SYSTEMATICS AND PALEOECOLOGY OF NORTHERN GREAT BASIN MYLAGAULIDAE (MAMMALIA: RODENTIA)

by

JONATHAN J. CALEDE

A THESIS

Presented to the Department of Geological Sciences
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Master of Science

June 2010

"Systematics and Paleoecology of Northern Great Basin Mylagaulidae (Mammalia: Rodentia)," a thesis prepared by Jonathan J. Calede in partial fulfillment of the requirements for the Master of Science degree in the Department of Geological Sciences. This thesis has been approved and accepted by:

Dr. Samantha S.B. Hopkins, Chair of the Examining Committee

5-28-10
Date

Committee in Charge:
Dr. Samantha S.B. Hopkins, Chair
Dr. Madonna Moss
Dr. Gregory J. Retallack

Accepted by:

Dean of the Graduate School

An Abstract of the Thesis of

Jonathan J. Calede for the degree of Master of Science

in the Department of Geological Sciences to be taken June 2010

Title: SYSTEMATICS AND PALEOECOLOGY OF NORTHERN GREAT BASIN MYLAGAULIDAE (MAMMALIA: RODENTIA)

Approved: [redacted]

Dr. Samantha S.B. Hopkins

Burrowing rodents are important ecosystem engineers in today's environments. The fossil record offers the opportunity to study patterns and processes in the evolution of the burrowing rodent guild through the Cenozoic. During the Miocene, this guild was very diverse, including numerous families ranging in ecology from semi-fossorial to subterranean. I use the emblematic family Mylagaulidae, a group of subterranean rodents, to test hypotheses of abiotic and biotic controls on mammalian evolution with the goal of better understanding turnover in the composition of the fossorial rodent guild in the Miocene of the Great Basin. I investigate the relative contributions of climate and biotic interactions to the purported intraguild competition between mylagaulids and geomyids with an emphasis on differences and similarities in patterns of occurrence and diet. Patterns of site occupancy and microwear suggest the importance of habitat changes in driving changes in guild composition among burrowers.

CURRICULUM VITAE

NAME OF AUTHOR: Jonathan J. Calede

[redacted]

[redacted]

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
Université Lyon I Claude Bernard, Villeurbanne, France

DEGREES AWARDED:

Master of Science, Geological Sciences, 2010, University of Oregon
Licence de Sciences de la Terre et de l'Environnement mention Geosciences fondamentales, 2008, Université Lyon I Claude Bernard, Villeurbanne

AREAS OF SPECIAL INTEREST:

Small Mammal Paleoecology
Evolution of Fossoriality
Drivers of Mammalian Evolution
Mammalian Community Structure

PROFESSIONAL EXPERIENCE:

Teaching and Research Assistant, Department of Geological Sciences, University of Oregon, Eugene, 2008-2010

Curatorial Assistant, Museum of Natural and Cultural History, University of Oregon, Eugene, 2009

GRANTS, AWARDS AND HONORS:

Weiser Scholarship, University of Oregon, Department of Geological Sciences, 2010

Ewart Baldwin Fellowship, University of Oregon, Department of Geological Sciences, 2009

Kenneth E. and Annie Caster Student Research Award, The Paleontological Society, 2009

Society of Vertebrate Paleontology Student Travel Grant, 2008

James Stovall Fellowship Award, University of Oregon, Department of Geological Sciences, 2008

National Society of Collegiate Scholars, since 2008

Dean's List Fall 2007, Winter 2008, University of Oregon, College of Arts and Sciences.

Full scholarship from Exchange Program to study abroad at the University of Oregon, 2007 - 2008

PUBLICATIONS:

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ACKNOWLEDGMENTS

I would like to thank my advisor Samantha Hopkins and Edward Davis for their endless support and advice since 2007. They introduced me to vertebrate paleontology and helped me develop this project with patience and encouragements. Their guidance has been invaluable and I am very grateful for it. I would also like to thank the other members of my committee. Greg Retallack is an amazing source of experience, ideas, and hypotheses to be tested. Madonna Moss kindly agreed to be part of my committee and brought a different perspective to paleoecological data. This research benefited from the critical comments of Stephen Frost, Rebecca Dorsey, Katharine Cashman, and Ted Fremd among many. I would also like to thank all the people who have provided technical help or insights into the methods used in this research: John Donovan and Paula Matano at the Scanning Electron Microscopy Facility, Emily Henderson Guthrie, and many people in the microwear community. This research would not have been possible without access to collections. Thank you to Edward Davis and Madonna Moss (UO), Jeff Bradley and Ron Eng (UWBM), Pat Holroyd (UCMP), Vanessa Rhue and Sam McLeod (LACM), Chris Schierup and Ted Fremd (JODA) for loans and access to specimens used in this project. Thank you to Qusheng Jin for suggesting early on I pursue my studies at the University of Oregon. Thank you to everyone involved in the Université Claude Bernard Lyon I exchange program with the University of Oregon which started this great experience.

This research was funded from the Paleontological Society Kenneth E. and Annie Caster Student Research Award and the University of Oregon Department of Geological Sciences Ewart Baldwin Award. Support from the department and my advisor through research fellowships and the Weiser Scholarship were critical. The Museum of Natural and Cultural History provided an additional source of employment that granted me the invaluable experience of working with collections. I thank the former and current members of the Hopkins Lab for their help and support throughout this research. In particular, I'd like to thank John Orcutt whose experience, guidance, and friendship have been very important to me. Thank you also to Rowan and Graham Davis for their cheerful presence. Thank you also to everyone who helped collect data from the UOMNH collections: Allison Lent, Bobbette Chichmanian, and most importantly Winifred Kehl. Dr. James Orcutt and Barbara Orcutt, Marlena and John Cannon, and Taimi and Erkki Mäki-Kihniä provided welcome housing while visiting collections. Thank you very much to Davina Mendiburu, Chris Henderson, Kristen Bianchi, John and Marlena Cannon for their friendship along those two years. More than anyone else, I need to thank Winifred Kehl who helped collecting data, provided assistance while visiting collections, provided advice throughout this research, read over drafts of this Thesis and, moreover, endlessly helped and supported me. Since my early years my parents, my brother, and the rest of my family have encouraged my goals and provided me with the means and will to study hard. My family has taught me the importance of education and always supported my passion. Thank you very much to all of you for trusting me. Thank you for letting me go far from you and your love.

To my parents who have encouraged and supported my passion all those years,

TABLE OF CONTENTS

LIST OF FIGURES

Figure Page

Chapter II

Figure Page

Chapter III

Chapter IV

Figure Page

LIST OF TABLES

Table Page

Chapter II

Chapter III

Table Page

Chapter IV

Table Page

CHAPTER I

INTRODUCTION: MYLAGAULID PALEOECOLOGY AND DRIVERS OF MAMMALIAN EVOLUTION

In light of the recent climate change, concerns have risen over declining diversity and changing ecologies of animals. Ongoing global warming and the resulting changes in habitat have consequences for the ecology and diversity of mammals (e.g., Root et al. 2003, Parmesan and Yohe 2003, Pounds et al. 1999) and in particular for small mammals (e.g., Myers et al. 2009). Small mammals (mammals weighing less than 5 kilograms,) are important members of modern mammalian communities. Rodents, in particular, represent about 40% of modern mammalian faunas and their diverse ecologies often make them keystone species in communities (Brown and Heske 1990, Merritt 2010, Kay and Hoekstra 2008). Beavers are very famous for their logging and damming behavior (Jenkins and Busher 1979, Nolet et al. 1994, Hillman 1998) and burrowing animals greatly impact the soils, plants, and other animals in their environments (Reichman and Seabloom 2002, Reichman and Jarvis 1989, Cameron 2000). The effects of current shifts in habitats, extirpations, and global variations in temperature, precipitation, or seasonality on the diversity and ecology of these ecosystem engineers are critical to our understanding of future changes in mammalian communities. The fossil record is critical to understanding past patterns in mammalian evolution and extinctions and to avoiding future extinctions (Hadly 2003, Hadly and Barnosky 2009, Barnosky et al. 2003, Barnosky and Bell 2003). The study of the taxonomic succession of fossorial rodents in the late Cenozoic of North America has been the subject of much study (e.g., Samuels and Van Valkenburgh 2009, Hopkins 2007b) and has recently been stimulated by the interest in better understanding the family Mylagaulidae (Hopkins 2005, Hopkins 2008a, Korth 1999, Korth 2000). This family of subterranean rodents is abundant in the terrestrial Miocene of North Americaand is characterized by peculiar cranial and dental morphology. Those particularities have long made this group of rodents an emblematic member of Miocene faunas (e.g., Cope 1881a, Cope 1881b, Riggs 1899). The mylagaulid fossil record in the Great Basin is very rich and ranges from the Hemingfordian to the Hemphillian (Shotwell, 1958a, Korth 1999). Here I review the systematics of the Mylagaulidae in order to use them as a case study in understanding the relative contributions of climate and biotic interactions to the purported intraguild competition between mylagaulids and geomyids (Baskin 1980). Indeed, while several authors (Baskin 1980; Hopkins 2005, 2007; Samuels and Van Valkenburgh 2009) have suggested various processes may drive the changes in diversity of mylagaulids and other fossorial rodent groups, none has formally investigated the competitive hypothesis of mylagaulids and geomyids. The revised systematics provides a framework for a paleoecological analysis of the changes in the fossorial rodent guild in the Miocene of the Great Basin dominated by the mylagaulids. In the third chapter of this Thesis, I investigate patterns of occurrence of mylagaulids, and their purported competitors, the geomyids, as well as summarize and build upon the paleoenvironmental data for southeastern Oregon and northwestern Nevada, geographical focus of the study. In the fourth chapter of this Thesis, I use microwear analysis to constrain the diet of fossil burrowing rodents to test the hypotheses that the distribution of rodents over the landscape might be a result of the dietary needs of mylagaulids and geomyids.

The integration of microwear analysis and faunal analysis in studying the mylagaulid fauna from the northern Great Basin may provide clues in the patterns of burrowing mammal evolution and the processes that drive them. The focus of this thesis is on the evolutionary ecology of the Mylagaulidae and, in particular, their use of the landscape in relation to other members of the community, global climate changes, and environmental variations, as well as their diet through time, space, and across taxa. The insight gained from such study can offer a snapshot of the future of the burrowing rodent guild;

CHAPTER II

INTRASPECIFIC VERSUS INTERSPECIFIC VARIATION IN MIOCENE GREAT BASIN MYLAGAULIDS: IMPLICATIONS FOR SYSTEMATICS AND EVOLUTIONARY HISTORY

INTRODUCTION

The family Mylagaulidae is an extinct clade of North American burrowing rodents whose peculiar tooth morphology has made it an iconic member of Miocene faunas. It includes a wide variety of species of large fossorial animals, including the unusual horned burrower *Ceratogaulus* (Matthew, 1902). Since Cope (1878) named the first two species within the genus *Mylagaulus*, numerous discoveries have added to our understanding of the diversity of the mylagaulid family (e.g., Douglass 1903; Matthew 1902; Gidley 1907; Matthew 1924; Hibbard and Phillis 1945; Korth 1999, 2000). As a consequence, extensive taxonomic problems have arisen; only recently have revisions (i.e. Korth 2000, Hopkins 2008a) begun to address the systematics of the whole family. In particular, numerous specimens had been referred to the genus *Mylagaulus.* This genus was described on the basis of inadequate type specimens which prevents confident assignment to this taxon. Korth (2000) addressed this problem in Nebraska in his reexamination of the northern Great Plains mylagaulids. Korth (1999) made an effort to update the systematics of the Mylagaulidae in the Great Basin; however, he had at his disposal only a limited sample consisting primarily of previously described specimens. New unpublished material primarily from the Barstovian and Clarendonian North American Land Mammal Ages (NALMAs) enables systematic description of additional Great Basin mylagaulids beyond those revised by Korth.

Ontogeny is a critical issue in mylagaulid systematics because these rodents exhibit a hypsodont dentition worn down throughout an individual's life. As a consequence, there appears to be great variation in occlusal morphology of the teeth because of the different ages of individuals at time of death. Most of the fossil record of the Mylagaulidae consists of dental remains (Hopkins 2008a), and, as a result, teeth are critical to systematic and phylogenetic understanding of this family of rodents. In addition to wear-related variation within an individual's lifetime, the expected non-wear-related intraspecific variation in mylagaulids has been poorly documented, creating challenges in the effort to diagnose species.

Here we present a study of intra- and interspecific variations in the Mylagaulidae of the Great Basin. Shotwell (1958a) first summarized mylagaulid systematics in this region of the western United States. In his review, Shotwell interpreted most of the specimens as belonging to genera known from the Great Plains or left them taxonomically unassigned. Since then, the age control on the mylagaulid localities of the Great Basin has been greatly improved. Korth (1999) reexamined some of Shotwell's specimens and recognized two new species both from a new genus: *Hesperogaulus gazini* from the Barstovian and *H. wilsoni* from the Hemphillian NALMA of Oregon. We extended the geographic range of Korth's work to include localities from Oregon and Nevada, focusing primarily on the northern part of the Great Basin (Fig. 1). We consider mylagaulids from the late Hemingfordian (LHMF) to the early late Hemphillian (ELHP). A summary of the Formations and Faunas included in this study is provided in Table 1.

In addition, we also consider the odd assemblage of the Warm Springs Fauna (Dingus 1990). This fauna includes mylagaulid specimens surprisingly more derived than expected this early in the evolution of the Mylagaulidae. Woodburne and Robinson (1977) and Dingus (1990) have discussed this peculiar mammal fauna and diverge in their interpretation of its age, and its relationship to other units of the Basin. Indeed, Woodburne and Dingus (1977) interpreted this fauna as Late Hemingfordian. Tedford et al. (2004) prefer an early Hemingfordian interpretation (EHMF). Later work considering all members of this fauna will shed light on the exact affinities of the mammalian fauna from Warm Springs.

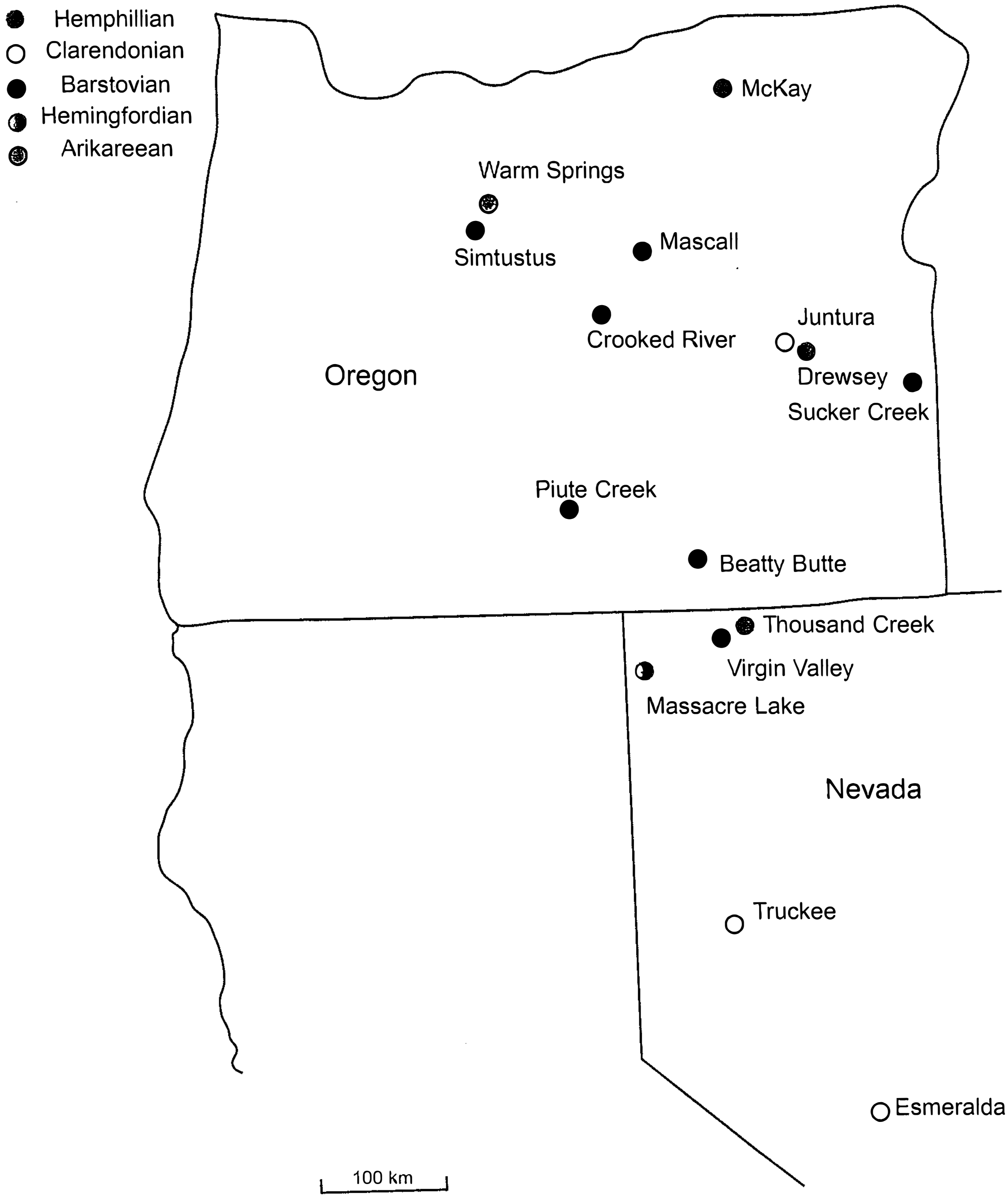


FIGURE 1: Map of the area considered in this study with the localities and North American Land Mammal Ages.

TABLE 1: Constraints on the ages of Great Basin formations and faunas. Data are from Tedford et al. 2004, Smith 1986, Carrasco et al. 2005. Ages in Ma. Faunas in parentheses.

Formation	(Massacre Lake)	Virgin Valley	(Beatty Buttes)	Sucker Creek	Mascall	Simtustus	Esmeralda	Truckee	Juntura	Thousand Creek	Drewsey	McKay	Chalk Butte
NALMA	LHMF	EBAR	EBAR	EBAR	EBAR	EBAR	MCLA	LCLA	LCLA	EEHP	LEHP	ELHP	ELHP
Max Age	16.60	15.90	15.90	15.90	15.77	15.90	11.7	10	10.0	8.00	7.50	6.70	6.70
Mean Age	16.55	15.54	15.35	15.35	15.29	15.70	11.35	9	9.7	7.75	7.30	5.90	6.30
Min Age	16.50	15.18	14.80	14.80	14.80	15.80	11.00	9.5	9.4	7.50	7.10	6.30	5.90
+/-	0.05	0.36	0.55	0.55	0.48	0.10	0.35	0.5	0.3	0.25	0.20	0.30	0.40

Nevertheless, the mylagaulid specimens from these localities are relevant to understanding late promylagaulines and mesogaulines and the evolution of early mylagaulines in the Great Basin. Understanding the mylagaulids from the Great Basin is critical to better comprehend the evolutionary history of the family as a whole. In addition, mylagaulids are fossorial rodents and as such act as ecosystem engineers; this study will thus facilitate future paleoecological studies and analyses of community structure. The rich mylagaulid fossil record of the Great Basin is typical of the family: cranial material is rare, dental remains are common, and there are few, sparse, isolated postcranial elements often without associated dental material. The dental morphology of mylagaulids is unusual because the tooth row is characterized by an enlarged fourth premolar that dominates the adult dentition. Juvenile specimens retain the first molar when the adult P4 first erupts, but as the P4 occlusal surface erodes, it becomes larger toward the root, progressively driving out the first and sometimes even the second molars in the toothrows of older adult individuals. Thus, the typical dental formula for a juvenile individual is 1/1, 0/0, 1/1, 3/3; that of adults is 1/1, 0/0, 1/1, 2/2. The premolars in particular are high-crowned, deeply rooted in the jaws, and are worn down throughout the life of the individual, apparently from an abrasive diet and possibly the exogenous grit associated with burrowing. The cusps of unworn teeth become blunt and wear away, leaving lakes of enamel (i.e. fossettes on the upper teeth, fossetids on lower ones) surrounded by exposed dentine on the occlusal surface of the tooth row. The changes in morphology of those lakes with wear have previously been discussed in a limited sample of *Umbogaulus monodon* (McGrew 1941) and in Mesogaulinae (Black and Wood 1956) but never between multiple species of derived mylagaulids. We offer new insights into ontogenetic and phylogenetic changes in occlusal morphology in Mylagaulinae, a subfamily of derived mylagaulids.

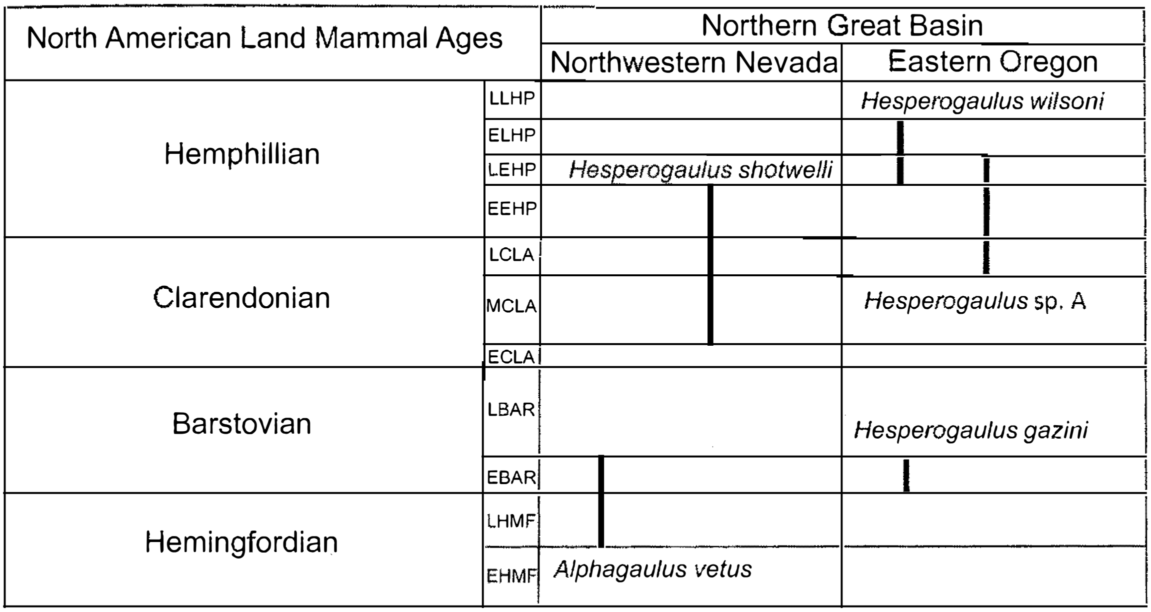
The rich fossil record of the Great Basin offers large enough sample sizes of isolated premolars to investigate changes in occlusal morphology within and between species, thus allowing us to revisit the species diversity of Mylagaulidae in the Miocene of the Great Basin. We describe a new species in the genus *Hesperogaulus* and a new occurrence of *Alphagaulus vetus* (Matthew 1924) in addition to the previously described *H. gazini*, and *H. wilsoni* (Korth 1999). We also discuss new rare and large mylagaulid specimens that exhibit complex occlusal morphologies.

Institutional abbreviations

AMNH	American Museum of Natural History, New York, NY
CM	Carnegie Museum, Pittsburgh, PA
F:AM	Frick Collection, American Museum of Natural History, New York, NY
FMNH	Field Museum, Chicago, IL
JODA	John Day Fossil Beds National Monument, Dayville, OR
LACM	Los Angeles County Museum, Los Angeles, CA
MCZ	Museum of Comparative Zoology, Harvard University, MA
UCMP	University of California Museum of Paleontology, Berkeley, CA
UOMNH	University of Oregon Museum of Natural and Cultural History Condon Fossil Collection, Eugene, OR.
YPM	Yale Peabody Museum, New Haven, CT

MATERIAL AND METHODS

The material described here consists of numerous specimens from Nevada and Oregon ranging in age from 18 to 6 Ma. They are compared with specimens from the published literature (Korth 1999, 2000), two juvenile (UWBM 59077 and UWBM 54683) and one adult (UWBM 32664) specimen of *Alphagaulus pristinus* (Calede and Hopkins unpubl. data), adult and juvenile specimens of *Aplodontia rufa* (UOMNH R-8568 and UOMNH R-8453, respectively) from the University of Oregon Museum of Natural and Cultural History collections. *A. rufa* was chosen because it is the closest living relative of mylagaulids in addition to exhibiting adaptations to burrowing and hypsodont teeth (Hopkins 2008a). A summary of the newly established species ranges are presented in Fig. 2.



North American Land Mammal Ages		Northern Great Basin	
		Northwestern Nevada	Eastern Oregon
Hemphillian	LLHP		*Hesperogaulus wilsoni*
	ELHP		
	LEHP	*Hesperogaulus shotwelli*	
	EEHP		
Clarendonian	LCLA		
	MCLA		*Hesperogaulus* sp. A
	ECLA		
Barstovian	LBAR		*Hesperogaulus gazini*
	EBAR		
Hemingfordian	LHMF		
	EHMF	*Alphagaulus vetus*	

FIGURE 2: Revised range of the mylagaulid species present in the Great Basin. Stratigraphy after Tedford et al. 2004. Abbreviations: EHMF, Early Hemingfordian; LHMF, Late Hemingfordian; EBAR, Early Barstovian; LBAR, Late Barstovian; ECLA, Early Clarendonian; MCLA, Middle Clarendonian; LCLA, Late Clarendonian; EEHP, Early early Hemphillian; LEHP, Late early Hemphillian; ELHP, Early Late Hemphillian; LLHP, Late late Hemphillian.

The taxonomic and phylogenetic framework of this study is provided by Hopkins (2008a), Calede and Hopkins (unpubl. data), and Korth (1999, 2000). We coded and added a newly described species of the genus *Hesperogaulus* to the revised character matrix of Calede and Hopkins (unpubl. data) and recoded *Alphagaulus vetus*, *H. gazini*, and *H. wilsoni*. All described mylagaulid species except *Mesogaulus ballensis* (Riggs 1899), which is known only from a specimen with teeth too worn to code most of the characters, are included as Operational Taxonomic Units (OTUs), in addition to the new material described here. The character matrix for this analysis is detailed in Appendix A. The character matrix was constructed in Mesquite 2.72 (Maddison and Maddison 2002). The phylogeny was analyzed in PAUP 4.0b 10 (Swofford 2003) using the semi-ordered character configuration of Hopkins (2008a). Searches were run using stepwise addition of taxa and maximum parsimony as the criterion for tree selection, over 1000 random addition replicates. *Meniscomys uhtoffi* and *Aplodontia rufa* were used as outgroups. The measurements mentioned in this paper are either drawn from the literature or were taken on the specimens using Mitutoyo Absolute Digimatic CD-6"C calipers. The nomenclature used follows Wahlert (1974) for skull terminology and cranial foramina. The terminology for dentition follows Shotwell (1958a) and Hopkins (2008a). It is worth noting that the parafossette of Korth (1999, 2000) is equivalent to the anterofossette of Shotwell (1958a). A detailed summary of the dental terminology is provided in Fig. 3. The occlusal surfaces of the teeth were digitized using a LEICA MZ 95 stereomicroscope. The variation in lakes across individuals and species were analyzed by focusing on the homologies of the fossettes and fossettids. I recognized and coded the lakes according to their affinity. Lakes that split with ontogeny are thus recognized as having a similar origin. Differences across species and within taxa can therefore be recognized and form the basis for the systematics presented in this paper.

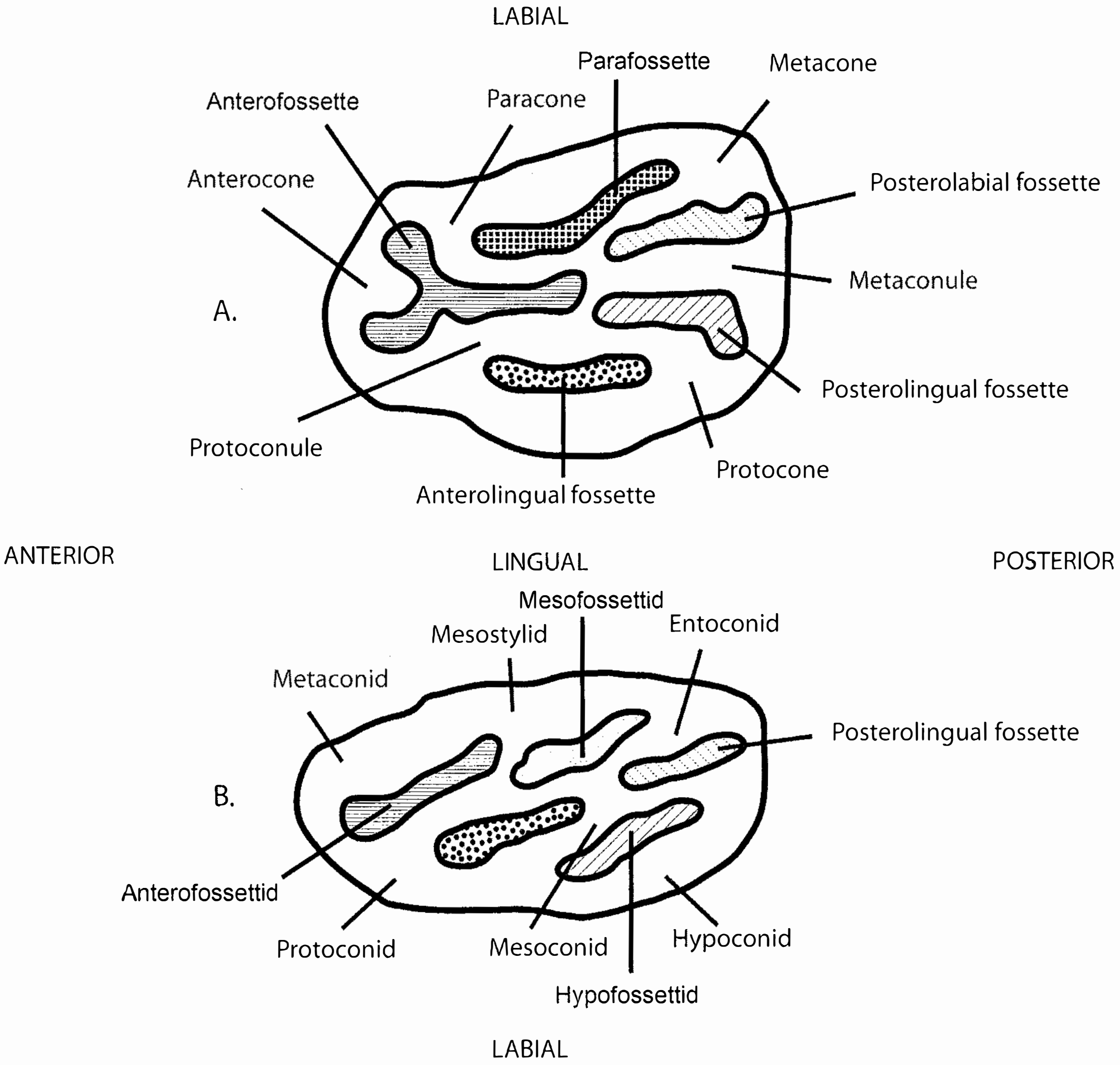


FIGURE 3: Summary of the dental morphology of mylagaulids (redrafted and modified from Hopkins 2008a). A. P4 of a mylagaulid (*Alphagaulus vetus*); B. p4 of a Mylagaulid (*Alphagaulus vetus*).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1785

RODENTIA Bowdich, 1821

APLODONTOIDEA Matthew, 1910

MYLAGAULIDAE Cope, 1881

MESOGAULINAE Korth 2000

MYLAGAULODON ANGULATUS (Sinclair, 1903)

Fig. 4

Synonymy: *Mylagaulodon angulatus* Sinclair, 1903
Mylagaulodon cf. *angulatus* MacDonald, 1963
Mylagaulodon cf. *angulatus* MacDonald, 1970
Mylagaulodon cf. *angulatus* McGrew, 1941
Mylagaulodon angulatus Shotwell, 1958a

Type Specimen: UCMP 1652, partial skull with right incisor, P3-P4, left incisor, P3 (Sinclair, 1903: fig.1) from John Day Formation, Oregon (UCMP 863, Black Bow Hill).

Referred Material: From Rosebud Beds by McGrew, 1941: FMNH P26266, isolated P4. From John Day Fm. (JDNM 150, Warm Springs): JODA 4666, isolated p4. From John Day Formation (V76124, Drees 2): UCMP 76887, partial dentary with p4-m3.

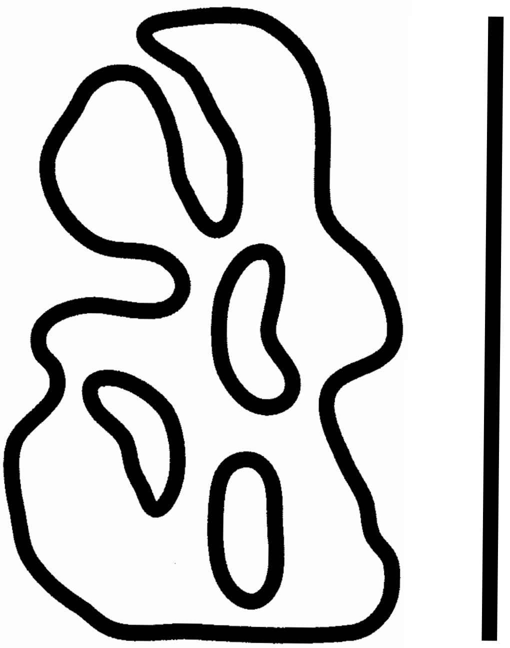


FIGURE 4: Occlusal morphology of the p4 of *Mylagaulodon angulatus* from the John Day Formation of Oregon. Scale bar equals 0.5 cm.

Distribution: Late early Arikareean of Rosebud Beds of South Dakota (McGrew 1941, MacDonald 1963, 1970) and Late early to Early late Arikareean of the John Day Fm., Oregon (Sinclair 1903, Shotwell 1958a, this paper).

Discussion: This taxon is known from rare, very incomplete material. The specimen from Warm Springs, an isolated p4, is identical in morphology to the specimen from Drees 2.

MYLAGAULINAE Cope, 1881

ALPHAGAULUS VETUS (Matthew, 1924)

Figs.5,6,7

Synonymy: *Mylagaulus pristinus* (in part) Kellogg, 1910

Mylagaulus vetus Matthew, 1924

Mesogaulus vetus Cook and Gregory, 1941

Alphagaulus vetus Korth, 2000

Mylagaulus sp. (in part) Downs 1956

Type Specimen: AMNH 18905, right mandible with incisor and p4, m2 (Sutton and Korth, 1995:fig. 3H) from Thompson Quarry, Sheep Creek Formation, Nebraska.

Referred Material: From type locality (Thompson Quarry, Sheep Creek Formation) by Korth (2000): AMNH 20504, 20507, 90734; F:AM 65515, 65517 – 65520, 65523, 65526, 65527. From Observation Quarry by Korth (2000): F:AM 65532, 65534 – 65536, 65538 – 65551, 65556, 65558, 65559, 65561. From Split Rock Local Fauna by Munthe (1988):

UCMP 121693, an almost complete skull and mandibles of an adult specimen (V69190, Third Bench); UCMP 121694, a partial adult skull (V77144, Split Rock Microsite); UCMP 121679, an isolated P4 (V69190, Third Bench); CM 14268 and CM 14269, isolated M1; UCMP 121680, UCMP 121685, isolated M2 (V69191, Second Bench); UCMP 121688, UCMP 121689, isolated M2 (V69192, First Bench); CM 13998, isolated dp4; UCMP 121686, isolated dp4 (V69191, Second Bench); UCMP 121690, isolated dp4 (V69192, First Bench); MCZ 7318, CM 14700, isolated p4; UCMP 121681, isolated p4 (V69190, Third Bench); MCZ 6224, isolated m1; UCMP 121692, isolated m1 (V77147, Split Rock Eagle's Nest); CM 14695, CM 15825, isolated m2; UCMP 121682, isolated m2 (V69190, Third Bench); UCMP 121687, isolated m2 (V69191, Second Bench); UCMP 121691, isolated m3 (V77144, Split Rock Microsite). From Virgin Valley Fm.: UCMP 11540, UCMP 11683, UCMP 11684, UCMP 11843, UCMP 40988, UCMP 130241, isolated p4 (UCMP 1090, Virgin Valley 9); UCMP 12580, isolated p4 (UCMP 1095, Virgin Valley 14); UCMP 130245, isolated p4 (V73056, Prospect 1); UCMP 152493, UCMP 152495, isolated p4 (V90052, Gooch Table NE 3); UCMP 130239, UCMP 130240, UCMP 130242, UCMP 40955, UCMP 40993, isolated P4 (UCMP 1090, Virgin Valley 9); UCMP 130243, isolated P4 (V73056, Prospect 3); UCMP 130244, UCMP 130246 – 130248, isolated P4 (V73056, Prospect 1); UCMP 11303, partial isolated P4 (UCMP 1095, Virgin Valley 14); UCMP 130251, partial isolated P4 (V73056, Prospect 1); UCMP 130249, partial isolated 4th premolars with associated partial distal humerus (V73056, Prospect 1); UCMP 130250, isolated partial right P4 with associated caudal vertebra, partial distal left humerus, and a partial edentulous maxilla (V73056, Prospect 1); UCMP 130252, isolated M3 (V73056, Prospect 1); UCMP 11686, isolated M3 (UCMP 1090, Virgin Valley 9). From Massacre Lake Local Fauna (RV7043, Massacre Lake 1): UCMP 315432, UCMP 315433, UCMP 315686, UCMP 316010, UCMP 316431, UCMP 316433 – 316435, isolated p4; UCMP 315431, UCMP 315685, UCMP 315988, UCMP 315989, UCMP 316007 – 316009, UCMP 316430, UCMP 316432, UCMP 319237, isolated P4; UCMP 318368, partial right mandible fragment with m2; UCMP 316072, partial right mandible with incisor fragment; UCMP 316436, partial right mandible with incisor and p4; UCMP 316438, partial right mandible with dp4, m1-m3; UCMP 318367, a partial left mandible with dp4, m1-m2; UCMP 315684, a partial skull with left P4, M2-M3 and right P4, M2; UCMP 316437, partial skull of a juvenile with left and right P4, M1-M2 and left M3. From Massacre Lake Local Fauna (V6161, Massacre Lake 2): UCMP 61709, a partial left mandible with p4, m2-m3; UCMP 61710, a partial skull of a juvenile with left and right P4, M1-M3. From Mascall Fm. (Crooked River): UOMNH F-16722, UOMNH F-16898, isolated p4. From Mascall Fm.: YPM 14311, isolated P4; YPM 14310, isolated p4.

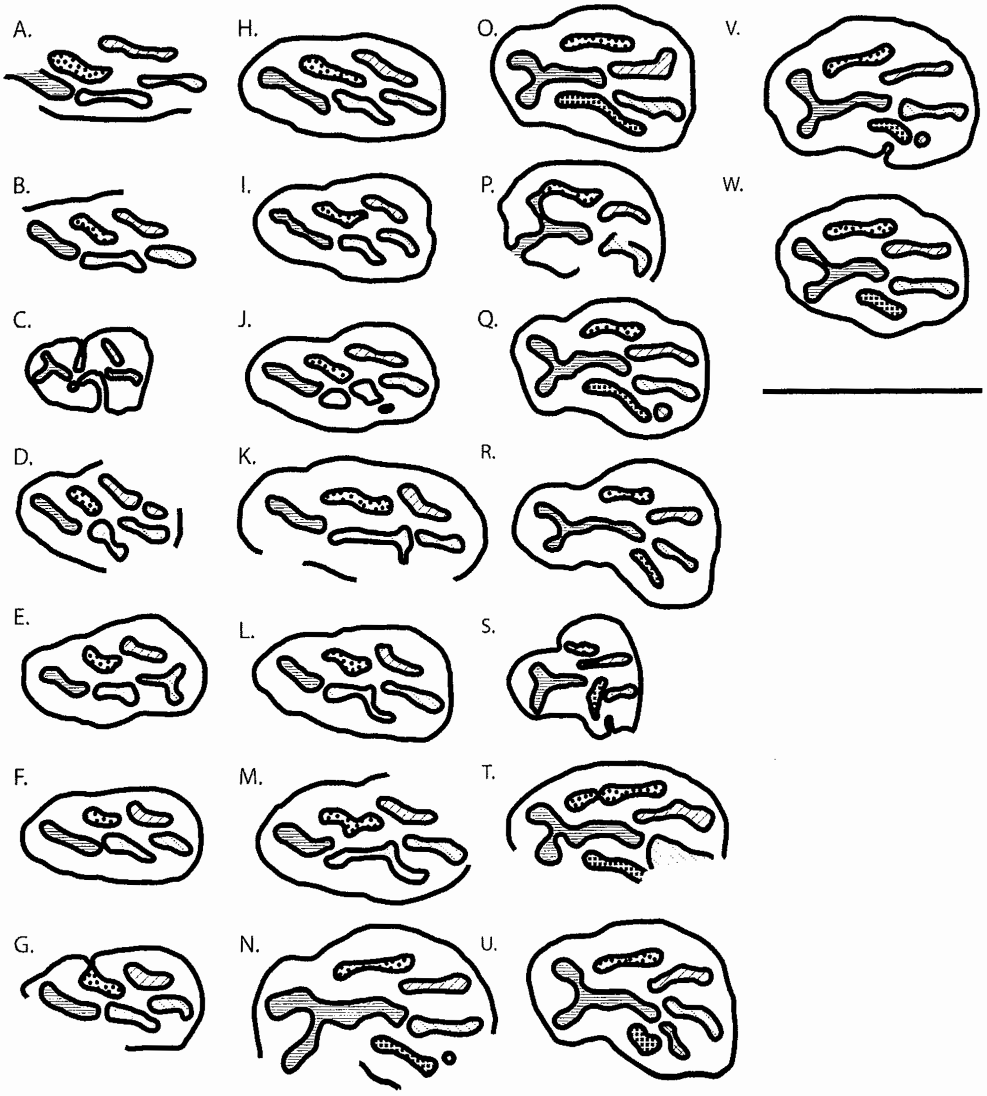


FIGURE 5: Occlusal morphology of the 4th premolars of *Alphagaulus vetus*. Scale bar equals 1 cm. A. UCMP 61709, left p4 (mirrored); B. UCMP 316433, left p4 (mirrored); C. UCMP 318367 left p4 (mirrored), D. UCMP 316434, left p4 (mirrored); E. UCMP 316431, left p4 (mirrored); F. UCMP 311843, left p4 (mirrored); G. UCMP 11540, left p4 (mirrored); H. UCMP 11684, left p4 (mirrored); I. UCMP 315432, left p4 (mirrored); J. UCMP 316435, right p4; K. 316010, right p4; L. UCMP 315686, right p4; M. UCMP 316430, right p4; N. UCMP 315431, left P4 (mirrored); O. UCMP 130244, left P4 (mirrored); P. UCMP 316008, left P4 (mirrored); Q. UCMP 152495, left P4 (mirrored); R. UCMP 316007, right P4; S. UCMP 316437, right P4; T. 130247, right P4; U. UCMP 319237, right P4; V. UCMP 15684, right P4; W. UCMP 130240, right P4.

Distribution: Late Hemingfordian of Sheep Creek Formation of Nebraska (Sutton and Korth 1995, Korth 2000), Split Rock Fauna of Wyoming (Munthe 1988), and Massacre Lake Fauna of Nevada (this paper). Early Barstovian of Sand Canyon Beds Formation (Observation Quarry) of Nebraska (Korth 2000), Virgin Valley Formation of Nevada, and Mascall Formation of Oregon (this paper).

Description of the postcranial elements: Postcranial elements associated to dental material confidently identifiable as *Alphagaulus vetus* are shown in Fig. 7. The single anterior caudal vertebra of *A. vetus* belongs to specimen UCMP 130250 from the Virgin Valley Formation. It is antero-posteriorly elongated, more so than in *A. rufa* (even though there is little body size difference between the two species and the two specimens are juveniles).The zygapophyses are small. The transverse processes are broadened posteriorly. The epiphyses of the vertebra are missing from this juvenile specimen. The neural spine is very small.

The partial distal left humerus of UCMP 130250 only includes the distalmost part of the bone where it is enlarged. Relative to length, the distal humerus of *A. vetus* is broader than that of *A. rufa* or even than that of *A. pristinus*. The supracondyloid foramen is preserved enough to be described. It is ovoid and quite unlike that of *A. rufa* which is more rounded. It is quite large unlike that of *P. laevis* (Fagan 1960) or that of *A. pristinus*. The medial epicondyle bends posteriorly, consistently with *P. laevis* or *A. pristinus* (Fagan 1960). The fossa posterior to the medial epicondyle is comparable in depth to that of *A. pristinus* and deeper than that of *A. rufa*. This seems to be a characteristic of Mylagaulidae because it also occurs in *P. laevis* (Fagan 1960). The capitulum is slightly more broadened than the trochlea, which is in turn sharper and more elongated anteroposteriorly. The articular surface of *A. vetus* is, in this aspect, larger than that of *A. pristinus*. The olecranon fossa is shallow, as in other mylagaulids (Fagan 1960). This fossa is also similar to *A. pristinus* in that it is narrower than the capitulum and trochlea together.

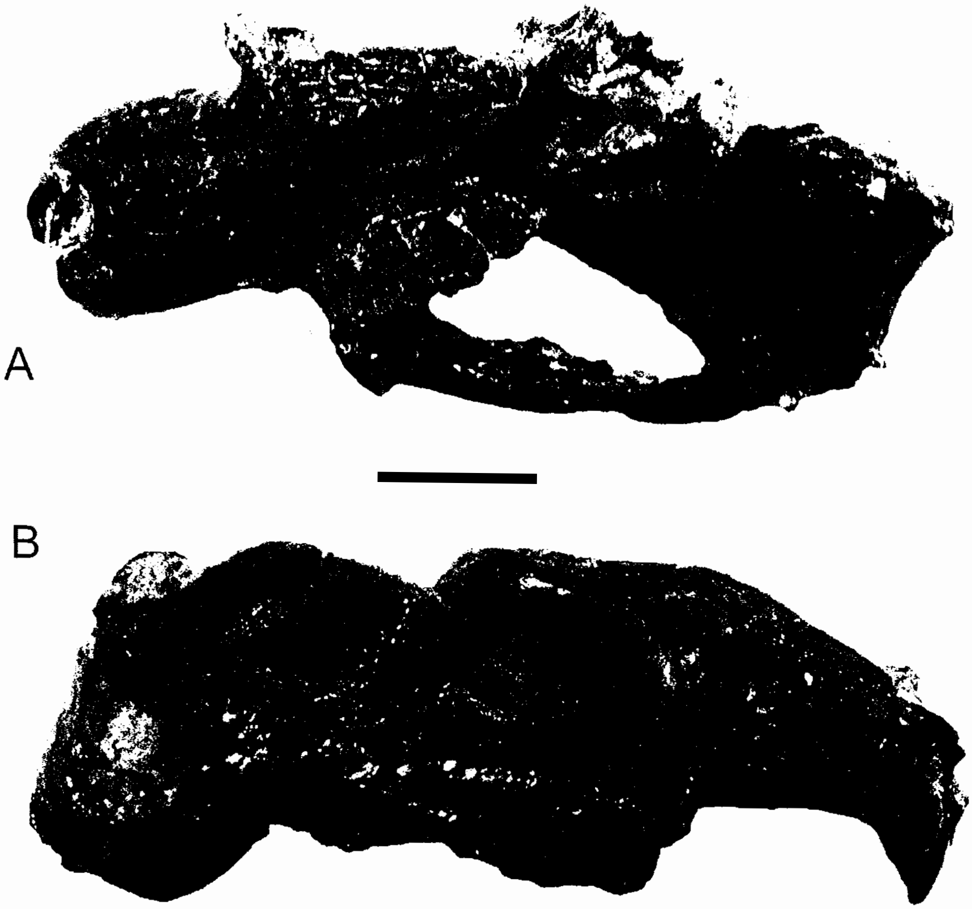


FIGURE 6: Cranial morphology of UCMP 316437, the skull of a juvenile *Alphagaulus vetus*. Scale bar equals 1 cm.

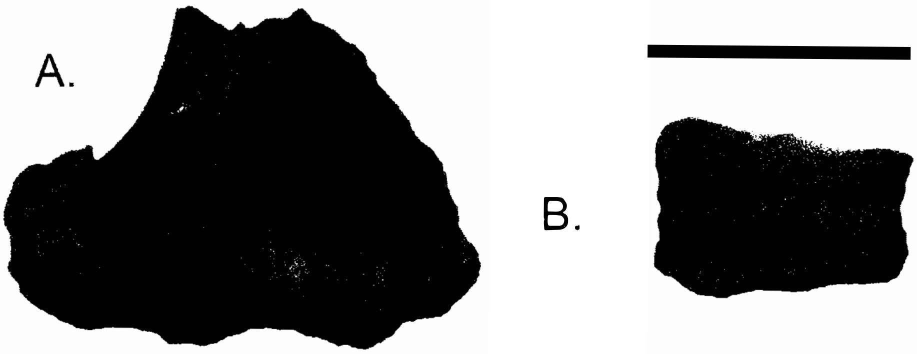


FIGURE 7: Postcranial morphology of UCMP 130250. A. partial distal humerus; B. caudal vertebra. Scale bar equals 1 cm.

Discussion: The genus *Alphagaulus* (Korth 2000) is a critical genus when trying to understand the evolutionary history of Mylagaulidae. This paraphyletic taxon at the base of the Mylagaulinae sheds light on the early history of the family Mylagaulidae. *Alphagaulus vetus* is particularly important, as it is represented by a more complete and geographically widespread fossil record than any other species of the genus *Alphagaulus* (Korth 2000). *A. vetus* is present in three different biogeographic regions (Nebraska: Northern Great Plains; Wyoming: Northern Rockies; Nevada: Columbia Plateau; Barnosky et al. 2005) and two NALMAs (Hemingfordian and Barstovian). Moreover, all stages of ontogeny are represented from juveniles to adults. The specimens from Crooked River (Mascall Formation) constitute the first record of *Alphagaulus vetus* from Oregon.

Fig. 5 shows the occlusal surface of the upper and lower fourth premolars of Nevadan specimens. There are five to six fossetids on the premolars, with the exception of

UCMP 16435 on which there are seven fossettids. Korth (2000) reported up to nine fossettids in Nebraskan specimens. The fossettids are not oriented antero-posteriorly but obliquely running from the posterolingual corner of the tooth to the anterolabial one. There are two fossettids in the anterolingual corner of the tooth (as noted by Korth 2000), a third one in the posterolabial corner, and two others running in between them. The fossetids that splitt include the posterolabial one (metafossettid, Shotwell 1958a) and the mesofossettid (Shotwell 1958a). Often, the mesofossettid and more occasionally the metafossettid and hypofossettid run more bucco-lingually in young individuals (e.g., UCMP 318367, UCMP 315686).The upper premolars exhibit a similar number of lakes (between four and six). Unlike the specimens from Nebraska that mostly show six or seven fossettes, most of the Nevadan specimens exhibit five lakes. As mentioned by Korth (2000) in the Great Plains specimens, the anterofossette is the largest fossette and remains branched very late in wear. The fossettes are more or less anteroposteriorly oriented. In late stages of wear, the anterofossette is the only lake to occupy the anterior lobe of the P4 and is still forked (e.g., UCMP 16007). In the DP4, the anterolingual fossette runs more bucco-lingually (e.g., UCMP 316437).

Comparisons of measurements between Nebraskan specimens and those of the Great Plains reported by Korth (2000) show very few differences (see Table 2). The width of the teeth is greater relative to the length in the Nevadan specimens than it is in those of the Great Plains or Rockies. The difference is within the published ranges for the species.

A juvenile specimen from the Massacre Lake Local Fauna (UCMP 316437, fig. 6) provides information on changes within *A. vetus* through ontogeny.

TABLE 2: Dental measurements of *Alphagaulus vetus* in the Great Plains, Rocky Mountains, and the Great Basin faunal provinces. Data for the Great Plains are from Korth (2000), Rockies data from Munthe (1988). No ranges were given by Munthe (1988). Only adults are included in the Virgin Valley and Thousand Creek samples.

	Measurement	Sample Size	Range	Mean	Std. Dev.
	Split Rock, WY (Late Hemingfordian)				
P4	Length	3	NA	7.4	0.4
	Width	3	NA	5.7	0.3
p4	Length	4	NA	8.2	1.1
	Width	4	NA	4.3	0.3
	Massacre lake, NV (Late Hemingfordian)				
P4	Length	7	5.59 – 8.6	7.86	0,7
	Width	7	5.1 – 7.22	6.025	0.9
p4	Length	4	6.42 – 8.85	7.53	0.85
	Width	4	3.55 – 4.8	4.26	0.4
	Sheep Creek, NE (Late Hemingfordian)				
P4	Length	4	7.5 – 8.0	7.8	0.2
	Width	5	5.0 – 5.6	5.2	0.2
p4	Length	12	7.3 – 9.3	8.1	0.7
	Width	12	4.1 – 5.2	4.6	0.3
	Observation Quarry, NE (Early Barstovian)				
P4	Length	15	7.3 – 9.0	8.0	0.5
	Width	15	4.7 – 6.1	4.7	0.4
p4	Length	31	6.9 – 9.3	8.4	0.6
	Width	31	3.3 – 5.6	4.4	0.5
	Virgin Valley, NV (Early Barstovian)				
P4	Length	6	7.21 – 8.45	7.57	0.51
	Width	6	4.77 – 5.6	5.23	0.3
p4	Length	5	6.45 – 9.48	7.87	1.3
	Width	5	3.83 – 5.05	4.39	0.5

This individual retains a juvenile dentition with the remaining deciduous P3 and P4, the retained M1, the adult M2, and the erupting M3. The skull is poorly sutured. As in *A. pristinus* and *H. gazini* (see discussion of *H. gazini* in this paper), there are a number of cranial features that change drastically between juveniles and adults. The zygomatic arch of UCMP 316437 is straight and gracile. It has been crushed taphonomically and thus brought closer to the midline of the skull. However, it could not have been as broad and as widely curving as it is in adult specimens prior to crushing. The infraorbital foramen is small, the partial occipital plate available for description is quite straight and doesn't slope posteroventrally as in adults (see Munthe 1988, fig. 8). The parasagittal and occipital crests, which differ importantly among early mylagaulines (Hopkins 2008a) are missing and therefore cannot be described.

HESPEROGAULUS GAZINI (Korth, 1999)

Figs. 8, 9

Synonymy: *Mylagaulus* cf. *laevis* Gazin 1932.

Mylagaulus cf. *laevis* Scharf 1935.

Mylagaulus cf. *laevis* Wallace 1946.

Mylagaulus sp. Downs (in part) 1956

Hesperogaulus gazini Korth 1999

Type Specimen: LACM (CIT) 68, skull with left P4, M2-M3 (Korth 1999: figs 2.1, 2.2) from Sucker Creek Formation of Oregon (Skull Springs).

Referred Material: From Skull Springs (Sucker Creek Formation) by Korth (1999): LACM (CIT) 69, LACM (CIT) 365 – 367, LACM 6018, LACM 4987, partial skulls or upper dentitions; LACM (CIT) 70, LACM (CIT) 368, LACM (CIT) 369, mandibles with dentition; LACM (CIT) 516 – 523, isolated p4, LACM (CIT) 524 – 531, isolated P4. From Beatty Buttes Fauna: UCMP 130331 (V84106, Dog-Leg Ridge SE), UCMP 130335 (V84100, Breakfast Square Butte 2), UOMNH F-17650 (UO 2418, Beatty Buttes), UOMNH F-21911 (UO 2418, Beatty Buttes), isolated P4; UOMNH F-17665 (UO 2418, Beatty Buttes), UOMNH F-21930 (UO 2418, Beatty Buttes), isolated p4, UOMNH F-17666 (UO 2418, Beatty Buttes), UCMP 188841 (V84103, Rattlesnake Butte (Pancake Butte) 2), partial isolated 4th premolars. From Mascall Fm.: JODA 3308, an almost complete skull with left partial P4 and complete M3 (V4827, Mascall 13); JODA 2330, isolated M2 (JDNM 4, Mascall Formation General). From Simtustus Fm.: JODA 8678, isolated P4 (Coburn Well).

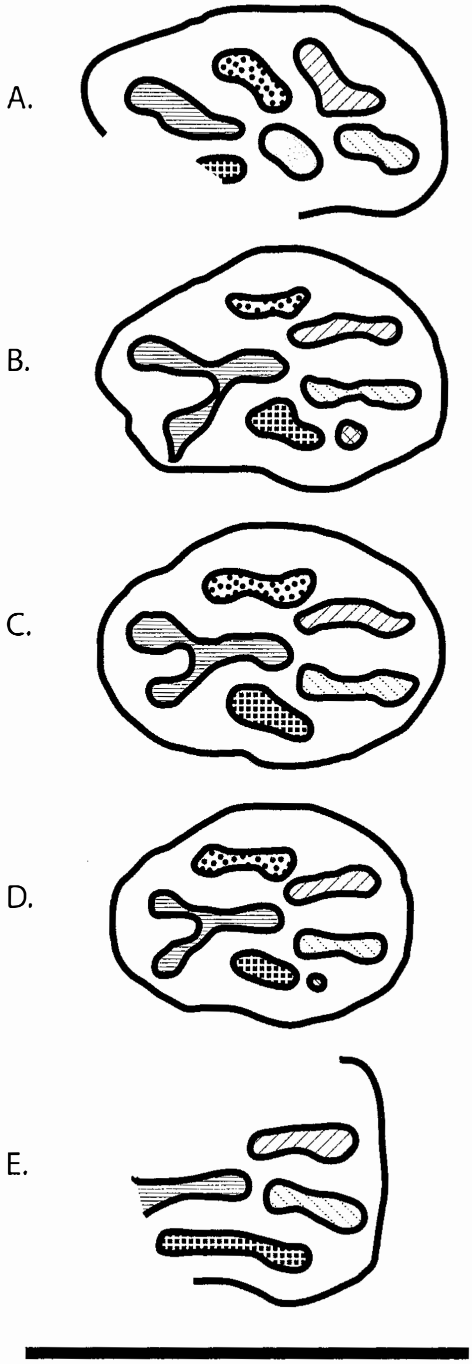


FIGURE 8: Occlusal morphology of the 4th premolars of *Hesperogaulus gazini*. A. CIT 521, left p4 (mirrored); B. CIT 524, right P4; C. CIT 525, right P4; D. CIT 527, right P4; E. JODA 3308, left P4 (mirrored). Scale bar equals 1 cm.

