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The rise of modern mammalian faunas:
tempo and mode of faunal turnover in western Montana during the Oligocene.

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Abstract

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The ongoing biodiversity crisis affects almost one in four mammal species. The main threat affecting them is the loss of their habitat with changes in their environment. Paleontological data allow an exploration of the patterns and processes that regulate such faunal turnovers linked to environmental change. I use the fossil record of the Arikareean (ca. 30 to 25.5 Ma), which records a major environmental change concurrent with the rise of many mammalian taxa, to shed light on the link between environmental change, ecological filtering by habitat, and taxonomic turnover over evolutionary timescales. I focus my work on the Cabbage Patch beds of western Montana, an area geographically intermediate between the well-studied John Day Formation of Oregon and Arikaree Group of the Great Plains. My detailed study of the preservation and depositional environments of the mammalian fossils from the Cabbage Patch beds demonstrates that many of the well sampled vertebrate microfossil assemblages from the beds can be considered isotaphonomic for the purpose of comparing biodiversity through time. Geometric morphometric analyses of the upper third molars and lower fourth premolars of entoptychine gophers, a very abundant group of mammals through the beds, demonstrate that even worn and isolated cheek-teeth can be used to identify these rodents to the genus, or even the species-level. These results, along with a detailed analysis of the taxonomic affinities of almost 1,000 specimens of fossil mammals through the beds, allow the assembly of the dataset necessary for an analysis of mammalian biodiversity in this area of the Rocky Mountains during the Arikareean. The study of the taxonomy and diversity of the mammalian fauna through the beds suggest that the timing of the faunal turnover of the Arikareean in the northern Rocky Mountains was more similar to the timing in Oregon than in the Great Plains. This pattern supports an eastward spread of the faunal transition of the Arikareean and a time transgressive mammalian turnover across the western United States that is associated to a stronger immigration from Eurasia than previously suggested. My analysis of the changes in dietary and locomotory ecologies through time at the scale of communities in the Cabbage Patch beds and a comparative dataset from Nebraska show evidence for a transition from assemblages dominated by mammals with affinities for forested and mesic environments to assemblages dominated by mammals with affinities for open environments ca. 27-26 Ma . Differences in ecologies across taxa suggest that these changes in the ecological composition of Arikareean mammalian assemblages were linked to taxonomic turnover from immigration and in situ evolution. These results suggest that the link between environmental change, ecological filtering, and taxonomic turnover acting over evolutionary timescales led to the rise of modern mammalian faunas.

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DEDICATION

To my wife, Winifred Kehl, for her unwavering love and support,

To my family who has fostered my passion and career for so many years,

Chapter 1. INTRODUCTION: THE RISE AND DEMISE OF MODERN MAMMALIAN FAUNAS

The consequences of ongoing climate and environmental changes on mammal communities are a major concern of conservation biology. Over 20% of extant mammalian species are currently threatened by extinction, and habitat loss is the greatest threat to mammal biodiversity (IUCN 2015). Deforestation, desertification, and vegetation changes, in particular, have been linked to decreases in species richness and ecological diversity (Malcolm and Ray 2000, Jones et al. 2003, Bateman and Ostoja 2004, Pardini 2004, Valone and Sauter 2005). Invasive species also play an important role in the extinction of mammals (IUCN 2015, see also Gibson et al. 2013 for an example). These threats have led to a growing body of ecological research seeking to disentangle the patterns and processes of taxonomic and ecological turnover of mammalian faunas (Manor et al. 2008, Meserve et al. 2011, Elmhagen et al. 2015). Although this work has focused on short term studies, long-term ecological research projects and studies taking advantage of historical data have sought to investigate changes in biodiversity over decades and centuries (e.g., Moritz et al. 2008, Rowe et al. 2011). Paleoecology offers the unique opportunity to extend this work even further to millennia and millions of years (Rull 2014). In addition to allowing the study of ecological processes over evolutionary timescales, paleoecology enables the investigation of the response of taxa and communities to a wider range of climatic and environmental perturbations than those observed in the modern and historical records (Dietl and Flessa 2011, Blois and Hadly 2009, Barnosky et al. 2003).

Such dramatic changes in climate and environment occurred in North America ca. 30–20 million years ago (Ma), a time called the Arikareean, when a globally stable climate was followed by successive episodes of global warming and global cooling (Zachos et al. 2008, 2001a, 2001b). Concurrently, the forests characteristic of the Eocene shrunk with the opening of the environment and the spread of the grasslands emblematic of the Miocene, first in the Great Plains and later in the Rocky Mountains (Strömberg 2005). The Arikareean also represents the beginning of modern mammalian faunas composed of extant families and subfamilies (Webb and Opdyke 1995, Woodburne 2004) when important immigration from Eurasia and the origination of many new taxa transformed the taxonomic composition of North American mammalian faunas. So what was the role of environmental change in the mammalian turnover of the Arikareean? I investigate this question focusing on the Cabbage Patch beds of western Montana, a series of fossil-bearing beds unique among Arikareean deposits for preserving a suite of vertebrate microfossil assemblages rich in small mammals spanning ca. 4.5 million years of the early Arikareean.

