known early Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian					
	Early					
Locality / Taxon	*C. neb.* AZ. Barstow	Mascall	Virgin Valley	Eubanks	Olcott	Ft. Polk
Desmatolagus cf. *D. schizopetrus*						
Oreolagus nebrascensis			G			
Oreolagus colteri						
Russellagus cf *R. vonhofi*						
Hypolagus parviplicatus	S	G	G			G
Hypolagus fontinalis						
Pronotolagus sp. indet.						

TABLE 54

Lagomorphs from Eastgate and comparisons to other known late Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian										
	Late										
Locality / Taxon	L. strirt. AZ Barstow	C. long. AZ Barstow	C. russ. AZ Barstow	Dome Springs	Tonapah	Quartz Basin	Anceney	Norden Bridge	Red Basin	Kleinfelder Fm.	Colter Formation
Desmatolagus cf. *D. schizopetrus*											
Oreolagus nebrascensis											
Oreolagus colteri											S
Russellagus cf *R. vonhofi*										S	
Hypolagus parviplicatus	S	S	S	G	G	G			G	G	G
Hypolagus fontinalis											
Pronotolagus sp. indet.											

TABLE 55

Aplodontids, mylaugulids, sciurids, castorids, and eomyids from Eastgate and comparisons to other known early Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian					
	Early					
Locality / Taxon	*C. neb.* AZ. Barstow	Mascall	Virgin Valley	Eubanks	Olcott	Ft. Polk
Tardontia nevadans			G			
Mesogaulus paniensis						
Protospermophilus dalquesti,						
Miospermophilus cf *M. bryanti*						
Miospermophilus hutchisoni						
Tamias sp. indet.						
Micropetauristodon vestali						
Petauristodon axelrodi						G
Petauristodon savagei						
Petauristodon czaplewskii						

TABLE 55 CONTINUED

Taxon \ Locality	Barstovian: Early: *C. neb.* AZ. Barstow	Mascall	Virgin Valley	Eubanks	Olcott	Ft. Polk
Monosaulax lotseei			G	G	G	
Pseudotheridomys woodburnei						
Pseudotheridomys cuyamensis						
Leptodontomys sp.						

TABLE 56

Aplodontids, mylaugulids, sciurids, castorids, and eomyids from Eastgate and comparisons to other known early Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian										
	Late										
Locality / Taxon	L. strirt. AZ Barstow	C. long. AZ Barstow	C. russ. AZ Barstow	Dome Springs	Tonapah	Quartz Basin	Anceney	Norden Bridge	Red Basin	Kleinfelder Fm.	Colter Formation
Tardontia nevadans											
Mesogaulus paniensis							G				
Protospermophilus dalquesti,									G		
Miospermophilus cf *M. bryanti*		G	G								
Miospermophilus hutchisoni											
Tamias sp. indet.	G	G	G				G	G	G	G	G
Micropetauristodon vestali											
Petauristodon axelrodi		G	G	G						G	G
Petauristodon savagei											
Petauristodon czaplewskii											

TABLE 56 CONTINUED

Taxon \ Locality	Barstovian: Late: L. strirt. AZ Barstow	C. long. AZ Barstow	C. russ. AZ Barstow	Dome Springs	Tonapah	Quartz Basin	Anceney	Norden Bridge	Red Basin	Kleinfelder Fm.	Colter Formation
Monosaulax lotseei	G	G				G	G		G		G
Pseudotheridomys woodburnei						G			G		G
Pseudotheridomys cuyamensis											
Leptodontomys sp.	S					S		G		S	

TABLE 57

Heteromyids, zapodids, and cricetids from Eastgate and comparisons to other known early Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian					
	Early					
Locality / Taxon	*C. neb.* AZ. Barstow	Mascall	Virgin Valley	Eubanks	Olcott	Ft. Polk
Lignimus cf. *L. transversus*						
Balantiomys cf. *B. borealis*						
Balantiomys nevadensis						
Cupidinimus eastgatensis	G					
Cupidinimus bamoskyi						
Cupidinimus boronensis						
Mojavemys cf. *M. magnumarcus*	G					
Macrognathomys shotwelli						
Copemys tenuis	G					G
Copemys russelli						
Copemys tyleri						
Copemys harperi						

TABLE 58

Heteromyids, zapodidis, and cricetids from Eastgate and comparisons to other known early Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian										
	Late										
Locality / Taxon	L. strirt. AZ Barstow	C. long. AZ Barstow	C. russ. AZ Barstow	Dome Springs	Tonapah	Quartz Basin	Anceney	Norden Bridge	Red Basin	Kleinfelder Fm.	Colter Formation
Lignimus cf. *L. transversus*										G	S
Balantiomys cf. *B. borealis*										S	
Balantiomys nevadensis											
Cupidinimus eastgatensis	G	G	G				G	G			G
Cupidinimus barnoskyi											
Cupidinimus boronensis											
Mojavemys cf. *M. magnumarcus*	G	G	G								S
Macrognathomys shotwelli											
Copemys tenuis	S	S				G	G	G	G		G
Copemys russelli		S	S								
Copemys tyleri											
Copemys harperi											

TABLE 59

Carnivores and ungulates from Eastgate and comparisons to other known early Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian					
	Early					
Locality / Taxon	*C. neb.* AZ. Barstow	Mascall	Virgin Valley	Eubanks	Olcott	Ft. Polk
Tomarctus cf. *T. brevirostris*		G	G		G	
Leptocyon sp. indet.						
Bassariscus cf. *B. parvus*			G		G	
cf. *Promartes* sp.						
Ticholeptus sp. indet.					G	
Aletomeryx sp. indet.						
Merychippus sp. indet.		G	G	G	G	G
Moropus sp. indet.					G	
Teleoceras sp. indet.					G	

TABLE 60

Carnivores and ungulates from Eastgate and comparisons to other known early Barstovian faunas from North America. S = presence of species, G = presence of genus, and blank cell = no occurrence.

	Barstovian										
					Late						
Locality / Taxon	L. strirt. AZ Barstow	C. long. AZ Barstow	C. russ. AZ Barstow	Dome Springs	Tonapah	Quartz Basin	Anceney	Norden Bridge	Red Basin	Kleinfelder Fm.	Colter Formation!
Tomarctus cf. *T. brevirostris*				G					G	G	
Leptocyon sp. indet.					G					G	
Bassariscus cf. B. parvus						G			G	G	
cf. *Promartes* sp.											
Ticholeptus sp. indet.						G				G	
Aletomeryx sp. indet.											
Merychippus sp. indet.						G	G			G	G
Moropus sp. indet.											
Teleoceras sp. indet.											

FIGURE LEGENDS

FIGURE 1. Eastgate study area. Black rectangle within Nevada state boundary indicates general geographic location of study area and topographic map below shows area (black square) Eastgate vertebrate fossil localities of Barstovian age and part of area prospected during 1996 field season by OMNH crew. Nevada state is modified from the USGS index to topographic map for state of Nevada, while topographic map was modified from part of Smith Creek Valley 36' Quad.

FIGURE 2. North-facing rock outcrops of Monarch Mill Formation showing beds dipping basinward, breccia (indicated by arrow and letter A), and conglomerate above breccia (indicated by arrow and letter B).

FIGURE 3. West-facing slope showing basal part of Monarch Mill Formation with breccia (indicated by arrow and letter A) and conglomerate (indicated by arrow and letter B). Individual in picture is about 1.8 m in height. Letters are same location as those in figure 2.

FIGURE 4. Panoramic view of North-west facing outcrops of Monarch Mill Formation showing topographic features separating most of fossil localities of Eastgate fauna.

FIGURE 5. South-facing slope of the Monarch Mill Formation with following fossil localities indicated by arrows and numbers: 1, UCMP V70144; 2, UCMP V70145; 3, UCMP V70142; 4, UCMP V70140; 5, UCMP V70143; 6, UCMP V87139; and 7, UCMP V8808. Stratigraphic unit 2 with three of five subunits (A-F) indicated by letters B, C, and F, respectively.

FIGURE 6. Horseshoe-shaped slope opening to west showing localities UCMP V70147, UCMP V74103, UCMP V67245, and OMNH V976 indicated with arrows and letters A-D, respectively.

FIGURE 7. West-facing slope showing localities UCMP V70138 and OMNH V974, which are indicated with arrows and letters A-B, respectivlely.

FIGURE 8A. Measurements taken on p3 of Eastgate lagomorphs. A-D: equals transverse width of tooth; E-F, equals anteroposterior length; B-D, equals depth of posterior external reentrant (PER); C-D, equals depth of anterior external reentrant (AER).

FIGURE 8B. Reentrants described and measured on P2 of lagomorphs are internal anterior reentrant (IAR), medial anterior reentrant (MAR), external anterior reentrant (EAR).

FIGURE 8C. Reentrants described and measured on p3 of lagomorphs are anterior internal reentrant (AIR), anterior reentrant (AR), anterior external reentrant (AER), thin enamel (TN), thick enamel (TH), posterior external reentrant (PER). Modified from White (1987).

FIGURE 9. Scatterplot of length vs. width (mean values) of P4s for species of Petauristinae from the Tertiary of North America taken from literature (Black, 1962; James, 1963; Lindsay, 1972; Pratt and Morgan, 1989) and Eastgate. Species numbers: 1) *P. pattersoni*; 2) *P. jamesi*; 3) *P. matthewsi*; 4) *P. savagei*; 5) *P. axelrodi*; 6) *P. minimus*.

FIGURE 10. Scatterplot of length vs. width (mean values) of M1 or M2s for species of Petauristinae from the Tertiary of North America taken from

literature (Black, 1962; James, 1963; Lindsay, 1972; Pratt and Morgan, 1989) and Eastgate. Species numbers: 1) *P. jamesi*; 2) *P. matthewsi*; 3) *P. pattersoni*; 4) *P. uphami*, 5) *P. axelrodi*; 6) *M. vestali*

FIGURE 11. Scatterplot of length vs. width (mean values) of M3s for species of Petauristinae from the Tertiary of North America taken from literature (Black, 1962; James, 1963; Lindsay, 1972; Pratt and Morgan, 1989) and Eastgate. Species numbers: 1) *P. pattersoni*; 2) *P. jamesi*; 3) *P. mattewsi*; 4) *P. uphami*, 5) *P. czaplewskii*, 6) *P. savagei*, 7) *P. axelrodi*; 8) *P. minimus*.

FIGURE 12. Scatterplot of length vs. width (mean values) of p4s for species of Petauristinae from the Tertiary of North America taken from literature (Black, 1962; James, 1963; Lindsay, 1972; Pratt and Morgan, 1989) and Eastgate. Species numbers: 1) *P. matthewsi*; 2) *P. pattersoni*; 3) *P. savagei*, 4) *P. axelrodi*.

FIGURE 13. Scatterplot of length vs. width (mean values) of m1 or m2s for species of Petauristinae from the Tertiary of North America taken from literature (Black, 1962; James, 1963; Lindsay, 1972; Pratt and Morgan, 1989) and Eastgate. Species numbers: 1) *P. pattersoni*; 2) *P. jamesi*; 3) *P. matthewsi*, 4) *P.* czaplewksii, 5) *P. savagei*, 6) *P. axelrodi*.

FIGURE 14. Scatterplot of length vs. width (mean values) of m3s for species of Petauristinae from the Tertiary of North America taken from literature (Black, 1962; James, 1963; Lindsay, 1972; Pratt and Morgan, 1989) and Eastgate. Species numbers: 1) *P. pattersoni*; 2) *P. jamesi*; 3) *P. matthewsi*, 4) *P.*

savagei, 5) *P. axelrodi.*

FIGURE 15. Scatterplot of length vs. width (mean values) of P4s for *Pseudotheridomys* species taken from literature (Wilson, 1960; Shotwell, 1967; Lindsay, 1974; Korth, 1992) and from Eastgate specimens. Species numbers: 1) *P. hesperus*; 2) *P. pagei*; 3) *P. cuyamensis*; 4) *P. cuyamensis* (Eastgate); 5) *P. woodburnei* n. sp.; 6) *P. tedfordi* n. sp.; 7) *P.* sp.

FIGURE 16. Scatterplot of length vs. width (mean values) of M1 or M2s for *Pseudotheridomys* species taken from literature (Wilson, 1960; Shotwell, 1967; Lindsay, 1974; Korth, 1992) and from Eastgate specimens. Species numbers: 1) *P. hesperus*; 2) *P. pagei*; 3) *P. cuyamensis*; 4) *P. cuyamensis*; 5) *P. woodburnei* n. sp.; 6) *P. tedfordi* n. sp.; 7) *P.* sp.

FIGURE 17. Scatterplot of length vs. width (mean values) of p4s for *Pseudotheridomys* species taken from literature (Wilson, 1960; Shotwell, 1967; Lindsay, 1974; Korth, 1992) and from Eastgate specimens. Species numbers: 1) *P. hesperus*; 2) *P. pagei*; 3) *P. cuyamensis*; 4) *P. cuyamensis*; 5) *P. woodburnei* n. sp.; 6) *P.* sp.

FIGURE 18. Scatterplot of length vs. width (mean values) of m1 or m2s for *Pseudotheridomys* species taken from literature (Wilson, 1960; Shotwell, 1967; Lindsay, 1974; Korth, 1992) and from Eastgate specimens. Species numbers: 1) *P. hesperus*; 2) *P. pagei*; 3) *P. cuyamensis*; 4) *P. cuyamensis*; 5) *P. woodburnei* n. sp.; 6) *P. tedfordi* n. sp.

FIGURE 19. Scatterplot of length vs. width (mean values) of M1s for

Copemys specimens of Eastgate. Species numbers: 1) *C. tyleri* n. sp.; 2) *C. harperi* n. sp.; 3) *C. russelli*; 4) *C. tenuis*.

FIGURE 20. Scatterplot of length vs. width (mean values) of m1s for *Copemys* specimens of Eastgate. Species numbers: 1) *C. tyleri* n. sp.; 2) *C. harperi* n. sp.; 3) *C. russelli*; 4) *C. tenuis*.

FIGURE 1

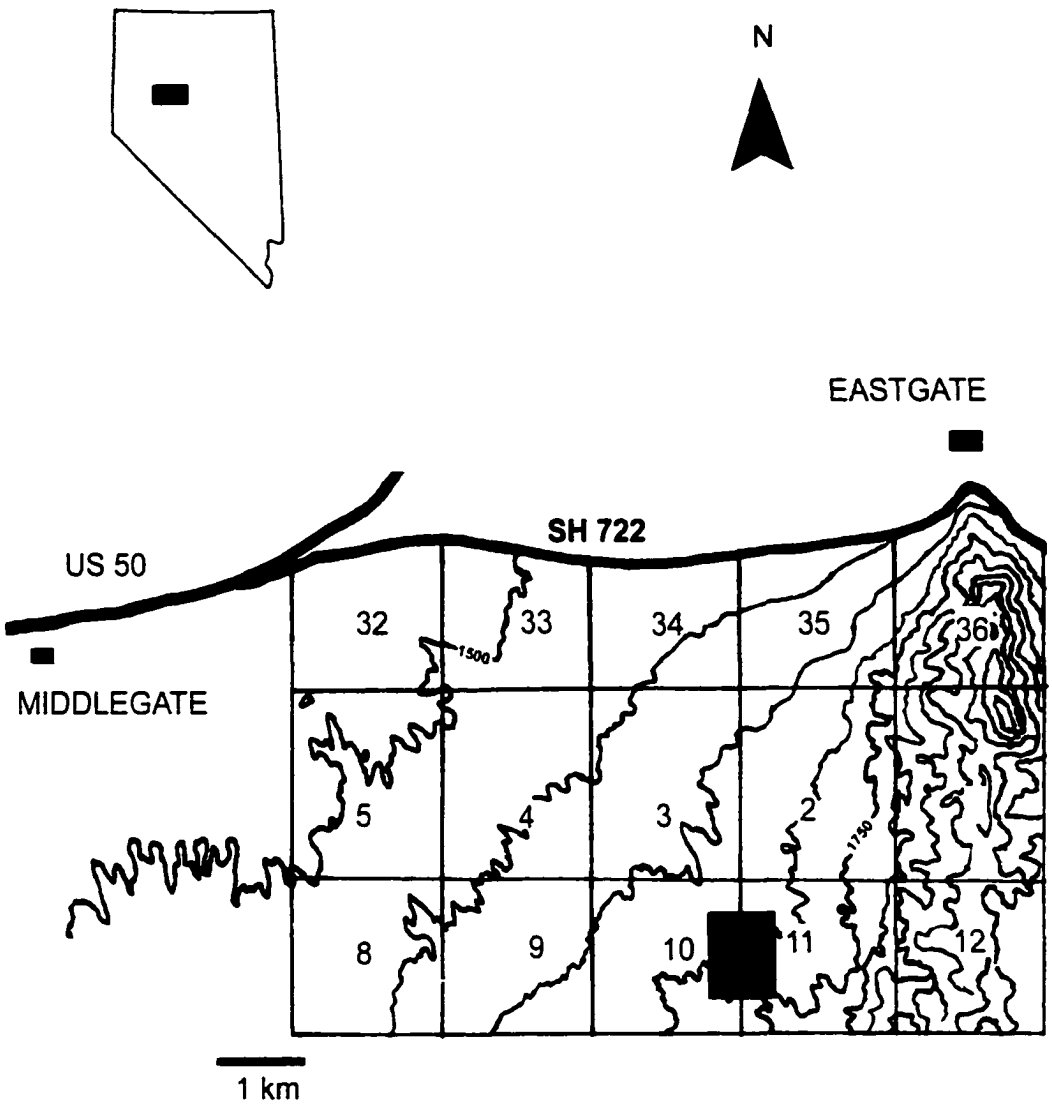

N
EASTGATE
SH 722
US 50
MIDDLEGATE
32
33
34
35
36
1500
5
4
3
2
1750
8
9
10
11
12
1 km

FIGURE 2

FIGURE 3

FIGURE 4

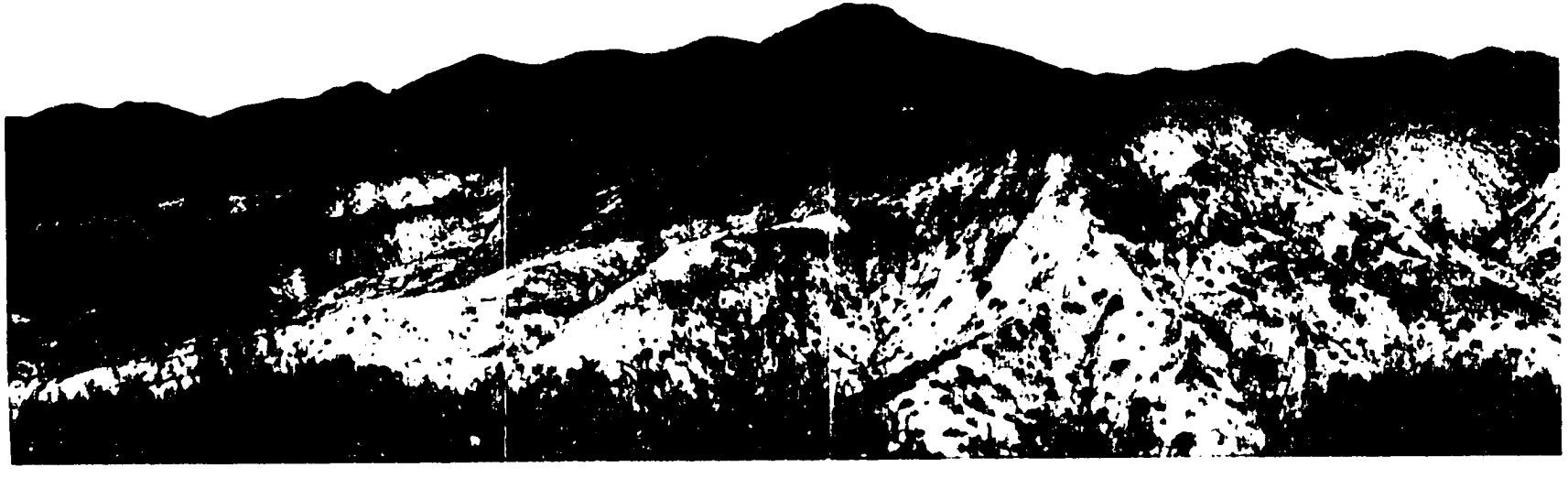


FIGURE 5

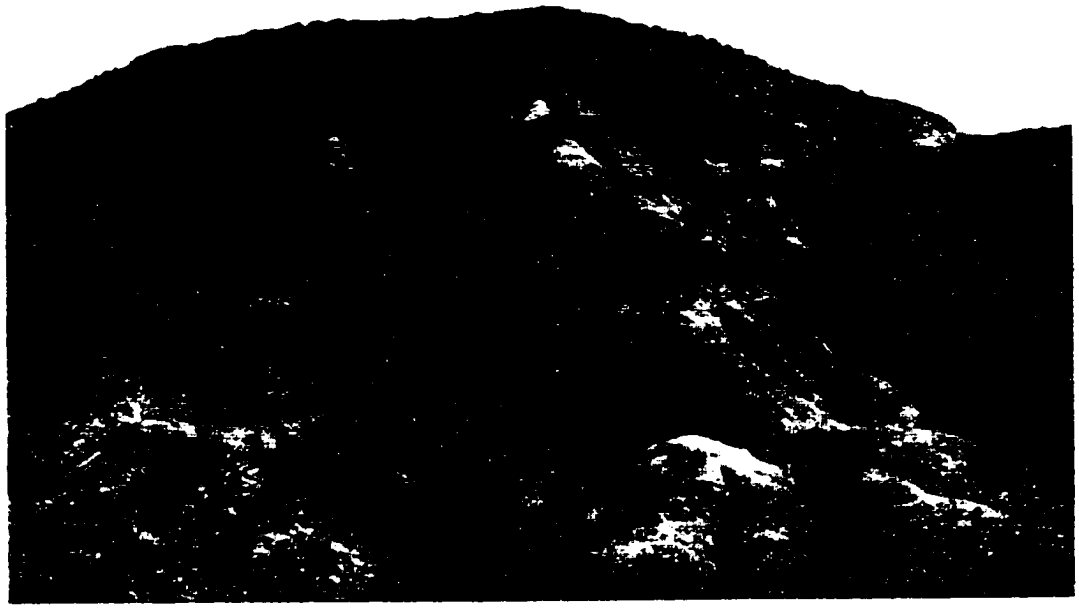


FIGURE 6

FIGURE 7

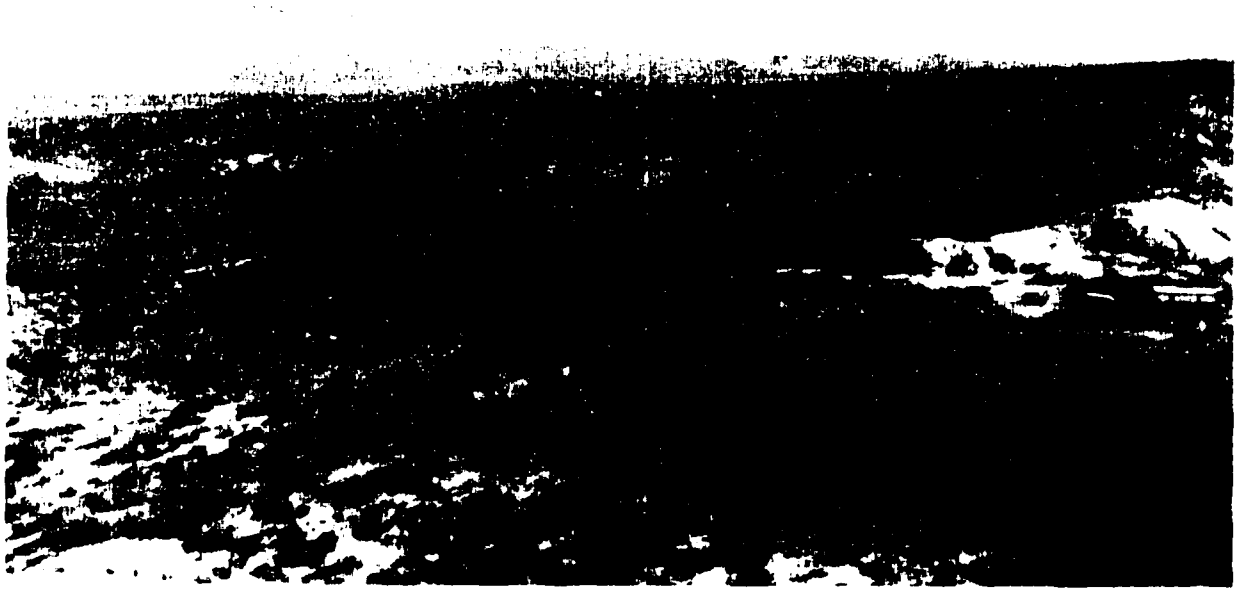
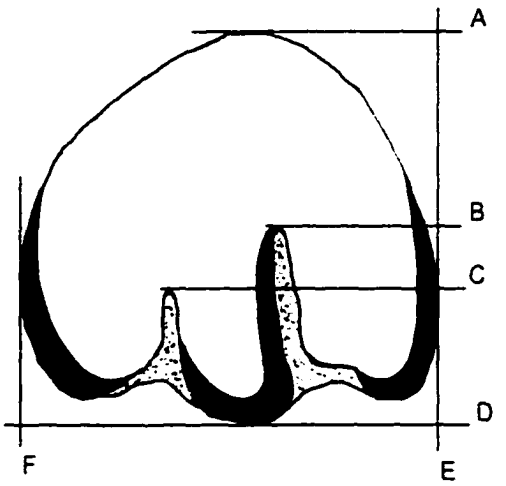


FIGURE 8



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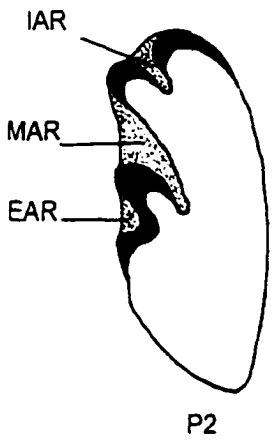

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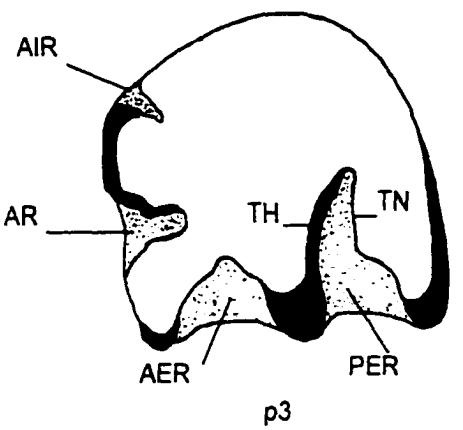


C

FIGURE 9

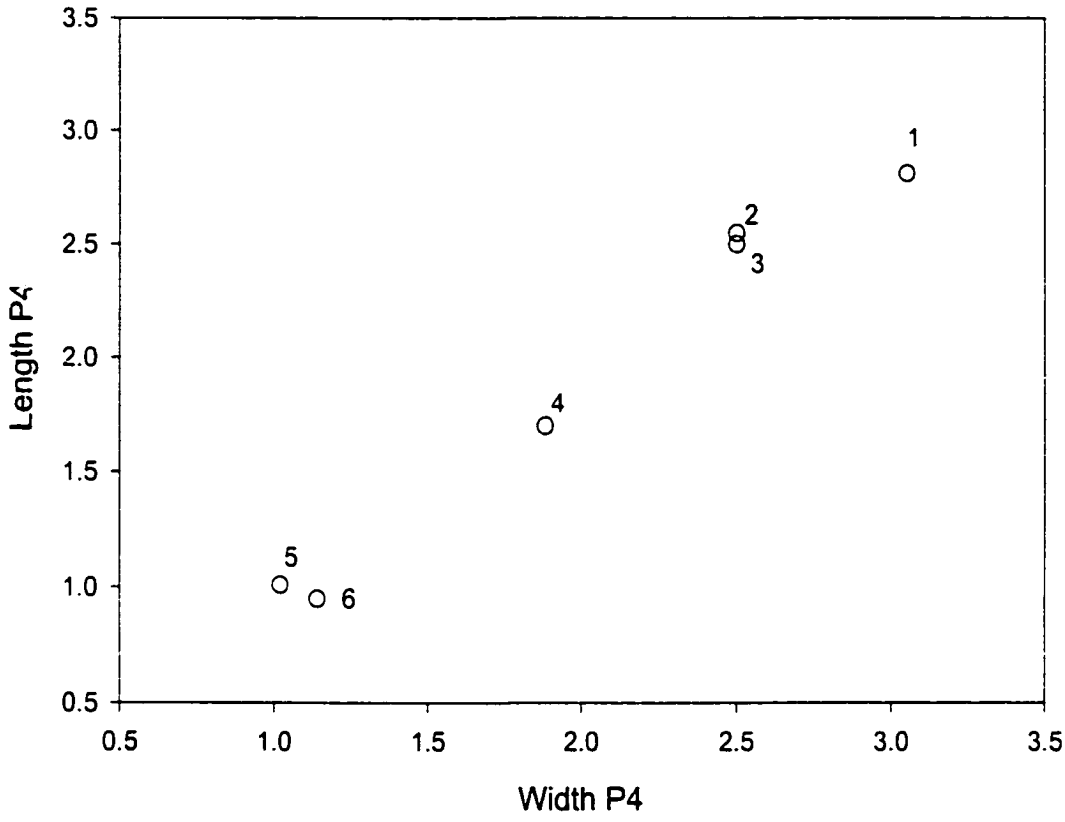
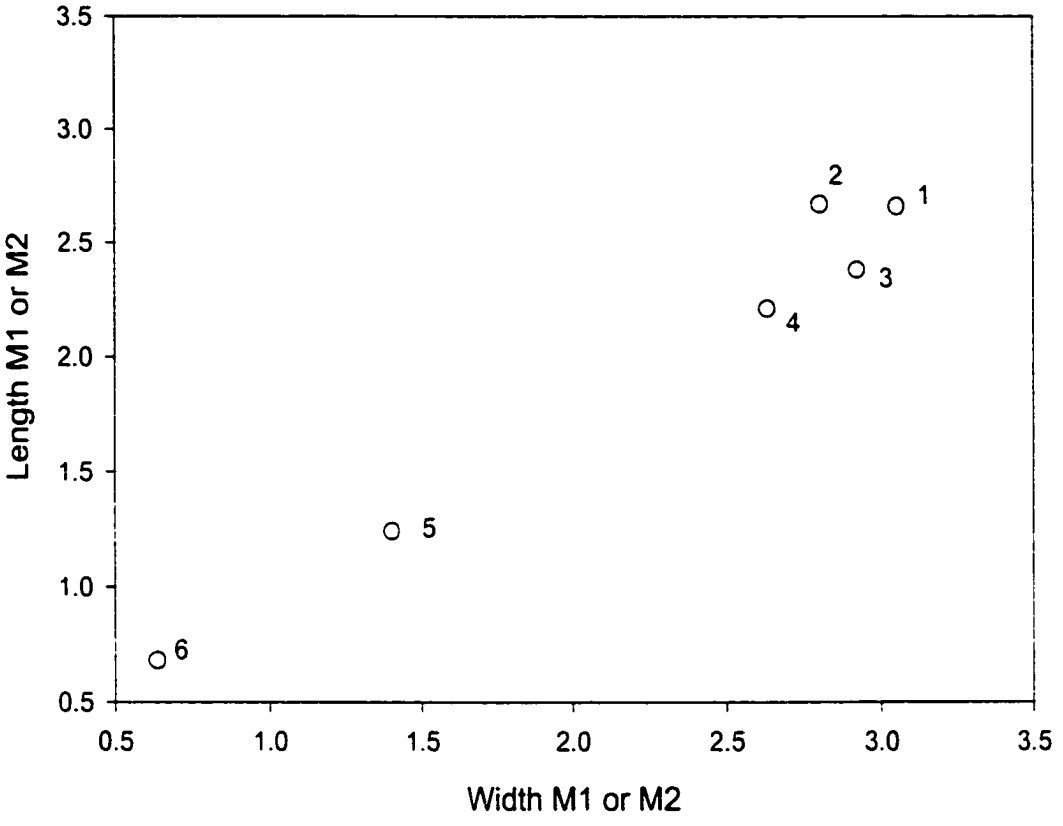


FIGURE 10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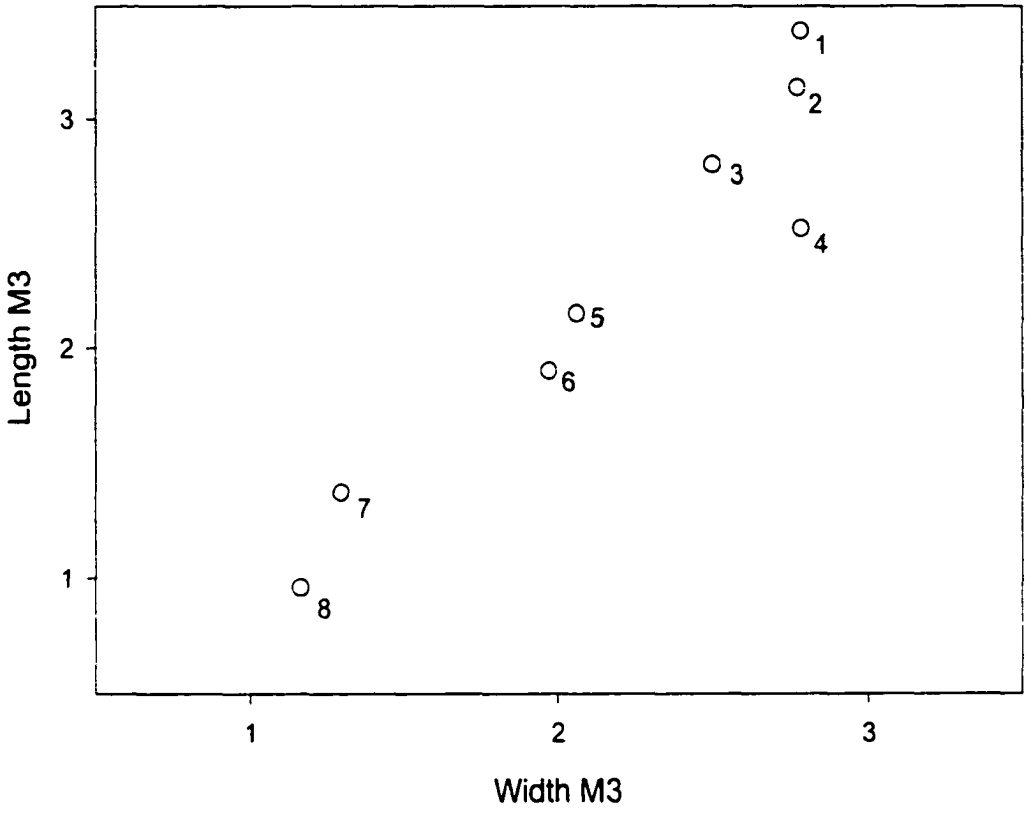
2.5
2.0
1.5
1.0
0.5
Length M1 or M2
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Width M1 or M2
1
2
3
4
5
6

FIGURE 11



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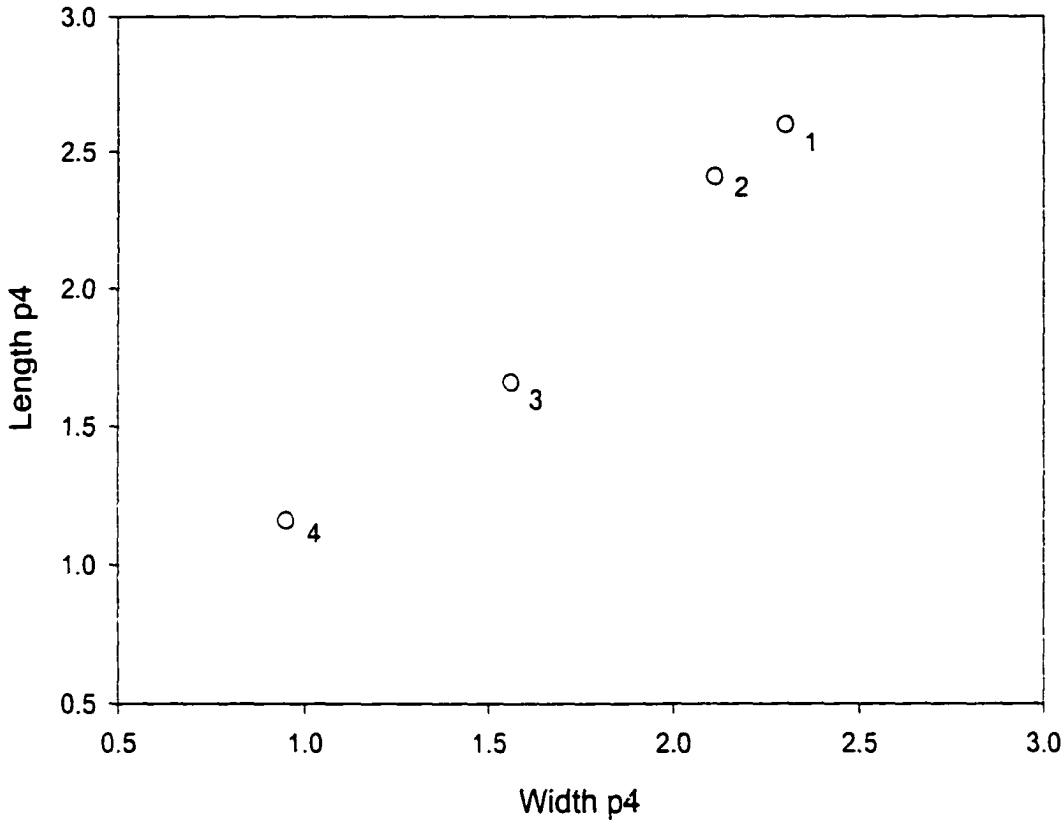