Distribution: Early Barstovian from the Sucker Creek (Korth 1999), Mascall, and Simtustus Formations, Beatty Buttes Fauna of Oregon (this paper).

Discussion: Korth (1999) described the species *Hesperogaulus gazini* with material restricted to the Sucker Creek Formation of Oregon. We present additional specimens from the Mascall, and Simtustus Formations as well as the Beatty Buttes Fauna of Oregon. We find that *H. gazini* is still restricted to the Early Barstovian. A single P4 from the Simtustus Formation is the first mylagaulid specimen to be published from this Miocene unit of central Oregon. This unit is stratigraphically equivalent to the better known Mascall Formation (Downs 1956) where other *H. gazini* specimens have been found. The Simtustus Formation is composed of volcaniclastic sandstones and mudstones interbedded with volcanic (tuff, lava flows) of the Columbia River Basalt Group. A date of 15.7 ±0.1 Ma (Smith 1986) is consistent with the stratigraphic correlations with the rest of the well-known central Oregon units. The isolated tooth from the Simtustus is that of an adult specimen at a mid-wear stage. The morphology of the lakes is consistent with the rather short bucco-lingually extended fossettes of the specimens described by Korth (1999, fig. 1). Similarly, in concordance with the published specimens, the lakes of the Simtustus tooth are anteroposteriorly oriented. The only major difference is in the shape and size of the posterolabial fossette. Unlike the specimens previously described, but similar to numerous specimens described herein, there is an unnamed posterolabial-most lake (see Fig. 6). The specimens from the Mascall Fm. include an isolated M2 from the

Mascall Ranch locality and an almost complete skull from Coburn Well (Fig. 9). The skull, although lacking much of the dentition, is very similar in cranial morphology to the type specimen (LACM (CIT) 68) of the species. Numerous isolated P4 and p4 from the Beatty Buttes Fauna. complete the material now available for *H. gazini.* The specimens from Beatty Buttes represent juvenile individuals. We therefore have an ontogenic series available from juvenile and young adult specimens at Beatty Buttes to young adult in the Mascall Formation to adults in the Sucker Creek Fm. (Fig. 6). This ontogenic series indicates important changes in the shape and size of the fossettes in *H. gazini* through development. The changes are greater in the anteriormost fossette. The separation of the branches of the anterofossette, is not a consistent character between specimens of the species *H. gazini.* Korth (1999) had noted some inconsistency and none of the additional specimens presented herein shed light on this issue. There is no evidence for a preferential separation of either branch of the anterofossette in the specimens observed in the JODA or LACM collections. Korth (1999) suggested *H. gazini* might be subject to sexual dimorphism expressed by differences in size and muscle development. The cranial material presented here does not resolve this issue. It most closely resembles (Fig. 9) the type specimen LACM(CIT) 68 illustrated by Korth (1999). There are now therefore two skulls for this morphotype of *H. gazini* versus one for the other morphotype (LACM 4987). The skull from the Mascall Formation is slightly smaller than the type and exhibits bumps on the anterior end of the nasal bones (a part of the skull not preserved in the type specimen of *H. gazini*) that are similar in size and shape to those of *H. wilsoni.* These bumps are also present in a third species of *Hesperogaulus* described later in this paper. The partial P4 available for description lacks the anterior part of the tooth but exhibits the two posteriormost lakes as well as the anterofossette and the anterobuccal lakes. The anterobuccal lake is unusually elongated anteroposteriorly, but the other lakes are consistent in morphology with those of the referred specimens of Korth (1999). Although Gazin (1932) provided a description of the type specimen, later completed by Korth's description of the species (1999), numerous features should be highlighted in reference to the new skull. The Mascall specimen differs from the type specimen in a few characters. The postorbital processes of the jugal and frontal are smaller in the Mascall specimen. The incisive foramina differ in shape between the two specimens with the Mascall skull exhibiting more fusiform and broader foramina. Finally, the infraorbital foramina are rounder in the Mascall specimen. In JODA 3308, the left foramen is essentially round, while the right one is oval with the long axis oriented dorsolaterally. The rest of the cranial morphology is consistent with the type where comparison is possible, although the two specimens are to some degree complementary in the areas of the skull that are preserved. The parietal region of JODA 3308 is missing whereas the basicranium is better preserved than in the type specimen. The nasal-maxilla, and the premaxilla-maxilla sutures can be observed on JODA 3308 but cannot be seen on LACM (CIT) 68. The Mascall specimen might thus be a younger individual than the holotype; the differences between the two specimens may thus be ontogenic. Calede and Hopkins (unpubl. data) observed in *Alphagaulus pristinus* numerous characters that change throughout ontogeny including the shape and size of the infraorbital foramen and zygomatic arch, the height of occipital and sagittal crests, and the size and position of the postorbital processes. The overall similarity in these cranial features between the two specimens of *H. gazini* examined and the fact that both specimens have a fully adult dentition (even though some teeth are missing from the JODA specimen) suggests that the JODA specimen is a young adult, not a juvenile.

The pattern seen in *H. gazini* is similar to that described for *A. pristinus*. It is worth noting that the angle of the occipital plate mentioned by Gazin (1932) and Korth (1999) also changes throughout the development of an individual. Therefore, ontogeny needs to be accounted for before to use this character. The fact that early Barstovian specimens are smaller was already noted by Korth (1999) and Shotwell (1958a) concerning the specimens from Sucker Creek and Virgin Valley. On the basis of the more complete cranial material available to us, we cannot discriminate two different species and retain *H.gazini* as the lone taxon, contrary to the possibility suggested by Korth (1999).

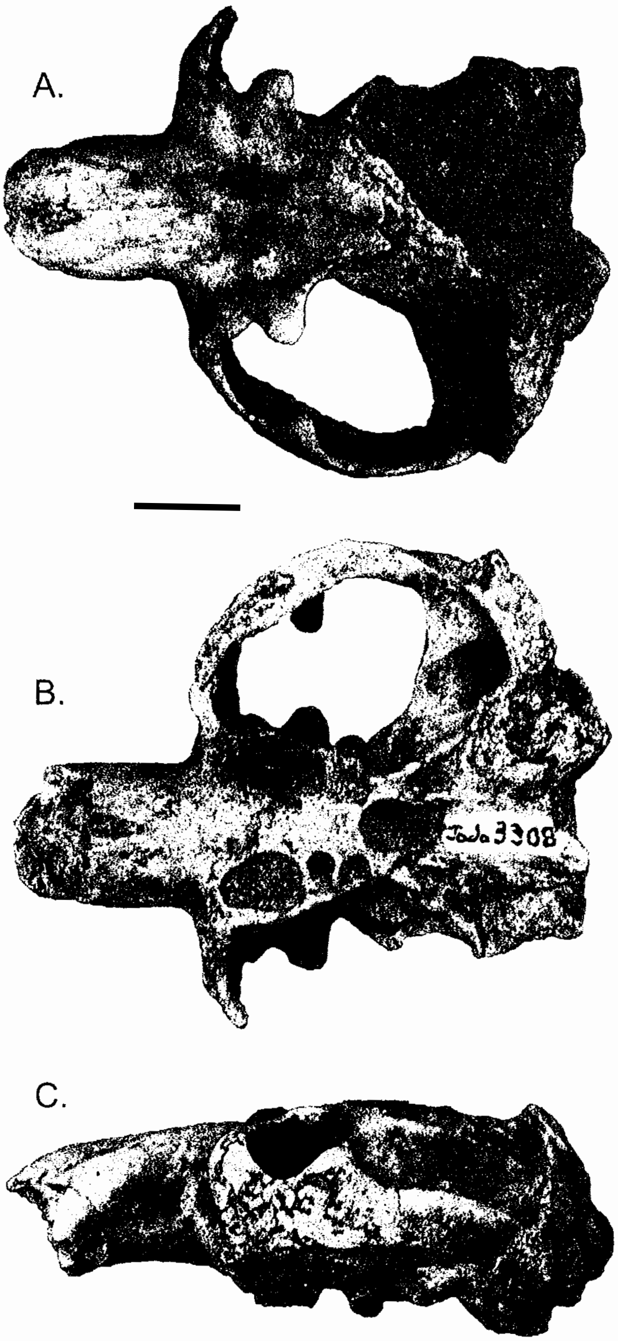


FIGURE 9: Cranial morphology of *Hesperogaulus gazini* from the Mascall Formation (JODA 3308). A. Dorsal view; B. Ventral View; C. Lateral View. Scale bar equals 1 cm.

HESPEROGAULUS SPECIES A (SP.NOV.)

Figs. 10, 11, 12

Synonymy: *Mylagaulus monodon (in part)* Kellogg 1910

Mylagaulus sp. MacDonald 1956

Mylagaulus sp. (in part). Shotwell 1958a

Mylagaulus sp. Hall 1930

Hesperogaulus sp. (in part) Korth 1999

Type Specimen: UCMP 320004, partial skull with left incisor, P4, M2-M3 and right incisor, M2-M3, and associated mandibles with left and right incisors, P4, M2-M3 from RV-8000, Thousand Creek General, Thousand Creek Formation, Nevada.

Referred Material: From Esmeralds Formation (V2804, Fish Lake Valley Fauna) by Korth (1999): UCMP 29637, isolated p4. From Thousand Creek Fm. by Korth (1999): F:AM 65871, FAM 65873, F:AM 65874. From Truckee Fm. (V4845, Brady Pocket 1): UCMP 38665, isolated p4; UCMP 152496, isolated P4. From Juntura Formation (Black Butte Fauna): UOMNH F-5425 (UO 2335), UOMNH F-5443 (UO 2334), UOMNH F-5557 (UO 2344), UOMNH F-5558 (UO 2344), UOMNH F-5772 (UO 2341), UOMNH F-6273 (UO 2340), UOMNH F-10977 (UO 2335), UOMNH F-17508 (UO 2334), isolated P4; UOMNH F-5771 (UO 2341), isolated p4. From Drewsey Fm.: UOMNH F-6113, UOMNH F-6115, UOMNH F-15697, isolated p4 (UO 2347, Otis Basin); UOMNH F-15691, isolated P4 (UO 2356, Stinking Water). From Thousand Creek Fm. (UCMP 1098, Thousand Creek 5): UCMP 11878, isolated P4.

Distribution: Middle Clarendonian through Late Early Hemphillian of the Esmeralda (Korth 1999, this paper), Truckee (this paper), and Thousand Creek Formations of Nevada (Korth 1999, this paper); Juntura and Drewsey Formations of Oregon (this paper).

Diagnosis: Species intermediate in size between *H. gazini* and *H. wilsoni* (upper tooth row length: 16.86 mm, lower tooth row length: 16.97 mm); six to nine fossettes on P4, more fossettes than in *H. gazini*, as many as in *H. wilsoni*; six to seven fossettids in p4, as many as in *H. gazini*; anterolingual and posterolabial fossettes split in *H.* species A unlike *H. gazini*, additional posterolingual fossette compared to *H. gazini*; shape of the outline of P4 intermediate between *H. gazini* and *H. wilsoni*; fossettids oriented obliquely unlike *H. wilsoni* but similar to *H. gazini*; Postorbital index (0.40) larger than in *Hesperogaulus gazini* or *H. wilsoni* (0.31-0.35 and 0.22-0.25 respectively); largest infraorbital foramen of the genus (6.5 by 3.95 mm).

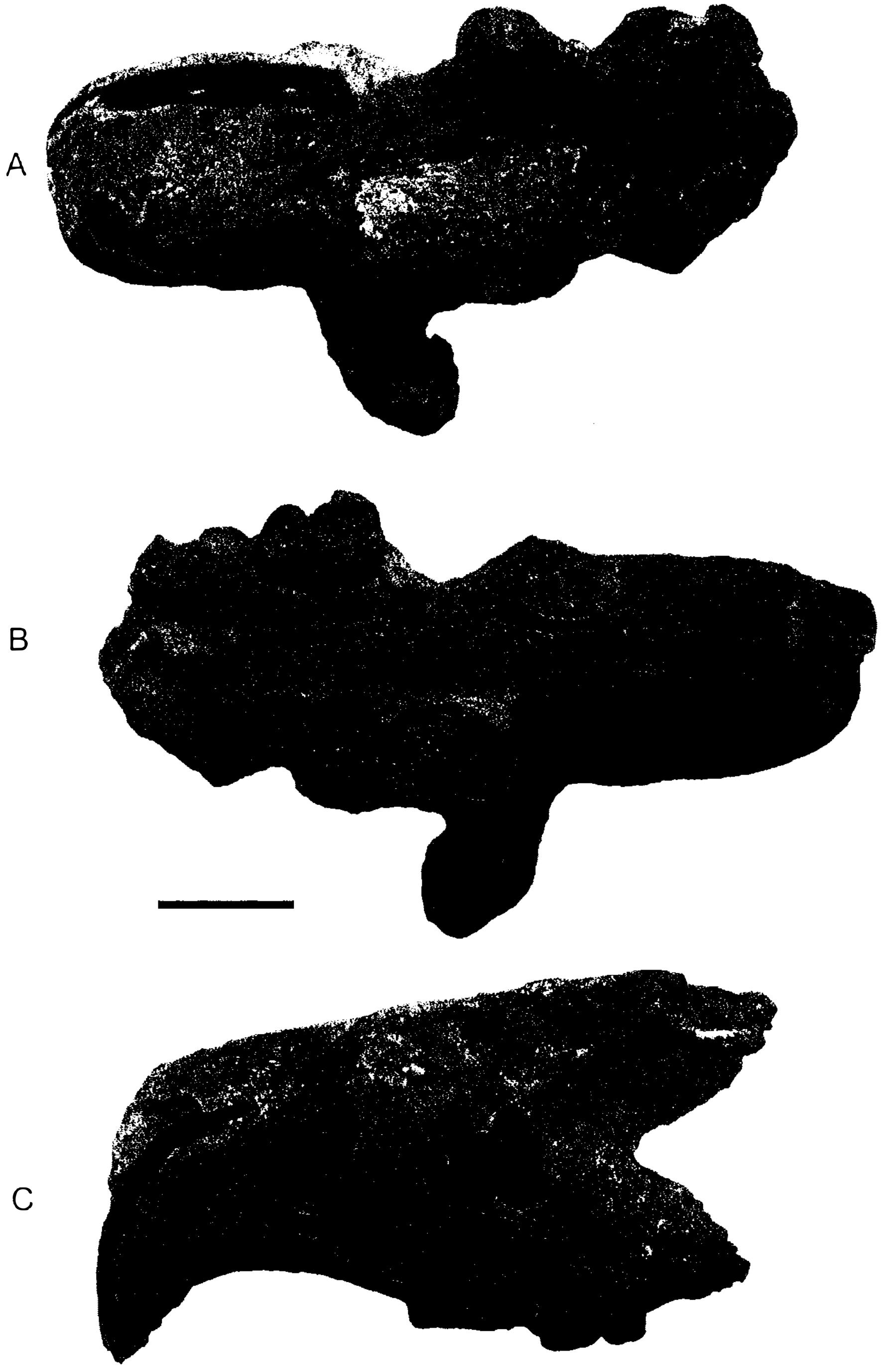


FIGURE 10: Cranial morphology of the type specimen of *Hesperogaulus* species A, UCMP 320004. Scale bar equals 1 cm. A. Dorsal view; B. Ventral view; C. Lateral view.

Description: The type specimen, UCMP 320004, of the species provides much information about the cranial and dental morphology of the species. The skull of *Hesperogaulus* species A is intermediate in depth and robustness between those of *H. gazini* and *H. wilsoni* (Fig. 10). The zygomatic arch is broken and mostly missing, but the zygomatic plate is very tall, taller than in *H. gazini*. The posterior part of the skull is missing. The maxillary-premaxillary suture begins at the posterior edge of the incisive foramina (as it does in most Aplodontidae). The diastema is long (17 mm, as in *A. pristinus*, Calede and Hopkins unpubl. data), moreso than in *H. gazini* from the Mascall Formation (11 mm). The rostrum is composed a large premaxilla and a slightly smaller maxilla. The P4 is placed about 6 mm posterior to the premaxilla-maxilla suture which continues dorsally up the lateral sides of the rostrum as a highly convoluted suture. The nasals are broken off laterally, exposing the root of the incisor in the upper jaw. There is a small bump on the dorsal surface of the nasal bones similar to that found in the specimen of *H. gazini* from the Mascall Fm. Wahlert (1974) noted that the interpremaxillary foramen is minute in derived mylagaulids; *H.* species A is no exception. The incisive foramina are about 8 mm long, close to half of the rostrum length. For comparison, they are only 5 mm long in *A. pristinus* that has a rostrum of similar length. There is no procumbency of the upper incisors. The anterior root of the zygomatic arch, the zygomatic plate, is thickened and almost as tall as the entire skull. This is a feature common to mylagaulids (Hopkins 2006). The dorsal edge of the zygomatic plate is thickened anteriorly and posteriorly above the foramen. It is high, extending from the alveolus of the P4 to the dorsalmost surface of the frontal. It is about 17.5 mm in height as compared to about 13.3 mm in the Mascall *H. gazini*. The anteriormost part of the zygomatic arch just posterior to the zygomatic plate is thick, thicker than in *H. gazini* but thinner than in *A. pristinus*. It therefore seems that the zygomatic plate is greatly enlarged relative to the jugal in *H.* species A compared to other mylagaulids. The postorbital process of the jugal is missing; that of the frontal is rounded and lobate in form and quite prominent. The Postorbital Index (POI) of Korth (2000) of *H.* species A is larger than those of *H. gazini* or *H. wilsoni* (0.40 versus 0.31-0.35 and 0.22-0.25 respectively, Korth, 2000). It falls within the range of the genus *Pterogaulus* from the Great Plains. This is primarily due to the narrow width of the frontal posterior to the postorbital process (parameter C of the POI equation of Korth 2000). The outline of the orbit indicates a very small opening for the eye. The infraorbital foramen is ovoid. It runs from the dorsolateral end of the plate (where the curvature of the zygomatic arch initiates) towards the medioventral end of it, dorsolaterally to P4. The infraorbital foramen of *H.* species A is close in shape to that of *Aplodontia*. It is very large with a length of 6.5 mm and a width of 3.95 mm. This is larger than for the *H. gazini* specimen from the Mascall Fm. whose very round infraorbital foramen is 4.8 mm wide. This latter measurement is at the high end of the range given for mylagaulids by Wahlert (1974), which ranges from 1.9 to 4.8 mm. *H.* species A's infraorbital foramen size is thus larger than the maximum of the published range. Because of the increased thickness of the zygomatic plate in mylagaulids, the infraorbital foramen appears to be positioned more dorsally than in

Aplodontia. The orbital region is well-preserved, but the bones of this area are fused as a consequence of the maturity of the specimen. Although the sutures cannot be distinguished, the foramina of the orbital area can. The optic foramen is very large for a mylagaulid, approaching the size of that of *Aplodontia rufa* (see Wahlert 1974). Nevertheless, *A. rufa*, and thus *H.* species A, have very small optic foramina relative to other rodents and can therefore be inferred to have very poor eyesight (Carraway and Verts 1993, Kay and Kirk 2000, see Hopkins 2005 for a discussion of the consequences of vision for behavior in mylagaulids). An interorbital foramen is also present immediately anterior to the optic foramen. This feature is also observed in *Allomys* and in *Aplodontia,* where there is a pit in front of the optic foramen where the rectus muscles of the eye originate (Wahlert 1974). The palate is strongly grooved as it is in *A. pristinus*, *A. vetus*, and other specimens of the genus *Hesperogaulus* (Korth 1999, figure 2, 3). The grooves terminate in the single pair of posterior palatine foramina. As in other mylagaulids with increased hypsodonty (Calede and Hopkins unpubl. data) and unlike in *Meniscomys* (Hopkins 2006), the maxilla is deep dorsal to the cheek teeth. The palate extends posteriorly down to the internal naris and terminates there, posterior to M3. The posterior maxillary foramen is missing due to taphonomic damage. Most of the basicranium is missing in this specimen but the pterygoid fossa and part of the pterygoid flanges are present. The pterygoid fossa is very deep, moreso than in *A. pristinus*, more as in *H. gazini* from the Mascall Fmormation or the modern *A. rufa*. Only the anteriormost parts of the pterygoid flanges are present. They are very similar to those of *H. gazini*. The portion of the dorsal surface of the skull available for description is very flat as in all mylagaulids. Both dentaries of UCMP 320004 are preserved. The dentaries are short but extremely robust (Fig. 11).

FIGURE 11: Mandibular morphology of the type specimen of *Hesperogaulus* species A, UCMP 320004. Scale bar equals 1 cm. A. Dorsal (Occlusal) view; Lateral view.

They are very deep (i.e. 11.5 mm at the diastema and 19.5 mm at its deepest point underneath the greatly hypsodont p4). This short, deep dentary is a common feature of mylagaulids. In addition, the lower jaw is also very wide in lateral dimension. In contrast with the members of the genus *Alphagaulus* such as *A. pristinus*, in which the short, deep lower jaw is gracile (Calede and Hopkins unpubl. data), the lower jaw of *H.* species A is thickened mediolaterally. This is emphasized by the bulge on the lateral surface of the lower jaw caused by the roots of p4. The tips of the lower incisors project slightly anteriorly, as in *A. pristinus* (Calede and Hopkins unpubl. data) or *A. vetus*. The root of the incisors can be observed curving below and around the cheek teeth to a point posterolateral to the m3, forming a half-circle. The diastema is long (about 10.2 mm). The mandibular symphysis is very long and covers the whole depth of the mandible. The dentaries are very strongly fused. There is a single mental foramen on the lateral side of each dentary ventral to the diastema, close to its posterior end, a few mm anterior to the root of p4. This foramen is large, almost 2 mm in diameter. It is almost round with a narrower end pointing anteriorly. The posterior end of both dentaries is missing, preventing the description of the masseteric fossa, the angular, condyloid, and coronoid processes. The mandibular foramen is present. It is ovoid and located a few mm posterior to m3. It cannot be easily measured but is larger than in *A. pristinus*. The dentition, as previously mentioned, is hypsodont. The roots of the left p4 can be seen and extend as much as 1.3 cm into the bone of the dentary. The total height of the p4 of this adult specimen is 1.7 cm.

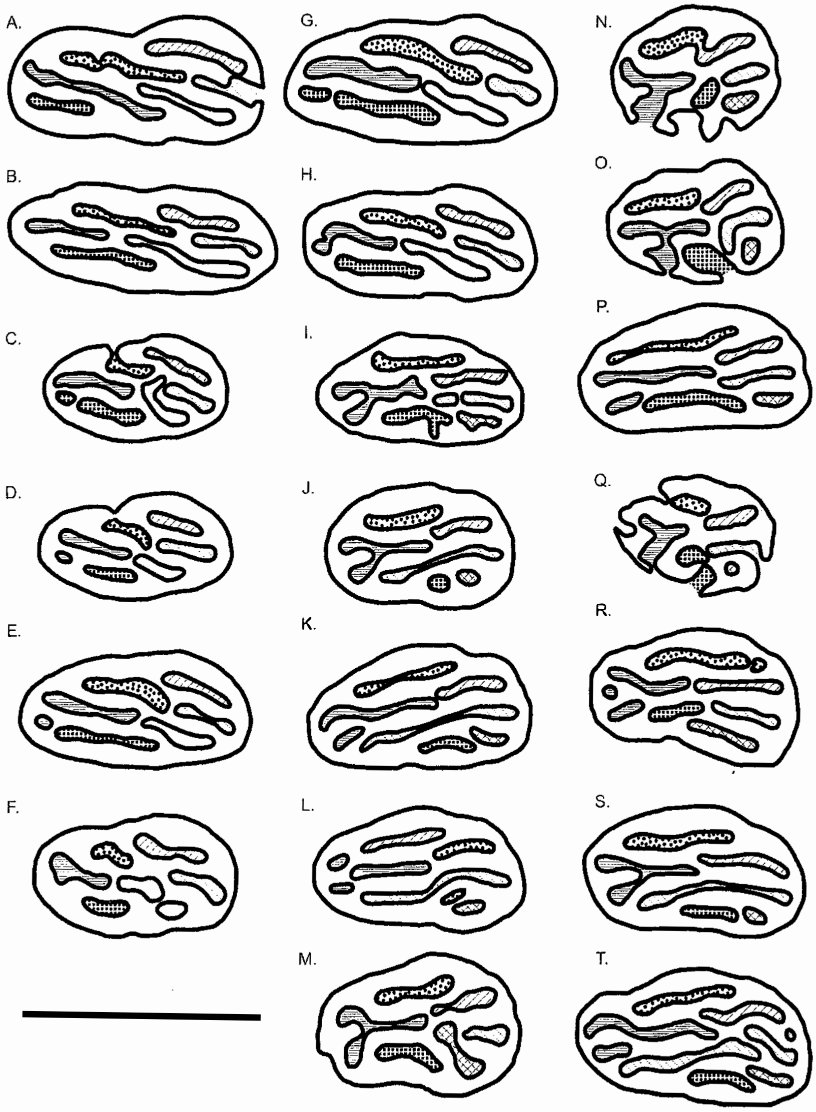


FIGURE 12: Occlusal morphology of the 4th premolars of *Hesperogaulus* species A. Scale bar equals 1 cm. A.UCMP 38665, left p4 (mirrored); B. UOMNH F-6115, left p4 (mirrored); C. UCMP 29637, left p4 (mirrored); D. UOMNH F-5771, right p4; E. UOMNH F-5771 sawed, right p4; F. UCMP 320004 (type), right p4; G. UOMNH F-6113, right p4; H. UOMNH F-15697, right p4; I. UOMNH F-17508, left P4 (mirrored); J. UOMNH F-5772, left P4 (mirrored); K. UOMNH F-5772 sawed, left P4 (mirrored); L. UOMNH F-5443 sawed, left P4 (mirrored); M. UCMP 320004 (type), left P4 (mirrored); N. UCMP 11878, left P4 (mirrored); O. UOMNH F-5557, right P4; P. UOMNH F-5771 sawed, right P4; Q. UOMNH F-5558, right P4; R. UOMNH F-5558 sawed, right P4; S. UOMNH F-15691, right P4; T. UOMNH F-10977, right P4.

The dentition is the same as in other derived mylagaulids; there is only one premolar retained, the p4 (and P4). The 1st molars are lost early in development as they are pushed out by the enlarged growing single premolar. As for all mylagaulids, the dental formula is therefore 1/1, 0/0, 1/1, 2/2 in adults. The total length of the cheek teeth is 16.9 mm for the upper left tooth row and 17.3 mm for the lower right one. The occlusal surface of the tooth rows is complex and characteristic of mylagaulids. The P4 of *H.* species A converges on the double-lobed shape of *A. pristinus* or *A. vetus* but because the indentation that separates the two lobes is not as strong in the new species, it still appears pear-shaped with a wider posterior end and a narrowing anterior one (see Fig. 12). There are six fossettes in the type specimen of the species that are mostly anteroposteriorly oriented. Other specimens discussed below display up to nine lakes. This is a greater number than in *H. gazini* and approaches that of *H. wilsoni.* The anterofossette is the largest fossette and is forked in the holotype. In later stages of wear, the labial branch of the anterofossette separates first later followed by the lingual one in a specimen in very late stage of wear (UOMNH F-5443). Other fossettes that separate include the hypofossette, parafossette, and the anterolingual fossette (protofossette of Shotwell 1958a). There are seven fossettids on the p4s of the holotype. This number varies between six and seven depending on the specimen considered. This is less than the maximum for *H. gazini* (eight lakes). The lakes on the p4 are elongated and obliquely oriented, running from the posterolingual corner of the tooth to the anterolabial one, as discussed above in *A. vetus*. There are some specimens (see Fig. 12) that show some rounder lakes. There are two lakes on the lingual edge of the tooth, two on the labial one and three aligned in between. The anterolabial fossettid and the anterior most fossettid split with wear.

Discussion: The assignment of *H.* species A (sp. nov.) to the genus *Hesperogaulus* is both consistent with the diagnosis of the genus and the presence of *H. gazini* and *H. wilsoni* in the Great Bain. These two species are the only other derived mylagaulids in Oregon. As a consequence, the decision to assign the new species to the genus *Hesperogaulus* is both consistent with morphology and the most parsimonious biogeographically. *H.* species A .also exhibits important morphological differences with the two previously described species of the genus. In addition, it also occurs in a time frame intermediate (with little overlap) between those of *H. gazini* and *H. wilsoni.* Those two features call for the publication of a new species.

The characters exhibited by *H.* species A are often either shared with *H. gazini* or *H. wilsoni*, or intermediate between the other species of the genus *Hesperogaulus.* There are a few exceptions, especially in the size and shape of the foramina, the POI, or in the morphology of the palatine region. Some specimens of *H.* species A display occlusal morphology that differs from that of the type specimen. This also occurs in other mylagaulids such as *H. wilsoni* (see above). I recognized in *H.* species A an extra posterolingual lake on both the upper and the lower premolars. Differences in the shape of the lakes between specimens (Fig. 12) correspond to the wear pattern from juveniles to late adults. Thus, few lakes of complex shapes in juveniles will separate into more numerous fossettes or fossettids of less complex shape in adults with wear.

HESPEROGAULUS WILSONI (Korth, 1999)

Fig. 13

Synonymy: *Mylagaulus* cf. *monodon* Wilson 1937
Mylagaulus sp. Shotwell 1958a
Hesperogaulus wilsoni Korth 1999

Type Specimen: LACM 142506, complete skull with incisors and right P4 from Rome Fauna (Drewsey Formation), Oregon.

Referred Material: From Drewsey Formation (Rome Fauna) by Korth (1999): LACM 142507, skull; LACM (CIT) 1952, LACM (CIT) 1953, LACM (CIT) 1955, isolated P4; LACM (CIT) 1954, LACM (CIT) 1956 – 1958, lower dentitions. From McKay Fm. (UO 2222, McKay Reservoir): UOMNH F-10349, isolated P4; UOMNH F-10347, UOMNH F-10348, isolated p4.

Distribution: Late early to early late Hemphillian of the Drewsey (Korth 1999) and McKay Formations of Oregon (this paper).

Discussion: Part of the material referred to *Hesperogaulus wilsoni* by Korth (1999) comes from the McKay Reservoir locality (UO2222). When first describing the fauna from the area, Shotwell (1956) hypothesized that this was a unit of the Shutler Formation. Since then, other authors (Wagner 1976, Feranec et al. 2005) have used the term Shutler Fm. when referring to the McKay specimens. However, Farooqui et al. (1981) and Newcomb (1971) proposed that the Shutler Fm. be broken up into the McKay Fm. that includes the locality UO 2222 and the Alkali Canyon Fm. (Farooqui et al. 1981). I therefore refer to the specimens from the McKay Reservoir as being part of the McKay Fm.

When describing *Hesperogaulus wilsoni*, Korth (1999) mentioned two specimens from the UOMNH collections. These specimens were figured by Shotwell (1958a) and attributed to *Mylagaulus* sp. There are actually three specimens from the McKay Formation (McKay Reservoir, UO 2222) of *Hesperogaulus wilsoni*. Fig. 7 shows the occlusal morphology of these three specimens. As mentioned by Korth (1999), the number of lakes in *H. wilsoni* is the greatest of the genus and in late stage of wear specimens can exhibit eight, nine, or even ten fossettids. The fossettids vary more in orientation than the fossettes, which are elongated and oriented anteroposteriorly. On the other hand, although usually the fossettids extend from the posterolingual corner of the tooth to the anterolabial one, the orientation seems to be more prone to changes with wear and among individuals. UOMNH F-10347, in particular, at a wear stage comparable to that of UOMNH F-10348, shows many more small smaller curved lakes with varying orientation. It is worth noting that in addition to the six main fossettids (see Shotwell

1958a, fig. 7), there are two other lakes of different homology, as both lower teeth exhibit an additional lingual lake. There is a posterolingual fossette, an anterolingual one, and a third one located in between. Furthermore, UOMNH F-10347 also shows another fossettid lingual to the anteriormost fossettid. A similar phenomenon is found in the upper tooth, UOMNH F-10349, as well as in the specimens figured by Korth (1999, figs. 1.3, 1.4) in which there is an additional lake in the posterolabial corner of the tooth. Within the species *H. wilsoni*, there is little variation in size of the premolar. All specimens from the UO as well as the specimens described by Korth (1999) are in the same size range (within a couple millimeters of each other) around 12 mm for the p4 (Table 3).

TABLE 3: Summary of the tooth row lengths and 4th premolars of the mylagaulids from the northern Great Basin. Tooth row length data for *Alphagaulus vetus*, *Hesperogaulus gazini* and *H. wilsoni* are from Hopkins 2007. The second set of P4 data and the p4 data for *H. gazini* come from (Korth 1999). Note that the size estimate of *H. wilsoni* is biased by the loss of the molars (the tooth row is reduced to the 4th premolar). *H. wilsoni* is actually the largest species of the genus (Korth 1999, this paper) as indicated by cranial material. The size of the 4th premolar by itself should not be considered as a proxy for body size since it may be affected by changes in ecology as well. Lower Tooth Row Length=LTRL, Upper Tooth Row Length=UTRL, N=sample size, S=standard deviation, M=mean.

Taxon	UTRL (mm)	LTRL (mm)	P4 length in mm: M, (N, S)	p4 length in mm: M, (N, S)
Alphagaulus vetus	14.46	16.04	7.70 (11,0.57)	7.7 (13,1.05)
Hesperogaulus gazini	15.52	18.24	7.8 (2,0.44), 8.38 (10,0.56)	9.03 (11, 0.62)
Hesperogaulus wilsoni	13.83	12	13.92 (1, NA)	13.39 (2,1.03)
Hesperogaulus species A	16.86	16.97	9.13 (8,0.78)	10.29 (6,1.55)
Mylagaulidae indet. from Beatty Buttes	NA	NA	8.96 (1, NA)	NA
Mylagaulidae indet. from Juntura	NA	NA	9.66 (1, NA)	11.75 (2,2.21)
Mylagaulidae indet. from Piute Creek West	NA	NA	10.36 (1, NA)	NA

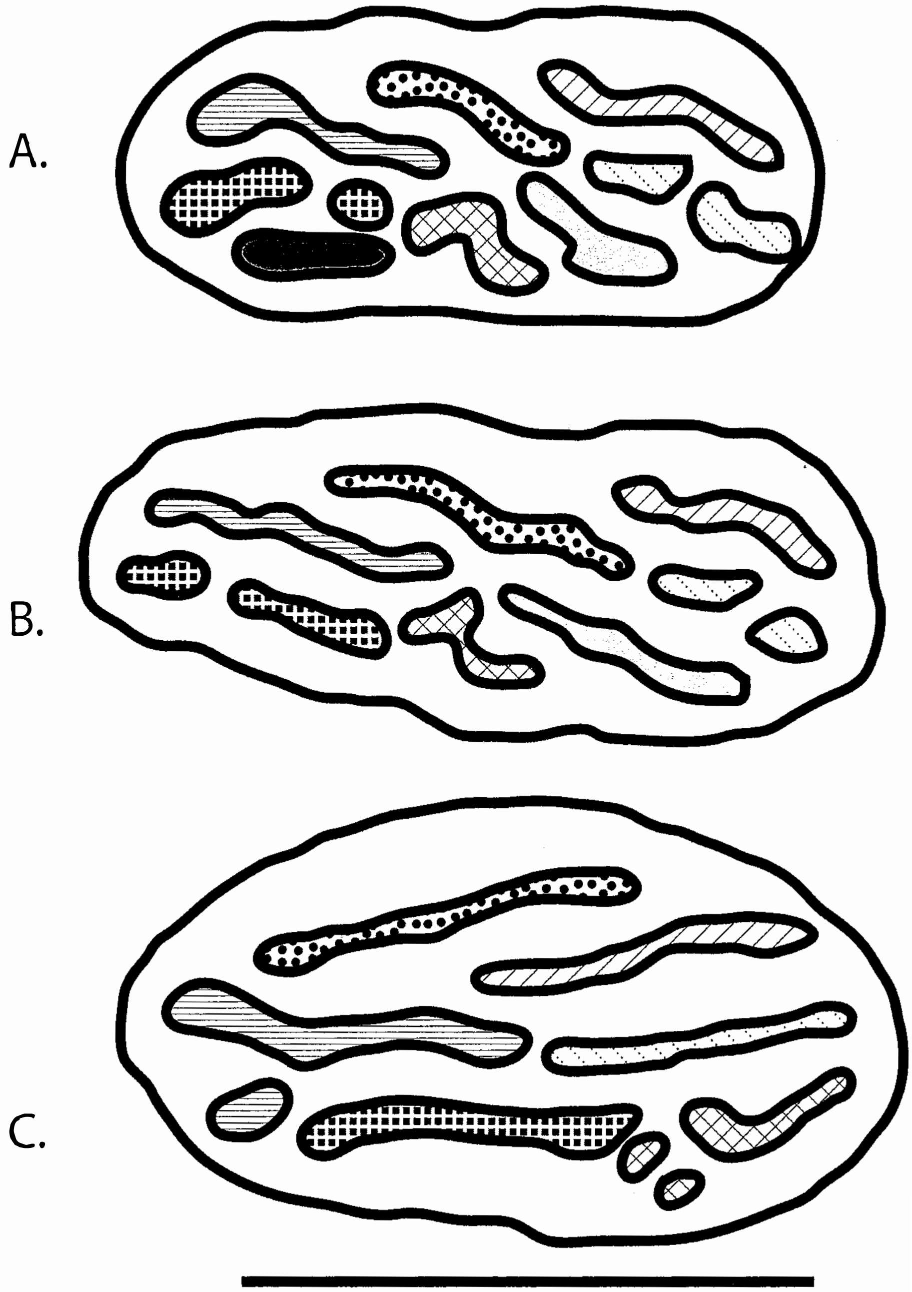


FIGURE 13: Occlusal morphology of the 4th premolars of *Hesperogaulus wilsoni*. A. UOMNH F-10347, left p4 (mirrored); B. UOMNH F-10348, right p4; C. UOMNH F-10349, right P4. Scale bar equals 1 cm.

MYLAGAULIDAE INDET.

Figs. 14, 15, 16

Synonymy: *Epigaulus minor* (in part) Shotwell 1958a

Mylagaulus sp. (in part) Shotwell 1963

Mylagaulus monodon (in part) Kellogg 1910

Mylagaulus sp. (in part) Shotwell 1958a

Referred Material: From Piute Creek West (UCMP V-85105, Formation unknown): UCMP 188927, isolated P4. From Juntura Fm. (Black Butte Fauna): UOMNH F-6165 (UO 2343), UOMNH F-6166 (UO 2343), isolated P4; UOMNH F-5451 (UO 2334), UOMNH F-15694 (UO 2339), isolated p4; UOMNH F-15695 (UO 2339), fragmentary fourth premolar; UOMNH F5770 (UO 2341), partial right mandible with m1. From Cox Butte (UO 2417, Beatty Buttes Fauna?): UOMNH F-17681, partial skull with left and right P4. From Massacre Lake Local Fauna (RV7043, Massacre Lake 1): UCMP 316439, UCMP 319224, partial incisors; UCMP 315687, partial mandible with partial incisor; UCMP 315730, partial juvenile cheek tooth. From John Day Fm. (RV7314, Warm Springs 1): UCMP 316526, isolated left P4. From Virgin Valley Fm.: UCMP 11326 (UCMP 1095, Virgin Valley 14), UCMP 152494 (V73056, Prospect 1), partial 4th premolars, UCMP 41026 (UCMP 1090, Virgin Valley 9), left and right mandibles with partial left incisor, left m2-m3, partial right incisor and right p4; UCMP 11572 (UCMP

1065, Virgin Valley), partial mandible with p4; UCMP 11662 (UCMP 1065, Virgin Valley), isolated p4. From Mascall Fm. (JDNM 4, Mascall Formation General): JODA 2329, partial left mandible with dp4-m2 and erupting p4.

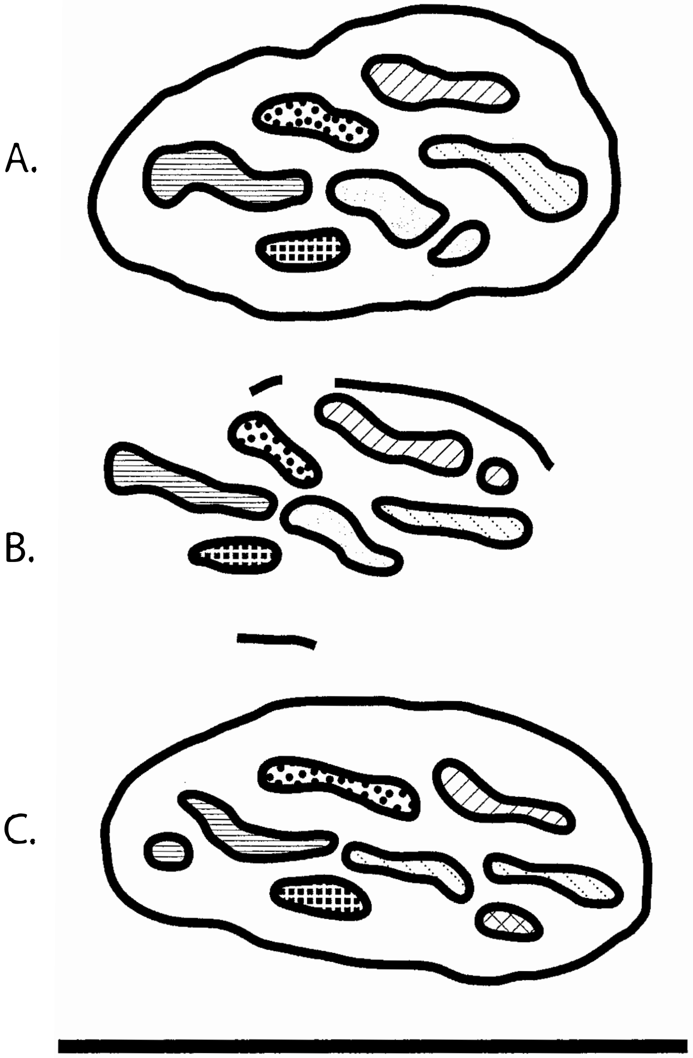


FIGURE 14: Occlusal morphology of the 4th premolars of the Virgin Valley specimens of indeterminate mylagaulids. A. UCMP 11572, left p4 (mirrored); B. UCMP 11662, right p4; C. UCMP 41026, right P4. Scale bar equals 1 cm.

Distribution: Early Hemingfordian John Day Fm., Oregon, Late Hemingfordian Massacre Lake Local Fauna, Nevada, Oregon; Early Barstovian Beatty Buttes Fauna, Virgin Valley Fm., and Mascall Fm. of Oregon; Late Clarendonian the Juntura Fm., Oregon. Barstovian of Piute Creek West (Formation unknown).

Discussion: The indeterminate specimens from the Massacre Lake Fauna and the Virgin Valley Fm. most likely belong to individuals of *A. vetus*. The lack of diagnostic features on those specimens does not, however, allow such assignment to be confidently made. Specimens UOMNH F-6165 and UOMNH F-6166 from Black Butte are curated with two different specimen numbers but they are premolars of opposite sides and Shotwell (1958a) reported they were collected on float a few inches apart from each other. They appear to represent the left and right P4 of a single individual, as the unusual fossette morphology and wear stage are identical. The outline of the tooth is simple, similar to other mylagaulids but the shape of the lakes shown in Fig. 15 is very complex. In particular, the anterofossette's branching is not a simple "Y" but rather consists of two parallel anteroposteriorly elongated lakes joined by a bucco-lingually oriented lake perpendicular to the first two. The anterolabial fossette of UOMNH F-6165 exhibits a high degree of complexity as well. It extends to the posterolingual side of the tooth and branches anteroposteriorly. The posterolabial fossette in both specimens is horseshoe-shaped and consists of the metafossette of Shotwell (1958a) joined to another, parallel labial fossette which, as described above for a specimen of *Hesperogaulus* sp., is an additional lake of different homology. The very peculiar lake morphology of these specimens and the large size of the teeth suggest that this single individual represent a new rare taxon. No formal description of this possible new species, sympatric with *H.* species A, will be undertaken here and awaits discovery of a more complete specimens. Specimen UOMNH F-5451 is a p4 in very early stage of wear. The tooth is damaged and no description or identification of it is possible. Specimen UCMP 188927 from the Barstovian is also a very large mylagaulid. The tooth is very wide bucco-lingually as well. This single upper left P4 shows no branching of the lakes. It is a late stage of wear and younger specimens of the same species would be expected to show some branching of the anterofossette. The fossettes are oriented and elongated antero-posteriorly. There is a total of seven fossettes on the occlusal surface of this tooth. As mentioned earlier for other taxa, there is an additional posterolabial fossette not homologous to the lakes described by Shotwell (1958a, fig. 7) or Hopkins (2008a, fig. 1). Because of its large size and its peculiar occlusal morphology, this individual may represent a rare, large species similar to the Black Butte specimen. Piute Creek West (V-85105), the site where the specimen was collected, is unpublished and very little information is available with which to better constrain the age of this specimen. UOMNH F-17681 from Cox Butte (Oregon) is a partial skull of a large mylagaulid. The P4s exhibit an occlusal morphology very close to that of *Alphagaulus vetus*, but with more elongated fossettes. The size of the teeth is within the range of *A. vetus* but the P4 of specimen UOMNH F-175681 is more elongated bucco-lingually, appearing rounder than that of an *A. vetus*. The outline of the teeth of the

Cox Butte specimen is different from that of the teeth of *A. vetus*. The tooth is still separated in an anterior and a posterior lobe but the posterolabial indentation found in UCMP 121693 (a mature individual of *A. vetus*) is not as pronounced in the Cox Butte specimen. The additional fossette of the posterolabial corner of the tooth described in other taxa in this paper is present in this specimen as well. This specimen possibly represents another rare new taxon. Dingus (1990) reported a mylagaulid left P4 from Warm Springs (RV-7314, early Hemingfordian, Oregon) that he attributed to *Alphagaulus* aff. *A.vetus*. Dingus (1990) mentioned that the specimen differed from *A. vetus* in having a slightly more posterior protocone, complete enamel covering on all roots, and a narrower bucco-lingual width. In addition to those differences, I find that the morphology of the posterior lakes of the Warm Springs P4 differs from that of *A. vetus*, in particular on its buccal side. As a consequence of these various differences, I assign the single Warm Springs specimen to Mylagaulidae indet. This specimen comes from the locality UCMP RV-7314 which is assigned to the early Hemingfordian by Woodburne and Robinson (1977). A single juvenile specimen (JODA 2329, fig. 16) from the Mascall Formation could not be confidently identified. It is most likely either one of *Alphagaulus vetus* or *Hesperogaulus gazini* present in the Mascall Formation. The lack of an adult dentition precludes definitive identification to a mylagaulid species. The m1 is close to being pushed out of the tooth row by the erupting p4. The absence of well-preserved lower second molars early in wear (in order to be comparable to that erupting in JODA 2329) and published deciduous lower fourth premolars for *A. vetus* and *H. gazini* make impossible a definitive assignment of this specimen to either one of the mylagaulids species found in the Mascall Fm. The partial mandible from the Juntura Fm. most likely belongs to *H.* species A. Because of the lack of diagnostic dental material, this specimen cannot be identified with confidence.

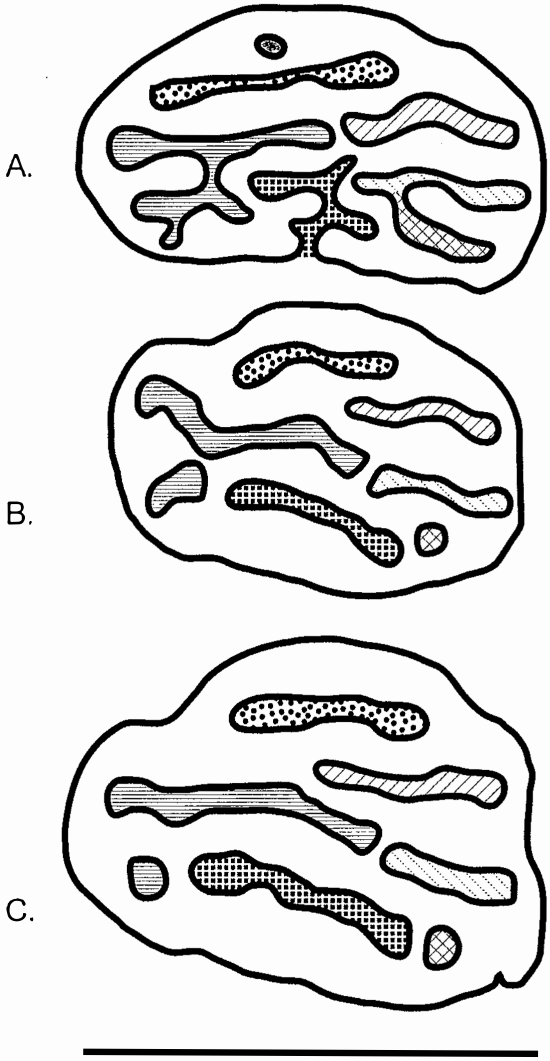


FIGURE 15: Occlusal morphology of the 4th premolars of indeterminate mylagaulids. A. UOMNH F-6166, right P4; B. UOMNH F-17681, right P4; C. UCMP 188927, left P4 (mirrored). Scale bar equals 1 cm.

Three specimens (UCMP 41026, UCMP 11572, UCMP 11662) of mylagaulids from the Early Barstovian Virgin Valley Formation exhibit a morphology intermediate between that of the commonly found sympatric *A. vetus* and *H. gazini* from the Early Barstovian of Oregon. The tooth size of these specimens is close to that of *H. gazini*. Similarly, the number of lakes in these specimens and in *H. gazini* is very close. In particular, they both exhibit an anterolingual fossettid absent in all *A. vetus* specimens. However, these Virgin Valley specimens share with *Alphagaulus vetus* a common general tooth shape. The shape of the fossettids of the three specimens is intermediate between *A. vetus* and *H. gazini*. The orientation of the lakes is closer to that of *A. vetus*. In UOMNH F-41026, I can also recognize an additional fossette located in the posterolabial corner of the tooth, labially to the metafossette and posteriorly to the parafossette of Shotwell (1958a, fig. 7). This character varies intraspecifically in other taxa (e.g., *Hesperogaulus* species A). These three specimens might represent evidence for a new taxon but the scarce material currently available prevents further description.

The occurrence of Great Baisn Mylagaulids in the formations and faunas of Oregon and Nevada is summarized in Table 4. The specimens of large rare mylagaulids from the Barstovian and Clarendonian of Oregon suggests that at least one additional lineage of large mylagaulids was present and lived sympatrically with the smaller *H.* species A and *H. gazini*. Further field work in the Miocene deposits of southeastern Oregon will hopefully recover additional material of this poorly-known taxon.

FIGURE 16: Occlusal morphology of the dp4-m2 of an indeterminate mylagaulid from the Mascall Formation of Oregon. Scale bar equals 1 cm.

TABLE 4: Summary of the occurrences of mylagaulids in the northern Great Basin.

Formations (Collection area)	Taxa present
(Massacre Lake)	*Alphagaulus vetus*, Mylagaulidae indet.
John Day	Mylagaulidae indet., *Mylagaulodon angulatus*
Virgin Valley	*Alphagaulus vetus*, Mylagaulidae indet.
Beatty Buttes	*Hesperogaulus gazini*, Mylagaulidae indet.
Sucker Creek	*Hesperogaulus gazini*
Mascall	*Hesperogaulus gazini, Alphagaulus vetus,* Mylagaulidae indet.
Simtustus	*Hesperogaulus gazini*
Drewsey	*Hesperogaulus wilsoni*, *Hesperogaulus* species A
McKay	*Hesperogaulus wilsoni*
Esmeralda	*Hesperogaulus* species A
Truckee	*Hesperogaulus* species A
Thousand Creek	*Hesperogaulus* species A
Juntura	*Hesperogaulus* species A, Mylagaulidae indet.
(Piute Creek West)	Mylagaulidae indet.

PHYLOGENETIC RESULTS

The phylogenetic analysis produced 166 most parsimonious trees. The consensus of these trees is shown in Fig. 17. The general topology is very different from that presented by Hopkins (2008a, Fig. 3). Among the major differences, the monophyletic Promylagaulinae previously found does not occur in this new analysis. *Promylagaulus* falls as the outgroup to the clade including *Galbreathia bettae* and all descendants of its common ancestor with other mylagaulids. The genus *Galbreathia* is paraphyletic. The reorganization at the base of the tree, where no taxa were recoded, suggests that the instability of the tree within the Mylagaulidae is great enough to make fine points of the phylogeny unreliable. I find the most basal Mylagaulinae to be *Alphagaulus tedfordi* and *A. douglassi* unlike Hopkins (2008a) who found *A. pristinus* as the most basal mylagauline. The genus *Alphagaulus* remains paraphyletic. The Massacre Lake *A. vetus* OTU is found to be a sister taxon to *A. vetus* thus confirming the taxonomy presented above. *Hesperogaulus* species A falls within a polytomy of all derived mylagaulids that includes the genera *Umbogaulus*, *Mylagaulus*, *Hesperogaulus*, *Pterogaulus* and *Ceratogaulus*, as well as the more primitive species *A. vetus* and *A. pristinus.* The support for the tree as a whole is very low and its configuration very unstable. The poor resolution of the tree is a consequence of the nature of the characters. Hopkins (2008a) used those characters to resolve the relationships between aplodontoid species. The characters use for the analysis yielded a rather well resolved tree for the whole super-order. Hopkins

(2008a), however, did mention that such characters may not offer a good resolution when considering mylagaulids only, because the dependence on characters related to the configuration of the cusps is problematic in a group with hypsodont dentition. Most of the characters used in this phylogenetic analysis are appropriate in differentiating between aplodontids and mylagaulids or between promylagaulines and mylagaulids. However, because all derived mylagaulines share many of these characters, the differentiation between two derived mylagaulines is sometimes impossible and leads to the numerous polytomies observed in the tree. Numerous characters are symplesiomorphic when considering the mylagaulines. A number of these characters differs between mylagaulid species because the morphology of the occlusal surface is not tightly constrained and may evolve rapidly rather than as a consequence of shared ancestry. The present analysis emphasizes this point and calls for further work on the phylogenetic relationships within the family Mylagaulidae. Reviews of the mylagaulid material such as this study may help build a character matrix that focuses on distinguishing the dentition of different derived mylagaulids species. The addition of more cranial and postcranial characters will also supplement the set of characters and allow a better understanding of the relationships within the Mylagaulinae.

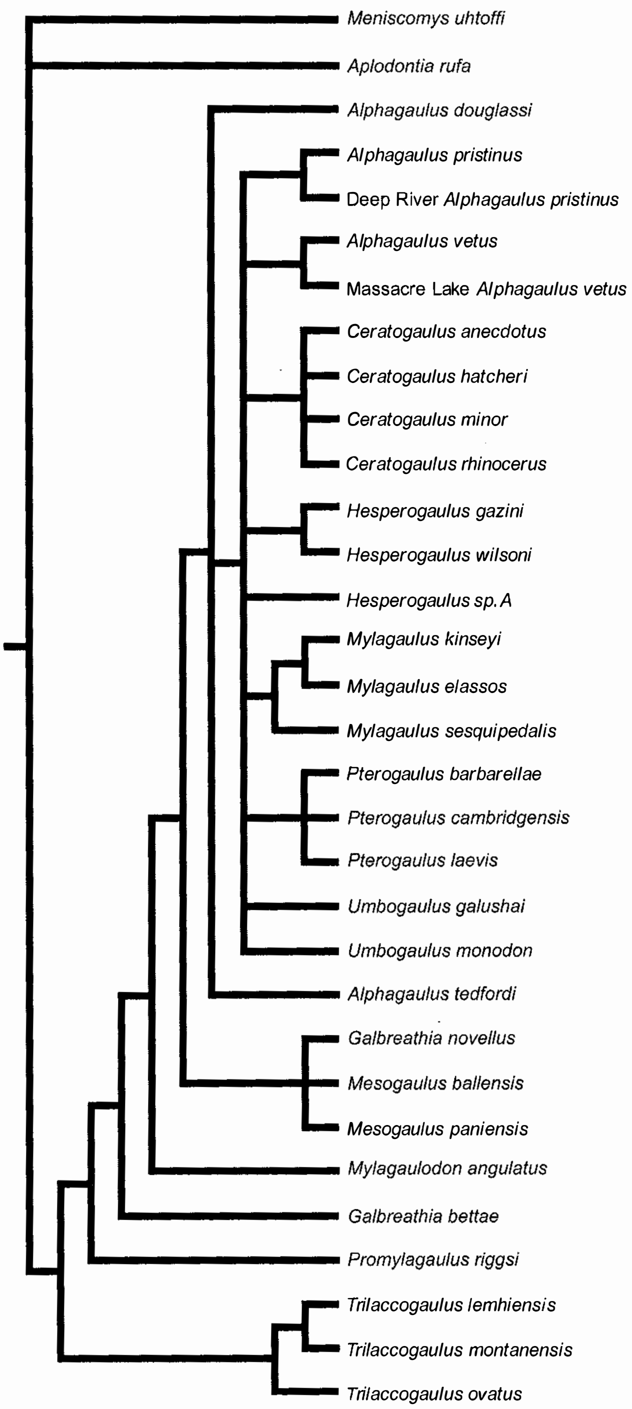


FIGURE 17: Consensus tree of the 166 most parsimonious trees of the phylogenetic relationships within the family Mylagaulidae.