Taphonomic processes can introduce biases in fossil deposits that can influence the composition of a fossil assemblage and thus confound perceived patterns of taxonomic or ecological diversity in space and time (Wing, Sues, Tiffney et al. 1992). In Chapter Two of my dissertation, I investigated the potential of the depositional environment and preservation of the fossils from select Cabbage Patch vertebrate microfossil assemblages to prevent comparisons through time of biodiversity patterns. Vertebrate microfossil assemblages are accumulations of isolated and fragmentary remains that can sometimes be difficult to assign to lower-level taxonomic groups. Yet, such taxonomic resolution is critical to track biodiversity through time. In Chapter Three, I studied the potential of tooth shape to inform the identification of isolated and worn teeth of entoptychine gophers, an abundant group of mammals in the Cabbage Patch beds. My collaborator and I used geometric morphometrics to study the shape of the cheek teeth of a large sample of modern gophers and applied this approach to entoptychine gophers, including many specimens from the Cabbage Patch beds. This work, as well as the taxonomic identification of almost 1,000 fossil specimens across the beds, enabled me to build the necessary dataset for an analysis of the timing of the transition from archaic to novel mammalian communities in western Montana, a region geographically intermediate between Oregon and Nebraska where coeval fossil assemblages have been more extensively studied. I present this analysis in Chapter Four and test the hypothesis that the faunal transition of the Arikareean in Montana was chronologically intermediate between Oregon and Nebraska, correlative with an eastward expansion of novel taxa. Could the faunal turnover of the Arikareean have been associated with the environmental change from closed forests to more open savanna-like environments? I investigate this question in Chapter Five by combining data on the dietary and locomotory ecology of fossil mammals with data on their biodiversity to analyze similarities in the ecological compositions of modern mammalian communities and mammalian fossil assemblages through the early Arikareean. Because of the asynchrony of environmental change across the northern United States (Strömberg 2005), I compared my results from the Cabbage Patch beds to those of an analysis of a comparable dataset from rare vertebrate microfossil assemblages of Nebraska.

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Chapter 2. COMPARATIVE TAPHONOMY OF THE MAMMALIAN REMAINS FROM THE CABBAGE PATCH BEDS OF WESTERN MONTANA (RENOVA FORMATION, ARIKAREEAN): CONTRASTING DEPOSITIONAL ENVIRONMENTS AND SPECIMEN PRESERVATION

ABSTRACT

The study of faunal change through time in the fossil record requires a careful assessment of the potential biases introduced by the filtering of death assemblages by depositional environments and other agents of accumulation like predators. I investigate the taphonomy of the mammalian remains from the Arikareean-aged Cabbage Patch beds of western Montana using both sedimentological evidence and characteristics of the preservation of the fossil specimens to test two hypotheses regarding their preservation pattern: (1) the pattern of faunal change through the section is not a product of differences in the preservation of fossils and (2) the taphonomic characteristics of fossil specimens are linked to the environments in which they were preserved. The interpretation of the sedimentological data, combined with the analyses of the taphonomic filtering of mammalian fossils, suggests that the attritional accumulation of fossils in floodplain settings was the result of predator activity and attrition reworked locally by fluvial processes. The fossils from these deposits experienced little transport. Moreover, despite complexities in the dataset, select specimen characteristics, including size, shape, and surface modifications, can be linked to the depositional environments determined from sedimentological data. The fossils

recovered from a high energy deposit of the lower Cabbage Patch are significantly different from those found at low energy deposits. These low depositional energy fossil assemblages appear to be taphonomically similar enough to each other to be used in analyses of faunal analyses despite a change in taphonomic filtering through the section.

1. INTRODUCTION

The fossil record enables the study of faunal change on evolutionary timescales through a range of climatic and environmental conditions not found in the modern and historical record (Dietl and Flessa 2011, Barnosky et al. 2003, Blois and Hadly 2009). Yet, this work should only be undertaken if the potential biases inherent to studying the fossil record are well understood (Behrensmeyer and Kidwell 1985, Brett and Baird 1986, Badgley 1986a, Wing, Sues, Tiffney et al. 1992, Kidwell and Flessa 1996, Kidwell and Holland 2002). The study of taphonomy can reduce the noise introduced by preservation processes and enhance the paleoecological signal by providing information about the environment that the organisms lived in and their relationships with it (Brett and Baird 1986). Analyzing the paleoecology of terrestrial vertebrates is particularly challenging because both the patterns of preservation of terrestrial bone assemblages and the processes controlling them are complex (Wolff 1973, Behrensmeyer and Hook 1992, Kidwell and Flessa 1996, Rogers and Kidwell 2000, Rogers and Brady 2010, Moore 2012).

Taphonomic processes can introduce biases in fossil deposits that are based on morphology (e.g., favoring the preservation of larger animals over smaller ones, Brown et al. 2013) or ecology (e.g., favoring the preservation of burrowing animals, Weissbrod and Zaidner 2014). These biases can influence the composition of a fossil assemblage and thus confound patterns of taxonomic or ecological diversity in space and time (Wing, Sues, Tiffney et al. 1992).

As a consequence, some paleoecological analyses of fossil vertebrates, particularly mammals (e.g., Clyde and Gingerich 1988), have been restricted to isotaphonomic assemblages, in which the preservation processes were similar (Wing, Sues, Potts et al. 1992). Other studies (e.g., Badgley 1982, 1986a) combined analyses of the environment and mode of deposition of fossils along with the paleoecological analyses to mitigate this problem.