FIGURE 13

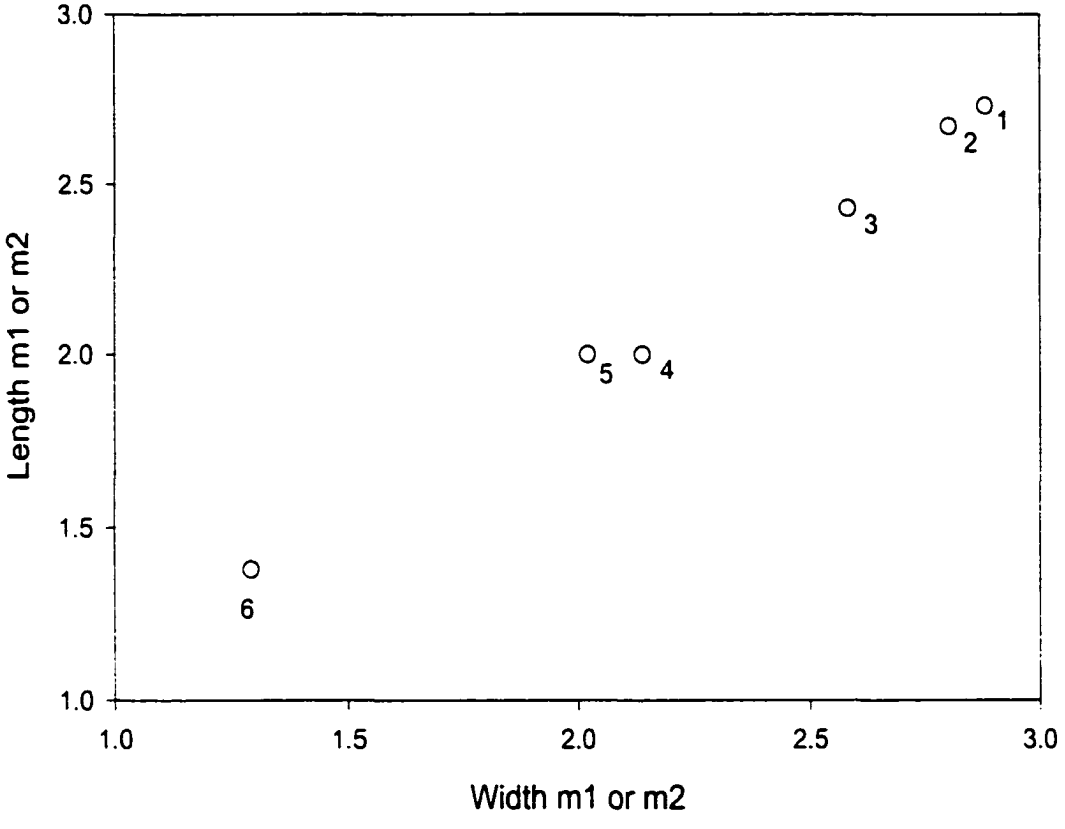


FIGURE 14

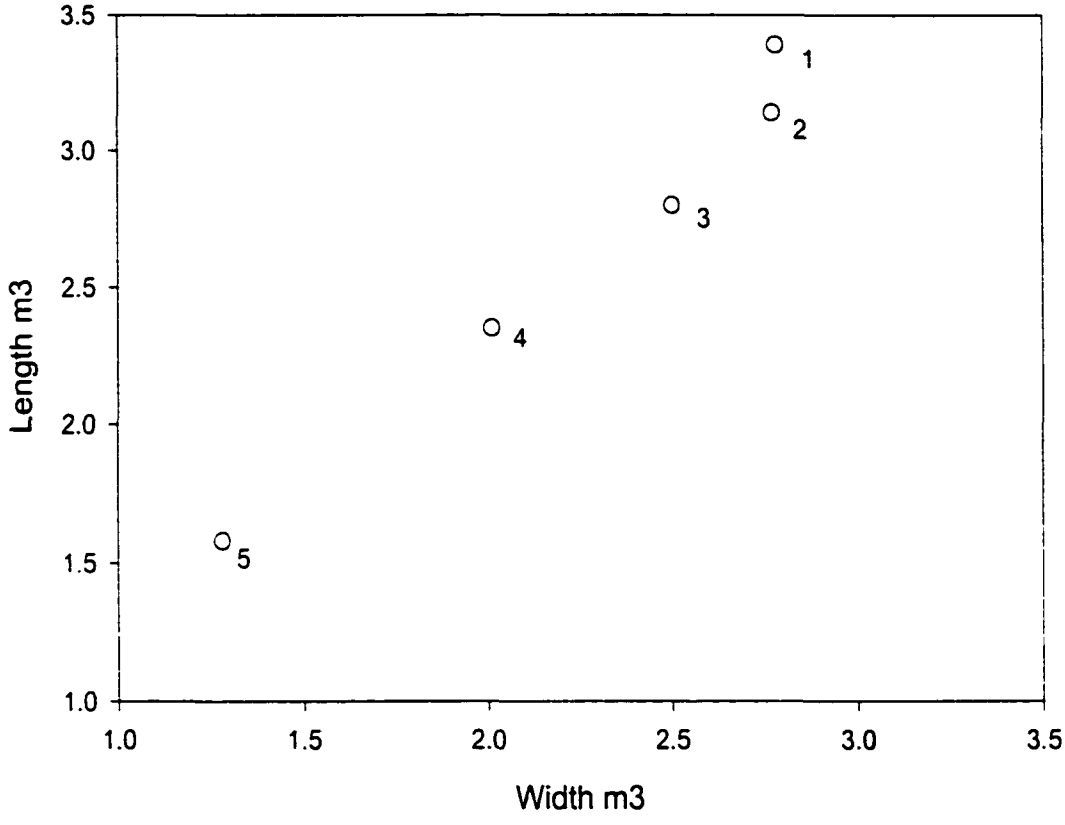
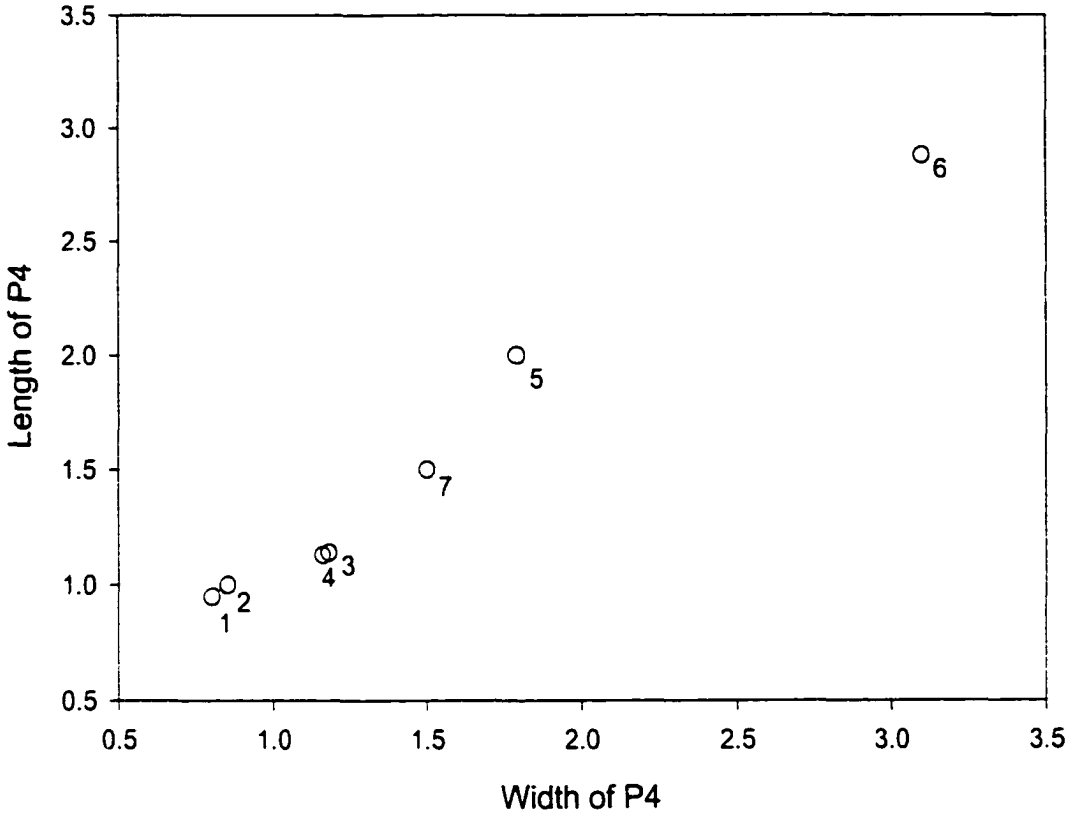


FIGURE 15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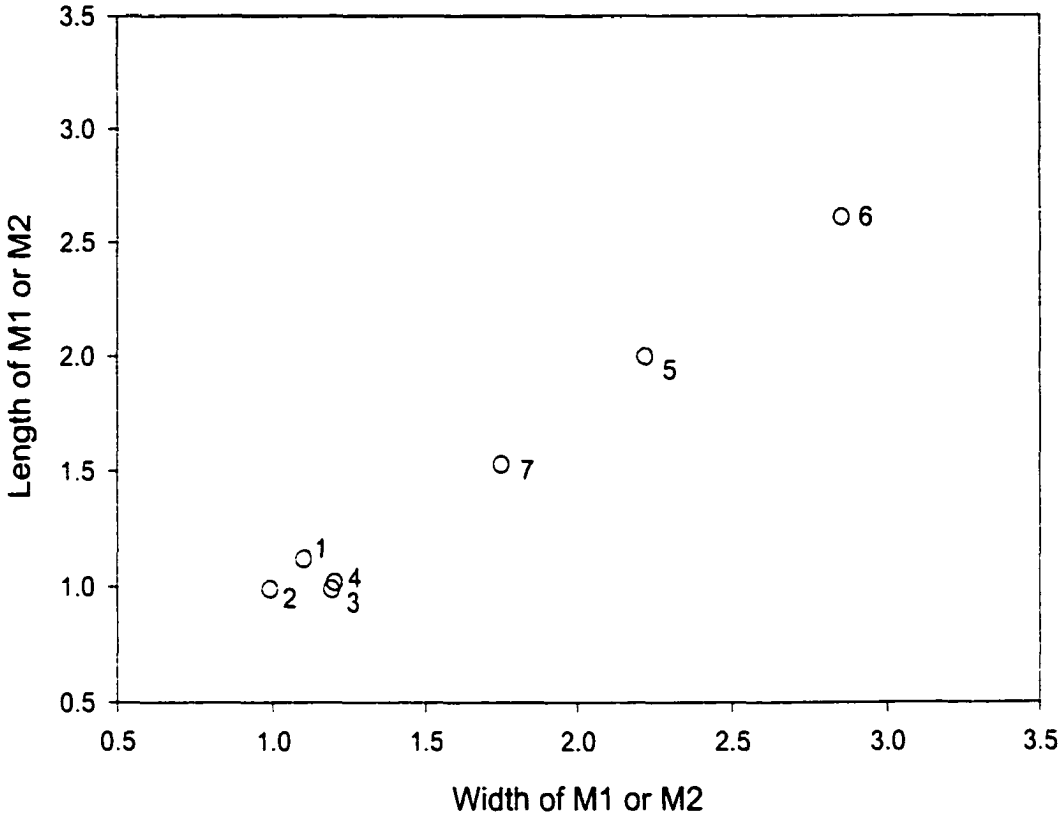
3.0
2.5
2.0
1.5
1.0
0.5
Length of P4
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Width of P4
1
2
3
4
5
6
7

FIGURE 16


Length of M1 or M2
Width of M1 or M2
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3.0
2.5
2.0
1.5
1.0
0.5
0.5
1.0
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2.5
3.0
3.5
1
2
3
4
5
6
7

FIGURE 17

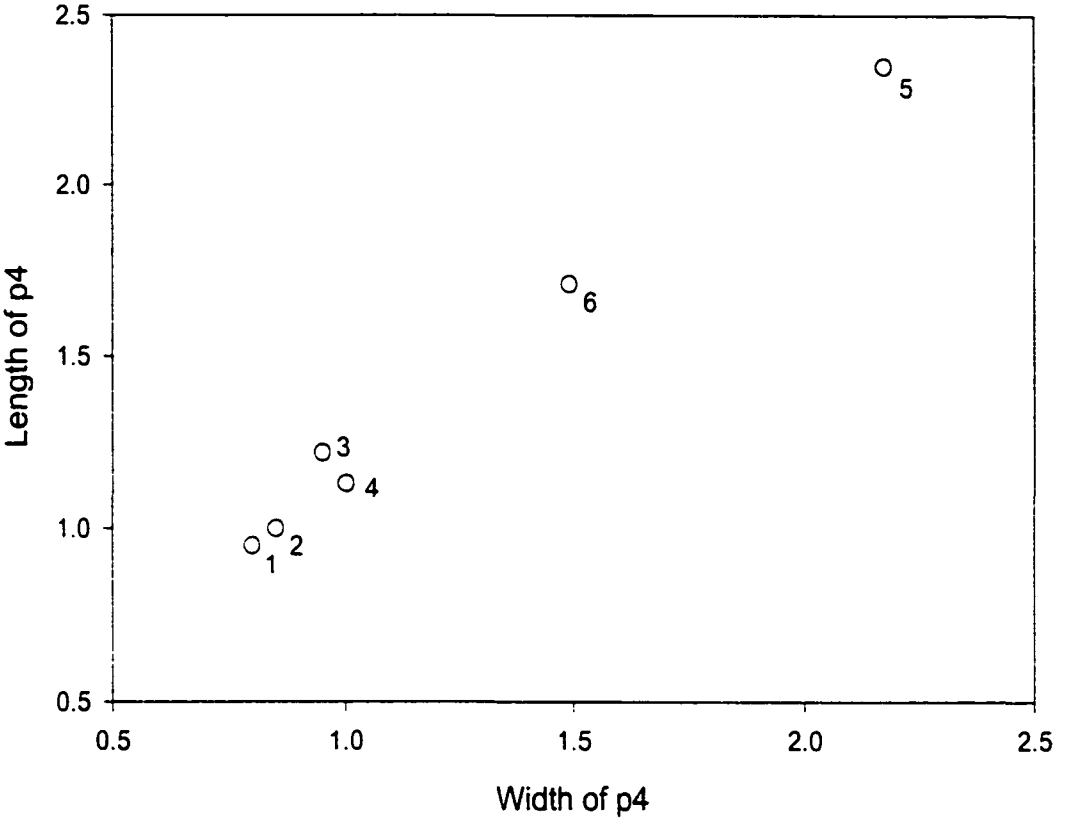


FIGURE 18

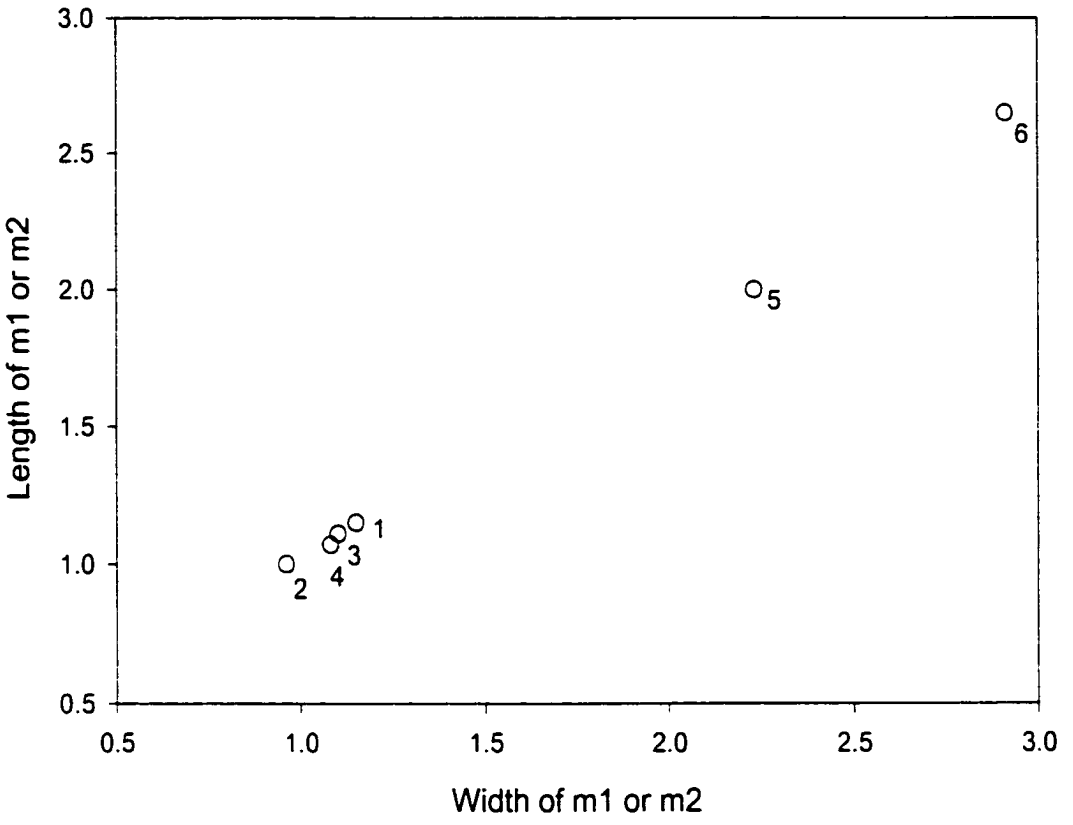
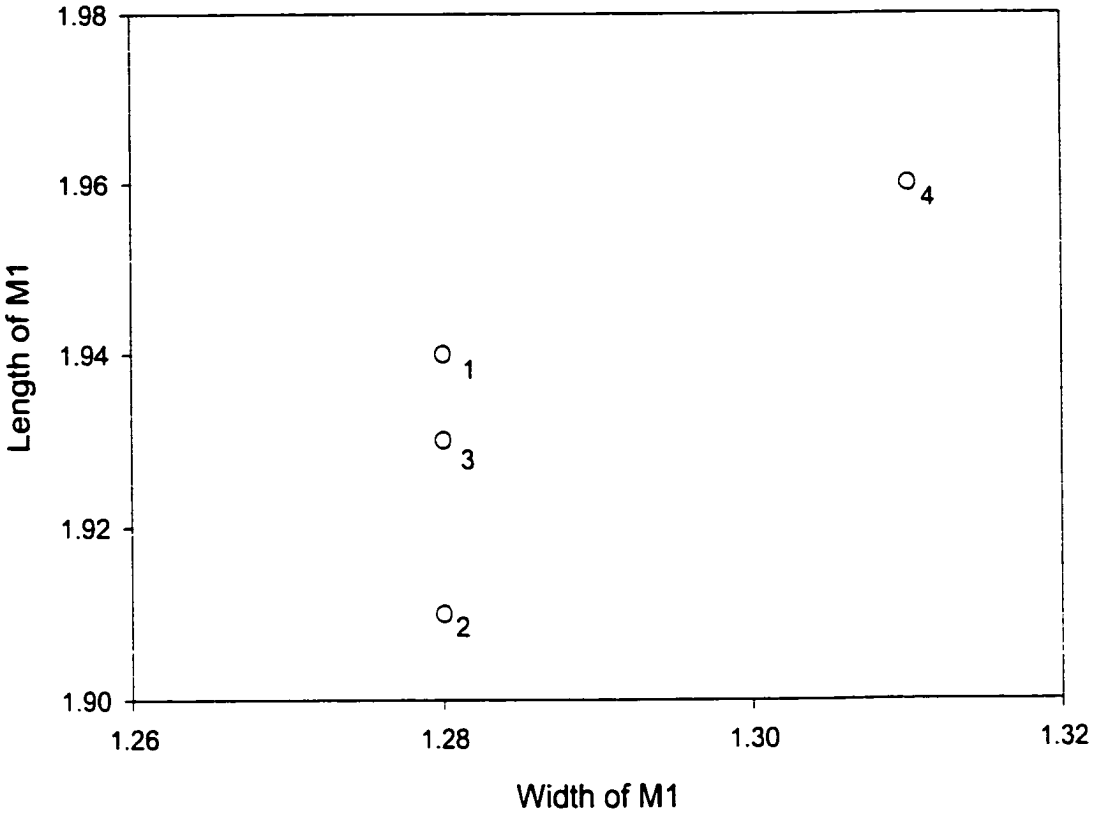

3.0
2.5
2.0
1.5
1.0
0.5
Length of m1 or m2
0.5
1.0
1.5
2.0
2.5
3.0
Width of m1 or m2
1
2
3
4
5
6

FIGURE 19


1.98
1.96
1.94
1.92
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Length of M1
1
2
3
4
1.26
1.28
1.30
1.32
Width of M1

FIGURE 20

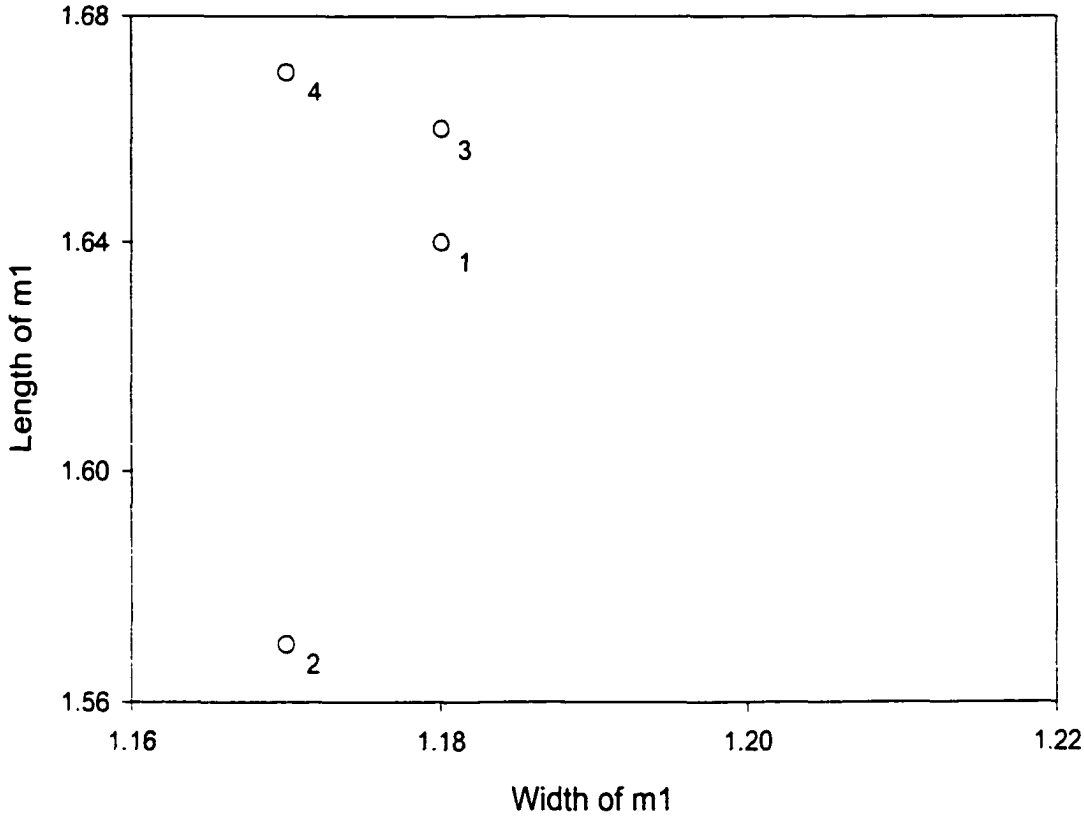

PLATE 1

A, *Plesiosorex* sp., OMNH 54956, labial view, left m2 fragment, X 11.8.

B, *Plesiosorex* sp., OMNH 54956, occlusal view, left m2 fragment, X 11.8.

C, *Plesiosorex* sp., OMNH 54956, lingual view, left m2 fragment, X 11.8.

D, *Meterix* sp., OMNH 54908, labial view, left dentary fragment, X 4.2.

E, *Meterix* sp., OMNH 54908, occlusal view, left dentary fragment, X 4.2.

F, *Meterix* sp., OMNH 54908, lingual view, left dentary fragment, X 4.2.

G, *Mystipterus vespertillo*, OMNH 54933, occlusal view, left P4, X 9.8.

H, *Mystipterus vespertillo*, OMNH 54933, lingual view, left P4, X 9.8.

Ii, *Mystipterus vespertillo*, OMNH 54931, occlusal view, left M2, X 12.3.

J, *Mystipterus vespertillo*, OMNH 54931, labial view, left M2, X 12.3.

K, *Mystipterus vespertillo*, OMNH 54931, lingual view, left M2, X 12.3.

L, *Mystipterus vespertillo*, OMNH 54931, occlusal view, left dentary fragment with m2, X 12.1.

M, *Mystipterus vespertillo*, OMNH 54931, labial view, left dentary fragment with m2, X 12.1.

N, *Mystipterus vespertillo*, OMNH 54931, lingual view, left dentary fragment with m2, X 12.1.

O, *Mystipterus vespertillo*, OMNH 54937, labial view, left m3, X 12.7.

P, *Mystipterus vespertillo*, OMNH 54937, occlusal view, left m3, X 12.7.

Q, *Mystipterus vespertillo*, OMNH 54937, lingual view, left m3, X 12.7.

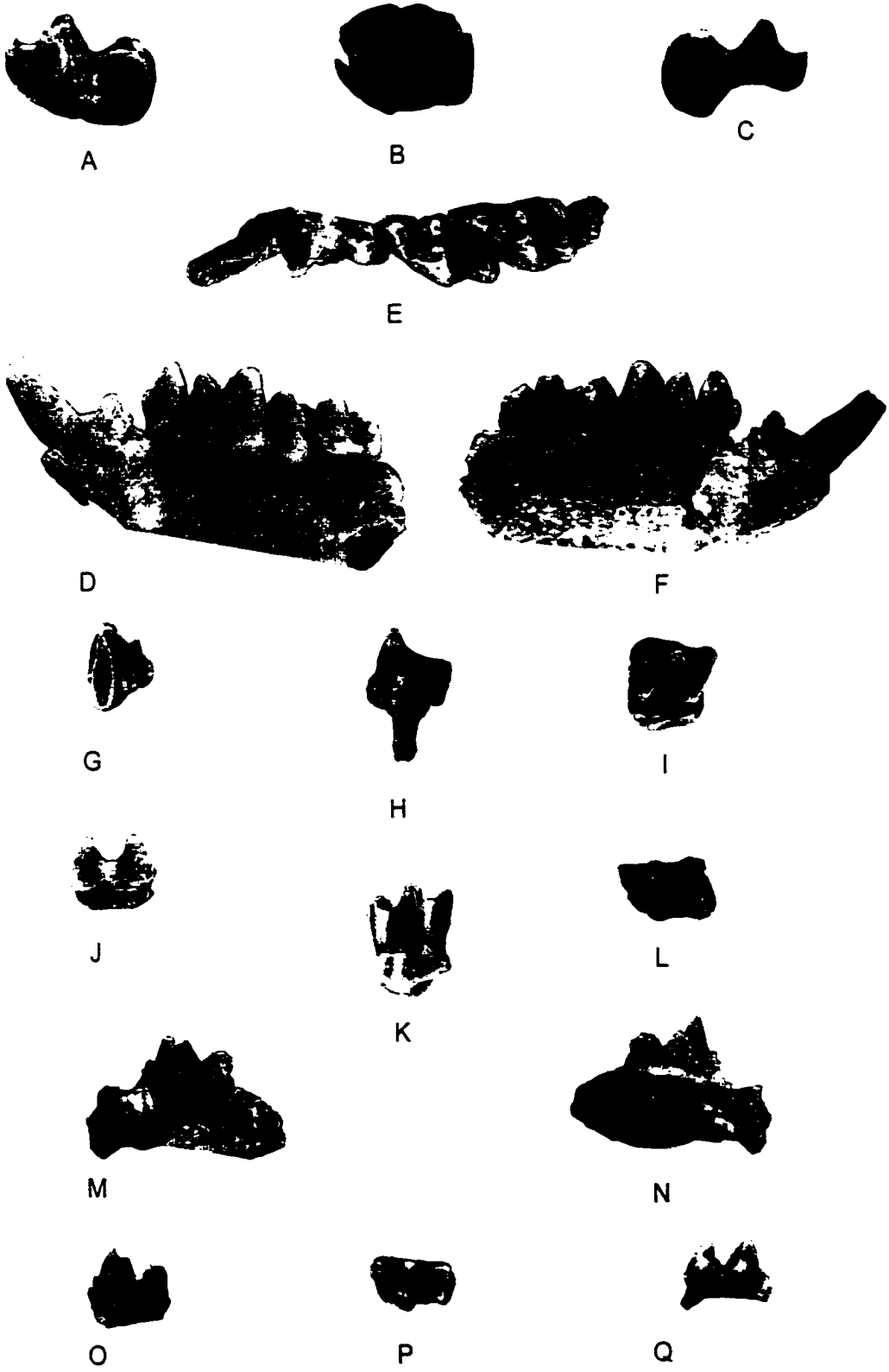
A
B
C
E
D
F
G
H
I
J
K
L
M
N
O
P
Q

PLATE 2

A, *Mystipterus* cf. *M. pacificus*, OMNH 54929, occlusal view, left M2, X 11.6.

B, *Mystipterus* cf. *M. pacificus*, OMNH 54929, labial view, left M2, X 11.6.

C, *Mystipterus* cf. *M. pacificus*, OMNH 54929, lingual view, left M2, X 11.6.

D, *Mystipterus* sp., OMNH 54959, occlusal view, left M3, X 12.5.

E, *Mystipterus* sp., OMNH 54959, labial view, left M3, X 12.5.

F, *Mystipterus* sp., OMNH 54959, lingual view, left M3, X 12.5.

G, *Mystipterus* sp., OMNH 54959, occlusal view, left m2, X 12.8.

H, *Mystipterus* sp., OMNH 54959, labial view, left m2, X 12.8.

I, *Mystipterus* sp., OMNH 54959, lingual view, left m2, X 12.8.

J, *Domninoides* sp., OMNH 54942, labial view, left dentary fragment with m1-m3, X 10.0.

K, *Domninoides* sp., OMNH 54942, occlusal view, left dentary fragment with m1-m3, X 10.0.

L, *Domninoides* sp., OMNH 54942, lingual view, left dentary fragment with m1-m3, X 10.0.

M, *Gaillardia* cf. *G. thomsoni*, OMNH 54950, labial view, left dentary fragment with m2, 7.4X.

N, *Gaillardia* cf. *G. thomsoni*, OMNH 54950, occlusal view, left dentary fragment with m2, 7.4X.

O, *Gaillardia* cf. *G. thomsoni*, OMNH 54950, lingual view, left dentary

fragment with m2, 7.4X.

Plate 2

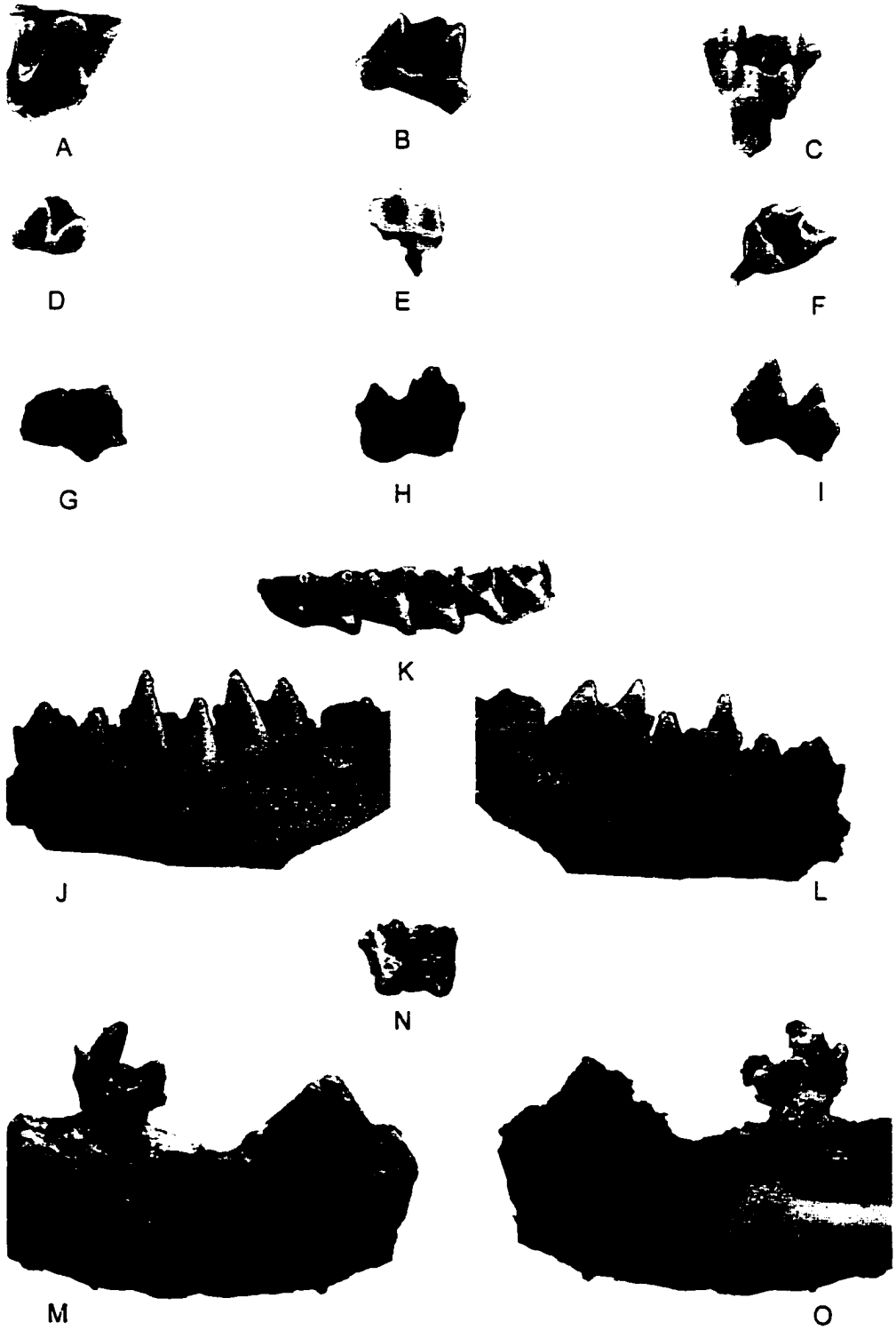

PLATE 3

A, *Pseudotrimylus cifelli*, n. sp., UCMP 141765-04, labial view, right dentary fragment with m1-m3, X 5.3.

B, *Pseudotrimylus cifelli*, n. sp., UCMP 141765-04, occlusal view, right dentary fragment with m1-m3, X 5.3.

C, *Pseudotrimylus cifelli*, n. sp., UCMP 141765-04, lingual view, right dentary fragment with m1-m3, X 5.3.

D, *Pseudotrimylus compressus*, UCMP 112209, labial view, left dentary fragment with m1-m3, X 5.6.

E, *Pseudotrimylus compressus*, UCMP 112209, occlusal view, left dentary fragment with m1-m3, X 5.6.

F, *Pseudotrimylus compressus*, UCMP 112209, lingual view, left dentary fragment with m1-m3, X 5.6.

G, *Pseudotrimylus* sp., UCMP 112214, labial view, left maxilla fragment with P2-M2, X 5.6.

H, *Pseudotrimylus* sp., UCMP 112214, occlusal view, left maxilla fragment with P2-M2, X 5.6.

I, *Pseudotrimylus* sp., UCMP 112214, lingual view, left maxilla fragment with P2-M2, X 5.6.

J, *Pseudotrimylus* sp., UCMP 112216, labial view, left I1, X 8.5.

K, *Pseudotrimylus* sp., UCMP 112216, lingual view, left I1, X 8.5.

L, *Pseudotrimylus* sp., UCMP 112227, lingual view, left i3, X 8.5.

M, *Pseudotrimylus* sp., UCMP 112227, labial view, left i3, X 8.5.

N, *Pseudotrimylus* sp., UCMP 112228, occlusal view, left maxilla fragment with M2-M3,, X 10.0.

O, *Pseudotrimylus* sp., UCMP 112228, labial view, left maxilla fragment with M2-M3,, X 10.0.

P, *Pseudotrimylus* sp., UCMP 112228, lingual view, left maxilla fragment with M2-M3,, X 10.0.

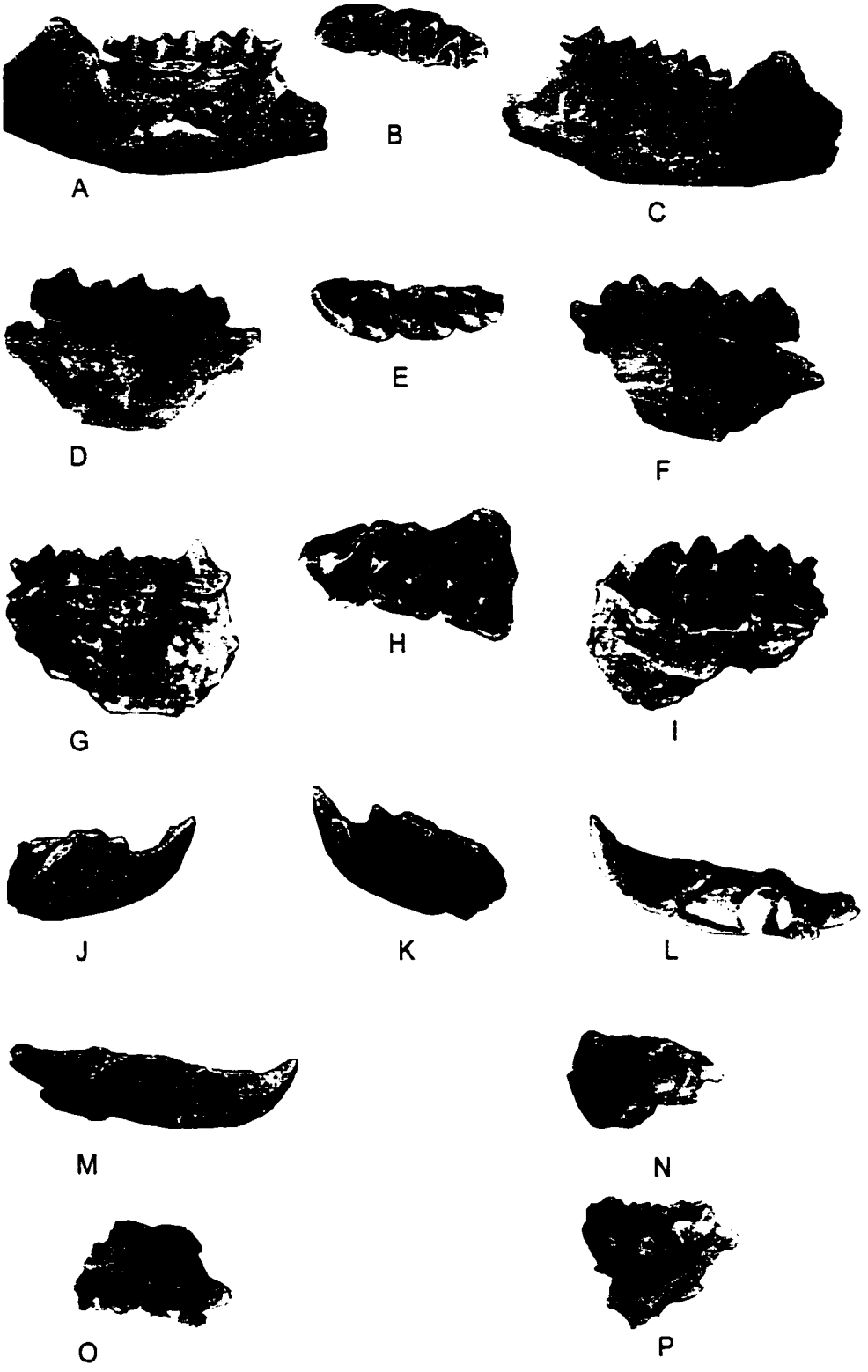
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PLATE 4

A, *Angustidens vireti*, OMNH 54920, labial view, right dentary fragment with p3-m3, X 7.8.

B, *Angustidens vireti*, OMNH 54920, occlusal view, right dentary fragment with p3-m3, X 7.8.

C, *Angustidens vireti*, OMNH 54920, lingual view, right dentary fragment with p3-m3, X 7.8.

D, *Limnoecus tricupsis*, UCMP 141768-02, labial view, right dentary fragment with p4-m3, X 10.0.

E, *Limnoecus tricupsis*, UCMP 141768-02, occlusal view, right dentary fragment with p4-m3, X 10.0.

F, *Limnoecus tricupsis*, UCMP 141768-02, lingual view, right dentary fragment with p4-m3, X 10.0.

G, *Limnoecus tricupsis*, OMNH 54911, labial view, left dentary fragment with m2 and partial m3, X 9.5.

H, *Limnoecus tricupsis*, OMNH 54911,occlusal view, left dentary fragment with m2 and partial m3, X 9.5.

I, *Limnoecus tricupsis*, OMNH 54911, lingual view, left dentary fragment with m2 and partial m3, X 9.5.

J, *Limnoecus niobrarensis*, OMNH 54918, labial view, right dentary fragment with i3, p3-m3, X 9.0.

K, *Limnoecus niobrarensis*, OMNH 54918, occlusal view, right dentary

fragment with i3, p3-m3, X 9.0.

L, *Limnoecus niobrarensis*, OMNH 54918, lingual view, right dentary fragment with i3, p3-m3, X 9.0.

M, *Limnoecus* sp., OMNH 54963, labial view, right I1, X 6.3.

N, *Limnoecus* sp., OMNH 54963, lingual view, right I1, X 6.3.

O, *Limnoecus* sp., UCMP 141765-03, occlusal view, right maxilla fragment with P3-M3, X 7.0.

P, *Limnoecus* sp., UCMP 141765-03, labial view, right maxilla fragment with P3-M3, X 7.0.

Q, *Limnoecus* sp., UCMP 141765-03, lingual view, right maxilla fragment with P3-M3, X 7.0.

R, *Limnoecus* sp., OMNH 54910, labial view, left dentary fragment with talonid of m1, m2-m3, X 8.2.

S, *Limnoecus* sp., OMNH 54910, occlusal view, left dentary fragment with talonid of m1, m2-m3, X 8.2.

T, *Limnoecus* sp., OMNH 54910, linguall view, left dentary fragment with talonid of m1, m2-m3, X 8.2.

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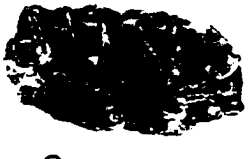

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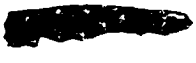

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PLATE 5

A, *Alluvisorex arcadentes*, UCMP 141769-03, labial view, left dentary fragment with i3, and p2, X 15.7.

B, *Alluvisorex arcadentes*, UCMP 141769-01, occlusal view, left dentary fragment with m2-m3, X 9.0.

C, *Alluvisorex arcadentes*, UCMP 141769-03, lingual view, left dentary fragment with i3, and p2, X 15.7.

D, *Alluvisorex arcadentes*, UCMP 141769-01, labial view, left dentary fragment with m2-m3, X 9.0.

E, *Alluvisorex arcadentes*, UCMP 141769-01, lingual view, left dentary fragment with m2-m3, X 9.0.

F, *Adeloblarina* sp., UCMP 141769-04, labial view, left dentary fragment with talonid of m1 and m2-m3, X 9.3.

G, *Adeloblarina* sp., UCMP 141769-04, occlusal view, left dentary fragment with talonid of m1 and m2-m3, X 9.3.

H, *Adeloblarina* sp., UCMP 141769-04, lingual view, left dentary fragment with talonid of m1 and m2-m3, X 9.3.

I, *Antesorex compressus*, OMNH 54913, labial view, left dentary fragment with m2, X 8.6.

J, *Antesorex compressus*, OMNH 54913, occlusal view, left dentary fragment with m2, X 8.6.

K, *Antesorex compressus*, OMNH 54913, lingual view, left dentary

fragment with m2, X 8.6.

L, *Antesorex* sp., UCMP 141768-03, labial view, right maxilla fragment with P3-M3, X 10.1.

M, *Antesorex* sp., UCMP 141768-03, occlusal view, right maxilla fragment with P3-M3, X 10.1.

N, *Antesorex* sp., UCMP 141768-03, lingual view, right maxilla fragment with P3-M3, X 10.1.

O, Chiroptera, OMNH 54955, labial view, isolated canine, X 10.8.

P, Chiroptera, OMNH 54955, occlusal view, isolated canine, X 10.8.

Plate 5

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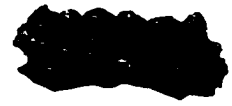

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PLATE 6

A, *Desmatolagus* cf. *D. schizopetrus*, UCMP 141719, labial view, right maxilla fragment with P3-M1, X 3.75.

B, *Desmatolagus* cf. *D. schizopetrus*, UCMP 141719, occlusal view, right maxilla fragment with P3-M1, X 3.75.

C, *Desmatolagus* cf. *D. schizopetrus*, UCMP 141719, lingual view, right maxilla fragment with P3-M1, X 3.75.

D, *Desmatolagus* cf. *D. schizopetrus*, UCMP 141750-01, labial view, right maxilla fragment with P3-M1, X 3.13.

E, *Desmatolagus* cf. *D. schizopetrus*, UCMP 141750-01, occlusal view, right maxilla fragment with P3-M1, X 3.13.

F, *Desmatolagus* cf. *D. schizopetrus*, UCMP 141750-01, lingual view, right maxilla fragment with P3-M1, X 3.13.

G, *Desmatolagus* cf. *D. schizopetrus*, UCMP 141736-03, labial view, right dp3, X 7.5.

H, *Desmatolagus* cf. *D. schizopetrus*, UCMP 141736-03, occlusal view, right dp3, X 7.5.

I, *Desmatolagus* cf. *D. schizopetrus*, UCMP 141736-03, lingual view, right dp3, X 7.5.

J, *Oreolagus nebrascensis*, UCMP 141720-17, anterior view, right P2, X 11.8.

K, *Oreolagus nebrascensis*, UCMP 141720-17, occlusal view, right P2, X

11.8.