ONTOGENETIC TRAJECTORIES AND TOOTH DEVELOPMENT

Black and Wood (1956) first approached the problem of interspecific versus intraspecific variation in Mylagaulidae. They used serial sections of 4th premolars to look at changes in lake patterns through wear in order to better understand age and individual variation. They concluded that species determination without serial sections was difficult as a consequence of the challenge of differentiating between interspecific and intraspecific variation. Shotwell (1958a) sectioned a number of specimens from Oregon (including several figured in this paper) to minimize the ontogenetic signal and review the systematics of Great Basin mylagaulids. In this study, I demonstrate that one can avoid such destructive protocol by using a large sample size of premolars to understand changes in occlusal morphology with different wear stages.

Isolated premolars of mylagaulids make up most of the fossil record of this family of burrowing rodents. There are extensive collections of upper and lower fourth premolars from numerous sites across the United States. Samples of many individuals from a single species in different ontogenic stages approximate the various wear stages of a single animal, avoiding a need for sectioning. As noted before by Shotwell (1958a), Korth (2000), and others, tooth wear through time triggers a change in tooth size, tooth shape, number of lakes on the occlusal surface of the tooth, and shape of these lakes. The number and length of the lakes increases through development whereas the width and complexity decreases. There is very little change in the orientation of the lakes throughout ontogeny.

Rectangular premolars in juvenile specimens tend to become more oval with wear. A number of teeth have a wear surface that is concave rather than flat. This occlusal curvature affects the morphology of the lakes both in their shapes and their dimensions by elongating the fossettes and fossettids antero-posteriorly. There is also a slight difference between individuals in the angle of the wear of the tooth. This tilting of the wear surface is very limited, but may be responsible for some inter-individual differences in fossette morphology. All of these wear patterns are tightly constrained by jaw mechanics; however, the hypsodonty of the tooth crown allows imprecise occlusion of the teeth, explaining some of the variability in the occlusal surface morphology of mylagaulids. In order to avoid such issues, numerous teeth must be examined with a focus on the adult wear stage. This need for a large sample size is one of the reasons I did not identify the specimens described as indeterminate mylagaulids to the species level. Intraspecific variation in mylagaulids includes variation in both tooth size and number of lakes, driven by tooth wear, but the orientation of the lakes and the shape and complexity of the lakes is consistent across individuals of the same wear stage. Between species, accounting for wear stage, the tooth size and the number of lakes differ, as do lake orientation and the shape and complexity of the lakes.

CHAPTER III

BIOTIC AND ABIOTIC DRIVERS OF TURNOVER IN BURROWING RODENTS

INTRODUCTION

Numerous studies have cited competitive replacement as a cause for the succession of taxa observed in the fossil record among invertebrates (e.g., Sepkoski et al. 2000) and vertebrates (e.g., Benton 1987) including burrowing insectivores (Barnosky 1981). Others have doubted the role of competition in evolution (e.g., Simpson 1944). Some authors (in particular Connell 1980) have suggested that detecting competition even in living species is very challenging, leading many to despair of ever detecting it in fossil ecosystems. However, a few studies of fossil animals have tested hypotheses of competitive replacement (i.e. Krause 1986, Van Valkenburgh 1999, Sepkoski et al. 2000). Studies of modern mammalian community ecology have provided evidence in favor of competition shaping mammalian community structure, and in particular within desert rodent species (e.g. Brown and Heske 1990, Hughes et al. 1994, Yunger et al. 2002).

Several researchers (e.g., Kennerly 1959) have suggested that interspecific competition in fossorial rodents is of minor importance, because they are mostly allopatric. More recent studies (e.g., Thaeler 1968, Miller 1964, Cameron 2000 and references therein) have shown that this allopatry is very often the result of interspecific competition, indicating that this process is a critical one in the distribution of burrowing rodents across the landscape. Cameron (2000) mentioned competition among subterranean rodents as having an important effect in shaping their distribution. Although subterranean rodents are rarely sympatric in modern ecosystems (Cameron 2000, references therein), numerous localities in the fossil record have two or more species of burrowing rodents in the same area (Shotwell 1963, 1968; Table 1). The goal of this study was to investigate the diversity pattern of fossorial rodents in the Miocene of the Northern Great Basin in search of the causes of turnover among burrowing rodents. Patterns of change in abundance were compared to global climate change, changes in vegetation, and the changes in abundance of other, potentially competing, burrowing rodent taxa. These comparisons should reveal whether biotic or abiotic forces are more important in driving the major changes in the burrowing herbivore guild during the late Miocene.

TABLE 1: List of the species of burrowing rodents considered in this study.

Family	Genus	Species
Aplodontidae	*Liodontia*	*alexandrae*
Aplodontidae	*Liodontia*	*dailyi*
Aplodontidae	*Liodontia*	*furlongi*
Aplodontidae	*Tardontia*	*occidentalis*
Geomyidae	*Brachygeomys*	sp.
Geomyidae	*Mojavemys*	*magnumarcus*
Geomyidae	*Mojavemys*	*mascallensis*
Geomyidae	*Pliosaccomys*	*magnus*
Geomyidae	*Pliosaccomys*	*minimus*
Mylagaulidae	*Alphagaulus*	*vetus*
Mylagaulidae	*Hesperogaulus*	*gazini*
Mylagaulidae	*Hesperogaulus*	species A
Mylagaulidae	*Hesperogaulus*	*wilsoni*
Sciuridae	*Ammospermophilus*	*junturensis*
Sciuridae	*Marmota*	*minor*
Sciuridae	*Eutamias*	sp.
Sciuridae	*Miospermophilus*	*wyomingensis*
Sciuridae	*Paenemarmota*	*nevadensis*
Sciuridae	*Petauristodon*	sp.
Sciuridae	*Protospermophilus*	*angusticeps*
Sciuridae	*Protospermophilus*	*malheurensis*
Sciuridae	*Spermophilus*	*tephrus*
Sciuridae	*Spermophilus*	*wilsoni*
Sciuridae	*Spermophilus*	*ridgewayi*

The guild of burrowing herbivores is composed of a rich and diverse group of rodents that dig extensive burrow systems for shelter, for food, and to protect their young. Some of the most extreme adaptations for this life habit occur in subterranean rodents, which spend almost all of their time underground and rarely come up to the surface. Today, subterranean rodents are dominated by the Geomyidae in North America (Lacey et al. 2000, Nevo 1999), but in the past this ecological role has been filled by a variety of taxa, including castorids and mylagaulids. This study focuses on animals with extensive underground life habits, encompassing both fossorial and subterranean forms. The term fossorial refers in this paper to both animals that hide and dig extensive networks of tunnels but reproduce and feed above ground on surface vegetation and/or animals (Reichman and Smith 1990), and subterranean rodents that live and reproduce underground, feeding mostly on roots and tubers (Reichman and Smith 1990, Lacey et al. 2000). This definition excludes many mammals that dig simple burrows but do not, as a consequence, exhibit osteological adaptations to a burrowing way of life.

Throughout the Cenozoic, the composition and importance of the burrowing herbivore guild has changed. In the Oligo-Miocene of North America, several groups of rodents replace one another as the most abundant member of the burrowing rodent fauna. In the early Arikareean (30 to 23 Ma), pleurolicine geomyids dominated the fauna, especially in eastern Oregon (Rensberger 1973, Samuels and Van Valkenburgh 2009). Later, in the late Arikareean (23 to 19 Ma), fossorial beavers (Palaeocastorinae) became more abundant, in particular in the fossil record of the Great Plains (Martin and Bennett 1977, Samuels and Van Valkenburgh 2009, Hopkins 2007). In the early Hemingfordian (19 to 17.5 Ma), mylagaulids became abundant, as shown in the Great Plains and Great Basin fossil record. They continued to be diverse and abundant until the late Hemphillian (5 Ma). In the Great Basin, in particular, they seem to be more abundant than in the Great Plains or the Rocky Mountains, whereas geomyids are conversely rarer in the northern

Great Basin. At this point, mylagaulids waned and the geomyids became more abundant in the Great Basin and even moreso in other areas of the west (e.g., Split Rock, WY). Members of the Aplodontidae are common in the Whitneyan to late early Arikareean (32 to 19 Ma), decline at the end of Oligocene (Hopkins 2007, Rensberger 1983), and remain at low diversity until the end of the Miocene. Aplodontids then disappear from the fossil record until the Pleistocene, when they are found in Californian cave deposits (Hopkins 2007, Lyman 2008).

Numerous hypotheses have been proposed to explain these successive changes in fauna. Samuels and Van Valkenburgh (2009) proposed that predator pressure from burrowing carnivores might have been important in driving fossorial beavers to extinction. Samuels and Van Valkenburgh (2009) as well as Hopkins (2007) have suggested that the rise of the Mylagaulidae could have been responsible for the competitive replacement of the Paleocastorinae. Conversely, Baskin (1980) suggested that the rise of the geomyids impacted the decline of the mylagaulids. Samuels and Van Valkenburgh (2009) suggested that similar processes to those affecting the evolutionary history of the fossorial beavers might have influenced the less fossorial ground squirrels and marmots (Sciuridae: Marmotini). Hopkins (2007), however, did not find a correlation between sciurid or castorid diversity and that of aplodontids. This project will further attempt to investigate possible interactions within the fossorial herbivore guild that would involve marmotins. Other researchers have preferred abiotic explanations to the diversity changes within the burrowing herbivore guild. Shotwell (1958a) favored an environmental explanation for changes in diversity of mylagaulids. He tied the radiation and decline of the Mylagaulidae to changes in the distribution of dry habitats. Shotwell (1958a) suggested that after the Hemingfordian, aplodontids occupied mesic forested environments while mylagaulids occupied drier savanna-like open environments (see also Baskin 1980). Hopkins (2007) tested many factors that could have affected the evolution of mylagaulids and aplodontids, and found no evidence coupling global climate change (as indicated by marine oxygen isotopes) with changes in aplodontid and mylagaulid diversity. She suggested that the changes in vegetation, in particular related to the rise of grasslands, might explain some of the decline in diversity during the late Oligocene and late Miocene (Hopkins 2007).

This study further investigates the drivers of fossorial mammal guild dynamics in the northern Great Basin (southeastern Oregon and northwestern Nevada). This area has a very rich fossil record that has been extensively collected (Davis and Pyenson 2007, Shotwell 1963). The terrestrial fossil record of this area spans the late Hemingfordian through early late Hemphillian, from 17.5 to 5.8 Ma, a time period critical to the spread of grasslands in North America (Strömberg 2005, Retallack 2007). This event has been suggested to be important in the evolution of some rodent taxa included in this study (Stirton 1947, Webb 1966, Hopkins 2007). The most abundant fossorial rodents during the late Hemingfordian and early Barstovian in the study area considered here are the mylagaulids. These large, highly fossorial to subterranean rodents are critical to understanding the ecology of burrowing rodents in the Miocene. They were purportedly involved in two competitive replacement events and radiated during the spread of grasslands (Hopkins 2007, 2008, Baskin 1980) at a critical time for climate change in the Miocene: the Mid-Miocene Climatic Optimum (Zachos et al. 2001, Retallack 2009). This event was the warmest and wettest time on Earth since the beginning of the Oligocene and corresponds to some predictions of global warming for the upcoming century (Zachos et al. 2001, Houghton et al. 2001, Solomon et al. 2007).

This study system provides the opportunity to set up a test of competition and its impact on changes in the burrowing rodent guild. Thus, the competitive interaction of mylagaulids and geomyids (Baskin 1980), should result in a negative relationship between the relative abundance of mylagaulids and that of a potential competitor: the Geomyidae. Alternatively, if mylagaulids are ecologically more like their close relatives, mylagaulid relative abundance should be negatively correlated with that of ground squirrels (Marmotini) or their fossorial sister clade, the Aplodontidae.

In light of the results of the tests of this hypothesis (see results and discussion), we also investigated climatic and environmental factors that could have driven changes in the burrowing herbivores.

MATERIAL AND METHODS

Study system

Data on the diversity of fossorial rodents in the Miocene of the Great Basin were collected from collection records. The time frame for this study starts with the peak of the Mid-Miocene Climatic Optimum (Miller et al. 1997, Zachos et al. 2001) and ends with the end of the Hemphillian (i.e. 17 Ma to 4.8 Ma). This time frame was chosen not only because of the abundant and well-dated fossil record but also because, in addition to a change in climate, it experienced substantial changes in flora and fauna.

The geographic area of this study was limited to southeastern Oregon and northwestern Nevada (Fig. 1) to represent the approximate scope of a modern ecosystem, encompassing a scale over which real ecological interactions would be expected to take place. Hopkins (2007) suggested that regional scale studies may be more appropriate for investigating the effects of changing environments on diversity. The geographic area considered in this study provides an area representative of a single ecosystem that allows such test. This area, the northern Great Basin, remains among the richest sequences available for this time period in North America. It includes parts of Oregon, Nevada, and Idaho and has been referred to by some paleontologists as the Columbia Plateau (Barnosky et al. 2005, Tedford et al. 2004). This region includes faunas from the Drewsey, Grassy Mountain, Juntura, Chalk Butte, Butte Creek Volcanic Sandstone, Deer

Butte, Sucker Creek, Thousand Creek, and Virgin Valley Formations as well as the Massacre Lake Local Fauna, Beatty Buttes, Piute Creek, and Rattlesnake Butte Faunas.

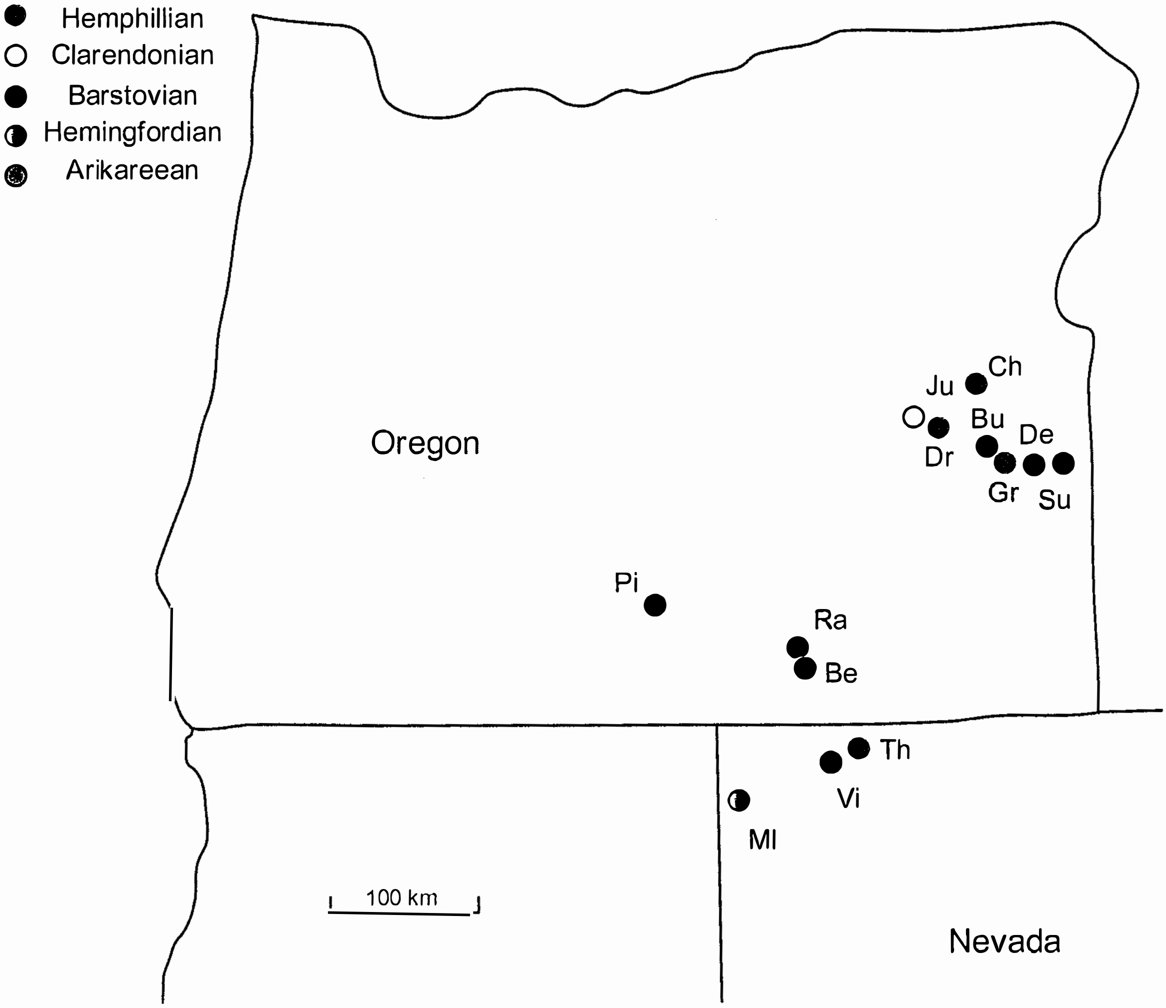


FIGURE 1: Map of the formations and collection areas included in this project with the North American Land Mammal Ages indicated. Abbreviations: Be. Beatty Buttes Fauna; Bu, Butte Creek Volcanic Sandstone Fm., Ch, Chalk Butte Fm.; De, Deer Butte Fm.; Dr. Drewsey Formation; Gr, Grassy Mountain Fm.; Ju. Juntura Fm.; Ml. Massacre Lake Fauna; Pi. Piute Creek Fauna; Ra, Rattlesnake Butte Fm.; Su. Sucker Creek Fm; Th. Thousand Creek Fm.; Vi. Virgin Valley Fm.

Southeastern Oregon and northwestern Nevada, which are the focus of this study, are the primary drainage basin of the Snake River and its tributaries (the Malheur and Owyhee Rivers). The area is bounded to the west by the southeastern Cascade Range and the northernmost Sierra Nevada, and to the east by the Owyhee Mountains. The northern boundary of the study area corresponds to the southern boundary of the Blue Mountains. The region of interest is thus primarily in Malheur, Lake, and Harney Counties in Oregon, and Humboldt and Washoe Counties in Nevada. The succession of basins and ranges (e.g., Juntura Basin, Steens Mountains, Harney Basin) in these counties is characteristic of the larger structure of horst and graben that was responsible for the Cenozoic extension in the larger geologic province of the Basin and Range that extends south of the province studied. The terrain where fossils occur in the region is a rugged, hilly and topographically complex high desert. Elevation varies greatly, reported by Kittleman et al. (1965) to range from 2,400 to 6,500 feet for Malheur County where many of the fossils used in this study were found. The modern habitat over much of this area is desert. Retallack (2004) found the area to be mostly dry in the Miocene as well (< 400 mm mean annual precipitation). The region is extensively covered by both extrusive volcanic rocks and ashy sediments of the Miocene through Pleistocene due to frequent volcanic events (see Kittleman et al. 1965).

The collection record of southeastern Oregon is believed to be representative of the original assemblage preserved in the rock, a result of systematic collecting efforts, designed for paleoecology studies, by Shotwell and his field assistants (Shotwell 1963, Hutchison 1968) to maximize the degree to which museum collections reflect the living ecology. Significant amounts of matrix (up to several hundred tons) were screened with standard and fine screens. The numerous localities of this region have yielded and still yield a very rich fossil record of Miocene mammals whose taxonomy and morphology is well understood (Hutchison 1966, 1968, Shotwell 1954, 1958a, 1958b, 1967a, 1967b, 1968, 1970). While the systematics of mammalian species in the northern Great Basin has been well studied, very few studies have attempted to decipher either small mammal paleoecology or their paleoenvironments in the northern Great Basin since the late 1960s (but see Davis and Pyenson 2007, and Davis 2005 for work on Thousand Creek and Virgin Valley as well as Retallack 2004 for work on southeastern Oregon paleoclimate).

The taxa included in this study, in addition to the Mylagaulidae, are the family Geomyidae as well as the Aplodontinae and Marmotini. These taxa have been suggested to be involved in competition within the guild of fossorial herbivores along with mylagaulids (Baskin 1980, Samuels and van Valkenburgh 2009). Fossorial castorids have been previously reported to be important in those events (Hopkins 2007, Samuels and van Valkenburgh 2009). However, although there are numerous occurrences of aquatic species of castorids (e.g., *Dipoides*, *Monosaulax*), there is none of burrowing beavers in the area considered during the time frame investigated. There is also no fossil of another possibly important group, the Arvicolinae (voles, lemmings, muskrats), in the area during the Miocene. A summary of the fossils considered in this study is provided in Table 1.

I follow the taxonomy and phylogeny of Korth (1999, 2000) and Hopkins (2008a) for mylagaulids. I follow Hopkins (2008a) for aplodontines and Black (1963) for sciurids. Geomyids of southeastern Oregon are extensively described in the work of Shotwell (1967b).

Data collection

The different hypotheses are investigated with the same original dataset: abundances of fossorial rodents relative to all small mammals (i.e. mammals with body mass <5 kg, Merritt 2010). The relative abundance data were derived from collection records of the University of California Museum of Paleontology (UCMP), the Los Angeles County Museum (LACM), and the University of Oregon Museum of Natural and Cultural History (UOMNH). Specimen data from UCMP were downloaded from the online catalog (http://www.ucmp.berkeley.edu/science/vertebrate_coll.php). Specimen data from the LACM were collected on-site from the electronic records of the collections. Specimen data from the UOMNH were obtained through digital cataloguing of all curated small mammal specimens from southeastern Oregon as well as additional curating and cataloguing of previously uncurated specimens from the area of interest by the author and collaborators. This additional curation and cataloguing focused on small mammals with the goal of covering all localities included in this study. All fossorial rodents available were curated and catalogued. Numerous, other, non fossorial, small mammals were also included. I address the potential issue of biases in abundance due to the lack of comprehensive curating and cataloguing of previously unrecorded non fossorial small mammals by using the MNI as well as occurrence data. The choice to use collection records rather than occurrences from databases was motivated by the inherent bias of publications (Davis and Pyenson 2007) as well as the focus of the study on southeastern Oregon, an area with substantial unpublished collections. In addition, the focus of this study on relative abundance necessitated the larger sample size of collections records.

For each locality where at least one of the burrowing rodent taxa of interest (i.e. Mylagaulidae, Aplodontidae, Marmotini, Geomyidae) was represented by at least one specimen, I gathered a complete faunal list with information covering taxonomic affinity and element represented. For each of the localities, I used the catalog information to determine the Number of Identified Specimens (NISPs) and the Minimum Number of Individuals (MNIs) for dental remains of all small mammals. All raw data are provided in Appendix B. Due to their adaptation to burrowing, fossorial rodents exhibit a very peculiar morphology that might bias the relative abundances of these taxa as a consequence of being more diagnostic than that of small mammals of more generalized ecology. Therefore, only adult teeth (including incisors) are used to determine the NISP for each taxon of interest (deciduous teeth are ignored since they could lead to overrepresentation with individuals counted both as juveniles and adults). The data from the collection records were analyzed using relative abundances because it is a better proxy of the importance of the taxon at a local to regional scale. The use of relative abundance was also motivated by the suggestion that relative abundance might be more relevant to studies of competitive replacement (Krause 1986). The relative abundance of each small mammal taxon at each locality was determined from the MNI. The relative abundances of taxa were lumped at the family level. MNIs were determined using the method of Binford (1978); when information on the side (i.e. left versus right) of the specimen was missing from the catalog records, MNIs were obtained from NISPs by considering all teeth (both left and right) and dividing by two (symmetrical elements). This method is efficient and allows use of data even when records don't have specimens completely sided, a frequent problem with unpublished specimens.

The data were analyzed in two different ways. I grouped the locality level information into collecting areas (i.e. formation or local fauna) as well as within subdivisions of North American Land Mammal Ages (NALMAs) to look for variation through time and across the landscape. All analyses were performed in R 2.10.1 (2009).

Whenever competitive replacement of one taxon by another is suggested, it is assumed that the replacing clade possesses a superior competitive ability over the replaced one. In such a case, when the two groups co-occur, the replacing clade will force the replaced clade out of its ecological niche and fill this newly available niche. If the diversity dynamics of some taxa are driven by competitive replacement, I should observe a double-wedge pattern (Benton 1987) in the abundance of taxa (Fig. 2). The presence of such a pattern is necessary but not sufficient to conclude that competition was the driver of evolution in the taxa studied. In order to fully test for competitive replacement, it is also necessary to consider the paleoecology of the organisms as a whole through habitat use, body size, and diet.

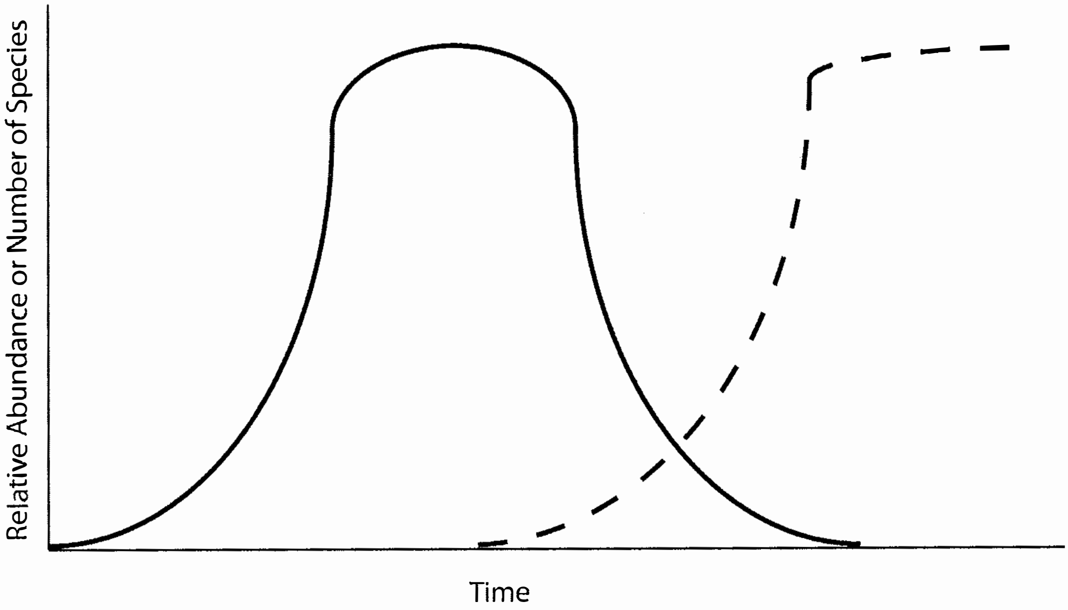


FIGURE 2: Expected diversity or abundance pattern of competing taxa (after Hopkins 2007).

I also collected data on the presence/absence of all mammalian taxa for all localities in the region studied (Appendix C). The nature of the collection record of the UOMNH did not allow relative abundance information to be gathered from the catalog for all mammals (only small ones). The presence/absence data for those collections were completed using published occurrences with the help of MIOMAP (Carrasco et al. 2005). Those published records come mostly from the work of Shotwell (e.g., 1963, 1968), Hutchison (1968), and Russell (1956) who provided extensive faunal lists for southeast Oregon.

Localities, stratigraphic and geographic information

Over 60 localities from southeastern Oregon and northwestern Nevada are included in this analysis. The accuracy of the dating varies greatly. Dating of the sediments of those localities relies on several methods including biostratigraphy, magnetostratigraphy, and radiometric dating. A few localities have been dated with limited accuracy using fossil assemblages, and cannot be assigned more accurately than to a NALMA. Although I found a few chronologically poorly-constrained localities to be relevant to the discussion of the results, I only analyzed data from localities that could be assigned to a subunit of NALMA. These subunits are most often less than two million years long (with the exception of the late Barstovian). Binning the data by subunits of NALMAs prevents inaccuracies in the dating of localities from influencing our results. These temporal bins are not equal in duration but this has little effect on diversity counts since there is no correlation between the length of each bin and the number of localities for these time periods (consider the early Barstovian versus the late Clarendonian for example) and since no locality spans the entire time represented by each subunit (see also Barnosky et al. 2005). All age assignments for NALMAs follow Tedford et al. (2004). For analyses binning taxa by collecting areas, I used the age of the formation as published (see Table 2 for ages and references).

TABLE 2: Summary of the data for the formations and collection areas considered in this study. Abbrevations for subdivisions of North American Land Mammal ages (NALMAs): LHMF, late Hemingfordian; EBAR, early Barstovian; LBAR, late Barstovian; LCLA, late Clarendonian; EEHP, early early Hemphillian; LEHP, late early Hemphillian; ELHP, early late Hemphillian. Collection areas in parentheses.

Formation	(Massacre Lake)	Virgin Valley	(Beatty Buttes)	Sucker Creek	Deer Butte	Butte Creek Volcanic Sandstone	Juntura	Thousand Creek	Drewsey	Grassy Mountain	Chalk Butte
NALMA	LHMF	EBAR	EBAR	EBAR	LBAR	LBAR	LCLA	EEHP	LEHP	LEHP	ELHP
Max Age (Ma)	16.60	15.9	15.90	15.90	14.77	14.80	10.00	8.00	7.50	7.50	6.70
Mean Age (Ma)	16.55	15.54	15.35	15.35	12.50	12.50	9.70	7.75	7.30	7.10	6.30
Min Age (Ma)	16.50	15.18	14.80	14.80	13.635	13.65	9.40	7.50	7.10	6.70	5.90
+/-	0.05	0.36	0.55	0.55	1.135	1.15	0.30	0.25	0.20	0.40	0.40

Ecological category assignment and predictions of competitive replacement

The biotic interactions examined by this study are possible competitive replacements within the burrowing herbivore guild. In order to assess if such interactions are of any importance in the evolution of mylagaulids, I compared both the relative abundance through time and the MNI through time of the mylagaulids and their potential competitors. These two proxies are expected to give very similar results (the relative abundance is derived from the MNI) but the MNI, unlike the relative abundance, does not consider the abundance of other small mammals in the area. Furthermore, I graphed the number of localities through time at which the taxa occur in order to look for a signal in the occupancy of the landscape by the clades studied. In addition to comparing data through time, I also looked at the locality data in search of sites where mylagaulids and their potential competitors co-occurred. I tested the randomness of the co-occurrence of the two taxa using the Chi-square test. It was not possible to plot the relative abundance of mylagaulids versus that of geomyids (or any other combination of the members of the guild) since the absence of one of the two taxa in most sites violates the assumptions of a linear regression.

The competitive replacements in which mylagaulids might have been involved must have also involved taxa with similar ecological requirements. For geomyids to replace mylagaulids in this niche, they must have shared very similar ecologies. Assessment of the ecological similarity between geomyids and mylagaulids consists here of contrasting their likely diets, body sizes, and habitat use. Similarly, I also assessed the potential overlaps in ecology between mylagaulids and sciurids as well as mylagaulids and aplodontids using similar variables. Although some information is missing for the species considered in this project, the families as a whole have good fossil records and their paleoecologies can be approximated accurately enough for family scale comparisons. These data allow for the ecologies of the four families to be estimated.

Important paleoecological characteristics of the taxa considered that can be approximated from the fossil record include: (1) body size, (2) diet and, (3) degree of fossoriality. Table 3 summarizes those data for each of the four families considered in this study.

TABLE 3: Summary of the paleoecological parameters for each of the taxa of the burrowing herbivore guild. Body size is indicated by the lower tooth row. Data for aplodontids, marmotins, and mylagaulids are from Hopkins (2007, Appendix 1), and Calede (second chapter of this thesis). Note that the size estimate of *H. wilsoni* is biased by the loss of the molars (the tooth row is reduced to the 4th premolar). *H. wilsoni* is actually the largest species of the genus (Korth 1999, first chapter of this thesis) as indicated by cranial material. The upper limit of the body size range of Geomyidae is based on the upper tooth row length. All measurements are in mm.

Taxon	Body Size Range	Diet	Degree of fossoriality
Aplodontidae	11.66 – 13.61	Abrasive diet feeding (above ground)	Semifossorial to fossorial
Geomyidae	4.20-5.36	Abrasive diet (underground)	Subterranean
Marmotini	6.6 – 11.35	Seeds, nuts, fungi, … (above ground)	Semifossorial to fossorial
Mylagaulidae	12 – 18.24	Abrasive diet (underground)	Subterranean

The body size of rodents, especially of non-muroids, can be accurately estimated from the toothrow length (Hopkins 2008b). Appendix 1 of Hopkins (2007) provides body size information for most taxa used in this study. I followed the method of Hopkins (2008b) to provide the missing body size data. When no complete tooth row was available, I added the lengths of each tooth to obtain measurements based on a composite tooth row.

The diets of the fossil taxa considered here have been studied very little. Diets are estimated from gross dental morphology, a method that has proven reasonably accurate (e.g., Janis 1995), though ongoing work to apply more precise proxies to this question will improve the accuracy of dietary reconstructions.

The degree of fossoriality of those variably burrowing rodents can be assessed through the qualitative study of postcranial elements or the use of quantitative morphological proxies (Mauk et al. 1999, Hopkins and Davis 2009). The humeral index has been used by Korth (2000) to approximate the degree of fossoriality of mylagaulids. Numerous other measurements of the limbs and skull can also be used when available (Hopkins and Davis 2009). Unfortunately, postcranial elements of most of the rodent taxa from the Great Basin are not well represented in the fossil record.

Another line of evidence available for the study of fossoriality in fossil rodents is ichnology and the morphology of preserved burrows. Although none have been recovered in the Great Basin, there are possible occurrences of fossorial rodent burrows in the tuff beds of the Beatty Buttes Fauna (Wallace 1946). Nevertheless, some Great Plains specimens shed light on the burrowing habits of related species both within mylagaulids and geomyids (Gobetz 2006, Gobetz and Martin 2006).

Geomyids and mylagaulids are found to have very similar burrowing habits. Both groups are highly fossorial to subterranean animals. The complex morphology of a recovered mylagaulid burrow from the Great Plains is similar to that of *Geomys* (eastern pocket gopher,) and indicates a highly subterranean way of life (Gobetz 2006). Gobetz and Martin (2006) described a gopher burrow from the Harrison Formation of Nebraska and presented evidence for fossorial chisel-tooth digging habits in an entoptychine (Geomyidae), thus confirming that the fossorial ecology widespread in modern gophers was already present in the early Miocene.

Geomyids differ from mylagaulids in their body size. The latter are large rodents (mass > 1 kg, Hopkins 2008a, b) comparable in size to their closest modern relative, the sewellel (*Aplodontia rufa*), whereas geomyids are much smaller animals that are no bigger than a few hundred grams. This difference in body size, however, may not be an obstacle to competition as shown in modern systems (e.g., Brown and Davidson 1977). There is no need for a precise size match but rather a size that is similar enough to imply similar use of food and space resources. The diet of the fossil forms is poorly known (but see fourth chapter of this thesis). Mylagaulids have been suggested to feed on very abrasive food (as indicated from their hypsodont dentition). Geomyids have quite a high-crowned dentition and wear down their teeth, leaving lakes of dentine surrounded by enamel at the occlusal surface. Modern gophers feed on grasses (Williams 1982) or underground food rich in nutrients, but also ingest exogenous grit (Jones and Baxter 2004). I can thus infer an abrasive diet for geomyids as well. These two groups of rodents seem to be likely competitors and further exploration of the hypothesis of Baskin (1980) is justified.

Marmotini and aplodontids differ somewhat in ecology from geomyids and mylagaulids. They are not as fossorial. They mostly feed above ground on a diversity of foods (Carraway and Verts 1993, Belk and Smith 1991, Frase and Hoffmann 1980, Gannon and Forbes 1995, Jenkins and Eshelman 1984). This diversity of food does not preclude overlap in diet with mylagaulids (in particular in light of the results of the fourth chapter of this thesis). Both aplodontids and marmotins are well above the body sizes of geomyids. However, both aplodontids and Marmotini are more similar in body size to mylagaulids (Kwiecinski 1998, Nagorsen 1987, Carraway and Verts 1993, Hopkins 2007, Hopkins 2008b). Aplodontids and Marmotini are close in size to each other. Aplodontids, on the other hand, are restricted to the genera *Liodontia* and *Tardontia.* These rodents are smaller than the modern mountain beaver (*Aplodontia rufa*), closer in size to ground squirrels, and may feed on rather abrasive food as indicated from their hypsodont dentition. There are no known postcrania of *Liodontia* that could inform the degree of fossoriality of this taxon. However, cranial morphology suggests burrowing habits close to those of *Meniscomys* (Morea 1981, Hopkins 2006), which are similar to those of ground squirrels. The distribution and ecologies as well as habitat requirements of modern Marmotini and mountain beavers are quite unlike each other. The modern *Aplodontia rufa* is present in a very restricted geographic area with temperate rainforest whereas ground squirrels and marmots are found in very diverse environments, some very dry (Caraway and Verts 1993, Belk and Smith 1991, Frase and Hoffmann 1980, Gannon and Forbes 1995, Jenkins and Eshelman 1984). The diversity in ecology within marmotins including overlaps with mylagaulids, and the similarities between mylagaulids and aplodontids (including their shared evolutionary history) supports the need for additional testing (see also Hopkins 2007) of the hypothesis that Marmotini (Samuels and Van Valkenburgh 2009) and aplodontids might have influenced the relative abundance of mylagaulids in the Miocene of the Great Basin.

Patterns in abundances within the fossorial herbivore guild

I also investigated variations in relative abundance and MNI for all burrowing rodent taxa through time. I present data on the changes in the relative contribution of each family to the burrowing herbivore guild throughout the mid to late Miocene. I analyze those with the help of chord distance analysis across subunits of NALMAs. Chord distance analysis is a measure of the difference based on the cosine of the angle between two vectors of abundance data (the relative contribution of each fossorial rodent group to the guild in two different NALMA subdivisions). Chord distance analysis is used to look for faunal turnover in mammalian assemblages (e.g., Frost 2007, Bobe et al. 2002). The measure of the chord distance between a sample j and a sample k runs from 0 to $2^{1/2}$ and is computed from the following formula (see Bobe et al. 2002):

$$CRD_{jk} = [2(1-ccos_{jk})]^{1/2} \qquad (1)$$

Using X_{ij}, the abundance of the ith taxon in sample j, X_{ik}, the abundance of the ith taxon in sample k, and X^S, the total number of taxa in both samples, $ccos_{jk}$ is computed with:

$$ccos_{jk} = \Sigma^S(X_{ij}\ X_{ik}) / [\Sigma^S X_{ij}^2\ \Sigma^S X_{ik}^2]^{1/2} \qquad (2)$$

The chord distance was calculated both for the MNI and the relative abundance of each fossorial rodent group within the guild across the subdivisions of NALMA to look for important changes in the composition of the guild through time. The early late Hemphillian was removed from this analysis due to the very small sample size of fossorial rodents in this time interval.

Climate and fossorial rodent diversity

There is very little local to regional information on the climate of the northern Great Basin. There is no information for southeastern Oregon and northwestern Nevada proper (but see Retallack 2004). The closest terrestrial area for which there is climatic data is the John Day Basin. Retallack (2007) has developed a climate curve for central Oregon (i.e. John Day area) from paleosol data, but this dataset lacks mean annual temperature information for the late Barstovian through the early late Hemphillian, which comprises most of the time frame spanned by this study. Nevertheless, the climate curve for central Oregon follows closely the global temperature trend as indicated by the stable isotope proxy $\partial_{18}O$ (Zachos et al. 2001). These data come from Pacific Ocean sediment cores spanning the Cenozoic. The data were binned by subunit of NALMAs in order to be comparable to the relative abundance of fossorial rodents. The influence of global temperature changes (as a proxy for regional changes) on the abundance of the fossorial rodent taxa was assessed through simple linear regressions of the relative abundance of the family against the $\partial_{18}O$. I tested the effect of changing climate on the abundance of fossorial rodents as a whole as well as on the mylagaulids and the geomyids.

Environmental and vegetational changes in the mid to late Miocene of Oregon

The spread of grasslands in the mid Miocene and the rise in C4 vegetation in North America has had a major impact on the changes in fauna, in particular within ungulates. While there is no C4 vegetation in eastern Oregon (Cerling et al. 1997), the spread of grasslands in Oregon might nevertheless have been a major driver of the evolution of mylagaulids and other fossorial rodent taxa. Hopkins (2007) focused her analysis of the vegetational changes and their potential relation to changes in aplodontid and mylagaulid diversity in the Great Plains but mentioned that the aplodontid and mylagaulid record of the northern Great Basin should be investigated as well. There are two sources of data when considering the switch from a more woodland-dominated early Miocene and a more grassland-dominated mid to late Miocene. Paleosol data can provide information on ecosystems in the area during the middle and late Miocene (e.g. Retallack 2007, Retallack et al. 2000). In addition, phytoliths have been used to study the spread of grasses in the Great Plains (e.g. Strömberg 2005). There is a small dataset of paleosol data from southeastern Oregon (Retallack 2004) that provides limited paleoenvironmental information. No phytolith data are yet available for the time frame or geographic range used in this study.

To look for differences across sites with little ancillary information, faunal differences can be evaluated as a proxy for microhabitats. Some taxa have very restricted environmental requirements, and mammalian faunal similarity provides a reasonable proxy for overall ecosystem similarity (van Dam 2006, Heikinheimo et al. 2007). I therefore performed a cluster analysis of the localities based on the presence or absence of other mammalian taxa as a proxy for environmental conditions. This analysis was run in R 2.10.1 (2009) using euclidean distances and the Ward clustering algorithm. For this analysis I only used localities where mylagaulids, geomyids, or both are present. I excluded from the faunal list the geomyid and mylagaulid taxa and only considered in the analysis localities for which five or more mammalian taxa are present and either recorded in catalogs or on MIOMAP (for the UOMNH localites). I excluded bats

(Vespertilionidae) from the dataset because they do not share a common taphonomy with land mammals because of their very fragile nature and their aerial ecology. This analysis allows the investigation of the possibility of an association of some fossorial taxa with microhabitats. A pattern of reciprocal exclusion between mylagaulids and geomyids might be evidence either for biotic interactions or for environmental preferences; consideration of the remainder of the fauna will make it possible to suggest which of these possibilities is most likely.

RESULTS

Sampling through time

Fig. 3 shows the sampling of the region's fossil record throughout the time frame considered. The early early Hemphillian represented by the Thousand Creek Formation (9-7 Ma) is the most poorly sampled subdivision of NALMAs with 162 specimens of small mammals versus 841 small mammal specimens in the late Barstovian (12.5-14.8 Ma). The early late Hemphillian is the most poorly sampled time interval for fossorial rodents (26 specimens). This is not associated with an overall decrease in small mammal sampling and might reflect a true trend in the abundance of small fossorial mammals (see Hutchison 1968 for a case study in moles). Nevertheless, this time subunit had to be discarded for some of the analyses described below and its data should be considered cautiously.

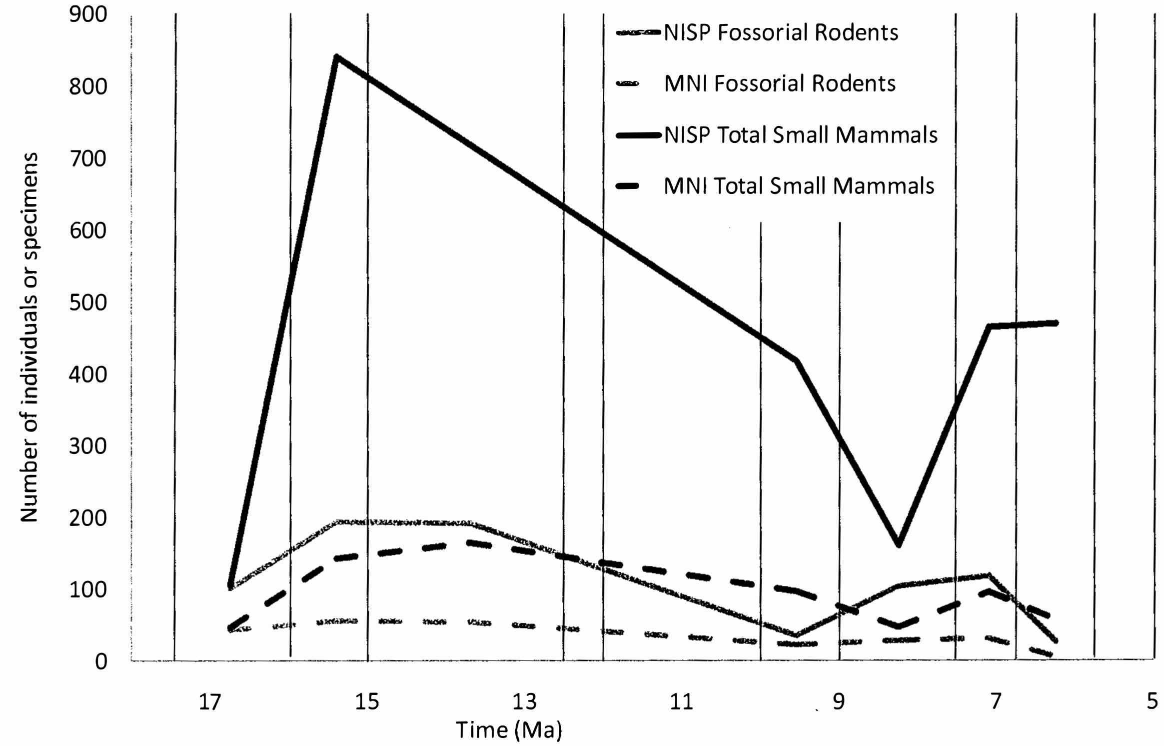


FIGURE 3: Sampling through time of all small mammals and fossorial rodents in the area of interest. Abbreviations: NISP, Number of Identified Specimens; MNI, Minimum Number of Individuals. Vertical bars indicate the limits of the subdivisions of North American Land Mammal Ages.

Biotic interactions within the burrowing herbivore guild

The trends in relative abundance through time of the burrowing herbivore guild show an overall decrease through time with the exception of the early early Hemphillian, when burrowing rodents, and geomyids in particular, are abundant in the Thousand Creek Formation (Fig. 4).

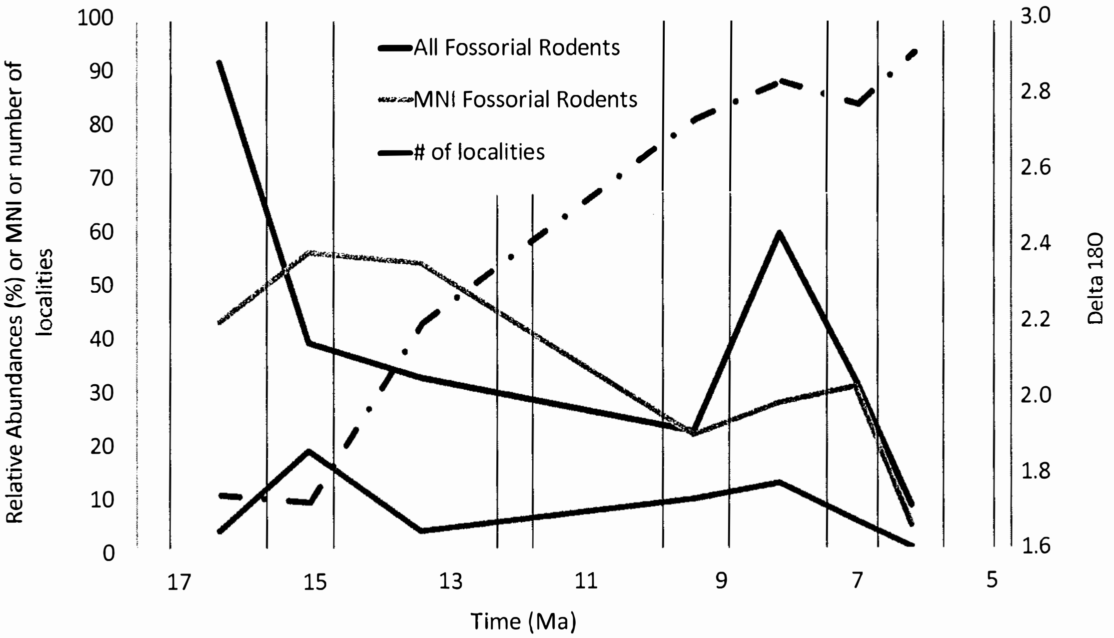


FIGURE 4: Relative abundance, Minimum Number of Individuals (MNI), and number of localities of all fossorial rodents and $\delta_{18}O$ through time as a proxy for global climate.

The mylagaulids, Marmotini, and aplodontids show a decline in relative abundance throughout the mid- to late Miocene (Fig. 4). The geomyids, on the other hand, show an increase in abundance up to the early early Hemphillian. This is followed by a decline in relative abundance in the late early Hemphillian and early late Hemphillian. The pattern observed between mylagaulids and geomyids is consistent with a negative correlation between the two taxa rather than the directional pattern of a double-wedge. The transition in relative abundance is unfortunately happening in a poorly-preserved interval (early early Hemphillian). There is no evidence for a double-wedge pattern between Marmotini and aplodontids. Most of the variation in the relative abundance of each fossorial rodent group is concentrated in the earliest (Barstovian) and latest (Hemphillian) parts of the time range studied. There are no substantial differences between the late Barstovian and the late Clarendonian where the largest gap in sampling is found. One would expect a longer unsampled time interval to lead to larger differences in faunas if change is relatively constant through time. This is not evident in this dataset and supports the hypothesis of events rather than directional trends driving the evolution of the community structure. This does not mean that the early and middle Clarendonian were uneventful; rather that those events did not trigger long term changes in the guild composition. When looking at the MNI values rather than the relative abundance, the data are more sensitive to sampling but support similar conclusions (Fig. 5). The pattern of negative correlation displayed by the geomyids and mylagaulids appears to be stronger with few geomyids in the Barstovian when mylagaulids are abundant and numerous gophers in the Hemphillian when mylagaulids are rarer. The curves intersect after the late Clarendonian as they do in the graph of the relative abundance. Once again, there is no pattern suggesting competitive interaction between ground-dwelling sciurids and aplodontids or between these groups and geomyids or mylagaulids.

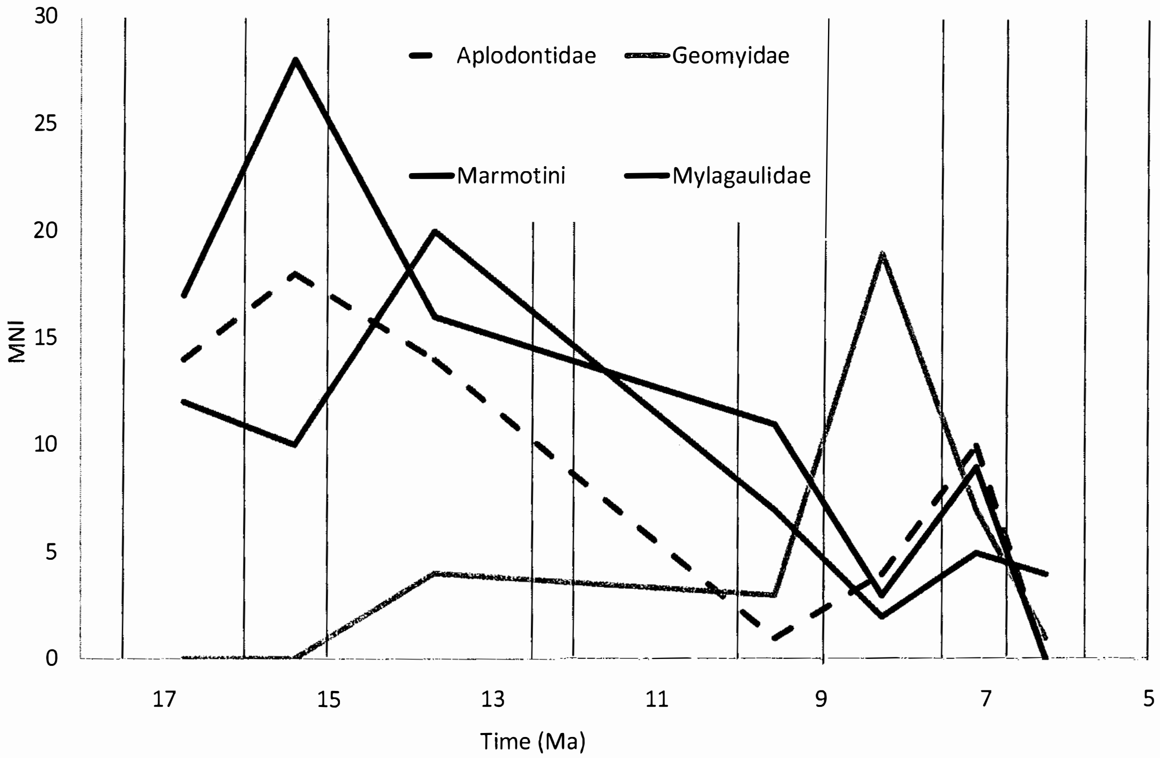


FIGURE 5: Changes in Minimum Number of Individuals (MNI) through time of each of the fossorial rodent groups.

Rather than considering the relative abundance of taxa at the localities, one can also look at the distribution of the taxa over the landscape. Fig. 6 shows the number of localities where at least one taxon is present through time. There is a greater number of localities occupied by fossorial rodents in the late Barstovian than in the Hemphillian. Mylagaulids and geomyids seem to follow opposite trends. Marmotini and Aplodontidae display a stronger double-wedge pattern than in the previous analyses but this trend doesn't hold in the late Hemphillian.

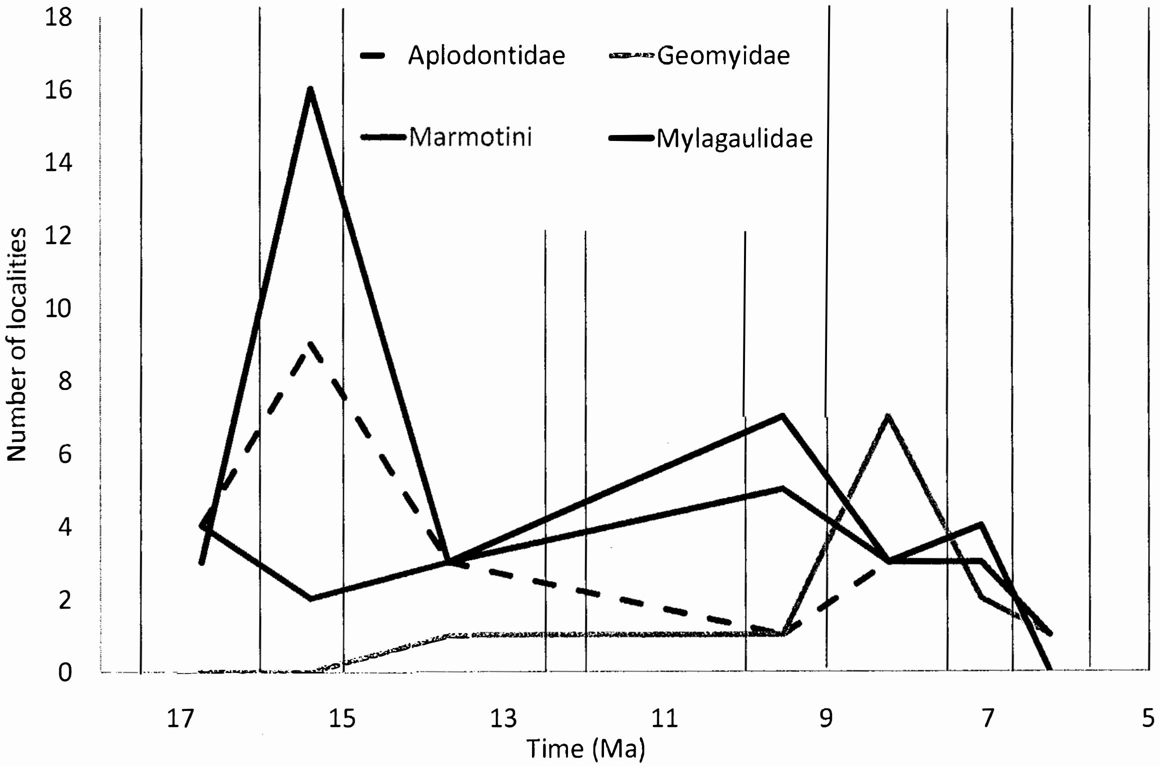


FIGURE 6: Changes in number of localities occupied by each of the fossorial rodent groups through time.

Because the curve of Fig. 6 is affected by sampling, I also normalized the number of localities where mylagaulids and geomyids occur by dividing the number of localities where each group is present by the total number of fossorial rodent localities (Fig. 7). These values show a very strong negative correlation between the two taxa. This pattern is suggestive of habitat tracking rather than direct competition. Trends in relative abundances of two competing taxa, illustrated by a double-wedge pattern, should be a directional pattern of the decrease in abundance of one of the taxa associated to the increase of the other. This pattern should be resolved once rather than exhibiting alternating abundances.