Different approaches have been adopted to characterize the taphonomy of vertebrate assemblages. Some have focused on specimen features such as size, shape, and taxonomic identity to compare the preservation of fossils across and within lithologies (e.g., Blob and Fiorillo 1996, Wilson 2008); sometimes using multiple regression to correlate these characteristics with the pattern of skeletal elements preservation within assemblages (Moore and Norman 2009). Others have focused on the analysis of fossils and their sedimentological context in the field to contrast vertebrate microfossil assemblages across depositional environments (e.g., Rogers and Brady 2010). These two approaches (specimen-based and sedimentological) can be integrated to determine the taphonomic history of mammalian fossil assemblages (e.g., Badgley 1986a).

In this study, I combine a field-driven sedimentological approach with an analysis of the preservational features (including size, shape, and surface modifications) of a large sample of fossil specimens to infer the depositional environment, mode and tempo of accumulation, and taphonomic filtering of the fossil mammals from seven different assemblages from the Oligocene of western Montana (following the framework of Badgley 1986a, fig. 1). I infer taphofacies (i.e. bodies of rocks defined by a specific set of taphonomic characteristics, Speyer and Brett 1996) to test the hypothesis that the faunal change through the beds is not a product of differential preservation across assemblages. I also seek to compare deposits within depositional environments to assess (1) how stable fossil preservation remained through the deposition of the Cabbage Patch beds, (2) whether or not differences in lithology (i.e., siltstone vs. mudstone) within deposits of similar energy are associated to differences in specimen preservation, and (3) how much contemporaneous fossil assemblages from the Flint Creek and Deer Lodge basins may differ. I expect that fossil assemblages from similar deposits will exhibit comparable specimen preservation, and that different depositional environments will have contrasting patterns of fossil preservation. The results of this taphonomic work will help guide future analyses of taxonomic and paleoecological changes in the Arikareean-aged Cabbage Patch beds of western Montana. I focus on the Arikareean because it is during this interval that the transition from more archaic to more modern faunas was initiated (Webb and Opdyke 1995, Woodburne 2004) as global and regional climate and regional vegetation changed (Strömberg 2005, Retallack 2007a, Zachos et al. 2008).

2. GEOLOGICAL SETTING: THE CABBAGE PATCH BEDS

The Cabbage Patch beds crop out in the Blackfoot, Deer Lodge, Divide, Douglas Creek, and Flint Creek intermontane basins of western Montana (Rasmussen and Prothero 2003, Calede and Rasmussen 2015). The tuffaceous Cabbage Patch beds are part of the upper Renova Formation (Rasmussen and Prothero 2003; Calede and Rasmussen 2015) and have been studied since the end of the 19th century, in part because of their abundant vertebrate fossils (e.g., Douglass 1903, Konizeski and Donohoe 1958, Riel 1964, Wood and Konizeski 1965, Tihen 1974, Rasmussen 1977, Tihen and Wake 1981, Henrici 1994, Calede and Rasmussen 2015). The geology of the Cabbage Patch beds (Rasmussen 1969, 1977, 2003, Rasmussen and Prothero 2003, Calede and Rasmussen 2015) and more broadly the Flint Creek (Portner and Hendrix

2005, Portner et al. 2011) and Deer Lodge (e.g., Berg 2004) basins have also been the subject of much attention. The Cabbage Patch beds unconformably overlap an Eocene-aged rhyolitic welded tuff dated to 48.64 ± 0.17 Ma (Portner et al. 2011). Based on the mollusk and mammal faunas, as well as magnetostratigraphic data, the Cabbage Patch beds have been divided into three biostratigraphic units (lower, middle, and upper; Fig. 1) ranging in age from approximately 28.2 to 23 Ma (Rasmussen and Prothero 2003). Recent radiometric dating suggests that the lower Cabbage Patch beds may be as old as 29.95 Ma in places (Mosolf 2015). Despite uncertainties in their absolute age, the Cabbage Patch beds have been interpreted as early Arikareean in age (Tedford et al. 2004).

The beds include rare paludal deposits, non-reworked eolian ash falls, and lacustrine delta fills as well as more abundant lacustrine deposits, and the dominant fluvial environments (Rasmussen 1977, table 2). Thanks largely to the work of Rasmussen (1969, 1977), fossils have been recovered from over 40 localities; mostly in fluvial and lacustrine deposits.

The Cabbage Patch beds were deposited as fine-grained sediments that are rich in volcanic glass. The deposits are at least 616 m thick. The parent material for these tuffaceous deposits might have been derived from air fall ash of the Paleogene Cascade volcanic arc (Sears and Ryan 2003). Other sources of the sediments of the Cabbage Patch beds likely include the Mount Powell batholith in the Flint Creek Range and the Lowland Creek volcanics (Portner 2005, Portner et al. 2011), the footwalls of the Anaconda core complex (Stroup et al. 2008, Portner et al. 2011), and the Boulder batholith as well as the Elkhorn Mountains volcanics (Rasmussen 1977, Lund et al. 2002, Vuke 2004). These sediments, including the air fall ashes, were reworked by fluvial and lacustrine processes.