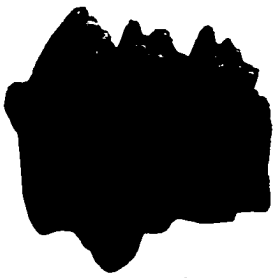
L, *Oreolagus nebrascensis*, UCMP 141716-05, occlusal view, left molariform cheektooth, X 17.5.

M, *Oreolagus nebrascensis*, OMNH 54970, labial view, right dentary fragment with dp3, dp4–m1, X 6.8.

N, *Oreolagus nebrascensis*, OMNH 54970, occlusal view, right dentary fragment with dp3, dp4–m1, X 6.8.

O, *Oreolagus nebrascensis*, OMNH 54970, lingual view, right dentary fragment with dp3, dp4–m1, X 6.8.

Plate 6



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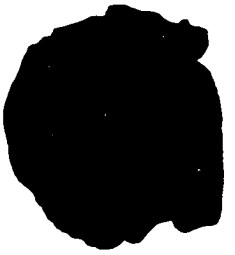

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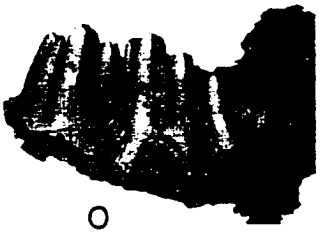

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PLATE 7

A, *Russellagus* cf. *R. vonhofi*, UCMP 141720-16, anterior view, right DP2, X 15.3.

B, *Russellagus* cf. *R. vonhofi*, UCMP 141720-16, occlusal view, right DP2, X 15.3.

C, *Russellagus* cf. *R. vonhofi*, UCMP 141737-20, labial view, left dp3, X 10.1.

D, *Russellagus* cf. *R. vonhofi*, UCMP 141737-20, occlusal view, left dp3, X 10.1.

E, *Russellagus* cf. *R. vonhofi*, UCMP 141737-20, lingual view, left dp3, X 10.1.

F, *Hypolagus parviplicatus*, UCMP 141751-03, occlusal view, right maxilla fragment with P2-M1, X 11.8.

G, *Hypolagus parviplicatus*, UCMP 141751-03, lingual view, right maxilla fragment with P2-M1, X 11.8.

H, *Hypolagus parviplicatus*, UCMP 141846, occlusal view, left dentary fragment with i1-m3, X 5.25.

I, *Hypolagus parviplicatus*, UCMP 141846, labial view, left dentary fragment with i1-m3, X 5.25.

J, *Hypolagus parviplicatus*, UCMP 141846, lingual view, left dentary fragment with i1-m3, X 5.25.

Plate 7

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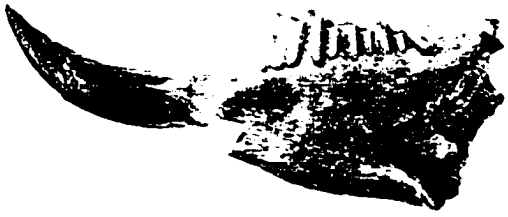

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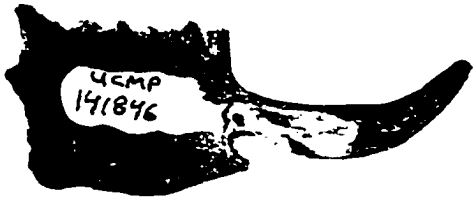

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PLATE 8

A, *Hypolagus fontinalis*, UCMP 141737-04, anterior view, right P2, X 8.7.

B, *Hypolagus fontinalis*, UCMP 141737-04, occlusal view, right P2, X 8.7.

C, *Hypolagus fontinalis*, UCMP 141550, lingual view, right dentary fragment wiht p3–m2, X 4.6.

D, *Hypolagus fontinalis*, UCMP 141550, labial view, right dentary fragment wiht p3–m2, X 4.6.

E, *Hypolagus fontinalis*, UCMP 141550, occlusal view, right dentary fragment wiht p3–m2, X 4.6.

F, *Pronotolagus* sp., UCMP 141720-11, lingual view, right p3, X 5.9.

G, *Pronotolagus* sp., UCMP 141720-11, occlusal view, right p3, X 5.9.

H, *Pronotolagus* sp., UCMP 141751-01, lingual view, right maxilla fragment with P2-P4, X 3.5.

I, *Pronotolagus* sp., UCMP 141751-01, lingual view, right maxilla fragment with P2–P4, X 3.5.

J, *Pronotolagus* sp., UCMP 141751-01, lingual view, right maxilla fragment with P2–P4, X 3.5.

Plate 8

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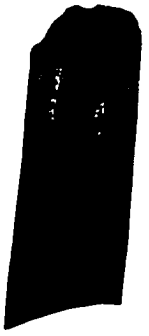

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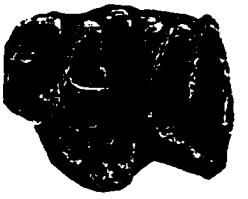

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PLATE 9

A, *Tardontia nevadans*, OMNH 54806, labial view, right dp4, X 4.6.

B, *Tardontia nevadans*, OMNH 54806, occlusal view, right dp4, X 4.6.

C, *Tardontia nevadans*, OMNH 54806, lingual view, right dp4, X 4.6.

D, *Tardontia nevadans*, UCMP 130161, labial view, left maxilla fragment with P3–M1, X 4.2.

E, *Tardontia nevadans*, UCMP 130161, occlusal view, left maxilla fragment with P3–M1, X 4.2.

F, *Tardontia nevadans*, UCMP 130161, lingual view, left maxilla fragment with P3–M1, X 4.2.

G, *Tardontia nevadans*, UCMP 130163, labial view, right dentary fragment with p4–m3, X 4.3.

H, *Tardontia nevadans*, UCMP 130163, lingual view, right dentary fragment with p4–m3, X 4.3.

I, *Tardontia nevadans*, UCMP 130163, occlusal view, right dentary fragment with p4–m3, X 4.3.

Plate 9

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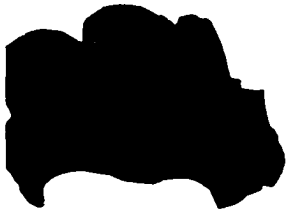

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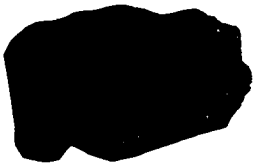

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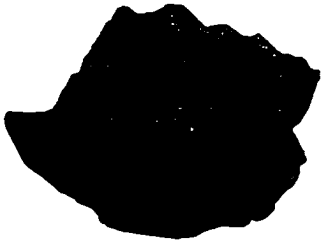

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PLATE 10

A, *Mesogaulus paniensis*, UCMP 130254, occlusal view, left P4, X 4.1.

B, *Mesogaulus paniensis*, UCMP 141799-01, occlusal view, left M2, X 4.6.

C, *Mesogaulus paniensis*, UCMP 141799-03, occlusal view, right M3, X 4.4.

D, *Mesogaulus paniensis*, UCMP 130256, occlusal view, left p4, X 4.9.

E, *Mesogaulus paniensis*, UCMP 141583, lingual view, right dentary fragment with p4, X 4.1.

F, *Mesogaulus paniensis*, UCMP 141583, labial view, right dentary fragment with p4, X 4.1.

G, *Mesogaulus paniensis*, UCMP 141583, occlusal view, right dentary fragment with p4, X 4.1.

Plate 10

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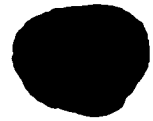

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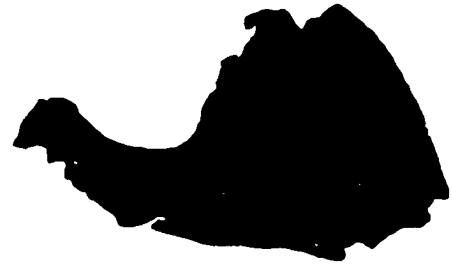

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PLATE 11

A, *Protospermophilus dalqesti*, UCMP 141630-01, labial view, right dentary fragment with p4–m3, X 4.5.

B, *Protospermophilus dalqesti*, UCMP 141630-01, occlusal view, right dentary fragment with p4–m3, X 4.5.

C, *Protospermophilus dalqesti*, UCMP 141630-01, lingual view, right dentary fragment with p4–m3, X 4.5.

D, *Protospermophilus dalqesti*, UCMP 141806-01, labial view, left maxillary fragment with P4, X 11.7.

E, *Protospermophilus dalqesti*, UCMP 141806-01, occlusal view, left maxillary fragment with P4, X 11.7.

F, *Protospermophilus dalqesti*, UCMP 141806-01, lingual view, left maxillary fragment with P4, X 11.7.

G, *Protospermophilus dalqesti*, UCMP 141806-02, labial view, right M1 or M2, X 12.2.

H, *Protospermophilus dalqesti*, UCMP 141806-02, occlusal view, right M1 or M2, X 12.2.

I, *Protospermophilus dalqesti*, UCMP 141806-02, lingual view, right M1 or M2, X 12.2.

J, *Miospermophilus* cf. *bryanti*, UCMP 141912, labial view, left maxilla fragment with P4–M3, X 8.0.

K, *Miospermophilus* cf. *bryanti*, UCMP 141912, occlusal view, left maxilla

fragment with P4–M3, X 8.0.

L, *Miospermophilus* cf. *bryanti*, UCMP 141912, lingual view, left maxilla fragment with P4–M3, X 8.0.

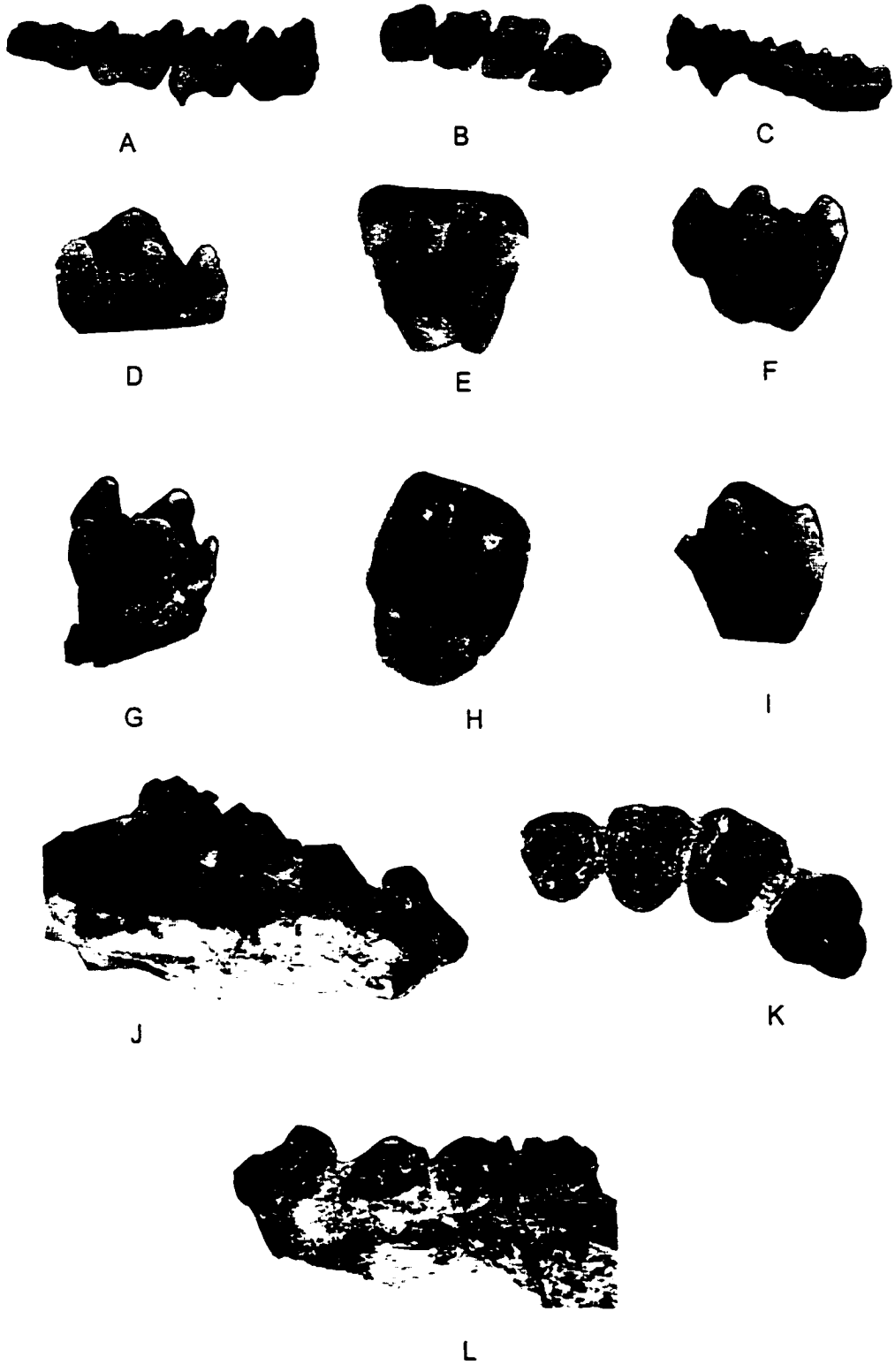
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PLATE 12

A, *Miospermophilus* cf. *bryanti*, UCMP 54578, labial view, right maxilla fragment with P3–M1, X 11.8.

B, *Miospermophilus* cf. *bryanti*, UCMP 54578, occlusal view,right maxilla fragment with P3–M1, X 11.8.

C, *Miospermophilus* cf. *bryanti*, UCMP 54578, lingual view, right maxilla fragment with P3–M1, X 11.8.

D, *Miospermophilus* cf. *bryanti*, UCMP 141829-17, labial view, right M1 or M2, X 14.8.

E, *Miospermophilus* cf. *bryanti*, UCMP 141829-17, occlusal view,right M1 or M2, X 14.8.

F, *Miospermophilus* cf. *bryanti*, UCMP 141829-17, lingual view, right M1 or M2, X 14.8.

G, *Miospermophilus* cf. *bryanti*, UCMP 141830-27, labial view, left M3, X 15.3.

H, *Miospermophilus* cf. *bryanti*, UCMP 141830-27, occlusal view, left M3, X 15.3.

I, *Miospermophilus* cf. *bryanti*, UCMP 141830-27, lingual view, left M3, X 15.3.

J, *Miospermophilus* cf. *bryanti*, OMNH 54548, labial view, left dentary fragment with i1–m3, X 7.6.

K, *Miospermophilus* cf. *bryanti*, OMNH 54548, occlusal view, left dentary

fragment with i1–m3, X 7.6.

L, *Miospermophilus* cf. *bryanti*, OMNH 54548, lingual view, left dentary fragment with i1–m3, X 7.6.

M, *Miospermophilus hutchisoni*, UCMP 131386, labial view, left dentary fragment with dp4, p4–m2, X 8.0.

N, *Miospermophilus hutchisoni*, UCMP 131386, occlusal view, left dentary fragment with dp4, p4–m2, X 8.0.

O, *Miospermophilus hutchisoni*, UCMP 131386, lingual view, left dentary fragment with dp4, p4–m2, X 8.0.

Plate 12

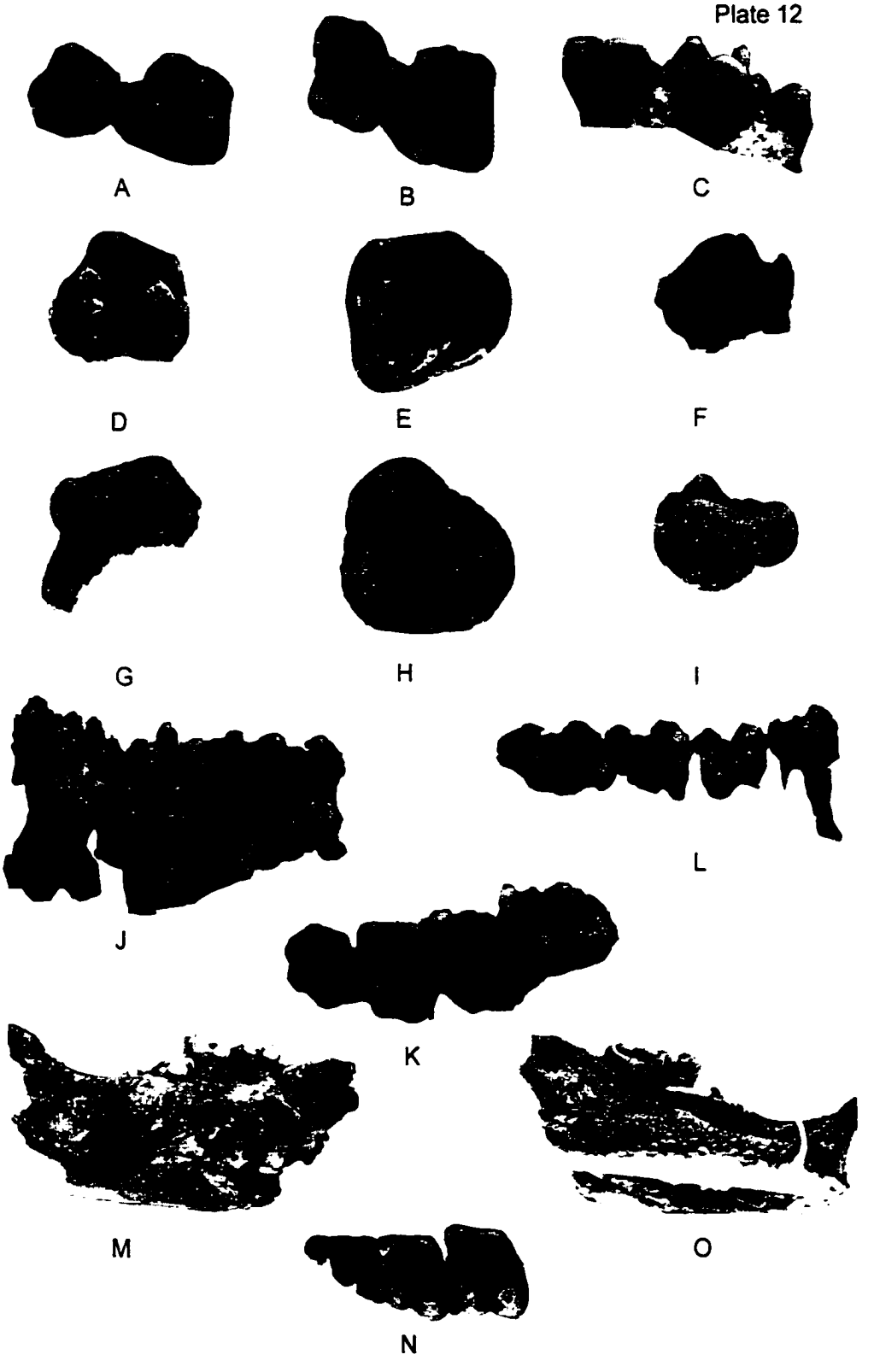

PLATE 13

A, *Tamias* sp., UCMP 141830-11, labial view, left DP4, X 14.8.

B, *Tamias* sp., UCMP 141830-11, occlusal view, left DP4, X 14.8.

C, *Tamias* sp., UCMP 141830-11, lingual view, left DP4, X 14.8.

D, *Tamias* sp., OMNH 54561, labial view, right P4, X 16.0.

E, *Tamias* sp., OMNH 54561, occlusal view, right P4, X 16.0.

F, *Tamias* sp., OMNH 54561, lingual view, right P4, X 16.0.

G, *Tamias* sp., UCMP 141829-08, labial view, left M1 or M2, X 11.4.

H, *Tamias* sp., UCMP 141829-08, occlusal view, left M1 or M2, X 11.4.

I, *Tamias* sp., UCMP 141829-08, lingual view, left M1 or M2, X 11.4.

J, *Tamias* sp., UCMP 141830-17, labial view, right M3, X 10.2.

K, *Tamias* sp., UCMP 141830-17, occlusal view, right M3, X 10.2.

L, *Tamias* sp., UCMP 141830-17, lingual view, right M3, X 10.2.

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PLATE 14

A, *Tamias* sp., UCMP 141691, labial view, right dentary fragment with i1–m3, X 4.3.

B, *Tamias* sp., UCMP 141691, occlusal view, right dentary fragment with i1–m3, X 4.3.

C, *Tamias* sp., UCMP 141691, lingual view, right dentary fragment with i1–m3, X 4.3.

D, *Tamias* sp., UCMP 141691, anterior view, right dentary fragment with i1–m3, X 6.2.

E, *Tamias* sp., UCMP 141601-22, labial view, right m1 or m2, X 14.7.

F, *Tamias* sp., UCMP 141601-22, occlusal view, right m1 or m2, X 14.7.

G, *Tamias* sp., UCMP 141601-22, lingual view, right m1 or m2, X 14.7.

H, *Micropetauristodon vestali*, OMNH 54564, labial view, left M1 or m2, X 33.0.

I, *Micropetauristodon vestali*, OMNH 54564, occlusal view, left M1 or m2, X 33.0.

J, *Micropetauristodon vestali*, OMNH 54564, lingual view, left M1 or m2, X 33.0.

K, *Petauristodon axelrodi*, UCMP 141805, labial view, right dentary fragment with p4, m2–m3, X 10.7.

L, *Petauristodon axelrodi*, UCMP 141805, occlusal view, right dentary fragment with p4, m2–m3, X 10.7.

M, *Petauristodon axelrodi*, UCMP 141805, lingual view, right dentary fragment with p4, m2–m3, X 10.7.

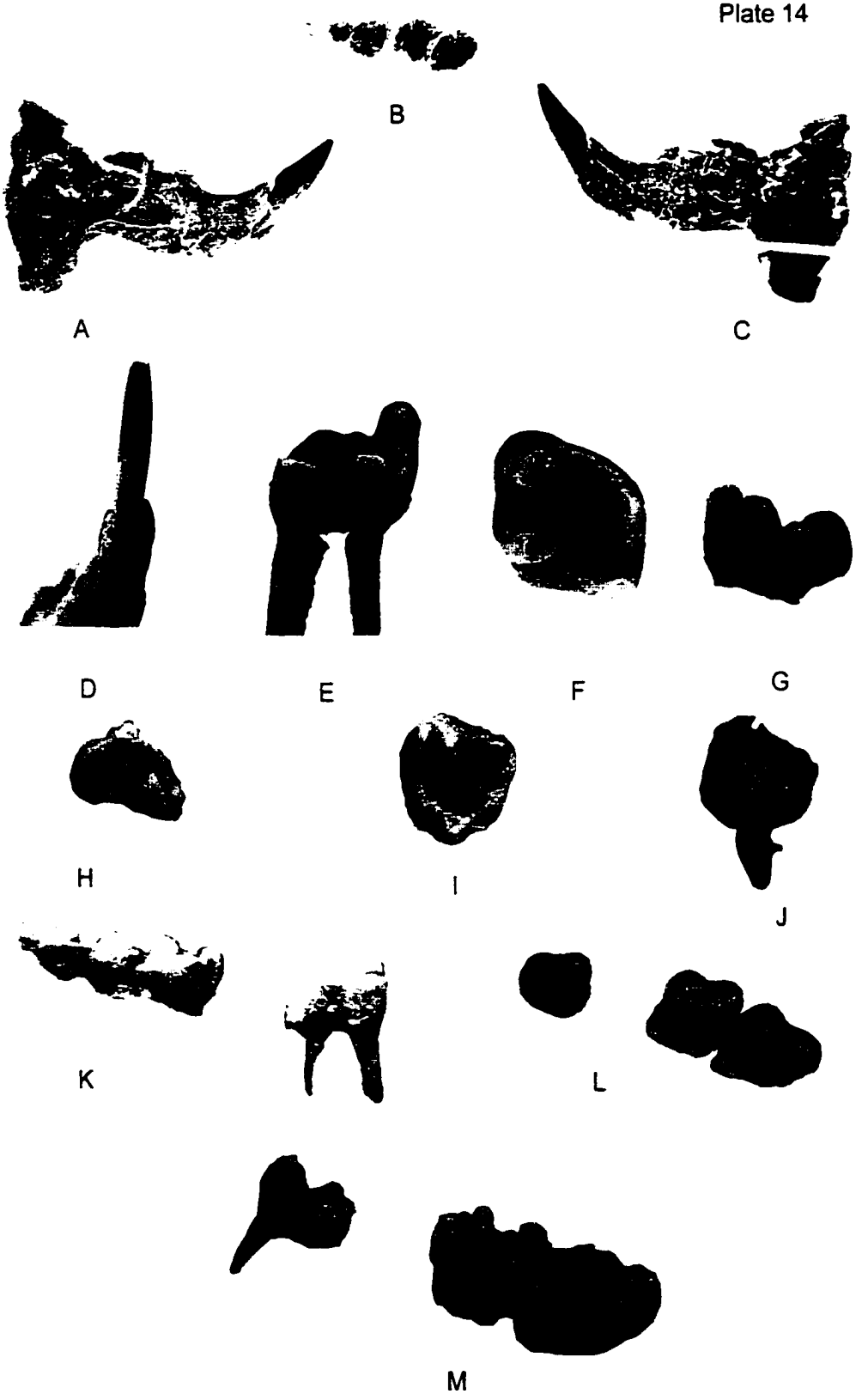
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PLATE 15

A, *Petauristodon axelrodi*, UCMP 141823-04, labial view, left P4, X 24.7.

B, *Petauristodon axelrodi*, UCMP 141823-04, occlusal view, left P4, X 24.7.

C, *Petauristodon axelrodi*, UCMP 141823-04, lingual view, left P4, X 24.7.

D, *Petauristodon axelrodi*, OMNH 54549, labial view, left M1 or M2, X 17.5.

E, *Petauristodon axelrodi*, OMNH 54549, occlusal view, left M1 or M2, X 17.5.

F, *Petauristodon axelrodi*, OMNH 54549, lingual view, left M1 or M2, X 17.5.

G, *Petauristodon axelrodi*, OMNH 54545, labial view, left M3, X 21.7.

H, *Petauristodon axelrodi*, OMNH 54545, occlusal view, left M3, X 21.7.

I, *Petauristodon axelrodi*, OMNH 54545, lingual view, left M3, X 21.7.

J, *Petauristidon savagei*, OMNH 54537, labial view, left dentary fragment with i1, m1–m3, X 8.3.

K, *Petauristidon savagei*, OMNH 54537, occlusal view, left dentary fragment with i1, m1–m3, X 8.3.

L, *Petauristidon savagei*, OMNH 54537, lingual view, left dentary fragment with i1, m1–m3, X 8.3.

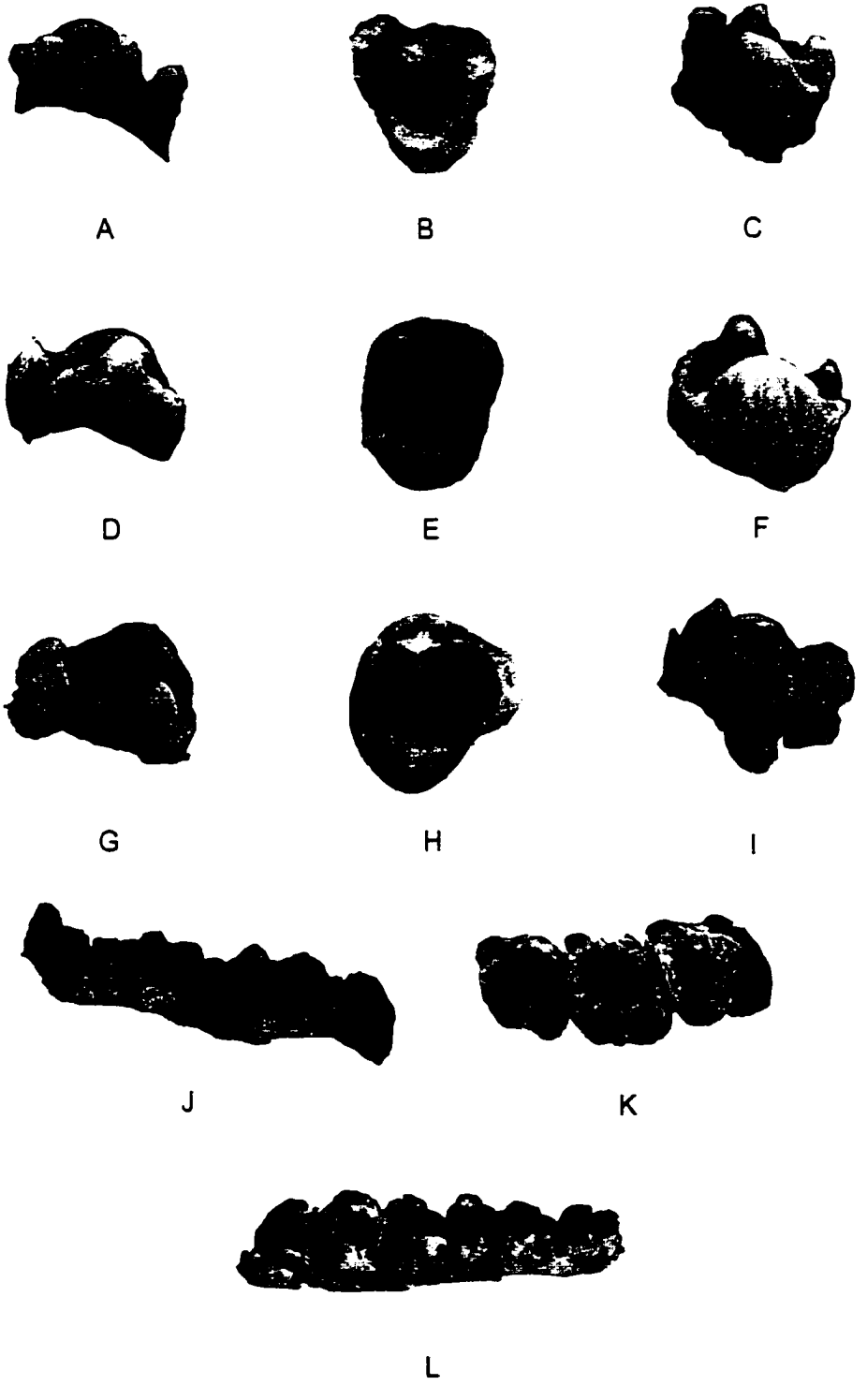
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PLATE 16

A, *Petauristidon savagei*, UCMP 141824-02, labial view, right P4, X 14.4.

B, *Petauristidon savagei*, UCMP 141824-02, occlusal view, right P4, X 14.4.

C, *Petauristidon savagei*, UCMP 141824-02, lingual view, right P4, X 14.4.

D, *Petauristidon savagei*, UCMP 141826-04, labial view, right M3, X 13.9.

E, *Petauristidon savagei*, UCMP 141826-04, occlusal view, right M3, X 13.9.

F, *Petauristidon savagei*, UCMP 141826-04, lingual view, right M3, X 13.9.

G, *Petauristidon savagei*, UCMP 141613-02, labial view, right dp4, X 12.3.

H, *Petauristidon savagei*, UCMP 141613-02, occlusal right dp4, X 12.3.

I, *Petauristidon savagei*, UCMP 141613-02, lingual view, right dp4, X 12.3.

J, *Petauristidon savagei*, UCMP 141629-02, labial view, right p4, X 13.9.

K, *Petauristidon savagei*, UCMP 141629-02, occlusal view, right p4, X 13.9.

L, *Petauristidon savagei*, UCMP 141629-02, lingual view, right p4, X 13.9.

Plate 16

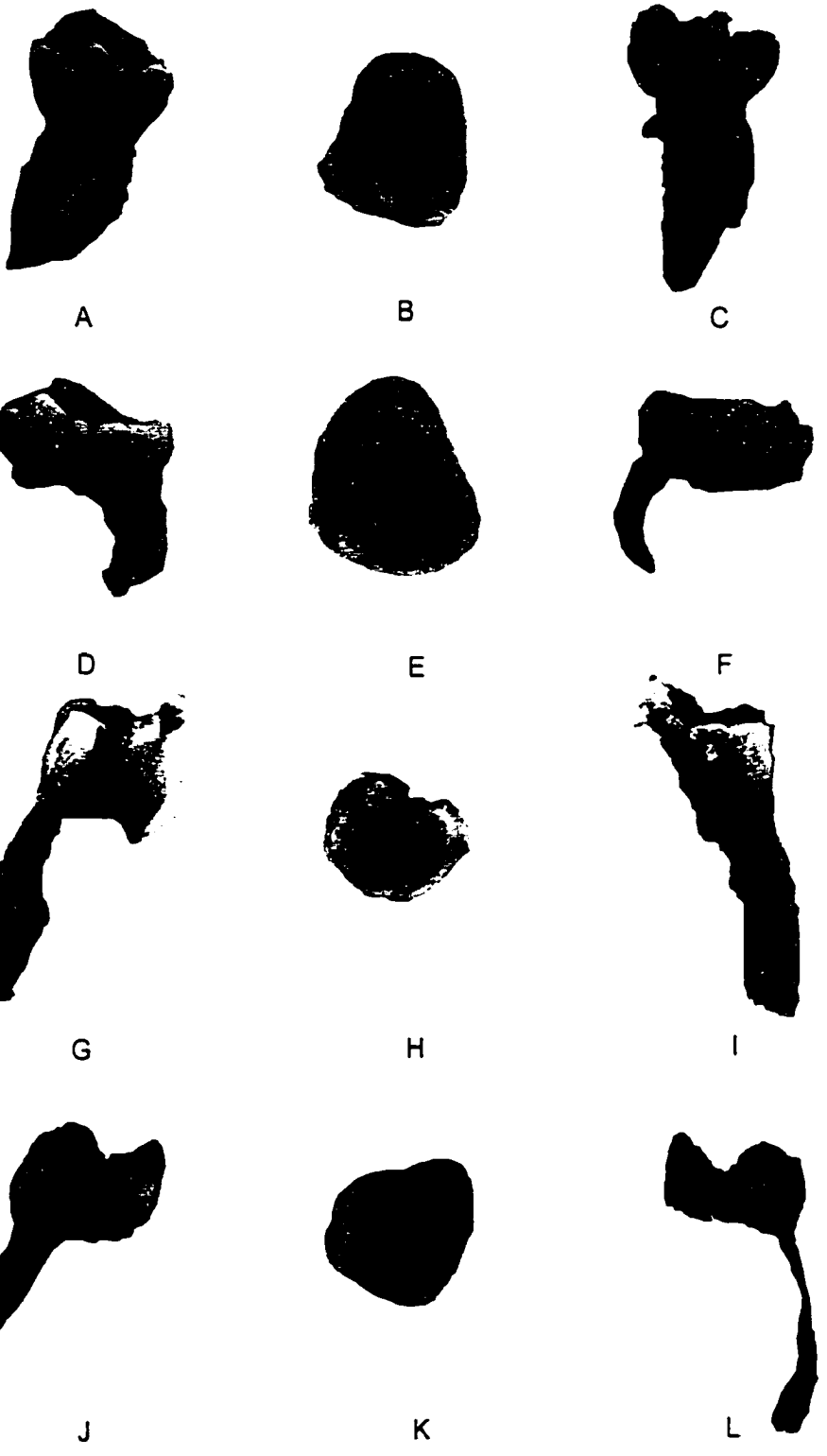

PLATE 17

A, *Petauristodon czaplewskii*, UCMP 141630-02, labial view, left dentary fragment with m1–m2, X 8.4.

B, *Petauristodon czaplewskii*, UCMP 141630-02, occlusal view, left dentary fragment with m1–m2, X 8.4.

C, *Petauristodon czaplewskii*, UCMP 141630-02, lingual view, left dentary fragment with m1–m2, X 8.4.

D, *Petauristodon czaplewskii*, UCMP 141830-26, labial view, right M3, X 10.0.

E, *Petauristodon czaplewskii*, UCMP 141830-26, occlusal view, right M3, X 10.0.

F, *Petauristodon czaplewskii*, UCMP 141830-26, lingual view, right M3, X 10.0.

G, *Petauristodon czaplewskii*, UCMP 141602-02, labial view, left m3, X 9.0.

H, *Petauristodon czaplewskii*, UCMP 141602-02, occlusal view, left m3, X 9.0.

I, *Petauristodon czaplewskii*, UCMP 141602-02, lingual view, left m3, X 9.0.

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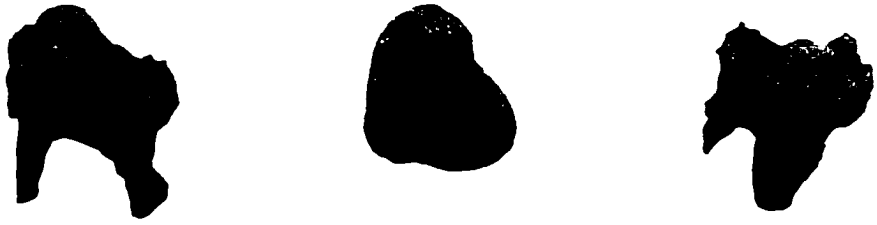

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PLATE 18

A, *Monosaulax lotseei* n. sp., UCMP 141542, labial view, right P4, X 5.0.

B, *Monosaulax lotseei* n. sp., UCMP 141542, occlusal view, right P4, X 5.0.

C, *Monosaulax lotseei* n. sp., UCMP 141542, lingual view, right P4, X 5.0.

D, *Monosaulax lotseei* n. sp., OMNH 54800, labial view, right dentary fragment with i1, p4-m3, X 4.0.

E, *Monosaulax lotseei* n. sp., OMNH 54800, occlusal view, right dentary fragment with i1, p4-m3, X 4.0.

F, *Monosaulax lotseei* n. sp., OMNH 54800, lingual view, right dentary fragment with i1, p4-m3, X 4.0.

G, *Monosaulax lotseei* n. sp., UCMP 141556, ventral view, palate fragment with left P4–m1 and right M1, X 2.3.

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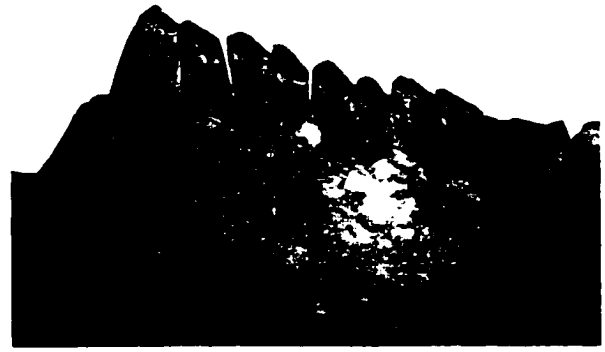

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PLATE 19

A, *Pseudotheridomys woodburnei* n. sp., UCMP 109300, labial view, dentary with p4–m3, X 3.5.

B, *Pseudotheridomys woodburnei* n. sp., UCMP 109300, lingual view, dentary with p4–m3, X 4.8.

C, *Pseudotheridomys n. woodburnei*, UCMP 109300, occlusal view, dentary p4–m3, X 4.8.

D, *Pseudotheridomys woodburnei* n. sp., UCMP 141774-01, labial view, left M1 or M2, X 9.2.

E, *Pseudotheridomys woodburnei* n. sp., UCMP 141774-01, occlusal view, left M1 or M2, X 9.2.

F, *Pseudotheridomys woodburnei* n. sp., UCMP 141774-01, lingual view, left M1 or M2, X 9.2.

G, *Pseudotheridomys woodburnei* n. sp., UCMP 141774-08, labial view, left P4, X 8.6.

H, *Pseudotheridomys woodburnei* n. sp., UCMP 141774-08, occlusal view, left P4, X 8.6.

I, *Pseudotheridomys woodburnei* n. sp., UCMP 141774-08, lingual view, left P4, X 8.6.

J. *Pseudotheridomys tedfordi* n. sp., UCR 15412, labial view, left maxilla with P4–M3, X 4.9.

K, *Pseudotheridomys tedfordi* n. sp., UCR 15412, occlusal view, left maxilla with P4–M3, X 4.9.

L, *Pseudotheridomys tedfordi* n. sp., UCR 15412, lingual view, left maxilla with P4–M3, X 4.9.

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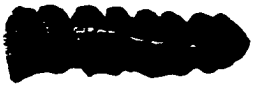

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PLATE 20

A, *Pseudotheridomys tedfordi* n. sp., UCR 15412, labial view, right dentary fragment with m1–m3, X 5.2.

B, *Pseudotheridomys tedfordi* n. sp., UCR 15412, occlusal view, right dentary fragment with m1–m3, X 5.2.

C, *Pseudotheridomys tedfordi* n. sp., UCR 15412, lingual view, right dentary fragment with m1–m3, X 5.2.

D, *Pseudotheridomys cuyamensis*, UCMP 141780-123, labial view, left maxilla fragment with P4–M3, X 12.5.

E, *Pseudotheridomys cuyamensis*, UCMP 141780-123, occlusal view, left maxilla fragment with P4–M3, X 12.5.

F, *Pseudotheridomys cuyamensis*, UCMP 141780-123, lingual view, left maxilla fragment with P4–M3, X 12.5.

G, *Pseudotheridomys cuyamensis*, UCMP 141780-235, labial view, right DP4, X 15.7.

H, *Pseudotheridomys cuyamensis*, UCMP 141780-235, occlusal view, right DP4, X 15.7.

I, *Pseudotheridomys cuyamensis*, UCMP 141780-235, lingual view, right DP4, X 15.7.

J, *Pseudotheridomys cuyamensis*, UCMP 141780-251, labial view, right dentary fragment with p4–m3, X 8.7.

K, *Pseudotheridomys cuyamensis*, UCMP 141780-251, occlusal view, right dentary fragment with p4–m3, X 8.7.

L, *Pseudotheridomys cuyamensis*, UCMP 141780-251, lingual view, right dentary fragment with p4–m3, X 8.7.

M, *Pseudotheridomys* sp. indet., OMNH 54593, labial view, left dp4, X 14.0.

N, *Pseudotheridomys* sp. indet., OMNH 54593, occlusal view, left dp4, X 14.0.

O, *Pseudotheridomys* sp. indet., OMNH 54593, lingual view, left dp4, X 14.0.