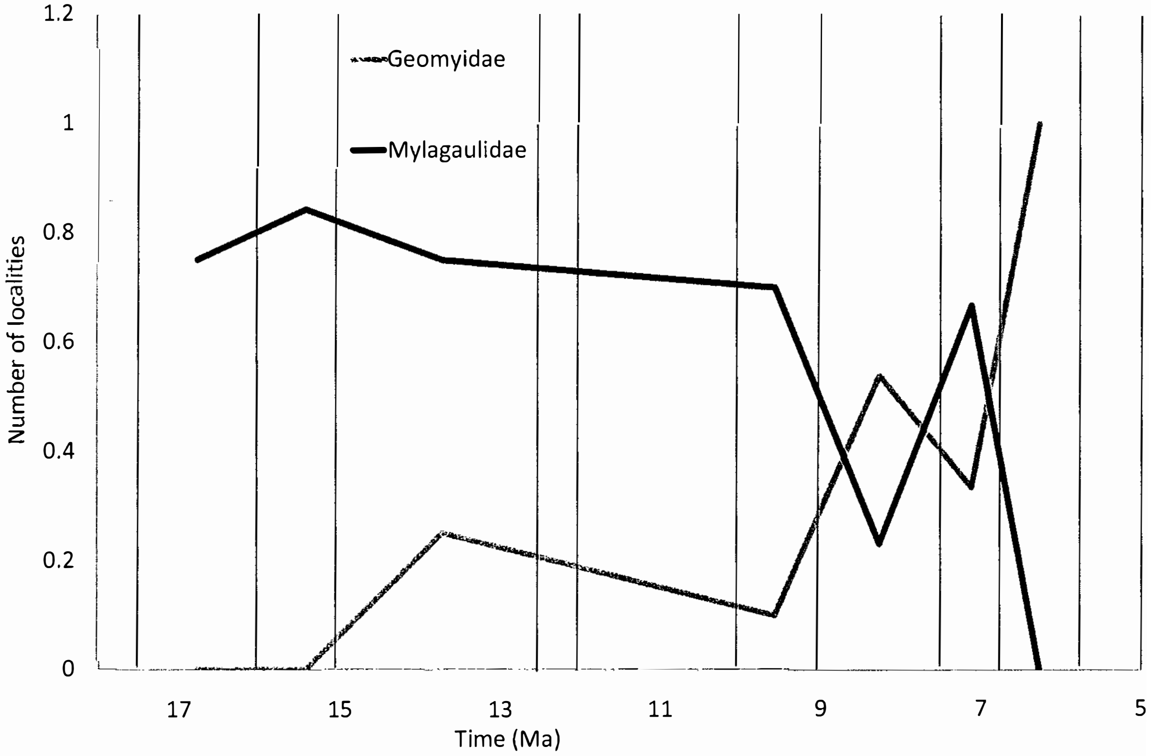


FIGURE 7: Changes in the normalized number of localities occupied by geomyids and mylagaulids through time.

The significant negative relationship between the presence of a mylagaulid in a site and the presence of a geomyid can be tested using a Chi-Square test on the numbers of sites where these animals do and do not co-occur. If those two taxa had similar habitat tolerances and did not interact with each other, their distribution relative to one another should be random. However, if these animals either competitively exclude each other or have very different environmental requirements, they would be expected to co-occur less frequently than predicted by random assortment. Table 4 shows the results of this test. Mylagaulids and geomyids co-occur only at three out of 52 sites and the difference from a random distribution is strongly significant.

TABLE 4: Summary of the Chi-square analysis on the number of localities where mylagaulids and geomyids co-occur. N = number of localities.

Taxon	N co-occurence	N no co-occurence	Total N	Proportion of localities without co-occurrence	X^2	p
Mylagaulidae	3	38	41	0.927	29.88	<0.005
Geomyidae	3	11	14	0.786	4.572	$0.05<p<0.25$

In addition to looking at changes in the relative abundance, minimum number of individuals, or number of localities of geomyids and mylagaulids through time, I also plotted those variables within each collecting area of the region studied. Relative abundances (Fig. 8) by collecting area show that for all but three of those areas, only one of the two potential competitors, mylagaulids or geomyids, is present. The Juntura, Thousand Creek, and Drewsey Formations include both taxa. In the Juntura and Drewsey Formations, mylagaulids are much more abundant than geomyids. In the Thousand Creek Formation, the pattern is reversed with a very strong geomyid presence and few mylagaulids. This pattern of co-occurrence of mylagaulids and geomyids within an area does not, however, translate as co-occurrence at the scale of localities.

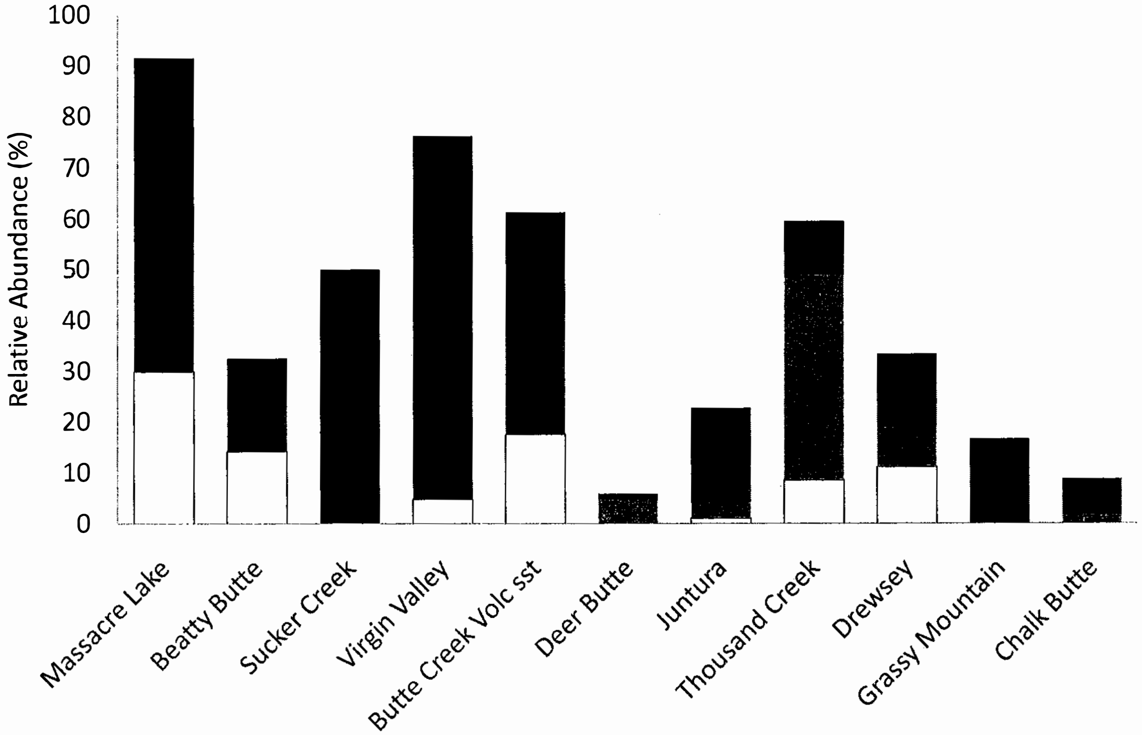


FIGURE 8: Abundance of each of the fossorial rodent groups relative to all small mammals in each of the formations and collection areas considered in this study.

The same pattern is observed in the MNI (Fig. 9). When looking at the number of localities normalized for sampling (in a similar method to that used for the normalization of the data binned by subunits of NALMA), the opposing pattern of landscape occupation is very clear (Fig. 10, 11). Interestingly, geomyids are present and mylagaulids absent in the late Barstovian Deer Butte Formation, and geomyids are absent in the presence of mylagaulids in the Butte Creek Volcanic Sandstone. This may be a consequence of collecting bias and is discussed later in the discussion of the cluster analysis.

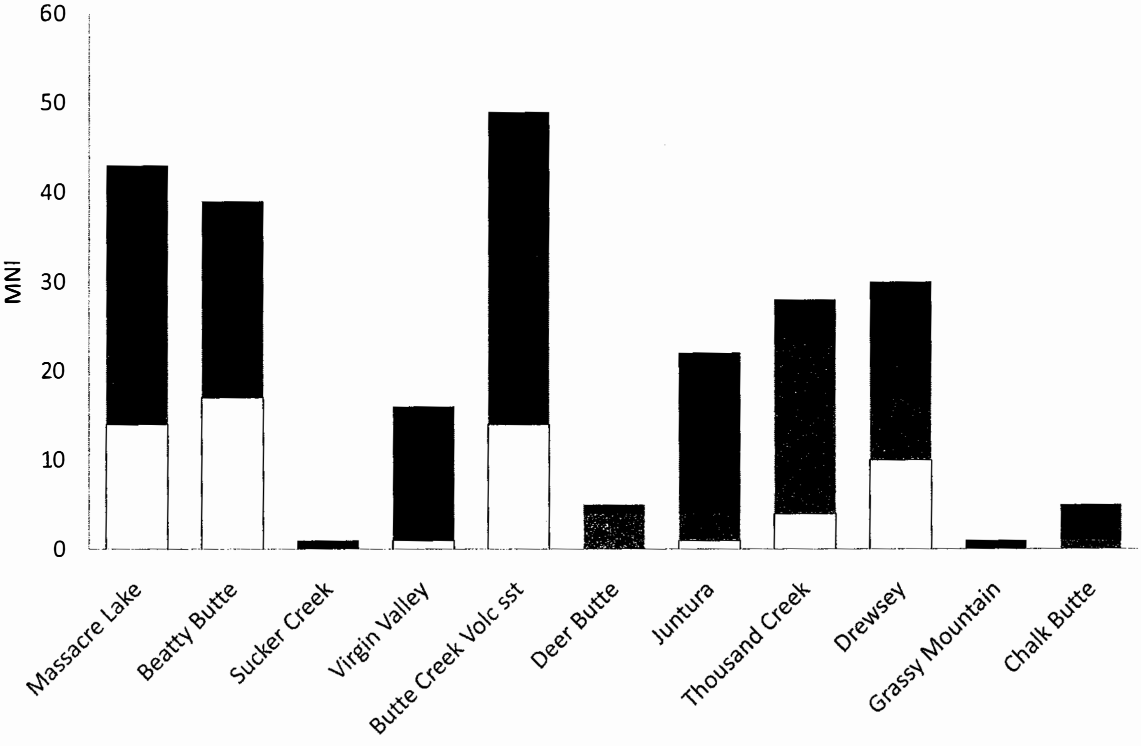


FIGURE 9: Minimum Number of Individuals (MNI) of each of the fossorial rodent groups in each of the formations and collection areas considered in this study.

Changes in the burrowing herbivore guild through time

To test the hypothesis that dynamics in the relative abundance of burrowing taxa took place as turnovers rather than slow gradual changes, I performed a chord distance analysis of the changes in the fauna across the subunits of NALMA from the late Hemingfordian to the early Hemphillian. Whether the analysis used MNI or the relative abundance of the taxa, the results (shown in Table 5) were the same. Fig. 12 shows the trend through time in the abundance of each group of the burrowing rodent guild relative to the whole guild.

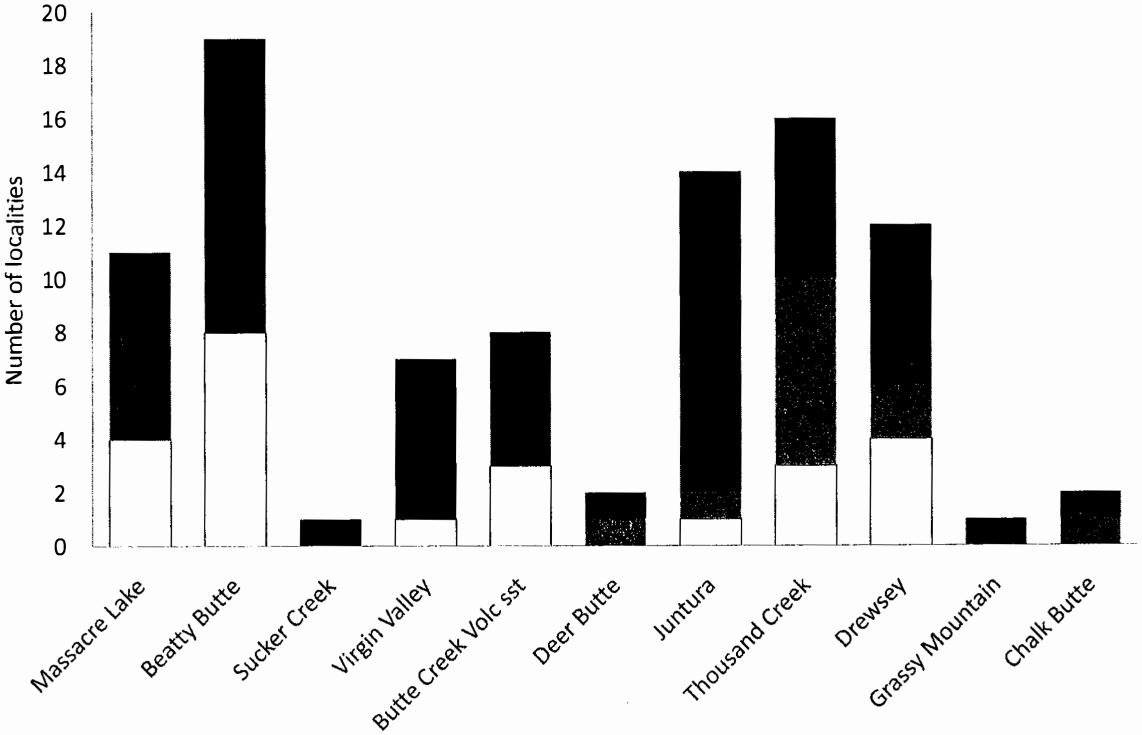


FIGURE 10: Number of localities where each of the fossorial rodent groups occur in each of the formations and collection areas considered in this study.

The general trend is similar to that described above and shown in Fig. 4. The result of the chord distance analysis suggests very little change within the guild during the late

Hemingfordian, the Barstovian and the Clarendonian. However, there are two very strong changes in burrowing rodent fauna between the end of the Clarendonian and the beginning of the Hemphillian as well as between the early early Hemphillian and the late early Hemphillian. The former may be affected by a shift in sample size but the change between the early early Hemphillian and the late early Hemphillian appears to be driven by the decrease in geomyids and the corresponding increase in mylagaulids and aplodontids.

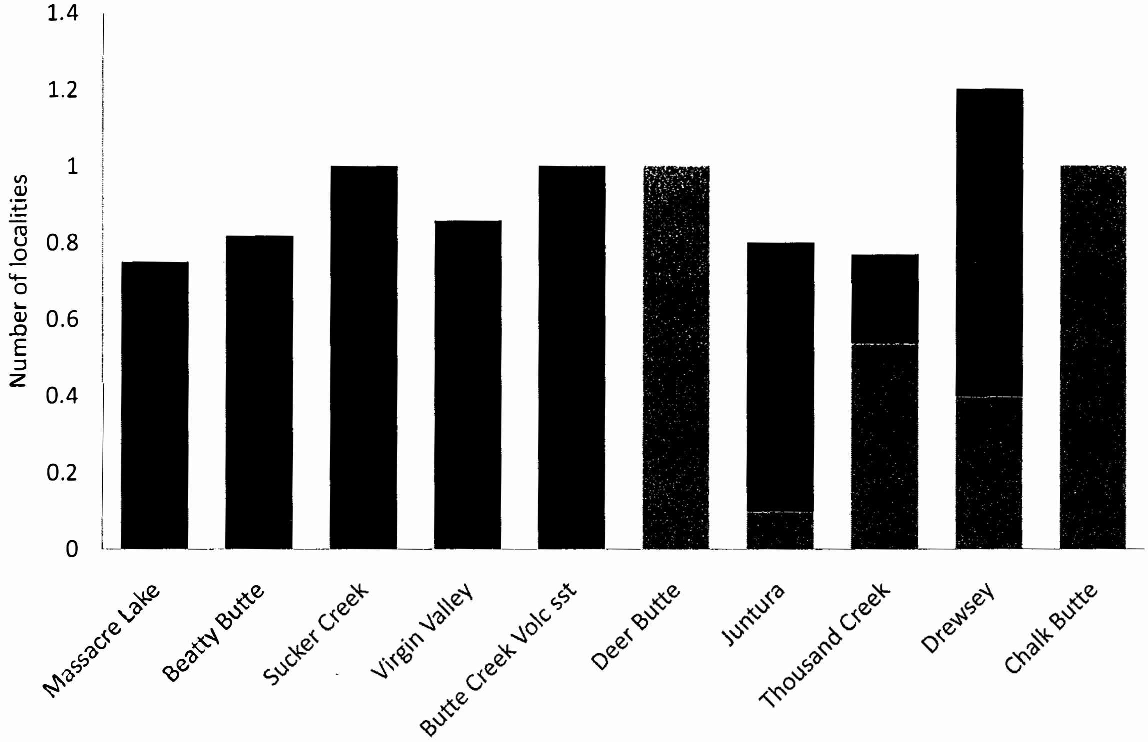


FIGURE 11: Normalized number of localities where geomyids and mylagaulids occur in each of the formations and collection areas considered in this study.

There is little change in the abundance of Marmotini through time. The results of this chord distance analysis support the hypothesis of geomyids and mylagaulids alternatively being more abundant than one another in the burrowing herbivore guild of southeastern Oregon.

TABLE 5: Summary of the Chord-distance analysis performed on the Minimum Number of Individuals of the burrowing herbivore guild taxa. Analysis of the relative abundance yielded the same results. A summary of the number of localities through time is provided in Appendix A. Abbreviations: LHMF, late Hemingfordian; EBAR, early Barstovian; LBAR, late Barstovian; LCLA, late Clarendonian; EEHP, early early Hemphillian, LEHP, late early Hemphillian.

Subdivision of NALMA	Aplodontidae	Geomyidae	Marmotini	Mylagaulidae	All	Chord Distance
LHMF	14	0	12	17	43	0.23
EBAR	18	0	10	28	56	0.49
LBAR	14	4	20	16	54	0.53
LCLA	1	4	7	11	23	1.01
EEHP	4	19	3	3	29	0.98
LEHP	10	4	5	10	29	

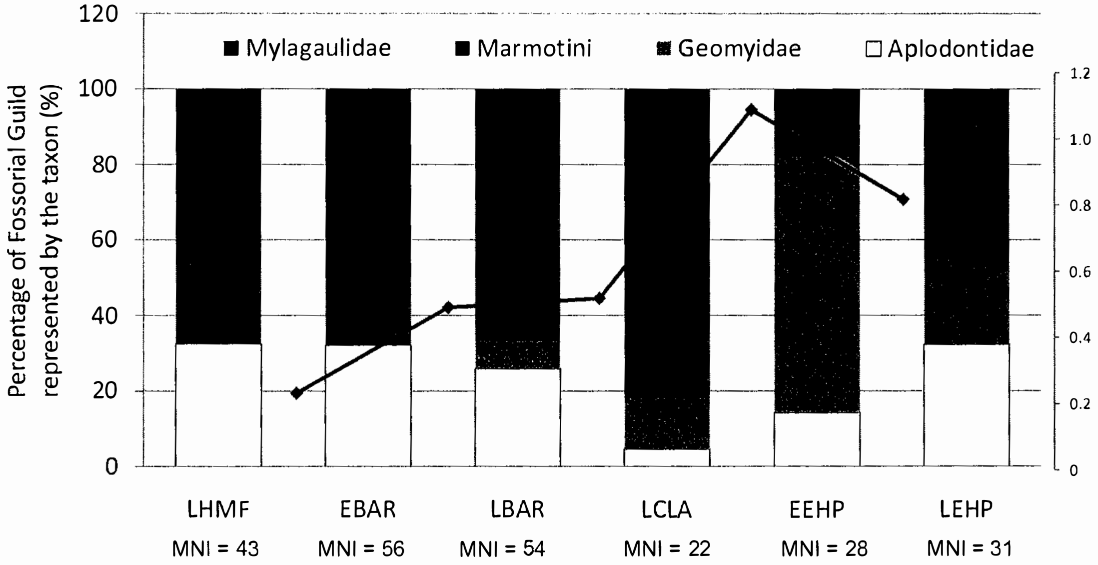


FIGURE 12: Abundance of each of the fossorial rodent groups relative to all fossorial rodents through time binned by subunits of North American Land Mammal Ages (NALMA) and curve of the chord distance analysis. The value under each bar of the graph indicates the Minimum Number of Individuals (MNI) for each subunit of land mammal age.

Effects of climate on fossorial herbivore abundance

The trend in climate through time versus the relative abundances of the fossorial herbivore group relative abundances is presented in Fig. 4. Regressions are shown in Figs. 13-15. Fossorial herbivores are very abundant in the late Barstovian, but experience a dramatic drop in the late Clarendonian despite little change in climate between those two time intervals. Fossorial rodents become very abundant in the early late Hemphillian even though there is no corresponding drastic change in climate.

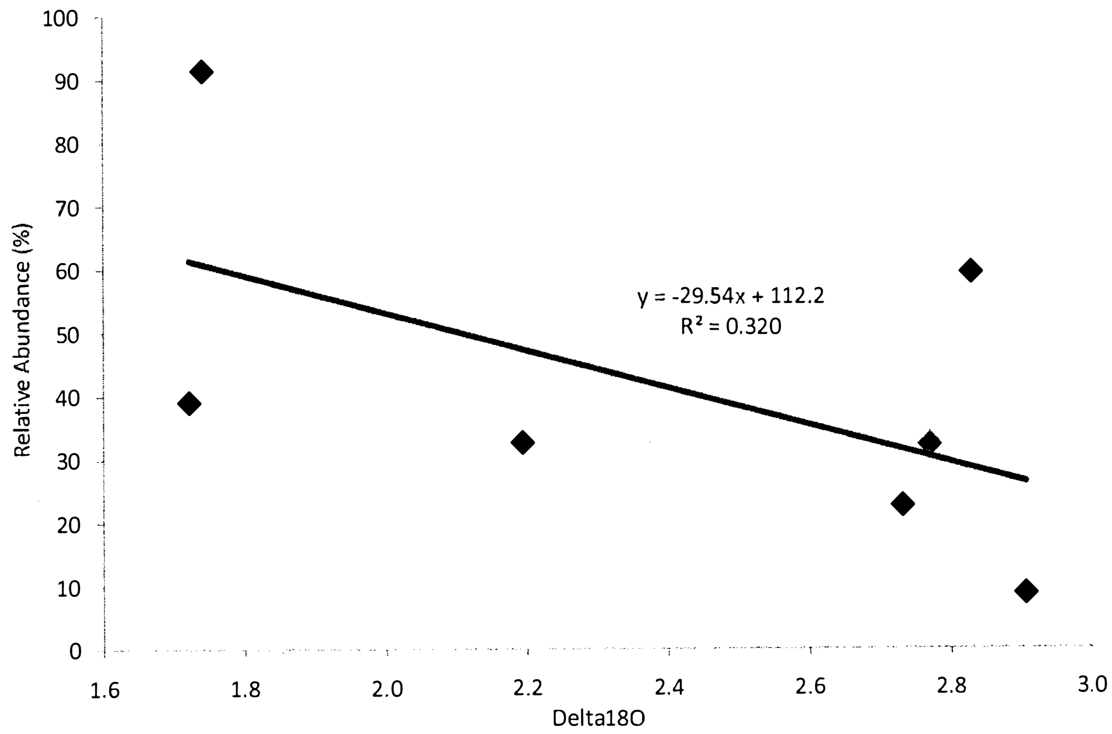


FIGURE 13: Regression of the relative abundance of all fossorial rodents versus $\delta_{18}O$. The regression of the relative abundance of the fossorial rodents versus the $\partial_{18}O$ value binned by subunits of NALMAs shown in Fig. 13 explains little of the variance for the abundance of burrowing herbivores as a whole ($R^2 = 0.321$, $p=0.185$).

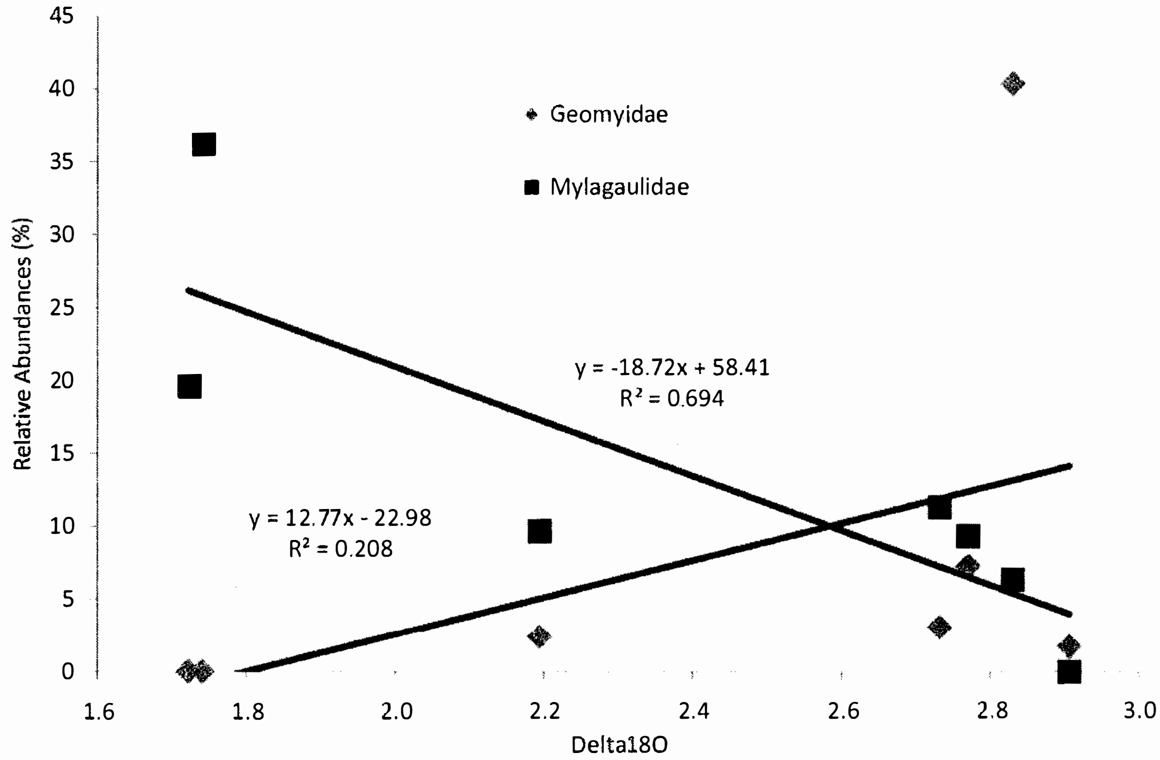


FIGURE 14: Regressions of the relative abundances of the Geomyidae and Mylagaulidae versus $\delta_{18}O$.

However when broken down by group of fossorial rodents, it seems that mylagaulids do show changes in relative abundance that are partially explained by changes in climate ($R^2 = 0.694$, $p = 0.020$). With increasing $\partial_{18}O$ and decreasing temperatures, mylagaulid relative abundance increases (Fig. 14). Geomyids do not seem to be affected much by climate ($R^2 = 0.208$, $p = 0.304$). Both aplodontids ($R^2 = 0.5597$, $p = 0.0531$) and Marmotini ($R^2 = 0.4387$, $p = 0.105$) display some correlation between climate and relative abundance but only about half of the variance is explained (Fig. 15).

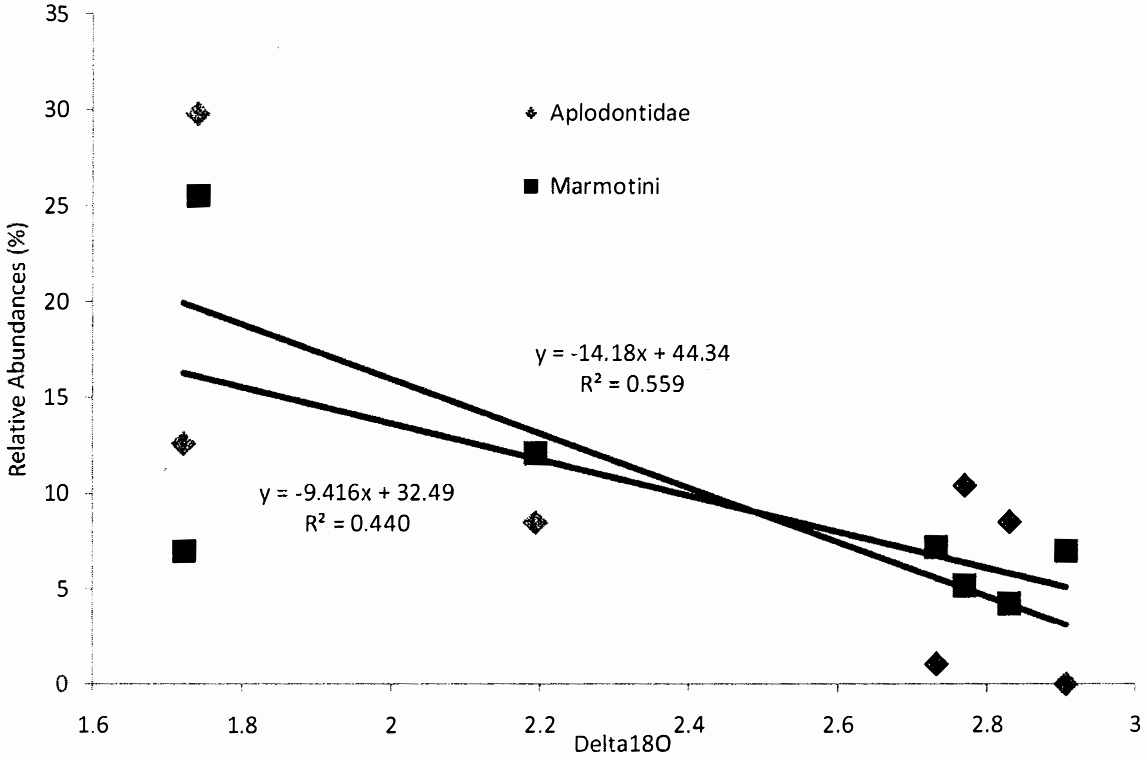


FIGURE 15: Regressions of the relative abundances of the Marmotini and Aplodontidae versus $\delta_{18}O$.

As a consequences of looking for climate affecting the relative abundance of different groups of fossorial rodents, I corrected the p value with the Bonferonni correction (p= 0.05/Number of tests, Shaffer 1995). Thus the threshold for significance is p=0.0125 for each test. None of the results are found to be significant. Additionally, this result should be considered very carefully due to the limited number of points this regression is run on.

Habitat differences among fossorial rodents

The cluster analysis of the fossil localities from the northern Great Basin where geomyids and/or mylagaulids are present yielded the results shown in Fig. 16. Four of the localities where geomyids occur alone are found to cluster together (UO 2500, UO 2239, UO 2337, UO 2516). A fifth locality (UO 2347) clusters very close to localities where only mylagaulids are present. This clustering of geomyid localities is independent of age and includes localities from the late Clarendonian Juntura formation (UO 2500, Black Butte) as well as the Little Valley site (UO 2516, Chalk Butte Formation) of the early late Hemphillian and UO 2337. UO 2465 (Quartz Basin) and UO 2495 (Red Basin) cluster together although only mylagaulids are present in UO 2495 and both are present in Quartz Basin. Another locality where only geomyids are present (V69114) clusters with mylagaulid localities of the Drewsey Formation (UO2358) and the Massacre Lake Fauna (V6160). This cluster is completed by a locality where both mylagaulids and geomyids occur (UO2347) and a mylagaulid locality (CIT62). All other clusters of localities obtained through this analysis include only mylagaulid localities with the exception of the locality V86028 (Rattlesnake Butte, Harney Basin) where both mylagaulids and geomyids occur together. This locality is an unpublished, poorly known locality from southeastern Oregon for which no stratigraphic or temporal data are available.

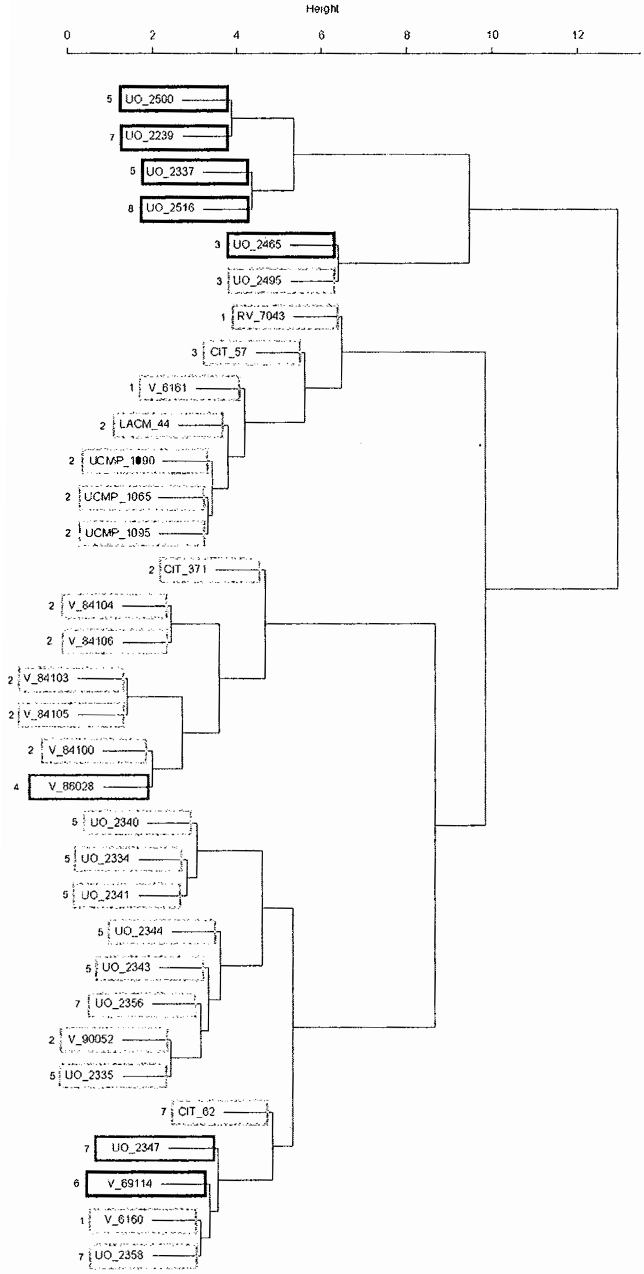


FIGURE 16: Cluster Analysis of the faunal assemblages of the localities of the area of study. Black boxes indicate those where only geomyids are present; dark grey where both geomyids and mylagaulids are present; light grey where only mylagaulids are present. Numbers indicate age of the locality: 1. LHMF, 2. EBAR, 3. LBAR, 4. BARS, 5. LCLA, 6. EEHP, 7. LEHP, 8. ELHP. Abbreviations as in Table 2.

DISCUSSION

Overall, the results do not allow me to reject the possibility of competitive interactions between mylagaulids and geomyids. Rather than the directional pattern of a double wedge suggestive of competitive replacement, I find a negative correlation between the relative abundance of geomyids and mylagaulids, which is more suggestive of habitat tracking.

When considering the relationship of climate through time to fossorial rodent group relative abundances, it appears that fossorial rodents as a whole and geomyids in particular are very little affected by climate (Figs. 13-15). Correlation between climate and mylagaulid relative abundance occurs but this may not be indicative of causation. The most drastic changes in $\partial_{18}O$ occurred between the early Barstovian and the late Barstovian as well as between the late Barstovian and the late Clarendonian without leading to important changes in the relative abundance of mylagaulids, suggesting that the relationship of mylagaulids to temperature is not a simple linear one.

The clustering of geomyid-containing localities based on faunal content is very interesting in light of previously published conclusions about the habitats they represent. The habitat interpretations of these localities by Shotwell (1963) on the basis of the mammalian assemblage present concluded that UO 2347 (Otis Basin) was most likely a border community (i.e. a unique arrangement of savanna, pond-bank, open grassland, and woodland, Shotwell 1963). In addition, UO 2500 (Black Butte) was interpreted as a pond-bank, slow moving stream habitat (Shotwell 1963). UO 2337 was also interpreted as a pond-bank community. This suggests a clustering of the pond-bank communities together as a favorable habitat for geomyids. Red Basin and Quartz Basin cluster together. These two localities from the late Barstovian share many similarities but also differ greatly in fauna. Shotwell (1968) reported, in particular, differences in body size with large ungulates and carnivores in Red Basin and small mammals in Quartz Basin. This may be an artifact of the sampling method used. Unlike Red Basin, Quartz Basin was very heavily screened for microvertebrate remains (three tons of matrix with standard screen, 400 pounds with fine screen, Hutchison 1968). In Red Basin (UO 2495), only mylagaulids are present, whereas in Quartz Basin (UO 2465), geomyids are present but mylagaulids are absent. Quartz Basin was interpreted as a stable, ponded, slow-moving water environment on the basis of its odd mammalian assemblage (Hutchison 1964). This is consistent with the interpretation of the close cluster of geomyid localities. The difference in fossorial herbivore fauna between the two localities may also be an artifact of collection methods.

Most of the numerous mylagaulid-only localities lack paleoenvironmental data that would allow discussion of the likely habitat preferences of mylagaulids. However, Shotwell (1963, p.18) mentioned that, on the basis of mammalian assemblages, the “savanna community is well represented in the Clarendonian Black Butte Fauna” (where most of the mylagaulid-only localities of the UOMNH are located). The clustering of localities yielded supports the hypothesis of differential habitat requirements between mylagaulids and geomyids in the northern Great Basin during the mid to late Miocene.

The paleopedology of the locality UO 2337 (Black Butte, late Clarendonian, Juntura Formation) was investigated by Retallack (2004). The section studied is dominated by gray siltstone and sandstone derived seasonally waterlogged soils. This is evidence for a riparian environment associated with moderately developed woodlands (Retallack 2004). The degree of development of the soils supports the hypothesis of a rather stable environment. The wetter environment of UO 2337 appears favorable to a geomyid, *Pliosaccomys* sp., although this particular genus of burrowing rodent is only represented by a single specimen. There are no mylagaulids at this locality. The few paleobotanic data from macrofloras of the Great Basin as well as a few isotopic analyses of mammalian enamel from the Juntura Formation and Quartz Basin locality indicate a MAT of about 13-18°C and MAP of 900-1000 mm (Retallack 2004, Kohn et al. 2002, Wolfe 1994, Wolfe et al. 1997, Graham 1999). Kohn et al. (2002) recommended further analyses of different taxa (i.e. not horses) from those areas.

Paleosol data from the Pawnee Creek Formation of northeastern Colorado where burrows of a mylagaulid occur indicate an environment vegetated by shrubs and hackberry trees (*Celtis* sp.) and a rich soil located above the water table in a floodplain environment (Gobetz 2006). This habitat would have been drier than that described for geomyids at UO 2337.

The cluster analysis supports the hypothesis that the apparent exclusion of geomyids and mylagaulids, rather than being a consequence of competition, is a result of the fact that mylagaulids and geomyids were habitat specialists. It may be difficult to determine precisely which taxa occupied which habitats without gathering additional paleoenvironmental data for the area studied. From studies of paleopedology in the Great Plains and the Great Basin, it appears that mylagaulids might have preferred a drier environment than geomyids. Modern data on the habitat preferences of geomyids indicate widespread heterogeneity in habitat preference within and across genera (Lacey et al. 2000). For example, *Thomomys bottae* generally favors alluvial areas for burrowing, and particularly creeks during droughts, although it may be relegated to drier, harder soils when in contact with other geomyid taxa (Jones and Baxter 2004). On the other hand, *Geomys pinetis* was found to be most abundant in dry soils (Pembleton and Williams 1978). It seems that the geomyids present in southeastern Oregon during the Miocene expressed affinities to wetter environments, maybe similar to those favored by *Thomomys* today, and did not associate with the dry habitats preferred by the modern *Geomys*. On the other hand, mylagaulids seem to show affinities for savanna habitats.

The local to regional scale differences in environment between wetter, more riparian habitats and drier savanna ones would explain the opposite expansions and contractions of the habitat range of each of the fossorial rodent families and the associated variation in the composition of the burrowing herbivore guild. Rather than an intra-family habitat partitioning observed in modern geomyids, geomyids and mylagaulids might have experienced inter-family habitat partitioning during the Miocene.

Shotwell's (1958a) hypothesis of the habitats from which these fossils were derived may well be confirmed with the caveat that although our data suggest that changes in the abundance of the mylagaulids are related to changes in habitats, I cannot conclusively tie those variations to the spread of grasslands as suggested by Shotwell (1958a) or Hopkins (2007). The results of my work also emphasize the similarities between paleoecological studies at different scales. With changes in global or local climates (Zachos et al. 2001, Kohn et al. 2002, Retallack 2004), the dominant habitat switched back and forth between drier, more savanna-like environments, and more mesic, riparian habitats. This seems to have led to turnover events in the burrowing herbivore guild. These turnovers may be related to the ability of the animal to burrow in different habitats. The ability to burrow determines the potential for escape from predators. Samuels and Van Valkenburgh (2009) hypothesized high predation pressure on fossorial rodents and Hopkins (2005) demonstrated that the evolution of the horns of the Great Plain mylagaulid *Ceratogaulus* was related to defense against predators. Burrowing herbivores might have been subject to important pressure from predation. If soils prevented burrowing because of a change in its physical properties (water content, induration, vegetation presence, nature of the parent material, etc), there could have been resulting changes in the predation pressures upon burrowing herbivores of different clades and, in turn, extirpation of one taxon or another.

From the late Hemingfordian to the late Clarendonian in the northern Great Basin, mylagaulids were more abundant than geomyids in the burrowing herbivore guild of the northern Great Basin. In the early early Hemphilian, without any evidence from global climate curve of an important change in climate, geomyids became more abundant. This may be the consequence of a switch to an environment promoting the habitat most favorable to geomyids. Alternatively, rather than being beneficial to geomyids, it is possible that the environment was very unfavorable to mylagaulids. Under this scenario, as the mylagaulids retreated with the contraction of their environment, they would have left room for geomyids that could have occupied the soils now hostile to the family Mylagaulidae. In the late early Hemphillian, another switch in climate led to the return of a microhabitat preferred by mylagaulids. Again, there does not seem to be a causative change in the global climate. Instead, an important local change in environment, causing a switch in habitat, appears to be imprinted on an apparently disconnected global trend that correlates but does not cause the change in fauna. This has been observed on a shorter time scale in the late Pleistocene of Washington state (Rensberger and Barnosky 1993). Further study of the paleopedology at the sites collected by Shotwell and others is needed to complete the paleoenvironmental data for the region and provide material for further analysis of the pattern described herein. The importance of habitat changes in mitigating or enhancing climate changes on mammalian taxa and the environmental preferences of mammals is believed to be a driving force of evolution in the Cenozoic (Blois and Hadly 2009). The present dataset does not allow me to conclude whether or not environmental changes are responsible for the decline of mylagaulids in North America as a whole, or for their final extinction at the end of the Miocene.

CONCLUSIONS

This study focused on the paleoecology of the burrowing herbivore guild from the late Hemingfordian through the early late Hemphillian in the northern Great Basin. I found that, rather than mutually exclusive causes for the waning of mylagaulids, climate, environmental variation, and biotic interactions may have come together to drive one of the most successful groups of burrowing rodents of the North American fossil record to its extinction. The first hypothesis formulated at the beginning of this paper of competitive interactions between mylagaulids and geomyids is not supported. Changes in the fossorial herbivore guild as a whole do not seem to be a gradual change in the composition of the guild but rather stasis in the early part of the record followed by a succession of turnover events falsifying the second hypothesis of competitive interactions between members of the fossorial herbivore guild. Those changes in faunal composition do not seem to be a consequence of global climate change. Environmental changes around turnovers in burrowing rodent fauna may have driven the changes in their relative abundances.

I present a new hypothesis for the decline of mylagaulids in which local to regional scale climatic changes triggered dramatic fluctuations in the dominant habitat, thus mediating competitive interactions by allowing one taxon to take over the other on the landscape as the fossorial rodent niche was left emptied in tracking a more favorable habitat. The observed pattern suggests that the Miocene burrowing herbivore guild was partitioned according to preferences in microhabitats at the local to regional scale.

CHAPTER IV

MICROWEAR ANALYSIS OF FOSSIL GEOMYIDAE AND MYLAGAULIDAE FROM THE GREAT BASIN

INTRODUCTION

The study of microwear features on the enamel surface of mammalian teeth is widely used to reconstruct paleodiets of extinct mammals (e.g., Solounias and Semprebon 2002, Merceron and Ungar 2005, Billet et al. 2009, Rivals and Solounias 2007, Ungar et al. 2007, and references therein). This technique has become increasingly popular for determining the diets of extinct mammalian taxa, particularly ungulates (e.g., Rivals and Semprebon 2006, Merceron, Zazzo et al. 2006), primates (Merceron, Taylor et al. 2006, Rafferty et al. 2002), moles (Talpidae; Silcox and Teaford 2002), sirenians (Sirenia; Beatty et al. 2009), carnivores (Carnivora; Goillot et al. 2009), and hyraxes (Hyracoidea; Walker et al. 1978). Few of these prior studies have focused on rodents and those that did often focused on a single taxon or a few related taxa (Rensberger 1978, Nelson et al. 2005, Hopley et al; 2006, Townsend and Croft 2008, Gomes Rodrigues et al. 2008, Hautier et al. 2009). The order Rodentia is very diverse, ranging widely in body size, behavior, habitat, and diet (Merritt 2010, Kay and Hoekstra 2008) and thus spans a wide variety of ecologies. Broad sampling is necessary in order to get representative modern taxa of different diets and behaviors. In particular, burrowing and the associated ingestion of exogenous grit have been recognized as having a major effect on the microwear signature of an animal (Daegling and Grine 1999) and must be considered in studies of diet and microwear of rodents.

Rodents are an important part of the fossil mammal communities of southeastern Oregon during the Miocene (Shotwell 1958a, 1963). The presence of several different species of subterranean rodents in this area of the northern Great Basin raises the question of the potential for interspecific competition over food resources and habitat specialization. Addressing these questions requires one to determine the diet of these animals. I focus on mylagaulids and geomyids, two groups of extinct subterranean rodents present in the Great Basin during the Miocene. The Mylagaulidae, a family of burrowing rodents from the Miocene of North America, include species of large (mass >1 kg) subterranean to fossorial herbivores. Previous paleoecological studies have benefited from data on the body size of the Mylagaulidae (Hopkins 2007, 2008b). Knowledge of their diet will allow further investigation of the paleoecology of this peculiar family of fossil rodents. This family of burrowing rodents exhibits an unusual dentition. They lose the first molar early in ontogeny and possess reduced second and third molars as well as a characteristic enlarged fourth premolar that provides most of the chewing surface. Those cheek teeth are hypsodont and this feature has been suggested to be related to an abrasive diet and the spread of grasslands in North America. This hypothesis has been tested by Hopkins (2007) but further investigation of this question can be undertaken with new lines of evidence. I use microwear analysis to further test this technique, and establish the diet of burrowing rodents and its bearing on species interactions. This association of hypsodonty, abrasive diet, and spread of grasslands has been extensively studied in ungulates (e.g., Janis et al. 2002, Webb 1977, but see Strömberg 2006) but only suggested in rodents (Stirton 1947, Webb 1966). Calede (third chapter of this thesis) suggested that mylagaulids may have been involved in habitat partitioning with other subterranean rodents: the geomyids. Divergent diets may not allow a definitive conclusion on habitat partitioning (third chapter of this thesis), they may provide additional evidence against direct competitive interactions.

The microwear signature of an organism can be defined as the proportion of scratches and pits on its tooth enamel; it is a direct consequence of feeding behavior (Walker et al. 1978). As abrasive food is ingested (e.g., grasses), the phytoliths of the cell walls mark the enamel surface with scratches (Merceron et al. 2004). The consumption of hard objects (e.g., seeds, nuts, fruit pits) creates pits (Rafferty et al. 2002). The resulting microwear signature is erased and replaced by subsequent feeding in 24 to 48 hours, so that microwear exhibits the "last supper effect" (i.e. the observed microwear signature is that of the last meal before the death of the individual; Grine 1986). Thus, it is possible to link the diet of an extant animal whose feeding behavior is known with the microwear signature observed on the surface of the enamel of its teeth. This calibration of microwear signature with diet using data from extant taxa can be used to assess the diet of an extinct animal. There are two main methods for observing and counting microwear features. Microwear was first studied using scanning electron microscopy to take pictures of the tooth at high magnification (i.e. 500x, Silcox and Teaford 2002). The other method only requires a stereomicroscope (magnification 30x to 75x) and uses transmitted light through transparent casts, therefore avoiding the mounting and coating of the specimens. The light microscope method is a much cheaper and faster method that allows for larger sample sizes (see Solounias and Semprebon 2002). Microwear studies have proven effective in distinguishing between broad diet categories such as browsing (where leaf material and sometimes hard foods such as fruits and nuts constitutes most of the diet), grazing (where grasses and forbs constitute most of the diet) and mixed feeding behavior (Solounias and Semprebon 2002, Ungar et al. 2007).

Unlike ungulates whose diets range along a browsing-grazing continuum, rodents exhibit a wider variety of feeding behaviors. Although most are herbivorous, some have omnivorous feeding behaviors or even carnivorous diets (e.g., *Tamias senex*, Gannon and Forbes 1995; *Onychomys torridus*, McCarty 1975). Indeed, small mammals exhibit a diversity of feeding behaviors that are more opportunistic and variable than that of most ungulates. Previous research (Townsend and Croft 2008) on microwear in rodents has attempted to cluster rodent species in dietary groups according to the proportion of seeds, fruits, grasses, and leaves in the diet. These categories were developed for caviomorph rodents in which herbivory is the dominant feeding behavior and green vegetation is almost always the main constituent of the diet. In this study, I include taxa with more diverse diets including fungivory as well as roots, tubers, bulbs, and corms. The microwear of extant taxa will be used to provide a framework for understanding the diet of extinct fossorial rodents and their bearing on the paleoecology of fossorial rodents. Low magnification microwear analysis should distinguish between broad and diverse dietary categories in the rodents included in this study as it has for other taxa (e.g., Solounias and Semprebon 2002, Semprebon et al. 2004, Nelson et al. 2005, Townsend and Croft 2008). I also expect to recognize burrowing behavior, with the associated ingestion of exogenous grit, from the microwear signature of extant rodents. Using the relationships between diet and microwear signature developed from the extant species, it should be possible to determine the diet and burrowing habits of extinct rodents on the basis of their microwear signature.

MATERIAL AND METHODS

Dietary categories

We implemented the categorization of Townsend and Croft (2008) that included three categories (i.e. grass-leaf, fruit-leaf, fruit-seed) to cover the more diverse diets of the taxa considered in this study. The categories are determined by the most important sources of food for the species and do not necessarily reflect secondary nutritional resources. Diet data and references for extant rodent taxa are drawn from the literature and are provided in Table 1. I was careful to consider seasonal variation in assigning species to categories as Townsend and Croft (2008) suggested. In addition to the categories of Townsend and Croft (2008) slightly redefined for the purpose of this study, I added two categories for feeding behaviors unobserved in caviomorph rodents. The categories used in this study include: (1) Abrasive food (i.e. grass-leaf group, the diet mostly comprises grasses and leaves, aquatic vegetation, other soft green vegetation), (2) Hard food (i.e. fruit-seed group, the animal relies on acorns, seeds, nuts, and fruit pits as its main nutritional source), (3) Mixed food (i.e. fruit-leaf group, the counterpart to the previously described groups, both green vegetation and seeds are important in the diet), (4) Underground food (i.e. root-bulb group, tubers, roots, corms, bulbs and buried food constitute most of the diet of the animal), (5) Fungivory (i.e. fungi are the main nutritional source).

Material studied

I included 11 species of modern rodents from six different families of rodents spanning phylogenetic as well as ecological diversity. All were museum specimens and adults with fully erupted dentition. Both males and females were sampled and individuals covered as much of the geographic range of the species as possible to account for variations in diet (and therefore microwear signature) across the landscape.

TABLE 1: Summary of the sample size and diet data of the extant taxa used in this study. N stands for sample size. References: 1, Carraway and Verts (1993); 2, Jarvis and Sherman (2002); 3, Woods (1973); 4, Jones and Baxter (2004); 5, Verts and Carraway (1999); 6, Williams and Kilburn (1991); 7, Kwiecinski (1998); 8, Koprowski (1994); 9, Caraway and Verts (1994); 10, Gannon and Forbes (1995); 11, Snyder (1982).

Family	Binomial Name	N	Dietary Category	Diet details	Habitat use	References
Aplodontidae	*Aplodontia rufa*	10	Abrasive food	Ferns, toxic plants	Fossorial	1
Bathyergidae	*Heterocephalus glaber*	11	Underground food	Underground food storages	Subterranean	2
Erethizontidae	*Erethizon dorsatum*	8	Mixed food	Bark, forbs, grasses, …	Terrestrial	3
Geomyidae	*Thomomys bottae*	7	Underground food	Acorn, bulbs, forage, …	Subterranean	4
Geomyidae	*Thomomys talpoides*	6	Abrasive food	Forbs, dandelions, roots, …	Subterranean	5
Heteromyidae	*Dipodomys ingens*	9	Hard food	seeds, fruits, green vegetation	Semi-fossorial	6
Sciuridae	*Marmota monax*	7	Mixed food	Halfalfa, fruits, and flowers	Fossorial	7
Sciuridae	*Sciurus carolinensis*	10	Hard food	nuts, flowers, grasses, …	Arboreal	8
Sciuridae	*Sciurus griseus*	8	Fungivory	fungi, pine nuts, acorns, …	Arboreal	9
Sciuridae	*Tamias senex*	6	Fungivory	fungi, seeds, insects, …	Arboreal	10
Sciuridae	*Tamias striatus*	7	Hard food	seeds, nuts, acorns, …	Semi-fossorial	11

Similarly, seasonal variations are critical, I was careful to include in our datasets specimens collected during different seasons throughout the year when available. Only taxa with a well-known diet were used. Because microwear studies require large data sets (i.e. numerous individuals sampled per taxon) to be reliable, I sampled 89 specimens for the extant taxa with an average of approximately 8 specimens per taxon. Details of the sample size for each taxon are provided in Table 1. Details about the provenance and season of death of each specimen are available online for all University of Washington Burke Museum specimens (at http://biology.burke.washington.edu/mammalogy/database/search.php) and are unavailable for University of Oregon Museum of Natural and Cultural History specimens.

I also investigated the diets of specimens of six species of fossil rodents in two families: the Mylagaulidae and the Geomyidae. I included 21 specimens from 4 different species of mylagaulids from the Hemingfordian through Hemphillian of the northern Great Basin (parts of Oregon, Nevada, and Idaho, second chapter of this thesis): (1) *Alphagaulus vetus*, (2) *Hesperogaulus gazini*, (3) *Hesperogaulus wilsoni*, (4) and a new species within the genus *Hesperogaulus* (see second chapter of this thesis). The sample size for these taxa varies considerably as dictated by the fossil record (Table 2). In addition to mylagaulids, I also examined the microwear of two species of geomyids from the same area (*Mojavemys mascallensis* and *Pliosaccomys magnus*). The familial assignment of *M. mascallensis* has been the subject of some controversy (Korth and Chaney 1999, Feranec et al. 2005, Flynn et al. 2008) and I follow Feranec et al. (2005) in this paper. Nevertheless, the results of this paper will not be invalidated if the suggestion that *M. mascallensis* is a dipodomyine (Flynn et al. 2008) is confirmed. Because of the challenges inherent to casting very small, isolated geomyid teeth and the lack of complete tooth rows to study, the sample size for each of those species is limited to three specimens.

TABLE 2: Summary of the data for the fossil species included in this study. Abbreviations for subdivisions of North American Land Mammal Ages (NALMA): LHMF, Late Hemingfordian; EBAR, Early Barstovian; LBAR, Late Barstovian; LCLA, Late Clarendonian; LEHP, Late Early Hemphillian. References: 1, Matthew 1924; 2, Munthe 1988; 3, Korth 2000; 4, Chapter two of this thesis; 5, Korth 1999; 6, Feranec et al. 2005; 7, Shotwell 1967b.

Family	Binomial Name	Formation	NALMA subdivision	References
Mylagaulidae	*Alphagaulus vetus*	Massacre Lake Fauna, Virgin Valley	LHMF, EBAR	1, 2, 3, 4
Mylagaulidae	*Hesperogaulus gazini*	Beatty Butte, Sucker Creek	EBAR	4, 5
Mylagaulidae	*Hesperogaulus* species A	Juntura, Drewsey	LCLA, LEHP	4
Mylagaulidae	*Hesperogaulus wilsoni*	Drewsey	LEHP	4,5
Geomyidae	*Mojavemys mascallensis*	Deer Butte	LBAR	6
Geomyidae	*Pliosaccomys magnus*	Drewsey	LEHP	7

There is a great diversity of occlusal patterns and tooth morphology in our dataset. Some rodents, such as geomyids, *Aplodontia rufa* and mylagaulids, are hypsodont and wear down their teeth to expose enamel bands of varying complexity. Others, such as squirrels and marmots (Sciuridae), exhibit a generalized pattern in their upper molars with an easily distinguishable protocone. To provide consistency, I collected microwear data from the upper second molar (M2) for all extant taxa. Because the microwear signal is consistent across associated maxillae and mandibles (Semprebon et al. 2004), when the upper tooth was not available, I selected its counterpart in the lower tooth row. More specifically, the data were gathered from the protocone or the analogous lingual enamel band. The same procedure was followed for fossil geomyids. Collecting microwear data from the second (upper or lower) molar has become the norm for microwear studies (e.g., Townsend and Croft 2008, Semprebon et al. 2004) and allows comparisons to be made across studies. Because much (if not all, as in *Hesperogaulus wilsoni*) of the chewing surface in mylagaulids is provided by the 4th premolars, and the 4th premolars constitute much of the fossil record of the Mylagaulidae, mylagaulid specimens were studied using the 4th premolars rather than the M2. This may induce a bias with differences in microwear signature across the tooth row. Several microwear studies have used different teeth in a single analysis as a consequence of fossil material available (e.g., Nelson et al. 2005).Other studies (e.g., Mahoney 2006) have shown that microwear may vary across the tooth row. This may be a consequence of differences in bite force across the tooth row, or in amount of dirt that contacts the different teeth. Further work comparing microwear in mylagaulids' fourth premolars and second molars may provide a better understanding of the potential pitfalls of the choice of teeth made here. Casts of specimens with obvious taphonomic damage (e.g., microwear-like features on both enamel and dentine) were rejected from the dataset and no features were counted on the casts. This was the case for most specimens of *Alphagaulus vetus* from the Virgin Valley Formation. Casts without any microwear visible (i.e. smooth enamel) were also rejected, a different taphonomic phenomenon (King et al. 1999) mostly observed in *Hesperogaulus wilsoni* in our sample.