In the Flint Creek basin, the deposition of the sediments took place on an Eocene-aged paleosurface (Portner 2005) bordered by the Flint Creek Range to the southeast, the Sapphire Range to the southwest, and the proto-Garnet Range to the North (see also Rasmussen 1973, 1977). The Cabbage Patch beds overlap the Douglas Creek beds unconformably on the northeastern end of the Flint Creek basin and overlap Cretaceous rocks of the Flint Creek Range to the south (see Rasmussen and Prothero 2003, Portner and Hendrix 2005). The paleo Flint Creek basin was thus likely fairly similar in size and shape to its current configuration, connected to the north to the Douglas Creek and Blackfoot basins and to the east to the Deer Lodge basin by rivers and lake systems (Rasmussen 1977). Studies of paleocurrents within the Flint Creek basin suggest a west to northwest directed paleoflow (Rasmussen 1973, 1977, 1989, Portner et al. 2011, Calede and Rasmussen 2015).

3. MATERIAL AND METHODS

Although the Cabbage Patch beds crop out at over 40 known localities, I focus on a few well-sampled fossil assemblages that make possible quantitative analyses of specimen characteristics (Table 1). My dataset includes seven vertebrate microfossil assemblages covering all three of the biostratigraphic units of the Cabbage Patch beds (Table 1), mainly from the Flint Creek basin where several adjacent and productive localities have been placed in a stratigraphic context (Rasmussen 1977, Rasmussen and Prothero 2003, Calede and Rasmussen 2015, Figs. 1-3). Because the Flint Creek basin localities from the upper Cabbage Patch beds are not very fossiliferous, I include a rich fossil assemblage from the Tavenner Ranch local fauna (C0173, Deer Lodge basin) located about 26 km from the Bert Creek area of the Flint Creek Basin (Fig. 1). To facilitate the comparison of this assemblage with those from the Flint Creek basin, I also include a lower Cabbage Patch assemblage from the Tavenner Ranch Local Fauna (MV6613, Deer Lodge basin).

At each locality, the crews of Rasmussen and myself recovered specimens from the surface as they eroded out and excavated fossils by quarrying productive horizons. Both crews collected all vertebrate fragments recovered in the field, including specimens not identifiable as a specific element of the vertebrate skeleton. Both crews also intensively used wet screenwashing with medium and fine mesh sizes (0.7 and 0.5 mm spacing respectively) to process several hundred kilos of fossiliferous matrix. This protocol allows the recovery of the smallest members of the vertebrate communities (Wolff 1975, Cifelli et al. 1996). The use of similar collecting methods by both investigators across all localities limits the potential for collecting to be a source of bias in both element representation and specimen modifications (from mechanical extraction and processing).

3.1. Sedimentology and depositional environments

Rasmussen (1969, 1977) undertook the initial detailed investigations of the fossiliferous horizons and their geological context. More recently, I reassessed the sedimentology of the fossiliferous horizons described herein. For C0173 and MV6613, I rely upon the work of Rasmussen (1977) as well as reanalyses of rock samples collected during the original study of the localities. In order to determine the depositional environment of the fossils, I collected data on the lithology, texture, sedimentary structures, and local context of each deposit. I determined the grain size, roundness, and sorting of the matrix in the field and later checked these characteristics in the lab on rock samples collected from the outcrops. I assessed the color of the matrix using a Munsell soil-color chart (Munsell 2009) as a measure of the degree of chemical oxidation and drainage of the weakly developed paleosols (entisols and inceptisols) of the Cabbage Patch beds (Retallack 2007b). Rock samples for the horizons described herein are reposited at the University of Washington Burke Museum (UWBM, Seattle, Washington). Fossils are reposited at the UWBM, the University of Montana Paleontology Center (UMPC, Missoula, Montana), and the University of Kansas Museum of Natural History (KUVP, Lawrence, Kansas). I used sedimentological data, fossil data (including vertebrates, invertebrates, and plants), and *in situ* taphonomic characteristics of the fossils (e.g., association, articulation, concentration within fossil-bearing horizon) to decipher the depositional environments of the fossil-bearing beds.

3.2. Bone preservation across assemblages

In an effort to assess similarities in taphonomic modifications across the vertebrate microfossil assemblages selected, I undertook an analysis of the preservation pattern of the fossil specimens. I restricted my analyses to mammalian remains, a well-known vertebrate group with a rich fossil record across the Cabbage Patch beds (Rasmussen 1977, Rasmussen and Prothero 2003, Calede and Rasmussen 2015). I used a large sample (Table 1) of mammalian specimens in this analysis, including fragmentary bones that could not be identified as a specific skeletal element. Fragments represent the majority of the fossils recovered from all Cabbage Patch assemblages studied (Table 1). Blob and Fiorillo (1996), Fiorillo (1988), as well as Rogers and Brady (2010) have suggested that fragments should be considered along with identifiable elements to get a better picture of the taphonomy of fossil assemblages including vertebrate microfossil deposits. To build composite datasets representative of the proportion of fossils in the assemblages (i.e., not biased against fragments and towards identifiable elements), I used a standardized amount of concentrate to calculate the ratio of elements to fragments in each assemblage (Table 1). I then randomly selected an appropriate number of identifiable elements for the number of fragments at each assemblage based on these ratios (Table 1, Appendix A2.6).