Plate 20

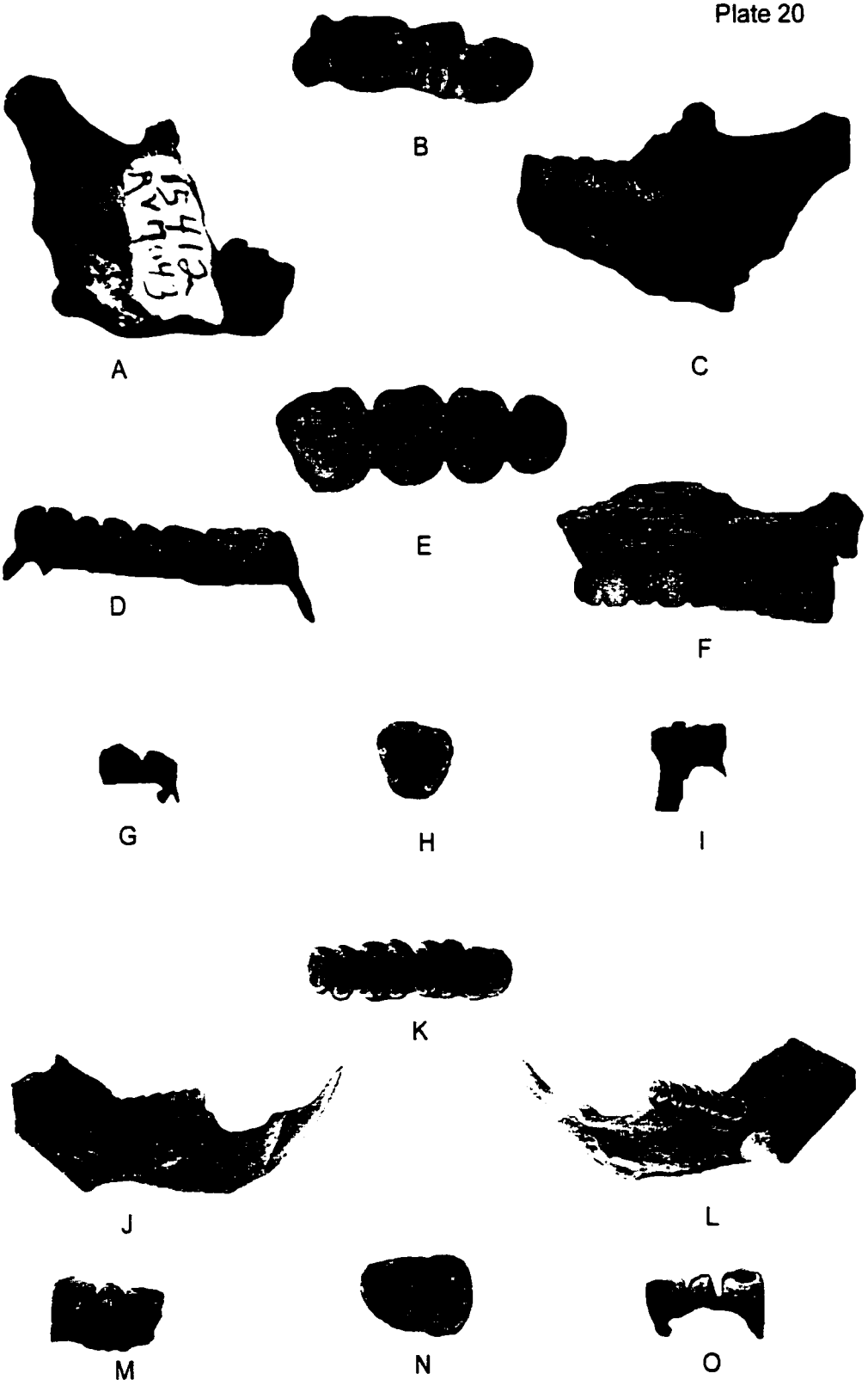

PLATE 21

A, *Lignimus* cf. *L. transversus*, UCMP 141792-02, labial view, left dentary fragment with p4, X 14.4.

B, *Lignimus* cf. *L. transversus*, UCMP 141792-02, occlusal view, left dentary fragment with p4, X 14.4.

C, *Lignimus* cf. *L. transversus*, UCMP 141792-02, lingual view, left dentary fragment with p4, X 14.4.

D, *Lignimus* cf. *L. transversus*, UCMP 141792-01, labial view, right dentary fragment with m2, X 9.6.

E, *Lignimus* cf. *L. transversus*, UCMP 141792-01, occlusal view, right dentary fragment with m2, X 9.6.

F, *Lignimus* cf. *L. transversus*, UCMP 141792-01, lingual view, right dentary fragment with m2, X 9.6.

G, *Lignimus* cf. *L. transversus*, UCMP 1417820-40, labial view, left m3, X 13.2.

H, *Lignimus* cf. *L. transversus*, UCMP 1417820-40, occlusal view, left m3, 13.2.

I, *Lignimus* cf. *L. transversus*, UCMP 1417820-40, lingual view, left m3, X 13.2.

J, *Balantiomys* cf. *B. borealis*, UCMP 141788-01, occlusal view, right maxilla fragment with P4–M1, X 17.0.

K, *Balantiomys* cf. *B. borealis*, UCMP 141788-01, labial view, right maxilla fragment with P4–M1, X 17.0.

L, *Balantiomys* cf. *B. borealis*, UCMP 141791, labial view, right dentary fragment with p4, m2–m3, X 10.1.

M, *Balantiomys* cf. *B. borealis*, UCMP 141791, occlusal view, right dentary fragment with p4, m2–m3, X 10.1.

N, *Balantiomys* cf. *B. borealis*, UCMP 141791, lingual view, right dentary fragment with p4, m2–m3, X 10.1.

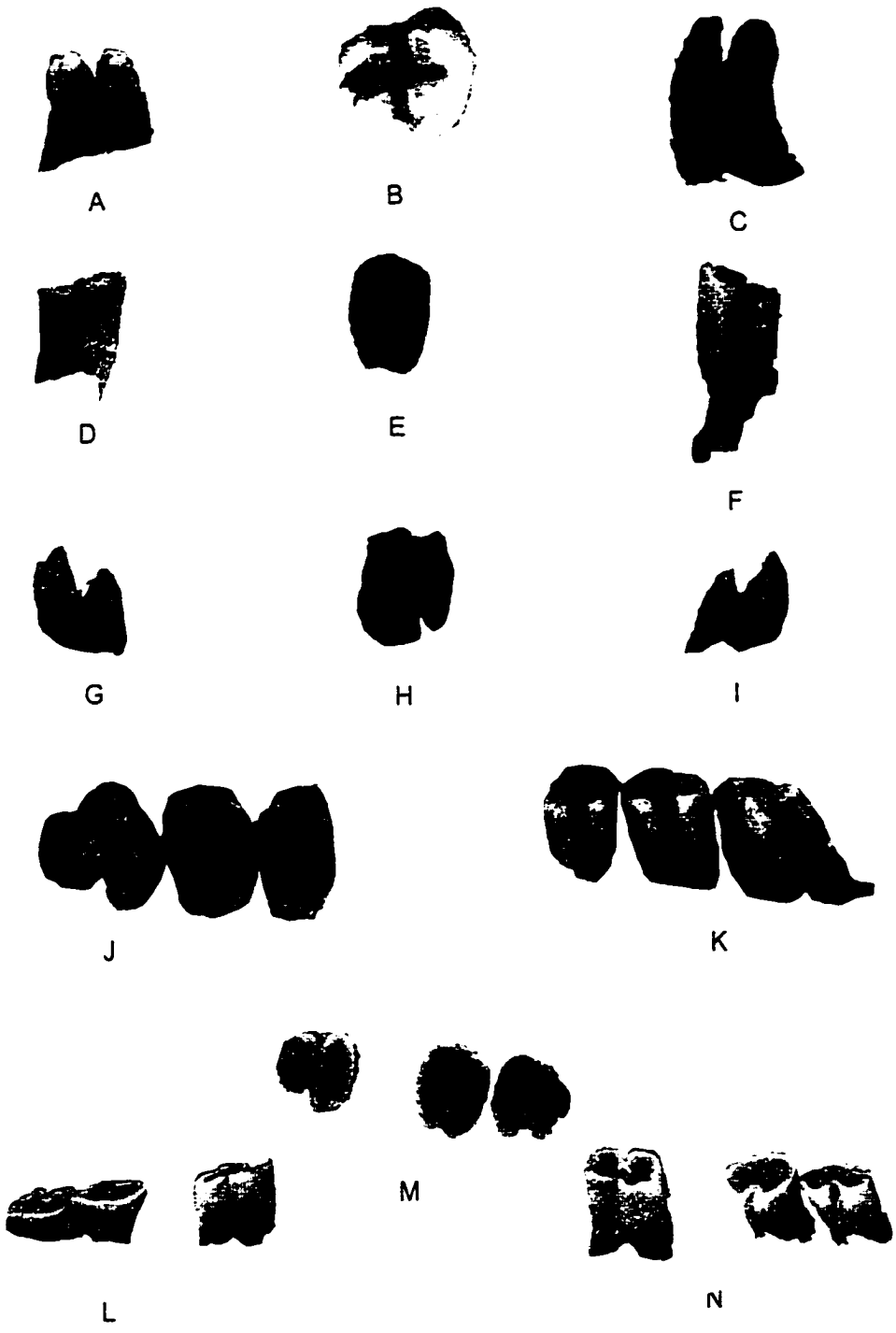
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PLATE 22

A, *Balantiomys nevadensis* n. sp.,OMNH 54762, labial view, left P4, X 17.0.

B, *Balantiomys nevadensis* n. sp.,OMNH 54762, occlusal view, left P4, X 17.0.

C, *Balantiomys nevadensis* n. sp.,OMNH 54762, lingual view, left P4, X 17.0.

D, *Balantiomys nevadensis* n. sp.,UCMP 141798, labial view, left maxilla fragment with M1–M3, X 13.7.

E, *Balantiomys nevadensis* n. sp.,UCMP 141798, occlusal view, left maxilla fragment with M1–M3, X 13.7.

F, *Balantiomys nevadensis* n. sp.,UCMP 141798, lingual view, left maxilla fragment with M1–M3, X 13.7.

G, *Balantiomys nevadensis* n. sp.,OMNH 54754, labial view, left dentary fragment with i1–m1, X 9.8.

H, *Balantiomys nevadensis* n. sp.,OMNH 54754, occlusal view, left dentary fragment with i1–m1, X 9.8.

I, *Balantiomys nevadensis* n. sp.,OMNH 54754, lingual view, left dentary fragment with i1–m1, X 9.8.

J, *Cupidinimus eastgatensis* n. sp., UCMP 141856, labial view, left dentary fragment with p4–m2, X 9.3.

K, *Cupidinimus eastgatensis* n. sp., UCMP 141856, occlusal view, left dentary fragment with p4–m2, X 9.3.

L, *Cupidinimus eastgatensis* n. sp., UCMP 141856, lingual view, left dentary fragment with p4–m2, X 9.3.

M, *Cupidinimus barnoskyi* n. sp., UCMP 141856, labial view, left dentary fragment with p4–m1, X 8.4.

N, *Cupidinimus barnoskyi* n. sp., UCMP 141856, labial view, left dentary fragment with p4–m1, X 8.4.

O, *Cupidinimus barnoskyi* n. sp., UCMP 141856, occlusal view, left dentary fragment with p4–m1, X 8.4.

P, *Cupidinimus boronensis*, OMNH 54763, lingual view, left maxilla fragment with P4–M1, X 10.1.

Q, *Cupidinimus boronensis*, OMNH 54763,occlusal view, left maxilla fragment with P4–M1, X 10.1.

R, *Cupidinimus boronensis*, OMNH 54763, lingual view, left maxilla fragment with P4–M1, X 10.1.

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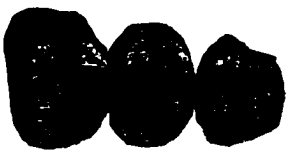

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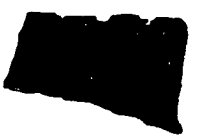

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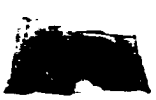

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PLATE 23

A, *Cupidinimus boronensis*, UCMP 141624, labial view, left dentary fragment with p4–m2, X 10.9.

B, *Cupidinimus boronensis*, UCMP 141624, occlusal view, left dentary fragment with p4–m2, X 10.9.

C, *Cupidinimus boronensis*, UCMP 141624, lingual view, left dentary fragment with p4–m2, X 10.9.

D, *Cupidinimus boronensis*, UCMP 141827-01, labial view, right m3, X 10.0.

E, *Cupidinimus boronensis*, UCMP 141827-01, occlusall view, right m3, X 10.0.

F, *Cupidinimus boronensis*, UCMP 141827-01, lingual view, right m3, X 10.0.

G, *Mojavemys* cf. *M. magnumarcus*, UCMP 141787-01, labial view, right P4, X 10.5.

H, *Mojavemys* cf. *M. magnumarcus*, UCMP 141787-01, occlusal view, right P4, X 10.5.

I, *Mojavemys* cf. *M. magnumarcus*, UCMP 141787-01, lingual view, right P4, X 10.5.

J, *Mojavemys* cf. *M. magnumarcus*, OMNH 54775, labial view, right m1 ofr m2, X 6.1.

K, *Mojavemys* cf. *M. magnumarcus*, OMNH 54775, occlusal view, right m1 ofr m2, X 6.1.

L, *Mojavemys* cf. *M. magnumarcus*, OMNH 54775, lingual view, right m1 ofr m2, X 6.1.

M, *Macrognathomys shotwelli* n. sp., UCMP 141603-11, occlusal view, right maxilla fragment with P4, X 11.5.

N, *Macrognathomys shotwelli* n. sp., UCMP 141603-07, occlusal view, left maxilla fragment with M1–M2, X 12.1.

0, *Macrognathomys shotwelli* n. sp., UCMP 141603-07, lingual view, left maxilla fragment with M1–M2, X 12.1.

P, *Macrognathomys shotwelli* n. sp., UCMP 141603-07, labial view, left maxilla fragment with M1–M2, X 12.1.

Q, *Macrognathomys shotwelli* n. sp., UCMP 141623, occlusal view, left dentary fragment with i1–m3, X 13.2.

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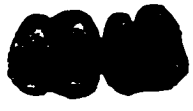

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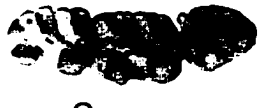

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PLATE 24

A, *Copemys tenuis*, UCMP 141777-15, labial view, right maxilla fragment with M1–M3, X 9.3.

B, *Copemys tenuis*, UCMP 141777-15, occlusal view, right maxilla fragment with M1–M3, X 9.3.

C, *Copemys tenuis*, UCMP 141777-15, lingual view, right maxilla fragment with M1–M3, X 9.3.

D, *Copemys tenuis*, UCMP 141733-01, labial view, left dentary with m1–m3, X 6.1.

E, *Copemys tenuis*, UCMP 141733-01, occlusal view, left dentary with m1–m3, X 6.1.

F, *Copemys tenuis*, UCMP 141733-01, lingual view, left dentary with m1–m3, X 6.1.

G, *Copemys russelli*, UCMP 141777-07, labial view, left maxilla fragment with M1–M2, X 9.3.

H, *Copemys russelli*, UCMP 141777-07, occlusal view, left maxilla fragment with M1–M2, X 9.3.

I, *Copemys russelli*, UCMP 141777-07, lingual view, left maxilla fragment with M1–M2, X 9.3.

J, *Copemys russelli*, OMNH 54414, labial view, right dentary fragment with i1, m1–m3, X 7.3.

K, *Copemys russelli*, OMNH 54414, occlusal view, right dentary fragment with i1, m1–m3, X 7.3.

L, *Copemys russelli*, OMNH 54414, lingual view, right dentary fragment with i1, m1–m3, X 7.3.

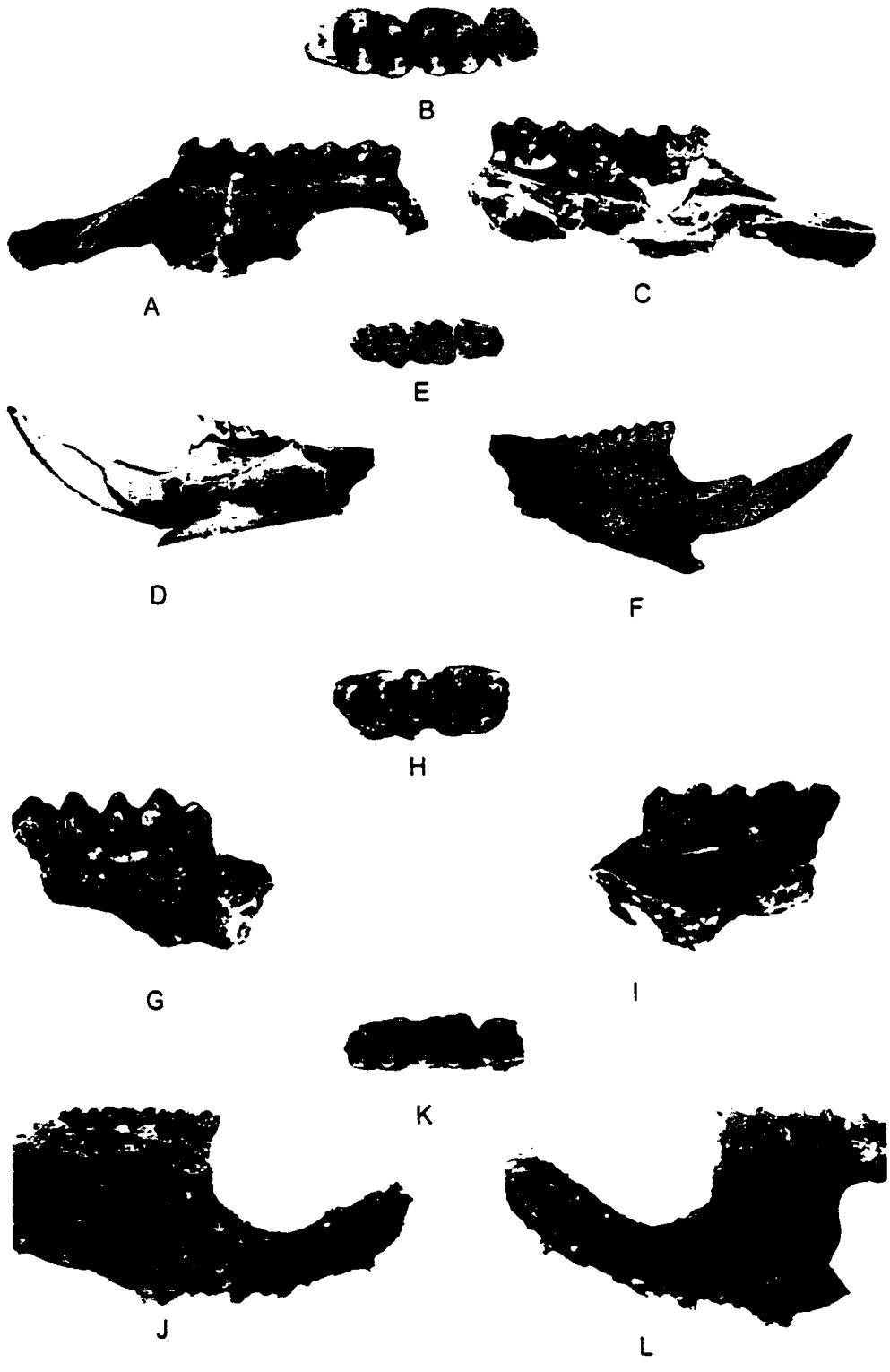
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PLATE 25

A, *Copemys tyleri* n. sp., OMNH 54905, labial view, right maxilla fragment with M1–M3, X 4.9.

B, *Copemys tyleri* n. sp., OMNH 54905, occlusal view, right maxilla fragment with M1–M3, X 4.9.

C, *Copemys tyleri* n. sp., OMNH 54905, lingual view, right maxilla fragment with M1–M3, X 4.9.

D, *Copemys tyleri* n. sp., OMNH 54371, labial view, right dentary fragment with m1–m3, X 4.7.

E, *Copemys tyleri* n. sp., OMNH 54371, occlusal view, right dentary fragment with m1–m3, X 4.7.

F, *Copemys tyleri* n. sp., OMNH 54371, lingual view, right dentary fragment with m1–m3, X 4.7.

G, *Copemys harperi* n. sp., UCMP 141777-36, labial view, left maxilla fragment with M1–M3, X 5.7.

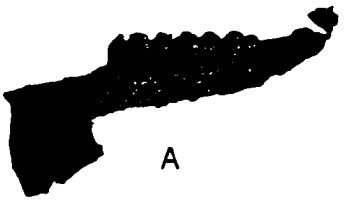
H, *Copemys harperi* n. sp., UCMP 141777-36, occlusal view, left maxilla fragment with M1–M3, X 5.7.

I, *Copemys harperi* n. sp., UCMP 141777-36, lingual view, left maxilla fragment with M1–M3, X 5.7.

J, *Copemys harperi* n. sp., UCMP 141767-10, labial vew, left dentary fragment with m1–m3, X 4.9.

K, *Copemys harperi* n. sp., UCMP 141767-10, occlusal view, left dentary fragment with m1–m3, X 4.9.

L, *Copemys harperi* n. sp., UCMP 141767-10, lingual view, left dentary fragment with m1–m3, X 4.9.



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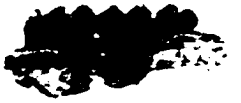

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PLATE 26

A, *Tomarctus* cf.*T. brevirostris*, UCMP 141908, occlusal view, left mandible with p2, p4, and fragmented m1, X 1.60.

B, *Tomarctus* cf.*T. brevirostris*, UCMP 141908, labial view, left mandible with p2, p4, and fragmented m1, X 1.60.

C, *Tomarctus* cf.*T. brevirostris*, UCMP 141908, lingual view, left mandible with p2, p4, and fragmented m1, X 1.60.

D, *Tomarctus* cf.*T. brevirostris*, UCMP 141916, occlusal view, isolated m2, X 2.34.

E, *Tomarctus* cf.*T. brevirostris*, UCMP 141916, labial view, isolated m2, X 2.34.

F, *Tomarctus* cf.*T. brevirostris*, UCMP 141916, lingual view, isolated m2, X 2.34.

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PLATE 27

A, *Leptocyon* sp., UCMP 141482, labial view, right m1, X 2.4.

B, *Leptocyon* sp., UCMP 141482, occlusal view, right m1, X 2.4.

C, *Leptocyon* sp., UCMP 141482, lingual view, right m1, X 2.4.

D, Canidae subfamily indet., UCMP 141911, labial view, maxilla fragment with P4, X 2.4.

E, Canidae subfamily indet., UCMP 141911, occlusal view, maxilla fragment with P4, X 2.4.

F, Canidae subfamily indet., UCMP 141911, lingual view, maxilla fragment with P4, X 2.4.

G, *Bassariscus* cf.*B. parvus*, UCMP 141928, labial view, left dentary fragment with p2–m2, X 0.9.

H, *Bassariscus* cf.*B. parvus*, UCMP 141928, occlusal view, left dentary fragment p2–m2, X 0.9.

I, *Bassariscus* cf.*B. parvus*, UCMP 141928, lingual view, left dentary fragment p2–m2, X 0.9.

J, *Promartes* cf sp., UCMP 113319, labial view, left dentary fragment with p3–m1, X 3.8.

K. *Promartes* cf sp., UCMP 113319, occlusal view, left dentary fragment with p3–m1, X 3.8.

L, *Promartes* cf sp., UCMP 113319, lingual view, left dentary fragment with p3–m1, X 3.8.

M, Felidae subfamily indet., UCMP 141531, labial view, left or right dentary fragment with partial p4, X 0.1.

N, Felidae subfamily indet.., UCMP 141531, occlusal view, left or right dentary fragment with partial p4, X 0.1.

O, Felidae subfamily indet., UCMP 141531, lingual view, left or right dentary fragment with partial p4, X 0.1.

Plate 27

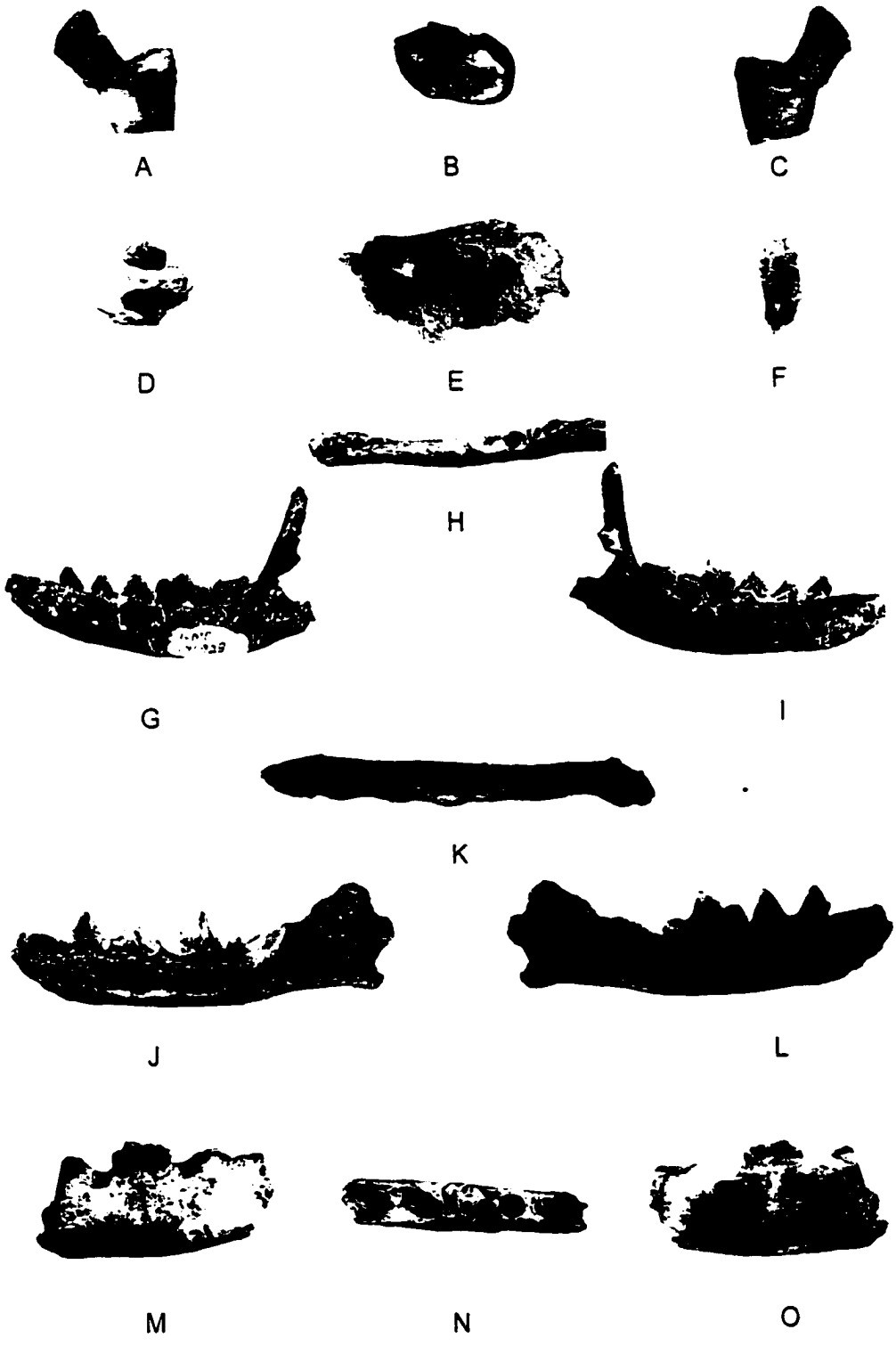

PLATE 28

A, *Ticholeptus* sp. indet., UCMP 141873, labial view, left dentary fragment with m1 and partial m2, X 0.9.

B, *Ticholeptus* sp. indet., UCMP 141873, occlusal view, left dentary fragment with m1 and partial m2, X 0.9.

C, *Ticholeptus* sp. indet., UCMP 141873, lingual view, left dentary fragment with m1 and partial m2, X 0.9.

D, *Aletomeryx* sp. indet., UCMP 141518, labial view, right dentary fragment with m1 fragment and complete m2–m3, X 0.8.

E, *Aletomeryx* sp. indet., UCMP 141518, occlusal view, right dentary fragment with m1 fragment and complete m2–m3, X 0.8.

F, *Aletomeryx* sp. indet., UCMP 141518, lingual view, right dentary fragment with m1 fragment and complete m2–m3, X 0.8.

G, *Aletomeryx* sp. indet., UCMP 141669, labial view, left dentary fragment with p3–m3, X 0.8.

H, *Aletomeryx* sp. indet., UCMP 141669, occlusal view, left dentary fragment with p3–m3, X 0.8.

I, *Aletomeryx* sp. indet., UCMP 141669, lingual view, left dentary fragment with p3–m3, X 0.8.

J, *Aletomeryx* sp. indet., UCMP 141524, labial view, maxillae fragment with M1–M2, X 1.0.

K, *Aletomeryx* sp. indet., UCMP 141524, occlusal view, maxillae fragment

with M1–M2, X 1.0.

L, *Aletomeryx* sp. indet., UCMP 141524, lingual view, maxillae fragment with M1–M2, X 1.0.

Plate 28

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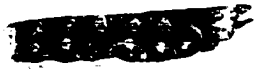

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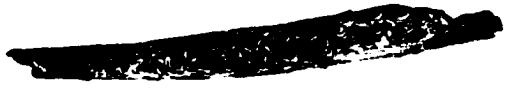

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PLATE 29

A, *Merychippus* sp. indet., UCMP 141921, posterior view, distal tibia, X 1.0.

B, *Merychippus* sp.indet., UCMP 141837, posterior view, astragalus, X 1.0.

C, *Merychippus* sp.indet.,UCMP 141889-01, medial view, proximal humerus, X 0.8.

D, *Merychippus* sp.indet., UCMP 141899-03, ? view, 2nd or 4th metatarsal, X 0.9.

E, *Merychippus* sp. indet., UCMP 141899-02, dorsal view, magnum, X 0.9.

F, *Moropus* sp. indet., UCMP 141946, posterior view, fragment of humerus, X 0.2.

A B

C

D

E

F

PLATE 30

A, *Teleoceras* sp., UCMP 120127, ventral view, palate with left P2–M3 and right P2–M3, X 0.2.

B, *Teleoceras* sp., UCMP 120127, vental view, symphosis of dentary fragment, X 0.3.

C, *Moropus* sp., UCMP 141954-01, dorsal view, ungual phalanx, X 0.9.

D, *Moropus* sp., UCMP 141954-01, lateral view, ungual phalanx, X 0.9.

E, *Moropus* sp., UCMP 141896, dorsal view, distal phalanx, X 0.7.

A

B

C

D

E

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Running head: *Leptodontomys* and phylogenetic relationships

NEW SPECIES OF *LEPTODONTOMYS* (RODENTIA: EOMYIDAE) AND PHYLOGENETIC RELATIONSHIPS WITHIN THE GENUS

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ABSTRACT

The Eastgate local fauna, Chuchill County, Nevada of Miocene (early Barstovian) age includes 25 families of mammals, as well as numerous fish, amphibians, reptiles and birds. Three new species of *Leptodontomys* (*L. korthi* n. sp., *L. schnelli* n. sp., and *L. protistopikos* n. sp.) are described based on a large sample (249 specimens) of maxillae, mandibles, incisors, and isolated upper and lower cheekteeth. Eighteen quantitative dental characters of the lower premolars for *Leptodontomys* provide reliable separation of species. Phylogeny including all species of *Leptodontomys* was constructed from 74 characters of the maxillae, mandibles, and upper and lower cheekteeth. Phylogenetic analyses show two of the new species, *L. schnelli* n. sp. and *L. protistopikos* n. sp., form a trifurcation with *L. stirtoni*. The third new species, *L. korthi*, does the same with *L. quartzi* and *L. russelli*.

Key words: Barstovian, *Leptodontomys*, Monarch Mill Formation, Nevada, Phylogenetics

INTRODUCTION

Five species of *Leptodontomys* have been described from Tertiary deposits in North America (Korth, 1994), the oldest is *L. douglassi*, is from the Oligocene (early Arikareean) of Slope County, North Dakota (Burke, 1934) and Dawes County, Nebraska (Korth and Bailey, 1992). Younger species of *Leptodontomys* include: *L. quartzi* and *Leptodontomys* sp. discovered in Oregon localities and Barstovian and Clarendonian in age, respectively (Shotwell,1967); *L. russelli* discovered in Saskatchewan, Canada, and Barstovian in age (Storer,1975); *L. stirtoni* from Barstow, California, and is Barstovian in age (Lindsay, 1972); and *L. oregonensis* recovered from deposits in Oregon, and are Hemphillian in age (Shotwell, 1956).

Leptodontomys is endemic to North America and occurred primarily in western North America and the Great Plains of the United States but with a single occurrence in southern Saskatchewan. A single specimen has been collected from Clarendonian deposits of the southern Great Plains (K. S. Smith, unpublished data).

Eomyids are rare in Miocene deposits in North America and, when present, usually consist of a single species represented by a single or few specimens (i.e., isolated cheekteeth, maxilla with one or more cheekteeth, and mandibles with one or more cheekteeth). Shotwell (1967) examined12 Miocene faunas of the northern Great Basin of Oregon as follows: Barstovian at Quartz Basin, Red Basin, and Mascall; Clarendonian at Black Butte; Hemphillian at Little

Valley, Bartlett Mountain, Otis Basin, Juniper Creek Canyon, Thousand Creek, Krebs Ranch I, Krebs Ranch II, and McKay Reservoir. Of these only four faunas included eomyids; the Barstovian Quartz Basin fauna included two genera *Pseudotheridomys* and *Leptodontomys*. The other three faunas (Clarendonian at Black Butte; and Hemphillian at Bartlett Mountain and McKay Reservoir) had only a single genus (*Leptodontomys*). Newly collected material from Eastgate, Nevada provides the best sample of *Leptodontomys* from a single fauna or collectively among all known faunas that contain this group.

Three genera of eomyids *Arikareeomys*, *Pseudotheridomys* and *Leptodontomys* in the Miocene of North America are represented (Korth, 1994). Two of these *(Pseudotheridomys* and *Leptodontomys*) have been reported from Barstovian localities by Lindsay (1972) and Shotwell (1967). To date, only Quartz Basin and Eastgate of the Barstovian vertebrate faunas have included genera of eomyids. At Eastgate, numerous specimens of two genera are represented. *Leptodontomys* is the focus of this paper.

Leptodontomys occurred from the Arikareean through Clarendonian (Smith, in preparation) in the Great Plains, Barstovian through Hemphillian in western North America, and Barstovian in the Great Plains of Saskatchewan where it was known from a single dentary. In fact, of the five previously described species of *Leptodontomys*, upper cheekteeth were known for only two (*L. douglassi* and *L. stirtoni*). The Eastgate fauna, by contrast, includes a large sample of dentaries, maxillae, cheekteeth, and the first reported skull for this genus. Thus the new material from Eastgate provides the best known sample

and allows a better understanding of the patterns of morphological variation and phylogeny of the genus.

The focus of this investigation is to: 1) provide an overview of the taxonomic history of the rodent genus *Leptodontomys* (Eomyidae); 2) evaluate morphological variation of the cheekteeth; 3) offer additional descriptive information for the dentary; 4) construct a hypothetical phylogeny for *Leptodontomys*; and 5) investigate the systematic paleontology of *Leptodontomys* recently collected from the Eastgate fauna, Churchill County, Nevada, including several new species.

TAXONOMIC HISTORY

The genus *Leptodontomys* was erected by Shotwell (1956), while describing *L. oregonensis*, which was recovered in an unamed and undescribed lithologic unit of Hemphillian age, and was part of the McKay Reservoir local fauna (Shotwell, 1956). Shotwell (1967) described another species of eomyid (*Adjidaumo quartzi*) collected from the Quartz Basin and Red Basin localities. In addition, he identified several teeth from the Black Butte and the Bartlett Mountain localities as *Leptodontomys* sp. Lindsay (1972) described a new species of *Pseudadjidaumo* (*P. stirtoni*). He also placed *Adjidaumo quartzi* in synonymy with *P. stirtoni*. Storer (1970) described *Adjidaumo russelli* and later placed it in *Pseudadjidaumo* (Storer, 1975). Engesser (1979) and Fahlbusch (1979) suggested that *Pseudadjidaumo stirtoni* Lindsay, 1972 was a junior

synonym of *Leptodontomys*. They did not believe the morphological differences (upper molars having a distinct lingual arm of anterior cingulum; lower molars having a distinct labial arm of anterior cingulid) described by Lindsay (1972) warranted generic distinction. Without elaboration, Korth and Bailey (1992) agreed with the synonomy of *Psedadjidaumo* and *Leptodontomys*. In fact, they suggested that all Barstovian species assigned to *Pseudadidjidaumo* should be included in *Leptodontomys*. Another eomyid, *A. douglassi*, was described by Burke (1934) based on a single specimen from the late Oligocene Killdeer Formation in North Dakota. Additional material referred to *A. douglassi* (see Korth, 1989) was recovered from the Cedar Ridge local fauna, Wyoming (Setoguchi, 1978), and the Harrison Ranch local fauna, South Dakota (Simpson, 1985). Korth and Bailey (1992) placed *A. douglassi* in *Leptodontomys* based on new specimens from Dawes County, Nebraska. In addition, Korth and Bailey (1992) suggested *Eomys* sp. from the Vedder fauna of the Branch Canyon Formation, Santa Barbara County, California (Lindsay, 1974) should be placed in the genus *Leptodontomys*, this being more consistent with the fossil record of eomyids in North America, where the Eurassian genus Eomys is otherwise unknown.

Thus, the following five species of *Leptodontomys* are recognized: 1) *Leptodontomys douglassi* (Burke, 1934) — Arikareean: Killdeer Formation, Slope County, North Dakota (Burke, 1934; Korth and Bailey, 1992); Gering Formation, Dawes County, Nebraska (Korth and Bailey, 1992). 2-4) *L. quartzi* Shotwell, 1967, *L. stirtoni* Lindsay, 1972, and *L. russelli* Storer, 1975 — Barstovian: Quartz

Basin and Red Basin faunas, Malheur County, Oregon (Shotwell, 1967); Barstow Formation, Barstow fauna, San Bernardino County, California (Lindsay, 1972); and Kleinfelder Farm locality, Wood Mountain Formation, Saskatchewan (Storer, 1975). 5) *L. oregonensis* — Hemphillian: McKay Reservoir fauna, Umatilla County, Oregon (Shotwell, 1956). Other specimens of *Leptodontomys* not yet identified are reported from the Arikareean at the following localities: Harrison Ranch local fauna, South Dakota (Simpson, 1985; Korth, 1989) and Vedder fauna, Branch Canyon Formation, Santa Barbara County, California (Lindsay, 1974); Clarendonian: Black Butte, Malheur County, Oregon (Shotwell, 1956, 1967); Whisenhunt Quarry local fauna, Laverne Formation, Beaver County, Oklahoma (Smith, in preparation); Hemphillian: Bartlett Mountain fauna, Harney County, Oregon (Shotwell, 1967).

METHODS AND MATERIALS

I examined 249 specimens of *Leptodontomys* from Eastgate. These specimens included mandibles, maxillae, and isolated teeth. The material was compared with 2 maxillae with cheekteeth and 8 mandibles with cheekteeth of *L. douglassi*; a single p4 of *L. oregonensis*; 6 mandibles with cheekteeth of *L. quartzi*; 4 DP4s, 4 P4s, 8 M2s, 3 M2s, 1 M3, 2p4s, 9 m1s, 9 m2s, and 1 m3 of *L. stirtoni*; and 1 mandible with cheeteeth of *L. russelli*.

Taxonomy follows Engesser (1979, 1999), Fahlbusch (1979), Korth and Bailey (1992), Shotwell (1956, 1967), and Storer (1975). For all Eastgate

specimens, length and width measurements are greatest crown dimensions and were made to the nearest 0.01 mm through a 3-D reflex microscope (MacLarnon, 1989). Additional length and width measurements, as well as other characters, were taken from the literature.

Eastgate fossils included are from 5 of the 20 localities in the Monarch Mill Formation of the Middlegate Basin described by Smith (2002). Fossil vertebrates from Eastgate were collected by individuals and field crews from the Univeristy of California Museum of Paleontology (UCMP) and the Oklahoma Museum of Natural History (OMNH). UCMP collections were made over a period of more than 30 years from 1958 into the early 1990s (D. E. Savage, personal communication) and those of the OMNH were made during a single field season (1995). Vertebrate fossils were collected by surface prospecting and by quarrying and screewnwashing of bulk matrix (Cifelli et al., 1996; Madsen, 1996).

The p4s were studied in greatest detail because they are most diagnostic tooth for this group; in addition, the p4 is the only tooth described for all known species of *Leptodontomys*. As with other rodent groups that possess P4/4, the M1/1 and M2/2s of *Leptodontomys* are not easily distinguished from one another, and morphological patterns of an M1 may differ from those of the M2 of the same specimen; likewise, the m1 may differ morphologically from that of an m2 of the same specimen. Therefore, species identifications based on a single upper or lower molar may be incorrect. In contrast, there is no mistaking a P4 for a p4 or for any of the upper or lower molars and, for *Leptodontomys*, the DP4/4s are easy to distinguish from the adult P4/4.

The coefficient of variation (CV), and three multivariate statistical techniques (principal components analysis, correspondence analysis, and cluster analysis) were employed to evaluate the interspecific and intraspecific variation of p4s in *Leptodontomys*. The two-dimensional scatter plots were constructed using SigmaPlot 2000 (SPSS Inc., 2000).

The CV, introduced by Simpson and Roe (1939) as a measure of relative variability, has been used in the study of fossil vertebrates to test a single-species null hypothesis (see Gingerich, 1979; Kay, 1982a, b: Freudenthal and Bescos, 1984; Cope and Lacy, 1992; Carrasco, 1998). Carrasco (1998) provided a comprehensive evaluation of the use of CV in determining variation and the presence of multiple species. I used the CV to evaluate the single-species null hypothesis for the p4s of *Leptodontomys* from Eastgate. A CV of greater than 10.0 has been used to indicate that more than a single species may be present in the sample (Carrasco, 1998, 2000).