Specimen preparation and stereomicroscopic observations

For, all specimens, I made clear, high-definition epoxy casts of the tooth of interest. Because of its optical properties, enamel cannot be directly observed under the stereomicroscope (Solounias and Semprebon 2002). Therefore, I molded specimens in the collections visited (see Appendix D) and later made casts following the method of Solounias and Semprebon (2002).

Casts were examined at 75x magnification using a Leica S8AP0 stereomicroscope. I examined a 0.3 mm x 0.3 mm area on the protocone (or analogous enamel band) of each specimen. On each tooth, I counted the number of pits and the number of scratches, subdivided by size and shape following Solounias and Semprebon (2002). Pits were identified as large pits, small pits, large puncture pits, and small puncture pits (Fig. 1).

Scratches were identified as fine scratches, coarse scratches, hypercoarse scratches, and gouges (Fig. 1). I scored all specimens for four different species of extant rodents (out of eleven) twice to assess intra-observer variation.

Intra-observer error and repeatability of counts

Low-magnification microwear analysis is a recently-developed method (Solounias and Semprebon 2002) whose reproducibility has been the subject of controversy (e.g., Teaford et al. 2008). Semprebon et al. (2004) provided support for the potential of this method to reconstruct diet and distinguish between broad dietary categories. They found that the method is subject to little intra-observer and inter-observer error. The common technique used to limit intra-observer error is to perform several (usually two) scorings of each specimen, average those data to obtain an average microwear signature for the specimen, and then later average the averages of all specimens of a given taxon to get the average microwear signature for the species (or genus) studied (e.g., Townsend and Croft 2008, Solounias and Semprebon 2002). This method, although yielding the central tendency of the microwear signature for a given cast, has the problem of pseudo-replication.

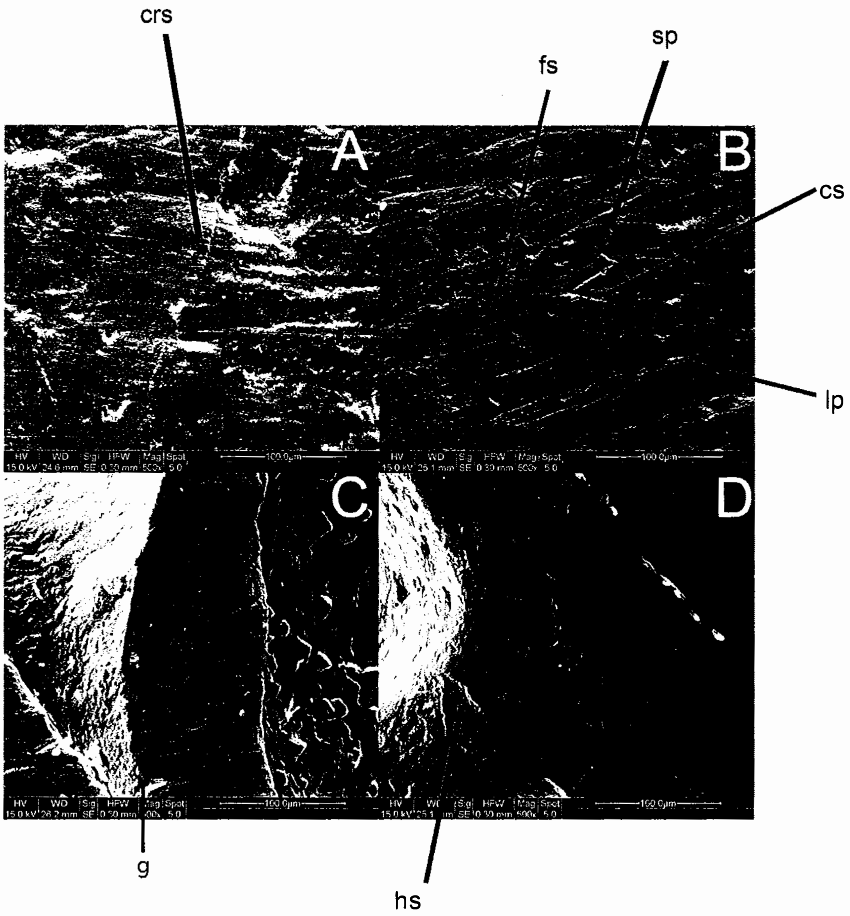


FIGURE 1: Scanning Electron Microscopy (SEM) photomicrographs of extant rodent taxa illustrating microwear features. A. *Aplodontia rufa*, B. *Sciurus griseus*, C. *Thomomys bottae*, D. *Tamias senex*. Abbreviations: crs, cross scratch; cs, coarse scratch; fs, fine scratch; g, gouge; hs, hypercoarse scratch; lp, large pits; sp, small pits.

The averaged data for the specimen are not an actual count of anything biologically real, and hence may increase the type II error rate unnecessarily (i.e. accepting the null hypothesis when the alternative is correct). I therefore did not score all specimens twice. Instead, I counted all specimens for a subset of the extant specimens twice and contrasted the two independent counts to assess the intra-observer error rate. The analyses are performed on actual counts from the specimens. The taxa used to assess intra-observer error rate are *Aplodontia rufa*, *Erethizon dorsatum*, *Sciurus carolinensis*, and *Marmota monax.* This set includes three of the five dietary categories considered in this study as well as various degrees of fossoriality. The intra-observer error was calculated using a linear regression of the first count of all pits against the second count for all pits. Similarly, a regression was run for all scratches. Because most of the pits are small and most of the scratches fine, I also ran regressions of the first count of the small pits versus the second and a regression of the first count all fine scratches versus the second.

Diet and burrowing behavior of rodents in relation to microwear signature

As a first attempt at differentiating the diets of extant and fossil rodents on the basis of microwear, I plotted the species means for the total number of scratches versus the total number of pits to look for the partitioning of dietary categories commonly reported in the microwear literature (e.g., Townsend and Croft 2008, fig. 4; Solounias and Semprebon 2002, fig. 8). I plotted these variables for each specimen to look for clustering of microwear signatures of animals with similar diets. These plots were then used to determine the magnitude of intraspecific variation in individual diets and to correlate the microwear signature of fossil taxa with those of extant ones of known diets. Outliers and clusters on the plots were checked against the specimen data to find potential links between microwear signature and specimen variables. All relationships uncovered from the plots were tested for significance using Chi-square tests. The commonly accepted convention is that the Chi-square test cannot be used when any of the cell counts is below five. However, this is only true of the expected count cell. Moreover, Bradley et al. (1979) have shown that small expected frequencies do not impair the test results. Hence, Chi-Square tests should be valid for these analyses in spite of the small sample sizes. I used two degrees of freedom for each of the tests (corresponding to the number of categories).

In order to test that the low-magnification microwear count of scratches and pits on the enamel surface of rodent teeth can accurately represent the ecology of the animals, I used several linear discriminant function analyses (DFA). I tested for the ability of the microwear features to differentiate the dietary category of each species on the basis of species mean values. Similarly, to test for a possible microwear signal from the exogenous grit ingested during burrowing by some taxa, I performed a linear discriminant function analysis comparing the various life habits (i.e. subterranean, fossorial, semi-fossorial, non-fossorial) of the taxa and differentiating this signal from their microwear. Finally, I ran a third DFA using the family-level identification of each species. This test was intended to determine whether phylogenetic differences were significant in generating the patterns of dental wear. I used the discriminant analysis developed from the extant taxa to determine the diet and burrowing behavior of the fossil taxa. The fossil taxa were treated as unknowns. I ran both non-jackknifed and jackknifed DFAs. All discriminant function analyses were run in JMP 8.0 (SAS).

I also used cluster analyses to find the extant species with the most similar diets to the six fossil taxa considered in this study. Those analyses were run using the average for the species considering all specimens counted. I ran analyses taking into account all of the detailed microwear feature categories excluding the total number of pits and the total number of scratches. This decision was made because these sums are not independent sets of variables and do not bring additional information to the dataset. I also ran analyses considering only the total number of pits and the total number of scratches. All cluster analyses were run in R 2.10.1 (2009). For each analysis, two clustering methods were used: Ward and average linkage. Both used euclidean distances.

Additionally, I used a principal component analysis (PCA) on the covariances of microwear feature distributions to find the features that explain most of the variance between taxa and to facilitate their visualization. This analysis was run excluding the total number of pits and scratches as explained above for the cluster analysis. The analysis was run in R 2.10.1 (2009) and the results were further investigated in JMP 8.0 (SAS) to determine the loadings of the different features on the principal components.

Finally, the data analysis was completed with two one way ANOVAs of the microwear features. This analysis is important to check for significant differences in microwear features within the dataset. The first ANOVAs were run on the total number of pits and scratches whereas the others considered all categories of microwear features. These ANOVAs were complemented by a Tukey-Kramer Honestly Significant Difference (HSD). This test is not as sensitive as the ANOVA and was only run when the null hypothesis of the ANOVA is rejected. It has the advantage of providing a comparison of the means for the feature studied across all taxa. The Tukey test assumes a parametric normal distribution of the data, an assumption violated by the microwear data. Rather, microwear data are distributed more like the nonparametric Poisson distribution. This only slightly violates the assumption of the Tukey test. A Wilcoxon test was also run to confirm the results of the ANOVA.

RESULTS

Intra-observer error

Results of the linear regressions are presented in Table 3 and shown in Fig. 2. The average R^2 (similarity between the two counts) for all pits is 0.74. It is largest (0.81) for *Sciurus carolinensis* and the smallest (0.63) for *Erethizon dorsatum*. When considering all scratches, the largest R^2 is for *Marmota monax* and smallest for *Erethizon dorsatum*. The average R^2 for all scratches is 0.73. There is no consistent trend in the relationship between the R^2 for all scratches or all pits and that of fine scratches and small pits respectively.

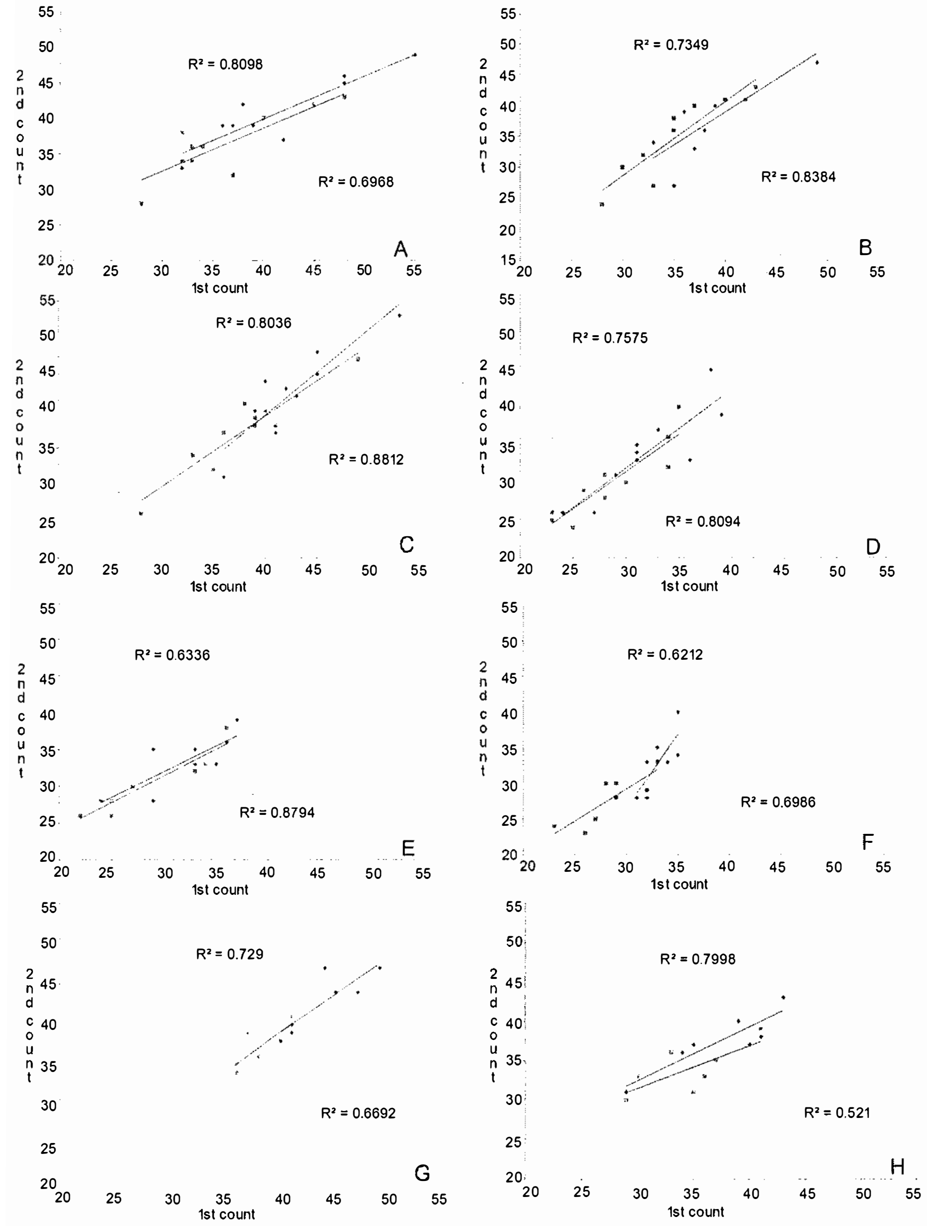


FIGURE 2: Linear regressions of counts of microwear features in four different taxa. Dark diamonds indicate total number of features (pits or scratches), grey squares counts of small pits or fine scratches. The R^2 above the regression line is for the total. A summary of the R^2 and p values is provided in Table 3. A. pits of *Sciurus carolinensis*, B. scratches of *S. carolinensis*, C. pits of *Aplodontia rufa*, D. scratches of *A. rufa*, E. pits of *Erethizon dorsatum*, F. scratches of *E. dorsatum*, G., pits of *Marmota monax*, H. scratches of *M. monax*.

TABLE 3: Results of the linear regressions for the intra-operator error.

Taxon	Variable	R^2	P
Sciurus carolinensis	small pits	0.6968	2.66E-03
	all pits	0.8098	3.89E-04
	fine scratches	0.8384	2.00E-04
	all scratches	0.7349	0.001523
Aplodontia rufa	small pits	0.8812	5.74E-05
	all pits	0.8036	0.0004438
	fine scratches	0.8094	3.92E-04
	all scratches	0.7575	0.001054
Erethizon dorsatum	small pits	0.8794	5.75E-04
	all pits	0.6336	0.01812
	fine scratches	0.6986	9.75E-03
	all scratches	0.6212	0.02015
Marmota monax	small pits	0.6692	2.45E-02
	all pits	0.729	0.01448
	fine scratches	0.521	6.70E-02
	all scratches	0.7998	0.00658

Some taxa (e.g., scratches in *Marmota monax*) display a high R^2 for the total counts of features (either scratches or pits) despite a low one for the most common finer feature (fine scratches or small pits respectively). Others (e.g., pits in *Erethizon dorsatum*) show a high R^2 for the fine scratches or small pits but a poor R^2 for the total of all features. The variation in microwear thus comes from either the main source of data (i.e. small pits/fine scratches) or the additional categories (larger and puncture pits, coarser scratches) depending on the taxon. Because I looked for significant relationships for both all pits and small pits as well as all scratches and fine scratches, I corrected the p value with the Bonferonni correction (p= 0.05/Number of tests, Shaffer 1995). Thus the threshold for significance is p=0.025 for each test. All relationships between the counts are significant.

Patterns of microwear features in relation to diet and burrowing behavior: graphical correlations

Fig. 3 shows the average number of scratches for the species plotted against the average number of pits. A summary of the counts for all taxa is provided in Table 4. All specimen counts are provided in Appendix D. The upper right corner of the graph shows species with high counts of both pits and scratches, including *Thomomys talpoides*, an extant gopher feeding above ground on abrasive food.

TABLE 4: Summary of the average microwear feature counts for all species included in the study. StD stands for Standard Deviation.

Taxon	N	Variable	# Small pits	# Large pits	# Large puncture pits	# Small puncture pits	Total number of pits	# Cross scratches	# Gouges	# Fine scratches	# Coarse scratches	# Hypercoarse scratches	Total number of scratches
A. rufa	10	Mean	37.20	1.60	1.40	2.60	42.80	0.40	0	30.10	2.30	1.10	33.90
		StD	5.63	1.17	1.07	1.35	6.00	0.52	0	4.98	2.06	1.10	5.72
D. ingens	9	Mean	46.67	4.33	4.67	4.11	59.78	0.56	0.1	31.56	2.22	1.00	35.44
		StD	4.95	1.12	1.50	2.85	7.33	0.88	0.3	5.17	1.39	1.00	5.20
E. dorsatum	8	Mean	30.13	1.25	0.75	1.25	33.38	1.88	0	27.75	2.38	1.00	33.00
		StD	4.09	0.89	0.89	1.04	3.81	2.10	0	3.45	1.30	0.93	3.85
H. glaber	11	Mean	43.27	3.64	2.09	1.82	50.82	0.64	0.2	45.27	5.64	1.00	52.73
		StD	8.05	1.86	1.70	1.40	7.97	1.29	0.4	5.20	2.62	1.41	5.22
M. monax	7	Mean	36.86	1.14	2.29	2.43	42.71	1.29	0.3	33.86	1.71	0.29	37.43
		StD	2.54	0.90	0.76	1.13	3.73	0.95	0.8	3.08	1.25	0.49	3.69
S. carolinensis	11	Mean	36.33	1.89	0.89	1.89	41.00	0.67	0	34.67	2.00	0.67	38.00

TABLE 4 (continued).

Taxon	N	Variable	# Small pits	# Large pits	# Large puncture pits	# Small puncture pits	Total number of pits	# Cross scratches	# Gouges	# Fine scratches	# Coarse scratches	# Hypercoarse scratches	Total number of scratches
S. griseus	8	Mean	31.13	2.13	2.00	1.63	36.88	1.13	0	42.00	1.13	0.75	45.00
		StD	4.32	0.83	1.41	1.77	5.03	1.25	0	3.02	1.13	0.46	2.83
T. bottae	7	Mean	53.00	3.29	1.57	1.86	59.71	1.29	0.7	48.14	4.14	1.00	55.29
		StD	13.54	5.09	1.27	1.95	11.13	1.60	1.0	9.28	4.71	1.15	11.84
T. senex	5	Mean	35.00	2.83	2.17	1.67	41.67	0.83	0	43.67	1.33	0.50	46.33
		StD	5.48	1.94	0.75	1.63	4.63	0.98	0	1.97	1.37	0.84	3.14
T. striatus	8	Mean	37.00	2.86	1.43	1.43	42.71	0.86	0	35.43	2.14	1.00	39.43
		StD	5.32	1.07	1.13	1.40	4.39	1.46	0	4.89	1.35	0.82	5.38
T. talpoides	6	Mean	62.33	3.83	1.50	0.83	68.50	1.50	0.2	60.83	3.00	0	65.50
		StD	7.06	1.33	1.64	0.75	6.92	2.07	0.4	3.37	1.55	0	3.78
H. species A	8	Mean	29.25	2.25	1.13	0.75	33.38	2.00	0	32.63	1.63	0.50	36.75

TABLE 4 (continued)

Taxon	N	Variable	# Small pits	# Large pits	# Large puncture pits	# Small puncture pits	Total number of pits	# Cross scratches	# Gouges	# Fine scratches	# Coarse scratches	# Hypercoarse scratches	Total number of scratches
H. gazini	7	Mean	34.14	2.00	1.14	2.57	39.86	2.71	0	32.43	2.14	0.57	37.86
		StD	5.43	2.08	1.21	2.15	6.44	3.40	0	3.91	1.68	0.53	2.19
A. vetus	5	Mean	35.20	1.80	2.40	1.20	40.60	2.60	0	28.80	1.60	1.00	34.00
		StD	5.17	1.79	1.67	0.84	3.65	1.34	0	3.11	0.89	1.00	4.30
P. magnus	3	Mean	67.33	3.33	4.67	2.67	78.00	4.67	0	64.67	1.33	1.33	72.00
		StD	4.62	2.31	4.16	2.31	5.29	2.31	0	7.57	1.15	1.15	5.29
M. mascallensis	3	Mean	64.67	4.00	5.33	0	74.00	3.33	0	62.67	4.00	0.67	70.67

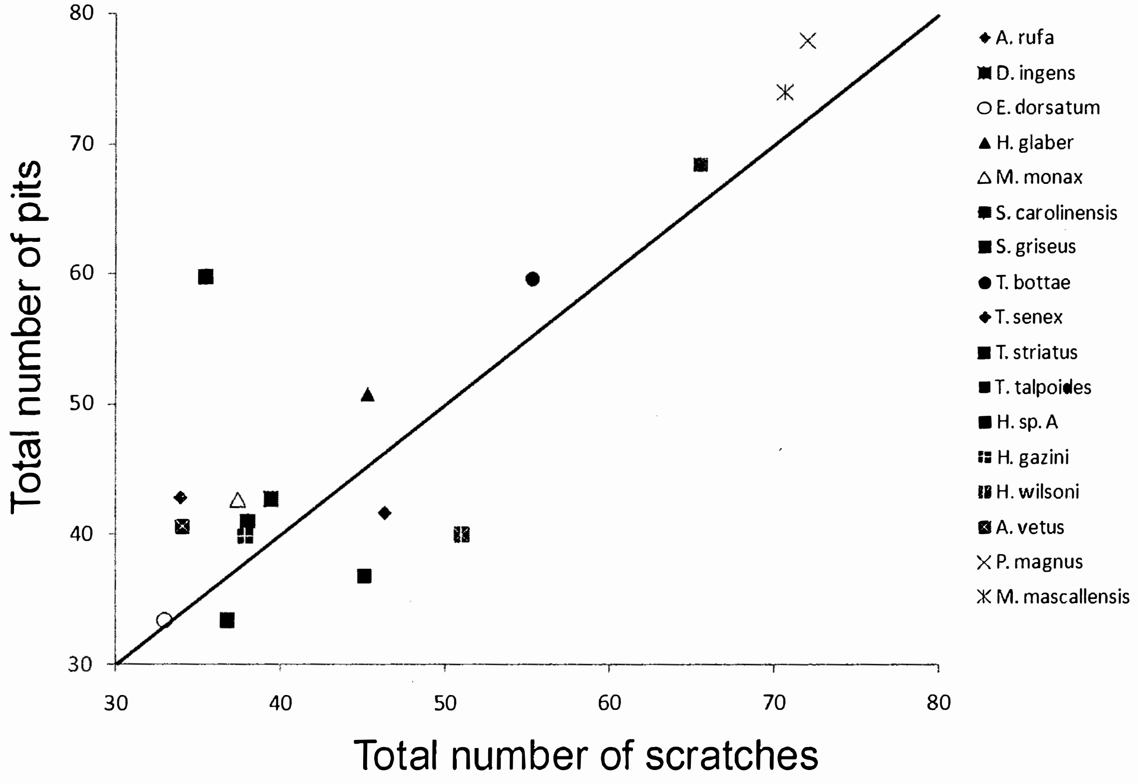


FIGURE 3: Bivariate plot of the counts of scratches versus pits averaged for each species included in this analysis. Symbols correspond to the following categories: empty, mixed feeders; black, underground feeders; dark gray, fungivores; dark gray with black lines, hard object feeders; light gray, abrasive food eaters; crosses, fossil geomyids; black with white lines, mylagaulids.

This species is above the one-to-one line and therefore exhibits more pits than scratches. Farther down the line but remaining above it, are other subterranean taxa, *Thomomys bottae* and *Heterocephalus glaber*, which both feed on the underground storage organs of plants (roots, tubers, corms, etc.). On the upper left corner of the graph with a low count of scratches but many pits is *Dipodomys ingens*, a hard-object-feeding semi-fossorial heteromyid. In the lower left corner on the graph with roughly equal numbers of scratches and pits is *Erethizon dorsatum*, a non-fossorial mixed feeder. To the right of the graph with more scratches than pits are the two fungivorous taxa included in this study: *Tamias senex* and *Sciurus griseus.* A cluster of four different species is located on the left of the graph and displays high counts of pits relative to the number of scratches. This group include, with the fewest scratches relative to pits *Aplodontia rufa*, a fossorial animal feeding on ferns and other above ground abrasive plants. Two taxa of hard-object-feeding rodents cluster together with the semi-fossorial *Tamias striatus* located just above *Sciurus carolinensis*. Located in between the abrasive food eating *A. rufa* and the hard object feeding squirrels is *Marmota monax*, a fossorial mixed feeder.

The microwear signature of fossil taxa can be qualified using counts of scratches and pits and visually compared to the distributions of extant taxa (Fig. 4). In order to obtain a first approximation of the diet of the fossil taxa studied, I first looked at where they plot in relation to modern taxa on a plot of scratches versus pits (Fig. 3). When considering the average for the species, the two species of fossil geomyids plot very close to one another in the upper right corner of the graph above *Thomomys talpoides*. The Mylagaulidae, however, display a very different microwear signature with much lower counts of both scratches and pits. *Hesperogaulus wilsoni* plots close to the fungivorous squirrels although it exhibits a few more scratches than *Tamias senex* or *Sciurus griseus. Hesperogaulus* sp. *A* is located in the lower left corner of the graph quite close to *Erethizon dorsatum* but again with a few more scratches.

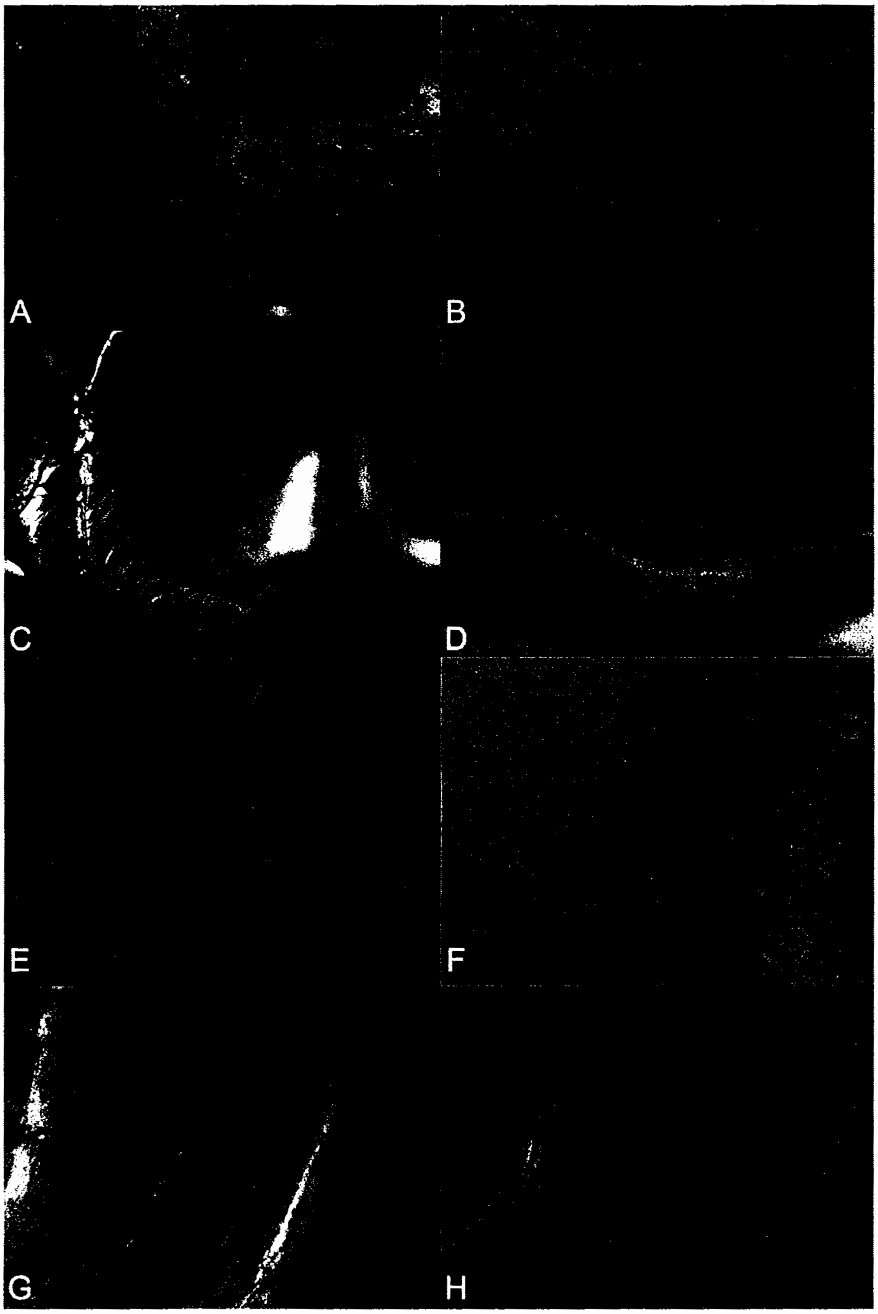


FIGURE 4: Views of the counting areas and microwear features of several species of rodents included in this study. All photos were taken at 37.5x magnification. A. *Dipodomys ingens*, B. *Erethizon dorsatum*, C. *Heterocephalus glaber*, D. *Sciurus carolinensis*, E. *Thomomys talpoides*, F, *Alphagulus vetus*, G, *Hesperogaulus sp. A*, H. *Hesperogaulus gazini*.

Alphagaulus vetus is closest to *Aplodontia rufa* but with fewer pits. The last species of mylagaulids, *Hesperogaulus gazini*, is plotting close to the cluster of *Sciurus carolinensis*, *Tamias striatus*, and *Marmota monax*, with fewer pits than *S. carolinensis*.

To get a better idea of the spread of the microwear signatures in fossil burrowing rodents, and their overlap with modern taxa, we can look at the specimen data shown in Fig. 5. Fossil Geomyidae cluster together and both overlap with *Thomomys talpoides*. The single specimen of *Hesperogaulus wilsoni* plots where a specimen of *Tamias striatus* plots and exhibits a few more scratches than fungivores. *Hesperogaulus* sp. *A* overlaps heavily with *Erethizon dorsatum*. It also spans the fields of *Aplodontia rufa*, *Sciurus griseus*, *Sciurus carolinensis* and slightly overlaps with *Tamias striatus* and *Marmota monax.* All specimens of *Alphagaulus vetus* but two are included in the field of *Aplodontia rufa*. One of the specimens excluded is on the very edge of the field and the last specimen is also very close to the limit of the range of *A. rufa*'s microwear signature. *Hesperogaulus gazini* overlaps with *A. rufa*, *Marmota monax*, or the two seed-eating sciurids. *Hesperogaulus wilsoni* does not overlap with any other mylagaulid. *A. vetus* and *Hesperogaulus* sp. *A* do overlap in the upper part of the field of *H.* sp. *A* and the lower left one of *A. vetus*. *Hesperogaulus gazini* overlaps with both *H.* sp. *A* and *A. vetus*.

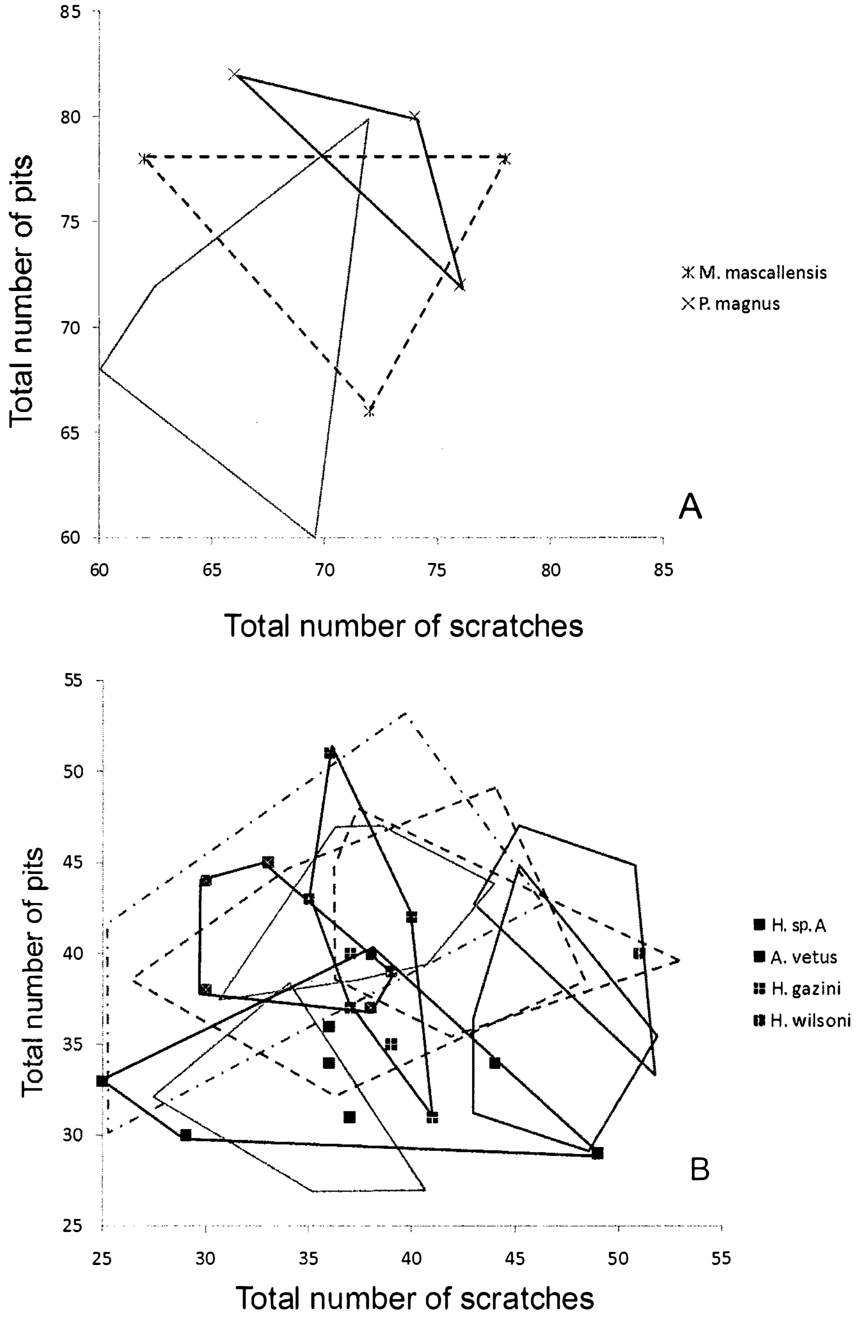


FIGURE 5: Microwear data of fossil specimens. A. Fossil geomyids and *Thomomys talpoides*. B. Mylagaulids and *A. rufa* (alternating dot-dash), *S. carolinensis* and *T. striatus* (dashes), and *E. dorsatum* and *M. monax* (gray full line).

Variations in microwear signature within taxa

Rather than looking at the average for the species which includes possible outliers and may not reflect finer clusterings, consequences of seasonal or geographic variations, we can also plot the average number of scratches and pits for all specimens of modern taxa (Fig. 6).

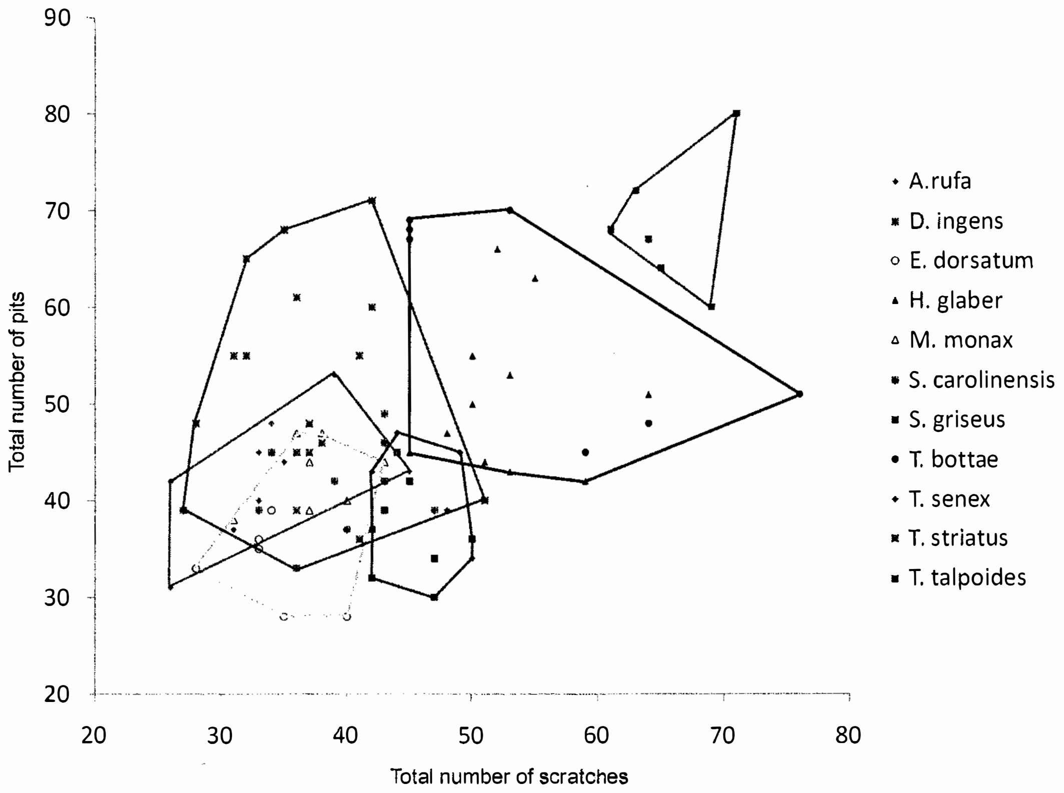


FIGURE 6: Bivariate plot of the counts of scratches versus pits for all specimens of all species included in this analysis. Black lines indicate underground feeders, dark gray lines indicate fungus eaters, medium gray indicates hard object feeders, light gray indicates abrasive food eating rodents, pale gray indicates mixed feeders.

All specimens of *Thomomys talpoides* cluster rather close to one another. There is no overlap with any other specimen of a different species. There is, however, some overlap between the two underground feeding rodents since some specimens of *Thomomys bottae* are very close to or even overlap with the field of *Heterocephalus glaber*. This latter species exhibits a very small overlap with the *Tamias senex* whose field overlaps heavily with that of *Sciurus griseus*. On the upper left corner of the graph, with numerous scratches and pits, are the specimens of the seed -specialist *Dipodomys ingens*. There is a lot of variation in the total number of pits and scratches of this species but it does not overlap with any other species. The lower left corner of the plot exhibits a lot of overlap between five species in three different dietary groups. Towards the bottom of this cluster, *Erethizon dorsatum*, is rather well constrained and occupies a field with low counts of pits. It is a mixed-feeder and overlaps with both an abrasive food eating species (*A. rufa*) and a seed-eating squirrel (*Sciurus carolinensis*). The first of these species spans counts of scratches from about 25 to 45 and pits from 30 to 50, thus occupying much of the space in this corner of the graph. All species with microwear signatures located in this corner of the plot overlap with *A. rufa*. The two species of seed eaters: *T. striatus* and *S. carolinensis* overlap almost entirely as well as with the mixed feeding *Marmota monax* which in turns also falls within the field of *A. rufa*. The lower left corner of the field of the seed eaters and the upper left one of the fungus-eaters overlap as well.

This general pattern of species' numbers of scratches vs. pits shows the diversity of microwear signatures within taxa. Numerous species such as *Thomomys bottae*, *Heterocephalus glaber*, and *Dipodomys ingens* span a wide range of microwear signatures along both axes. There is also a substantial overlap of the microwear signatures of four species in the lower left corner of the graph. Nevertheless, the diversity in microwear signatures within taxa can be understood by integrating geographic, seasonal, or sexual data from collection records (Fig. 7). These relationships are expected because microwear reflects the last meal of the individual and therefore (because it is not averaged) should represent variation in diet associated to season or foraging area. Linking microwear signatures to seasonal, geographic, and sexual data on specimens, has recently been undertaken in a quantitative manner by Merceron et al. (2010). It will only be approached qualitatively here.

There are five taxa for which it is possible to observe some variation introduced by seasonal, geographic, and other ecological differences. These relationships are not straightforward and should be further tested with larger sample sizes. In *Thomomys bottae*, four specimens from California, with high counts of pits (around 70) and lower counts of scratches (around 50), cluster together. There is another cluster with two specimens from Utah and one from California with higher counts of scratches (between 60 and 80) at lower pit counts (below 50). Similarly, in *Aplodontia rufa*, it seems that geographic origin (as a proxy for differences in regional environment) of the specimen may account for some of the discrepancies in microwear between the single specimen from Oregon (that exhibits the largest number of scratches) and the specimens from Washington. There is also a convergence between season of death and microwear.

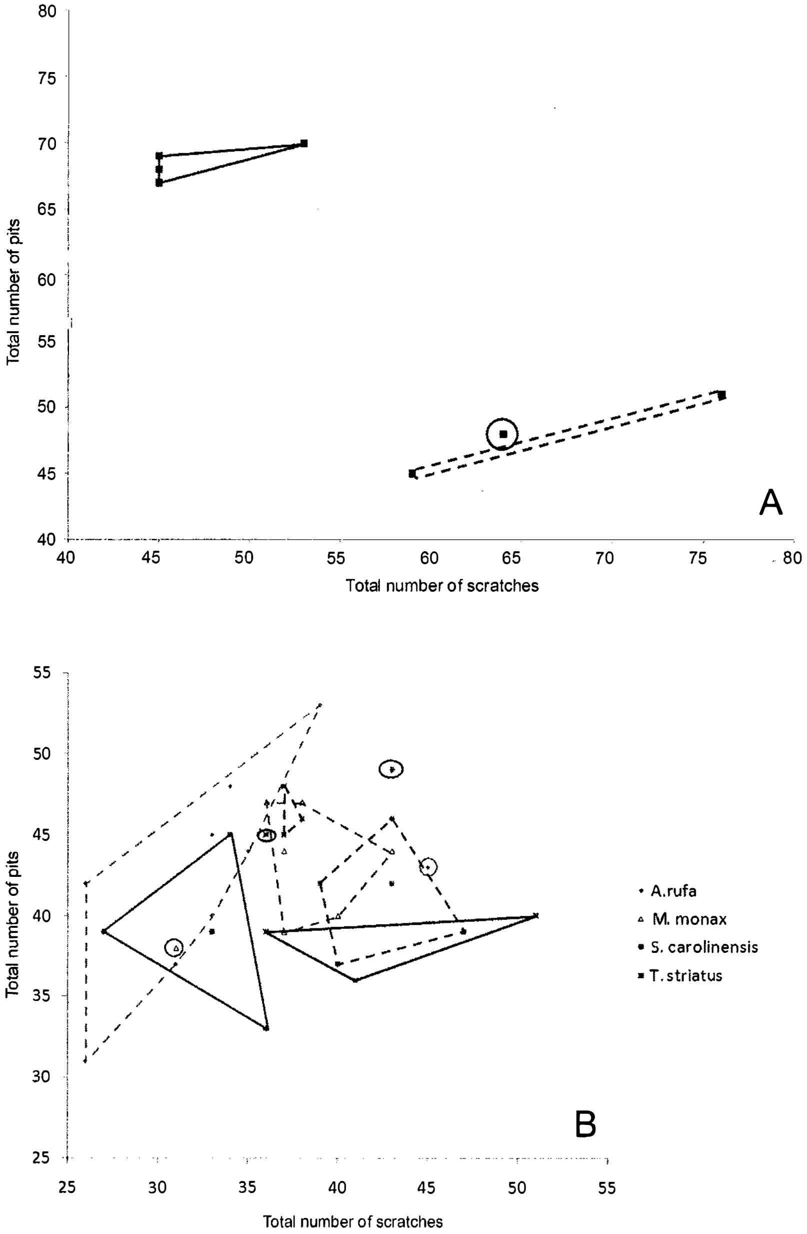


FIGURE 7: Variation among specimens of rodent taxa. A. *Thomomys bottae*: full line indicates Californian specimens, dashed line specimens from Utah. B. Black lines: *Tamias striatus*, solid line corresponds to male specimens, dashed line to female ones; dark gray lines: *Sciurus carolinensis*, dashed line unites spring and summer specimens, solid line fall and winter ones; light gray lines: *Aplodontia rufa*, dashed line indicates specimens from Washington, solid line the specimen from Oregon.

In *Marmota monax*, the specimen with the least number of pits and scratches died and was collected in winter, while the other specimens collected spring and summer cluster together in a tight window of scratches and pits. There is also a relationship between season and microwear signature in *Sciurus carolinensis* with the single specimen collected in fall or winter exhibiting few scratches and a cluster of specimens with higher counts of scratches including specimens collected in spring or summer (except for one specimen collected in February that has the highest number of pits recorded for the species). In *Tamias striatus*, a group of three specimens includes only males ranging widely in the number of scratches with very little variation in the number of pits. Another group includes four specimens with very tightly clustered microwear patterns (range of scratches: 36-38, range of pits: 45-48). This group includes mostly females; there is only one male specimen. This could represent differences in nutrition in relation to gestation or lactation. Those qualitative relationships can be checked for significance using a Chi-square test. The results are summarized in Table 5. As a consequences of looking for clusterings in different species, I corrected the p value with the Bonferonni correction (p= 0.05/Number of tests, Shaffer 1995). Thus the threshold for significance is p=0.01 for each test. None of the results are found to be significant. There is no particular clustering of the specimens' microwear for fossil taxa.

Two extant species show a very wide range of observed microwear patterns that does not relate to any obvious seasonal, geographic, or sexual data. All specimens of *Dipodomys ingens* were collected on the same day in the same place and yet display a very wide range of pit and scratch counts. Similarly, all specimens of *Heterocephalus glaber* were collected in the same place over the course of a few months and do not show any pattern consistent with the collection records. This suggests that a wide variety of food resources were consumed by the different individuals collected.

TABLE 5: Summary of the Chi-square tests for significance of intra-specific clusterings.

Taxon	Specimen data	Composition of cluster 1	Composition of Cluster 2	X^2	P
Sciurus carolinensis	Spring/Summer	0	5	6.8	0.043
	Fall/Winter	4	1		
Thomomys bottae	Utah	0	2	3.8	0.1496
	California	4	1		
Tamias striatus	Males	3	1	4	0.135
	Females	0	3		
Marmota monax	Winter	1	0	7	0.0302
	Spring/Summer	0	6		
Aplodontia rufa	Oregon	1	0	10	0.0674
	Washington	0	9		

Cluster analyses of microwear

In order to better constrain the diet of fossil burrowing rodents, I used cluster analyses to group the fossil taxa with the extant rodents with the most similar microwear signatures (Fig. 8-11). There are very few differences between the four analyses. All analyses agree on the clustering of the fossil geomyids with *Thomomys talpoides* as well as the position of *Hesperogaulus* sp. *A*, which clusters with *Erethizon dorsatum*.

Alphagaulus vetus groups consistently with *Aplodontia rufa*, and *Hesperogaulus wilsoni* is found to cluster with *Tamias senex* and *Sciurus griseus*. The grouping of species within clusters differs depending on the data used. Using all microwear features excluding totals, *S. griseus* and *T. senex* are found to be closer to each other with *H. wilsoni* falling outside, not clustered with any living taxon. However, when running the analyses with only the total number of scratches and pits, *H. wilsoni* is grouped with *T. senex* and *S. griseus* falls out of this cluster. Using Ward's method or average linkage did not make a difference. The two remaining clusters are less robust since some discrepancies are found across the analyses. All analyses but the one of all microwear features using average linkage find a cluster including *Heterocephalus glaber*, *Thomomys bottae*, and *Dipodomys ingens* with the first two grouping together. There are also differences in the clustering of *Hesperogaulus gazini*. Both analyses using only the total number of pits and scratches find *H. gazini* to cluster with *Sciurus carolinensis*. This cluster groups with another cluster including *Marmota monax* and *Tamias striatus*. Using all microwear features without totals, two very different topologies are found, both different from that found using totals only. The average linkage method yields clusters involving the same taxa as in the other analyses but in a different configuration. *T. striatus* and *S. carolinensis* cluster together with *M. monax* outside of this group and *H. gazini* outside of the cluster formed by the three Sciuridae. Finally, if I run the analysis using Ward's method on all microwear features, *H. gazini* clusters with other species since it falls outside of the group formed by *A. rufa* and *A. vetus*.

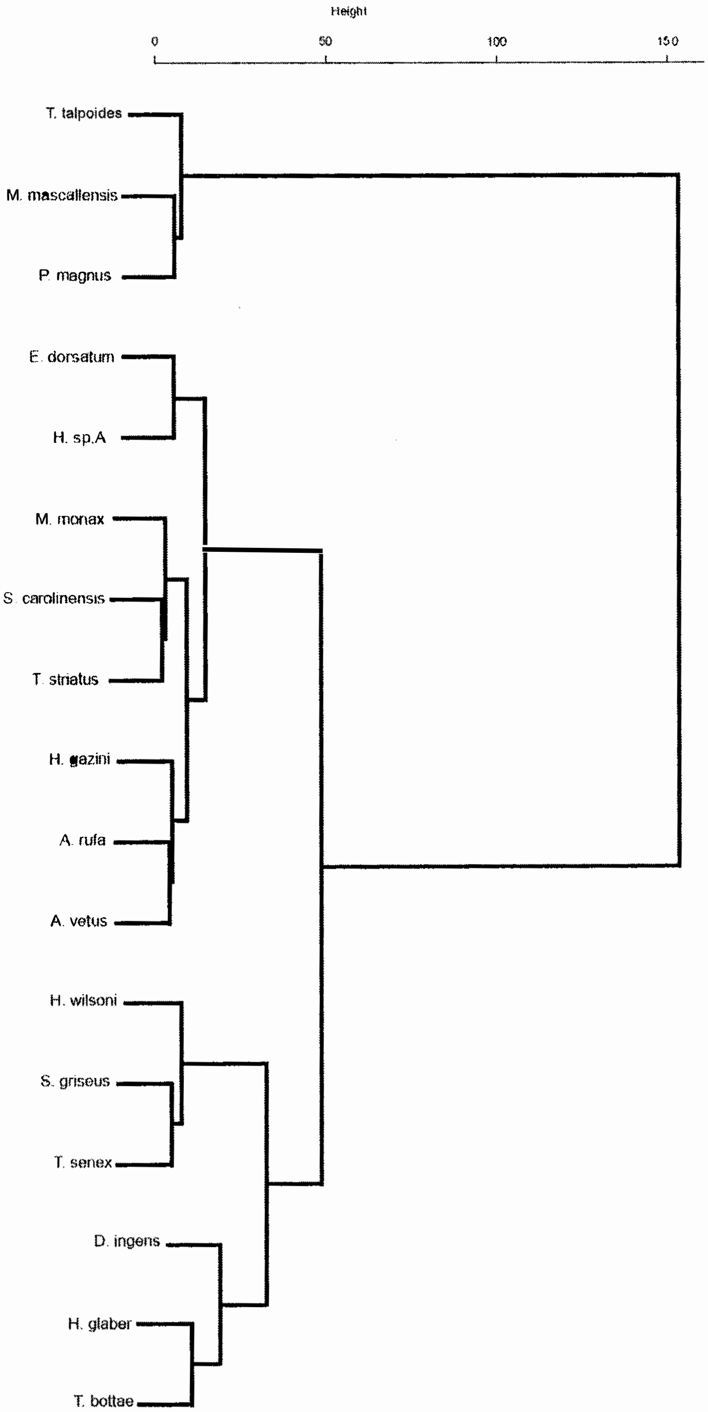


FIGURE 8: Cluster analysis of the microwear features using Ward's method on all microwear features.

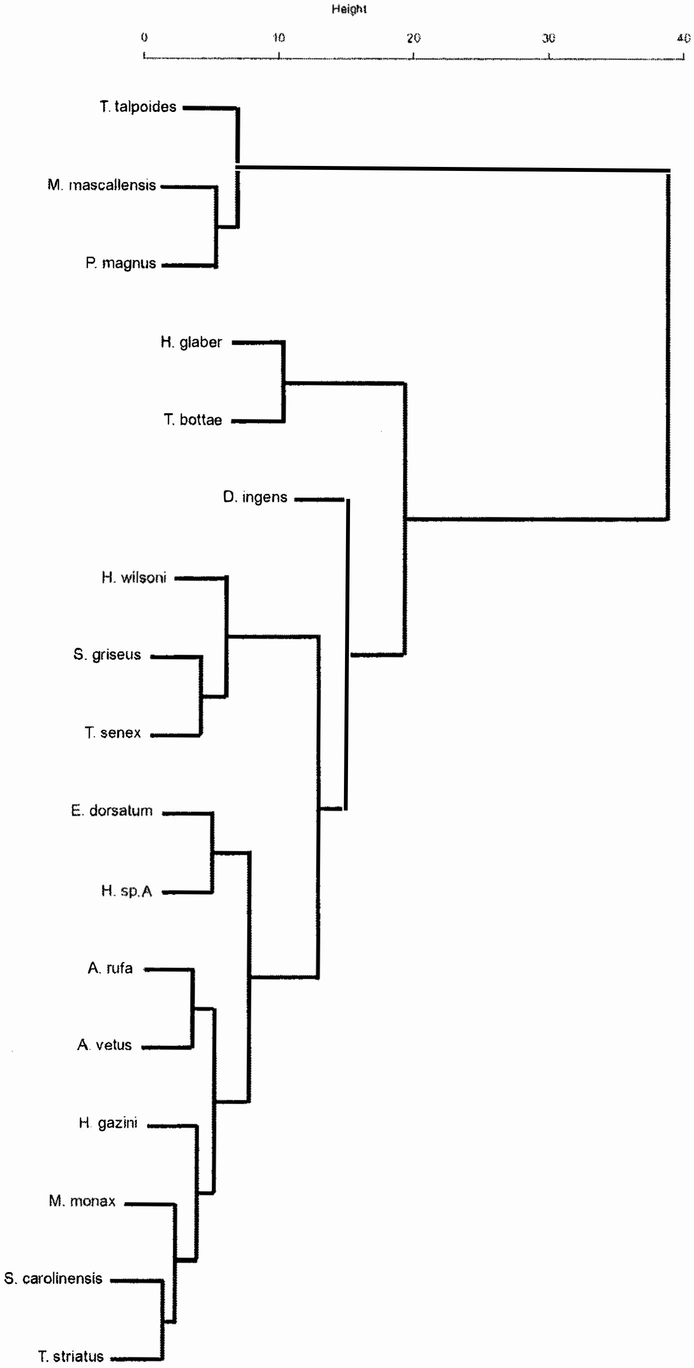


FIGURE 9: Cluster analysis of the microwear features using the average linkage method on all microwear features.

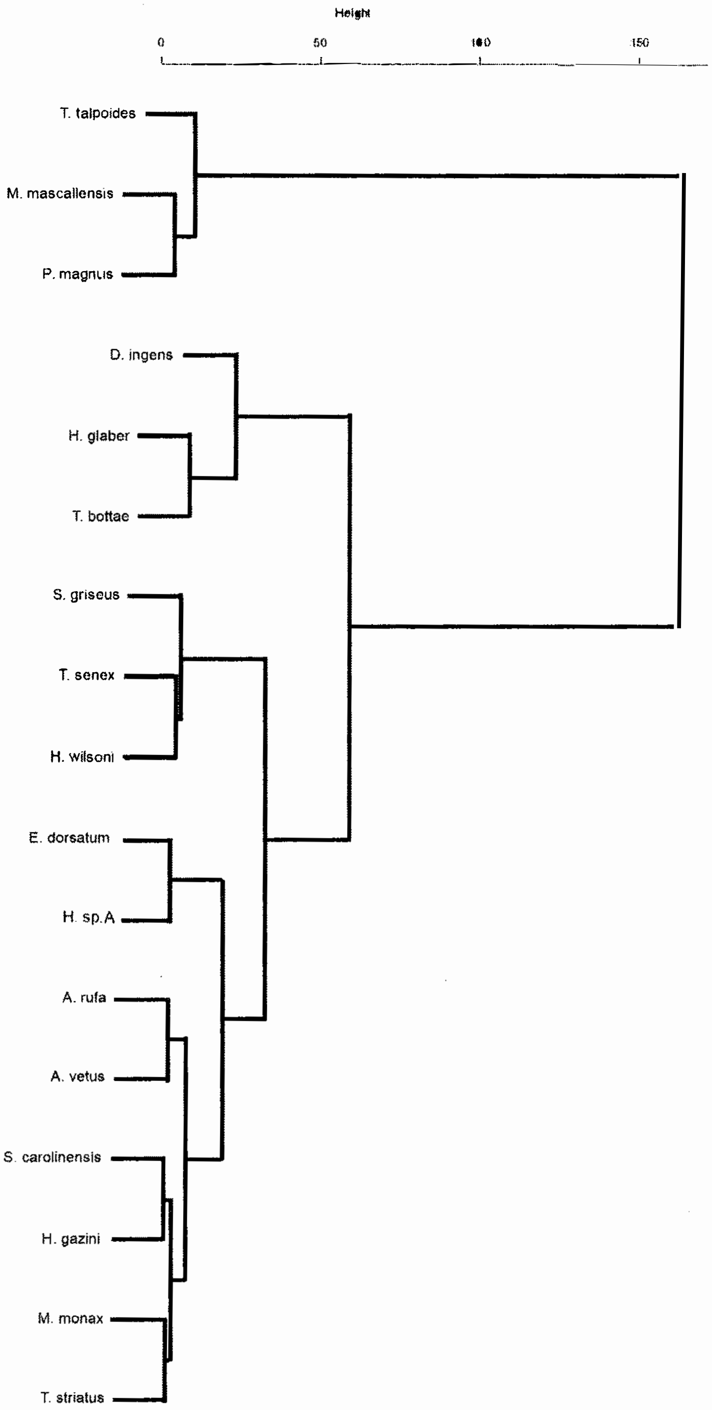


FIGURE 10: Cluster analysis of the microwear features using Ward's method on the total pits and scratches.