3.3. Data and analyses

The characteristics I collected from the fossil specimens cover bone surface modifications, completeness, shape, and size (Table 2). Bone surface modifications include weathering and abrasion. Weathering is the cracking and flaking of bones (Table S1). Abrasion is the rounding and polishing of bones (Table S2). I assessed both characteristics using the stages (0 through 3, Table 2) developed by Fiorillo (1988) and used by Wilson (2008) as well as Moore and Norman (2009) among others. Abrasion and weathering provide a measure of the breakdown and damage of the bones associated with bone handling and processing by predators, transport, surface exposure, and local conditions of degradation and burial (Behrensmeyer 1978, Andrews 1990, Moore and Norman 2009). Bone weathering can be influenced by climate, intrinsic characteristics of the bones, properties of the environment where they are breaking down, and exposure to the surface (Lyman and Fox 1989, Andrews 1990, Rogers 1990, Andrews and Whybrow 2005, Madgwick and Mulville 2011). Nevertheless, distinct patterns of weathering can be distinguished across environments (Cutler et al. 1999). I used the weathering of the fossils and their distribution within the horizons to determine the period of accumulation of the fossils across deposits. I used the abrasion of specimens as well as their size (see below) to infer the hydraulic regime, reworking, and interactions with the sediment load the specimens experienced (Badgley 1986a, Behrensmeyer et al. 2000 and references therein, Fernández-Jalvo and Andrews 2003).

I determined completeness by comparing the percentage of the volume preserved in a given fossil relative to a complete specimen (i.e., same element and taxon; rounded to the nearest 5%) following the method of Moore and Norman (2009). The completeness of the bones of an assemblage helps assess the fragmentation of the fossils and thus potentially the mode of accumulation and transport of the fossils (e.g., Behrensmeyer 1988, Terry 2007). I grouped fossils in three categories of completeness (fragmentary [less than 50% complete], partial [50 to 95 % complete], and complete [95 to 100% complete]) following Coombs and Coombs (1997) to characterize the degree of fragmentation of skeletal elements across assemblages. I determined weathering and abrasion under magnification (hand-lens, microscope) for all specimens, fragments included. I could only determine completeness for specimens identified as a specific element.

I took three measurements orthogonal to one another (Table 2) to determine the shape and size of all specimens (fragments and elements). All measurements were taken using Mitutoyo Digimatic CD-8” CX calipers and rounded to the nearest 0.1 mm. Shape has been suggested to be important in bone transport in fluvial environments because of hydraulic sorting (e.g., Boaz and Behrensmeyer 1976) and terrestrial environment because of displacement on slopes (Frostick and Reid 1983). I determined the shape of the specimens by calculating two different proxies: columnarity and flatness (Hofmann 1994, Moore and Norman 2009). Columnarity is the negative ratio of the length of the shortest axis to that of the longest axis of the fossils specimen (-L3/L1). The higher the value, the more pillar-like the fossil is (e.g., a humerus is more columnar than a vertebra). Flatness is the negative ratio of the length of the shortest axis to that of the median axis (-L3/L2; e.g., an ilium is flatter than a femur). I then categorized the shape of the specimens as flat, columnar, or compact following the classification used by Blob and Fiorillo (1996) and Wilson (2008). I defined flat specimens as having a depth equal to or less than half their width and columnar specimens as having a length of at least 1.5 times their width. When a specimen could be categorized as both flat and columnar following these guidelines, I used the largest ratio to classify the specimen as either columnar or flat. Specimens that could not be categorized as flat or columnar were classified as compact. I used length (L1) as a proxy for specimen size (Blob and Fiorillo 1996, Wilson 2008). I used the Shapiro-Wilk test to evaluate continuous variables (length, width, and depth as well as the derived flatness and columnarity) for normality. Based on the results of these analyses, I used non-parametric tests in my analyses. I also categorized skeletal elements according to their surface area to volume ratio (Table S3) using the method developed by Moore and Norman (2009). Surface area to volume ratio has been linked with skeletal element abundance in mammalian fossil assemblages (Moore and Norman 2009) and more specifically in bone transport (Coard 1999). Shape, completeness of the specimens, and representation of skeletal elements (see below) within assemblages help determine the agents of accumulation at each assemblage and the possible filtering of elements by depositional environments.

The representation of skeletal elements has been extensively used to help determine the agent of accumulation (e.g., predator type, fluvial environment) of fossil assemblages (e.g., Badgley 1986a, Pratt 1989, Kusmer 1990, Behrensmeyer 1991). I therefore collected data on the representation of elements for all Cabbage Patch assemblages studied as well as comparative assemblages from the literature including both biotic (i.e., predators) and abiotic (i.e., fluvial) agents of accumulation (Table 3) but focusing on small mammal assemblages comparable to those of the Cabbage Patch beds (Andrews and Nesbit Evans 1983, Cassiliano 1997, Lloveras 2008, Lloveras et al. 2012). Because the specimens from the Cabbage Patch beds included in my analyses are found isolated and no association can usually be made between elements, I used the number of identified specimens rather than the minimum number of individuals in my analyses (see Badgley 1986b). I grouped and split data on the frequency of skeletal elements from published accounts to be consistent with the Cabbage Patch data. Thus, I included maxillae and horncore fragments along with skull fragments, tusks and roots with isolated teeth, but excluded astragali and calcanea from the count of podials. Fibulae are not reported in some of the comparative datasets used in this study (e.g., Cassiliano 1997, Lloveras et al. 2012) and, along with sesamoid bones, were excluded from the analysis. Although the count of tibiae of Aslan and Behrensmeyer (1996) includes fibulae, this is unlikely to be a source of bias in the dataset; fibulae represent less than 1.5% of fossil assemblages (Appendix A2.5, Brown and Kraus 1981, Badgley 1986a). I used the number of specimens for each element to calculate the relative abundance of skeletal elements for each assemblage. I then log transformed these relative abundances and used them to calculate pairwise Bray-Curtis distances between assemblages. I chose to use Bray-Curtis distances because they can incorporate the low frequencies of elements present in the dataset better than other distances. These distances are represented in a non-metric multidimensional scaling ordination (NMDS), a technique commonly used in multivariate analyses of taphonomic data (e.g., Kidwell et al. 2005, Tomašových and Rothfus 2005, Moore 2012). I chose to use NMDS because it does not assume multivariate normality or linear associations and uses the rank order of distances (not the value themselves unlike principal coordinate analysis, Kruskal and Wish 1978). It is therefore not as sensitive to numerical differences between assemblages.