Principal components analysis (PCA) was used to evaluate the relationships between the specimens (p4s) and their morphological attributes by reducing a data set of 18 variables to 2 or 3 composite variables. Principal components can be useful for detecting structure among the original variables, and thus aid in separating the specimens into groups (e.g., species). PCA was performed using NTSYS-pc version 2.10q (Rohlf, 2001). A cross-tabulated matrix as defined by Hair et al. (1998) was constructed from a suite of 18 characters identified from a sample of 54 p4s of *Leptodontomys* from Eastgate. The data matrix consisted of discrete, multistate characters (i.e., 0, 1, and 2), and

thus there was no need to standardize. A correlation matrix was constructed and employed to determine the principal component axes (eigenvalues and eigenvectors). A scree test (Hair et al., 1998) was used to determine how many components should be retained. This test is used to identify the number of factors that can be extracted before unique variance dominates the common variance (Hair et al., 1998). The projections onto the first two or three components (based on unstandardized data) were plotted.

Correspondence analysis (CA) also was employed to determine associations between specimens and a set of descriptive characters was specified for the p4s. CA is based on transformation of chi-square values into metric measures of distance (Hair et al., 1998). CA was performed using NTSYS-pc, version 2.10q (Rohlf, 2001) to identify associations among the Eastgate specimens and their characters simultaneously (e.g., in joint space). Of the 18 characters of the p4s used in the PCA, only the 14 with complete data (i.e., no missing values) were used in the CA, which does not recognize missing data (Legendre and Legendre, 1998). As a result, characters 7, 11, 12, and 15 were excluded (see Table 1). Two-dimensional scatter plots were created from loadings in the row factor matrix (characters) and the column factor matrix (specimens). The number of dimensions selected for analysis was based on Hair et al. (1998), who stated that this number should have an inertia (eigenvalue) greater than 0.20. A major attribute of CA is its abilitiy to represent rows and columns in joint space, thus allowing for character-specimen relationships to be observed in a single perceptual map.

Cluster analysis allowed me to display the most similar specimens based on the 18 characters of the p4s. Because the data are qualitative (e.g., presence/absence), the matrix was not standardized. The unweighted pair-group method using arithmetic averages (UPGMA) of Euclidean distances was selected because it has been used effectively in similar studies involving dental variation (Best, 1993; Best and Schnell, 1974; Carrasco, 2000; Schnell et al., 1978). The cophenetic correlation coefficient (Sneath and Sokal, 1973) was calculated to evaluate the degree to which the resulting dendogram accurately represented the original multidimensional Euclidian distances.

A phylogenetic analysis was performed using PAUP 4.0b8 (Phylogenetic Analysis Using Parsimony; Swofford, 2001) and MacClade 4.0 (Maddison and Madison, 2001). Characters from all upper (P4–M3) and lower (p4–m3) cheekteeth and mandibles of *Leptodontomys* were evaluated. The data matrix consisted of 74 characters from upper cheekteeth, lower cheekteeth, and dentary for eight species of *Leptodontomys* (Table 2), including three new species described below. Most specimens of *Leptodontomys* lack many of the 74 characters evaluated and several of these characters are polymorphic. I followed Poes and Wiens (2000), who suggested the inclusion of polymorphic characters and missing values (even when 75% or greater of the data cells scored are for unknown data) because they may contain useful phylogenetic information. Inclusion of such characters increases accuracy (i.e., they provide a strong similarity between the estimated trees and the true phylogeny) (Poes and Wiens, 2000).

All characters were designated as unordered, and an outgroup (i.e., *Adjidaumo maximus*) was specified to polarize the character states of the ingroup taxa. The outgroup was chosen based on presence of shared, derived characters associated with the ingroup and its completeness in number of character states evaluated. Strict-consensus and 50%-majority-rule-consensus trees were produced from the several most-parsimonious trees constructed from the exhaustive search.

ABBREVIATIONS

Abbreviations are used in the text, figures, captions, plates, and tables. Institutional abbreviations: (CMNH) Carnegie Museum of Natural History; (KUVP) University of Kansas Museum of Natural History; (LACM) Los Angeles County Museum of Natural History; (OMNH) Oklahoma Museum of Natural History; (ROM) Royal Ontario Museum; (UCMP) University of California Museum of Paleontology; (UCR) University of California at Riverside; (UNSM) University of Nebraska State Museum; (UO) University of Oregon Museum of Natural History. Dentition: (I) upper incisor; (P4–M3) represents cheekteeth of maxilla; (P4) upper fourth premolasr; (DP4) deciduous upper fourth premolars; (M1) upper first molars; (M2) upper second molars; (M3) upper third molars; (i) lower incisor; (p4–m3) represents teeth of dentary; (dp4) lower deciduous fourth premolars; (p4) lower fourth premolars; (m1) lower first molars; (m2) lower second molasr; (m3) lower third molars; (DP4/4) upper and lower deciduous fourth premolars;

(P4/4) upper and lower fourth premolars; (M1/1) upper and lower first molars; (M2/2) upper and lower second molasr; (M3/3) upper and lower third molars; (id) suffix that refers to a lophid, a cingulid, or a cusp of lower cheektooth. Tooth measurement abbreviations: (AP) greatest anteroposterior length of tooth; (T) greatest transverse width of tooth; (TA) greatest transverse width of anterior half of tooth; (TP) greatest transverse width of posterior half of tooth. Miscellaneous abbreviations: (m) meter; (Ma) *mega-annum* (millions of years); (mm) millimeter; (P) fossil plant localities for UCMP; (V) vertebrate fossil localities for OMNH and UCMP.

VARIATION OF THE DENTITION

General characters.—The upper and lower cheekteeth of *Leptodontomys* are brachydont, with slightly bulbous walls. Three roots are present on all upper cheekteeth: a single large labial root and two smaller lingual roots. Two roots of the lower cheekteeth are present on the p4s, while three roots (one large anterior and two smaller posterior) occur on the lower molars. As with the upper cheekteeth, the lower m1 and m2 are similar in size to each other, but larger than the p4, which is larger than the smallest tooth in the tooth row, the m3. The upper and lower cheekteeth also possess the following: has a crown that is roughly rectangular (longer than wide) in occlusal outline, has a major cusp that occurs on each corner, has premolars that are usually molariform with a metaconid and protoconid that are much closer to each other than a paracone

and protocone of the M1 or M2s. A distinct anterior cingulum(id) is present on the M/1– M2/2, spanning nearly the entire width of these teeth; a distinct posterior cingulum(id) is also present on all first and second molars, but not as prominent as the anterior cingulum(id). An ectoloph(id) usually unites the hypocone(id) with the protocone(id) or the metaconid (p4 only). A hypoloph(id) unites the the hypocone(id) and metacone or entoconid and, although always present, the posterior cingulum(id) varies in its lateral sites of attachment, transverse length across the width of the tooth, and anteroposterior length. Below I describe occlusal patterns for the cheekteeth in detail (see also Korth and Bailey, 1992; Lindsay, 1972; Shotwell, 1956; 1967).

The upper and lower premolars are the main focus of species identification herein (see Tables 3-5). However, previous studies utilized characters of the upper and lower molars for identification of *Leptodontomys* species (see Lindsay, 1972; Korth and Bailey, 1992; Shotwell, 1956, 1967). The large sample of specimens from Eastgate show these characters to be variable, however, suggesting their taxonomic significance is questionable. For example, variations in the metalophid (see below) for the m1 can occur in consert with the same p4 morphotype, but different from that of the m2 for the same specimen as follows: the attachment of the anterior cingulid occurs centrally and high on the metalophid, or the anterior cingulid is attached centrally and low on the metalophid, and thus often being identifiable only in late stages of wear; or the anterior cingulid is unattached on the m1 but attached on the m2. If the m1 and m2 from the same jaw were found isolated from each other, criteria employed in

previous studies would have resulted in different taxonomic placement for the two molars. Another character previously used for species identification (Lindsay, 1972; Korth and Bailey, 1992; and Shotwell, 1956, 1967) is the mesolophid, which also is variable (it may be present or absent; if present, it can be long or short) and usually appears to be longer and more distinct on the m2 than m1 (This difference in mesolophid length may help to separate an m1 from an m2 of the same specimen, but is not reliable for determining tooth locus on different specimens or of isolated teeth; see Tables 6-7).

Unlike the p4s, the P4s appear to be much less variable and can be separated by few consistent characters. Thus, statistical analyses were limited to the p4s for all taxa.

Size.—Of all species of Leptodontomys, *L. stirtoni* has, by far, the largest P4, followed in size by *L. douglassi*, species C (Eastgate), *L. quartzi*, and species A (Eastgate; see Tables 8-9 and Fig. 1). The p4s of *L. stirtoni* are the largest, followed by *L. douglassi*, species B (Eastgate), *L. oregonensis*, *L. russelli*, *L. quartzi*, and species A (Eastgate) (see Tables 10-11 and Fig. 2). In general, the size relationships of upper and lower molars follow the pattern of their respective premolars (see Figs. 3-4). However, exceptions are as follows: the M1 and m1 are usually longer than wide compared to the M2 and m2, which are usually wider than long (except in *L. douglassi*, in which M1/1 and M2/2 length and width are nearly equal). Based on Lindsay (1972) and Korth and Bailey (1992), the M3s of *L. douglassi* are much smaller than those of *L. stirtoni*, but curiously, the m3s of *L. douglassi* are much larger than those of *L. stirtoni*. In other species of

Leptodontomys in which the M3 and m3 are known, they are similar in size, and thus the supposed size differences of the M3/3s of *L. douglassi* and *L. stirtoni* may be a an artifact of small sample size. It is also possible that the M3/3s were incorrectly attributed to *L. douglassi* by those authors.

Statistical analyses.—The CV values based on all p4s from Eastgate suggested the presence of more than one species. The p4s were then assigned to species groups, following results of other analyses. After the p4s were assigned to species groups, the new CV values calculated for these resorted samples were substantially lower, suggesting that the new samples were monospecific.

Gingerich (1974) indicated that a CV value of 10.0 or greater suggests that a sample may include two or more species. Recently, Carrasco (1998) examined geographic range, sexual dimorphism, and temporal mixing as possible explanations for the high variation (CV) of a population of extinct heteromyid rodents (*Cupidinimus*) from southwestern Montana. He suggested that geographic range was not an explanatory factor, because CV values from modern reference groups (e.g., *Perognathus*) of both large and small ranges were much lower than the fossil heteromyid population. Similarly, Carrasco (1998) found that the influence of sexual dimorphism was unlikely because other studies showed that sexual dimorphism does not significantly affect cheektooth size (Gingerich and Schoenginger, 1979; Gingerich and Winkler, 1979; Gingerich,1981). In addition, sexual dimorphism is low in extant populations of the closely related heteromyids (*Perognathus*) studied by Williams (1978).

Likewise, Carrasco (1998) suggested that temporal mixing is unlikely to have affected CV values for *Cupidinimus* because the sample represents a short time interval (0.2 ma), and thus is more time-constrained than any other species of *Cupidinimus* with lower CV values. Eomyids are closely related to heteromyids (Korth and Bailey, 1992; Korth 1994) and might resemble them in the ways in which their teeth vary. Therefore, based on Carrasco (1998) and the other studies cited above, the high CV values for the p4s of *Leptodontomys* from Eastgate are probably related to morphological variation and not to geographic range, sexual dimorphism, or temporal mixing.

The first four principal components of PCA explained 55.9% of the variance, with the first component accounting for 20.8% (Table 12). Character loadings on the first component were greater than 0.04, with the highest loadings on the following variables: separation of the protoconid and metaconid from each other (5) had a high positive loading; absence of the metalophid (6) and the anterior arm of the ectolophid joined to the metaconid (15) both had high negative loadings (Fig. 5). The second component explained 16.0% of the total variation, with negative loadings for absence of the mesolophid (9) and the posterior cingulid joined to the hypolophid centrally (18). The third component (10.6%) was characterized by two high negative loadings for an incomplete metalophid (9) and the absence of the anterior arm of the ectolophid (10) (Fig. 6). The fourth component (8.5%) had a single high negative loading for the absence of a mesostylid (character 16) (Fig. 7).

The first three axes of the correspondence analysis explained 49.6% of

the variance, with the first axis explaining 20.0%. One cluster of specimens (species A) occurred on the far right of the first axis and showed a strong correspondence with characters 2, 4, and 5, indicating that these specimens have a p4 that is equally as long as wide, may have an anteroconid, and have a separate protoconid and metaconid (Fig. 8). A second cluster of specimens (*L. quartzi*) are concentrated near the center of the first dimension and showed a correspondence with characters 1, 10, and 17, which indicated the presence of a trigonid that is equally as wide as long, an anterior arm of the ectolophid, and a posterior cingulid that usually is incomplete, respectively. The data points that grade toward the left side of the graph (Fig. 8) also represent *L. quartzi* and showed a strong correspondence with characters 3, 6, 14, and 16, indicating the presence of an anterior cingulid and metalophid, a straight posterior arm of the ectolophid, and the presence of a mesostylid, respectively. A single specimen (species B) occurred on the lower left side of the first dimension and showed a strong correspondence for characters 9 and 18, indicating that a mesolphid is present and a posterior cingulid arises near the hypoconid, respectively. This is the only species to possess these characters.

The second axis explained 16.7% of the total variance. The group of specimens (i.e., *L. quartzi*) in the center of the second axis showed a strong correspondence with characters 9, 14, and 18, indicating the absence of a mesolophid, a posterior arm of the ectolophid that tends to be bent (but is straight in a few specimens), and a posterior cingulid that arises centrally on the hypolophid, respectively.

The third axis explained 13.0.% of the total variance. The group of specimens (i.e., *L. quartzi*) near the center of this dimension showed a strong correspondence with characters 3, 14, and 16, indicating the presence of an anterior cingulid (present in three specimens of this group and in no other species of *Leptodontomys*), a posterior arm of the ectolophid that tends to be straight with few exceptions, and of a mesostylid that occurs in a few specimens, respectively (Fig. 9).

The cluster analysis grouped similar specimens based on 18 characters of the p4s (Tables 1, 2, and 13). In the resulting UPGMA dendrogram, specimens were partitioned into three main groups (Fig. 10). The first group included a single specimen (species B) that is the largest of all specimens (p4s) from Eastgate. The second group included two clusters that include specimens of species A. The first cluster included 9 specimens, while the second had 14. The third group also contained two clusters and represents specimens of *L. quartzi*. The first cluster contained 3 specimens, while the second cluster had 26. Cluster analysis produced groups of specimens similar to those discovered in PCA and CA.

In summary, five species of *Leptodontomys* can be recognized from the Eastgate local fauna, Churchill County, Nevada. Three species (species A, species B, and species C) from Eastgate are new (named below), whereas the other two species (*L. quartzi* and *L. stirtoni*) have been previously described. My results indicated that the upper and lower premolars (P4/4) are the most diagnostic for species identification. However, the upper molars may prove

useful in distinguishing the large species from the smaller species, but are not as reliable for species identifications among the smaller species (see Figs. 3 and 4).

The premolars of these species are easily distinguishable by size: *L. stirtoni* has the largest P4, followed by species C in which P4 is also longer anteroposteriorly compared to width than those of *L. quartzi*, species A, or *Leptodontomys* sp. indet. respectively. There are two groups of species based on the length and width of p4 (but widths are similar). The first group has a long p4, and consists of *L. stirtoni* and Eastgate species B. The second has shorter p4s and includes Eastgate species A and *L. quartzi*. For comparisons to other known species of *Leptodontomys*, see Figs. 1 and 2.

Unfortunately, two species of *Leptodontomys* from Eastgate are missing the p4, and thus those species were not included in the multivariate analyses. Species of *Leptodontomys* included in PCA and CA were *L. quartzi*, species A and species B. The PCA, CA, and cluster analysis separated p4s into three groups. Collectively, the characters that appear to contribute most to these groups are presence or absence of an anterior cingulid or anteroconid, separation of protoconid and metaconid, presence or absence of a metalophid, length and direction of mesolophid, attachment of the anterior arm of the ectolophid to the metaconid, and labial attachment of posterior cingulid.

Below, I provide detailed descriptions of *Leptodontomys* specimens from Eastgate, including three new species. In addition, a detailed comparison of the Eastgate material to other known specimens of *Leptodontomys* are included.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Eomyidae Eperet and Douxami, 1902

Subfamily Eomyinae Eperet and Douxami, 1902

Tribe Eomyini Eperet and Douxami, 1902

Genus *Leptodontomys* Shotwell, 1956

Leptodontomys korthi n. sp.

Plate 1 (A-H)

Holotype.—UCMP 141780-241, right dentary fragment with p4–m2.

Type locality.—Eastgate, UCMP V70140.

Etymology.—Named in honor of W. W. Korth for his contributions to knowledge of the genus *Leptodontomys* and other Tertiary rodents.

Localities.—Type and OMNH V974 and V976; UCMP V70138, and V70147.

Age.—Barstovian.

Stratigraphic and geographic occurrence of species.—Barstovian: Monarch Mill Formation, Eastgate fauna, Churchill County, Nevada.

Hypodigm.—Type and OMNH 54699, right maxilla fragment with P4; OMNH 54703, right maxilla fragment with M1–M2; OMNH 54706, right P4; OMNH 54707, left maxilla fragment with P4; OMNH 54712, left P4; OMNH 54715, left p4; OMNH 54720, right dentary fragment with p4; OMNH 54724, right dentary fragment with p4–m2; OMNH 54725, right dentary fragment with p4–m1;

OMNH 54732, left m1or 2; OMNH 54733, left M1 or 2; OMNH 54736, left m1or 2; OMNH 54739, right m1or 2; OMNH 54880, right m1 or 2; UCMP 141705 palate with right P4–M1; UCMP 141780-33, left m1or 2; UCMP 141780-40, right m1or 2; UCMP 141780-44, left M1 or 2; UCMP141780-60, left M1 or 2; UCMP 141780-61, right m1or 2; UCMP 141780-85, left M1 or 2; UCMP 141780-89, right maxilla fragment with P4–M1; UCMP 141780-96, right maxilla with P4–M1; UCMP 141780-99, right P4.; UCMP 141780-107, left dentary fragment with p4; UCMP 141780-108, left m1or 2; UCMP 141780-127, left p4; UCMP 141780-133, right M1 or 2; UCMP 141780-135, left m1or 2; UCMP 141780-136, left m1or 2; UCMP 141780-137, left P4; UCMP 141780-155, right m1or 2; UCMP 141780-172, right P4; UCMP 141780-182, right M1 or 2; UCMP 141780-206, right m1or 2; UCMP 141780-236, right P4-M1; UCMP 141780-237, left maxilla fragment with P4–M2; UCMP 141780-242, right dentary fragment with p4; UCMP 141780-244, right dentary fragment with p4–m1; UCMP 141780-245, left dentary fragment with p4-m2; UCMP 141780-248, left dentary fragment with p4–m1; UCMP 141780-250, right dentary fragment with p4–m1; UCMP 141780-254, right dentary fragment with p4; UCMP 141780-262, right dentary fragment with m1–m3; UCMP 141780-263, left maxilla fragment with P4; UCMP141780–264, right dentary fragment with p4-m1; UCMP 141780-266, left dentary fragment with p4–m2; UCMP 141780-267, left dentary fragment with p4; UCMP 141780-268, right dentary fragment with p4-m1; UCMP 141780-277, left dentary fragment with p4–m1; UCMP 141780-278, right dentary fragment with p4–m1; UCMP 141780-282, left dentary fragment with p4; UCMP 141780-283, left maxilla

fragment with P4– M1.

Measurements.—See Tables 9 and 11.

Diagnosis.—This small species of *Leptodontomys* differs from *L. stirtoni* and *L. douglassi* in having the following characters of the P4: anterocone present in 18% of specimens (no other species possesses this character); paracone larger than other three cusps (except *L. stirtoni*); paracone and protocone transversely aligned; lingual arm of the protoloph short to absent; labial arm of the protoloph submerged; lingual arm of the metaloph less distinct than labial arm; equal anteroposterior length of lingual and labial basins; posterior cingulum anteroposteriorly narrow and open labially (except *L. stirtoni*). The M1–M2s of *L. korthi* differ from *L. stirtoni* and *L. douglassi* in having: a labial attachment for the anterior cingulum that lies along the anteromedial margin of the protocone; arms of the anterior cingulum equal in size (except *L. stirtoni*); and lingual and labial arms of the protoloph and metaloph that are less distinct and more distinct, respectively.

The dentary of *L. korthi* differs from those of *L. douglassi*, *L. oregonensis*, *L. quartzi*, and *L. russelli* (the dentary of *L. stirtoni* is not known) in possessing the following characters: the mental foramen occurs level with the distal end of the masseteric scar (except *L. oregonensis*); the masseteric scar ends distally below the middle of the p4 (except *L. douglassi*); the dorsal shelf of the masseteric scar is absent to weak (except *L. quartzi*); the ventral shelf of the masseteric scar is strong; and there is a single foramen on the lingual surface below the anterior root of the m1. The p4 of *L. korthi* differs from those of *L.*

stirtoni, *L. douglassi*, *L. russelli*, *L. quartzi*, and *L. oregonensis* in the following: anterior cingulid present (except *L. oregonensis*, in which an isolated anterior cingulid is present); protoconid and metaconid are separate (except *L. oregonensis* and *L. stirtoni*); and metalophid lacking (except *L. stirtoni*).

Description.—The M1 is the largest cheektooth, followed in size by the M2, P4 and M3. The P4 is subquadrate, molariform and low crowned. The talon is noticeably narrower than the trigon. The anterior cingulum is absent, but a shallow concavity occurs between the bases of the paracone and protocone. An anterocone is present below the apex of the protocone in 18% of the specimens. The paracone is the largest of the four major cusps with all others being subequal in size. The paracone is transversely aligned with the protocone, but the metacone is placed anterior to the hypocone; anteroposteriorly, the paracone–metacone and the protocone–hypocone are aligned, respectively; and the distance between the protocone and hypocone is greater than that between paracone and metacone. The paracone and protocone are set far apart but united by a high, *V*-shaped protoloph. A protolophule is absent. The lingual arm of the protoloph is short or absent, while the labial arm of the protoloph is submerged within the paracone. The protoloph is not as wide transversely as the metaloph. The anterior arm of the ectoloph (=posterior arm of protocone; see Lindsay, 1972; Korth and Bailey, 1992) is short, arises near the posterolabial margin of the protocone, and is directed about 45° posterolabially (or directly posteriorly) to join the mesocone. The mesocone is distinct and occurs in the middle of the central basin between the paracone and metacone. A mesoloph is

present, while a mesostyle and labial cingulum are absent. The posterior arm of the ectoloph (= anterior arm of hypocone; see Lindsay, 1972) is short and extends anteroposteriorly in a straight line to join the center of the metaloph. The lingual arm of the metaloph is less distinct than that of the labial arm of the metaloph. The shape and direction of the ectoloph define a *C*-shaped labial basin or valley (if a mesoloph is present and directed labially and oblique to the ectoloph, it forms a *Y*-shaped labial basin; see Shotwell, 1967). The labial and lingual basins are equal in their anteroposterior length and open laterally. The metacone and hypocone are far apart from each other but joined by a metaloph. The metaloph forms a high, sharp ridge that rises high on the anterolingual side of the metacone (labial arm of the metaloph = anterior arm of the metacone; see Lindsay, 1972) and is directed strongly anterolingually toward the center of the tooth where it intersects the ectoloph and becomes redirected strongly posterolingually to join the hypocone (lingual arm of the metaloph = anterior arm of the hypocone; see Lindsay, 1972). The posterior cingulum arises high on the labial margin of the hypocone (posterior arm of the hypocone; see Lindsay, 1972) and descends as it traverses labially in a straight line to join low on the posteromedial margin of the metacone. Also, the posterior cingulum is anteroposteriorly narrow and open labially.

On the anterolabial surface of the M1, the anterior cingulum arises low on the anteromedial margin of the protocone and ascends to join the middle of the protoloph by an adloph, then descends lingually to attach on the anteromedial margin of the paracone. Although the labial and lingual arms of the anterior

cingulum are equally well developed, they do not traverse the entire width of the tooth. Four major, subequal cusps are present on this tooth. The lingual arm of the protoloph is short and less distinct than that of the labial arm. The protoloph is equal in width to the metaloph. The anterior arm of the ectoloph arises at the posterolabial margin of the protocone and traverses posterolabially at about a 5° angle to join the mesocone. The mesocone is distinct and occurs in the anteromedial part of the central basin between the paracone and metacone. The mesoloph is directed anterolabially toward the posterolingual base of the paracone but does not reach the paracone. The lingual arms of the protoloph and metaloph are equal to each other and are more distinct than the respective labial arms.

The M2 differs from the M1 in that it is wider than long, and has a more distinct adloph, an anterior arm that extends in a transversely straight line from the posterolabial margin of the protocone, and a more distinct, anterolabially directed mesoloph. M3 is unknown for this species.

The ventral margin of the dentary, seen in lateral view, is slightly convex ventrally. The diastema is deep and short. A distinct mental foramen occurs high on the diastema; the ventralmost edge of the foramen is level with the anteromost of the masseteric scar. Anteroposteriorly, the foramen lies midway between p4 and the anteromost part of the diastema. The foramen opens anterodorsally. The masseteric scar terminates below the middle of p4. Posterior to its distal end, the massteric scar forms a strong ventral shelf that grades ventrally with the ramus, while the dorsal shelf is absent (weak in a few

specimens). A shallow fossa occurs between p4 and the masseteric scar. The ascending ramus arises lateral to the middle part of m2. On the lingual surface of the diastema, a small secondary mental foramen (dorsoventrally centered and separate from the mental foramen) occurs in a distinct fossa below the anterior root of the m1.

The lower incisor possesses the following: the distal end occurs at the level of the tooth row; and the tooth is rounded labially with little enamel present on the medial surface, while about one-quarter of the lateral side of the tooth is covered with enamel. In cross section, the tooth is oblong.

The p4 is as wide as it is long. The trigonid is slightly narrower than the talonid. An anterior cingulid occurs in 10% of specimens and an anteroconid occurs in 39% of specimens referred to this species. The protoconid is the largest cusp on this tooth. The protoconid and metaconid are not joined; a metalophid is absent. The ectolophid may possess two arms (anterior and posterior) or a single arm (posterior). The anterior arm of the ectolophid, if present, is weak or strong, bent or straight, and attached to the protoconid or the metaconid. In contrast, the posterior arm of the ectolophid is always present and attached to the hypoconid; it varies in strength and straightness. The mesoconid occurs along the ectolophid and is variable in that it may occur as a distinct, triangular conid or may be submerged (embedded within the ectolophid and not noticeable). The mesolophid and mesostylid are always absent. A posteriorly bent hypolophid joins the hypoconid and entoconid and may posssess a hypolophulid (difficult to assertain after considerable wear to the occlusal

surface). When a hypolophulid is present, it generally is located where the posterior cingulid joins the hypolophid. The posterior cingulid is complete. It arises at the center of the hypolophid and descends to attach to the posteromedial margin of the entoconid.

The m1 is longer than wide and has three roots (two small anterior and one large posterior). The trigonid is slighlty wider than the talonid. The central and labial basins are much deeper than the anterior or posterior basins and all basins are open. The anterior cingulid is anteroposteriorly expanded centrally, narrows laterally to traverse nearly the entire width of the tooth, is slightly sigmoid shaped, and arises low near the anterolabial base of the protoconid. The anterior cingulid gradually ascends lingually, reaching an apex at the middline of the tooth (or at the anteroconid where that cusp is present), then descends lingually in a gradual fashion, terminating low at the anterolabialmost margin of the metaconid. The anterior cingulid is attached to the middle of the metalophid (this character is variable for *Leptodontomys*). The anterior and posterior arms of the ectolophid are slightly bent and attach to the posterolingual and anterolingual parts of the protoconid and hypoconid, respectively. The mesoconid is usually distinct; the mesolophid, where present, extends lingually in a short, straight line. The mesostylid is absent. A posteriorly bent hypolophid joins hypoconid to entoconid. The lingual arm of the hypolophid is less distinct than the labial arm. A hypolophulid (which disappears early in wear) occurs along the middle of the hypolophid and gives rise to the posterior cingulid. The posterior cingulid also attaches laterally along the posterolabial margin of the entoconid; the posterior

basin is open lingually. In addition to extending lingually from its point of attachment with the hypolophulid, the posterior cingulid extends labially and terminates at the posteromedial margin of the entoconid.

The m2 differs from m1 in that it is wider than long and the anterior cingulid is attached to the center of the metalophid by an adlophid. The lingual arm of the metalophid is less distinct than the labial arm (a character that is variable within *Leptodontomys*). The mesolophid of m2 extends more lingually (is longer) than on the m1, but it does not reach the lingual border of the tooth. The posterior arm of the posterior cingulid is less distinct than on m1.

The m3 differs from the preceding molars in that the lingual arm of the metalophid is absent; a distinct mesolophid is present and extends lingually halfway across the central basin; a weak, low hypolophid joins the hypoconid and entoconid; the entoconid is greatly reduced; the posterior cingulid is absent; and the talonid is noticeably narrower than the trigonid.

Comparison and discussion.—No upper cheekteeth are known for *L. quartzi*. The dentary of *L. korthi* differs from that of *L. quartzi* in having the ventralmost edge of the mental foramen lying above the masseteric scar, whereas in *L. quartzi* it occurs below the masseteric scar; a masseteric scar ends below the middle part of the p4, not the anteromost part of the p4 as in *L. quartzi*; the dorsal shelf of the masseteric scar is absent to weak and the ventral shelf is strong for *L. korthi*, but the opposite is true for *L. quartzi*; ventral shelf of the masseteric scar is weak; on the lingual surface of the diastema, a small foramen occurs within a distinct fossa and below the m1 in *L. korthi*, but below the p4 in *L.*

quartzi; and a single small foramen occurs on the lingual surface between the i1 and p4 and not in a fossa below p4.

The p4 of *L. korthi* differs from that of *L. quartzi* in having a trigonid that is slightly narrower than the talonid, while the talonid is narrower for *L. quartzi*; an anterior cingulid occurs in 10% of *L. korthi*, but is not present in *L. quartzi*; an anteroconid occurs less often in *L. korthi* than in *L. quartzi* (39% and 52%, respectively); a metalophid is absent in *L. korthi*, but present in *L. quartzi*; the protoconid and metaconid are separate in *L. korthi*, but joined in *L. quartzi*; a mesostylid is absent in *L. korthi*, but occurs in 18% of *L. quartzi*.

The m1–m2 of *L. korthi* have an anterior cingulid that arises on the anterolabialmost part of the metaconid, while in *L. quartzi* it arises on the lingual side of the metaconid; the labial arm of the metalophid is distinct and the lingual arm of the metalophid is weak to absent in *L. korthi*, the opposite is true in *L. quartzi*; the anterior and posterior arms of the ectolophid are bent in *L. korthi*, while they are straight in *L. quartzi*; the mesolophid is short in *L. korthi*, but can be long in *L. quartzi*; the lingual arm of the hypolophid is distinct and labial arm is weak in *L. korthi*, but the opposite is true in *L. quartzi*; and a labial arm of the posterior cingulid is present in *L. korthi*, but not *L. quartzi*.

In 18% of *specimens referred to L. korthi*, the P4 possesses an anterocone, whereas it is consistently absent in *L. stirtoni*. *Leptodontomys korthi* has a paracone and protocone that are transversely in line with each other, while in *L. stirtoni* the paracone is anterior to the protocone. The protolophule and protoloph are present in *L. korthi* but absent in *L. stirtoni*, whereas the mesostyle

is absent in *L. korthi* but present in *L. stirtoni*. The lingual and labial arms of the metaloph are less distinct and more distinct, respectively in *L. korthi* (condition opposite in *L. stirtoni*). In *L. korthi*, the lingual and labial basins are equal in length to each other, while the lingual basin is long and the labial basin is short in *L. stirtoni*. The M1–M2 of *L. korthi* have an anterior cingulum that attaches along the anteromedial margin of the paracone, while it attaches at the anterolingual margin of the paracone in *L. stirtoni*. The lingual and labial arms of the protoloph are less distinct and more distinct for *L. korthi*, respectively, while in *L. stirtoni* they are more distinct and less distinct, respectively. In *L. korthi*, the posterior arm of the ectoloph attaches at the center of the metaloph, whereas in *L. stirtoni* it attaches lingual to the center of the metaloph. The lingual and labial basins of *L. korthi* are equal, while in *L. stirtoni* the labial basin is anteroposteriorly longer than the lingual basin. In *L. korthi*, the mesostyle and labial cingulum are absent, whereas in *L. stirtoni* they are variably present. The posterior cingulum of *L. korthi* attaches at the posteromedial margin of the metacone, while in *L. stirtoni* it attaches at the posterolabial margin of the metacone.

The dentary is unknown for *L. stirtoni*, but isolated p4s, m1s, and m2s can be compared with those of *L. korthi*. The p4s of *L. korthi* possess an anterior cingulid in 10% of specimens, whereas they are always absent in *L. stirtoni*. In *L. korthi*, an anteroconid occurs in 39% of specimens, while in *L. stirtoni* it is always absent. A mesolophid is absent in *L. korthi*, but is present and anteriorly directed in *L. stirtoni*. The mesostylid is always absent in *L. korthi*, but present in 50% of specimens referred to *L. stirtoni*.

The m1–m2 of *L. korthi* have an anterior cingulid that variably attaches to the metalophid or is free (not attached to the metalohid); in *L. stirtoni* it is usually attached centrally but is never free. In *L. korthi* a mesostylid is absent, whereas in *L. stirtoni* it is occurs in 50% of specimens. There are too few m3s to allow for a comparison between these taxa.

The P4 of *L. korthi* does not possess an anterior cingulum, which is present in *L.* douglassi. The paracone is the largest cusp in *L. korthi*, but all cusps are equal-sized in *L. douglassi*. A mesostyle is absent in *L. korthi* but present in *L. douglassi*. A distinct mesocone and mesoloph are present in *L. korthi*; both are absent in *L. douglassi*.

The M1–M2 of *L. korthi* have an anterior cingulum that arises labially at the anteromedial margin of the paracone, while in *L. douglassi* it continues labially around the paracone. The mesostyle is absent in *L. korthi* but present in *L. douglassi*. The posterior cingulum ends along the posteromedial margin of the metacone in *L. korthi* but extends the entire width of the tooth in *L. douglassi*.

The p4s of *L. korthi* may possess an anterior cingulid; *L. douglassi* never has an anterior cingulid. The protoconid and metaconid are separate in *L. korthi* but joined in *L. douglassi*. A metalophid and mesolophid are always absent in *L. korthi* but present in *L. douglassi*. The posterior cingulid always arises at the center of the hypolophid and ends at the posteromedial margin of the entoconid in *L. korthi*, while in *L. douglassi* it may arise directly from the hypoconid and does not reach the entoconid.

The m1–m2 of *L. korthi* have labial and lingual arms of the anterior

cingulid that are equal and join the center of the metalophid, while in *L. douglassi* the lingual arm is transversely wider than the labial arm and they join the protoconid. The mesolophid is shorter in *L. korthi* than in *L. douglassi*. The posterior cingulid of *L. korthi* attaches at the posterior margin of the entoconid, while in *L. douglassi* it does not reach the entoconid. There are too few m3s to allow for a comparison between these taxa.

The dentary of *L. russelli* is similar to that of *L. quartzi* (see Storer, 1975); see comparisons between *L. korthi* and *L. quartzi* above. The p4 of *L. korthi* may possess an anterior cingulid or an anteroconid, while *L. russelli* never possesses either of these characters. The protoconid and metaconid are not joined in *L. korthi* but are in *L. russelli*. A metalophid is absent in *L. korthi* but present in *L. russelli*. In *L. korthi*, a distinct mesoconid is present, while it is submerged in *L. russelli*. The posterior cingulid reaches the posteromedial margin of the entoconid in *L. korthi*, while it does not reach the entoconid in *L. russelli*.

The m1–m2 of *L. korthi* have an anterior cingulid that nearly spans the entire width of the tooth, while in *L. russelli* it is reduced and does not reach either of the lateral margins. A distinct mesoconid and mesolophid occur in *L. korthi* but are never present in *L. russelli*. The posterior cingulid of *L. korthi* reaches the posterior border of the entoconid, while in *L. russelli* it does not reach the entoconid. There are no known upper cheekteeth for *L. russelli*. There are too few m3s to allow for a comparison between these taxa.

Tthe dentary of *L. korthi* has a masseteric scar that ends below the middle part of p4, while in *L. oregonensis* it ends below the posteriormost part of p4.

The dorsal shelf is strong and the ventral shelf is weak in *L. korthi*, while in *L. oregonensis* they are opposite. On the lingual surface, there is a single foramen below the anterior root of the m1 in *L. korthi*, while in *L. oregonensis* there are numerous foramina on the lingual surface. The p4 of *L. korthi* may possess an anteroconid, while *L. oregonensis* never possesses an anteroconid. The protoconid and metaconid are separate in *L. korthi*, while in *L. oregonensis* they are joined by a metalophid. The mesoconid may be submerged in *L. korthi*, while in *L. oregonensis* it is always distinct. The mesolophid is absent in *L. korthi* but present in *L. oregonensis*. There are no other lower or upper cheekteeth known for *L. oregonensis*.

Among previously described species, *L. korthi* most closely resembles *L. stirtoni*. Notable similarities in P4 include lack of anterior cingulum, dominance of the paracone among the four cusps (with the other three subequal to each other), and distinctness of the mesocone. The M1–M2 of *L. korthi* resemble those of *L. stirtoni*, with the two species sharing the following structures: the lingual and labial arms of the anterior cingulum are equal in length, the protoloph and metaloph are equal in length, the paracone and protocone are transversely aligned, and the metacone occurs anterior to the hypocone.

On p4, the two species are most similar in having a separate protoconid and metaconid, the metalophid is absent, and a mesostylid is present. The m1–m2 of *L. korthi* resemble those of *L. stirtoni* in sharing an anterior cingulid attached to the center of the metalophid, a distinct mesoconid with a short mesolophid, and a posterior cingulid attached to the entoconid.

Leptodontomys schnelli n. sp.

Plate 2 (A-C)

Holotype.—OMNH 54716, right dentary fragment with p4-m2.

Type locality.—Eastgate, UCMP V70147.

Etymology.—Named in honor of Gary D. Schnell for his helpful and generous advice.

Age.—Barstovian.

Stratigraphic and geographic occurrence of species.—Barstovian: Monarch Mill Formation, Eastgate fauna, Churchill County, Nevada.

Hypodigm.—Type only.

Measurements.—See Table 11.

Diagnosis.—Compared to other species of *Leptodontomys*, *L. schnelli* is a medium-sized species of *Leptodontomys*. The p4 of *L. schnelli* differs from all known species in having an anteriorly directed distinct metalophid (except *L. stirtoni*), absence of an anteroconid (except *L. stirtoni*, *L. oregonensis*, and *L. russelli*); and a strong anterior and posterior arm of the ectolophid.

Description.—The holotype dentary is incomplete anteriorly: it is broken through the distal edge of the diastema, and thus no descriptions of the diastema, incisor, or mental foramen are possible. Posteriorly, the dentary is broken through the posterior alveolus of the m2, so that no description can be given for the ascending ramus. In addition, the dentary is poorly preserved and does not reveal other relevant structures.

The cheekteeth show little occlusal wear. The p4 and m3 are similar in size, while the m1 and m2 are larger than the other cheekteeth but similar in size to each other. The m3 is the smallest.

The p4 has two roots and is wider than long. The trigonid is slightly narrower than the talonid; an anterior cingulid and anteroconid are absent. The four principal cusps of p4 are subequal in size. The protoconid and metaconid are joined by a short, weak metalophid. The anterior arm of the ectolophid is the more distinct of the two; it is straight and is attached to the protoconid. The posterior arm of the ectolophid is weak, slightly bent, and attached to the hypoconid. The mesoconid is submerged within the middle of the ectolophid. The mesolophid is distinct, anterolingually directed, and nearly reaches the posteromedial margin of the metaconid. The mesostylid is absent. A weak, low posteriorly bent hypolophid joins the hypoconid and entoconid; a hypolophulid is lacking. The posterior cingulid is complete. It arises posterior to (but at the same level as) the hypolophid and descends to attach to the posteromedial margin of the entoconid.

The m1 has three roots and is longer than wide; the middle of the tooth is expanded labiolingually, so that the crown appears oblong rather than rectangular in occlusal outline. The trigonid is similar in width to the talonid. The central and labial basins are much deeper than the anterior or posterior basins; all except the posterior basin are open. The anterior cingulid is anteroposteriorly expanded centrally, narrows laterally, and spans nearly the entire width of the tooth. It is slightly sigmoid-shaped. The anterocingulid arises low near the

anterolabial base of the protoconid and gradually ascends lingually to the anteroconid, then descends lingually in a gradual fashion to end low at the anteromedial margin of the metaconid. The anterior cingulid joins the metalophid labial to its center near the protoconid. The lingual arm of the metalophid is weak, while the labial arm is submerged within the protoconid. The anterior and posterior arms of the ectolophid are slightly bent, subequal in size, and attached to the posterolingual and anterolingual parts of the protoconid and hypoconid, respectively. The mesoconid is distinct, with a mesolophid that extends anterolingually nearly reaching the posteromedial margin of the metaconid. The mesostylid is absent. A posteriorly bent hypolophid joins the hypoconid and entoconid. The lingual arm of the hypolophid is more distinct than the labial arm. A hypolophulid occurs labial to the middle of the hypolophid and gives rise to the posterior cingulid. The posterior cingulid also attaches along the posteromedial margin of the entoconid; the posterior basin is closed lingually.

The m2 differs from m1 in the following characters: it is wider than long (square-shaped), the anterior cingulid is attached to the center of the metalophid by an adlophid, the lingual arm of the metalophid is distinct, and a mesolophid extends lingually but does not reach the lingual border of the tooth. No m3s are known for this species.