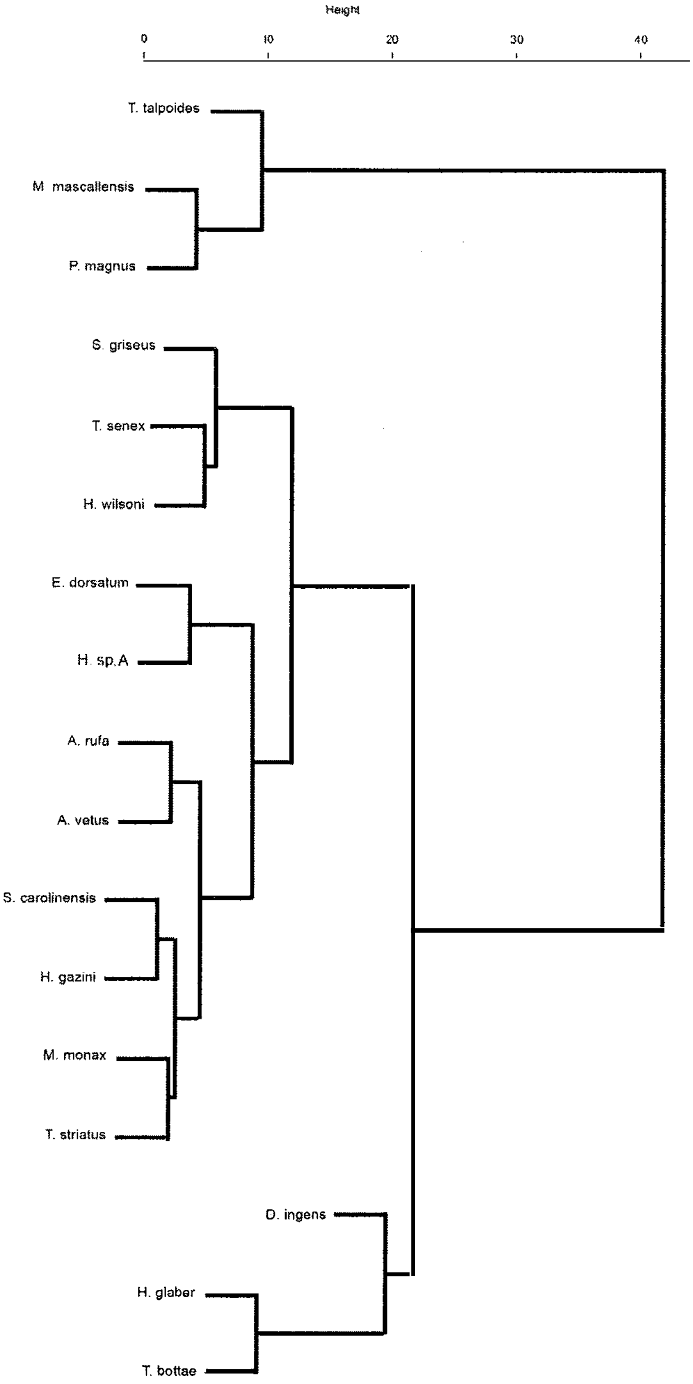


FIGURE 11: Cluster analysis of the microwear features using the average linkage method on the total pits and scratches.

Discriminant function analyses of microwear signatures: can various diets and burrowing behaviors be differentiated?

I ran several DFAs to test for the potential of microwear to reflect dietary categories, burrowing behavior, and phylogenetic affinity. The non-jackknifed DFAs categorized all extant taxa correctly according to their degree of fossoriality, dietary category, or family identification. The DFA obtained from the dataset of extant rodents can be applied on fossil ones to attempt to better understand their ecology from their microwear. The first DFA run, including extant and extinct rodents, discriminated taxa on the basis of the counts of microwear features on their enamel and their degree of fossoriality. The results of this analysis are provided in Table 6. The two geomyids were assigned high degrees of fossoriality (fossorial and subterranean) whereas the mylagaulids were mostly assigned low degrees of fossoriality. *Alphagaulus vetus* was classified as fossorial whereas all species of the genus *Hesperogaulus* were classified as non-fossorial. This puzzling result is further discussed in the discussion. The categorization of fossil species in dietary categories by the DFA is similarly giving a uniform signal across geomyids of an abrasive diet whereas within the mylagaulids much diversity is observed. Almost all categories of diets are represented within the family. *Alphagaulus vetus* is interpreted as a hard object feeder (i.e. nuts and seeds). Within the genus *Hesperogaulus*, *H. gazini* is associated to a mixed food diet, *H. wilsoni* to a diet of underground storage organs, and *H.* sp. A to a diet of fungi. The final analysis, concerned with taxonomic identification, properly classified all extant and fossil taxa in their respective families, indicating the presence of phylogenetic signal in the microwear, a troubling result.

TABLE 6: Summary of the proposed diet and fossoriality results for fossil species.

Taxon	Graphical correlation using specimen data	Graphical correlation using species average	Cluster analyses using totals only	Cluster analyses using all features	DFA treated as unknowns
Pliosaccomys magnus	Abrasive-Subterranean	Abrasive-Subterranean	Abrasive-Subterranean	Abrasive-Subterranean	Abrasive-Subterranean
Mojavemys mascallensis	Abrasive-Subterranean	Abrasive-Subterranean	Abrasive-Subterranean	Abrasive-Subterranean	Abrasive-Fossorial
Alphagaulus vetus	Abrasive-Fossorial	Abrasive-Fossorial	Abrasive-Fossorial	Abrasive-Fossorial	Hard food-Fossorial
Hesperogaulus gazini	Mixed-Fossorial	Mixed-Non-fossorial	Hard food-Non-fossorial	Abrasive-Fossorial Mixed-Fossorial	Fungivory-Non-fossorial
H. species A	Mixed-Non-fossorial	Mixed-Non-fossorial	Mixed-Non-fossorial	Mixed-Non-fossorial	Mixed-Non-fossorial
H. wilsoni	Hard food-Semi-fossorial	Fungivory-Non-fossorial	Fungivory-Non-fossorial	Fungivory-Non-fossorial	Underground-Non-fossorial

I also ran DFAs jackknifing the data to check for the stability of the results obtained without withholding taxa from the DFA. A summary of the results for the jackknifed DFAs on dietary categories and burrowing behavior are provided in Table 7 and 8.

TABLE 7: Actual (rows) versus predicted (columns) dietary category results for extant taxa.

	Abrasive	Hard	Underground	Fungivory	Mixed
Abrasive	0	1	1	0	0
Hard	0	0	1	1	1
Underground	1	0	1	0	0
Fungivory	0	1	0	1	0
Mixed	0	1	0	1	0

TABLE 8: Actual (rows) versus predicted (columns) burrowing category results for extant taxa.

	Non Fossorial	Semi-fossorial	Fossorial	Subterranean
Non Fossorial	1	2	1	0
Semi-fossorial	1	0	1	0
Fossorial	0	1	1	0
Subterranean	0	0	2	1

For dietary categories, only 18% of the taxa (i.e. *Sciurus griseus*, *Heterocephalus glaber*) were properly categorized *a posteriori.* The DFA for burrowing behavior properly classified only 27% of the taxa in their burrowing behavior category (i.e. *Marmota monax*, *Sciurus griseus*, *Thomomys bottae*). It was not possible to run jackknifed analyses on the family identifications since numerous families are represented by a single taxon.

In addition to poor results with extant taxa, I observed important variations in the results for fossil taxa from the jackknifed DFAs. A summary of the results for the fossil taxa is provided in Tables 9 and 10.

TABLE 9: Results of the jackknifed Discriminant Function Analyses for dietary categories. The first row indicates the taxon witheld from the analysis. Diet Abbreviations: A, Abrasive; M, Mixed; H, Hard; U, Underground; F, Fungivory. Taxa Abbreviations: A, *Aplodontia rufa*; Av, *Alphagaulus vetus*; D, *Dipodomys ingens*; E, *Erethizon dorsatum*; H, *Heterocephalus glaber*; Hg, *Hesperogaulus gazini*; Hs, *Hesperogaulus* species A; Hw, *Hesperogaulus wilsoni*; M, *Marmota monax*; Mm, *Mojavemys mascallensis*; Sc, *Sciurus carolinensis*; P, *Pliosaccomys magnus*; Sg, *Sciurus griseus*; Tb, *Thomomys bottae*; Te, *Tamias senex*; Ts, *Tamias striatus*; Tt, *Thomomys talpoides*.

	A	*D*	*E*	*H*	*M*	*Sc*	*Sg*	*Tb*	*Te*	*Ts*	*Tt*
Hs	M	M	H	F	M	F	M	F	M	F	M
Hg	F	U	U	F	M	M	M	F	M	M	F
Hw	F	U	U	U	M	F	U	F	U	F	F
Av	M	M	H	M	H	H	M	M	M	F	M
Mm	A	A	M	A	A	H	M	U	M	A	U
Pm	A	U	H	F	M	A	M	F	M	A	U

TABLE 10: Results of the jackknifed discriminant function analyses for burrowing behavior categories. The first row indicates the taxon witheld from the analysis. Fossoriality Abbreviations: N, Non-fossorial; SF, Semi-fossorial; F, Fossorial; SU, Subterranean. Taxa Abbreviations: A, *Aplodontia rufa*; Av, *Alphagaulus vetus*; D, *Dipodomys ingens*; E, *Erethizon dorsatum*; H, *Heterocephalus glaber*; Hg, *Hesperogaulus gazini*; Hs, *Hesperogaulus* species A; Hw, *Hesperogaulus wilsoni*; M, *Marmota monax*; Mm, *Mojavemys mascallensis*; Sc, *Sciurus carolinensis*; P, *Pliosaccomys magnus*; Sg, *Sciurus griseus*; Tb, *Thomomys bottae*; Te, *Tamias senex*; Ts, *Tamias striatus*; Tt, *Thomomys talpoides*.

	A	*D*	*E*	*H*	*M*	*Sc*	*Sg*	*Tb*	*Te*	*Ts*	*Tt*
	N	SF	SF	N	N	N	N	N	SF	N	N
*H*s	N	F	SF	N	N	N	N	N	N	SF	N
Hg	N	SF	SF	N	N	N	SU	SF	SU	N	SU
Hw	SF	F	SF	SF	F	SF	F	F	N	F	F
Av	SU	F	SU	SU	SU	SU	SU	SU	SU	F	F
Mm	SU	F	SU	SU	SU	SF	F	SU	N	SF	F

Most taxa are categorized into three or more (up to all) categories at least once. For the analysis bearing on the dietary categories, the best result is obtained for *Alphagaulus vetus* which is categorized in 64% of the analyses as a mixed feeder. *Hesperogaulus* sp. A is categorized 55% of the time in this category. *Pliosaccomys magnus* is categorized in any one of the dietary groups depending on the analysis. The analysis concerned with burrowing behavior yields slightly better results. *H. gazini* is categorized in 82% of the analyses as a non fossorial animal. *H.* sp. A and *Mojavemys mascallensis* are categorized respectively as non fossorial or subterranean in 73% of the analyses. Overall, these analyses give very equivocal results. In addition to not being statistically reliable, some burrowing behavior results may not be plausible in light of additional data. In particular, the fossorial to subterranean mylagaulids are often categorized as non-fossorial animals.

Principal component analysis of microwear

The results of the PCA are summarized in Table 11 and Fig. 12. Two of the eleven components explain much of the variation in the dataset. PC 1 in particular explains 90% of the variation in microwear. PC 2 explains 8% and the following components less than 2% altogether.

TABLE 11: Summary of the results of the principal component analysis.

Principle Component	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9
Variance explained (%)	90.23	8.056	0.65	0.438	0.275	0.190	0.118	0.026	0.016

A summary of the eigenvectors for the first two principal components is provided in Table 12. The loadings on the first component are most heavily relying on the number of small pits and the number of fine scratches. All loadings for PC 1 are positive with the exception of the small puncture pits. The loadings seem to reflect the proportion of each feature in an average microwear pattern. The loadings of PC 2, however, although strongly influenced by the small pits and the fine scratches alike PC 1, displays numerous negative loadings including the most important loading, "fine scratches." Large puncture pits also appear to be contributing to PC 2. The values of PC 1 and PC 2 for all taxa are summarized in Table 13. The values of PC 1 are of particular interest. Indeed, all positive values for PC 1 belong to subterranean taxa. All negative ones belong to non-fossorial, semi-fossorial, or fossorial taxa. No clear link between ecology and PC 2 can be drawn.

TABLE 12: Summary of the eigenvectors for PC1 and PC2. Abbreviations: SP. small puncture pits; LP. large pits; LPP. large puncture pits; SPP. small puncture pits; CRS. cross scratches; G. gouges; FS. fine scratches; CS. coarse scratches; HS. hypercoarse scratches.

Variables	Loadings PC 1	Loadings PC 2
SP	0.72023	0.67769
LP	0.03962	-0.07295
LPP	0.05279	0.12167
SPP	-0.01056	0.07487
CRS	0.03461	0.01477
G	0.00093	-0.04585
FS	0.68913	-0.71417
CS	0.02651	0.03196
HS	0.00011	0.04028

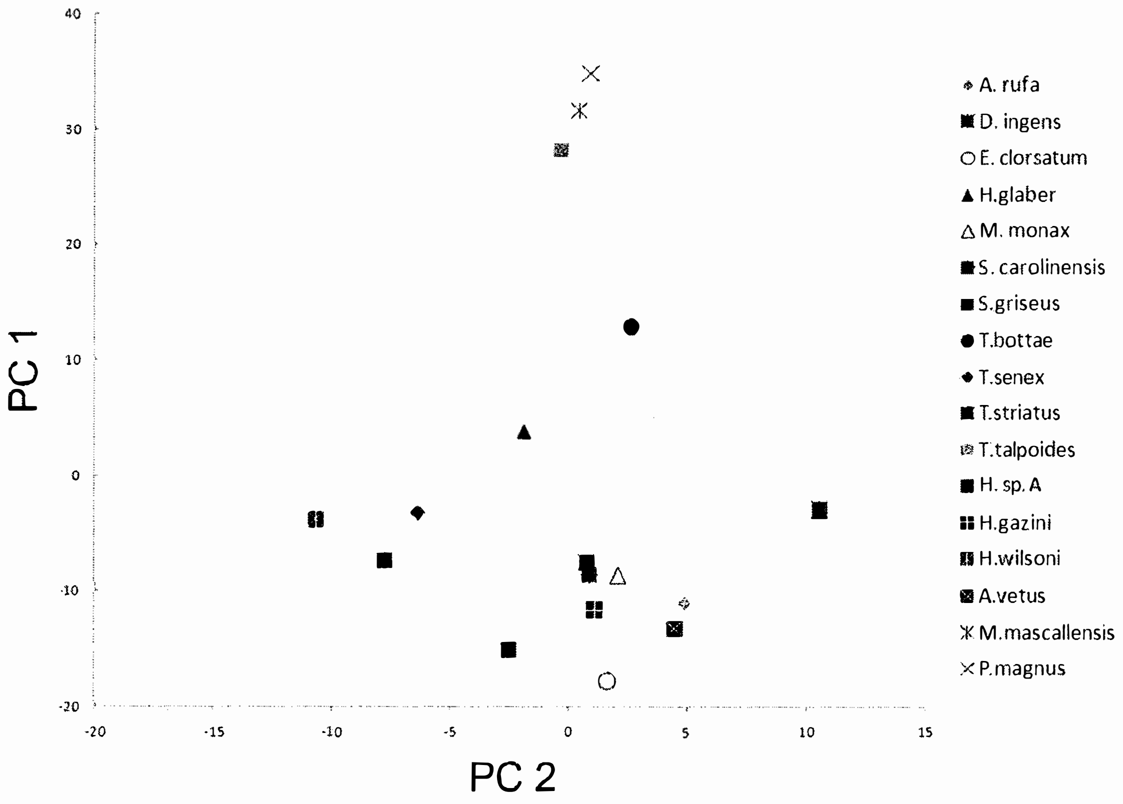


FIGURE 12: Plot of PC2 versus PC1 for all rodent species (fossil and extant). Symbols correspond to the following categories: empty, mixed feeders; black, underground feeders; dark gray, fungivores; dark gray with black lines, hard object feeders; light gray, abrasive food eaters; crosses, fossil geomyids; black with white lines, mylagaulids.

TABLE 13: Summary of the Principal Components value for all taxa.

Taxon	PC 1	PC 2
Aplodontia rufa	-11.14204	4.84664246
Dipodomys ingens	-3.0469607	10.5241505
Erethizon dorsatum	-17.834108	1.59943705
Heterocephalus glaber	3.90634237	-1.8990315
Marmota monax	-8.7498997	2.00841649
Sciurus carolinensis	-8.6259197	0.83400186
Sciurus griseus	-7.2560911	-7.8445843
Thomomys bottae	12.8334623	2.54784562
Tamias senex	-3.2867776	-6.4500868
Tamias striatus	-7.5375044	0.72635327
Thomomys talpoides	28.3032513	-0.3660256
Hesperogaulus sp. A	-15.055792	-2.5885814
Hesperogaulus gazini	-11.66217	1.0534733
Hesperogaulus wilsoni	-3.8087891	-10.705663
Alphagaulus vetus	-13.345285	4.42803265
Mojavemys mascallensis	31.5640576	0.39089678
Pliosaccomys magnus	34.7442244	0.89472243

Analysis of variance of microwear and significant differences across taxa

The one way ANOVA analyses of the total number of scratches and the total number of pits both yielded highly significant results ($p<0.0001$), indicating that species had significantly different numbers of scratches and pits. The species were grouped into six and five different groups respectively on the basis of these ANOVAs. The Wilcoxon tests for both analyses confirmed the ANOVA results ($p<0.0001$).

The Tukey test for each of those comparisons yielded the results summarized in Table 14.

TABLE 14: Summary of the results of the Tukey test for the one-way ANOVA of the total number of scratches and pits. Taxa that are not connected by the same letter are significantly different from one another. Abbreviations as in Table 12.

Taxa	*Pliosaccomys magnus*	*Mojavemys mascallensis*	*Thomomys talvoides*	*Thomomys bottae*	*Heterocephalus glaber*	*Hesperogaulus wilsoni*	*Tamias senex*	*Sciurus griseus*	*Tamais striatus*	*Sciurus carolinensis*	*Hesperogaulus gazini*	*Marmota monax*	*Hesperogaulus shotwelli*	*Dipodomys ingens*	*Alphagaulus vetus*	*Aplodontia rufa*
total scratches	A	A	AB	BC	C	ABCDEF	CD	CDE	DEF	DEF	DEF	DEF	DEF	EF	EF	F
total pits	A	AB	AB	BC	CD	CDE	DE	E	DE	E	E	DE	E	BC	DE	DE
sp	A	A	A	AB	BCD	BCDE	CDE	E	CDE	CDE	DE	CDE	E	BC	CDE	CDE
lp	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
lpp	ABC	AB	CD	CD	BCD	ABCD	ABCD	BCD	CD	CD	CD	ABCD	CD	A	ABCD	CD
spp	AB	B	B	AB	AB	AB	AB	AB	AB	B	AB	B	A	AB	AB	AB
crs	A	AB	AB	AB	B	AB	AB	AB	AB	B	AB	AB	AB	B	AB	B
g	BC	BC	BC	AB	BC	A	C	C	C	C	C	BC	C	BC	BC	C
fs	A	A	A	B	B	ABCD	BC	BC	CD	CD	D	CD	D	D	D	D
cs	AB	AB	AB	AB	A	AB	B	B	B	B	B	B	B	B	B	B

When considering only the ANOVA performed on the total number of scratches, *Pliosaccomys magnus*, *Mojavemys mascallensis*, and *Thomomys talpoides* do not significantly differ from one another. In addition, *Hesperogaulus wilsoni* is not statistically different from any of the taxa, most likely as a consequence of the very small sample size for this species. The two species of the genus *Thomomys* are not statistically different from each other either. *Thomomys bottae* and *Heterocephalus glaber*, the two underground feeders, are not statistically different from the fungi eaters *Sciurus griseus* and *Tamias senex*. Similarly, all members of the family Sciuridae along with the mylagaulids *Hesperogaulus* sp. A, and *H. gazini* cannot be considered significantly different. It is not possible to significantly differentiate taxa from the abrasive food (except *Thomomys talpoides*), mixed food, and hard food dietary categories. Another cluster of taxa that do not statistically differ from one another includes *S. griseus*, *Tamias striatus*, *S. carolinensis*, *H. gazini*, *Marmota monax*, *H.* sp. A, *Dipodomys ingens*, and *Alphagaulus vetus*.

The Tukey test performed on the ANOVA of the total number of pits yielded mostly different results. *Pliosaccomys magnus*, *Mojavemys mascallensis*, and *Thomomys talpoides* are not statistically different from each other, nor are *M. mascallensis*, *T. talpoides*, *Dipodomys ingens*, and *T. bottae*. Another group of taxa not statistically different from each other includes the two underground feeders, *T. bottae* and *Heterocephalus glaber*, along with *D. ingens* and *Hesperogaulus wilsoni*. As for the previous Tukey test, *H. wilsoni* does not significantly differ from many taxa. Along with the mylagaulids *H. wilsoni* and *A. vetus*, *Aplodontia rufa*, *H. glaber*, *T. striatus*, *M. monax*, and *T. senex* are not significantly different from one another. Nor are the taxa of the abrasive food, mixed food, hard food (with the exception of *Dipodomys ingens*), and fungivory dietary categories.

Among the one way ANOVAs run for each category of microwear features, the one based on hypercoarse scratches is not significant. The Wilcoxon tests confirm the non-significance of this analysis. All other ANOVAs are found to be significant and the Wilcoxon tests confirmed these (Table 15).

TABLE 15: Summary of the significance of the ANOVAs and Wilcoxon tests on all microwear feature categories. Abbreviations as in Table 12.

Feature	SP	LP	LPP	SPP	CRS	G	FS	CS	HS
ANOVA p > F	<0.0001	0.033	<0.0001	0.0068	0.0086	<0.0001	<0.0001	0.0007	0.564
Wilcoxon p > Chi-square	<0.0001	0.004	0.002	0.044	0.041	0.005	<0.0001	0.019	0.433

The first grouping of species significantly different from all other taxa suggested by the first ANOVA, based on small pits, includes all species of the family Geomyidae. *Hesperogaulus wilsoni* is not statistically different from any species of the data set except for *Pliosaccomys magnus*, *Mojavemys mascallensis*, and *Thomomys talpoides*. The second group of taxa comprises underground feeders and *Dipodomys ingens*. There are three other groups suggested by this Tukey test. A first one includes *D. ingens*, *Heterocephalus glaber*, *Aplodontia rufa*, *Tamias striatus*, *Marmota monax*, *Sciurus carolinensis*, *Alphagaulus vetus*, and *T. senex*. A second group includes *H. glaber*, *A. rufa*, *T. striatus*, *M. monax*, *S. carolinensis*, *A. vetus*, *T. senex*, and *H. gazini*. The last group includes *A. rufa*, *T. striatus*, *M. monax*, *S. carolinensis*, *A. vetus*, *T. senex*, and *H. gazini*, *S. griseus*, *E. dorsatum*, and *H.* sp. A. The second Tukey test based on large pits does not allow any species to be significantly differentiated from any other in the dataset. The third test relying on large puncture pits yields four different groups. In this test, *H. wilsoni* cannot be differentiated from many species in the dataset. A first group of taxa consists of the two fossil geomyids, *Alphagaulus vetus*, *Dipodomys ingens*, *Marmota monax*, and *Tamias senex*. A second group includes *M. mascallensis*, *P. magnus*, *A. vetus*, *M. monax*, *T. senex*, *H. glaber*, and *S. griseus*. A third group includes all taxa but *D. ingens*, *M. mascallensis*, and *E. dorsatum*. A last group includes all species but *M. mascallensis*, *D. ingens*, and *P. magnus*. A fourth Tukey test, based on small puncture pits, yields two different groups. The first one includes all taxa except *Sciurus carolinensis*, *Erethizon dorsatum*, *Thomomys talpoides*, *Hesperogaulus* sp. A, and *Mojavemys mascallensis*. The second group includes all taxa but *Dipodomys ingens.* The Tukey test based on cross scratches is not very informative and very close in its results to that based on small puncture pits. The first group includes all taxa but four (*H. glaber*, *D. ingens*, *S. carolinensis*, and *A. rufa*). The second group only excludes *P. magnus*. Another test based on gouges finds *T. bottae* and *H. wilsoni* to not be statistically different from each other. The second group of taxa includes all subterranean taxa, *M. monax*, *D. ingens*, and *A. vetus*. The last group of taxa comprises all species but those of the first group. In the following Tukey test, *H. wilsoni* cannot be differentiated from any group. In addition, one group of taxa includes the subterranean abrasive feeders. Another group consists of fungivores and subterranean rodents. A third group comprises all Sciuridae. One last group of taxa includes mixed feeders, hard object feeders, fossorial abrasive food eating rodents, in addition to *H. gazini* and *H.* sp. A. The last Tukey test, based on coarse scratches, yields two different groups of taxa. The first one comprises all extant subterranean rodents, and the fossil geomyids, in addition to *E. dorsatum* and *H. wilsoni*. The other group includes all taxa except *Heterocephalus glaber*.

DISCUSSION

The goal of this study is to further address the use of microwear analysis in determining the diet of extinct rodents with an emphasis on the consequence of fossorial behavior on microwear. To apply microwear analysis to fossil burrowing rodents, the validity of the method already investigated by Townsend and Croft (2008) and Nelson et al. (2005) must be further evaluated focusing on burrowing taxa. The results from the assessment of the intra-operator error suggest that counts of microwear features at low-magnification are, for the most part, reliable with almost 80% of the variance explained by the regressions of the second count against the first one. Some of this difference can be explained by inconsistency in counting, but some is also a result of variation across the tooth surface, because the two counts did not necessarily cover the exact same area on the tooth. With the limits of the repeatability of the technique in mind, we can now appreciate the validity of the method and its links to diet, burrowing behaviors, as well as potential evolutionary baggage.

The results of the non-jackknifed DFAs may suggest that microwear features recorded on the enamel surface of the protocone or lingual band of enamel of rodents can accurately predict broad dietary categories to which the species belong. However, it seems that this doesn't hold up when taxa are successively withheld from the analysis, an important test of the validity of the result, especially given the small number of different taxa (REF). The results of the jackknifed DFAs presented here provide better information on how likely an unknown is to be misclassified. The jackknifed results obtained suggest a very poor ability of the DFA in discriminating between diets or burrowing behaviors on the basis of microwear. The predicted results for extant taxa are not coherent with actual ones, suggesting that the performance with additional unknowns, such as the fossil taxa, may be poor. In addition, fossil taxa are not assigned to dietary or burrowing behavior categories in a consistent way. This suggests that the non-jackknifed DFA results are not reliable. This may be a consequence of the small number of taxa and specimens included in this study or of the use of averages in the analyses. It is common in the microwear literature to use DFAs on species averages (e.g., Townsend and Croft 2008). This takes some of the variation in the dataset out of the analysis, increases differences due to sample size (i.e. a fossil species represented by a single individual is compared to an extant one represented by 10+ specimens), and changes the distribution of the data. Moreover, as mentioned above for the intra-operator error, those values are not actual counts for any specimen in the dataset. Working with species-level averages may be obscuring the pattern. It is a reliable method when working on animals with tightly constrained diets (such as some ungulates, Solounias and Semprebon 2002). However, when used on small mammals with a high diversity of diet within taxa (because of the more opportunistic feeding behavior of small highly active animals), it appears that microwear analysis is not as reliable in giving a sense of the central tendency for the species. Specimen-level data are reliable and give a sense of the within species variation in food resources.

Further work improving the sample size of this study may more accurately determine the link between microwear signature and diet or fossoriality in rodents by considering all of the variation within taxa. In addition to the results of the DFA, plots of scratches versus pits suggest an overlap of microwear signatures in taxa of similar diets. Furthermore, taxa of intermediate diet (e.g., mixed feeders) do partially overlap with abrasive feeders and hard object eaters. High counts of pits, in particular puncture pits, associated with low counts of scratches seem to be typical of taxa with a high intake of seeds in their diet (e.g., *Dipodomys ingens*) as suggested in previous studies (Townsend and Croft 208). Fungivores seem to be characterized by high counts of fine scratches and low counts of pits. Unlike Townsend and Croft (2008), I do not find abrasive food eaters to have very high counts of pits (unless they are highly fossorial). The two fungivorous taxa partially overlap with the two seed-eating squirrels. This is most likely a consequence of the diet of the fungivorous animals included in this dataset. Although fungi are a very important part of their diet, they do not feed exclusively on fungi and both include some amounts of hard fruits (e.g., acorns) in their diet. Abrasive food eating rodents, mixed feeders and hard object feeding squirrels heavily overlap. The mixed feeding taxa are expected to overlap with both hard object eaters and abrasive food eaters. When looking at the plot of the averages for the species, *Marmota monax* plots between *Aplodontia rufa* and *Tamias striatus*. *Erethizon dorsatum*, the North American porcupine, is an arboreal animal that mostly feeds in trees. Unlike the porcupine, the woodchuck, *M. monax*, is a fossorial animal that digs and lives in burrows. The exogenous grit induced by such behavior may account for the higher counts of pits in the marmot than in the porcupine. The two seed eaters plot on top of each other as well as sharing some of their scratches vs. pits field with *Aplodontia rufa*. The mountain beaver is a fossorial animal that may exhibit as many pits on its enamel as hard-object-feeding animals as a consequence of its fossoriality. It otherwise mostly feeds on a variety of aboveground abrasive foliage and green vegetation. There is no overlap between the hard-object-eating squirrels and *D. ingens*. The heteromyid has a much coarser diet than any of the other hard-feeding taxa. The proportion of each food in the overall diet of the animal as well as the availability of these food resources at the time the animal died may explain why it does not cluster with other animals whose diet is mainly based on seeds, nuts, or acorns but may include larger amounts of fungi and vegetation in their diet. The three subterranean taxa included in this study plot in the upper right corner of the graph. The presence of a large number of pits associated with the absence of a large number of puncture pits is probably a consequence of the subterranean lifestyle of these rodents and the resulting exogenous grit. The high counts of scratches reflect the abrasive diet of these animals (due to grasses for *Thomomys talpoides* and underground storage units for *T. bottae* and *H. glaber*). The diet of *Thomomys talpoides*, although including roots and tubers, consists mostly of aboveground abrasive grasses and forbs. This may explain the higher counts of scratches observed in this taxon compared to *Thomomys bottae.*

From the dataset available to us, it seems that microwear features may not accurately predict the degree of fossoriality of taxa. It also seems that microwear features allow for family identifications of the rodent taxa to be predicted. This suggests a substantial taxonomic and/or phylogenetic signal to microwear. Shared evolutionary history can, either directly, or indirectly through ecological baggage inherited from a common ancestor, be reflected in microwear.

In addition, these general trends in microwear and their relationship to diet and burrowing behaviors need to be considered with reservation because of the small sample size of the present analysis. This is particularly concerning since microwear has been shown to reflect the "last supper" of the animal therefore yielding data on a snapshot in the dietary habits of an individual rather than an average diet over longer time spans (Grine 1986).

Some of the overlap described above and pictured in Figure 6 may be explained when specimen data from collection records are integrated in the analysis. Nevertheless, this variation may obscure the link between microwear and diet, in particular because we do not have the necessary data for fossils. There is a very strong seasonal control on availability of food and therefore on diet. This is turns creates variation in the microwear of individuals as shown here in the case of *Marmota monax* and *Sciurus carolinensis.* *Marmota monax* is reported to easily switch food preferences on the basis of availability dictated by season (Kwiecinski 1998). The diet of *Sciurus carolinensis* also varies with seasons. Fungi and insects are eaten in summer, corn and wheat in winter, gravel and soil are ingested by females in winter and spring (Koprowski 1994). In addition, *S. carolinensis* feeds on a very wide variety of plants (as many as 97 species, Koprowski 1994) whose availability may vary with seasons. The diet of *Erethizon dorsatum* is reported as being highly seasonally influenced. Because of the lack of data on the specimens, it is not possible to test the hypothesis that the two specimens located in the lower right corner of the species field (high counts of scratches, low counts of pits) died in a different season than those located in the left part of the field displaying low counts of scratches and higher ones of pits. *Sciurus griseus* is expected to show seasonal differences in feeding that should be observable in the microwear of the specimens (Caraway and Verts 1994). The range in specimen data presented in Figure 6 does not match the expected clustering of diets due to seasons. Specimens from fall/winter and spring/summer do not clearly cluster together. This suggests that it remains challenging to link specimen data to microwear because, again, of the diversity of foods individuals of a same species forage on, even within a season where limited food supplies (in nature rather than quantity) are available. Constraining the diet of fossil species may be challenging and requires large sample size to span the diversity of microwear signatures within the species in addition to providing statistical power. One species of mylagaulids is represented in this dataset by a single specimen and will require further study to be confidently categorized in a dietary group.

Numerous analyses (graphical, cluster analyses, DFAs, and AVOVAs) have yielded various results concerning the potential diet of the fossil species considered in this study (Tables 6, and 9). This diversity of results suggests that it may be difficult to reconstruct the diet of fossil small mammals because (1) there is a large variation in diet within small mammal taxa, (2) some of the dietary signal may be overprinted by phylogenetic constraint on ecology, (3) a larger dataset spanning more taxa and including more specimens is needed. With these limitations in mind, we can attempt to draw broad conclusions on the diet of the fossil mylagaulids and geomyids included in this study. We can use graphical correlation of the specimen data of the fossil species with specimen data for extant taxa to approach the ecology of the mylagaulids and fossil geomyids. Thus, both *Pliosaccomys magnus* and *Mojavemys mascallensis* plot where *Thomomys talpoides* plots. This modern rodent is subterranean and feeds mostly above ground on forbs, dandelions or grasses in addition to supplementing its diet with roots and tubers. This may suggest that *M. mascallensis* and *P. magnus* were subterranean and ate aboveground vegetation. Similarly, *Hesperogaulus wilsoni* plots where a specimen of *Tamias striatus* plots, suggesting a similar habit of eating seeds, nuts, and acorns as a main source of food. *Alphagaulus vetus* is close to *Aplodontia rufa*, *Hesperogaulus* sp. A to *Erethizon dorsatum*, and *Hesperogaulus gazini* covers much of the taxa from abrasive food feeders to hard-object-eating rodents through mixed feeders. It therefore most likely is a mixed feeder feeding on a variety of food resources as dictated by availability. Overall, within the family Mylagaulidae, there is a wide variety of feeding behaviors. I also compared fossil species to extant ones qualitatively on a diagram of scratches vs. pits diagram using species averages. Using this technique, the results change only for two taxa. *Hesperogaulus wilsoni* is now recognized as being closest to non-fossorial fungivores while *Hesperogaulus gazini* falls next to *Sciurus carolinensis*.

The results of the cluster analyses also reflect dietary categories. Extant taxa with similar ecologies group together (e.g., *Thomomys bottae* with *Heterocephalus glaber*). Some clusters reflect similarities in microwear despite differences in diet. For example, *Dipodomys ingens* clusters with the underground feeding subterranean animals because of the high number of pits in its microwear. Subterranean rodents have a high number of pits in their diet as a consequence of fossoriality as discussed for *Chinchilla lanigera* by Townsend and Croft (2008). It is possible to differentiate a dietary signal from a burrowing signal in the number of pits with the number of puncture pits. *D. ingens* exhibits the highest counts of puncture pits of the dataset (as expected for an animal feeding heavily on seeds and nuts) whereas the extant subterranean rodents feeding on underground organs have lower counts of puncture pits, closer to those of sciurids. Cluster analyses only show the pattern of the microwear and do not provide clues to the process by which it is acquired (i.e. diet, burrowing behavior, or phylogenetic constraints). The two fossil geomyids cluster with *Thomomys talpoides*, *H. wilsoni* with fungivores, *A. vetus* with *A. rufa*, *H.* sp. A with *E. dorsatum.* Only *H. gazini* seems to be more unstable and groups with hard-feeding animals, mixed feeding ones, or abrasive-food-eating rodents. This may be a consequence of a larger sample size for this taxon associated to opportunistic feeding.

The results of the jackknifed analyses do not support a particular conclusion regarding the diet or burrowing behavior of the fossil taxa. However we can observe some general trends. *Hesperogaulus* sp. A and *H. gazini* are more often categorized as mixed feeders or fungi eaters. *H. wilsoni* is either interpreted as a fungi eater or an underground storage unit eating rodent. *Alphagaulus vetus* is more often categorized as a mixed feeder although it sometimes is also categorized as a hard object feeder. Although abrasive food dominates the categorization of *Mojavemys mascallensis*, mixed food is also a dietary category this geomyids is assigned to. The results for *Pliosaccomys magnus* are very equivocal.

The Tukey tests also suggest some clusters of taxa that are not significantly different from one another. Throughout the Tukey tests, *Hesperogaulus wilsoni*, because of its very small sample size, cannot be statistically differentiated from most or all categories therefore precluding its categorization. It seems as though the total number of scratches groups together the fossil geomyids with *Thomomys talpoides*. This is consistent with their convergent ecologies suggested by other analyses and other tests confirm this cluster. These three geomyids seem to be more different from everything else than any other signal in the data. The two species of *Thomomys* are also found to not be significantly different. This may be a taxonomic signal. Underground feeders and fungus eaters aren't different may be because of their similar diet of high calorie, unabrasive terrestrial food. Another taxonomic signal may be found in the grouping of the Sciuridae. Other groupings that do not seem to relate to ecological or taxonomic signals emphasize the poor discriminatory power of this analysis on the data and the noise of the overlapping abrasive, mixed, and hard food diets. Evolutionary history affects the ecology of species by not allowing for all ecological niches to be explored. It also affects jaw mechanics, and hence the likelihood that a given food will generate microwear features. This in turns impacts the diet and burrowing behavior and therefore the microwear signature. The issues encountered with the Tukey tests may be similar to those of the jackknifed DFAs in which noise obscures the signals.

The grouping of the fossil geomyids with *Thomomys talpoides* is supported by numerous other Tukey tests based on different microwear features. The test based on the total number of pits also groups together the underground feeders reflecting the relationship between pitting and burrowing ecology. This group is associated with *Dipodomys ingens*, a hard-object feeder whose microwear converges on that of subterranean rodents because of diet. A similar situation is observed in the grouping of the two extant geomyids, the fossil *M. mascallensis* and *D. ingens*. As for the test based on scratches, that based on pits cannot differentiate between the taxa with low counts of scratches and pits overlapping in the scratches to pits graph.

Another taxonomic signal is obtained from the Tukey test based on small pits that finds no significant difference between geomyids. Underground feeders and *Dipodomys ingens* are once again clustered together. Overall the results of this test are very similar to that based on all pits because small pits make up most of the pits counted for any given taxon. Similarly for the fine scratches, subterranean abrasive food eaters are grouped together. Fungivores and subterranean rodents are also not significantly different from each other. All sciurids fall together in a third group suggesting a taxonomic signal again. *Hesperogaulus gazini*, *H. sp. A* and the extant taxa grouping in the lower left corner of the scratches to pits plot also appear to not be significantly different from one another. The other Tukey tests for rarer, coarser features of both scratches and pits are do not support any particular pattern.

Overall, it seems like the Tukey tests support the already heavily-supported association of the fossil geomyids with *Thomomys talpoides*. In addition, they suggest a taxonomic or phylogenetic signal for the sciurids and geomyids. Subterranean animals can be confused with hard object feeders when considering pits or with fungivores when considering scratches. It is challenging to differentiate mixed feeders from abrasive food eaters or hard object feeders.

The results of the PCA, DFAs and cluster analyses, in conjunction with those of the graphical correlations, can also be used to approach the degree of fossoriality of the fossil taxa. The first principal component (PC 1) of the PCA suggests a grouping of the two fossil geomyids with *Heterocephalus glaber*, *Thomomys bottae*, and *Thomomys talpoides*. This clustering of subterranean rodents with different diets (abrasive food or subterranean food) hints at the subterranean lifestyle expected for those geomyids and suggested by some of the other analyses (Table 9). Although, a few of the jackknifed DFAs suggest that *Mojavemys mascallensis* is a fossorial taxon, most analyses converge in classifying or associating the fossil geomyids to a subterranean ecology. However, the results for the mylagaulids are much more diverse. *Alphagaulus vetus* is often interpreted as a fossorial taxon. *Hesperogaulus* sp. A is often classified as non-fossorial. The results for the other species of the genus *Hesperogaulus* are more equivocal. *H. gazini* and *H. wilsoni* are either interpreted as non-fossorial or semi-fossorial. Cranial (e.g., Korth 2000, Hopkins 2005), postcranial (e.g., Fagan 1960), and ichnological evidence (Gobetz 2006) suggest that mylagaulids are fossorial to subterranean animals digging complex branching burrows. *Hesperogaulus* sp. A is fossorial and although very similar in microwear to the porcupine, *Erethizon dorsatum*, according to these analyses would be expected (for a similar diet) to be closer in ecology (and therefore in microwear signature) to *Marmota monax*. Microwear is not convergent with other lines of evidence when it comes to fossoriality. Further research including larger sample sizes and a more diverse dataset of modern rodents may provide clues as to how this issue can be resolved but it may be that some diets erase the microwear signature of burrowing thus leaving no evidence of the effect of exogenous grit.

Most of the interest of microwear analysis of fossil taxa has focused on determining the diet of extinct animals. In this study, I show that integrating collection records with microwear data in modern rodents may shed light on some of the variation displayed within species. No similar patterns of outliers and diversity in microwear signature in fossil species could be understood by differences in locality or time interval origin of the specimens. The diverse microwear observed in mylagaulids does not appear to relate to specimen information, suggesting diverse diets within taxa.

CONCLUSIONS

Cautious interpretation of the data obtained in this study suggests some possible feeding habits in fossil burrowing rodents. Comparisons between the microwear of extant rodents and two species of fossil geomyids, *Pliosaccomys magnus* and *Mojavemys mascallensis*, suggest that these two species of Miocene rodents had ecologies very similar to each other in addition to being similar to that of *Thomomys talpoides*, the northern pocket gopher. They were most likely subterranean rodents that fed mostly above ground with additional feeding on roots and tubers. The microwear of mylagaulids, however, displays a wide range of variation in the number of pits and scratches across species. This suggests a diversity of diets and ecologies within and across taxa.

Alphagaulus vetus appears to have been very similar in its feeding and burrowing behaviors to its closest modern relative, *Aplodontia rufa*, feeding on an abrasive diet of above ground plants although it may have included significant amounts of hard objects in its diet closing in on a mixed feeding behavior. *Hesperogaulus* sp. A displays a microwear pattern closest to that of the North American porcupine therefore hinting at a mixed feeder diet. *Hesperogaulus gazini* overlaps with numerous species ranging in diet from abrasive food to hard object feeding and may have been an opportunistic feeder. Data for *Hesperogaulus wilsoni* are scarce, but initial results suggest that it could have fed on a diet of fungi and fruits similar to that of modern chipmunks.

Burrowing does not seem to consistently affect microwear. King et al (1999) have shown that taphonomy is readily observable in dental microwear and that, rather than modifying microscopic features, taphonomy obliterates them. Taphonomy therefore does not explain why some mylagaulid taxa expected to be fossorial fall out near non-fossorial animals (no taphonomy signature can be observed for those specimens). However, some diets may be over-imprinting the signal from burrowing, erasing evidence for an underground way of life. This may explain the discrepancies between the degree of fossoriality of mylagaulids as suggested by microwear and that demonstrated by cranial and skeletal evidence.

Those new dietary information for fossil burrowing herbivores provide additional data to address the question of fossorial herbivore paleoecology in the Miocene. The conclusions on the likely diets of mylagaulids and geomyids do not reject nor confirm the habitat partitioning proposed in the third chapter of this thesis. However, it is further evidence that competition, at least over diet, may not have been an important factor in determining the paleoecology and evolution of mylagaulids and geomyids in the Miocene of the Great Basin. The two fossil geomyids studied seem to be ecologically similar to *Thomomys talpoides*. Mylagaulids exhibit very diverse diets both across and within species. They seem to be more opportunistic in their feeding behavior. Further research involving larger sample sizes and additional taxa for both extant and extinct rodents is needed to improve our understanding of fossorial herbivore paleoecology. This study does not support the use of low magnification microwear analysis on small mammals as strongly as previous studies did (Townsend and Croft 2008, Nelson et al. 2005). It appears that the possibility to link microwear signature to ecological variables (i.e. diet and fossoriality) is challenged by the conflict between those two signals, the variability in diet in opportunistically feeding small mammals, and a possible evolutionary baggage. This last issue suggests the need for a more careful examination of the influence of phylogeny on microwear signature using an extended dataset thus providing clues to how phylogenetic signal may be removed from paleodiet studies using microwear. Such study should include more extant taxa with closely related species of similar and different diets in addition to distantly related species with similar diets. The taxa selected should be carefully sampled across the rodent phylogeny.

CHAPTER V

CONCLUSIONS ON THE SYSTEMATICS AND PALEOECOLOGY OF GREAT BASIN MYLAGAULIDS

The mylagaulid fauna from the Great Basin includes, in addition to rare large mylagaulids of uncertain taxonomic affinity, four species of mylagaulids distributed throughout Oregon and Nevada from the late Hemingfordian through the early late Hemphillian: *Alphagaulus vetus*, *Hesperogaulus gazini*, *Hesperogaulus wilsoni*, and a new species from the genus *Hesperogaulus*. This new species ranges from the middle Clarendonian through the late early Hemphillian of Oregon and Nevada. It is intermediate in morphology between the early Barstovian *H. gazini* and the Hemphillian *H. wilsoni* from Oregon. A phylogenetic analysis of the family including the newly described material calls for further work on the phylogenetic relationships within the family Mylagaulidae. Reviews of the mylagaulid material such as this study may help build a character matrix that focuses on distinguishing the dentition of different derived mylagaulid species. The addition of more cranial and postcranial characters will also supplement the set of characters and allow a better understanding of the relationships within the Mylagaulinae.

In this study, I demonstrate that one can use large sample sizes of premolars to understand changes in occlusal morphology with different wear stages. As noted before by Shotwell (1958a), Korth (2000), and others, tooth wear through time triggers a change in tooth size, tooth shape, number of lakes on the occlusal surface of the tooth, and shape of these lakes. The number and length of the lakes increases through development whereas the width and complexity decreases. There is very little change in the orientation of the lakes throughout ontogeny. Rectangular premolars in juvenile specimens tend to become more oval with wear. A number of teeth have a wear surface that is concave rather than flat. This occlusal curvature affects the morphology of the lakes both in their shapes and their dimensions by elongating the fossettes and fossettids antero-posteriorly. There is also a slight difference between individuals in the angle of the wear of the tooth. This tilting of the wear surface is very limited, but may be responsible for some inter-individual differences in fossette morphology. All of these wear patterns are tightly constrained by jaw mechanics; however, the hypsodonty of the tooth crown allows imprecise occlusion of the teeth, explaining some of the variability in the occlusal surface morphology of mylagaulids. In order to avoid such issues, numerous teeth must be examined with a focus on the adult wear stage. Intraspecific variation in mylagaulids includes variation in both tooth size and number of lakes, driven by tooth wear, but the orientation of the lakes and the shape and complexity of the lakes is consistent across individuals of the same wear stage. Between species, accounting for wear stage, the tooth size and the number of lakes differ, as do lake orientation and the shape and complexity of the lakes.

This new taxonomic framework allows a better understanding of the paleoecology of the fossorial herbivore guild, of which mylagaulids are members, in the mid to late Miocene of the Great Basin. The hypothesis of competitive interactions between mylagaulids and geomyids is not supported. Changes in the fossorial herbivore guild as a whole do not seem to be a gradual change in the composition of the guild but rather stasis in the early part of the record followed by a succession of turnover events. This result is inconsistent with the hypothesis of competitive interactions between members of the fossorial herbivore guild. Those changes in faunal composition do not seem to be the consequence of global climate change. Environmental changes around turnover events in burrowing rodent fauna may have driven the changes in their relative abundances.

I present a new hypothesis for the decline of mylagaulids in which local to regional scale climatic changes triggered dramatic fluctuations in the dominant habitat, thus mediating taxonomic dominance by shifting the proportion of the landscape covered in habitats that favor one taxon or another. The observed pattern suggests that the Miocene burrowing herbivore guild was partitioned according to preferences in microhabitats at the local to regional scale.

In addition to better understanding their diversity dynamics, I also investigated the likely diet of geomyids and mylagaulids. Cautious interpretation of the data obtained in this study suggests some possible feeding habits. Comparisons between the microwear signatures of extant rodents and two species of fossil geomyids, *Pliosaccomys magnus* and *Mojavemys mascallensis*, suggest that these two species of Miocene rodents had ecologies very similar to each other in addition to being similar to that of *Thomomys talpoides*, the northern pocket gopher. They were most likely subterranean rodents that fed mostly above ground with some dietary input from roots and tubers.

The microwear signature of mylagaulids, however, displays a wide range of variation in the number of pits and scratches across species. This suggests a diversity of diets and ecologies within and across taxa. *Alphagaulus vetus* appears to have been very similar in its feeding behavior to its closest modern relative, *Aplodontia rufa*, feeding on an abrasive diet of above ground plants although it may have included significant amounts of hard objects in its diet closing in on a mixed feeding behavior. *Hesperogaulus* species A displays a microwear signature closest to that of the North American porcupine therefore hinting at a mixed feeder diet. *Hesperogaulus gazini* overlaps with numerous species ranging in diet from abrasive food to hard object feeding and may have been an opportunistic feeder. Data for *Hesperogaulus wilsoni* are scarce, but initial results suggest that it could have fed on a diet of fungi and fruits similar to that of modern chipmunks.

Additionally, we find that some diets may be over-imprinting the signal from burrowing, erasing evidence for an underground way of life. This may explain the discrepancies between the degree of fossoriality of mylagaulids as suggested by microwear and that demonstrated by cranial and skeletal evidence.

Those new dietary information for fossil burrowing herbivores do not reject nor confirm the habitat partitioning proposed in this thesis. However, it is further evidence that competition, at least over diet, may not have been an important factor in determining the paleoecology and evolution of mylagaulids and geomyids in the Miocene of the Great Basin. This study does not support the use of low magnification microwear analysis on small mammals as strongly as previous studies did (Townsend and Croft 2008, Nelson et al. 2005). It appears that the effort to link dental microwear to ecological variables (i.e. diet and fossoriality) is challenged by the conflict between those two signals, the variability in diet in opportunistically feeding small mammals, and possibly by evolutionary baggage. This last issue suggests the need for a more careful examination of the influence of phylogeny on microwear using a larger dataset thus providing clues to how phylogenetic signal may be removed from paleodiet studies using microwear.