Density impacts bone preservation as a consequence of its role in fluvial transport (e.g., Boaz and Behrensmeyer 1976, Coard 1999, Evans 2014), its importance in the processing, fragmentation, and sorting of skeletal elements by predators (e.g., Richardson 1980, Andrews and Armour-Chelu 1998, Faith et al. 2007), and its bearing on bone trampling (Andrews and Armour-Chelu 1998). I here use data on extant small mammal bone density (Pavao and Stahl 1999, Lyman et al. 1992) to determine the relative abundance of low, medium, and high density elements and assess the potential for density mediation of bone accumulation in the Cabbage Patch assemblages. I use the same small mammal data to determine the relative abundance of low, medium, and high density elements in the small mammal-dominated fluvial assemblages of the Palm Springs Formation (Cassiliano 1997), and those accumulated by predators (Andrews and Nesbit Evans 1983, Lloveras 2008, Lloveras et al. 2012). I use the data on large mammals of Behrensmeyer (1975) for the assemblages from the Siwalik (Badgley 1986a) and the modern fluvial assemblage (Aslan and Behrensmeyer 1996). Skulls were excluded from the small-mammal dataset in the absence of density data. This is unlikely to be of much importance because skulls represent less than 6% of elements recovered from the Cabbage Patch assemblages and only represent over 8% in the Pliocene-aged channel fill deposits of the Palm Springs Fm. Because density readily changes with decay, weathering, drying, and wetting (Evans 2014) and may be difficult to assess (Lyman 1984, Evans 2014), the results should be interpreted with much caution. All analyses were performed in R 3.1.3 (R Development Core Team 2015) using RStudio 0.98.1103 (R Studio 2015) and the packages vegan 2.2-1 (Oksanen et al. 2015), PMCMR 1.1 (Pohlert 2014), Hmisc 3.15-0 (Harrell 2015), and biostats (McGarigal 2015).

4. DEPOSITIONAL ENVIRONMENTS OF THE CABBAGE PATCH BEDS

The sedimentology and field taphonomy of the assemblages studied (Fig. 4) are described in stratigraphic order starting with the lowest (i.e., oldest) horizons in the appendix and summarized in tables 4 and 5. These data support two different categories of depositional environments for the Cabbage Patch deposits studied.

Six of the assemblages are derived from low energy deposits characterized by poorly sorted, fine-grained sedimentary rocks (mudstones and siltstones) that display no particular bedding and often incorporate air fall ash deposits (Table 4). These characteristics typify the low energy environments associated with weakly developed paleosols in floodplain deposits (Bown and Kraus 1987, Kraus and Gwinn 1997, Aslan 2003, Laute and Beylich 2010). Other evidence of the close proximity with water bodies includes the presence in the deposits of freshwater snails that can be very common and often well-preserved (Pierce 1993), ostracods, fish bones, and amphibians (mainly frogs) that are sometimes very abundant. The presence of diatoms and freshwater snails along with root traces and invertebrate burrows (bioturbation) in thin, poorly developed horizons suggest repeated flooding events. One assemblage (MV6613) includes occasional thin lenses of arkosic sand that indicate temporary returns of a higher energy environment, possibly crevasse splays. Across the low energy deposits (C1708, C1721, MV6613, C1704, C0174, and C0173), there are few differences in fine-grained lithologies (all mudstones to siltstones), poor sorting (poorly to moderately sorted sand grains and silt-sized volcanic glass shards), roundness (mostly subrounded to subangular), yellow color (all but MV6613 have hues of 5Y to 2.5Y), and lack of sedimentary features (beyond bioturbation by roots) following pedogenic modification (i.e., the beds are massive with no features). There are, however, finer scale differences in lithological and paleontological characteristics between low energy deposits that may be indicative of environmental variation across assemblages. For example, fish, freshwater snails, and even frogs are not as abundant at C1704 as they are at C1708. Also present at C1704 are insect burrow casts, slug shells, and plethodontid as well as salamandrid salamanders (see Appendix A2.1), which can be some of the most terrestrial batrachians (Wake and Deban 2000). Together, these faunal data suggest that the environment at C1704 may not be as wet as it was at C1708, a low energy environment that was likely periodically ponded. The biodiversity of freshwater molluscs at another assemblage (C0174) has been interpreted to indicate more permanent water bodies (Pierce 1993). There, the deposits suggest ephemeral lacustrine to lacustrine delta fill depositional regimes interbedded with a low energy fluvial influence or possibly a sediment-starved ash-choked stream.