Comparison and discussion.—Comparisons of *Leptodontomys schnelli* to other species of *Leptodontomys* are limited to the p4, m1, and m2. The p4 of *L. schnelli* does not possess an anterior cingulid or anteroconid, while both may be present in *L. korthi*. In *L. schnelli*, the protoconid and metaconid are joined by a

metalophid, whereas in *L. korthi* the protoconid and metaconid are separate and a metalophid is lacking. A mesoconid is always absent but a mesolophid is distinct and anteriorly directed (nearly reaching the metaconid) in *L. schnelli*, while in *L. korthi* a mesoconid may be present and a mesolophid is absent. The m1–m2 of *L. schnelli* have an anterior cingulid that attaches lingual to the center near the protocone, while in *L. korthi* it attaches in the middle of the metaloph. In *L. schnelli*, a distinct mesoconid is always present, together with a mesolophid that is anterolingually directed and nearly reaches the metaconid, but in *L. korthi* a mesoconid with a short, straight mesolophid is usually present. The posterior cingulid in *L. schnelli* attaches to the posteromedial margin of the entoconid, while in *L. korthi* it terminates at the posterolabial margin of the entoconid.

The p4 of *L. schnelli* has a weak, short metalophid, whereas in *L. quartzi* it is distinct and transversely elongate. A distinct, anterolingually directed mesolophid is present in *L. schnelli* but absent in *L. quartzi*. The m1–m2 of *L. schnelli* have an anterior cingulid that joins the metalophid labial to the crown midline, while *L. quartzi* it is either free or joins the center of the metalophid. In *L. schnelli*, the mesolophid is distinct and anterolingually directed, nearly reaching the metaconid, whereas in *L. quartzi* the mesolophid is directed laterally in a straight line. The posterior cingulid attaches along the posteromedial margin of the metaconid in *L. schnelli*, but it attaches along the posterolabial margin in *L. quarzti*.

In *L. schnelli*, the p4 has a metalophid that joins the protoconid and metaconid, while in *L. stirtoni* a metalophid is absent and the protoconid and

metaconid are separate from each other. A mesostylid is absent in *L. schnelli* but present in *L. stirtoni*. The m1– m2 of *L. schnelli* have a labial arm of the anterior cingulid that terminates along the anterolabial margin of the protocone, whereas in *L. stirtoni* it ends along the anteromedial margin of the protocone. The metalophid is always complete in *L. schnelli*, but in *L. stirtoni* it may be incomplete (missing the lingual arm). A metastylid is absent in *L. schnelli*, while in *L. stirtoni* it is present.

The p4 of *L. schnelli* has a mesoconid that is submerged within a distinct mesolophid that is anterolingually directed, and nearly reaches the metaconid; in *L. douglassi* the mesoconid is distinct and the mesolophid is short and extends laterally in a straight line. The posterior cingulid of *L.* schnelli reaches the posteromedial margin of the entoconid, but in *L. douglassi* it does not reach the entoconid. The m1–m2 of *L. schnelli* have an anterior cingulid that has equal arms (lingual and labial) and attaches labial to the center of the metalophid (near the protoconid), whereas in *L. douglassi* the lingual arm is more distinct than the labial arm and the cingulid attaches on the protoconid. The mesolophid is anterolingually directed and nearly reaches the metaconid in *L. schnelli*, while in *L. douglassi* it extends laterally in a straight line and does not reach the lingual margin of the tooth. The posterior cingulid attaches to the posteromedial margin of the entoconid in *L. schnelli* but does not reach the entoconid in *L. douglassi*.

The p4 of *L. schnelli* has a distinct, anterolingually directed mesolophid that nearly reaches the metaconid, whereas in *L. russelli* a mesolophid is absent. The posterior cingulid joins the posteromedial margin of the entoconid in *L.*

schnelli but does not reach the entoconid in *L. russelli*. The m1–m2 of *L. schnelli* have an anterior cingulid that nearly spans the entire width of the tooth, while it is reduced and does not reach either of the lateral margins in *L. russelli*. A distinct mesoconid and anterolingually directed mesolophid that nearly reaches the metaconid are present in *L schnelli*, but both are absent in *L. russelli*. The posterior cingulid joins the posteromedial margin of the ectoconid in *L. schnelli* but does not reach the entoconid in *L. russelli*.

The p4 of *L. schnelli* has a protoconid and metaconid that are very close to each other; in *L. oregonensis*, these cusps are farther apart. The mesoconid is submerged in *L. schnelli* but always distinct in *L. oregonensis*. The mesolophid is anterolingually directed nearly reaching the metaconid in *L. schnelli* but is short, linear, and laterally directed in *L. oregonensis*. There are no other lower or upper cheekteeth known for *L. oregonensis*.

Leptodontomys *schnelli* is similar to *L. russelli*, differing chiefly in size. Notable shared attributes include absence of an anterior cingulid or anteroconid, protoconid and metaconid closely approximated and joined by a short metalophid, and absence of a mesostylid and labial cingulid.

Leptodontomys protistopikos n. sp.

Plate 2 (D-I)

Holotype.—OMNH 54695, partial skull with palate.

Type locality.—Eastgate, OMNH V974.

Etymology.—*Protistos*, Gr., the very first; *topikos*, Gr., a place or locale; in reference to the first OMNH locality I discovered in the Monarch Mill Formation.

Localities.—Type locality only.

Age.—Barstovian.

Stratigraphic and geographic occurrence of species.—Barstovian: Monarch Mill Formation, Eastgate fauna, Churchill County, Nevada.

Hypodigm.—Type and OMNH 54698, right M1 or M2; OMNH 54702, right M1 or M2; OMNH 54704, right M1 or M2; OMNH 54705, right M1 or M2; UCMP 141780-41, left M1 or M2; UCMP 141780-97, right M1 or M2; UCMP 141780-122, left M1 or M2; UCMP 141780-131, right M1 or M2.

Measurements.—See Table 9.

Diagnosis.—This small species of *Leptodontomys* has the following unique characteristics of the P4: anterior cingulum and anterocone absent; all four principal cusps subequal in size, labial cusps occur slightly anterior to lingual cusps; protolophule absent; protoloph much wider than metaloph; mesocone submerged with metaloph; mesoloph, mesostyle, and labial cingulum absent; and labial basin anteroposteriorly longer than lingual basin.

The upper M1-M2 of *L. protistopikos* are distinctive in the following:

anterior cingulum almost spans width of tooth and labial arm is more distinct than lingual arm; four principal cusps subequal in size; labial cusps transversely aligned with lingual cusps; protoloph much wider than metaloph; mesocone distinct; mesostyle and labial cingulum absent; mesoloph present; and labial basin anteroposteriorly longer than lingual basin.

Description.—The P4 is subquadrate, molariform, and unworn in the type specimen. The talon and trigon are nearly equal in width. A small but distinct anterior cingulum is present between the paracone and protocone. An anterocone is absent. The placement of the four cusps relative to each other is as follows: the paracone and metacone lie anterior to the protocone and hypocone, respectively; anteroposteriorly, the paracone is transversely aligned with the metacone and the protocone is transversely aligned with the hypocone. The distance between paracone and metacone is greater than that between protocone and hypocone. The paracone and protocone are set far apart but are united by a high, *V*-shaped protoloph. A protolophule is absent. The lingual arm of the protoloph is distinct, whereas the labial arm of the protoloph is submerged with the paracone. The protoloph is as wide transversely as the metaloph. The anterior arm of the ectoloph arises high at the posterolabial margin of the protocone and traverses posterolabially at about 90° to join the mesocone in the middle of the central basin. The mesocone is distinct and lies in the middle of the central basin, posterior to the paracone and metacone. A mesoloph is present, whereas a mesostyle and labial cingulum are absent. The posterior arm of the ectoloph is posteriorly directed from the mesocone and joins the center of the

metaloph. The lingual arm of the metaloph is more distinct than the labial arm of the metaloph. The shape and direction of the ectoloph define a *C*-shaped labial basin. The labial basin is anteroposteriorly longer than the lingual basin but both are open laterally. The metacone and hypocone are set far apart but are joined by a metaloph. The metaloph forms a high, *V*-shaped ridge that rises high on the anterolingual side of the metacone and is directed strongly anterolingually toward the center of the tooth where it intersects with the ectoloph and becomes re-directed strongly posterolingually to join the hypocone. The posterior cingulum arises high on the labial margin of the hypocone and descends labially in a straight, transverse line to join low on the posteromedial margin of the metacone. The posterior cingulum is anteroposteriorly elongate and closed labially.

The M1 possesses an anterior cingulum that arises low on the anterolingual margin of the protocone and ascends toward the midline of the tooth and continues lingually in a gradual descent and attaches to the anterolabial margin of the paracone. The anterior cingulum and protoloph are joined centrally by an adloph. Thus, the anterior cingulum traverses nearly the entire width of the tooth. The labial arm of the anterior cingulum is more distinct than the lingual arm. The placement of the four cusps relative to each other is as follows: the posterior surface of the paracone is anterior to the anterior surface of the protocone; the metacone is noticeably anterior to the hypocone; anteroposteriorly, the paracone and metacone are equidistant from the midline of the tooth; and the protocone and hypocone are equidistant from the midline. The paracone and protocone are set far apart but are united by a high, *V*-shaped

protoloph. The lingual arm of the protoloph is distinct, while the labial arm is submerged within the paracone. The protoloph is as wide as the metaloph. The anterior arm of the ectoloph arises at the posterolabial margin of the protocone and traverses 5° posterolabially to join the mesocone in the middle of the central basin. The mesocone is distinct and lies in the middle of the central basin midway between the paracone and metacone. The mesoloph is directed anterolabially toward the posterolingual base of the paracone but does not reach that cusp. A mesostyle and labial cingulum are absent. The posterior arm of the ectoloph is posteriorly directed from the mesocone and joins lingual to the center of the metaloph. The lingual arm of the metaloph is anterolabially directed and more distinct than the labial arm. The lingual arms of the protoloph and metaloph are equal to each other and are more distinct than the labial arms of these lophs. The metacone and hypocone are far apart but are joined by a metaloph. The metaloph forms a high, sharp-ridge that rises high on the anterolingual side of the metacone and is directed strongly anterolingually toward the center of the tooth, where it intersects with the ectoloph and becomes strongly redirected posterolingually to join the hypocone. The posterior cingulum arises high on the labial margin of the hypocone and descends as it traverses the back of the crown to join the metacone low on its posteromedial margin. The posterior cingulum is anteroposteriorly elongated and closed labially.

The M2 differs from M1 in being wider than long and in having protocone and hypocone more closely approximated. The M3 is distinguished from the preceding molars by the following characteristics: noticeably wider than long;

smallest tooth of the tooth battery; the paracone and protocone occur far apart; and the metacone and hypocone are much reduced.

Comparison and discussion.—The P4 of *L. protistopikos* has a distinct anterior cingulum but lacks an anterocone, whereas in *L. korthi* an anterior cingulum is absent and an anterocone may be present. The four principal cusps are subequal in *L. protistopikos*, while in *L. korthi* the paracone is the largest cusp. The labial cusps (paracone, metacone) are anterior to the lingual cusps (protocone, hypocone) in *L. protistopikos*, but the anterior cusps (paracone, protocone) are transversely aligned with each other in *L. korthi*. A protolophule is absent in *L. protistopikos*, but present in *L. korthi*. The lingual arm of the protoloph is distinct in *L. protistopikos*, while it is short or absent in *L. korthi*. The protoloph is as wide as the metaloph in *L. protistopikos*, whereas they are not equal to each other in *L. korthi*. A distinct mesocone lies posterior to a transverse line between the posteromost part of the paracone and protocone in *L. protistopikos*, whereas in *L. korthi* it occurs anterior to that line. The lingual arm of the metaloph is distinct in *L. protistopikos*, while it is less distinct in *L. korthi*. In *L. protistopikos*, the labial basin is anteroposteriorly longer than the lingual basin, whereas in *L. korthi* they are equal in length. The posterior cingulum is anteroposteriorly elongated and closed labially in *L. protistopikos*, while in *L. korthi* it is narrow and open. The M1–M2 of *L. protistopikos* have an anterior cingulum that arises at the anterolingual margin of the protocone, while in *L. korthi* it arises at the anteromedial margin of the protocone. The anterior cingulum attaches at the anterolabial margin of the paracone in *L. protistopikos*,

while it attaches to the anteromedial margin of the paracone in *L. korthi*. In *L. protistopikos*, the labial arm of the anterior cingulum is more distinct than the lingual arm, whereas in *L. korthi* the opposite holds true. The labial cusps are anterior to those of the lingual side in *L. protistopikos*, while in *L. korthi* the anterior cusps are aligned, but the posterior cusps (metacone, hypocone) are not aligned. The lingual arm of the protoloph is distinct in *L. protistopikos*, while it is the labial arm that is distinct in *L. korthi*. In *L. protistopikos*, the labial basin is anteroposteriorly longer than the lingual basin, while in *L. korthi* they are equal. The posterior cingulum is anteroposteriorly elongated and closed labially in *L. protistopikos*, whereas in *L. korthi* it is narrow and open labially.

In *L. protistopikos*, the P4 has a distinct anterior cingulum, lacking in *L. stirtoni*. The four cusps are subequal in *L. protistopikos*, whereas in *L. stirtoni* the paracone is distinctly larger than the remaining cusps. The mesostyle and labial cingulum are absent in *L. protistopikos*, but present in *L. stirtoni*. The M1–M2 of *L. protistopikos* have an anterior cingulum that attaches at anterorlabial margin of the paracone, while in *L. stirtoni* it attaches to the anterolingual margin of the paracone. In *L. protistopikos*, the posterior arm of the ectoloph joins the center of the metaloph, whereas in *L. stirtoni* it joins lingual to the center of the metaloph. In *L. protistopikos*, a mesostyle and labial cingulum are absent, but may be present in *L. stirtoni*. The posterior cingulum in *L. protistopikos* attaches at the posteromedial margin of the metacone, while in *L. stirtoni* it attaches at the posterolabial margin of the metacone.

The P4 of *L. protistopikos* does not possess a mesostyle, while in *L.*

douglassi a mesostyle is present. A distinct mesocone and mesoloph are present in *L. protistopikos*, whereas they are both absent in *L. douglassi*. The M1–M2 of *L. protistopikos* lack a mesostyle, whereas a mesostyle is present in *L. douglassi*. The posterior cingulum joins the posteromedial margin of the metacone in *L. protistopikos*, but it extends past the posteromedial margin in *L. douglassi*. Comparisons with other species are precluded by differential representation of teeth in known specimens.

Excluding the great differences in size, *L. protistopikos* is similar to *L. douglassi* in most dental characters. These shared characters are as follows: P4, an anterior cingulum is present, while an anterocone is absent, the four principal cusps are subequal in size, the paracone and protocone are set far apart, the protoloph and metaloph are equally wide, a mesoloph is present, and labial cusps are anterior to the lingal cusps. On M1–M2, the anterior cingulum attaches to or near the protocone, the four principal cusps are subequal in size, the paracone and protocone are set far apart, the protoloph and metaloph are equally wide, a short mesoloph is present, and the labial cusps lie anterior to the lingal cusps.

Leptodontomys quartzi Shotwell, 1967

Plate 3 (A-I)

Localities.—Eastgate, UCMP V70138, V70140, V70147.

Age.—Barstovian.

Stratigraphic and geographic occurrence of species.—Barstovian: Quartz Basin fauna, Malheur County, Oregon (Shotwell, 1967); Monarch Mill Formation, Eastgate fauna, Churchill County, Nevada.

Referred specimens.—OMNH 54696, right maxilla fragment with P4–M2; OMNH 54700, right M1 or M2; OMNH 54708, right P4; OMNH 54709, left P4; OMNH 54710; left P4; OMNH 54711, right P4; OMNH 54713, left maxilla fragment with P4; OMNH 54714, left dentary fragment with p4–m3; OMNH 54718, left dentary fragment with i1–p4; OMNH 54719, left dentary fragment with i1–m1; OMNH 54721, right dentary fragment with p4; OMNH 54722, right dentary fragment with p4–m3; OMNH 54723, right dentary fragment with p4; OMNH 54726, left dentary fragment with p4–m1; OMNH 54727, left dentary fragment with p4; OMNH 54728, left dentary fragment with m1–m2; OMNH 54729, right m1 or m2; OMNH 54734, left m1 or m2; OMNH 54735, right m1 or m2; OMNH 54737, right m1 or m2; OMNH 54738, right m1 or m2; OMNH 54740, left m1 or m2; OMNH 54741, right m1 or m2; OMNH 54859, left dentary fragment with p4–m1; OMNH 54875, right maxilla fragment with P4–M1; UCMP 141611, right dentary fragment with m1–m2; UCMP 141675-13, left dentary fragment with i1, m2; UCMP 141679-02, left m1 or m2; UCMP 141779-04, left p4; UCMP

141780-06, left M1 or M2; UCMP 141780-13, right M1 or M2; UCMP 141780-43, left m1 or m2; UCMP141780-52, right m1 or m2; UCMP 141780-58, left M1 or M2; UCMP141780-62, left p4; UCMP 141780-64, right m1 or m2; UCMP 141780-68, left m1 or m2; UCMP 141780-71, right M1 or M2; UCMP 141780-81, left M1 or M2; UCMP 141780-111, left M1 or M2; UCMP 141780-143, left P4; UCMP 141780-147, left P4; UCMP 141780-154, left P4; UCMP 141780-159, left M1 or M2; UCMP 141780-165, right m1 or m2; UCMP 141780-167, left m1 or m2; UCMP 141780-168, right dentary fragment with p4–m1; UCMP 141780-173, left maxilla fragment with P4–M1; UCMP 141780-188, left m1 or m2; UCMP 141780-196, left p4; UCMP 141780-211, right p4; UCMP 141780-219, left m1 or m2; UCMP 141780-222, right m1 or m2; UCMP 141780-243, left dentary fragment with i1–p4; UCMP 141780-246, left dentary fragment with i1–m2; UCMP 141780-256, left dentary fragment with i1–p4; UCMP 141780-257, right dentary fragment with i1–m2; UCMP 141780-260, left dentary fragment with p4–m1; UCMP 141780-261, right dentary fragment with p4–m3; UCMP 141780-265, left dentary fragment with p4–m2; UCMP 141780-270, right p4–m3; UCMP 141780-273, right dentary fragment with p4–m1; UCMP 141780-274, left maxilla fragment with P4–M1; UCMP 141780-276, left dentary fragment with p4–m1; UCMP 141780-279, right dentary fragment with p4; UCMP 141878, right p4.

Measurements.—See Tables 9 and 11.

Description.—The P4 has a talon that is slightly narrower than the trigon. The anterior cingulum is absent, but a shallow concavity occurs between the

bases of the paracone and protocone. An anterocone is absent. The placement of the four principal cusps relative to each other is as follows: the paracone is slightly anterior to the protocone and the metacone is slightly anterior to the hypocone; anteroposteriorly, the paracone is aligned with the metacone and the protocone is aligned with the hypocone; and the distance between the protocone and hypocone is greater than that between paracone and metacone. The paracone and protocone are closely approximated and are united by a low, slightly *V*-shaped protoloph. A protolophule is absent. The lingual and labial arms of the protoloph are short and subequal to each other. The protoloph is noticeably narrower than the metaloph. The anterior arm of the ectoloph is short, very weak (almost absent), arises low near the posterolabial margin of the protocone, and is directed about 45° posterolabially (or directly posteriorly) to join the mesocone in the middle of the central basin. The mesocone is submerged within the ectoloph. A mesoloph, mesostyle, and labial cingulum are absent. The posterior arm of the ectoloph is short and extends anteroposteriorly in a straight line to join the center of the metaloph. The lingual arm of the metaloph is less distinct than the labial arm of the metaloph. The labial basin is anteroposteriorly longer than the lingual basin; both are open laterally. The metacone and hypocone are closely approximated and are joined by a metaloph. The metaloph forms a high, *V*-shaped ridge that rises high on the anterolingual side of the metacone and is directed strongly anterolingually toward the center of the tooth, where it intersects the ectoloph and becomes strongly redirected posterolingually to join the hypocone. The posterior cingulum arises high on the

labial margin of the hypocone and descends as it traverses labially. It is strongly bowed anteriorly as it extends to join low on the posteromedial margin of the metacone. The posterior cingulum is anteroposteriorly elongated and open labially.

The M1 has an anterior cingulum that arises low near the anterolingual margin of the protocone and descends gradually to the middle of the tooth, where it joins the center of the protoloph by an adloph, then it descends lingually, nearly reaching the lingual margin of the tooth. The labial arm of the anterior cingulum is more distinct than the lingual arm. The paracone and metacone are transversely aligned with protocone and hypocone, respectively. The paracone and protocone are far apart and united by a high, slightly *V*-shaped protoloph. The lingual arm of the protoloph is short and less distinct than the labial arm. The protoloph is transversely wider than the metaloph. The mesocone is distinct and lies in the anteromedial part of the central basin, between paracone and metacone. The mesoloph is directed anterolabially toward the posterolingual base of the paracone but does not reach that cusp. A mesostyle and labial cingulum are absent. The lingual arm of the metaloph is anterolabially directed and more distinct than the anterolingually directed labial arm. The labial basin is anteroposteriorly longer than the lingual basin; both are open laterally. The lingual arm of the protoloph is less distinct than the metaloph, while the labial arm of the protoloph is more distinct than the metaloph. The metacone and hypocone are far apart but joined by a metaloph. The posterior cingulum arises high on the labial margin of the hypocone and descends rapidly as it traverses the back of

the crown to join low on the posteromedial margin of the metacone. The posterior cingulum is anteroposteriorly elongated and open labially. The M2 differs from the M1 only in being wider and shorter, and in having a more distinct adloph and a more distinct, anterolabially directed mesoloph.

The M3 is distinguished from the preceding molars by the following characteristics: noticeably wider than long; smallest tooth of the tooth battery; anterior cingulum reduced and not connected to the protoloph; paracone and protocone occur far apart; metacone and hypocone greatly reduced; posterior arm of ectoloph reduced; and posterior cingulum reduced.

The dentary has a diastema that is deep and short. The mental foramen occurs high on the side of the jaw below the diastema but slightly below the anteriormost projection of the masseteric scar, anteroposteriorly in front of p4, and opens anterodorsally. The masseteric scar terminates below the anterior root of p4. Posterior to its distal end the massteric scar forms a weak dorsal shelf that grades dorsally with the ascending ramus, while a weak ventral shelf is also present and extends anteriorly to below the posteriormost part of m2. A distinct fossa occurs between p4 and the masseteric scar. The ascending ramus arises lateral to the middle part of the m2. On the lingual surface of the diastema, a small foramen occurs midway between the incisor and the p4; it is dorsoventrally centered.

The lower incisor is rounded with a little enamel on the medial surface, while one-third of the lateral side of the tooth is covered with enamel; in cross section, the tooth is oblong.

The p4 has two roots and is equally wide and long. The trigonid is much narrower than the talonid (equal in several specimens), an anteroconid occurs in 52.0% of the Eastgate specimens, and the protoconid is the largest cusp. The protoconid and metaconid are joined by a metalophid. The metalophid may be complete (spanning the distance from protoconid to metaconid) or incomplete (the metalophid may attach separately to both the protoconid and metaconid but not form a complete lophid between them). The ectolophid may possess two arms (anterior, posterior) or a single arm (posterior). The posterior arm is always present and attaches to the hypoconid but may be weak or strong and bent or straight, while the anterior arm is variable in its occurrence as well as shape. The anterior arm of the ectolophid, if present, is weak or strong, and bent or straight. In addition, it may attach to either the protoconid or metaconid. The mesoconid occurs along the ectolophid and is variable in that it may occur as a distinct, triangular conid or may be submerged (embedded within the ectolophid and not noticeable). The mesolophid is absent, while a mesostylid occurs in 18% of the Eastgate specimens. A posteriorly bent hypolophid joins the hypoconid and entoconid and may posssess a hypolophulid (difficult to ascertain after considerable wear to the occlusal surface). Usually, if a hypolophulid is present, it is at the junciton of the posterior cingulid with the hypolophid. The posterior cingulid may be complete (forming a single posterior shelf that attaches along the center of the hypolophid and near the ectoconid) or incomplete (a posterior shelf formed by a series of two or more discontinuous enamel ridges).

The m1 has a trigonid that is slighlty wider than the talonid. The central

and labial basins are much deeper than the anterior or posterior basins; all basins are open. The anterior cingulid is anteroposteriorly expanded centrally, narrows transversely to traverse nearly the entire width of the tooth, and is slightly sigmoid shaped. It attaches low near the anterolabial base of the protoconid and gradually ascends lingually as it reaches the anteroconid, then descends lingually in a gradual fashion to join the metaconid. The anteroconid is small and centrally located along the anterior cingulid; it disappears with little wear to the occlusal surface. The anterior cingulid is free and does not join the metalophid. The lingual arm of the metalophid is distinct, while the labial arm is less distinct. The anterior and posterior arms of the ectolophid are straight and attach to the posterolingual and anterolingual part of the protoconid and hypoconid, respectively. The mesoconid is usually distinct, with a mesolophid that extends lingually in a short, straight line. A few specimens lack a mesolophid but all lack a mesostylid. A posteriorly bent hypolophid joins the hypoconid and entoconid. The lingual arm of the hypolophid is more distinct than the labial arm. A hypolophulid (which disappears early in wear) occurs along the middle of the hypolophid and gives rise to the posterior cingulid. The posterior cingulid also attaches along the posterior border of the entoconid; the posterior basin is open lingually.

The m2 is very similar to m1; however, there are subtle differences. The m2 is wider than long, the anterior cingulid attaches to the center of the metalophid by an adlophid, the lingual and labial arms of the metalophid are equal in size, and a mesolophid extends farther lingually (is longer) than on m1

but does not reach the lingual border of the tooth. The m3 differs from the preceding molars in having a reduced entoconid, so that the talonid is noticeably narrower than the trigonid.

Comparison and discussion.—The P4 of *L. quartzi* does not possess an anterocone, whereas in *L. korthi* an anterocone is variably present. The principal cusps are subequal in *L. quartzi*, while the paracone is the largest cusp in *L. korthi* with the other three being subequal. In *L. quartzi*, the paracone is anterior to the protocone, while in *L. korthi* there cusps are transversely aligned. The paracone and protocone are closely approximated in *L. quartzi* but are farther apart in *L. korthi*. The lingual and labial arms of the protoloph are short in *L. quartzi*, whereas in *L. korthi* they are absent and submerged within the labial arm of the protoloph, respectively. The mesocone is submerged in *L. quartzi*, it is distinct in *L. korthi*. In *L. quartzi*, the mesoloph is absent, while in *L. korthi* it is present. The labial and lingual basins differ in size in *L.* quartzi, but are equal in *L. korthi*. The posterior cingulum of *L. quartzi* is anteroposteriorly elongated, while that of *L. korthi* is narrow. The M1–M2 of *L. quartzi* have an anterior cingulum that arises at the anterolingual margin of the protocone, while in *L. korthi* it arises at the anteromedial margin of the protocone. In *L. quartzi*, the labial arm of the anterior cingulum is more distinct than the lingual arm, while in *L. korthi* the arms are equal in expression. The metacone is transversely aligned with the hypocone in *L. quartzi*, while in *L. korthi* the metacone is anterior to the hypocone. The protoloph is wider than the metaloph in *L. quartzi*, whereas in *L. korthi* they are similar in width. The labial basin is anteroposteriorly longer than

the lingual basin in *L. quartzi*, while in *L. korthi* both basins are equal in length to each other. The lingual arms of the protoloph and metaloph are unequal in *L. quartzi* but equal to each other in *L. korthi*. The posterior cingulum is anteroposteriorly wide in *L. quartzi*, but in *L. korthi* it is narrow.

The dentary of *L. quartzi* has a mental foramen that lies below the masseteric scar, while in *L. korthi* it is level with the masseteric scar. In L. *quartzi*, the masseteric scar ends below the anterior root of the p4, has weak dorsal and ventral shelves, and a single foramen on the lingual side; whereas in *L. korthi* the masseteric scar ends below the middle of the p4, has an absent to weak dorsal shelf and a strong ventral shelf, and a single lingual foramen below the anterior root of the m1. The p4 of *L. quartzi* has a metalophid that joins a protoconid to metaconid; this lophid is lacking in *L. korthi*, where the cusps are not joined. A mesostylid is present in *L. quartzi* and absent in *L. korthi*. The m1–m2 of *L. quartzi* have a distinct lingual arm of the hypolophid, while *L. korthi* has a weak lingual arm of the hypolophid.

The p4 of *L. quartzi* may have an anteroconid, lacking in *L. schnelli*. In *L. quartzi*, the metalophid may be complete or incomplete, while in *L. schnelli* it is complete. The mesoconid is distinct without a mesolophid in *L. quartzi*, whereas in *L. schnelli* it is submerged but possesses a mesolophid. A mesostylid may be present in *L. quartzi*, but it is absent in *L. schnelli*. The posterior cingulid may be incomplete in *L. quartzi* but complete in *L. schnelli*. The m1–m2 of *L. quartzi* have a lingual arm of the metalophid that is distinct, whereas it is weak in *L. schnelli*. In *L. quartzi*, the mesolophid extends laterally in a short, straight line,

while in *L. schnelli* it is directed anterolingually and nearly reaches the metaconid.

The P4 of *L. quartzi* does not possess an anterior cingulum, present in *L. protistopikos*. The protoloph is wider than the metaloph in *L. quartzi*, whereas they are equal to each other in *L. protistopikos*. The lingual arm of the protoloph is shorter or subequal to the labial arm in *L. quartzi*, but in *L. protistopikos* the lingual arm is distinct and the labial arm is submerged within the paracone. The mesocone is submerged and the mesoloph is absent in *L. quartzi*, while in *L. protistopikos* the mesocone is distinct and a mesoloph is present. The lingual arm of the metaloph is weak in *L. quartzi*, while it is distinct in *L. protistopikos*. The posterior cingulum is open labially in *L. quartzi* but closed in *L. protistopikos*. On the M1–M2 of *L. quartzi*, the labial cusps are transversely aligned with the lingual cusps, in contrast with *L. protistopikos*. The protoloph is transversely wider than the metaloph in *L. quartzi*, whereas the lophs are equally developed in *L. protistopikos*. The posterior cingulum is open in *L. quartzi*, while it is closed in *L. protistopikos*.

The P4 of *L. quartzi* has a protoloph, while it is absent in *L. stirtoni*. A mesoloph, mesostyle, and labial cingulum are absent in *L. quartzi*, but all are present in *L. stirtoni*. The lingual and labial arms of the metaloph are less and more distinct, respectively, in *L. quartzi*. The opposite is true of *L. stirtoni*. The M1–M2 of *L. quartzi* have an anterior cingulum that joins the protoloph centrally, but in *L. stirtoni* it joins the anterolingual margin of the paracone. The lingual and labial arms of the protoloph are less distinct and more distinct, respectively, in *L. quartzi*, whereas in *L. stirtoni* the opposite is true. In *L. quartzi*, the posterior arm

of the ectoloph joins the center of the metaloph, while in *L. stirtoni* it joins lingual to the center of the metaloph. A mesostyle and labial cingulum are absent in *L. quartzi*, while they are present in *L. stirtoni*.

In *L. quartzi*, the p4 has an anteroconid, a cusp consistently lacking in *L. stirtoni*. A metalophid joins the protoconid and metaconid in *L. quartzi*, whereas in *L. stirtoni* the metalophid is absent, and the protoconid and metaconid are separate. The mesolophid is absent in *L. quartzi*, while it is present in *L. stirtoni*. The m1–m2 of *L. quartzi* have an anterior cingulid that is free or attaches centrally to the metalophid, while in *L. stirtoni* the anterior cingulid always attaches to the metalophid. A mesostylid is absent in *L. quartzi* but present in *L. stirtoni*.

The P4 of *L. quartzi* does not possess an anterior cingulum, which is present in *L. douglassi*. The four principal cusps are subequal in *L. quartzi*, but the paracone is the largest of the cusps in *L. douglassi*. A mesostyle, absent in *L. quartzi*, occurs in *L. douglassi*. The M1–M2 of *L. quartzi* have an anterior cingulum that arises labially at the anteromedial margin of the paracone, while in *L. douglassi* it continues labially around the paracone. A mesostyle is absent in *L. quartzi*, but present in *L. douglassi*. The posterior cingulum terminates along the posteromedial margin of the metacone in *L. quartzi* but extends the entire width of the tooth for *L. douglassi*.

The p4 of *L. quartzi* has an anteroconid but is lacking in *L. douglassi*; the mesolophid is absent in *L. quartzi* but present in *L. douglassi*. The posterior cingulid always arises at the center of the hypolophid and ends at the

posteromedial margin of the entoconid in *L. quartzi*, whereas in *L. douglassi* it may arise directly from the hypoconid. In the latter it never reaches the entoconid. The m1–m2 of *L. quartzi* have labial and lingual arms of the anterior cingulid that are equal and join the center of the metalophid, whereas in *L. douglassi* the lingual arm is transversely wider than the labial arm and they join the protoconid. The mesolophid is shorter in *L. quartzi* than in *L. douglassi*. The posterior cingulid of *L. quartzi* attaches at the posterior margin of the entoconid, while in *L. douglassi* it does not reach the entoconid.

The p4 of *L. quartzi* possesses an anteroconid, mesoconid and mesolophid, all of which are lacking in *L. russelli*. The posterior cingulid reaches the posteromedial margin of the entoconid in *L. quartzi*, while it does not in *L. russelli*. The m1–m2 of *L. quartzi* have an anterior cingulid that nearly traverses the entire width of the tooth, while in *L. russelli* it is reduced and does not reach either of the lateral margins. A distinct mesoconid and mesolophid occur in *L. quartzi*, absent in *L. russelli*. The posterior cingulid of *L. quartzi* reaches the posterior border of the entoconid, while in *L. russelli* it does not reach the entoconid.

The dentary of *L. quartzi* has a masseteric scar that ends below the anterior root of p4, whereas in *L. oregonensis* it ends below the posteriormost part of p4. The dorsal shelf is absent or weak, and the ventral shelf is strong in *L. quartzi*, while the opposite conditions are apparent in *L. oregonensis*. On the lingual surface, there is a single foramen that occurs between the i1 and p4 in *L. quartzi*, while in *L. oregonensis* there are numerous lingual foramina. The p4 of

L. quartzi possesses an anteroconid, which is lacking in *L. oregonensis*. The metalophid of *L. quartzi* is variably incomplete, while in *L. oregonensis* it is consistently complete.

The lower cheekteeth of *L. quartzi* closely resembles those of *L. russelli*; in fact, present evidence suggests that the two taxa are conspecific. Only a single specimen of *L. russelli*, the type, is known. Thus, an adequate diagnosis for the species should include important features (presence or expression of the anteroconid, mesoconid, anterior arm of the ectolophid, and mesostylid) observed in *L. quartzi* and other species of *Leptodontomys*. These characters are variable within species, and the significance of the condition in *L. russelli* cannot be evaluated. For this study, I provisionally recognize both species.

Leptodontomys stirtoni (Lindsay, 1972)

Plate 4 (A-F)

Localities.—Eastgate, UCMP V70140 and V70147.

Age.—Barstovian.

Stratigraphic and geographic occurrence of species.—Barstovian: Barstow Formation, Barstow fauna, San Bernardino County, California (Lindsay, 1972); Monarch Mill Formation, Eastgate fauna, Churchill County, Nevada.

Referred specimens.—OMNH 54701, left maxilla fragment with P4; UCMP 141780-22, right M1 or M2; UCMP 141780-95, left maxilla fragment with P4; UCMP 141780-98, right M1 or M2; UCMP 141780-101, left M1 or M2; UCMP

141780-142, left maxilla fragment with P4-M1; UCMP 141780-210, right maxilla fragment with M2; UCMP 141780-238, left maxilla fragment with P4; UCMP 141822-15, right M1 or M2.

Measurements.—See Table 9.

Description.—The P4 possesses a talon that is nearly as wide as the trigon. The anterior cingulum is absent, but a shallow concavity occurs between the bases of the paracone and protocone. An anterocone is absent. The paracone is the largest of the principal cusps, with the others being subequal in size. The paracone and metacone are slightly anterior to the protocone and hypocone, respectively, so that the cusps are not transversely aligned. Anteroposteriorly, the paracone is aligned with the metacone and the protocone with the hypocone; the distance between protocone and hypocone is greater than that between the paracone and metacone. The paracone and protocone are set far apart and not united by a protoloph. A protolophule occurs between the paracone and protocone. The lingual and labial arms of the protoloph are absent. The mesocone is distinct and lies in the middle of the central basin between the paracone and metacone. A mesoloph may be present, while a mesostyle is present in 67% of specimens. A labial cingulum is absent. The posterior arm of the ectoloph is short and extends anteroposteriorly in a straight line to join the center of the metaloph. The lingual and labial arms of the metaloph are equal in length. The labial basin is anteroposteriorly longer than the lingual basin, but both open laterally. The metacone and hypocone are far apart, but joined by a metaloph. The metaloph forms a high, *V*-shaped ridge that

rises high on the anterolingual side of the metacone and is directed strongly anterolingually toward the center of the tooth, where it intersects the ectoloph and becomes re-directed strongly posterolingually to join the hypocone. The posterior cingulum arises high on the labial margin of the hypocone and descends, as it traverses labially in a straight line, to join the metacone low on its posteromedial margin. The posterior cingulum is anteroposteriorly narrow and open labially.

The M1 has an anterior cingulum that arises low near the anterolingual base of the protocone and ascends to the middle of the tooth, where an adloph unites them at the center of the protoloph; the cingulum then descends lingually to attach on the anterolingual margin of the paracone. Although the labial and lingual arms of the anterior cingulum are equally developed, they do not traverse the entire width of the tooth. The four major cusps are subequal in size. The paracone is transversely aligned with the protocone, but the metacone lies slightly anterior relative to the hypocone. Anteroposteriorly, the paracone and protocone are aligned with metacone and hypocone, respectively. The paracone and protocone are set far apart but united by a high, *V*-shaped protoloph. The lingual arm of the protoloph is more distinct than the labial arm. The protoloph and metaloph are equidistant in width. The mesocone is distinct and occurs in the anteromedial part of the central basin but posterior to a transverse line between paracone and metacone. The mesoloph is directed anterolabially toward the posterolingual base of the paracone but does not reach that cusp. A mesostyle is present in 67% of the Eastgate specimens, whereas a labial

cingulum occurs in 33%. The posterior arm of the ectoloph is posteriorly directed from the mesocone and joins lingual to the center of the metaloph. The metacone and hypocone are far apart but joined by a metaloph. The lingual arm of the metaloph is anterolabially directed and less distinct than the labial arm. The labial arm of the metaloph is directed lingually in a straight line, joining the lingual arm of the metaloph. The labial basin is anteroposteriorly longer than the lingual basin; both basins are open laterally. The posterior cingulum arises high on the labial margin of the hypocone and descends gradually as it traverses the posteriormost part of the tooth to join the metacone low on the posterolabial margin. The posterior cingulum is anteroposteriorly elongated and open labially.

Comparison and discussion.—The P4 of *L. stirtoni* has paracone and metacone anterior to the protocone and hypocone, respectively, whereas the paracone and metacone are transversely aligned and the metacone is anterior to the hypocone in *L. korthi*. The paracone and protocone are not joined by a protoloph, and a protolophule is absent in *L. stirtoni*; the opposite is true in *L. korthi*. A mesostyle, present in *L. stirtoni*, is absent in *L. korthi*. The lingual and labial arms of the metaloph are equally distinct in *L. stirtoni*, while in *L. korthi* they are less and more distinct, respectively. The lingual basin is anteroposteriorly elongate in *L. stirtoni*, while in *L. korthi* they are equal. The M1–M2 of *L. stirtoni* have an anterior cingulum that arises along the anterolingual base of the protocone and ends at the anterolingual margin of the paracone, whereas in *L. korthi* it arises along the anteromedial margin of the protocone and ends along the anteromedial margin of the paracone. The lingual arm of the protoloph is

more distinct than the labial arm in *L. stirtoni*, whereas in *L. korthi* the opposite is true. A mesostyle and labial cingulum are present in *L. stirtoni*; in *L. korthi* these features are lacking. The posterior cingulum joins the posterolabial margin of the metacone in *L. stirtoni*, while it joins the posteromedial margin in *L. korthi*. The posterior cingulum is anteroposteriorly elongate in *L. stirtoni*, while it is narrow in *L. korthi*.

The P4 of *L. stirtoni* does not posses an anterior cingulum, which is present in *L. protistopikos*. The paracone is the largest of principal cusps in *L. stirtoni*, whereas all cusps are subequal in *L. protistopikos*. A protolophule, present in *L. stirtoni*, is absent in *L. protistopikos*. The distance between paracone and protocone is less than between the metacone and hypocone in *L. stirtoni*, while in *L. protistopikos* these distances are equal. A mesostyle is present in *L. stirtoni*, but absent in *L. protistopikos*. The lingual and labial arms of the metaloph are equal in *L. stirtoni*, while in *L. protistopikos* the lingual arm is more distinct. The posterior cingulum is anteroposteriorly narrow and open in *L. stirtoni*; it is anteroposteriorly elongate and closed in *L. protistopikos*. The M1–M2 of *L. stirtoni* have an anterior cingulum that joins the anterolingual margin of the paracone, while *L. protistopikos* it joins the anterolabial margin of that cusp. The lingual and labial arms of the anterior cingulum are equal in *L. stirtoni*, whereas in *L. protistopikos* the labial arm is more distinct than the lingual arm. The labial and lingual cusps are transversely aligned in *L. stirtoni*, but in *L. protistopikos* the labial cusps occur anterior to those of the lingual side. A mesostyle and labial cingulum are present in *L. stirtoni*, but in *L. protistopikos*

both are absent. The posterior cingulum joins the posterolabial margin of the metacone and opens labially in *L. stirtoni*, while in *L. protistopikos* it joins the posteromedial margin of the metacone and closes labially.