APPENDIX A

CHARACTER MATRIX USED IN THE PHYLOGENETIC ANALYSIS OF GREAT BASIN MYLAGAULIDS

Modified and completed after Hopkins 2008a

Taxa	Characters															
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Meniscomys uhtoffi	1	1	1	2	1	2	1	2	0	0	0	1	1	0	1	1
Aplodontia rufa	2	1	1	0	1	2	1	2	0	0	0	0	1	0	0	0
Alphagaulus douglassi	0	1	?	0	1	0	1	2	0	0	0	?	?	1	1	1
Alphagaulus pristinus	0	1	?	0	1	0	1	2	0	?	0	?	?	?	1	1
Alphagaulus pristinus from Deep River Formation	0	1	1	0	1	0	1	2	0	0	0	0	?	1	1	1
Alphagaulus tedfordi	1	1	?	0	1	2	1	2	0	?	?	?	?	1	1	1
Alphagaulus vetus	0	1	1	0	1	0	1	2	0	0	0	0	0	1	1	1
Alphagaulus vetus from Massacre Lake Fauna	0	1	1	0	1	0	1	2	0	0	0	0	0	0	1	1
Ceratogaulus anecdotus	0	?	?	?	1	0	1	2	0	?	?	?	?	1	1	1
Ceratogaulus hatcheri	0	?	?	?	1	0	1	2	0	?	?	?	?	1	1	1
Ceratogaulus minor	0	?	?	?	1	0	1	2	0	?	0	0	?	1	1	1
Ceratogaulus rhinocerus	0	?	?	?	1	0	1	2	0	?	0	0	?	1	1	1
Galbreathia bettae	1	?	?	?	1	1	1	2	0	?	0	?	?	0	1	1
Galbreathia novellus	1	1	1	0	1	0/1	1	2	0	0	0	0	0	1	1	1
Hesperogaulus gazini	0	?	1	?	1	0	1	2	0	0	0	0	0	1	1	1
Hesperogaulus wilsoni	0	1	?	0	1	0	1	2	0	?	0	?	?	1	1	1
Hesperogaulus species A	0	1	1	0	1	0	1	2	0	0	0	0	0	1	1	1
Mesogaulus ballensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mesogaulus paniensis	1	1	1	0	1	1	1	2	0	?	0	?	0	0	1	1
Mylagaulodon angulatus	1	1	1	0	1	0/1	1	2	0/1	?	0	?	?	?	?	1
Mylagaulus kinseyi	0	?	?	?	1	0	1	2	0	?	?	?	?	?	1	1
Mylagaulus elassos	0	?	?	?	1	0	1	2	0	?	?	?	?	?	1	1
Mylagaulus sesquipedalis	0	?	?	?	1	0	1	2	0	?	?	?	?	1	1	1
Promylagaulus riggsi	1	1	1	0/2	1	0/1	1	2	0	0	0	?	?	1	1	1
Pterogaulus barbarellae	0	?	?	?	1	0	1	2	0	?	?	?	?	1	1	1
Pterogaulus cambridgensis	0	?	?	?	1	0	1	2	0	?	?	?	?	?	1	1
Pterogaulus laevis	0	1	?	?	1	0	1	2	0	0	0	0	?	1	1	1
Trilaccogaulus lemhiensis	0	1	?	0	1	0/1	1	2	0	0	?	?	?	0	1	1
Trilaccogaulus montanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trilaccogaulus ovatus	0	0	1	0	1	0/1	1	2	0	?	0	?	0	0/1	1	1
Umbogaulus galushai	0	?	?	?	1	0	1	2	0	?	?	?	0	1	1	1
Umbogaulus monodon	0	?	?	?	1	0	1	2	0	0	?	?	?	1	1	1

Appendix A (extended)

Taxa	**Characters**															
	17	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Meniscomys uhtoffi	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Aplodontia rufa	1	0	1	0	1	0	0	0	0	0	0/1	0	0	0	0	2
Alphagaulus douglassi	1	0	?	0	0	0	?	0	0	0	1	0	0	0	0	2
Alphagaulus pristinus	1	?	?	?	?	?	?	?	?	0	1	?	?	?	?	2
Alphagaulus pristinus From Deep River Formation	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2
Alphagaulus tedfordi	1	0	?	?	?	0	?	?	?	0	1	1	?	0	?	2
Alphagaulus vetus	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	2
Alphagaulus vetus from Massacre Lake Fauna	1	0	1	0	0	0	0	0/1	0	0	1	0	0	0	0	2
Ceratogaulus anecdotus	1	?	1	?	?	?	?	?	?	0	1	1	?	0	?	?
Ceratogaulus hatcheri	1	?	1	?	?	?	?	?	?	0	1	1	?	0	?	?
Ceratogaulus minor	1	0	1	0	0	0	?	?	0	0	1	1	0	0	0	2
Ceratogaulus rhinocerus	1	0	1	0	0	0	?	0	0	0	1	1	0	0	0	2
Galbreathia bettae	1	?	?	?	?	?	?	?	?	0	1	1	?	0	0	?
Galbreathia novellus	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0	2
Hesperogaulus gazini	1	0	1	0	0	0	?	0	0	0	1	1	0	0	0	2
Hesperogaulus wilsoni	1	0	1	?	?	0	?	?	0	0	1	1	?	0	?	?
Hesperogaulus species A	1	0	1	0	0	0	1	0	0	0	1	1	0	0	0	2
Mesogaulus ballensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mesogaulus paniensis	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	2
Mylagaulodon angulatus	1	0	1	0	?	?	?	?	0	0	1	1	0	0	0	2
Mylagaulus kinseyi	1	?	1	?	?	?	?	?	?	0	1	0	?	0	?	?
Mylagaulus elassos	1	?	1	?	?	?	0	?	?	0	1	0	?	0	?	?
Mylagaulus sesquipedalis	1	?	1	?	?	?	?	?	?	0	1	1	?	0	?	?
Promylagaulus riggsi	1	0	1	0	0	0	?	0	0	0	1	0	?	0	0	?
Pterogaulus barbarellae	1	0	1	0	0	0	0	?	0	0	1	1	0	0	0	2
Pterogaulus cambridgensis	1	?	1	?	?	?	?	?	?	0	1	1	?	0	?	?
Pterogaulus laevis	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	2
Trilaccogaulus lemhiensis	1	0	1	0	?	0	?	0	0	0	1	?	?	1	0	?
Trilaccogaulus montanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trilaccogaulus ovatus	1	0	1	0	?	?	?	0	0	0	1	0	0	1	0	2
Umbogaulus galushai	1	?	1	?	?	?	?	?	?	0	1	1	?	0	?	?
Umbogaulus monodon	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	2

Appendix A (extended)

Taxa	**Characters**															
	33	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
Meniscomys uhtoffi	1	1	2	1	0/1	0	0	?	?	1	0	0	0	0	0	1
Aplodontia rufa	1	1	?	1	1	1	0	?	?	1	1	0	0	0	0	1
Alphagaulus douglassi	1	1	2	1	2	1	0	?	?	0	1	0	0	0	0	1
Alphagaulus pristinus	?	1	2	1	?	1	0	?	?	?	1	?	0	0	0	1
Alphagaulus pristinus from Deep River Formation	0	1	2	1	2	1	0	?	?	0	1	0	0	0	0	1
Alphagaulus tedfordi	?	1	2	1	2	1	0	?	?	?	1	?	0	0	0	1
Alphagaulus vetus	1	1	2	1	2	1	0	?	?	0	1	0	0	0	0	1
Alphagaulus vetus from Massacre Lake Fauna	0	1	2	1	2	1	0	?	?	0	1	0	0	0	0	1
Ceratogaulus anecdotus	?	1	?	?	2	1	0	?	?	?	1	?	0	0	?	1
Ceratogaulus hatcheri	?	1	?	?	2	1	0	?	?	?	1	?	0	0	?	1
Ceratogaulus minor	?	1	2	1	2	1	0	?	?	0	1	0	0	0	0	1
Ceratogaulus rhinocerus	1	1	2	1	2	1	0	?	?	0	1	0	0	0	0	1
Galbreathia bettae	?	1	?	?	2	1	?	?	?	0	1	?	0	0	0	1
Galbreathia novellus	0	1	2	1	2	1	0	0	?	0	1	0	0	0	0	1
Hesperogaulus gazini	1	1	2	1	2	1	0	0	?	0	1	0	0	0	0	1
Hesperogaulus wilsoni	?	1	2	?	2	1	0	0	?	0	1	?	0	0	0	1
Hesperogaulus species A	0	1	2	1	2	1	0	0	?	0	1	0	0	0	0	1
Mesogaulus ballensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mesogaulus paniensis	1	1	2	1	2	1	0	?	?	0	1	0	0	0	0	1
Mylagaulodon angulatus	?	1	2	1	2	1	0	0	?	0	1	0	0	0	0	1
Mylagaulus kinseyi	?	?	2	?	2	1	0	0	?	?	1	?	0	0	0	1
Mylagaulus elassos	?	1	2	?	2	1	0	0	?	?	1	?	0	0	0	1
Mylagaulus sesquipedalis	?	?	2	?	2	1	0	0	?	?	1	?	0	0	0	1
Promylagaulus riggsi	?	1	2	1	2	1	0	?	?	1	1	0	0	0	0	1
Pterogaulus barbarellae	?	0	2	1	2	1	0	0	?	0	1	0	0	0	0	1
Pterogaulus cambridgensis	?	?	2	?	2	1	0	0	?	0	1	?	0	0	?	1
Pterogaulus laevis	?	1	2	1	2	1	0	0	?	0	1	0	0	0	0	1
Trilaccogaulus lemhiensis	1	1	?	1	2	1	0	?	?	1	1	0	0	0	0	1
Trilaccogaulus montanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trilaccogaulus ovatus	?	1	2	1	2	1	0	?	?	?	1	0	0	0	0	1
Umbogaulus galushai	?	1	2	?	2	1	0	?	?	?	1	?	0	0	?	1
Umbogaulus monodon	0	1	2	1	2	1	0	?	?	0	1	0	0	0	0	1

Appendix A (extended)

Taxa	Characters															
	49	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**
Meniscomys uhtoffi	0	1	1	0	1	2	1	1	1	1	1	0	0	0	0	0
Aplodontia rufa	1	1	1	1	0	0	1	1	1	1	0	1	0	0	1	0
Alphagaulus douglassi	0	2	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Alphagaulus pristinus	?	?	2	0	0	?	0	1	1	0	?	0	?	1	0	?
Alphagaulus pristinus From Deep River Formation	0	2	2	0	0	?	0	1	1	0	0	0	2	1	0	1
Alphagaulus tedfordi	?	2	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Alphagaulus vetus	0	2	2	0	0	0	0	1	1	0	0	0	2	1	0	1
Alphagaulus vetus from Massacre Lake Fauna	0	2	2	0	0	0	0	1	1	0	0	0	2	1	0	1
Ceratogaulus anecdotus	?	?	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Ceratogaulus hatcheri	0	2	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Ceratogaulus minor	0	2	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Ceratogaulus rhinocerus	0	2	2	0	0	?	0	1	1	0	?	0	2	1	0	0
Galbreathia bettae	?	?	1/2	0	0	0	0	1	1	0	?	0	2	0	0	1
Galbreathia novellus	0	2	1/2	0	0	0	0	1	1	0	1	0	1	0	0	0
Hesperogaulus gazini	0	2	2	0	0	?	0	1	1	0	?	0	2	0	0	1
Hesperogaulus wilsoni	0	2	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Hesperogaulus species A	0	2	2	0	0	0	0	1	1	0	0	0	2	1	0	1
Mesogaulus ballensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mesogaulus paniensis	0	2	1/2	0	0	1	0	1	1	0	0	0	1	0	0	0
Mylagaulodon angulatus	0	2	1	0	?	?	0	1	1	0	?	0	1	0	0	0
Mylagaulus kinseyi	?	?	2	0	0	?	0	1	1	0	?	0	2	0	0	1
Mylagaulus elassos	?	?	2	0	0	?	0	1	1	0	?	0	2	0	0	1
Mylagaulus sesquipedalis	?	?	2	0	0	?	0	1	1	0	?	0	2	0	0	1
Promylagaulus riggsi	0	2	1	0	0	0	0	1	1	1	0	0	1	0	0/1	0
Pterogaulus barbarellae	0	2	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Pterogaulus cambridgensis	?	?	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Pterogaulus laevis	0	2	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Trilaccogaulus lemhiensis	0	2	1/2	0	0	?	0	1	1	0	0	0	2	0	1	1
Trilaccogaulus montanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trilaccogaulus ovatus	?	2	1/2	0	0	0	0	1	1	0	0	0	2	0	1	1
Umbogaulus galushai	?	?	2	0	0	?	0	1	1	0	?	0	2	1	0	1
Umbogaulus monodon	0	2	2	0	0	?	0	1	1	0	?	0	2	1	0	1

Appendix A (extended)

Taxa	**Characters**															
	65	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**
Meniscomys uhtoffi	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1
Aplodontia rufa	0	0	1	2	0	0	0	0	0	1	1	3	0	1	0	1
Alphagaulus douglassi	2	1	1	0	0	0	0	1	2	1	1	2	1	1	1	?
Alphagaulus pristinus	?	1	1	0	0	1	1	1	1	1	1	2	?	1	1	1
Alphagaulus pristinus from Deep River Formation	0	0/1	1	0	0	1	1	1	1	1	1	2	1	1	1	1
Alphagaulus tedfordi	0	1	1	0	0	1	0	1	2	1	1	2	?	1	1	?
Alphagaulus vetus	0	1	0	0	0	1	1	1	1	1	1	2	1	1	1	1
Alphagaulus vetus from Massacre Lake Fauna	0	1	0	0	0	1	1	1	0	1	1	2	1	1	1	1
Ceratogaulus anecdotus	2	1	1	1	0	1	1	1	2	1	1	2	1	1	1	0
Ceratogaulus hatcheri	2	1	1	0	0	1	1	1	2	1	1	2	1	1	1	?
Ceratogaulus minor	1	1	1	?	0	1	1	1	2	1	1	2	1	1	1	?
Ceratogaulus rhinocerus	2	1	1	0	0	1	1	1	2	1	1	2	1	1	1	0
Galbreathia bettae	0	0	1	0	0	1	0	1	2	0	1	1	?	?	1	1
Galbreathia novellus	0	1	1	0	0	1	0	1	2	0	1	1	0	1	1	1
Hesperogaulus gazini	0	0	1	0	0	1	1	1	3	1	1	2	1	1	1	?
Hesperogaulus wilsoni	0	0	1	0	0	1	1	1	3	1	1	2	1	1	3	1
Hesperogaulus species A	0	0	0	0	0	1	1	1	3	1	1	2	1	1	1	1
Mesogaulus ballensis	?	?	?	?	?	?	?	?	?	1	1	1	?	?	1	?
Mesogaulus paniensis	0	1	1	0	0	1	0	1	1	1	1	1	0	1	1	1
Mylagaulodon angulatus	0	1	1	0	0	1	0	1	0	0	1	1	0	0	1	1
Mylagaulus kinseyi	1	1	1	0	0	1	0	1	0	1	1	2	1	?	?	?
Mylagaulus elassos	1	1	1	0	0	1	0	1	0	1	1	2	1	1	?	1
Mylagaulus sesquipedalis	1	1	1	0	0	1	0	1	0	1	1	2	1	?	?	?
Promylagaulus riggsi	0	0	0	0	0	0	0	0	?	0	1	1	0	?	0	?
Pterogaulus barbarellae	?	0	1	1	0	1	1	1	1	1	1	2	1	1	2	1
Pterogaulus cambridgensis	?	0	1	1	0	1	1	1	1	1	1	2	1	1	2	?
Pterogaulus laevis	?	1	1	1	0	1	1	1	?	1	1	2	1	1	1	?
Trilaccogaulus lemhiensis	0	0	1	1	?	1	0	0	?	0	1	1	?	?	0	1
Trilaccogaulus montanensis	?	?	?	?	?	?	?	?	?	0	1	1	?	?	0	1
Trilaccogaulus ovatus	0	0	0	1	1	1	0	0	?	0	1	1	0	?	0	1
Umbogaulus galushai	?	1	1	0	0	0	0	1	0	1	1	2	1	1	1	?
Umbogaulus monodon	?	1	1	0	0	0	1	1	1/2	1	1	2	1	1	1	?

Appendix A (extended)

Taxa	**Characters**															
	81	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**
Meniscomys uhtoffi	0	0	0	0	3	0	1	1	0	0	0	0	1	1	?	1
Aplodontia rufa	2	0	5	0	0	0	0	1	0	0	1	0	1	2	1	0
Alphagaulus douglassi	?	1	3	?	?	?	?	?	?	1	?	2	1	?	?	?
Alphagaulus pristinus	0	?	?	?	?	?	?	?	?	1	?	?	1	?	?	?
Alphagaulus pristinus from Deep River Formation	0	2	1/2	?	?	?	?	?	?	1	?	1	1	1	1	0
Alphagaulus tedfordi	?	1	?	?	?	?	?	?	?	1	?	?	1	?	?	?
Alphagaulus vetus	0	2	2	?	?	?	?	?	?	1	?	1	1	0	0	0
Alphagaulus vetus from Massacre Lake Fauna	0	2	2	0	0	1	0	1	0	1	0	1	1	0	0	0
Ceratogaulus anecdotus	0	2	3	?	?	?	?	?	?	1	?	?	1	?	?	?
Ceratogaulus hatcheri	?	2	3	?	?	?	?	?	?	1	?	?	1	?	?	?
Ceratogaulus minor	0	2	?	?	?	?	?	?	?	1	?	2	1	?	0	0
Ceratogaulus rhinocerus	0	0	2	?	?	?	?	?	?	1	?	2	1	?	?	0
Galbreathia bettae	0	0	?	?	?	?	?	?	?	?	?	?	1	?	?	?
Galbreathia novellus	0	1	0	0	0	1	0	2	0	1	0	2	1	0	0	0
Hesperogaulus gazini	?	2	3	?	?	?	?	?	?	1	?	2	1	?	?	?
Hesperogaulus wilsoni	0	2	?	?	?	?	?	?	?	1	?	2	1	?	?	?
Hesperogaulus species A	0	1	3	?	?	?	?	?	?	1	?	2	1	0	?	0
Mesogaulus ballensis	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mesogaulus paniensis	0	0	0	0	2	1	0	2	0	0	0	2	1	1	1	1
Mylagaulodon angulatus	0	0	0	0	0	1	0	2	0	0	1	1	1	0	0	0
Mylagaulus kinseyi	?	1	?	?	?	?	?	?	?	1	?	?	?	?	?	?
Mylagaulus elassos	0	1	3	?	?	?	?	?	?	1	?	?	?	?	0	0
Mylagaulus sesquipedalis	?	?	2	?	?	?	?	?	?	1	?	?	1	?	?	?
Promylagaulus riggsi	?	0	?	0	3	0	0	2	0	0	0	1	1	1	1	1
Pterogaulus barbarellae	0	1	2	?	?	?	?	?	?	1	?	2	1	0	?	0
Pterogaulus cambridgensis	?	1	3	?	?	?	?	?	?	1	?	?	1	?	?	?
Pterogaulus laevis	0	1	2	?	?	?	?	?	?	1	?	2	1	?	0	0
Trilaccogaulus lemhiensis	0	0	0	0	3	1	0	2	0	0	0	1	1	?	0	1
Trilaccogaulus montanensis	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trilaccogaulus ovatus	0	0	?	?	?	?	?	?	?	0	?	1	1	2	?	1
Umbogaulus galushai	0	0	3	?	?	?	?	?	?	1	?	2	1	?	?	?
Umbogaulus monodon	0	1	1	?	?	?	?	?	?	1	?	2	1	0	0	0

Appendix A (extended)

Taxa	**Characters**															
	97	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**
M. uhtoffi	0	0	?	0	1	0	1	1	0	1	0	0	1	1	1	0
A. rufa	1	0/1	0	0	1	0	0	0	1	0	0	1	1	1	1	0
A. douglassi	0	0	?	0	1	1	0	0	?	?	?	?	?	?	?	?
A. pristinus	?	?	?	?	?	?	?	?	0	1	?	0	1	1	0	?
DR *A. pristinus*	0	0	?	0	1	1	0	0	0	1	0	1	1	1	0	0
A. tedfordi	?	?	?	?	?	?	?	?	?	1	?	0	1	1	0	0
A. vetus	0	0	?	0	1	1	0	0	0	1	0	0	1	1	0	0
ML *A. vetus*	0	0	?	0	1	1	0	0	0	1	0	0	1	1	0	0
C. anecdotus	?	?	?	?	?	?	?	?	?	1	?	?	1	1	0	?
C. hatcheri	?	?	?	?	?	?	?	?	?	1	?	?	1	1	0	?
C. minor	0	0	?	0	1	1	0	?	?	1	?	?	1	1	0	?
C. rhinocerus	0	0	?	0	1	1	0	0	?	1	?	?	1	1	0	?
G. bettae	?	?	?	?	?	?	?	?	0	?	?	0/2	1	1	0	?
G. novellus	0	0	?	0	1	0	0	0	0	1	0	0/2	1	1	0	0/1
H. gazini	0	0	?	0	1	1	0	0	?	1	?	?	1	1	0	?
H. wilsoni	0	0	?	0	?	1	0	0	0	1	?	?	1	1	0	0
H. species A	0	0	1	0	1	1	?	0	0	1	?	0	1	1	0	0
M. ballensis	?	?	?	?	?	?	?	?	?	1	?	?	1	1	0	?
M. paniensis	0	0	0	0	1	0	?	?	0	1	0	0	1	1	0	?
M. angulatus	?	?	?	0	1	?	?	?	0	1	?	0	1	1	0	0
M. kinseyi	?	?	?	?	?	?	?	?	?	1	?	?	1	1	0	?
M. elassos	?	?	?	?	?	?	?	?	?	1	?	?	1	1	0	?
M. sesquipedalis	?	?	?	?	?	?	?	?	?	1	?	?	1	1	0	?
P. riggsi	1	0/1	?	?	?	1	0	0	0	1	0	0/2	1	1	0	0/1
P. barbarellae	0	0	?	0	1	1	0	0	0	1	0	0	1	1	0	0
P. cambridgensis	?	?	?	?	?	?	?	?	?	1	?	?	1	1	0	?
P. laevis	0	0	?	0	1	1	0	0	?	?	?	?	1	1	0	?
T. lemhiensis	1	0/1	?	?	?	?	?	?	0	1	0	2	1	1	1	1
T. montanensis	?	?	?	?	?	?	?	?	0	1	0	2	1	1	1	1
T. ovatus	?	?	?	0	1	?	?	?	0	1	0	2	1	1	1	1
U. galushai	?	?	?	?	?	?	?	?	0	1	0	0	1	1	0	0
U. monodon	0	0	?	0	1	1	0	0	0	1	?	0	1	1	0	0

Appendix A (extended)

Taxa	**Characters**															
	113	**114**	**115**	**116**	**117**	**118**	**119**	**120**	**121**	**122**	**123**	**124**	**125**	**126**	**127**	**128**
M. uhtoffi	0	0	1	3	1	1	0	1	0	3	0	0	0	1	0	0
A. rufa	0	0	1	1	1	1	0	1	1	1	0	1	0	1	1	0
A. douglassi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
A. pristinus	1	?	1	3	0	1	1	1	0	0	0	?	0	1	1	2
DR *A. pristinus*	1	0	1	3	0	1	1	1	1	0	0	0	0	1	1	2
A. tedfordi	1	1	1	?	?	1	1	?	?	?	0	0	?	1	1	2
A. vetus	1	0	1	3	0	1	1	1	1	0	0	0	0	1	1	2
ML *A. vetus*	0	1	1	3	0	1	0	1	1	0	0	0	0	1	1	2
C. anecdotus	?	0	0	?	?	?	1	?	1	0	0	0	?	0	1	2
C. hatcheri	?	?	0	?	?	?	1	?	?	?	0	?	?	0	1	2
C. minor	?	1	0	3	0	?	1	1	?	0	0	0	?	0	1	2
C. rhinocerus	?	1	0	?	?	?	1	1	?	?	?	0	?	0	1	2
G. bettae	?	0	0	3	?	?	1	1	1	?	0	?	?	1	1	?
G. novellus	1	0	0	3	0	1	1	1	1	0	0	?	0	1	1	2
H. gazini	?	0	0	?	?	?	1	1	?	2	0	0	?	0	1	2
H. wilsoni	1	0	0	3	0	1	1	1	1	2	0	0	?	0	1	2
H. species A	0	1	1	3	0	1	1	1	1	?	0	0	0	0	1	2
M. ballensis	?	0	1	?	0	?	1	?	?	?	0	?	?	1	1	2
M. paniensis	0	0	1	3	0	1	1	1	1	0	0	0	0	1	1	2
M. angulatus	1	0	0	3	0	1	1	1	?	0	0	0	0	1	1	2
M. kinseyi	?	0	1	?	?	?	1	?	?	?	0	?	?	0	1	2
M. elassos	?	0	1	?	?	?	1	?	?	?	0	?	?	0	1	2
M. sesquipedalis	?	0	1	?	?	?	1	?	?	?	0	0	?	0	1	2
P. riggsi	1	1	0	3	0	1	1	1	1	0	0	0	0	1	1	0
P. barbarellae	1	1	1	3	?	1	1	1	1	?	0	0	?	0	1	2
P. cambridgensis	?	1	1	?	?	?	1	?	?	?	0	?	?	0	1	2
P. laevis	?	1	1	?	0	?	1	?	?	?	0	0	?	0	1	2
T. lemhiensis	1	1	1	3	0	1	1	1	1	2	0	0	0	1	1	0/1
T. montanensis	1	1	1	3	0	1	1	1	1	2	0	0	0	1	1	0
T. ovatus	1	1	1	3	?	1	1	1	1	0	0	0	0	1	1	0/1
U. galushai	1	1	1	3	0	1	1	1	1	0	0	0	0	0	1	2
U. monodon	1	1	1	3	0	1	1	1	1	0	0	0	0	0	1	2

Appendix A (extended)

Taxa	Characters															
	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144
M. uhtoffi	0	0	0	0	2	1	0	1	0	0	0	2	0	0	0/2	0
A. rufa	0	1	0	1	3	0	?	2	1	0	0	0	0	0	0	0
A. douglassi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
A. pristinus	1	?	?	2	3	2	?	2	0	1	1	2	1	0	2	0
DR *A. pristinus*	1	?	0	2	3	2	0	2	0	1	1	2	1	0	2	0
A. tedfordi	1	?	0	?	3	?	0	2	0	1	1	2	1	0	2	0
A. vetus	1	0	0	2	3	2	0	2	0	1	1	2	1	0	2	0
ML *A. vetus*	1	0	0	2	3	2	0	2	0	1	1	2	1	0	2	0
C. anecdotus	1	?	?	?	3	?	?	2	?	1	1	2	1	1	2	0
C. hatcheri	1	?	?	?	3	?	?	2	?	1	1	2	1	1	2	0
C. minor	1	?	0	?	3	?	?	2	?	1	1	2	1	1	2	0
C. rhinocerus	1	?	?	?	3	?	?	2	?	1	1	2	1	1	2	0
G. bettae	1	?	?	2	3	2	?	2	?	1	0	2	0	0	2	0
G. novellus	1	0	0	2	3	2	0	2	0	1	1	2	1	0	2	0
H. gazini	1	0	0	?	3	2	?	2	?	1	1	2	1	0	0	0
H. wilsoni	?	0	0	?	3	2	?	2	0	1	1	2	1	0	2	0
H. species A	1	0	0	2	3	2	0	2	0	1	1	2	1	0	2	0
M. ballensis	?	?	0	?	3	?	?	2	?	1	1	2	1	0	?	?
M. paniensis	1	?	0	2	3	2	0	2	0	1	1	2	1	0	0	1
M. angulatus	1	0	0	2	3	2	0	2	0	1	1	2	1	0	0	1
M. kinseyi	1	?	0	?	3	?	?	2	?	1	1	2	1	1	2	0
M. elassos	1	0	0	2	3	?	0	2	0	1	1	2	1	1	2	0
M. sesquipedalis	1	?	?	?	3	?	?	2	?	1	1	2	1	1	2	0
P. riggsi	?	0	0	2	2	0	0	2	0	0	0	1	0	0	0	0
P. barbarellae	1	?	0	2	3	2	0	2	0	1	1	2	1	1	2	0
P. cambridgensis	1	?	?	?	3	?	?	2	?	1	1	2	1	1	2	0
P. laevis	1	?	?	?	3	?	?	2	?	1	1	2	1	1	2	0
T. lemhiensis	?	0	0	1/2	2	0	0	2	0	1	0	2	1	0	0	1
T. montanensis	?	0	0	1	2	1	0	2	0	1	1	2	1	0	0	0
T. ovatus	1	0	0	1	2	1	0	2	0	0	0	2	1	0	0	1
U. galushai	1	0	0	2	3	2	0	2	0	1	1	2	1	1	2	0
U. monodon	1	?	0	2	3	2	0	2	0	1	1	2	1	1	2	0

Appendix A (extended)

Taxa	**Characters**															
	145	**146**	**147**	**148**	**149**	**150**	**151**	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**	**160**
M. uhtoffi	1	0	0	0	0	0	1	0	1	1	2	1	0	0	1	0
A. rufa	1	0	0	1	0	0	1	2	1	2	2	0	0	0	1	0
A. douglassi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
A. pristinus	1	0	?	0	0	1	1	2	0	1	2	1	0	0	1	1
DR *A. pristinus*	1	?	?	?	?	1	1	2	0	1	2	1	0	0	1	1
A. tedfordi	?	?	?	?	?	?	1	?	?	1	2	1	0	0	?	1
A. vetus	1	0	0	0	0	0	1	2	0	1	2	1	1	1	1	1
ML *A. vetus*	1	0	0	0	0	0	1	2	2	1	2	1	1	1	1	1
C. anecdotus	?	?	?	?	?	?	1	?	?	1	2	1	1	1	?	1
C. hatcheri	?	?	?	?	?	?	1	?	?	1	2	1	1	1	?	1
C. minor	1	?	?	?	?	?	1	?	?	1	2	1	1	1	?	1
C. rhinocerus	?	?	?	?	?	?	1	?	?	1	2	1	1	?	?	1
G. bettae	?	0	?	0	0	?	1	?	0	1	2	1	0	0	1	1
G. novellus	1	0	0	0	0	0	1	2	1	1	2	1	0	0	1	1
H. gazini	?	?	?	?	?	1	1	?	?	1	2	1	1	0	?	1
H. wilsoni	?	?	?	?	?	1	1	?	?	1	2	1	1	0	?	1
H. species A	1	?	?	?	?	0	1	2	0	1	2	1	1	0	1	1
M. ballensis	1	?	?	?	?	?	1	2	?	?	2	1	0	0	?	1
M. paniensis	1	0	?	?	?	0	1	2	1	1	2	1	0	0	1	1
M. angulatus	1	?	?	?	?	1	1	2	0	1	2	1	0	0	1	1
M. kinseyi	?	?	?	?	?	?	1	?	?	1	2	1	1	0	?	1
M. elassos	?	?	?	?	?	?	1	?	0	1	2	1	1	0	1	1
M. sesquipedalis	?	?	?	?	?	?	1	?	?	1	2	1	1	0	?	1
P. riggsi	1	0	0	0	0	1	1	2	1	1	2	1	0	0	1	1
P. barbarellae	?	?	?	?	?	?	1	?	1	1	2	1	1	0	1	1
P. cambridgensis	?	?	?	?	?	?	1	?	?	1	2	1	1	0	?	1
P. laevis	?	?	?	?	?	?	1	?	?	1	2	1	1	0	?	1
T. lemhiensis	1	0	0	0	0	1	1	2	1	1	2	1	0	0	1	1
T. montanensis	1	0	0	0	0	?	1	2	1	1	2	1	0	0	1	1
T. ovatus	1	0	0	0	0	?	1	?	1	1	2	1	0	0	1	1
U. galushai	1	0	0	?	0	1	1	2	2	1	2	1	1	0	1	1
U. monodon	1	0	?	?	?	0	1	2	0	1	2	1	1	0	1	1

Appendix A (extended)

Taxa	**Characters**															
	161	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**	**171**	**172**	**173**	**174**	**175**	**176**
M. uhtoffi	1	0	0	0	2	1	2	1	1	0	0	1	0	1	1	0
A. rufa	1	?	0	1	2	1	2	0	2	1	0	1	0	1	0	0
A. douglassi	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	0
A. pristinus	1	1	0	0	0	1	1	0	1	3	?	2	1	2	1	?
DR *A. pristinus*	1	1	0	0	?	1	1	0	1	3	0	2	1	2	1	0
A. tedfordi	1	1	?	0	0	1	?	0	1	0	1	?	1	2	1	1
A. vetus	1	1	0	0	0	1	1	0	1	0	0	2	1	2	1	1
ML *A. vetus*	1	1	0	0	0	1	1	0	1	3	0	2	1	2	?	1
C. anecdotus	1	1	?	0	0	1	?	?	?	?	0	?	1	?	?	?
C. hatcheri	1	1	?	0	0	1	?	?	?	?	1	2	1	2	1	?
C. minor	1	1	?	0	0	1	?	?	1	0	1	2	1	2	1	?
C. rhinocerus	1	1	?	0	0	1	?	?	?	?	1	2	1	2	1	1
G. bettae	1	1	0	0	0	1	?	0	1	0	0	?	0	1	?	?
G. novellus	1	1	0	0	0	1	?	0	1	0	0	2	1	2	1	1
H. gazini	?	1	?	0	0	1	?	?	1	0	0/1	2	1	2	1	?
H. wilsoni	1	1	?	0	0	1	?	0	1	0	1	2	1	2	?	1
H. species A	1	1	0	0	0	1	2	0	1	3	1	2	1	2	1	1
M. ballensis	1	1	?	0	0	1	?	0	?	?	0	2	1	2	1	?
M. paniensis	1	1	0	0	0	1	1	0	1	0	0	2	1	2	1	0
M. angulatus	1	1	?	0	0	1	1	?	1	3	0	2	0	1	1	0
M. kinseyi	1	1	0	0	0	1	?	0	?	?	1	?	1	2	?	?
M. elassos	1	1	0	0	0	1	?	0	1	0	1	?	1	2	1	?
M. sesquipedalis	1	1	?	0	0	1	?	?	?	?	0	?	1	?	1	?
P. riggsi	1	1	0	0	0	1	2	1	1	2	0	1	0	1	?	?
P. barbarellae	1	1	0	0	0	1	?	0	1	0	0	2	1	2	1	1
P. cambridgensis	1	1	?	0	0	1	?	?	?	?	0	?	1	?	?	1
P. laevis	1	1	0	0	0	1	?	?	?	?	0	2	1	2	?	1
T. lemhiensis	1	0	0	0	0	1	2	1	1	2	0	1	0	1	?	?
T. montanensis	1	0	0	0	0	1	2	1	1	2	0	1	0	1	?	?
T. ovatus	1	0	0	0	0	1	?	?	1	2	0	1	0	1	?	?
U. galushai	1	1	0	0	0	1	1	0	1	3	1	2	1	2	1	1
U. monodon	1	1	0	0	0	1	1	0	1	3	1	2	1	2	1	1

Appendix A (extended)

Taxa	**Characters**															
	177	**178**	**179**	**180**	**181**	**182**	**183**	**184**	**185**	**186**	**187**	**188**	**189**	**190**	**191**	**192**
M. uhtoffi	0	1	1	3	1	1	0	0	0	0	0	1	1	2	0	1
A. rufa	0	1	2	3	0	0	1	0	0	1	1	0	1	2	2	0
A. douglassi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
A. pristinus	0	1	3	3	?	0	0	0	0	1	1	1	?	?	1	1
DR *A. pristinus*	0	1	3	3	0	0	0	0	0	1	1	1	1	2	1	1
A. tedfordi	0	1	2	3	0	0	0	0	0	?	?	1	1	?	1	?
A. vetus	1	1	3	2	0	0	1	0	0	1	1	1	2	2	1	1
ML *A. vetus*	?	?	?	2	0	0	1	?	0	?	?	1	2	?	1	?
C. anecdotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
C. hatcheri	1	1	3	?	0	0	?	?	?	?	1	1	1	?	?	?
C. minor	1	1	3	2	0	0	1	1	0	?	?	?	1	?	?	?
C. rhinocerus	1	1	3	2	0	0	0	0	0	?	1	?	1	?	1	?
G. bettae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
G. novellus	1	1	3	2	1	0	1	1	0	0	?	1	2	2	1	?
H. gazini	1	?	?	?	?	?	?	0	0	?	?	?	?	?	1	1
H. wilsoni	1	1	3	2	0	0	0	1	1	1	?	1	1	?	1	?
H. species A	?	?	?	2	0	0	0	?	0	?	?	?	2	?	?	?
M. ballensis	0	1	3	3	0	0	?	0	?	?	?	?	1	?	?	?
M. paniensis	0	1	3	3	0	0	0	0	0	1	1	1	1	?	1	1
M. angulatus	0	?	2	3	?	?	0	?	0	?	?	?	?	?	1	?
M. kinseyi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. elassos	1	1	2	?	0	0	1	1	0	?	?	?	1	?	?	?
M. sesquipedalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. riggsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. barbarellae	1	1	3	2	0	0	1	0/1	0/1	0	1	?	1	2	1	1
P. cambridgensis	1	1	?	2	0	0	0	0/1	1	?	?	?	2	?	?	?
P. laevis	1	1	3	3	0	0	0	0	0	?	?	?	1	?	?	?
T. lemhiensis	0	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?
T. montanensis	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?
T. ovatus	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?
U. galushai	1	1	3	3	0	0	0	0	0	?	1	?	1	?	?	?
U. monodon	1	1	3	2	0	0	0	1	0	0	1	?	0/1	?	1	?

Appendix A (extended)

Taxa	Characters															
	193	**194**	**195**	**196**	**197**	**198**	**199**	**200**	**201**	**202**	**203**	**204**	**205**	**206**	**207**	**208**
M. uhtoffi	0	0	0	1	1	?	0	?	1	0	0	1	1	0	0	0
A. rufa	1	1	0	1	2	0	0	2	1	0	1	1	0	0	0	1
A. douglassi	?	?	?	?	1	?	1	?	?	?	1	0	2	0	?	1
A. pristinus	1	1	0	1	2	?	1	2	1	0	1	0	1	0	?	?
DR *A. pristinus*	1	?	0	1	?	1	1	2	1	0	1	0	1	0	1	1
A. tedfordi	1	1	0	1	1	1	1	2	1	0	1	0	2	0	1	1
A. vetus	1	1	1	0	1	1	1	2	1	0	1	0	1	0	1	1
ML *A. vetus*	1	1	?	?	?	1	1	2	1	0	?	0	1	0	1	1
C. anecdotus	?	?	2	1	2	1	1	?	1	0	1	?	1	?	1	?
C. hatcheri	1	1	2	1	2	1	1	2	1	0	1	0	0/1	0	1	1
C. minor	1	1	1	0	2	?	1	?	1	0	1	0	1	0	1	1
C. rhinocerus	1	1	1	0	2	1	1	1	1	0	1	0	1	0	1	1
G. bettae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
G. novellus	1	1	0	1	0	1	0	1	1	0	1	1	1	0	1	0
H. gazini	1	1	2	1	2	1	1	2	1	0	1	0	1	0	1	1
H. wilsoni	1	1	2	0	2	1	1	2	1	0	1	0	1	0	1	1
H. species A	?	1	?	?	?	?	1	?	?	?	?	0	1	1	?	1
M. ballensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. paniensis	1	1	0	1	0	?	1	1	1	0	1	1	1	0	1	1
M. angulatus	?	?	?	?	?	?	?	?	?	?	?	0	1	0	?	0
M. kinseyi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. elassos	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
M. sesquipedalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. riggsi	?	0	?	?	?	?	?	?	?	?	?	0	?	0	?	1
P. barbarellae	1	1	1	1	2	1	1	2	1	1	1	0	2	1	1	1
P. cambridgensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. laevis	?	?	1	?	?	?	?	?	1	1	1	0	2	1	1	1
T. lemhiensis	?	?	?	?	?	1	0	?	1	?	?	?	?	?	1	?
T. montanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
T. ovatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
U. galushai	1	1	1	?	2	?	1	2	1	0	1	0	2	0	1	1
U. monodon	1	1	1	1	2	1	1	2	1	0	1	0	2	0	1	1

Appendix A (extended)

Taxa	**Characters**															
	209	**210**	**211**	**212**	**213**	**214**	**215**	**216**	**217**	**218**	**219**	**220**	**221**	**222**	**223**	**224**
M. uhtoffi	?	0	0	?	2	1	1	0	1	0	0	1	1	0/1	2	1
A. rufa	2	0	0	?	3	1	0	1	1	0	1	0	1	0	0	1
A. douglassi	2	0	1	?	1	1	?	0/1	0	1	1	1	0	1	2	?
A. pristinus	?	0	?	?	?	?	1	0	0	1	0	1	0	0	?	1
DR *A. pristinus*	2	0	0	?	1	1	1	0	0	1	0	1	?	?	?	1
A. tedfordi	2	0	0	?	1	1	2	?	?	0	0	1	?	?	?	1
A. vetus	2	0	0	?	1	1	2	0	0	1	1	1	0	1	0	1
ML *A. vetus*	?	?	0	?	?	1	2	0	0	1	?	1	0	1	0	1
C. anecdotus	?	?	2/3	1	?	?	?	?	?	?	?	?	?	?	?	1
C. hatcheri	1	1	3	0	2	1	2	0	0	1	0	1	?	?	?	1
C. minor	?	?	2	?	?	?	?	?	?	?	?	1	?	?	?	1
C. rhinocerus	1	1	2	1	1	1	1	0/1	0	0	1	1	0	?	?	1
G. bettae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
G. novellus	2	0	0	?	2	1	2	1	0	0	1	1	?	1	?	0
H. gazini	2	1	1	?	?	1	2	0	0	1	0	1	0	?	0	1
H. wilsoni	2	?	1	?	?	?	2	?	?	0	1	1	?	?	?	1
H. species A	?	1	1	?	1	1	2	0	0	1	1	1	0	1	0	1
M. ballensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
M. paniensis	2	0	0	?	2	1	2	0	0	1	1	1	1	1	?	1
M. angulatus	?	0	0	?	?	?	?	?	?	1	1	1	?	?	?	1
M. kinseyi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
M. elassos	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
M. sesquipedalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
P. riggsi	2	?	0	?	0	?	1	1	0	0	1	1	?	1	2	1
P. barbarellae	2	0	0	?	1	1	2	0	0	1	0	1	0	1	0	1
P. cambridgensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
P. laevis	2	0	0	?	2	1	?	0	0	1	1	1	?	?	?	1
T. lemhiensis	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0
T. montanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
T. ovatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
U. galushai	2	1	1	?	1	1	2	0	0	?	?	?	?	?	?	1
U. monodon	2	1	1	?	2	1	2	0	0	0	0	1	?	1	?	1

Appendix A (extended)

Taxa	**Characters**															
	225	**226**	**227**	**228**	**229**	**230**	**231**	**232**	**233**	**234**	**235**	**236**	**237**	**238**	**239**	**240**
M. uhtoffi	0	?	0	0	0	0	0	0	1	0	1	1	1	1	1	1
A. rufa	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	1
A. douglassi	?	?	?	?	0	?	0	?	?	?	?	?	?	1	1	1
A. pristinus	1	0	1	0	1	1	0/1	0	0	0	1	1	1	1	1	1
DR *A. pristinus*	1	0	1	0	1	?	0	0	1	0	1	1	?	1	1	1
A. tedfordi	1	0	1	?	1	?	0	0	?	0	?	?	?	1	1	1
A. vetus	1	0	1	0	1	1	1	0	0	0	1	1	1	1	1	1
ML *A. vetus*	1	0	1	0	1	1	1	0	0	0	1	1	1	1	1	1
C. anecdotus	1	?	?	?	1	?	1	0	?	?	1	?	?	1	1	1
C. hatcheri	1	?	?	?	1	?	1	0	?	?	?	?	?	1	1	1
C. minor	1	0	1	?	1	?	1	0	?	?	?	?	?	1	1	1
C. rhinocerus	1	?	?	?	1	?	1	0	?	?	1	?	?	1	1	1
G. bettae	1	?	1	?	0	1	1	0	1	0	1	1	1	1	1	1
G. novellus	1	0	1	0	0	1	1	0	1	0	1	1	1	1	1	1
H. gazini	1	?	?	?	1	?	2	0	?	?	?	?	?	1	1	1
H. wilsoni	1	0	1	?	1	?	2	0	1	0	1	1	?	1	1	1
H. species A	1	0	1	0	1	?	2	0	1	0	1	1	?	1	1	1
M. ballensis	?	?	1	?	0	?	2	0	?	0	?	?	?	1	1	1
M. paniensis	1	0	1	0	0	1	2	0	1	0	1	1	?	1	1	1
M. angulatus	1	0	1	0	0	?	0	0	0	0	1	1	?	1	1	1
M. kinseyi	1	0	?	?	1	?	1	0	?	?	?	?	?	1	1	1
M. elassos	1	0	1	?	1	?	1	0	1	0	1	1	1	1	1	1
M. sesquipedalis	1	?	?	?	1	?	0	0	?	?	?	?	?	1	1	1
P. riggsi	0	1	0	0	0	1	0	1	1	0	1	1	1	1	1	1
P. barbarellae	1	0	1	?	1	1	2	0	1	0	1	1	?	1	1	1
P. cambridgensis	1	?	?	?	1	?	2	0	?	?	?	?	?	1	1	1
P. laevis	1	?	?	?	1	?	1	0	?	?	?	?	?	1	1	1
T. lemhiensis	0	1	0	0	0	?	0	0	1	0	1	1	1	1	1	1
T. montanensis	0	1	0	?	0	1	0	0	0	0	1	1	1	1	1	1
T. ovatus	0	1	0	?	0	1	0	0	1	0	1	1	1	1	1	1
U. galushai	1	0	1	0	1	1	2	0	1	0	1	1	1	1	1	1
U. monodon	1	0	1	0	1	1	2	0	1	0	1	1	?	1	1	1

Appendix A (extended)

Taxa	**Characters**									
	241	242	243	244	245	246	247	248	249	250
M. uhtoffi	2	?	?	0	1	1	0	0	0	0
A. rufa	2	?	?	0	1	1	1	1	0	0
A. douglassi	2	?	?	0	1	1	0	?	0	0
A. pristinus	2	?	?	0	1	1	?	0	1	0
DR *A. pristinus*	2	?	?	0	1	1	0	0	1	0
A. tedfordi	2	?	?	0	1	1	0	0	0	0
A. vetus	2	?	?	0	1	1	0	0	1	0
ML *A. vetus*	2	?	?	0	1	1	0	0	1	0
C. anecdotus	2	?	?	0	1	1	0	0	0	0
C. hatcheri	2	?	?	0	1	1	0	0	0	0
C. minor	2	?	?	0	1	1	0	0	0	0
C. rhinocerus	2	?	?	0	1	1	0	0	0	0
G. bettae	2	?	?	0	1	1	0	0	1	0
G. novellus	2	?	?	0	1	1	0	0	1	0
H. gazini	2	?	?	0	1	1	0	0	1	0
H. wilsoni	2	?	?	0	1	1	0	0	1	0
H. species A	2	?	?	0	1	1	0	0	1	0
M. ballensis	2	?	?	0	1	1	?	0	?	0
M. paniensis	2	?	?	0	1	1	0	0	0	0
M. angulatus	2	?	?	0	1	1	0	0	0	0
M. kinseyi	2	?	?	0	1	1	0	0	0	0
M. elassos	2	?	?	0	1	1	0	0	0	0
M. sesquipedalis	2	?	?	0	1	1	0	0	0	0
P. riggsi	2	?	?	0	1	1	0	0	0	0
P. barbarellae	2	?	?	0	1	1	0	0	1	1
P. cambridgensis	2	?	?	0	1	1	0	0	1	1
P. laevis	2	?	?	0	1	1	0	0	1	1
T. lemhiensis	2	?	?	0	1	1	0	0	0	0
T. montanensis	2	?	?	0	1	1	?	0	0	0
T. ovatus	2	?	?	0	1	1	0	0	0	0
U. galushai	2	?	?	0	1	1	0	0	1	0
U. monodon	2	?	?	0	1	1	0	0	1	0

APPENDIX B

NUMBER OF IDENTIFIED SPECIMENS, MINIMUM NUMBER OF INDIVIDUALS, AND NUMBER OF LOCALITIES OF FOSSORIAL HERBIVORES USED IN CHAPTER III

Abbreviation: MNI, Minimum Number of Individuals; N, Number; NISP, number of Identified Specimens.

Abbreviations of North American Land Mammal Ages (NALMAs): LHMF, Late Hemingfordian; EBAR, Early Barstovian; LBAR, Late Barstovian; BARS, Barstovian; LCLA, Late Clarendonian; EEHP, Early early Hemphillian; LEHP, Late early Hemphillian; ELHP, Early late Hemphillian.

Data for fossorial rodents				
Collecting Area	NALMA subdivision	Family	NISP	MNI
Massacre Lake	LHMF	Aplodontidae	34	14
Massacre Lake	LHMF	Geomyidae	0	0
Massacre Lake	LHMF	Marmotini	21	12
Massacre Lake	LHMF	Mylagaulidae	46	17
Massacre Lake	LHMF	All Fossorial rodents	101	43
Beatty Butte	EBAR	Aplodontidae	103	17
Beatty Butte	EBAR	Geomyidae	0	0
Beatty Butte	EBAR	Marmotini	23	10
Beatty Butte	EBAR	Mylagaulidae	33	12
Beatty Butte	EBAR	All Fossorial rodents	159	39
Sucker Creek	EBAR	Aplodontidae	0	0
Sucker Creek	EBAR	Geomyidae	0	0
Sucker Creek	EBAR	Marmotini	0	0
Sucker Creek	EBAR	Mylagaulidae	2	1
Sucker Creek	EBAR	All Fossorial rodents	2	1
Virgin Valley	EBAR	Aplodontidae	1	1
Virgin Valley	EBAR	Geomyidae	0	0
Virgin Valley	EBAR	Marmotini	0	0
Virgin Valley	EBAR	Mylagaulidae	32	15
Virgin Valley	EBAR	All Fossorial rodents	33	16
Butte Creek Volc sst	LBAR	Aplodontidae	26	14
Butte Creek Volc sst	LBAR	Geomyidae	0	0
Butte Creek Volc sst	LBAR	Marmotini	86	19
Butte Creek Volc sst	LBAR	Mylagaulidae	60	16
Butte Creek Volc sst	LBAR	All Fossorial rodents	172	49
Deer Butte	LBAR	Aplodontidae	0	0
Deer Butte	LBAR	Geomyidae	17	4
Deer Butte	LBAR	Marmotini	3	1
Deer Butte	LBAR	Mylagaulidae	0	0
Deer Butte	LBAR	All Fossorial rodents	20	5
Juntura	LCLA	Aplodontidae	3	1
Juntura	LCLA	Geomyidae	4	4
Juntura	LCLA	Marmotini	14	7
Juntura	LCLA	Mylagaulidae	15	11

Appendix B (continued)

Data for fossorial rodents				
Collecting Area	NALMA subdivision	Family	NISP	MNI
Juntura	LCLA	All Fossorial rodents	36	23
Thousand Creek	EEHP	Aplodontidae	5	4
Thousand Creek	EEHP	Geomyidae	94	19
Thousand Creek	EEHP	Marmotini	3	3
Thousand Creek	EEHP	Mylagaulidae	3	3
Thousand Creek	EEHP	All Fossorial rodents	105	29
Drewsey	LEHP	Aplodontidae	50	10
Drewsey	LEHP	Geomyidae	9	4
Drewsey	LEHP	Marmotini	29	4
Drewsey	LEHP	Mylagaulidae	16	10
Drewsey	LEHP	All Fossorial rodents	104	28
Grassy Mountain	LEHP	Aplodontidae	0	0
Grassy Mountain	LEHP	Geomyidae	0	0
Grassy Mountain	LEHP	Marmotini	3	1
Grassy Mountain	LEHP	Mylagaulidae	0	0
Grassy Mountain	LEHP	All Fossorial rodents	3	1
Chalk Butte	ELHP	Aplodontidae	0	0
Chalk Butte	ELHP	Geomyidae	2	1
Chalk Butte	ELHP	Marmotini	22	4
Chalk Butte	ELHP	Mylagaulidae	0	0
Chalk Butte	ELHP	All Fossorial rodents	24	5
Piute Creek	BARS	Aplodontidae	1	1
Piute Creek	BARS	Geomyidae	1	1
Piute Creek	BARS	Marmotini	0	0
Piute Creek	BARS	Mylagaulidae	5	4
Piute Creek	BARS	All Fossorial rodents	7	6
Rattlesnake Butte	BARS	Aplodontidae	7	2
Rattlesnake Butte	BARS	Geomyidae	2	1
Rattlesnake Butte	BARS	Marmotini	0	0
Rattlesnake Butte	BARS	Mylagaulidae	11	6
Rattlesnake Butte	BARS	All Fossorial rodents	20	9

Appendix B (continued)

Data for all small mammals			
Collecting Area	NALMA subdivision	NISP	MNI
Massacre Lake	LHMF	106	47
Beatty Butte	EBAR	796	120
Sucker Creek	EBAR	3	2
Virgin Valley	EBAR	42	21
Butte Creek Volc sst	LBAR	279	80
Deer Butte	LBAR	440	85
Juntura	LCLA	419	98
Thousand Creek	EEHP	162	48
Drewsey	LEHP	446	90
Grassy Mountain	LEHP	19	6
Chalk Butte	ELHP	472	58
Piute Creek	BARS	9	8
Rattlesnake Butte	BARS	31	13

Appendix B (continued)

Data for fossorial rodents			
Collecting Area	NALMA subdivision	Family	Relative abundance (MNI)
Massacre Lake	LHMF	Aplodontidae	29.79
Massacre Lake	LHMF	Geomyidae	0.00
Massacre Lake	LHMF	Marmotini	25.53
Massacre Lake	LHMF	Mylagaulidae	36.17
Massacre Lake	LHMF	All Fossorial rodents	91.49
Beatty Butte	EBAR	Aplodontidae	14.17
Beatty Butte	EBAR	Geomyidae	0.00
Beatty Butte	EBAR	Marmotini	8.33
Beatty Butte	EBAR	Mylagaulidae	10.00
Beatty Butte	EBAR	All Fossorial rodents	32.50
Sucker Creek	EBAR	Aplodontidae	0.00
Sucker Creek	EBAR	Geomyidae	0.00
Sucker Creek	EBAR	Marmotini	0.00
Sucker Creek	EBAR	Mylagaulidae	50.00
Sucker Creek	EBAR	All Fossorial rodents	50.00
Virgin Valley	EBAR	Aplodontidae	4.76
Virgin Valley	EBAR	Geomyidae	0.00
Virgin Valley	EBAR	Marmotini	0.00
Virgin Valley	EBAR	Mylagaulidae	71.43
Virgin Valley	EBAR	All Fossorial rodents	76.19
Butte Creek Volc sst	LBAR	Aplodontidae	17.50
Butte Creek Volc sst	LBAR	Geomyidae	0.00
Butte Creek Volc sst	LBAR	Marmotini	23.75
Butte Creek Volc sst	LBAR	Mylagaulidae	20.00
Butte Creek Volc sst	LBAR	All Fossorial rodents	61.25
Deer Butte	LBAR	Aplodontidae	0.00
Deer Butte	LBAR	Geomyidae	4.71
Deer Butte	LBAR	Marmotini	1.18
Deer Butte	LBAR	Mylagaulidae	0.00
Deer Butte	LBAR	All Fossorial rodents	5.88

Appendix B (continued)

Data for fossorial rodents

Collecting Area	NALMA subdivision	Family	Relative abundance (MNI)
Juntura	LCLA	Aplodontidae	1.02
Juntura	LCLA	Geomyidae	4.08
Juntura	LCLA	Marmotini	7.14
Juntura	LCLA	Mylagaulidae	11.22
Juntura	LCLA	All Fossorial rodents	23.47
Thousand Creek	EEHP	Aplodontidae	8.33
Thousand Creek	EEHP	Geomyidae	39.58
Thousand Creek	EEHP	Marmotini	6.25
Thousand Creek	EEHP	Mylagaulidae	6.25
Thousand Creek	EEHP	All Fossorial rodents	60.42
Drewsey	LEHP	Aplodontidae	11.11
Drewsey	LEHP	Geomyidae	4.44
Drewsey	LEHP	Marmotini	4.44
Drewsey	LEHP	Mylagaulidae	11.11
Drewsey	LEHP	All Fossorial rodents	31.11
Grassy Mountain	LEHP	Aplodontidae	0.00
Grassy Mountain	LEHP	Geomyidae	0.00
Grassy Mountain	LEHP	Marmotini	16.67
Grassy Mountain	LEHP	Mylagaulidae	0.00
Grassy Mountain	LEHP	All Fossorial rodents	16.67
Chalk Butte	ELHP	Aplodontidae	0.00
Chalk Butte	ELHP	Geomyidae	1.72
Chalk Butte	ELHP	Marmotini	6.90
Chalk Butte	ELHP	Mylagaulidae	0.00
Chalk Butte	ELHP	All Fossorial rodents	8.62
Piute Creek	BARS	Aplodontidae	12.50
Piute Creek	BARS	Geomyidae	12.50
Piute Creek	BARS	Marmotini	0.00
Piute Creek	BARS	Mylagaulidae	50.00
Piute Creek	BARS	All Fossorial rodents	75.00

Appendix B (continued)

Data for fossorial rodents

Collecting Area	NALMA subdivision	Family	Relative abundance (MNI)
Rattlesnake Butte	BARS	Aplodontidae	15.38
Rattlesnake Butte	BARS	Geomyidae	7.69
Rattlesnake Butte	BARS	Marmotini	0.00
Rattlesnake Butte	BARS	Mylagaulidae	46.15
Rattlesnake Butte	BARS	All Fossorial rodents	69.23

Data for fossorial rodents

Collecting Area	NALMA subdivision	Family	N localities
Rattlesnake Butte	BARS	Aplodontidae	1
Rattlesnake Butte	BARS	Geomyidae	1
Rattlesnake Butte	BARS	Marmotini	0
Rattlesnake Butte	BARS	Mylagaulidae	1
Rattlesnake Butte	BARS	All Fossorial rodents	1

Appendix B (continued)

Data for fossorial rodents

Collecting Area	NALMA subdivision	Family	N localities
Massacre Lake	LHMF	Aplodontidae	4
Massacre Lake	LHMF	Geomyidae	0
Massacre Lake	LHMF	Marmotini	4
Massacre Lake	LHMF	Mylagaulidae	3
Massacre Lake	LHMF	All Fossorial rodents	4
Beatty Butte	EBAR	Aplodontidae	8
Beatty Butte	EBAR	Geomyidae	0
Beatty Butte	EBAR	Marmotini	3
Beatty Butte	EBAR	Mylagaulidae	9
Beatty Butte	EBAR	All Fossorial rodents	11
Sucker Creek	EBAR	Aplodontidae	0
Sucker Creek	EBAR	Geomyidae	0
Sucker Creek	EBAR	Marmotini	0
Sucker Creek	EBAR	Mylagaulidae	1
Sucker Creek	EBAR	All Fossorial rodents	1
Virgin Valley	EBAR	Aplodontidae	1
Virgin Valley	EBAR	Geomyidae	0
Virgin Valley	EBAR	Marmotini	0
Virgin Valley	EBAR	Mylagaulidae	6
Virgin Valley	EBAR	All Fossorial rodents	7
Butte Creek Volc sst	LBAR	Aplodontidae	3
Butte Creek Volc sst	LBAR	Geomyidae	0
Butte Creek Volc sst	LBAR	Marmotini	2
Butte Creek Volc sst	LBAR	Mylagaulidae	3
Butte Creek Volc sst	LBAR	All Fossorial rodents	3
Deer Butte	LBAR	Aplodontidae	0
Deer Butte	LBAR	Geomyidae	1
Deer Butte	LBAR	Marmotini	1
Deer Butte	LBAR	Mylagaulidae	0
Deer Butte	LBAR	All Fossorial rodents	1
Juntura	LCLA	Aplodontidae	1
Juntura	LCLA	Geomyidae	2

Appendix B (continued)

Data for fossorial rodents

Collecting Area	NALMA subdivision	Family	N localities
Juntura	LCLA	Marmotini	5
Juntura	LCLA	Mylagaulidae	7
Juntura	LCLA	All Fossorial rodents	10
Thousand Creek	EEHP	Aplodontidae	3
Thousand Creek	EEHP	Geomyidae	6
Thousand Creek	EEHP	Marmotini	2
Thousand Creek	EEHP	Mylagaulidae	3
Thousand Creek	EEHP	All Fossorial rodents	13
Drewsey	LEHP	Aplodontidae	4
Drewsey	LEHP	Geomyidae	2
Drewsey	LEHP	Marmotini	2
Drewsey	LEHP	Mylagaulidae	4
Drewsey	LEHP	All Fossorial rodents	5
Grassy Mountain	LEHP	Aplodontidae	0
Grassy Mountain	LEHP	Geomyidae	0
Grassy Mountain	LEHP	Marmotini	1
Grassy Mountain	LEHP	Mylagaulidae	0
Grassy Mountain	LEHP	All Fossorial rodents	1
Chalk Butte	ELHP	Aplodontidae	0
Chalk Butte	ELHP	Geomyidae	1
Chalk Butte	ELHP	Marmotini	1
Chalk Butte	ELHP	Mylagaulidae	0
Chalk Butte	ELHP	All Fossorial rodents	1
Piute Creek	BARS	Aplodontidae	1
Piute Creek	BARS	Geomyidae	1
Piute Creek	BARS	Marmotini	0
Piute Creek	BARS	Mylagaulidae	2
Piute Creek	BARS	All Fossorial rodents	3

APPENDIX C

PRESENCE/ABSENCE DATA OF MAMMALIAN TAXA FOR THE LOCALITIES IN THE NORTHERN GREAT BASIN INCLUDED IN THE CLUSTER ANALYSIS OF CHAPTER III

	Achlyoscapter	*Acritohippus*	*Adjidaumo*	*Aelurodon*	*Alluvisorex*	*Amebelodon*
1065	0	0	0	0	0	0
1083	0	0	0	0	0	0
1090	0	0	0	0	0	0
1095	0	0	0	0	0	0
1098	0	0	0	0	0	0
1100	0	0	0	0	0	0
1103	0	0	0	0	0	0
1104	0	0	0	0	0	0
1105	0	0	0	0	0	0
3351	0	0	0	0	0	0
V6160	0	0	0	0	0	0
V6161	0	0	0	0	0	0
RV7043	0	0	0	0	0	0
RV7317	0	0	0	0	0	0
RV7319	0	0	0	0	0	0
RV7322	0	0	0	0	0	0
RV7324	0	0	0	0	0	0
V65593	0	0	0	0	0	0
RV68136	0	0	0	0	0	0
V69114	0	0	0	0	0	0
V73056	0	0	0	0	0	0
V78080	0	0	0	0	0	0
V84100	0	0	0	0	0	0
V84101	0	0	0	0	0	0
V84102	0	0	0	0	0	0
V84103	0	0	0	0	0	0
V84104	0	0	0	0	0	0
V84105	0	0	0	0	0	0
V84106	0	0	0	0	0	0

Appendix C (extended)

	Ammospermophilus	*Amphicyon*	Amphicyonidae	*Anchitherium*	*Anouroneomys*
1065	0	0	0	0	0
1083	0	0	0	0	0
1090	0	0	0	0	0
1095	0	0	0	0	0
1098	0	0	0	0	0
1100	0	0	0	0	0
1103	0	0	0	0	0
1104	0	0	0	0	0
1105	0	0	0	0	0
3351	0	0	0	0	0
V6160	0	0	0	0	0
V6161	0	0	0	0	0
RV7043	0	1	1	1	0
RV7317	0	0	0	1	0
RV7319	0	0	0	0	0
RV7322	0	0	0	0	0
RV7324	0	0	0	0	0
V65593	0	0	0	0	0
RV68136	0	0	0	0	0
V69114	0	0	0	0	0
V73056	0	0	0	0	0
V78080	0	0	0	0	0
V84100	0	0	0	0	0
V84101	0	0	0	0	0
V84102	0	0	0	0	0
V84103	0	0	0	0	0
V84104	0	0	0	0	0
V84105	0	0	0	0	0
V84106	0	0	0	0	0

Appendix (extended)