One of the deposits (C1707) displays characteristics of a channel-lag (see Appendix A2.1). These features include a coarse-grained sedimentology (i.e., sandstone), the presence of cross-bedding, and an upward-fining sequence without bioturbation or air fall ash deposits (Table 4). Fossils, including numerous aquatic vertebrate remains (i.e., fish and amphibians), are concentrated at the bottom of this upward-fining horizon along with the coarser component of the sediments. The high degree of breakage of the fossil vertebrates and freshwater snails is consistent with the higher energy environment evidenced by the cross-bedding. The channel cuts into the finer-grained underlying siltstone.

5. PRESERVATION PATTERN OF MAMMALIAN BONES ACROSS HORIZONS

5.1. Intra-observer error

I assessed the reliability of measurements and scores across all assemblages by scoring and measuring 101 specimens a second time several months after the initial scoring and measurements. The sample used to assess intra-observer error includes fragments and elements from all assemblages (see Appendix A2.7). The second set of values was only used to assess error. The first set of scores and measurements was included in the analyses to be consistent with the specimens that were scored and measured only once.

Measurement errors are small (Table 6). The mean error for length corresponds to less than 3.5% of the standard deviation of the sample. Mean errors for width and depth represent less than 4.5% of the standard deviation of the sample. Average errors for columnarity and flatness represent respectively 8.8 and 16.5% of the standard deviation of the sample. The mean error in the assessment of completeness is around 2%. Because completeness is rounded to the closest 5% and subsequent analyses group specimens in three broad breakage categories, this error is negligible. I did not detect any mistake in the categorization of elements according to their surface area to volume ratio. Surface modifications (weathering and abrasion) were the least reliable scores collected; 27 of the 101 specimens rescored were not categorized properly. However, 25 of those specimens were only misclassified by one category (most often substitutions between categories 0 and 1 as well as 1 and 2). Similarly, abrasion was misclassified for 30 out of 101 specimens (24 when specimens of low abrasion (categories 0 and 1) were grouped together). None were misclassified by more than one step (substitutions between 1 and 2 as well as 2 and 3). These results are consistent with the conclusions of Rothfus (2004) that surface alterations (e.g., weathering) and edge modification (e.g., abrasion) are difficult to reliably assess and suggest caution in interpreting weathering and abrasion results, particularly from small sample sizes.

5.2. Size and shape

Small mammals (<5kg) are abundant in all Cabbage Patch assemblages (Table 1). They represent about 97 to 100% of the fauna from each assemblage. Large mammals (e.g., Equidae, Merycoidodontidae, Rhinocerotidae, some Canidae) are rare (<4.2% of the fauna) through the section (see SI text). The other fossil vertebrates present are also small animals (fish and amphibians mostly) preserved as isolated and fragmentary bones that rarely exceed a centimeter.

The smallest and most consistently sized specimens are found at C1707, the assemblage from higher depositional energy (Table 7). Specimen size is different across assemblages (Kruskal-Wallis χ^2=75.43, df=6, p < 0.001; Fig. 6). Post-hoc pairwise comparisons (Nemenyi-test, Table S4) show evidence for significant differences between C1707 and all low energy deposit assemblages from the lower and upper Cabbage Patch beds, but not from the middle Cabbage Patch. Some differences exist across lower energy deposits as well (Table 8). However, they appear to be consequences of the presence of a few very large specimens, most of them fragments, at C1708 and MV6613 (Fig. 6, Table 7, Appendix A2.6).

There is no significant difference in flatness or columnarity between high and low depositional energy assemblages (Kruskal-Wallis χ^2=0.851, df=1, p=0.36 and χ^2=0.148, df=1, p =0.70 respectively; Table 9). No significant differences are found either when comparing proportions of specimens in shape categories (flat, columnar, compact) across lithologies (χ^2= 0.668, df = 4, p= 0.96) or assemblages (Table 9).

5.3. Weathering and abrasion

Across all assemblages, all four weathering stages are represented (Table 9). However, there is a significant difference in weathering across assemblages (χ^2= 48.44, df = 18, p-value = 1.10^{-4}). Post-hoc Chi square pairwise comparisons (Table S5) show evidence for significant differences between the higher energy deposits of C1707 and some lower energy ones of the middle (C1704 and C0174) and lower Cabbage Patch (C1721). C1707 includes very few specimens that are little weathered (stage 0) and the highest proportion of very weathered specimens (stage 3) of any assemblage (Table 9). The significant difference between two low energy assemblages (C0174 and C1721) is likely an artefact; most of the difference is in the proportions of specimens scored as stages 0 and 1, which may not be reliable (Table 6). One low depositional energy assemblage, C1708 includes a high proportion of more weathered specimens. It is significantly different from C1704 and C1721; even accounting for some specimens assigned to the wrong weathering category.

The lowest proportion of specimens with low abrasion (stages 0 and 1) is found at C1707, where the highest proportion of very abraded (stage 3) specimens is also found (Table 9). Specimen abrasion at C1707, the highest depositional energy environment studied, is significantly different from that of all low energy deposits except C1704 (Table S6).