The P4 of *L. stirtoni* has a paracone that is distinctly larger than remaining cusps, whereas in *L. quartzi* all cusps are subequal in size. A protolophule is present in *L. stirtoni* but not in *L. quartzi*. The mesocone is distinct in *L. stirtoni*, while it is submerged in *L. quartzi*. In *L. stirtoni*, the mesoloph and mesostyle are present; both are absent in *L. quartzi*. The lingual and labial arms of the metaloph are equal in *L. stirtoni*, while in *L. quartzi* the lingual arm is less distinct. The metacone and hypocone occur far apart in *L. stirtoni*, while in *L. quartzi* they are closely approximated. The posterior cingulum is anteroposteriorly narrow in *L. stirtoni*; it is anteroposteriorly elongate in *L. quartzi*. The M1–M2 of *L. stirtoni* have an anterior cingulum with equally developed lingual and labial arms, whereas in *L. quartzi* the labial arm is more distinct. In *L. stirtoni*, the lingual arm of the protoloph is more distinct and the labial arm is less so, while in *L. quartzi* the lingual arm is less distinct. A mesostyle and labial cingulum are present in *L. stirtoni*; both are absent in *L. quartzi*. The posterior cingulum joins the posterolabial margin of the metacone in *L. stirtoni*, while in *L. quartzi* it joins the posteromedial margin of the metacone.

The P4 of *L. stirtoni* lacks an anterior cingulum, present in *L. douglassi*. A distinct mesocone and mesoloph are present in *L. stirtoni*; both are absent in *L douglassi*. The M1–M2 of *L. stirtoni* have an anterior cingulum that joins the paracone at its anterolingual margin, while in *L. douglassi* it continues labially

around the paracone. A labial cingulum is present in *L. stirtoni*; absent in *L. douglassi*.

Leptodontomys sp. indet.

Plate 4 (G-I)

Locality.—Eastgate, UCMP V70140.

Age.—Barstovian.

Stratigraphic and geographic occurrence.—Barstovian: Monarch Mill Formation, Eastgate fauna, Churchill County, Nevada.

Referred specimens.—UCMP 141780-88, left P4; UCMP 141780-163, left P4.

Measurements.—UCMP 141780-88: AP = 0.70, T = 0.73; UCMP 141780-163: AP = 0.65, T = 0.69.

Description.—The P4 occlusal outline is trapizoidal and not molariform. The talon is nearly as wide as the trigon. The anterior cingulum arises at, and level with, the middle of the protoloph, extending labially to the labial margin of the tooth. An anterocone is absent. The four major cusps are subequal. The paracone and metacone are transversely aligned with protocone and hypocone, respectively. Anteroposteriorly, the paracone and protocone are aligned with the metacone and hypocone, respectively. The distance between paracone and metacone is similar to that between the protocone and hypocone. The paracone and protocone are closely approximated and united by a protoloph. A

protolophule is absent. The lingual arm of the protoloph is more distinct than the labial arm. The mesocone is distinct and occurs in the middle of the central basin, posterior to a line traversing the posteriormost part of the paracone and metacone. A mesoloph is absent, while a mesostyle is present in one of the two specimens. A labial cingulum is absent. The posterior arm of the ectoloph is short and extends anteroposteriorly in a straight line to join the center of the metaloph. The lingual arm of the metaloph is less distinct than the labial arm. The labial basin is anteroposteriorly longer than the lingual basin; both are open laterally. The metacone and hypocone are far apart but joined by a metaloph. The metaloph forms a high, *V*-shaped ridge that rises high on the anterolingual margin of the metacone and is directed strongly anterolingually toward the center of the tooth, where it intersects the ectoloph and becomes redirected strongly posterolingually to join the hypocone. The posterior cingulum arises high on the labial margin of the hypocone and descends as it traverses labially in a straight line to join the metacone low on the posterolingual margin. The posterior cingulum is anteroposteriorly narrow and open labially.

Comparison and discussion.—No other species of *Leptodontomys* have a P4 similar in occlusal outline, size, or morphology to these specimens. These teeth appear to belong to the permanent (rather than deciduous) dentition because their roots are straight, not divergent. When better material becomes available for study, these teeth may prove to represent a new species of *Leptodontomys*.

PHYLOGENETIC ANALYSIS

Past phylogenetic investigations for Leptodontomys.—Several authors (Fahlbusch, 1973, 1979; Walhert, 1978; Storer, 1987, and Korth and Bailey, 1992) have addressed the phylogenetic relationships of eomyids, but none have focused on phylogenetic relationships within *Leptodontomys*. Storer (1987) identified three groups of Uintan–Chadronian eomyids:

1) *Adjidaumo–Paradjidaumo*, with an increased crown height resulting from increased height of the base of the tooth crown (not accompanied by increased cusp height), enlarged bulbous cusps, and a mesoconid lacking a mesolophid; 2) *Yoderimyinae*, the only group possessing a P3 and an anterior displacement of the central basin on lower molars; and 3) *Namatomys*, having a mesoconid that extends lingually and labially, an adloph (see Kelly and Whistler, 1998) that joins the anterior cingulum lingual to the center of the protoloph near the protocone, and an adlophid (see Kelly and Whistler, 1998) that joins the anterior cingulid lingual to the center on the metalophid near the protoconid. Storer (1987) indicated that *Adjidaumo* could be separated from the *Paradjidaumo* group based on a primitive condition of the latter. In this primitive condition, the central basin has an anterior position in the upper cheekteeth and a posterior position in the lower cheekteeth (Storer, 1987). *Adjidaumo* was considered a proximal relative of *Leptodontomys* relative to *Paradjidaumo*. *Adjidaumo* is derived in having shallow basins, a protoconid and metaconid that are closely approximated and joined, and a mesolophid that is short and high (Storer, 1987). These derived

characters are shared, in part, by *Leptodontomys*.

Korth and Bailey (1992) listed four characters of the cheekteeth of *Leptodontomys* that are derived compared to those of *Adjidaumo*: the anterior cingulid joins the metalophid lingual to the protoconid; the posterior cingulid joins the hypolophid centrally; a lingual arm of the anterior cingulum is present on the upper molars; and a central basin that is deeper than the anterior or posterior basins. The geologically oldest known species of *Leptodontomys* is *L. douglassi*. It and other species of *Leptodontomys* can be distinguished from *Adjidaumo* in that *Leptodontomys* has the following: p4 more molariform; metalophid and hypolophid nearly equal in transverse width; shorter mesolophs and mesolophids; an anterior cingulid of the lower molars that does not traverse the entire width of the tooth; an adlophid that joins the anterior cingulid near the center of the metalophid; and a hypolophid that joins the posterior cingulid of the molars lingually (near its center). According to Korth and Bailey (1992), *A. maximus* is the only species of *Adjidaumo* that shares the last character with *Leptodontomys*.

Outgroup selection.—Korth and Bailey (1992) suggested *L. douglassi* as the most primitive species of *Leptodontomys* and a possible transitional species between *Adjidaumo* sp. and *Leptodontomys*. In addition, these authors considered *Adjidaumo* sp. of Orellan age from the Tepee Trail Formation, Cedar Ridge local fauna, Natrona County, Wyoming, as the most recent common ancestor for the genus *Leptodontomys*. However, after close evaluation of all the species of *Adjidaumo*, I believe *A. maximus* described by Korth (1989) of Orellan

age from the Brule Formation, Sioux County, Nebraska shows closer affinities with *Leptodontomys* than any of the other species of *Adjidaumo*. Characters present for *A. maximus* and *Leptodontomys*, but not occurring in any other species of *Adjidaumo*, include a mesostylid on the lower cheekteeth (except m3) and a short posteriorly directed hypolophid that joins the posterior cingulid of the lower molars lingually (near the center of the posterior cingulid). The latter character is shared by all *Leptodontomys*. Based on these characters and other similarities between *A. maximus* and *Leptodontomys*, I have used the former as the outgroup for the phylogenetic analyses. In addition, *A. maximus* has 99% of all characters evaluated in the phylogenetic analyses.

The characters taken from the literature and characters identified herein are listed in Appendix I. They were scored for *A. maximus* and all species of *Leptodontomys*, which includes *L. douglassi*, *L. stirtoni*, *L. quartzi*, *L. russelli*, *L. korthi*, *L. schnelli*, *L. protistopikos*, and *L. oregonensis* (Table 14). The matrix includes 74 characters, which were evaluated for the ingroup and outgroup. Completeness of all characters is indicated in Table 14.

Results.—An exhaustive search resulted in 14 most-parsimonious trees with the following statistics: tree length 133; consistency index 0.76; and retention index 0.49. Consensus trees (strict and 50%-majority-rule) were produced from 14 most-parsimonious trees. The 50%-majority-rule consensus tree had an ingroup with two clusters. One cluster included a single species, *L. douglassi*; the other was a tricotomy of the remaining seven species of *Leptodontomys*. This tricotomy consisted of a single species, *L. oregonensis*,

and the two other daughter groups included three species each. One daughter group (*L. stirtoni*), included *L. stirtoni*, *L. schnelli*, and *L. protistopikos*. The second daughter group (*L. quartzi*), included *L. quartzi*, *L. korthi*, and *L. russelli* (Fig. 11).

Character evolution was traced for all 74 characters on the 50%-majority-rule tree and revealed the following. Character 2 grouped all species of the three daughter groups *L. douglassi*, *L. stirtoni*, and *L. korthi*, sharing a derived state 1 (P4 with variable anterocone). Character 5, state 1 (P4 protolophule absent) and character 17, state 1 (P4 with lingual arm of anterior cingulum present) clustered all species of the ingroup. Characters 13, state 1 (P4 metaloph lingual arm less distinct than labial arm); 53, state 1 (m1–m2 with labial arm of anterior cingulid attached along anterolabial margin of protoconid); and 68, state 0 (m1–m2 with hypolophid posteriorly bent) clustered the *L.* stirtoni group (*L. stirtoni*, *L. schnelli*, and *L. protistopikos*) with *L. quartzi* group (*L. quartzi*, *L. korthi*, and *L. russelli*). Character 14, state 2 (P4 with lingual basin anteroposteriorly shorter than labial basin) defined the branches with all species of the ingroup except *L. korthi*, which has state 1 (P4 with lingual and labial basins equal). Character 23, state 2 (M1–M2 with labial arm of protoloph more distinct than lingual arm) clustered all species, except *L. schnelli* (for which the state is unknown) of the ingroup, with *L. stirtoni* having a derived state 1 (M1–M2 with labial arm of protoloph less distinct than lingual arm). The following clustered *L. quartzi* with *L. korthi*: character 26, state 1 (M1–M2 with paracone and protocone transversely aligned); character 36, state 1 (p4 with anteroconid variable);

character 44, state 1 (p4 with anterior arm of ectolophid variable); character 45, state 1 (p4 with posterior arm of ectolophid variable); and character 73, state 1 (dentary with dorsal shelf of masseteric scar weak). Additional derived characters that clustered all species of the *L. quartzi* group include: character 41, state 2 (p4 with mesolophid absent); character 57, state 2 (m1–m2 with labial arm of metalophid more distinct than lingual arm); and character 65, state 1 (m1–m2 with labial and lingual basins equal), which clustered *L. quartzi* and *L. russelli* of the *L. quartzi* group, but not *L. korthi* having a state 2 (m1–m2 with labial basin shorter than lingual basin).

CONCLUDING REMARKS

The Eastgate local fauna is considered early Barstovian (see Smith, 2002). Five species of *Leptodontomys* were identified from the Eastgate local fauna of the Monarch Mill Formation, Churchill County, Nevada. These include two known species (*L. stirtoni* and *L. quartzi*) and three new species (*L. korthi* n. sp., *L. schnelli* n. sp., and *L. protistopikos* n. sp.) for the genus.

Leptodontomys has a temporal range from the Arikareean, Barstovian, and Clarendonian of North America. No species of *Leptodontomys* are known from the Hemingfordian. The oldest is *L. douglassi*, whereas the youngest is *L. oregonensis*. The Barstovian species are *L. stirtoni*, *L. quartzi*, and *L. russelli*. Of these species, only the Barstovian species are known from Eastgate, thus, supporting a Barstovian age for the Eastgate fauna as reported by Smith (2002).

Only two *Leptodontomys* species, *L. douglassi* and *L. russelli*, have been reported from the Great Plains. In contrast, *L. stirtoni* and *L. quarzti* are known only known from the West Coast and Great Basin, respectively. The presence of *L. stirtoni* at Eastgate extends the geographic range from the southwestern part of California to the Great Basin. To date, there are no known species of *Leptodontomys* reported from the Rocky Mountains of North America. The lack of *Leptodontomys* from the Rocky Mountains may be attributed to the differences in climate and vegetation between these geographically separate sites or it may reflect the rarity of *Leptodontomys* in the fossil record.

Phylogenetic analyses for *Leptodontomys* indicate this is a monophyletic

group. Two clusters are evident with a single species (L. douglassi) in one cluster and seven species of *Leptodontomys* in the other cluster. This second cluster has three daughter groups. The first daughter group contains a single species (*L. oregonensis*), whereas the other two daughter groups (*L. stirtoni* and *L. quartzi*) include three species each. The second daughter group (*L. stirtoni*) includes *L. stirtoni*, *L. schnelli*, and *L. protistopikos*. The third daughter group (*L. quartzi*) contains *L. quartzi*, *L. korthi*, and *L. russellli*. The species of the *L. stirtoni* cluster have shared, derived character states not possessed by any other species of this genus. These character states include: the P4 with a posterior cingulum that is open; the M2 with an anterior cinguum that attaches along the anterolabial margin, and labial basin that is anteroposteriorly longer than the lingual basin; the p4 with an anteriorly directed mesolophid, posterior cingulid that joins the hypoconid directly; and the m1 with an anteriorly directed mesolophid and posterior cingulid that joins the entoconid along the posteromedial margin. The species of the *L. quartzi* cluster have defining shared, derived character states: a p4 that may lack the mesolophid and m1–m2 with labial arms of metalophids more distinct than those of the lingual arms.

The species relationships resolved within *Leptodontomys* are very robust even though limited material was available for most of the species of *Leptodontomys*. For example, when *L. oregonensis* (known from a single lower jaw fragment with p4 only) was removed from the phylogenetic analyses, three most-parsimonious trees (rather than 14 most-parsimonious trees) were produced. However, the strict-consensus and 50%-majority-rule-consensus

trees from these 3 most-parsimonious trees were identical and had a similar resolution of relationships among the remaining seven species of *Leptodontomys* as when the *L. oregonensis* was present in the analyses. In addition, when the character states for variable characters (= 2) were coded as being polymorphic (i.e., 1 & 0) the outcome of the consensus trees was similar to that in Fig. 11. The only difference in the two cladograms was the latter presented *L. quartzi* and *L. russelli* as sister taxa, rather than *L. quartzi* and *L. korthi*.

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APPENDIX I

Descriptions of characters and character states used in phylogenetic analyses.

1. P4: anterior cingulum present (0) or absent (1).

2. P4: anterocone; anterocone present (0), variable among two or more specimens within a given taxon (1), or absent (2).

3. P4: all principal cusps subequal to each other (0) or paracone is the largest cusp with others being subequal (1).

4. P4: paracone and protocone transversely aligned (0) or paracone is anterior to protocone (1).

5. P4: protolophule present (0) or absent (1).

6. P4: lingual arm of protoloph short (0), distinct (1), variable among two or more specimens within a given taxon (2), or absent (3).

7. P4: labial arm of protoloph distinct (0), equal to lingual arm of protoloph (1), or submerged (2).

8. P4: protoloph/metaloph; protoloph narrower (0) or equal (1).

9. P4: mesocone submerged (0) or distinct (1).

10. P4: mesoloph absent (0) or present (1).

11. P4: mesostyle always absent (0) or variable among two or more specimens within a given taxon (1).

12. P4: labial cingulum absent (0) or variable among two or more specimens within a given taxon (1).

13. P4: lingual arm of metaloph more distinct (0) or less distinct than labial

arm (1).

14. P4: lingual basin anteroposteriorly longer (0), equal (1), or shorter (2) than labial basin.

15. P4: posterior cingulum anteroposteriorly elongated (0) or narrow (1).

16. P4: posterior cingulum is open (0) or closed (1).

17. M1–M2: anterior arm of cingulum absent (0) or present (1).

18. M1–M2: lingual arm of anterior cingulum attaches along anteromedial margin (0) or anterolingual margin (1).

19. M1– M2: labial arm of anterior cingulum attaches along anteromedial margin (0), anterolingual margin (1), or anterolabial margin (2).

20. M1–M2: labial arm of anterior cingulum compared to lingual arm distinct (0) or equal (1).

21. M1– M2: anterior cingulum attaches along center of protoloph (0), lingual to center of protoloph near protocone (1), or directly on the protocone (2).

22. M1–M2: lingual arm of protoloph more distinct than labial arm (0), or less distinct (1), or submerged (2).

23. M1–M2: labial arm of protoloph submerged (0), less distinct than the lingual arm of protoloph (1), or more distinct than lingual arm of the protoloph (2).

24. M1–M2: protoloph wider than metaloph (0), equal (1), or protoloph narrower than metaloph(2).

25. M1–M2: labial arm of metaloph more distinct than lingual arm (0) or less distinct (1).

26. M1–M2: paracone occurs in slightly anterior position relative to

protocone (0) or paracone and protocone are transversly aligned (1).

27. M1–M2: metacone positioned slightly anterior relative hypocone (0) or metacone and hypocone are transversely aligned (1).

28. M1–M2: posterior arm of ectoloph joins metaloph lingual to center (0) or centrally (1).

29. M1–M2: posterior cingulum joins metacone along posteromedial margin (0) or posterolabial margin (1).

30. M1–M2: posterior cingulum anteroposteriorly narrow (0) or elongated (1).

31. M1–M2: labial end of posterior cingulum open (0) or closed (1).

32. M1–M2: labial basin and lingual basin equal in length (0), lingual basin anteroposteriorly longer than labial basin (1), or labial basin anteroposteriorly longer than lingual basin (2).

33. M1–M2: mesostyle absent (0) or variable among two or more specimens within a given taxon (1).

34. M1–M2: labial cingulum absent (0) or variable among two or more specimens within a given taxon (1).

35. p4: anterior cingulid absent (0) or variable among two or more specimens within a given taxon (1).

36. p4: anteroconid always absent (0), variable among two or more specimens within a given taxon (1), or always present (2).

37. p4: protoconid and metaconid joined (0) or separated (1).

38. p4: metalophid: metalophid present (0) or absent (1).

39. p4: metalophid state: if metalophid is present, it may be complete (attaches to both protoconid and metaconid and is continuous along entire path) (0) or variable among two or more specimens within a given taxon (1).

40. p4: mesoconid distinct (0), variable among two or more specimens within a given taxon (1), or submerged (2).

41. p4: mesolophid present (0), absent (2), or variable among two or more specimens within a given taxon (1).

42. p4: if present, mesolophid short (0) or anterolingually directed (1).

43. p4: anterior arm of ectolophid present (0), variable among two or more specimens within a given taxon (1), or absent (2).

44. p4: if present, anterior arm of ectolophid attaches to protoconid (0), or is variable among two or more specimens within a given taxon (1).

45. p4: posterior arm of ectolophid; posterior arm of ectolophid distinct (0), variable among two or more specimens within a given taxon (1), or weak (2).

46. p4: mesostylid present (0), variable among two or more specimens within a given taxon (1), or absent (2).

47. p4: labial cingulid absent (0) or variable among two or more specimens within a given taxon (1).

48. p4: posterior cingulid joins hypolophid centrally (0), or directly on hypoconid (1).

49. p4: lingual end of posterior cingulid ends along posterolabial margin of entoconid (0) or along posteromedial margin (1).

50. p4: lingual end of posterior cingulid open (0) or closed (1).

51. m1–m2: the anterior cingulid attached to metalophid (0) or variable among two or more specimens within a given taxon (1).

52. m1–m2: anterior cingulid; if attached, attaches to metalophid directly on protoconid (0), near protoconid (1), or to centrally (2).

53. m1–m2: labial arm of anterior cingulid attaches along anteromedial margin of protoconid (0) or along anterolabial margin (1).

54. m1–m2: lingual arm of anterior cingulid attaches to metaconid along anteromedial margin (0), anterolingual margin (1), or anterolabial margin (2).

55. m1–m2: labial arm of anterior cingulid less distinct than lingual arm (0), equal (1), or more distinct (2).

56. m1–m2: linual arm of metalophid more distinct than in labial arm of metalophid (0), less distinct (1), or submerged (2).

57. m1–m2: labial arm of metalophid submerged with lingual arm (0), less distinct than lingual arm (1), or more distinct (2).

58. m1–m2: metalophid narrower than hypolophid (0) or equal in transverse width to hypolophid (1).

59. m1–m2: mesoconid distinct (0), variable among two or more specimens within a given taxon (1), or submerged (2).

60. m1–m2: mesolophid present (0), variable among two or more specimens within a given taxon (1), or absent (2).

61. m1–m2: if mesolophid present, it is short (0), long (1), or anterolingually directed (2).

62. m1–m2: lingual arm of hypolophid more distinct than labial arm (0) or

less distinct (1).

63. m1–m2: entoconid anterior to hypoconid (0) or transversely aligned (1).

64. m1–m2: posterior cingulid joins entoconid along posterolabial margin (0) or posteromedial margin (1).

65. m1–m2: labial basin anteroposteriorly longer than lingual basin (0), basins equal (1), or labial basin shorter (2).

66. m1–m2: mesostylid present (0), variable among two or more specimens within a given taxon (1), or absent (2).

67. m1–m2: labial cingulid absent (0), present (1), or variable among two or more specimens within a given taxon (2).

68. m1–m2: hypolophid posteriorly bent (0), transversely straight (1), or variable (2).

69. dentary: ledge structure of lateral side of ascending ramus weakly developed (0) or strongly developed (1).

70. dentary: placement of mental foramen along dorsoventral axis of mandible level with anteriormost part of masseteric scar (0), below level of anteriormost part of masseteric scar (1), or above level of anteriormost part of masseteric scar (2).

71. dentary: distal end of masseteric scar ends below anteriormost part of p4 (0), below middle part of p4 (1), or below posteromost part of p4 (2).

72. dentary: small shelf occurring posterior to knob for base of lower incisor on ascending ramus absent (0), present (1), or variable among two or

more specimens within a given taxon (2).

73. dentary: dorsal shelf of masseteric scar absent (0), weak (1), or strong (2).

74. dentary: ventral shelf of masseteric scar absent (0), weak (1), or strong (2).

Table 1.–List of characters for principal components analysis and, in part, for correspondence analysis of p4s for *Leptodontomys*.

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1. Trigonid vs talonid: (0) talonid noticeably wider than trigonid; (1) equal.

2. Length vs width: (0) longer than wide (greater than 0.5 mm); (1) equal (less than 0.5 mm); (2) wider than long (greater than 0.5 mm).

3. Anterior cingulid: (0) absent; (1) present.

4. Anteroconid: (0) absent; (1) present.

5. Relationship of protoconid to metaconid: (0) joined except at apex of cusps (at or level with ectolophid); (1) separate entire height of cusp (anteroposterior valley present between the protoconid and metaconid, and thus not joined by a metalophid).

6. Metalophid: (0) absent; (1) present.

7. If metalophid present, it is: (0) incomplete; (1) complete.

8. Mesoconid: (0) distinct; (1) submerged.

9. Mesolophid: (0) absent; (1) present.

10. Anterior arm of ectolophid: (0) absent; (1) present.

11. If anterior arm present, it is: (0) weak; (1) strong.

12. If anterior arm present, it is: (0) bent; (1) straight.

13. Posterior arm of ectolophid: (0) weak; (1) strong.

14. Posterior arm of ectolophid: (0) bent; (1) straight.

15. Ectolophid unites with trigonid: (0) metaconid; (1) protoconid.

Table 1.–Continued.

16. Mesostylid: (0) absent; (1) present.

17. Posterior cingulid: (0) incomplete; (1) complete (is continuous across its entire width).

I8. If posterior cingulid complete it unites: (0) with hypolophid centrally at hypoconulid; (1) near hypoconid.

Table 2.–Data matrix of absence (0) and presence (1) scores for p4s of *Leptodontomys* from Eastgate.

Specimen	[a] Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
OMNH 54716	0	1	0	0	0	1	1	1	0	1	1	0	1	0	1	0	1	1
UCMP 141780-247	1	0	0	0	0	1	1	0	0	1	1	0	1	0	1	0	1	0
UCMP 141780-253	1	0	0	0	0	1	1	0	0	1	1	0	1	0	1	0	1	0
OMNH 54722	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	1	0
OMNH 54719	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0
OMNH 54727	1	0	0	0	0	1	1	0	0	1	0	1	0	0	1	0	0	0
UCMP 141780-211	0	1	0	1	0	1	1	0	0	1	0	0	0	0	1	1	1	0
UCMP 141780-246	0	1	0	0	0	1	1	0	0	0	-	-	0	0	-	0	0	0
OMNH 54714	0	1	0	1	0	1	0	0	0	0	-	-	1	0	-	0	1	0
UCMP 141780-257	1	0	0	0	0	1	1	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-273	1	0	0	0	0	1	1	0	0	1	0	1	0	1	1	1	1	0

Table 2.–Continued.

Specimen	[a] Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
UCMP 141780-276	1	1	0	1	0	1	0	0	0	0	-	-	0	0	-	0	0	0
OMNH 54726	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	1	1	0
UCMP 141780-279	1	1	1	0	0	1	0	0	0	0	-	-	1	0	-	1	1	0
OMNH 54723	1	0	0	1	0	1	0	0	0	0	-	-	1	0	-	0	0	0
UCMP 141780-265	1	1	1	0	0	1	1	0	0	1	1	1	1	0	1	0	1	0
OMNH 54721	1	1	0	1	0	1	1	0	0	0	-	-	0	0	-	0	0	0
UCMP 141780-168	1	0	0	0	0	1	1	0	0	1	0	1	0	0	1	1	1	0
UCMP 141780-62	1	0	0	0	0	1	1	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-256	0	0	0	1	0	1	1	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-270	1	1	1	0	0	1	1	0	0	0	-	-	1	0	-	0	1	0
UCMP 141780-196	1	0	0	0	0	1	1	0	0	0	-	-	0	0	-	0	1	0

Table 2.–Continued.

Specimen	[a] Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
UCMP 141878	0	0	0	1	0	1	1	0	0	1	1	1	0	0	1	1	1	0
UCMP 141780-261	1	1	0	0	0	1	1	0	0	1	0	1	0	0	1	0	1	0
OMNH 54718	1	0	0	0	0	0	-	1	0	1	1	0	1	0	0	0	1	0
UCMP 141780-243	1	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	1	0
OMNH 54859	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	1	0
UCMP 141780-260	1	0	0	1	0	1	1	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-04	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	1	0
OMNH 54715	1	0	0	0	1	0	-	0	0	1	0	1	0	0	1	0	1	0
OMNH 54720	0	2	0	0	1	0	-	1	0	1	0	0	0	0	0	0	0	0
UCMP 141780-127	1	0	0	1	1	0	-	1	0	1	0	0	0	0	0	0	1	0
UCMP 141780-241	0	1	0	0	1	0	-	0	0	0	-	-	0	0	-	0	1	0

Table 2.–Continued.

Specimen	[a] Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
UCMP 141780-242	0	0	0	1	1	0	-	1	0	1	0	0	0	0	0	0	1	0
UCMP 141780-244	1	0	0	1	1	0	-	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-245	0	2	0	0	1	0	-	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-248	1	0	0	1	1	0	-	0	0	0	-	-	0	0	-	0	0	0
UCMP 141780-250	1	1	0	0	1	0	-	1	0	1	0	0	0	0	0	0	0	0
UCMP 141780-254	0	1	0	0	1	0	-	0	0	1	0	0	0	0	1	0	1	0
UCMP 141780-262	1	0	0	0	1	0	-	0	0	1	0	0	0	0	0	0	0	0
UCMP 141780-264	1	0	0	1	1	0	-	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-266	1	0	0	1	1	0	-	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-267	1	1	0	0	1	0	-	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-268	1	1	0	1	1	0	-	0	0	0	-	-	0	0	-	0	1	0

Table 2.–Continued.

Specimen	[a] Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
UCMP 141780-277	1	2	0	0	1	0	-	0	0	1	0	0	0	0	0	0	1	0
UCMP 141780-278	1	0	0	1	1	0	-	0	0	1	0	1	0	0	1	0	1	0
UCMP 141780-282	1	2	0	1	1	0	-	0	0	0	-	-	0	0	-	0	1	0
UCMP 141780-107	1	1	0	1	1	0	-	1	0	1	0	0	0	0	0	0	1	0
OMNH 54724	1	0	0	0	1	0	-	0	0	0	-	-	0	0	-	0	0	0
OMNH 54725	1	1	0	1	1	0	-	0	0	1	0	0	0	0	0	0	1	0

[a] Dash indicates missing value.

Table 3.–Characteristics of p4 used to separate species of *Leptodontomys*.

Character	Taxon				
	L. quartzi	L. *russelli*	*L. oregonensis*	*L. douglassi*	*L. stirtoni*
Length (AP) of p4	0.59-0.69	0.60	0.70	0.82-0.93	0.85-0.92
Trigonid vs talonid	narrower	narrower	equal	narrower	narrower
Length vs width	equal to slightly longer than wide	slightly wider than long	much wider than long	much longer than wide	slightly wider than long
Anterior cingulid	absent	absent	isolated	absent	absent
Anteroconid	absent	absent	absent	present	absent
Protoconid/ metaconid	joined	joined	separate	joined	separate
Metalophid	present	present	present	present	absent
Mesoconid	submerged	submerged	distinct	distinct	

Table 3.–Continued.

Character	Taxon				
	L. quartzi	L. *russelli*	*L. oregonensis*	*L. douglassi*	*L. stirtoni*
Mesolophid	absent	absent	present	variable	anteriorly directed
Ectolophid					
anterior arm	weak/bent	absent	strong/bent	weak/straight	weak/straight
posterior arm	weak/bent	weakj/bent	weak/bent	weak/straight	weak/straight
joins protoconid	yes	no	yes	yes	yes
joins metaconid	no	no	no	no	no
unattached	no	yes	no	no	no
Mesostylid	absent	absent	absent	absent	50%
Posterior cingulid joins	hypoconid	hypolophulid	hypoconid	hypolophulid	hypolophulid

Table 4.–Characteristics of p4 used to separate species of *Leptodontomys* from Eastgate.

	Taxon		
Character	*L. korthi*	*L. quartzi*	*L. schnelli*
Length (AP) of p4	0.59-0.76	0.54-0.79	0.71
Anterior cingulid	10%	absent	absent
Anteroconid	39%	52%	absent
Protoconid/ metaconid	separate	joined	joined
Metalophid	absent	present	present
Mesoconid	variable	variable	distinct

Table 4.–Continued.

Character	Taxon		
	L. korthi	*L. quartzi*	*L. schnelli*
Mesolophid	absent	absent	anterolingually directed
Ectolophid	variable	variable	variable
anterior arm	variable	variable	strong/bent
posterior arm	variable	variable	strong/bent
joins protoconid	variable	variable	yes
joins metaconid	variable	variable	no
unattached	variable	variable	no
Mesostylid	absent	18%	absent
Posterior cingulid			
joins	hypolophulid centrally	hypolophulid centrally	hypolophulid near entoconid

Table 5.–Characteristics of P4 used to separate species of *Leptodontomys* from Eastgate.

Character	Taxon			
	L. korthi	*L. protistotopikos*	*L. quartzi*	*L. stirtoni*
Width of P4	0.69-0.81	0.75-0.78	0.60-0.85	0.75-0.96
Anterior cingulum	absent	distinct	absent	absent
Anterocone	18%	absent	absent	absent
Size relation of major Cusps/ largest	paracone	all subequal	all subequai	paracone
Paracone				
Anterior to protocone	no	yes	yes	yes
In line with protocone	yes	no	no	no
Metacone				
Anterior to hypocone	yes	yes	yes	yes

Table 5.--Continued.

Character	Taxon			
	L. korthi	*L. protistotopikos*	*L. quartzi*	*L. stirtoni*
Protolophule	absent	absent	absent	present
Protoloph				
Lingual arm	variable	distinct	equal	absent
Labial arm	submerged	submerged	equal	absent
Protoloph width vs Metaloph width	narrow/wide	equal	narrow/wide	unknown/wide
Mesocone	distinct	distinct	submerged	distinct
Mesoloph	present	present	absent	variable
Mesostyle	absent	absent	absent	67%
Labial cingulum	absent	absent	absent	absent

Table 5.–Continued.

Character	Taxon			
	L. korthi	*L. protistotopikos*	*L. quartzi*	*L. stirtoni*
Metaloph				
Lingual arm/labial arm	less/more	more/less	less/more	equal
Basins				
Lingual/labial	equal	short/long	short/long	long/short
Posterior cingulum				
AP length	narrow	elongated	elongated	narrow
Lingual end	open	closed	open	open

Table 6.--Characteristics of m1--m2 used to separate species of *Leptodontomys*.

Character	Taxon				
	L. quartzi	L. *russelli*	*L. oregonensis*	*L. douglassi*	*L. stirtoni*
AP m1 or m2	0.65-0.83	0.70		0.91-1.06	0.80-1.03
Anterior cingulid					
free or attached	variable	attached		attached	attached
Anteroconid					
present/absent	present	present		present	present
Adlophid					
present/absent	variable	present		present	present
attachment site	central	central		protoconid	central

Table 6.--Continued.

Character	Taxon				
	L. quartzi	L. *russelli*	*L. oregonensis*	*L. douglassi*	*L. stirtoni*
Metalophid	complete	complete		complete	variable
Mesoconid	distinct	submerged		distinct	distinct
Mesolophid	present	absent		present	present
length	short			short	short
direction	transverse			transverse	transverse
Mesostylid	absent	50%		absent	50%

Table 7.–Characteristics of M1–M2 used to separate species of *Leptodontomys*.

	Taxon			
Character	*L. korthi*	*L. quartzi*	*L. stirtoni*	*L. protistopikos*
Width of M1 or M2	0.78-0.92	0.77-0.96	0.81-1.12	0.69-0.86
Anterior cingulum				
Lingual attachment	anteromedial	anterolingual	anterolingual	anterolabial
Lingual arm	equal	less distinct	equal	less distinct
Labial arm	equal	more distinct	equal	more distinct
Medial attachment	center of protoloph	center of protoloph	center of protoloph	near protocone
Protoloph				
Lingual arm	less distinct	less distinct	more distinct	more distinct
Labial arm	more distinct	more distinct	less distinct	submerged
Protoloph/metaloph	equal	protoloph wider	equal	equal

Table 7.–Continued.

Character	Taxon			
	L. korthi	*L. quartzi*	*L. stirtoni*	*L. protistopikos*
Metaloph				
Lingual arm	less distinct	more distinct	less distinct	more distinct
Labial arm	more distinct	less distinct	more distinct	less distinct
Paracone				
Anterior to protocone	no	no	no	yes
In line with protocone	yes	yes	yes	no
Metacone				
Anterior to hypocone	yes	no	yes	yes
In line with hypocone	no	yes	no	no
Ectoloph, posterior arm				
Attaches to metaloph	centrally	centrally	lingual of center	centrally

Table 7.–Continued.

Character	Taxon			
	L. korthi	*L. quartzi*	*L. stirtoni*	*L. protistopikos*
Posterior cingulum				
Labial attachment	posteromedial	posteromedial	posterolabial	posteromedial
Basins				
Lingual	equal	equal	AP short	AP short
Labial	equal	equal	AP long	AP long
Mesostyle	absent	absent	67%	absent
Labial cingulum	absent	absent	33%	absent

Table 8.–Measurements (mean, range, and n) of upper cheekteeth of *Leptodontomys*.

Tooth	Character	[a] *L. douglassi*	[b] *L. stirtoni*
P4	AP	0.80, 0.72-0.88, 2	0.94, 0.90-1.00, 4
	T	0.86, 0.76-0.95, 2	0.98, 0.93-1.02, 4
M1	AP	0.84, 1	0.93, 0.88-1.00, 8
	T	0.88, 1	1.07, 1.01-1.11, 8
M2	AP	0.78, 1	0.85, 0.81-0.87, 3
	T	0.89, 1	1.04, 1.02-1.06, 3
M3	AP	0.53, 1	0.85, 1
	T	0.64, 1	0.89, 1

[a] Data from Korth and Bailey (1992). [b] Data from Lindsay (1972).

Table 9.–Measurements (mean, range, and n) of upper cheekteeth of four species of *Leptodontomys* from Eastgate. [a]

Tooth	Character	*L. quartzi*	*L. korthi*	L. *stirtoni*	*L. protistopikos*
P4	AP	0.72, 0.64-0.82, 12	0.71, 0.62-0.80, 14	0.82, 0.74-0.89, 4	0.75, 0.73-0.77, 2
	T	0.76, 0.60-0.85, 12	0.74, 0.69-0.81, 14	0.89, 0.75-0.96, 4	0.76, 0.75-0.78, 2
M1/ 2	AP	0.77, 0.66-0.83, 13	0.76, 0.70-0.83, 17	0.92, 0.81-1.12, 5	0.78, 0.69-0.86, 12
	T	0.84, 0.77-0.96, 13	0.84, 0.78-0.92, 17	1.01, 0.83-1.23, 5	0.82, 0.75-0.89, 12
M3	AP	0.52, 1			0.42, 1
	T	0.73, 1			0.67, 1

[a] See text for measurements of *Leptodontomys* sp.

Table 10.–Measurements (mean, range, and n) of lower cheekteeth of *Leptodontomys*.

Tooth	Character	*L. douglassi*	L. *oregonensis*	L. *quartzi*
p4	AP	0.88, 0.82-0.93, 2	0.70, 1	0.60, 0.59-0.60, 2
	T	0.73, 0.71-0.75, 2	0.80, 1	0.62, 0.59-0.64, 2
m1	AP	0.99, 0.91-1.06, 5		0.76, 0.65-0.83, 5
	T	0.90, 0.84-0.96, 5		0.73, 0.66-0.79, 5
m2	AP	0.98, 0.94-1.00, 4		0.74, 0.68-0.81, 5
	T	0.91, 0.82-0.96, 4		0.75, 0.72-0.81, 5
m3	AP	0.90, 1		
	T	0.90, 1		

Table 10.–Continued.

Tooth	Character	*L. russelli*	*L. stirtoni*
p4	AP	0.60, 1	0.89, 0.85-0.92, 2
	T	0.65, 1	0.83, 0.80-0.86, 2
m1	AP	0.70, 1	0.95, 0.88-1.03, 9
	T	0.75, 1	0.95, 0.86-1.07, 9
m2	AP	0.75, 1	0.91, 0.80-0.97, 9
	T		0.75, 0.72-0.81, 5
m3	AP		0.81, 1
	T		0.81, 1

[a] Data from Korth and Bailey (1992), Lindsay (1972), Shotwell (1956, 1967), and Storer (1975).

Table 11.–Measurements (mean, range, and n) of *Leptodontomys* lower cheekteeth from Eastgate. [a]

Tooth	Character	*L. quartzi*	*L. schnelli*	*L. korthi*
p4	AP	0.67, 0.54-0.79, 24	0.77, 1	0.66, 0.59-0.76, 19
	T	0.62, 0.51-0.76, 24	0.79, 1	0.64, 0.52-0.78, 19
m1/ 2	AP	0.80, 0.71-0.95, 39	0.81, 0.79-0.83, 2	0.78, 0.70-0.85, 28
	T	0.79, 0.68-0.93, 39	0.88, 0.86-0.89, 2	0.77, 0.69-0.84, 28
m3	AP	0.67, 0.62-0.75, 11		
	T	0.60, 0.54-0.80, 11		

[a] See text for measurements of *Leptodontomys* sp.

Table 12.–Character loadings on first four principal components based on characters of p4s. Numbers in bold indicate relatively high absolute values.

	Component			
Character	I	II	III	IV
1	0.042	0. 434	0.045	0.073
2	0.213	-0.227	0.165	0.190
3	-0.462	0.070	0.464	0.067
4	0.361	-0.042	0.284	-0.327
5	**0.793**	-0.057	-0.060	0.364
6	**-0.777**	0.224	0.027	-0.307
7	-0.051	0.019	**-0.601**	0.247
8	0.251	-0.683	-0.180	-0.491
9	-0.364	**-0.723**	-0.297	0.231
10	-0.081	-0.208	**-0.601**	-0.381
11	-0.640	-0.444	0.359	-0.058
12	-0.442	0.653	-0.149	0.172
13	-0.634	-0.388	0.494	0.026
14	-0.236	0.355	-0.344	-0.232

Table 12.–Continued.

Character	Component I	II	III	IV
15	**-0.742**	0.361	-0.231	0.367
16	-0.319	0.168	-0.191	**-0.515**
17	-0.268	-0.044	-0.211	-0.094
18	-0.364	**-0.723**	-0.297	0.321
Eigenvalue	3.75	2.88	1.90	1.53
Percent explained	20.82	16.00	10.60	8.49

Table 13.–Specimen number (as occurs in phenogram; see Fig. 10), code name, and catalog number of specimens (p4s) from Eastgate.

Specimen number	Code name	Specimen number
1.	8o716	OMNH 54716
2.	1u247	UCMP 141780-247
3.	1u253	UCMP 141780-253
4.	1o722	OMNH 54722
5.	1o719	OMNH 54719
6.	1o727	OMNH 54727
7.	1u211	UCMP 141780-211
8.	1u246	UCMP 141780-246
9.	1o714	OMNH 54714
10.	1u257	UCMP 141780-257
11.	1u273	UCMP 141780-273
12.	1u276	UCMP 141780-276
13.	1o726	OMNH 54726
14.	1u279	UCMP 141780-279
15.	1o723	OMNH 54723
16.	1u265	UCMP 141780-265
17.	1o721	OMNH 54721
18.	1u168	UCMP 141780-168

Table 13.–Continued.

Specimen number	Code name	Specimen number
19.	1u62	UCMP 141780-62
20.	1u256	UCMP 141780-256
21.	1u270	UCMP 141780-270
22.	1u196	UCMP 141780-196
23.	1u878	UCMP 141878
24.	1u261	UCMP 141780-261
25.	1o718	OMNH 54718
26.	1u243	UCMP 141780-243
27.	1o859	OMNH 54859
28.	1u260	UCMP 141780-260
29.	1u04	UCMP 141780-04
30.	2o715	OMNH 54715
31.	2o720	OMNH 54720
32.	2u127	UCMP 141780-127
33.	2u241	UCMP 141780-241
34.	2u242	UCMP 141780-242
35.	2u244	UCMP 141780-244
36.	2u245	UCMP 141780-245
37.	2u248	UCMP 141780-248

Table 13.–Continued.