	Antecalomys	Antilocapridae	*Aphelops*	Aplodontidae	*Archaeohippus*	*Arctomys*	*Acritohippus*
1065	0	0	0	0	0	0	1
1083	0	0	0	0	0	1	0
1090	0	0	0	0	0	0	0
1095	0	0	0	0	0	0	0
1098	0	0	0	0	0	0	0
1100	0	1	0	0	0	0	0
1103	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	1	0
3351	0	0	0	0	0	0	0
V6160	0	0	0	0	0	0	0
V6161	0	0	0	0	0	0	0
RV7043	0	0	1	0	0	0	0
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	1	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	0	0	1	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0
V84104	0	0	0	0	0	0	0
V84105	0	0	0	0	0	0	0
V84106	0	0	0	0	0	0	0

Appendix C (extended)

	Balantiomys	*Barbouromeryx*	*Bassaricyonoides*	*Bassariscus*	*Blastomeryx*
1065	0	0	0	0	1
1083	0	0	0	0	0
1090	0	0	0	0	1
1095	0	0	0	0	0
1098	0	0	0	0	0
1100	0	0	0	0	0
1103	0	0	0	0	0
1104	0	0	0	0	0
1105	0	0	0	0	0
3351	0	0	0	0	0
V6160	0	0	0	0	0
V6161	0	0	0	0	1
RV7043	0	1	1	0	0
RV7317	0	0	0	0	0
RV7319	0	0	0	0	0
RV7322	0	0	0	0	0
RV7324	0	0	0	0	0
V65593	0	0	0	0	0
RV68136	0	0	0	0	0
V69114	0	0	0	0	0
V73056	0	0	0	0	0
V78080	0	0	0	0	0
V84100	0	0	0	0	0
V84101	0	0	0	0	0
V84102	0	0	0	0	0
V84103	0	0	0	0	0
V84104	0	0	0	0	0
V84105	0	0	0	0	0
V84106	0	0	0	0	0

Appendix C (extended)

	Bouromeryx	*Brachypsalis*	Camelidae	Canidae	*Canis*	*Castor*	Castoridae	*Chalicomys*
1065	0	0	0	0	0	0	0	0
1083	0	0	0	0	0	0	0	0
1090	0	0	0	0	0	0	0	0
1095	0	0	0	0	0	0	0	0
1098	0	0	0	0	0	0	0	0
1100	0	0	0	0	1	0	0	0
1103	0	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0	0
V6160	0	0	0	0	0	0	0	0
V6161	0	0	0	0	0	0	0	0
RV7043	1	0	0	0	0	0	1	0
RV7317	1	0	0	0	0	0	0	0
RV7319	0	0	0	1	0	0	0	0
RV7322	0	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0	0
V84104	0	0	0	0	0	0	0	0
V84105	0	0	0	0	0	0	0	0
V84106	0	0	0	1	0	0	0	0

Appendix C (extended)

	Chalicotheriidae	*Copemys*	*Cosoryx*	*Cranioceras*	Cricetidae	*Cupidinimus*	*Cynorca*	*Desmathyus*
1065	0	0	0	0	0	0	0	0
1083	0	0	0	0	0	0	0	0
1090	0	0	0	0	0	0	0	0
1095	0	0	0	0	0	0	0	0
1098	0	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0	0
1103	0	0	0	0	0	1	0	0
1104	0	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0	0
V6160	0	0	0	1	0	0	0	0
V6161	0	0	0	1	0	0	0	1
RV7043	0	0	1	0	0	0	1	1
RV7317	0	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0	1
RV7324	0	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0	0
V69114	0	0	0	0	1	0	0	0
V73056	0	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0	0
V84104	0	0	0	0	1	0	0	0
V84105	0	0	0	0	0	0	0	0
V84106	0	0	0	0	0	0	0	0

Appendix C (extended)

	Diceratherium	*Didelphis*	*Dinohippus*	*Dipoides*	*Diprionomys*	*Domnina*
1065	0	0	0	0	0	0
1083	0	0	0	0	0	0
1090	0	0	0	0	0	0
1095	0	0	0	0	0	0
1098	0	0	0	0	0	0
1100	0	0	0	0	0	0
1103	0	0	0	1	1	0
1104	0	0	0	0	0	0
1105	0	0	0	0	0	0
3351	0	0	0	0	0	0
V6160	0	0	0	0	0	0
V6161	1	0	0	0	0	0
RV7043	0	0	0	0	0	0
RV7317	0	0	0	0	0	0
RV7319	0	0	0	0	0	0
RV7322	0	0	0	0	0	0
RV7324	0	0	0	0	0	0
V65593	0	0	0	0	0	0
RV68136	0	0	0	0	0	0
V69114	0	0	0	0	1	0
V73056	0	0	0	0	0	0
V78080	0	0	0	0	1	0
V84100	0	0	0	0	0	0
V84101	0	0	0	0	0	0
V84102	0	0	0	0	0	0
V84103	0	0	0	0	0	0
V84104	0	0	0	0	0	0
V84105	0	0	0	0	0	0
V84106	0	0	0	0	0	0

Appendix C (extended)

	Domninoides	*Dromomeryx*	Eomyidae	*Epicyon*	Equidae	Erinaceidae	*Eucastor*	*Eucyon*
1065	0	1	0	0	1	0	0	0
1083	0	0	0	0	0	0	0	0
1090	0	1	0	0	0	0	0	0
1095	0	1	0	0	0	0	0	0
1098	0	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0	0
1103	0	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0	0
3351	0	1	0	0	1	0	0	0
V6160	0	0	0	0	0	0	0	0
V6161	0	1	0	0	1	0	0	0
RV7043	0	1	0	0	1	0	0	0
RV7317	0	0	0	0	0	0	0	0
RV7319	0	0	0	0	1	0	0	0
RV7322	0	0	0	0	0	0	0	0
RV7324	0	0	0	0	1	0	0	0
V65593	0	0	0	0	0	0	0	0
RV68136	0	1	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0	0
V84100	0	0	0	0	1	0	0	0
V84101	0	0	0	0	1	0	0	0
V84102	0	0	0	0	0	0	0	0
V84103	0	0	0	0	1	1	0	0
V84104	0	0	0	0	0	1	0	0
V84105	0	0	0	0	1	1	0	0
V84106	0	0	0	0	1	0	0	0

Appendix C (extended)

	Euoplocyon	*Eutamias*	Felidae	Gomphotheriidae	*Goniodontomys*	*Hemicyon*	*Hesperhys*
1065	0	0	0	0	0	0	0
1083	0	0	0	0	0	0	0
1090	0	0	0	0	0	0	0
1095	0	0	0	0	0	0	0
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0
1103	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0
V6160	0	0	0	0	0	0	0
V6161	0	0	0	0	0	0	0
RV7043	0	0	0	0	0	0	1
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	1	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0
V84104	0	0	0	0	0	0	0
V84105	0	0	0	0	0	0	0
V84106	0	0	0	0	0	0	0

Appendix C (extended)

	Hesperolagomys	*Hesperosorex*	Heteromyidae	*Heterosorex*	*Hypohippus*	*Hypolagus*	*Hystricops*
1065	0	0	0	0	1	1	0
1083	0	0	0	0	0	0	0
1090	0	0	0	0	1	0	0
1095	0	0	0	0	1	0	0
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	1	0
1103	0	0	0	0	0	1	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	1	0	0
V6160	0	0	0	0	1	0	0
V6161	0	0	0	0	1	0	0
RV7043	0	0	0	0	0	0	0
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	1	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	0	1	0
V73056	0	0	0	1	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	0	1	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	1	0	0	0	0
V84104	0	0	1	0	0	0	0
V84105	0	0	1	0	0	1	0
V84106	0	0	1	0	0	0	0

Appendix C (extended)

	Ilingoceros	*Indarctos*	*Ingentisorex*	*Lantanotherium*	Leporidae	*Leptodontomys*
1065	0	0	0	0	0	0
1083	0	0	0	0	0	0
1090	0	0	0	0	0	0
1095	0	0	0	0	0	0
1098	0	0	0	0	0	0
1100	1	0	0	0	0	0
1103	0	0	0	0	0	0
1104	0	0	0	0	0	0
1105	0	0	0	0	0	0
3351	0	0	0	0	0	0
V6160	0	0	0	0	0	0
V6161	0	0	0	0	0	0
RV7043	0	0	0	0	0	0
RV7317	0	0	0	0	0	0
RV7319	0	0	0	0	0	0
RV7322	0	0	0	0	0	0
RV7324	0	0	0	0	0	0
V65593	0	0	0	0	0	0
RV68136	0	0	0	0	0	0
V69114	0	0	0	0	0	0
V73056	0	0	0	0	0	0
V78080	0	0	0	0	0	0
V84100	0	0	0	0	0	0
V84101	0	0	0	0	0	0
V84102	0	0	0	0	0	0
V84103	0	0	0	0	0	0
V84104	0	0	0	0	1	0
V84105	0	0	0	0	0	0
V84106	0	0	0	0	1	0

Appendix C (extended)

	Limnoecus	*Liodontia*	*Macrognathomys*	*Mammut*	Mammutidae	*Marmota*
1065	0	0	0	0	0	0
1083	0	0	0	0	0	0
1090	0	0	0	0	0	0
1095	0	0	0	0	0	0
1098	0	0	0	0	0	0
1100	0	1	0	0	0	0
1103	0	1	0	0	0	0
1104	0	0	0	0	0	0
1105	0	0	0	0	0	1
3351	0	1	0	1	0	0
V6160	0	1	0	0	0	0
V6161	0	1	0	0	0	0
RV7043	0	1	0	0	0	0
RV7317	0	1	0	0	0	0
RV7319	0	0	0	0	0	0
RV7322	0	0	0	0	0	0
RV7324	0	0	0	0	0	0
V65593	0	0	0	0	0	0
RV68136	0	0	0	0	0	0
V69114	0	1	0	0	0	0
V73056	0	0	0	0	0	0
V78080	0	0	0	0	0	0
V84100	0	1	0	0	0	0
V84101	0	1	0	0	0	0
V84102	0	0	0	0	0	0
V84103	0	1	0	0	0	0
V84104	0	1	0	0	0	0
V84105	0	1	0	0	0	0
V84106	0	1	0	0	0	0

Appendix C (extended)

	Martes	Megalonychidae	*Megapeomys*	*Megatylopus*	*Merychippus*	*Merychyus*	*Merycodus*
1065	0	0	0	0	1	0	0
1083	0	0	0	0	0	0	0
1090	0	0	0	0	1	0	1
1095	0	0	0	0	1	1	0
1098	0	0	0	0	1	0	0
1100	0	0	0	0	0	0	0
1103	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	1	0	0
V6160	0	0	0	0	0	0	0
V6161	0	0	0	0	1	0	0
RV7043	0	0	1	0	0	0	0
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	1	0	0
RV68136	0	0	0	0	1	0	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	0	1	0	0
V84104	0	0	0	0	0	0	0
V84105	0	0	0	0	1	0	0
V84106	0	0	0	0	0	0	0

Appendix C (extended)

	Merycoidodontidae	*Metalopex*	*Metatomarctus*	*Meterix*	*Miospermophilus*	*Monosaulax*	*Moropus*
1065	0	0	1	0	0	0	1
1083	0	0	0	0	0	0	0
1090	0	0	0	0	0	1	0
1095	0	0	0	0	0	0	1
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0
1103	0	1	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0
V6160	0	0	0	0	0	0	0
V6161	0	0	0	0	0	0	0
RV7043	0	0	0	0	1	0	0
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	1	0
V78080	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0
V84104	0	0	0	0	0	0	0
V84105	0	0	0	0	0	0	0
V84106	0	0	0	0	0	0	0

Appendix C (extended)

	Mustela	Mustelidae	*Mystipterus*	*Neohipparion*	*Nothodipoides*	*Oreodon*	Oreodontidae
1065	0	0	0	0	0	0	0
1083	0	0	0	0	0	0	0
1090	0	0	0	0	0	0	0
1095	0	0	0	0	0	0	0
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0
1103	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0
V6160	0	1	0	0	0	0	0
V6161	0	1	0	0	0	0	0
RV7043	0	0	0	0	0	0	0
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0
V84104	0	0	0	0	0	0	0
V84105	0	0	0	0	0	0	0
V84106	0	0	0	0	0	0	0

Appendix C (extended)

	Oreolagus	Palaeomerycidae	*Paracosoryx*	*Paracynarctus*	*Paradomnina*	*Parahippus*	*Parapliohippus*
1065	0	0	0	1	0	0	0
1083	0	0	0	0	0	0	0
1090	0	1	0	0	0	1	0
1095	0	0	0	0	0	1	0
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0
1103	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0
V6160	0	0	0	0	0	0	0
V6161	0	0	0	1	0	1	0
RV7043	0	0	0	1	0	1	1
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	1	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	1	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	1	0	0	0	0	0	0
V84104	1	0	0	0	0	0	0
V84105	1	0	0	0	0	0	0
V84106	1	0	0	0	0	0	0

Appendix C (extended)

	Paratomarctus	*Perchoerus*	*Peridomys*	*Perognathus*	*Peromyscus*	*Petauristodon*	*Platygonus*
1065	0	0	0	0	0	0	0
1083	0	0	0	0	0	0	0
1090	0	0	0	0	0	0	0
1095	0	1	0	0	0	0	0
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0
1103	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0
V6160	0	0	0	0	0	0	0
V6161	0	0	0	0	0	0	0
RV7043	0	0	0	0	0	0	0
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	1	0	0
V84100	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0
V84104	0	0	0	0	0	0	0
V84105	0	0	0	0	0	0	0
V84106	0	0	0	0	0	0	0

Appendix C (extended)

	Plesiadjidaumo	*Plesiosminthus*	*Plesiosorex*	*Pliocyon*	*Pliogale*	*Pliohippus*	*Pliotaxidea*
1065	0	0	0	0	0	0	0
1083	0	0	0	0	0	0	0
1090	0	0	0	0	0	0	0
1095	0	0	0	0	0	0	0
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	1	0
1103	0	0	0	0	1	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0
V6160	0	0	0	0	0	0	0
V6161	0	0	0	0	0	0	0
RV7043	0	0	0	0	0	0	0
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0
V84104	0	0	0	0	0	0	0
V84105	0	0	0	0	0	0	0
V84106	0	0	0	0	0	0	0

Appendix C (extended)

	Probassariscus	*Procamelus*	*Prodipodomys*	*Prosthennops*	*Protohippus*	*Protospermophilus*	*Pseudaelurus*
1065	0	0	0	0	0	0	0
1083	0	0	0	0	0	0	0
1090	0	0	0	0	0	0	0
1095	1	0	0	0	0	0	0
1098	0	0	0	1	0	0	0
1100	0	0	0	0	0	0	0
1103	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	1	0	1	0	0
3351	0	0	0	0	0	0	0
V6160	0	0	0	0	0	0	0
V6161	0	0	0	0	0	1	0
RV7043	0	0	0	0	0	1	0
RV7317	0	0	0	0	0	1	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0
V84104	0	0	0	0	0	1	0
V84105	0	0	0	0	0	0	0
V84106	0	0	0	0	0	1	0

Appendix C (extended)

	Pseudotheridomys	*Pseudotrimylus*	*Rakomeryx*	Rhinocerotidae	*Satherium*	*Scalopoides*	*Scapanoscapter*
1065	0	0	0	0	0	0	0
1083	0	0	0	0	0	0	0
1090	0	0	0	1	0	0	0
1095	0	0	0	0	0	0	0
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0
1103	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	1	0	0	0
V6160	0	0	0	0	0	0	0
V6161	0	0	0	1	0	0	0
RV7043	1	0	0	1	0	0	0
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	1	0	0	0
V84104	0	0	0	0	0	0	0
V84105	0	0	0	1	0	0	0
V84106	0	0	0	0	0	0	0

Appendix C (extended)

	Scapanus	Sciuridae	*Sciurus*	Soricidae	*Spermophilus*	*Sphenophalos*	*Sthenictis*
1065	0	0	0	0	0	0	0
1083	0	0	0	0	0	0	0
1090	0	0	0	0	0	0	0
1095	0	0	0	0	0	0	0
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	1	0
1103	0	0	0	0	0	1	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0
V6160	0	0	0	0	1	0	0
V6161	0	0	0	0	1	0	0
RV7043	0	0	0	0	0	0	0
RV7317	0	0	0	0	0	0	0
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	1	1	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	1	0	1	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	1	0	0	0	0	0
V84103	0	1	0	0	0	0	0
V84104	0	1	0	1	0	0	0
V84105	0	1	0	0	0	0	0
V84106	0	1	0	0	0	0	0

Appendix C (extended)

	Talpidae	Tapiridae	*Tardontia*	Tayassuidae	*Teleoceras*	*Tephrocyon*	*Ticholeptus*
1065	0	0	0	0	0	0	1
1083	0	0	0	0	0	0	0
1090	0	0	0	0	0	1	1
1095	0	0	0	0	0	0	0
1098	0	0	0	0	0	0	0
1100	0	0	0	0	0	0	0
1103	0	0	0	0	0	0	0
1104	0	0	0	0	0	0	0
1105	0	0	0	0	0	0	0
3351	0	0	0	0	0	0	0
V6160	0	0	0	0	0	0	1
V6161	0	0	0	0	0	0	1
RV7043	0	0	0	0	0	0	1
RV7317	0	0	0	0	0	0	1
RV7319	0	0	0	0	0	0	0
RV7322	0	0	0	0	0	0	0
RV7324	0	0	0	0	0	0	0
V65593	0	0	0	0	0	0	0
RV68136	0	0	0	0	0	0	0
V69114	0	0	0	0	0	0	0
V73056	0	0	0	0	0	0	0
V78080	0	0	0	0	0	0	0
V84100	0	0	0	0	0	0	0
V84101	0	0	0	0	0	0	0
V84102	0	0	0	0	0	0	0
V84103	0	0	0	0	0	0	0
V84104	1	0	0	0	0	0	0
V84105	0	0	0	0	0	0	0
V84106	0	0	0	0	0	0	0

Appendix C (extended)

	Tomarctus	*Trimylus*	*Ursavus*	Ursidae	*Vulpes*	Zapodidae
1065	0	0	0	0	0	0
1083	0	0	0	0	0	0
1090	0	0	0	0	0	0
1095	0	0	0	0	0	0
1098	0	0	0	0	0	0
1100	0	0	0	0	0	0
1103	0	0	0	0	0	0
1104	0	0	0	0	0	0
1105	0	0	0	0	0	0
3351	0	0	0	0	1	0
V6160	0	0	0	0	0	0
V6161	1	0	0	0	0	0
RV7043	1	0	1	0	0	0
RV7317	0	0	0	0	0	0
RV7319	0	0	0	0	0	0
RV7322	0	0	0	0	0	0
RV7324	0	0	0	0	0	0
V65593	0	0	0	0	0	0
RV68136	0	0	0	0	0	0
V69114	0	0	0	0	0	0
V73056	0	0	0	0	0	0
V78080	0	0	0	0	0	0
V84100	0	0	0	0	0	0
V84101	0	0	0	0	0	0
V84102	0	0	0	0	0	0
V84103	0	0	0	0	0	0
V84104	0	0	0	0	0	0
V84105	0	1	0	0	0	0
V84106	0	0	0	0	0	0

Appendix C (continued)

	Achlyoscapter	*Acritohippus*	*Adjidaumo*	*Aelurodon*	*Alluvisorex*	*Amebelodon*
V85100	0	0	0	0	0	0
V85105	0	0	0	0	0	0
V86028	0	0	0	0	0	0
V90052	0	0	0	0	0	0
LACM44	0	0	0	0	0	0
CIT57	0	0	0	0	0	0
CIT62	0	0	0	0	0	0
CIT371	0	0	0	0	0	0
2500	0	0	0	0	0	0
2239	0	0	0	0	0	0
2334	0	0	0	0	0	0
2335	0	0	0	0	0	0
2337	0	0	0	0	0	0
2516	0	0	0	0	0	0
2465	1	0	1	1	1	0
2495	1	1	0	0	1	0
2338	0	0	0	0	0	0
2339	0	0	0	0	0	0
2340	0	0	0	0	0	0
2341	0	0	0	0	0	0
2343	0	0	0	1	0	0
2344	0	0	0	1	0	0
2347	0	0	0	0	0	0
2356	0	0	0	0	0	0
2357	0	0	0	0	0	1
2358	0	0	0	0	0	0
2417	0	0	0	0	0	0
2418	0	0	0	0	0	0
2469	0	0	0	0	0	0

Appendix C (extended)

	Ammospermophilus	*Amphicyon*	Amphicyonidae	*Anchitherium*	*Anouroneomys*
V85100	0	0	0	0	0
V85105	0	0	0	0	0
V86028	0	0	0	0	0
V90052	0	0	0	0	0
LACM44	0	0	0	0	0
CIT57	0	1	0	0	0
CIT62	0	0	0	0	0
CIT371	0	1	0	0	0
2500	1	0	0	0	1
2239	0	0	0	0	0
2334	1	0	0	0	0
2335	0	0	0	0	0
2337	0	0	0	0	1
2516	1	0	0	0	0
2465	0	0	0	0	0
2495	0	1	0	0	0
2338	1	0	0	0	0
2339	0	0	0	0	0
2340	0	0	0	0	0
2341	1	0	0	0	0
2343	0	0	0	0	0
2344	0	0	0	0	0
2347	0	0	0	0	0
2356	0	0	0	0	0
2357	0	0	0	0	0
2358	0	0	0	0	0
2417	0	0	0	0	0
2418	0	0	0	0	0
2469	0	0	0	0	0

Appendix C (extended)

	Antecalomys	Antilocapridae	*Aphelops*	Aplodontidae	*Archaeohippus*	*Arctomys*	*Acritohippus*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0
V90052	0	1	0	0	0	0	0
LACM44	0	0	0	0	0	0	0
CIT57	0	0	0	0	0	0	0
CIT62	0	0	0	0	0	0	0
CIT371	0	0	1	0	1	0	0
2500	0	0	0	0	0	0	0
2239	0	0	0	1	0	0	0
2334	0	1	0	0	0	0	0
2335	0	0	0	0	0	0	0
2337	0	0	0	0	0	0	0
2516	1	0	0	0	0	0	0
2465	0	0	1	0	0	0	0
2495	0	0	1	0	0	0	0
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0
2343	0	1	0	0	0	0	0
2344	0	0	0	0	0	0	0
2347	0	0	0	0	0	0	0
2356	0	1	0	1	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	1	0	0	0
2469	0	0	0	0	0	0	0

Appendix C (extended)

	Balantiomys	*Barbouromeryx*	*Bassaricyonoides*	*Bassariscus*	*Blastomeryx*
V85100	0	0	0	0	0
V85105	0	0	0	0	0
V86028	0	0	0	0	0
V90052	0	0	0	0	0
LACM44	0	0	0	0	0
CIT57	0	0	0	0	1
CIT62	0	0	0	0	0
CIT371	0	0	0	0	0
2500	0	0	0	0	0
2239	0	0	0	0	0
2334	0	0	0	0	0
2335	0	0	0	0	0
2337	0	0	0	0	0
2516	0	0	0	0	0
2465	1	0	0	1	0
2495	1	0	0	0	0
2338	0	0	0	0	0
2339	0	0	0	0	0
2340	0	0	0	0	0
2341	0	0	0	0	0
2343	0	0	0	0	0
2344	0	0	0	0	0
2347	0	0	0	0	0
2356	0	0	0	0	0
2357	0	0	0	0	0
2358	0	0	0	0	0
2417	0	0	0	0	0
2418	0	0	0	0	0
2469	0	0	0	0	0

Appendix C (extended)

	Bouromeryx	*Brachypsalis*	Camelidae	Canidae	*Canis*	*Castor*	Castoridae	*Chalicomys*
V85100	0	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0	0
V90052	0	0	1	0	0	0	0	0
LACM44	0	0	1	1	0	0	0	1
CIT57	0	0	0	1	0	0	0	0
CIT62	0	0	1	1	0	1	0	0
CIT371	0	0	0	1	0	0	0	0
2500	0	0	0	0	0	0	0	0
2239	0	0	0	0	0	0	0	0
2334	0	0	0	1	0	0	0	0
2335	0	0	1	0	0	0	0	0
2337	0	0	0	0	0	0	1	0
2516	0	0	0	0	0	0	0	0
2465	0	1	0	1	0	0	0	0
2495	0	1	1	1	0	0	0	0
2338	0	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0	0
2343	0	0	1	0	0	0	0	0
2344	0	0	1	0	0	0	0	0
2347	0	0	0	0	0	0	0	0
2356	0	0	1	0	0	0	0	0
2357	0	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	1	0
2417	0	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0	0

Appendix C (extended)

	Chalicotheriidae	*Copemys*	*Cosoryx*	*Cranioceras*	Cricetidae	*Cupidinimus*	*Cynorca*	*Desmathyus*
V85100	0	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0	0
V90052	0	0	0	0	0	0	0	0
LACM44	0	0	0	0	0	0	0	0
CIT57	1	0	0	0	0	0	0	0
CIT62	0	0	0	0	0	0	0	0
CIT371	0	0	0	0	0	0	0	0
2500	0	1	0	0	1	0	0	0
2239	0	0	0	0	1	0	0	0
2334	0	0	0	0	0	0	0	0
2335	0	0	0	0	0	0	0	0
2337	0	1	0	0	0	0	0	0
2516	0	1	0	0	0	0	0	0
2465	0	1	0	0	0	0	0	0
2495	0	1	0	0	1	0	0	0
2338	0	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0	0
2343	0	0	0	0	0	0	0	0
2344	0	0	0	0	0	0	0	0
2347	0	0	0	0	0	0	0	0
2356	0	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0	0

Appendix C (extended)

	Diceratherium	*Didelphis*	*Dinohippus*	*Dipoides*	*Diprionomys*	*Domnina*
V85100	0	0	0	0	0	0
V85105	0	0	0	0	0	0
V86028	0	0	0	0	0	0
V90052	0	0	0	0	0	0
LACM44	0	0	0	0	0	0
CIT57	0	0	0	0	0	0
CIT62	0	0	0	1	0	0
CIT371	0	0	0	0	0	0
2500	0	0	0	0	1	0
2239	0	0	0	0	1	0
2334	0	0	0	0	0	0
2335	0	0	0	0	0	0
2337	0	0	0	0	0	0
2516	0	0	0	1	1	0
2465	0	1	0	0	0	0
2495	0	0	0	0	0	1
2338	0	0	0	0	0	0
2339	0	0	0	0	0	0
2340	0	0	0	0	0	0
2341	0	0	0	0	0	0
2343	0	0	0	0	0	0
2344	0	0	0	0	0	0
2347	0	0	1	0	0	0
2356	0	0	0	1	0	0
2357	0	0	0	0	0	0
2358	0	0	0	1	0	0
2417	0	0	0	0	0	0
2418	0	0	0	0	0	0
2469	0	0	1	1	0	0

Appendix C (extended)

	Domninoides	*Dromomeryx*	Eomyidae	*Epicyon*	Equidae	Erinaceidae	*Eucastor*	*Eucyon*
V85100	0	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0	0
V86028	0	0	0	0	1	0	0	0
V90052	0	0	0	0	1	0	0	0
LACM44	0	1	0	0	1	0	0	0
CIT57	0	1	0	0	1	0	0	0
CIT62	0	0	0	1	0	0	0	0
CIT371	0	1	0	0	1	1	0	0
2500	0	0	0	0	0	0	0	0
2239	0	0	1	0	0	0	0	0
2334	0	0	0	0	1	0	1	0
2335	0	0	0	0	1	0	0	0
2337	0	0	0	0	1	0	1	0
2516	0	0	0	0	0	0	0	1
2465	1	0	0	0	0	0	0	0
2495	0	1	0	0	0	0	0	0
2338	0	0	0	0	1	0	0	0
2339	0	0	0	0	0	0	0	0
2340	0	0	0	0	1	0	0	0
2341	0	0	0	0	1	0	1	0
2343	0	0	0	0	1	0	0	0
2344	0	0	0	0	1	0	1	0
2347	0	0	0	0	0	0	0	0
2356	0	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0	0
2358	0	0	0	0	1	0	0	0
2417	0	0	0	0	1	0	0	0
2418	0	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0	1

Appendix C (extended)

	Euoplocyon	*Eutamias*	Felidae	Gomphotheriidae	*Goniodontomys*	*Hemicyon*	*Hesperhys*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0
V90052	0	0	0	0	0	0	0
LACM44	0	0	0	0	0	0	0
CIT57	1	0	0	1	0	1	0
CIT62	0	0	0	1	1	0	0
CIT371	0	0	0	0	0	0	0
2500	0	1	0	0	1	0	0
2239	0	1	0	0	1	0	0
2334	0	0	0	0	0	0	0
2335	0	0	0	0	0	0	0
2337	0	0	0	0	0	0	0
2516	0	0	0	0	0	0	0
2465	0	0	0	0	0	0	0
2495	0	1	0	0	0	0	0
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	1	0	0	0
2341	0	0	0	0	0	0	0
2343	0	0	1	0	0	0	0
2344	0	0	0	0	0	0	0
2347	0	0	0	0	0	0	0
2356	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	1	0	0	0	0

Appendix C (extended)

	Hesperolagomys	*Hesperosorex*	Heteromyidae	*Heterosorex*	*Hypohippus*	*Hypolagus*	*Hystricops*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0
V90052	0	0	0	0	0	0	0
LACM44	0	0	0	0	1	0	0
CIT57	0	0	0	0	1	1	0
CIT62	0	0	0	0	0	1	0
CIT371	0	0	0	0	1	0	0
2500	1	1	1	0	0	1	0
2239	0	0	1	0	0	1	1
2334	0	0	0	0	0	1	0
2335	0	0	0	0	0	0	0
2337	1	1	1	0	0	1	0
2516	0	0	1	0	0	1	0
2465	0	0	1	0	0	1	0
2495	0	0	0	1	1	0	0
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	1
2341	0	0	0	0	0	0	0
2343	0	0	0	0	0	0	0
2344	0	0	0	0	0	0	0
2347	0	0	0	0	0	0	0
2356	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	1	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	0	1	0

Appendix C (extended)

	Ilingoceros	*Indarctos*	*Ingentisorex*	*Lantanotherium*	Leporidae	*Leptodontomys*
V85100	0	0	0	0	0	0
V85105	0	0	0	0	0	0
V86028	0	0	0	0	0	0
V90052	0	0	0	0	0	0
LACM44	0	0	0	0	0	0
CIT57	0	0	0	0	0	0
CIT62	0	0	0	0	0	0
CIT371	0	0	0	0	1	0
2500	0	0	0	0	0	1
2239	0	0	0	0	0	1
2334	0	0	0	0	0	0
2335	0	0	0	0	1	0
2337	0	0	0	0	0	0
2516	0	0	0	0	0	0
2465	0	0	1	1	0	0
2495	0	0	0	1	0	0
2338	0	0	0	0	0	0
2339	0	0	0	0	0	0
2340	0	0	0	0	0	0
2341	0	0	0	0	0	0
2343	0	0	0	0	0	0
2344	0	0	0	0	1	0
2347	0	0	0	0	0	0
2356	0	0	0	0	0	0
2357	0	0	0	0	0	0
2358	0	0	0	0	1	0
2417	0	0	0	0	0	0
2418	0	0	0	0	0	0
2469	0	1	0	0	0	0

Appendix C (extended)

	Limnoecus	*Liodontia*	*Macrognathomys*	*Mammut*	Mammutidae	*Marmota*
V85100	0	1	0	0	0	0
V85105	0	1	0	0	0	0
V86028	0	1	0	0	0	0
V90052	0	0	0	0	0	0
LACM44	0	0	0	0	0	0
CIT57	0	1	0	0	0	0
CIT62	0	0	0	0	0	0
CIT371	0	1	0	0	0	0
2500	0	0	1	0	0	0
2239	0	0	1	0	0	0
2334	0	0	0	0	0	0
2335	0	0	0	0	0	0
2337	0	0	0	0	0	0
2516	0	0	0	0	0	0
2465	0	0	1	0	0	0
2495	1	1	0	0	0	0
2338	0	0	0	0	0	0
2339	0	0	0	0	0	0
2340	0	0	0	0	0	0
2341	0	0	0	0	0	0
2343	0	0	0	1	0	0
2344	0	0	0	0	0	0
2347	0	1	0	1	0	0
2356	0	0	0	0	0	0
2357	0	0	0	0	0	0
2358	0	1	0	0	1	0
2417	0	0	0	0	0	0
2418	0	0	0	0	0	0
2469	0	0	0	0	0	0

Appendix C (extended)

	Martes	Megalonychidae	*Megapeomys*	*Megatylopus*	*Merychippus*	*Merychyus*	*Merycodus*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	1	0	0
V86028	0	0	0	0	1	0	0
V90052	0	0	0	0	0	0	0
LACM44	0	0	0	0	1	1	1
CIT57	1	0	0	0	1	0	1
CIT62	0	0	0	0	0	0	0
CIT371	0	0	0	0	1	0	1
2500	0	0	0	0	0	0	0
2239	0	0	0	0	0	0	0
2334	0	0	0	1	0	1	0
2335	0	0	0	0	0	0	0
2337	0	0	0	0	0	0	0
2516	1	0	0	0	0	0	0
2465	0	0	0	0	1	0	1
2495	0	0	0	0	1	0	0
2338	0	0	0	1	0	0	0
2339	0	0	0	1	0	0	0
2340	0	0	0	1	0	1	0
2341	0	0	0	0	0	1	0
2343	0	0	0	1	0	0	0
2344	0	0	0	0	0	0	0
2347	0	1	0	0	0	0	0
2356	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	1	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	1	0	0	0

Appendix C (extended)

	Merycoidodontidae	*Metalopex*	*Metatomarctus*	*Meterix*	*Miospermophilus*	*Monosaulax*	*Moropus*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0
V90052	1	0	0	0	0	0	0
LACM44	0	0	0	0	0	0	1
CIT57	1	0	0	0	0	0	0
CIT62	0	0	0	0	0	0	0
CIT371	0	0	0	0	0	0	0
2500	0	0	0	1	0	0	0
2239	0	0	0	0	0	0	0
2334	0	0	0	0	0	0	0
2335	1	0	0	0	0	0	0
2337	0	0	0	0	0	0	0
2516	0	0	0	0	0	0	0
2465	0	0	0	1	0	1	0
2495	0	0	0	1	0	1	0
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0
2343	0	0	0	0	0	0	0
2344	0	0	0	0	0	0	0
2347	0	0	0	0	0	0	0
2356	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0

Appendix C (extended)

	Mustela	Mustelidae	*Mystipterus*	*Neohipparion*	*Nothodipoides*	*Oreodon*	Oreodontidae
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0
V90052	0	0	0	0	0	0	0
LACM44	0	1	0	0	0	1	0
CIT57	0	0	0	0	0	0	0
CIT62	0	0	0	0	0	0	0
CIT371	0	0	0	0	0	0	0
2500	0	1	1	0	1	0	0
2239	0	0	0	0	0	0	0
2334	0	1	0	0	1	0	0
2335	0	0	0	0	0	0	0
2337	0	0	0	0	1	0	0
2516	0	0	0	0	0	0	0
2465	1	0	1	0	0	0	1
2495	0	0	1	0	0	0	0
2338	0	0	0	1	0	0	0
2339	0	0	0	0	0	0	0
2340	0	1	0	0	0	0	0
2341	0	0	0	0	1	0	0
2343	0	0	0	0	0	0	0
2344	0	0	0	0	1	0	0
2347	0	0	0	0	0	0	0
2356	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0

Appendix C (extended)

	Oreolagus	Palaeomerycidae	*Paracosoryx*	*Paracynarctus*	*Paradomnina*	*Parahippus*	*Parapliohippus*
V85100	0	0	0	0	0	0	0
V85105	1	0	0	0	0	0	0
V86028	1	0	0	0	0	0	0
V90052	0	0	0	0	0	0	0
LACM44	0	0	0	0	0	1	0
CIT57	0	0	0	0	0	1	0
CIT62	0	0	0	0	0	0	0
CIT371	1	0	0	0	0	1	0
2500	0	0	0	0	0	0	0
2239	0	0	0	0	0	0	0
2334	0	0	0	0	0	0	0
2335	0	0	0	0	0	0	0
2337	0	0	0	0	0	0	0
2516	0	0	0	0	0	0	0
2465	0	0	1	0	0	0	0
2495	0	0	1	0	1	0	0
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0
2343	0	0	0	0	0	0	0
2344	0	0	0	0	0	0	0
2347	0	0	0	0	0	0	0
2356	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0

Appendix C (extended)

	Paratomarctus	*Perchoerus*	*Peridomys*	*Perognathus*	*Peromyscus*	*Petauristodon*	*Platygonus*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0
V90052	0	0	0	0	0	0	0
LACM44	0	0	0	0	0	0	0
CIT57	1	0	0	0	0	0	1
CIT62	0	0	0	0	0	0	0
CIT371	0	0	0	0	0	0	0
2500	0	0	0	1	1	0	0
2239	0	0	0	1	1	0	0
2334	0	0	0	0	0	0	0
2335	0	0	0	0	0	0	0
2337	0	0	0	0	1	0	0
2516	0	0	0	1	1	0	0
2465	0	0	1	0	0	0	0
2495	0	0	1	0	1	1	0
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0
2343	0	0	0	0	0	0	0
2344	0	0	0	0	0	0	0
2347	0	0	0	0	0	0	0
2356	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	1	0	0

Appendix C (extended)

	Plesiadjidaumo	*Plesiosminthus*	*Plesiosorex*	*Pliocyon*	*Pliogale*	*Pliohippus*	*Pliotaxidea*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0
V90052	0	0	0	0	0	0	0
LACM44	0	0	0	0	0	0	0
CIT57	0	0	0	1	0	0	0
CIT62	0	0	0	0	1	1	0
CIT371	0	0	0	0	0	0	0
2500	0	0	0	0	0	0	0
2239	0	0	0	0	0	0	1
2334	0	0	0	0	0	0	0
2335	0	0	0	0	0	0	0
2337	0	0	0	0	0	0	0
2516	0	0	0	0	0	0	0
2465	1	1	1	0	0	0	0
2495	0	1	0	0	0	0	0
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0
2343	0	0	0	0	0	0	0
2344	0	0	0	0	0	1	1
2347	0	0	0	0	0	0	0
2356	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0

Appendix C (extended)

	Probassariscus	*Procamelus*	*Prodipodomys*	*Prosthennops*	*Protohippus*	*Protospermophilus*	*Pseudaelurus*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0
V90052	0	0	0	0	0	0	0
LACM44	0	0	0	1	0	0	0
CIT57	0	0	0	0	0	0	0
CIT62	0	0	0	1	0	0	0
CIT371	0	0	0	0	0	1	0
2500	0	0	0	0	0	0	0
2239	0	0	0	0	0	0	0
2334	0	0	0	0	0	0	1
2335	0	0	0	0	0	0	1
2337	0	0	0	1	0	0	0
2516	0	0	0	0	0	0	0
2465	0	0	1	1	0	0	0
2495	0	0	0	0	0	1	1
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	1
2341	0	0	0	0	0	0	0
2343	0	0	0	0	0	0	1
2344	0	0	0	0	0	0	0
2347	0	1	0	0	0	0	0
2356	0	0	0	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0

Appendix C (extended)

	Pseudotheridomys	*Pseudotrimylus*	*Rakomeryx*	Rhinocerotidae	*Satherium*	*Scalopoides*	*Scapanoscapter*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	1	0	0	0
V86028	0	0	0	1	0	0	0
V90052	0	0	0	1	0	0	0
LACM44	0	0	0	1	0	0	0
CIT57	0	0	1	1	0	0	0
CIT62	0	0	0	0	1	0	0
CIT371	0	0	0	1	0	0	0
2500	0	0	0	0	0	1	0
2239	0	0	0	0	0	1	0
2334	0	0	0	0	0	0	0
2335	0	0	0	0	0	0	0
2337	0	0	0	0	0	0	0
2516	0	0	0	0	0	0	0
2465	1	0	0	0	0	1	0
2495	1	0	1	0	0	1	1
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0
2343	0	0	0	0	0	0	0
2344	0	0	0	0	0	0	0
2347	0	0	0	0	0	0	0
2356	0	0	0	1	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0

Appendix C (extended)

	Scapanus	Sciuridae	*Sciurus*	Soricidae	*Spermophilus*	*Sphenophalos*	*Sthenictis*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	1	0	1	0	0	0
V90052	0	1	0	0	0	0	0
LACM44	0	0	0	0	0	0	0
CIT57	0	0	0	0	1	0	0
CIT62	0	0	0	0	0	1	0
CIT371	0	1	1	0	0	0	0
2500	1	0	0	1	1	0	1
2239	1	0	0	1	1	0	0
2334	0	1	0	0	0	0	0
2335	0	0	0	0	0	0	0
2337	1	0	0	0	1	0	0
2516	1	0	0	1	1	0	0
2465	0	0	0	1	1	0	0
2495	0	0	0	0	1	0	0
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0
2343	0	0	0	0	0	0	0
2344	0	0	0	0	0	0	1
2347	1	0	0	0	1	0	0
2356	0	0	0	0	0	1	0
2357	1	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	1	1	0

Appendix C (extended)

	Talpidae	Tapiridae	*Tardontia*	Tayassuidae	*Teleoceras*	*Tephrocyon*	*Ticholeptus*
V85100	0	0	0	0	0	0	0
V85105	0	0	0	0	0	0	0
V86028	0	0	0	0	0	0	0
V90052	0	0	0	0	0	0	0
LACM44	0	0	0	0	0	0	1
CIT57	0	1	0	1	0	0	1
CIT62	0	0	0	0	0	0	0
CIT371	0	0	0	0	0	0	0
2500	1	0	1	0	0	0	0
2239	1	0	1	0	1	0	0
2334	0	1	0	0	0	0	0
2335	0	0	0	0	0	0	0
2337	0	0	0	0	0	0	0
2516	1	0	0	0	0	0	0
2465	1	0	0	1	0	0	0
2495	1	0	0	0	0	1	1
2338	0	0	0	0	0	0	0
2339	0	0	0	0	0	0	0
2340	0	0	0	0	0	0	0
2341	0	0	0	0	0	0	0
2343	0	1	0	0	0	0	0
2344	0	0	0	0	0	0	0
2347	0	0	0	1	1	0	0
2356	0	0	1	0	0	0	0
2357	0	0	0	0	0	0	0
2358	0	0	0	0	0	0	0
2417	0	0	0	0	0	0	0
2418	0	0	0	0	0	0	0
2469	0	0	0	0	0	0	0

Appendix C (extended)

	Tomarctus	*Trimylus*	*Ursavus*	Ursidae	*Vulpes*	Zapodidae
V85100	0	0	0	0	0	0
V85105	0	0	0	0	0	0
V86028	0	0	0	0	0	0
V90052	0	0	0	0	0	0
LACM44	0	0	0	0	0	0
CIT57	0	0	0	0	0	0
CIT62	0	0	0	0	0	0
CIT371	0	0	0	0	0	0
2500	0	0	0	0	0	1
2239	0	0	0	0	0	1
2334	0	0	0	0	0	0
2335	0	0	0	0	0	0
2337	0	0	0	0	1	0
2516	0	0	0	0	0	0
2465	0	0	0	1	0	0
2495	1	1	0	0	0	0
2338	0	0	0	0	0	0
2339	0	0	0	0	0	0
2340	0	0	0	0	0	0
2341	0	0	0	0	0	0
2343	0	0	0	0	0	0
2344	0	0	0	0	0	0
2347	0	0	0	0	0	0
2356	0	0	0	0	0	0
2357	0	0	0	0	0	0
2358	0	0	0	0	0	0
2417	0	0	0	0	0	0
2418	0	0	0	0	0	0
2469	0	0	0	0	0	0

APPENDIX D

MICROWEAR DATA FOR ALL SPECIMENS INCLUDED IN CHAPTER IV

For specimens scored twice, both counts are included.

Abbrevaitions: Ap, all pits; As, all scratches; sp, small puncture pits; lp, large pits; lpp, large puncture pits; spp, small puncture pits; crs, cross scratches; g, gouges; fs, fine scratches; cs, coarse scratches; hs, hypercoarse scratches.

Taxonomic Abbreviation: *S. carol.*, *Sciurus carolinensis.*

Museum Abbreviations: CIT , Los Angeles County Museum, CA; UCMP, University of California Museum of Paleontology, Berkeley, CA; UO-F, University of Oregon Museum of Natural and Cultural history Condon Fossil Collections, Eugene ,OR; UWBM, University of Washington Burke Museum., Seattle, WA.

Taxon	Museum	Number	sp	lp	lpp	spp	Ap	crs	g	fs	cs	hs	As
M. monax	UWBM	39792	36	0	2	3	41	0	0	37	1	1	39
M. monax	UWBM	42167	36	1	3	1	41	1	2	35	2	0	40
M. monax	UWBM	42164	37	3	1	3	44	1	0	36	4	0	41
M. monax	UWBM	42165	41	3	2	3	49	0	0	33	1	0	34
M. monax	UWBM	42166	40	1	1	3	45	0	0	41	2	0	43
M. monax	UWBM	12951	36	0	2	2	40	0	0	29	0	0	29
M. monax	UWBM	42154	38	1	3	5	47	0	0	30	4	1	35
M. monax	UWBM	39792	35	0	3	2	40	2	0	35	2	1	40
M. monax	UWBM	42167	34	1	3	1	39	2	2	31	2	0	37
M. monax	UWBM	42164	39	2	2	4	47	1	0	33	4	0	38
M. monax	UWBM	42165	41	2	2	2	47	0	0	36	0	0	36
M. monax	UWBM	42166	38	1	3	2	44	2	0	39	1	1	43
M. monax	UWBM	12951	35	0	1	2	38	0	0	30	1	0	31
M. monax	UWBM	42154	36	2	2	4	44	2	0	33	2	0	37
H. glaber	UWBM	36428	35	5	0	2	42	0	0	50	9	0	59
H. glaber	UWBM	36443	41	4	1	1	47	0	0	37	10	1	48
H. glaber	UWBM	36460	58	1	4	3	66	2	0	44	6	0	52
H. glaber	UWBM	36464	37	5	3	0	45	0	0	37	8	0	45
H. glaber	UWBM	36427	54	2	4	3	63	4	0	44	5	2	55
H. glaber	UWBM	36466	37	6	0	0	43	0	1	46	5	1	53
H. glaber	UWBM	36461	41	6	1	2	50	0	1	48	1	0	50
H. glaber	UWBM	36435	36	4	2	2	44	1	0	46	4	0	51
H. glaber	UWBM	36465	53	1	1	0	55	0	0	44	6	0	50
H. glaber	UWBM	36434	40	4	5	4	53	0	0	47	3	3	53
H. glaber	UWBM	36462	44	2	2	3	51	0	0	55	5	4	64
H. wilsoni	CIT	1956	32	6	0	2	40	1	2	46	2	0	51
H. species A	UO-F	5771	30	2	1	0	33	0	0	22	2	1	25
H. species A	UO-F	15691	23	6	1	0	30	0	0	26	2	1	29
H. species A	UO-F	5772	26	5	0	0	31	1	0	33	2	1	37
H. species A	UO-F	5443	27	3	2	2	34	4	0	29	3	0	36
H. species A	UO-F	5425	35	1	0	0	36	4	0	31	0	1	36
H. species A	UO-F	17508	28	1	3	2	34	5	0	39	0	0	44
H. species A	UO-F	10977	36	0	2	2	40	2	0	36	0	0	38
H. species A	UO-F	6115	29	0	0	0	29	0	0	45	4	0	49
H. gazini	CIT	527	33	2	1	6	42	1	0	33	5	1	40

Appendix D (continued)

Taxon	Museum	Number	sp	lp	lpp	spp	Ap	crs	g	fs	cs	hs	As
H. gazini	CIT	525	45	0	3	3	51	3	0	31	1	1	36
H. gazini	CIT	528	30	1	0	0	31	1	0	38	1	1	41
H. gazini	CIT	70	31	0	0	4	35	1	0	34	4	0	39
H. gazini	CIT	517	35	2	0	3	40	3	0	33	1	0	37
H. gazini	LACM	4987	36	3	2	2	43	0	0	33	2	0	35
H. gazini	UCMP	130331	29	6	2	0	37	10	0	25	1	1	37
E. dorsatum	UO-R	8662	36	1	0	0	37	0	0	32	3	0	35
E. dorsatum	UO-R	9251	27	2	1	3	33	0	0	29	2	1	32
E. dorsatum	UO-R	8519	34	1	1	0	36	4	0	27	2	0	33
E. dorsatum	UO-R	8513	25	0	1	3	29	0	0	29	5	0	34
E. dorsatum	UO-R	8408	24	2	4	3	33	0	0	23	6	3	32
E. dorsatum	UO-R	8511	33	0	0	2	35	1	0	26	4	0	31
E. dorsatum	UO-R	4023	25	3	1	0	29	0	0	28	3	2	33
E. dorsatum	UO-R	1998	22	2	0	0	24	0	0	33	2	0	35
E. dorsatum	UO-R	8662	38	0	0	1	39	1	0	29	3	1	34
E. dorsatum	UO-R	9251	30	1	2	2	35	0	0	30	2	1	33
E. dorsatum	UO-R	8519	33	1	1	1	36	6	0	25	1	1	33
E. dorsatum	UO-R	8513	28	2	2	3	35	2	0	28	3	0	33
E. dorsatum	UO-R	8408	28	3	0	2	33	1	0	24	3	0	28
E. dorsatum	UO-R	8511	32	1	0	0	33	0	0	23	4	1	28
E. dorsatum	UO-R	4023	26	1	0	1	28	4	0	30	0	1	35
E. dorsatum	UO-R	1998	26	1	1	0	28	1	0	33	3	3	40
D. ingens	UWBM	46911	48	4	6	10	68	2	0	30	3	0	35
D. ingens	UWBM	46921	38	5	4	1	48	0	0	26	2	0	28
D. ingens	UWBM	46902	47	3	4	1	55	0	0	29	2	1	32
D. ingens	UWBM	46912	47	3	7	4	61	0	0	36	0	0	36
D. ingens	UWBM	46914	53	5	4	3	65	0	0	27	2	3	32
D. ingens	UWBM	46901	42	3	5	5	55	0	0	38	2	1	41
D. ingens	UWBM	46920	46	5	2	2	55	0	0	25	5	1	31
D. ingens	UWBM	46925	45	5	4	6	60	2	1	36	1	2	42
D. ingens	UWBM	46910	54	6	6	5	71	1	0	37	3	1	42
A. rufa	UWBM	35998	35	1	2	3	41	0	0	23	6	0	29
A. rufa	UWBM	35966	28	3	2	3	36	0	0	25	2	0	27

Appendix D (continued)

Taxon	Museum	Number	sp	lp	lpp	spp	Ap	crs	g	fs	cs	hs	As
A. rufa	UWBM	9643	33	6	0	0	39	0	0	28	3	0	31
A. rufa	UWBM	31867	49	2	2	0	53	1	0	34	2	2	39
A. rufa	UWBM	9638	36	8	0	1	45	0	0	26	4	1	31
A. rufa	UWBM	79564	39	1	2	1	43	0	0	23	1	0	24
A. rufa	UWBM	20207	39	2	0	1	42	0	0	35	2	1	38
A. rufa	UWBM	34065	38	1	0	1	40	0	0	30	1	0	31
A. rufa	UWBM	42317	40	1	2	2	45	0	0	34	2	0	36
A. rufa	UWBM	9571	41	4	0	0	45	2	0	28	2	1	33
A. rufa	UWBM	35998	32	2	1	2	37	0	0	25	5	1	31
A. rufa	UWBM	35966	26	0	2	3	31	1	0	24	1	0	26
A. rufa	UWBM	9643	34	2	3	1	40	0	0	31	2	0	33
A. rufa	UWBM	31867	47	2	2	2	53	0	0	36	1	2	39
A. rufa	UWBM	9638	37	4	2	5	48	0	0	29	4	1	34
A. rufa	UWBM	79564	38	0	2	2	42	0	0	26	0	0	26
A. rufa	UWBM	20207	39	2	0	2	43	0	0	40	2	3	45
A. rufa	UWBM	34065	41	1	0	2	44	1	0	30	2	2	35
A. rufa	UWBM	42317	40	1	2	2	45	1	0	32	0	0	33
A. rufa	UWBM	9571	38	2	0	5	45	1	0	28	6	2	37
A. vetus	UCMP	315685	42	2	1	0	45	1	0	31	1	0	33
A. vetus	UCMP	130246	28	4	5	1	38	2	0	26	1	1	30
A. vetus	UCMP	130239	37	3	3	1	44	2	0	25	3	0	30
A. vetus	UCMP	130240	36	0	1	2	39	4	0	32	1	2	39
A. vetus	UCMP	319237	33	0	2	2	37	4	0	30	2	2	38
T. talpoides	UWBM	38493	56	4	0	0	60	0	0	65	4	0	69
T. talpoides	UWBM	45118	75	4	1	0	80	5	0	61	5	0	71
T. talpoides	UWBM	36483	56	3	4	1	64	1	0	60	4	0	65
T. talpoides	UWBM	52514	63	2	1	1	67	0	0	63	1	0	64
T. talpoides	UWBM	58264	64	6	0	2	72	0	0	61	2	0	63
T. talpoides	UWBM	44956	60	4	3	1	68	3	1	55	2	0	61
T. bottae	UWBM	44627	34	14	3	0	51	4	2	56	14	0	76
T. bottae	UWBM	44802	67	0	2	0	69	1	0	39	5	0	45
T. bottae	UWBM	44628	39	3	1	2	45	0	0	57	1	1	59
T. bottae	UWBM	44697	64	1	0	5	70	0	0	48	5	0	53

Appendix D (continued)

Taxon	Museum	Number	sp	lp	lpp	spp	Ap	crs	g	fs	cs	hs	As
T. bottae	UWBM	44644	44	0	3	1	48	1	0	59	1	3	64
T. bottae	UWBM	44698	61	0	2	4	67	3	1	37	2	2	45
T. bottae	UWBM	44643	62	5	0	1	68	0	2	41	1	1	45
T. striatus	UWBM	43395	43	1	1	0	45	3	0	34	0	0	37
T. striatus	UWBM	43390	41	2	1	2	46	3	0	31	2	2	38
T. striatus	UWBM	60304	35	4	1	0	40	0	0	46	3	2	51
T. striatus	UWBM	43411	35	3	1	0	39	0	0	33	2	1	36
T. striatus	UWBM	43404	40	4	1	3	48	0	0	34	3	0	37
T. striatus	UWBM	60305	38	3	1	3	45	0	0	34	1	1	36
T. striatus	UWBM	43391	27	3	4	2	36	0	0	36	4	1	41
T. senex	UWBM	43339	25	5	2	2	34	1	0	45	4	0	50
T. senex	UWBM	43357	35	2	2	0	39	2	0	45	1	0	48
T. senex	UWBM	43354	35	2	3	3	43	0	0	42	0	0	42
T. senex	UWBM	43355	40	0	3	4	47	0	0	43	1	0	44
T. senex	UWBM	43342	35	5	1	1	42	2	0	41	1	1	45
T. senex	UWBM	80625	40	3	2	0	45	0	0	46	1	2	49
S. griseus	UWBM	52456	25	2	4	3	34	0	0	43	3	1	47
S. griseus	UWBM	75741	37	2	3	3	45	1	0	40	2	1	44
S. griseus	UWBM	76898	26	3	1	0	30	0	0	46	0	1	47
S. griseus	UWBM	76909	32	1	3	3	39	3	0	39	1	0	43
S. griseus	UWBM	74094	28	3	1	0	32	1	0	40	1	0	42
S. griseus	UWBM	74093	35	1	0	0	36	0	0	47	2	1	50
S. griseus	UWBM	73385	33	3	1	0	37	1	0	40	0	1	42
S. griseus	UWBM	42266	33	2	3	4	42	3	0	41	0	1	45
S. carol.	UWBM	43900	45	1	1	1	48	0	0	40	1	2	43
S. carol.	UWBM	42256	37	4	1	0	42	0	0	35	3	1	39
S. carol.	UWBM	80912	28	0	4	0	32	2	0	30	5	1	38
S. carol.	UWBM	43899	32	3	1	0	36	0	0	43	4	2	49
S. carol.	UWBM	42245	32	4	1	0	37	1	0	28	4	2	35
S. carol.	UWBM	42229	48	2	3	2	55	0	0	42	0	1	43
S. carol.	UWBM	42232	40	6	0	2	48	0	0	32	1	0	33
S. carol.	UWBM	39505	33	7	1	4	45	0	0	35	1	0	36
S. carol.	UWBM	39796	33	3	1	2	39	2	0	33	1	1	37

Appendix D (continued)

Taxon	**Museum**	**Number**	**sp**	**lp**	**lpp**	**spp**	**Ap**	**crs**	**g**	**fs**	**cs**	**hs**	**As**
S. carol.	UWBM	42234	34	4	0	0	38	2	0	37	3	1	43
S. carol.	UWBM	43900	42	1	0	3	46	0	0	41	1	1	43
S. carol.	UWBM	42256	32	2	1	2	37	0	0	36	2	2	40
S. carol.	UWBM	80912	28	0	1	4	33	0	0	30	5	1	36
S. carol.	UWBM	43899	38	1	0	0	39	2	0	43	2	0	47
S. carol.	UWBM	42245	34	4	0	1	39	0	0	24	3	0	27
S. carol.	UWBM	42229	43	1	1	4	49	0	0	41	1	1	43
S. carol.	UWBM	42232	40	3	0	2	45	0	0	32	2	0	34
S. carol.	UWBM	39505	36	4	1	1	42	0	0	38	1	0	39
S. carol.	UWBM	39796	34	1	4	0	39	4	0	27	1	1	33
S. carol.	UWBM	42234	36	1	2	3	42	0	0	40	3	0	43
P. magnus	UO-F	26067	62	6	8	4	80	2	0	70	2	0	74
P. magnus	UO-F	26068	70	2	0	0	72	6	0	68	0	2	76
P. magnus	UO-F	26062	70	2	6	4	82	6	0	56	2	2	66

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