Specimen number	Code name	Specimen number
38.	2u250	UCMP 141780-250
39.	2u254	UCMP 141780-254
40.	2u262	UCMP 141780-262
41.	2u264	UCMP 141780-264
42.	2u266	UCMP 141780-266
43.	2u267	UCMP 141780-267
44.	2u268	UCMP 141780-268
45.	2u277	UCMP 141780-277
46.	2u278	UCMP 141780-278
47.	2u282	UCMP 141780-282
48.	2u107	UCMP 141780-107
49.	2o724	OMNH 54724
50.	2o725	OMNH 54725

Table 14.–Data matrix, showing states for 74 characters of 9 eomyid taxa (*Leptodontomys* and *Adjidaumo*) studied.

	Character			
	0000000001	1111111112	2222222223	3333333334
Taxon	1234567890	1234567890	1234567890	1234567890
L. douglassi	0201112100	1002001000	1221000101	0110021000
L. stirtoni	1100100111	1112111120	0112000011	0211000170
L. quartzi	1201101000	0012001110	0120111101	0000011011
L. russelli	??????????	??????????	??????????	????001002
L. korthi n. sp.	1110122011	0011101001	0121010100	0000110172
L. schnelli n. sp.	??????????	??????????	??????????	????001002
L. protistopikos n. sp.	0201112111	0012011120	2221100101	1200??????
L. oregonensis	??????????	??????????	??????????	????021000
A. maximus	0000000000	0000000?00	0000000000	0000000000

Table 14.–Continued.

Taxon	Characters			
	4444444445	5555555556	6666666667	7777
	1234567890	1234567890	1234567890	1234
L. douglassi	1000020000	0000000000	0000221200	1221
L. stirtoni	0100010110	1211001100	2001010000	????
L. quartzi	2?01110010	1210212101	0001120011	0111
L. russelli	2?2?021000	0212122022	?000122000	????
L. korthi n. sp.	2?11120011	1212112111	0100220000	1012
L. schnelli n. sp.	0100220111	0110100000	2011020000	????
L. protistopikos n. sp.	??????????	??????????	??????????	????

Table 14.–Continued.

Taxon	Characters			
	4444444445	5555555556	6666666667	7777
	1234567890	1234567890	1234567890	1234
L. oregonensis	0000020017	??????????	??????????	????
A. maximus	0000000000	0000000000	000000000?	????

? Indicates missing data.

FIGURE LEGEND

Fig. 1.–Mean length and width measurements of P4s of *Leptodontomys* species from literature and from specimens in Eastgate fauna for: 1) *L. stirtoni* (from Barstow); 2) *L. douglassi*; 3) *L. protistopikos* n. sp.; 4) *L. korthi* n. sp.; 5) *L. stirtoni* (from Eastgate); *L. schnelli* n. sp.; 6) *L. quartzi* (from Eastgate); and 7) *Leptodontomys* sp. (from Eastgate).

Fig. 2.–Mean length and width measurements of p4s of *Leptodontomys* species taken from literature and from specimens in Eastgate fauna for: 1) *L. quartzi*; 2) *L. russelli*; 3) *L. quartzi* (from Eastgate); 4) *L. korthi* n. sp.; 5) *L. schnelli* n. sp.; 6) *L. oregonensis*; 7) *L. douglassi*; and 8) *L. stirtoni*.

Fig. 3.–Mean length and width measurements of the M1 or M2s of *Leptodontomys* specimens from literature and from specimens in Eastgate fauna for: 1) *L. stirtoni* (M1); 2) *L. stirtoni* (M2); 3) *L. douglassi* (M1); 4) *L. douglassi* (M2); 5) *L. protistopikos* n. sp.; 6) *L. korthi* n. sp.; 7) *L. stirtoni* (M1 or M2 from Eastgate); and 8) *L. quartzi* (M1 or M2 from Eastgate).

Fig. 4.–Mean length and width measurements of the m1 and m2s of *Leptodontomys* species taken from literature and from specimens in Eastgate fauna for: 1) *L. quartzi*; 2) *L. russelli*; 3) *L. quartzi* (from Eastgate); 4) *L. korthi* n. sp.; 5) *L. schnelli* n. sp.; 6) *L. oregonensis*; 7) *L. douglassi*; 8) *L. stirtoni*; 9) *L. douglassi* (m2); 10) *L. stirtoni* (m1); and 11) *L. stirtoni* (m2).

Fig. 5.–Projections of specimens onto the first and second principal components based on characters of the p4 of *Leptodontomys* from the Eastgate fauna. Open circles represent *L. quartzi* (from Eastgate), open squares *L. korthi*

n. sp., and solid-filled triangle *L. schnelli* n. sp. Numbers represent characters of p4s (see Tables 1 and 2).

Fig. 6.–Projections of specimens onto the first and third principal components based on characters of the p4 of *Leptodontomys* from the Eastgate fauna. Open circles represent *L. quartzi* (from Eastgate), open squares *L. korthi* n. sp., and solid-filled triangle *L. schnelli* n. sp. Numbers represent characters of p4s (see Tables 1 and 2).

Fig. 7.–Projections of specimens onto the first and fourth principal components based on characters of the p4 of *Leptodontomys* from the Eastgate fauna. Open circles represent *L. quartzi* (from Eastgate), open squares *L. korthi* n. sp., and solid-filled triangle *L. schnelli* n. sp.

Fig. 8.–Axis I and II of correspondence analysis for p4s of *Leptodontomys* from Eastgate fauna, evaluating character-specimen relationships. Open circles represent *L. quartzi* (from Eastgate), open squares *L. korthi* n. sp., (=species A) and solid-filled triangle *L. schnelli* n. sp. (=species B). Numbers represent characters of p4s (see Tables 1 and 2).

Fig. 9.–Axis I and III of correspondence analysis for p4s of *Leptodontomys* from Eastgate fauna, evaluating character-specimen relationships. Open circles represent *L. quartzi* (from Eastgate), open squares *L. korthi* n. sp., (=species A) and solid-filled triangle *L. schnelli* n. sp. (=species B). Numbers represent characters of p4s (see Tables 1 and 2).

Fig. 10.–Dendogram resulting from cluster analysis of 18 characters of p4s. Cluster analysis was performed using the distance matrix. Numbers at

terminal end of branches represent specimens (see Table 13).

Fig. 11.–Majority-rule consensus tree of 4 most-parsimonious trees generated from exhaustive search option of PAUP. Outgroup is *A. maximus*. Tree had 133 steps (consistency index = 0.767; retention index = 0.49).

Figure 1

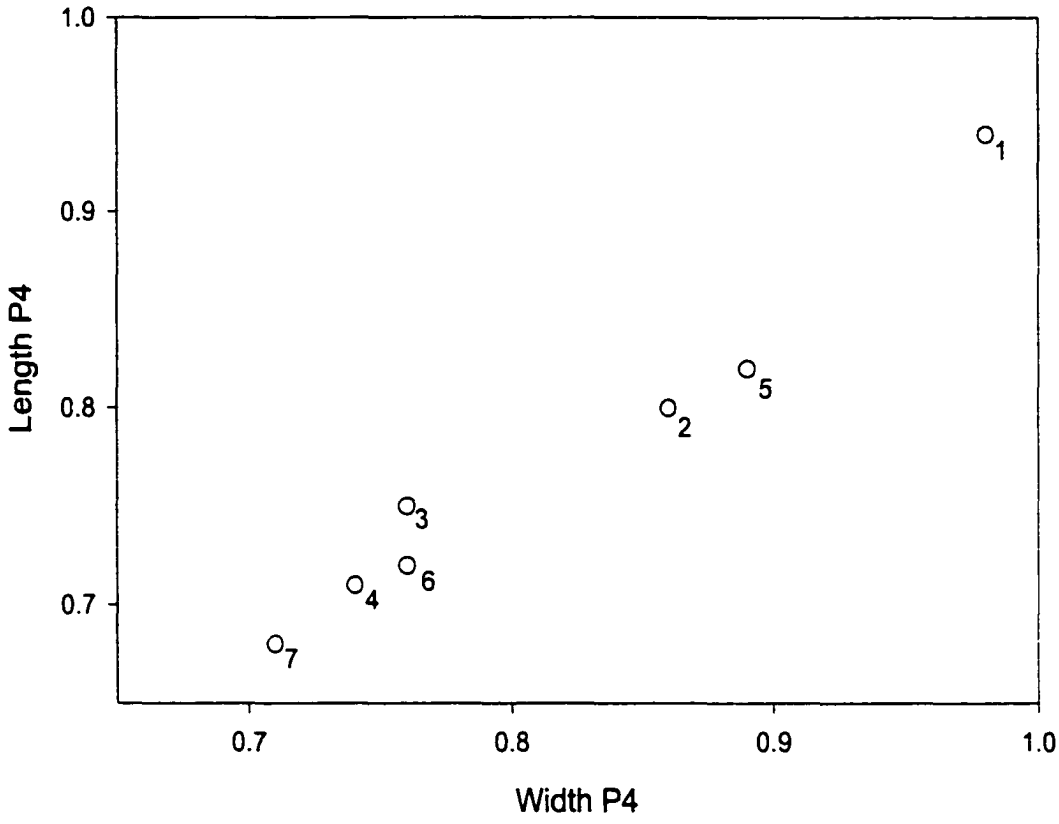


Figure 2

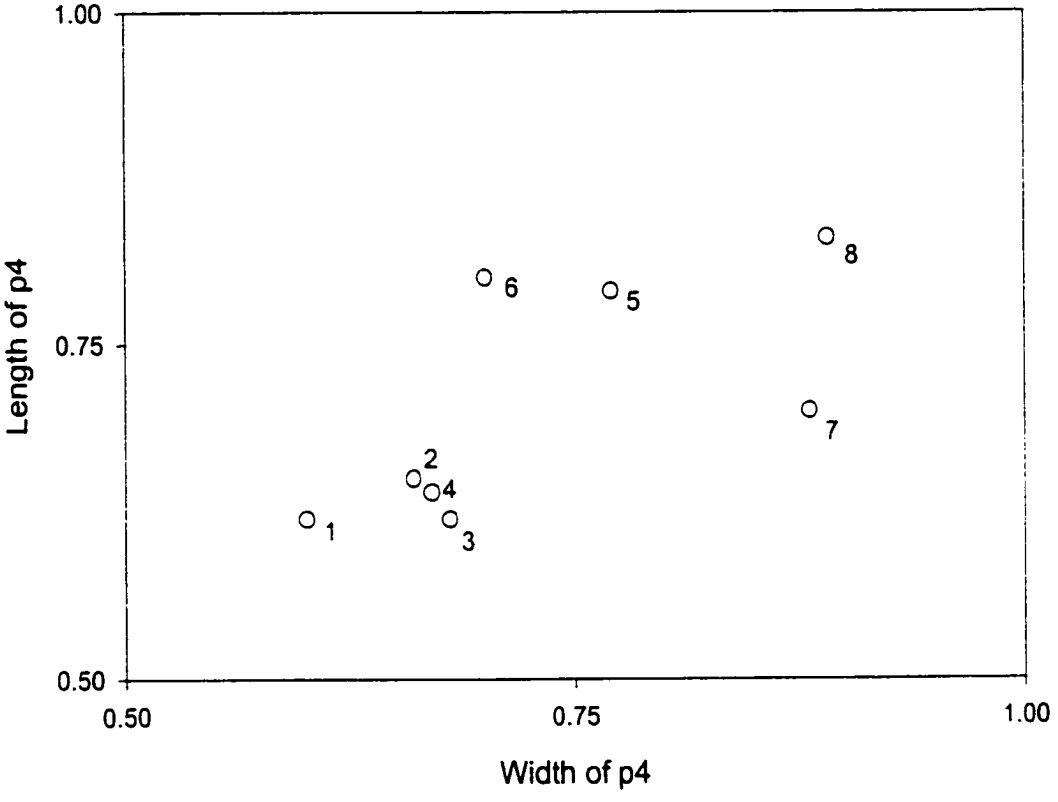
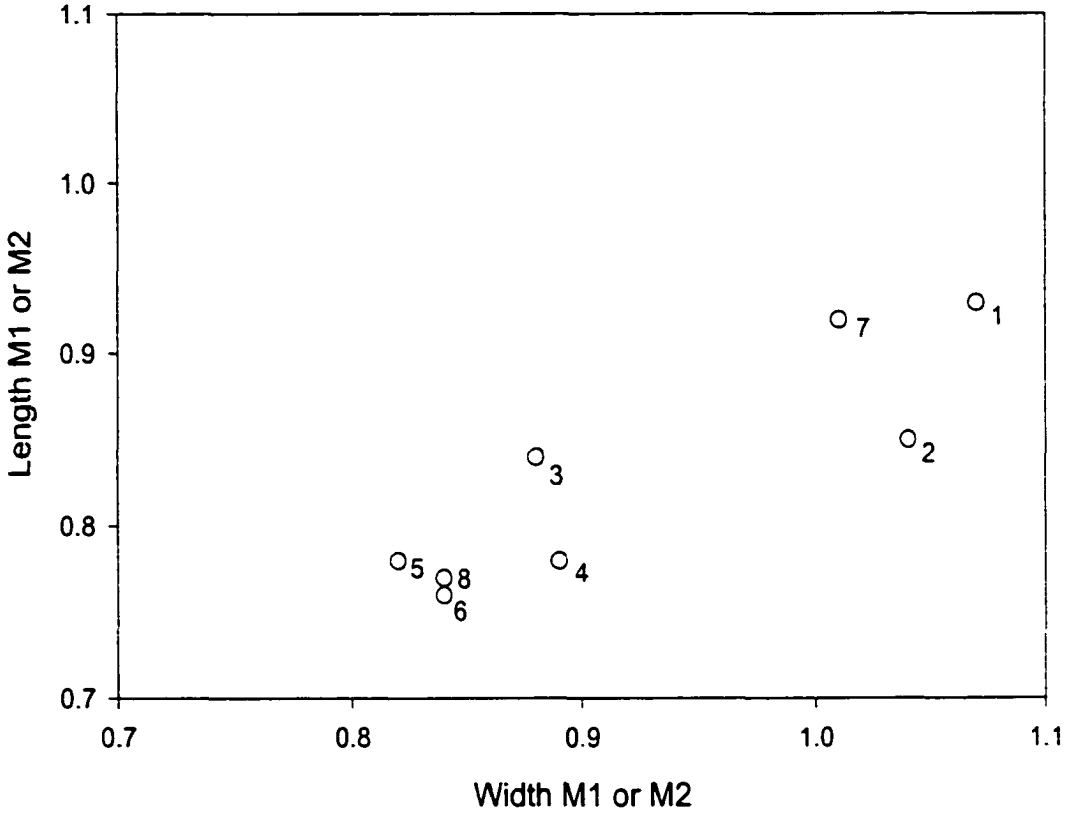


Figure 3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Width M1 or M2
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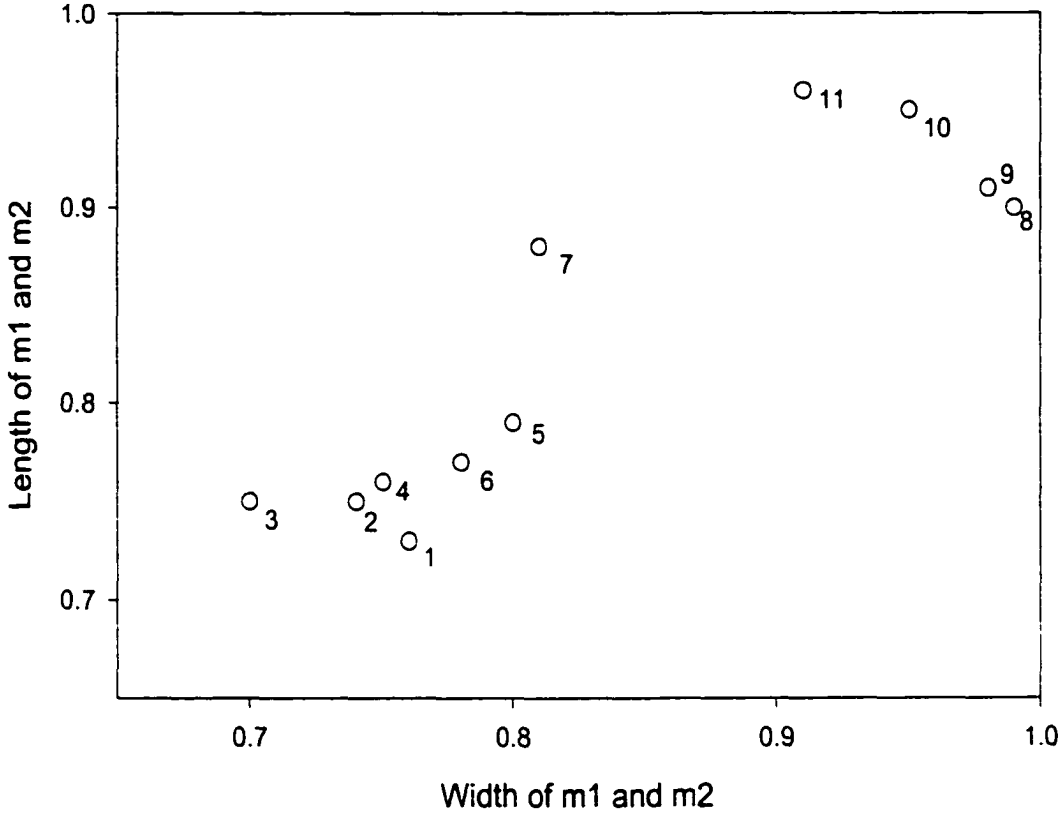
7
8

Figure 4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0.7
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3
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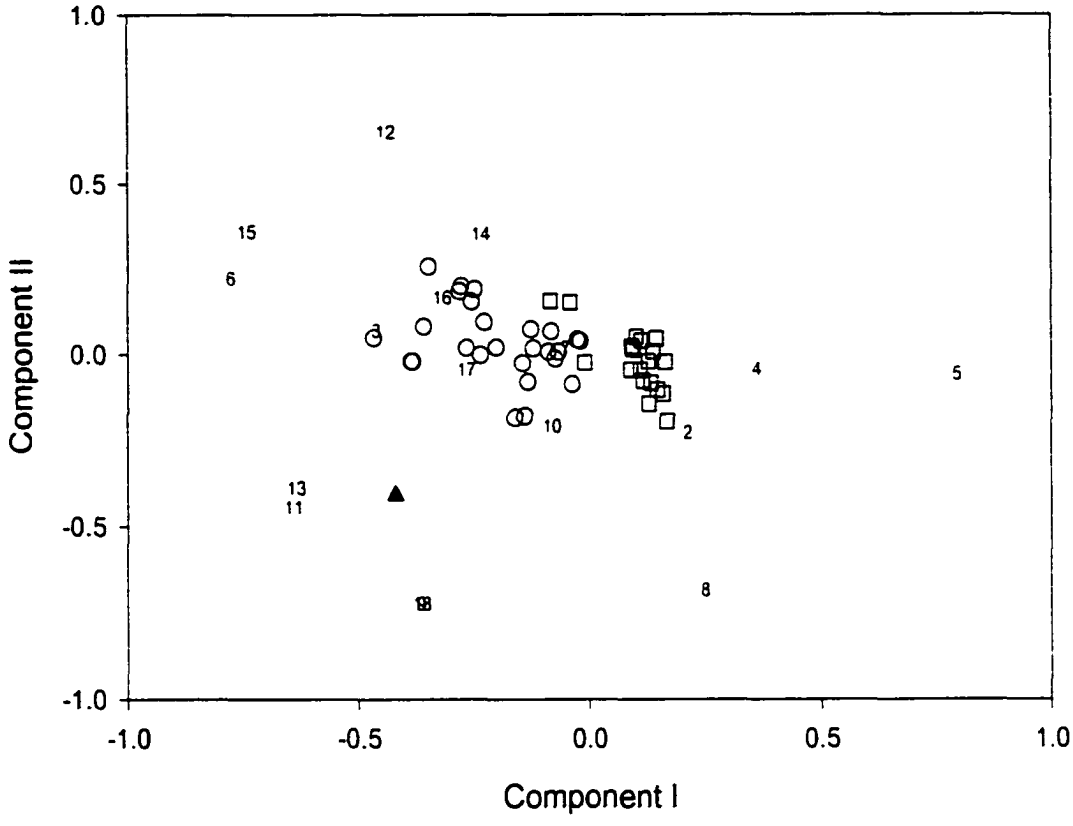
1

Figure 5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Component I
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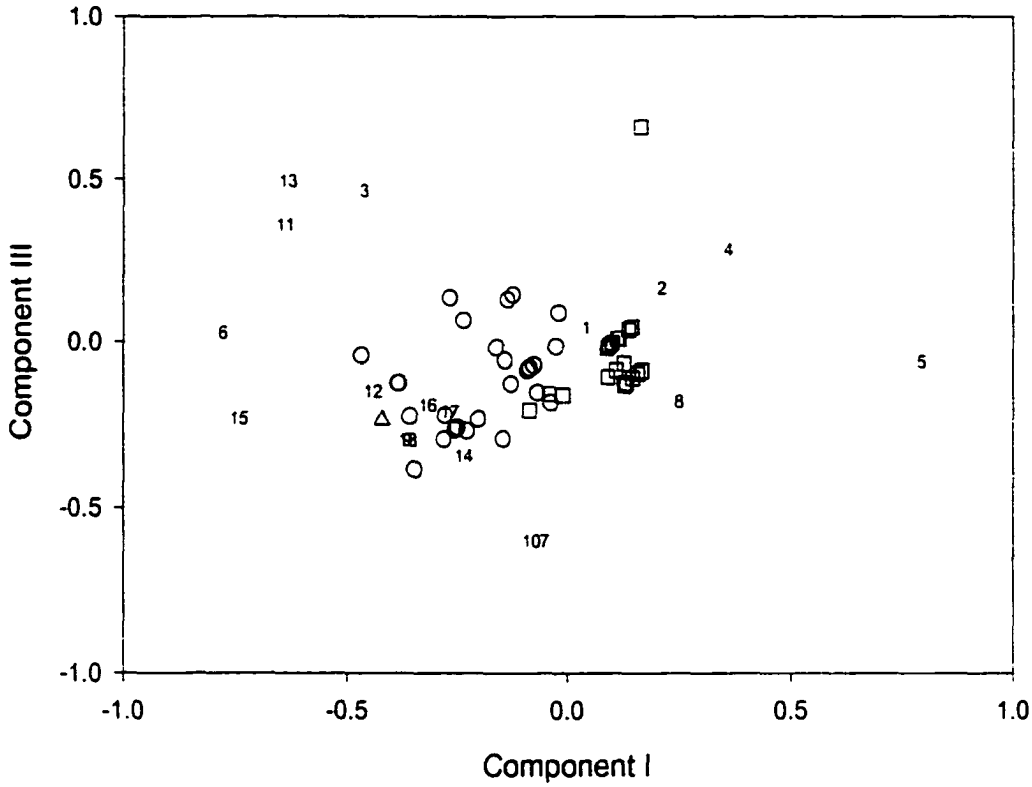
10
2
13
11
8

Figure 6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Component III
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Component I
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2
6
1
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12
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8
15
14
107

Figure 7

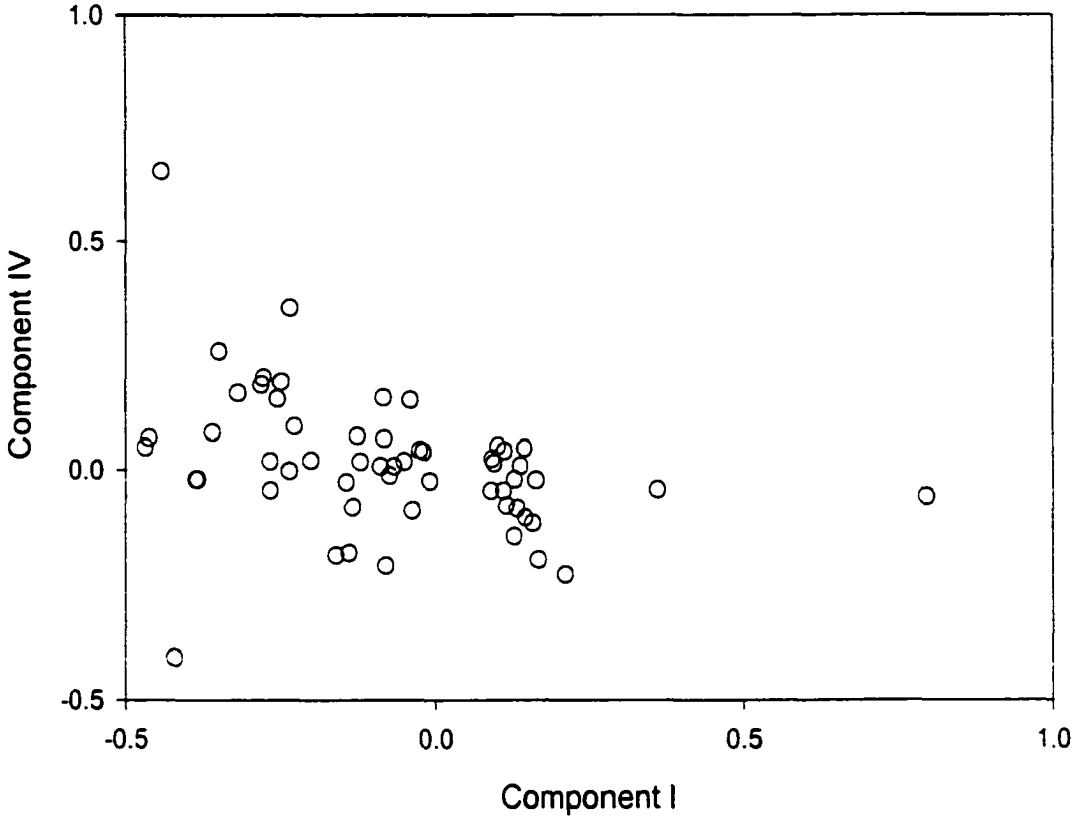


Figure 8

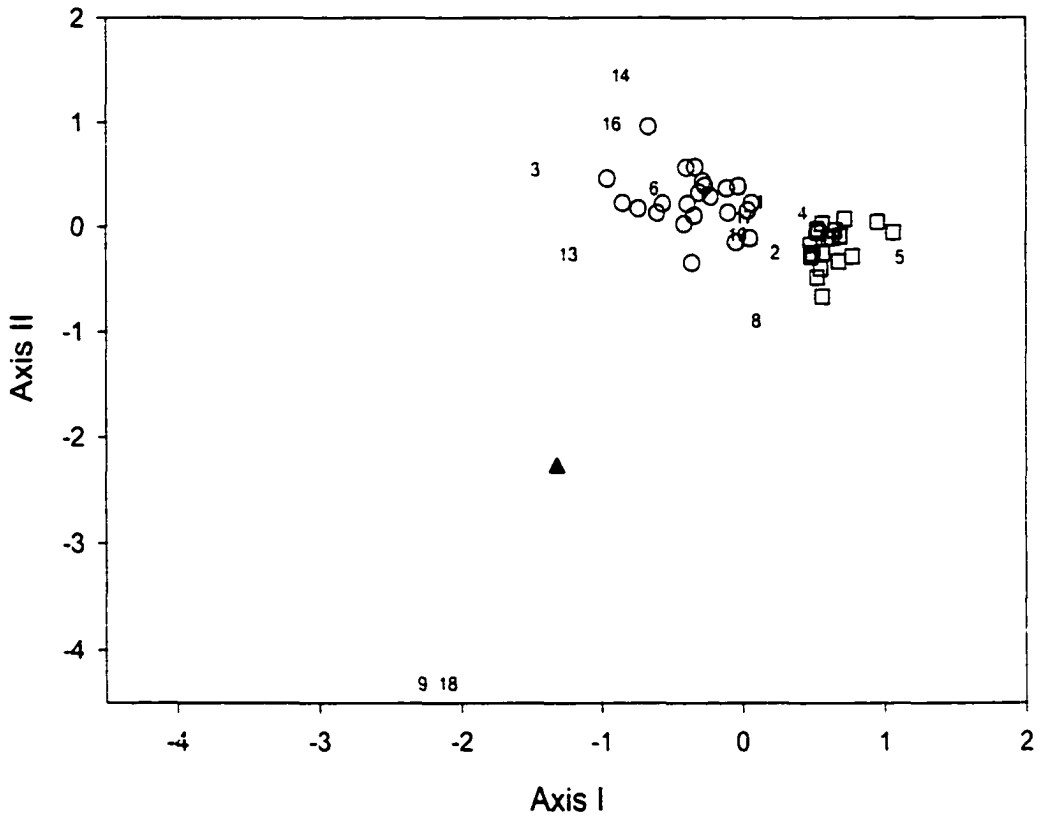


Figure 9

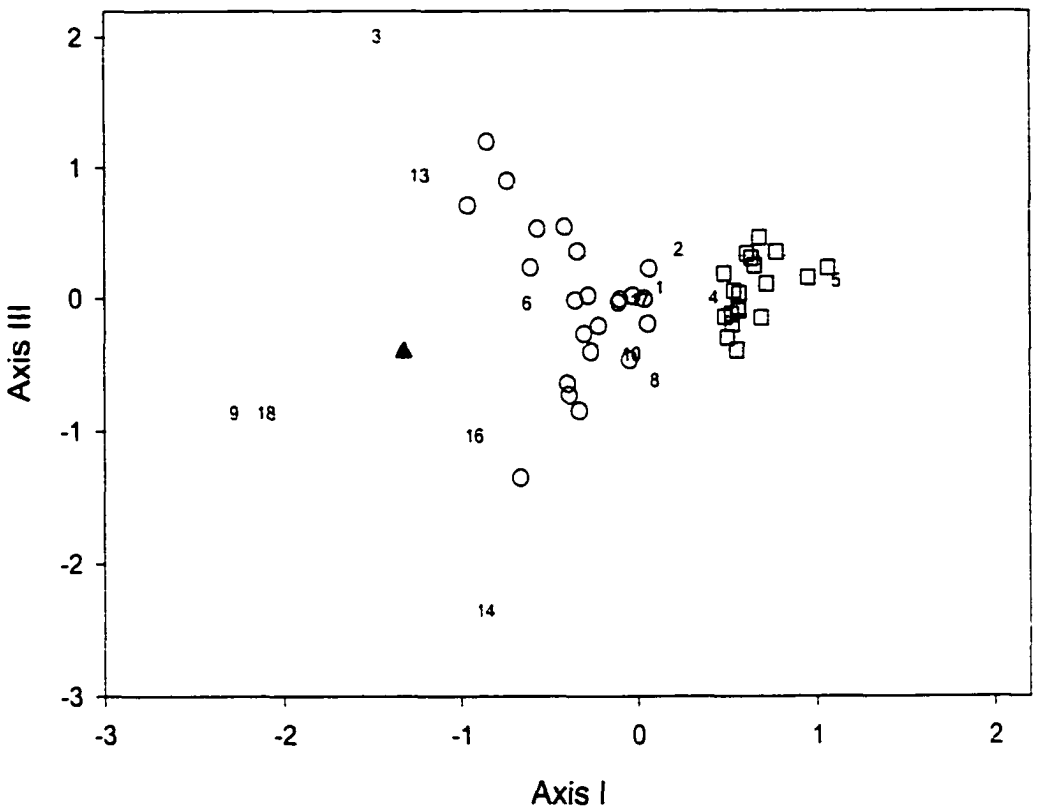
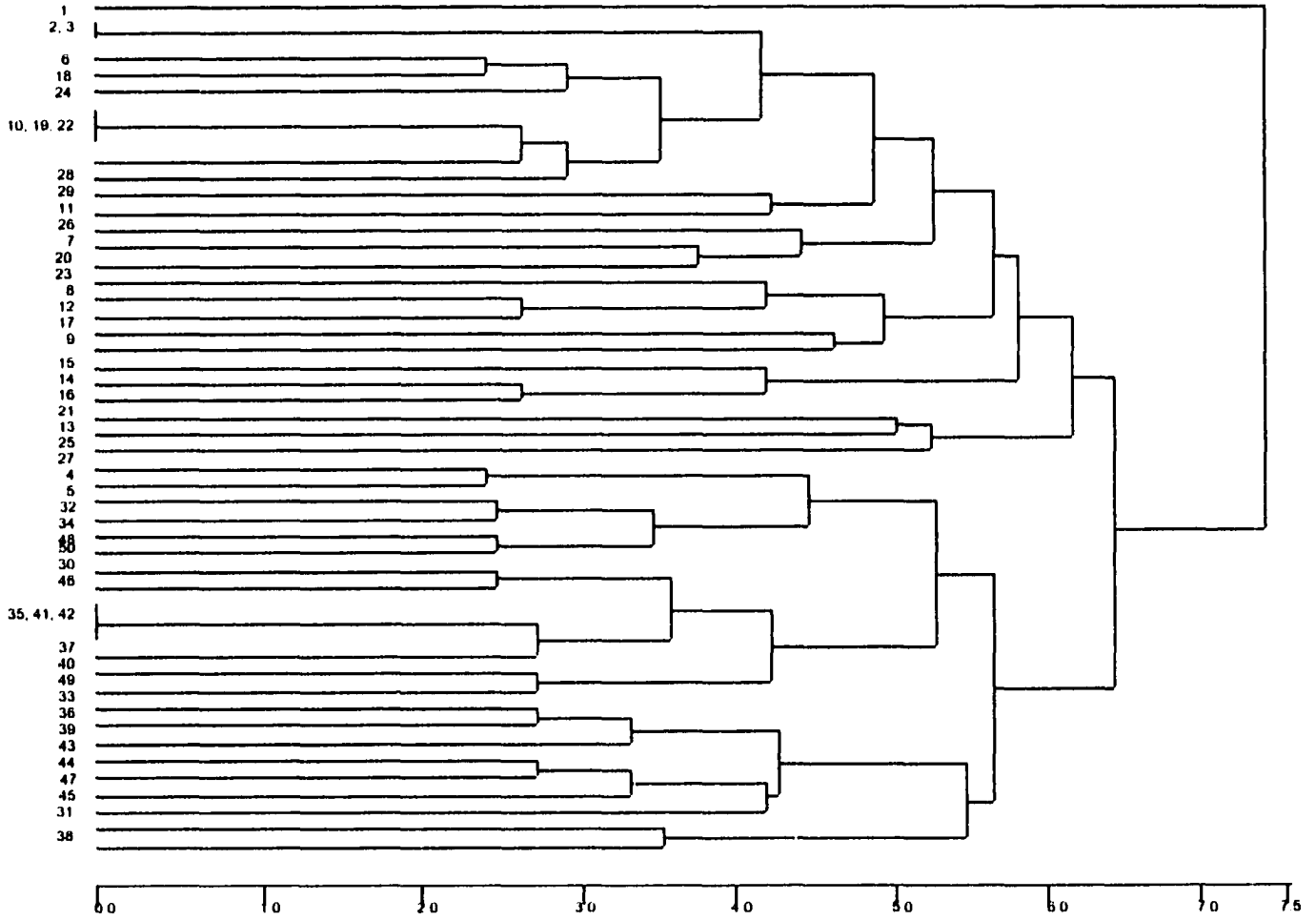


Figure 10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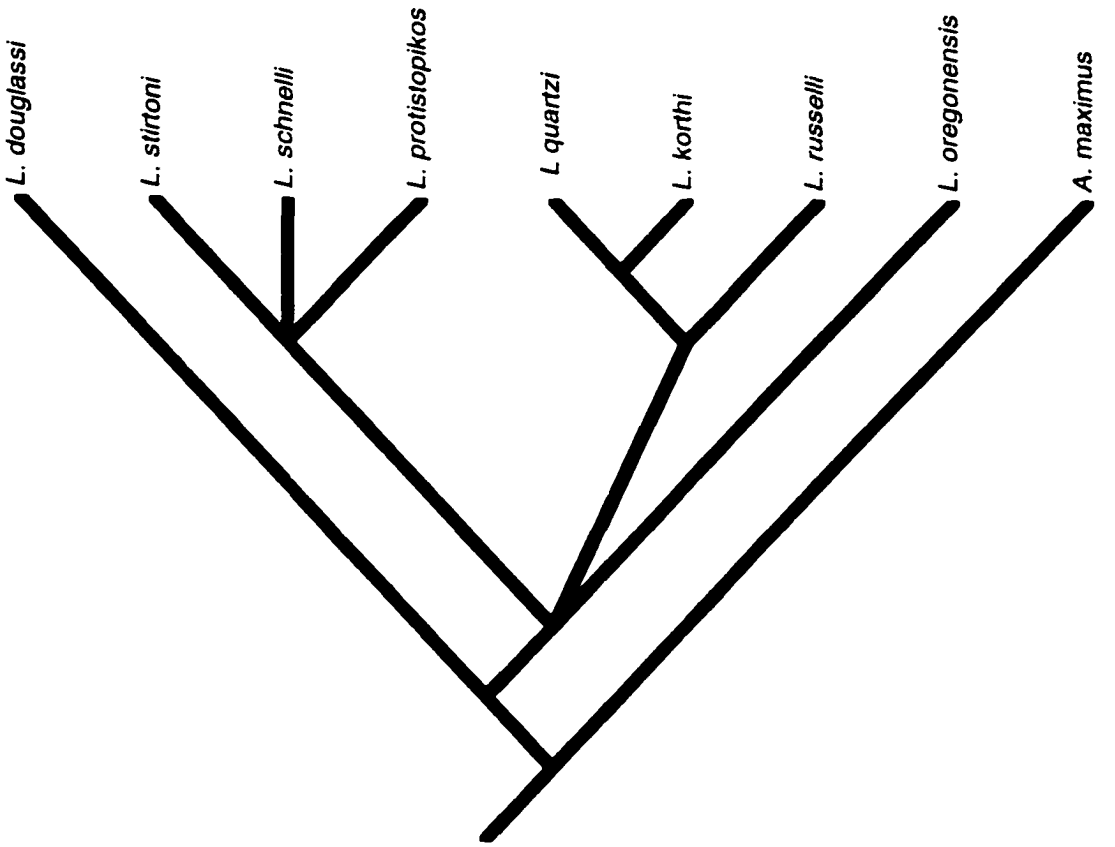
75

Figure 11


L. douglassi
L. stirtoni
L. schnelli
L. protistopikos
L quartzi
L. korthi
L. russelli
L. oregonensis
A. maximus

PLATES LEGEND

Plate 1.—Holotype of *Leptodontomys korthi* n. sp. (Eomyidae; Barstovian; Churchill County, Nevada): A) UCMP 141780-241 right dentary fragment with p4-m2 in occlusual view, B) in labial view, and C), in lingual view; upper and lower cheekteeth of *L. korthi* n. sp., D) OMNH 54699, right maxilla fragment with P4-M2 in occlusual view, E) in labial view, and F) in lingual view; G) UCMP 141780-282 left dentary fragment with i2-p4 in labial view, 6.5 X; and H) OMNH 54720 right m3 in occlusal view, 14.5 X. Unless otherwise indicated all are 13.9 X.

Plate 2.—Holotype of *Leptodontomys schnelli* n. sp. (Eomyidae; Barstovian; Churchill County, Nevada): A) OMNH 54716, right dentary fragment with p4-m2 in occlusal view, B) in labial view, and C) in lingual view, all at 14.3 X; Holotype of *L. protistopikos* n. sp. (Eomyidae; Barstovian; Churchill County, Nevada): D) OMNH 54695 left maxilla with P4–M3 in occlusal view, E) in labial view, and F) in lingual view, all at 14.3 X; G) OMNH 54695 right maxilla with P4–M2 in occlusal view, H) in labial view, all at 14.3 X, and I) in lingual view; and J) occlusal view of palate at 6.5 X.

Plate 3.—Upper and lower cheekteeth of *Leptodontomys quartzi* (Eomyidae; Barstovian; Churchill County, Nevada): A) OMNH 54696 right maxilla fragment with P4–M3 in occlusal view, B) in labial view, and C) in lingual view; D) OMNH 54714 left dentary fragment with p4–m3 in occlusal view, E) in labial view, and F) in lingual view; and G) UCMP 141780-246 left dentary fragment with p4–m2 in occlusal view, H) in labial view, and I) in lingual view, all are 12.7 X.

Plate 4.—Upper cheekteeth of *Leptodontomys stirtoni* (Eomyidae; Barstovian; Churchill County, Nevada): A) UCMP 141780-95 maxilla fragment with P4 in occlusal view, B) in labial view, and C) in lingual view, all are 12.8 X; D) UCMP 141780-142 left maxilla fragment with P4–M1 in occlusal view, E) in labial view, and F) in lingual view, all are 12.3 X; and *Leptodontomys* sp. (Eomyidae; Barstovian; Churchill County, Nevada): G) UCMP 141780-163 left P4 in occlusal view, H) in labial view, and I) in lingual view, all are 12.3 X.

PLATE 1

A

B

C

D

E

F

G

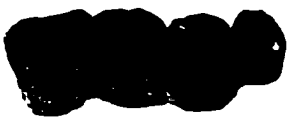
H

PLATE 2

A

B

C



D

E

F

G

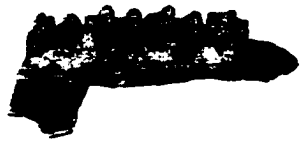
H

I

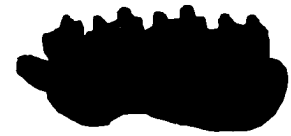
J

PLATE 3

A

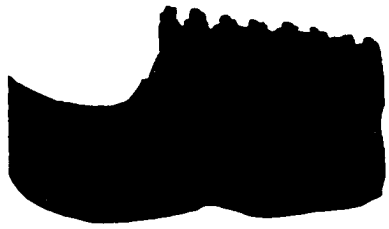


B



C

D

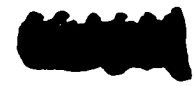


E

F

G

H



I

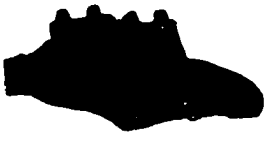
PLATE 4

A

B

C

D



E

F

G

H

I