5.4. Surface area to volume ratio and element representation

There are significant differences in the distribution of identifiable elements across surface area to volume ratio categories across assemblages (Table 9; $\chi^2 = 40.998$, df = 12, $p < 0.001$). Elements with very low or very high ratios are rare across all assemblages (≤15.5%), particularly at C1707 where no category 1 and very few category 5 elements have been recovered (Table 9). The distribution of specimens across surface area to volume ratio categories at C1707 is significantly different from that at C1704 and C1708, two of the low energy deposits (Table S7). There are also differences across the low depositional energy assemblages (Tables 11 and S7). C1708, in particular, significantly differs from almost all other low depositional energy assemblages, a consequence of its very high proportion of dentaries and low proportion of limb bones.

The relative abundance of skeletal elements across Cabbage Patch and in comparative assemblages is summarized in table 3. These data were used to produce a two-dimensional NMDS (Fig. 7A, Table S8; stress=13.5%; Monte Carlo randomization test of stress value with k=2 and 100 replicates: p=0.01). An additional analysis not figured (k=3, stress=7%) shows a similar pattern. The low stress values of these analyses suggest a good fit between the observed ordination pattern and the dissimilarities between assemblages (McCune and Grace 2002). The distances in the ordination accurately represent the pairwise dissimilarities across assemblages (correlation of the fitted values and ordination distances: non-metric fit R^2=0.98, linear fit R^2=0.91).

The ordination (Fig. 7A) displays similarities in element representation between three low depositional energy assemblages (C1708, C1704, and C1721) that are rich in teeth. These three assemblages are similar to the Pliocene floodplain deposits from the Palm Springs Formation of southern California (Cassiliano 1997) in that respect (Table 3). The two deposits from the Deer Lodge basin, C0173 and MV6613, are very similar to one another. MV6613 is also close to the Pliocene-aged channel fill deposits of the Palm Spring Fm. (Cassiliano 1997). These two assemblages are rich in dentaries. The two youngest assemblages, C0173 and C0174, are similar to the late Miocene deposits of the Siwalik IV locality from Pakistan, a predator accumulated assemblage on a floodplain land surface (Badgley 1986a). They are very close to the centroid of the ordination; the proportion of bones at these assemblages is very close to average. The high energy deposit (C1707) is most similar to C0174 and the deposits produced by mongooses (Andrews and Nesbit Evans 1993). Both C0174 and C1707 stand close to the centroid of the ordination with average proportions of teeth, tibiae, radii/ulnae, vertebrae, and femora.

Pairwise Spearman rank order correlations (as in Behrensmeyer 1975, Badgley 1986a, Pratt 1989) between all assemblages (Table 10, A2.8) support similarities between C0173 (upper Cabbage Patch beds, Deer Lodge basin), C0174 (middle Cabbage Patch beds, Flint Creek basin), MV6613 (lower Cabbage Patch beds, Deer Lodge basin), and the floodplain deposits from the Palm Springs Formation. They also find C1704 (middle Cabbage Patch beds, Flint Creek basin), C1708 (lower Cabbage Patch, Flint Creek basin), the Pliocene floodplain assemblage, and C0173 to be similar to one another. C1707 (lower Cabbage Patch, Flint Creek basin) is found to be most similar to MV6613, deposits accumulated by coyotes (*Canis latrans*) and red fox (*Vulpes vulpes*), and C0173.

5.5. Density

The assemblages included in the analysis form three distinctive clusters based on the dominant category of element density represented (low, medium, or high density). C1704, C1708, and C1721, all low depositional energy environments rich in teeth, cluster in the high density element region of the graph along with the low energy floodplain deposits of the Palm Springs Formation (NMDS using Bray-Curtis distances, k=2, stress=3.4%, p= 0.0099, non-metric fit R^2=0.999, linear fit R^2=0.995, Table S9, Fig. 7B). No Cabbage Patch assemblage is found to cluster in the medium density region along with the Siwalik assemblages, the modern river deposits, and the channel fill deposits of the Palm Springs Fm. The remaining Cabbage Patch assemblages are found to be most similar to the low density-dominated assemblages formed by mammalian and avian predators. The density composition at MV6613 thus overlaps that of an avian predator assemblage (Lloveras et al. 2012) and the density composition at C0174 overlaps with that formed by Lynx (Lloveras 2008).

5.6. Completeness

The ratio of elements to fragments (Table 1) is higher overall in the Deer Lodge (C0173, MV6613) than the Flint Creek basin assemblages (C0174, C1704, C1707, C1708, and C1721). It is also higher in the upper and middle units of the beds than in the lower unit. There is no correlation between the ratio of elements to fragments and the completeness of elements (e.g., proportion of fragmentary elements) across assemblages. The proportion of fragmentary specimens (0-50% complete) is highest in the high depositional energy assemblage of C1707 and lowest in the low energy deposits of C1704 (Table 9). Overall, the proportion of complete specimens (95-100 % complete) is lower in the lower Cabbage Patch assemblages (MV6613, C1708, C1721, and C1707) and higher in the middle and upper assemblages (C1704, C0174, and C0173). The higher depositional energy assemblage of C1707 is similar to the low energy assemblages from the middle and upper Cabbage Patch in its proportion of partial specimens (50 to 95% complete). Within the low depositional energy assemblages, the distribution of specimens across the three completeness categories (Table 9) is significantly different between the lower Cabbage Patch (pairwise chi-square tests: C1708 [$p = 0.007$], C1721 [$p = 0.015$], and MV6613 [$p = 0.003$]) and the middle Cabbage Patch assemblage C1704. The two assemblages from the Deer Lodge basin (C0173 and MV6613) are also significantly different from each other ($p = 0.016$).

5.7. Multivariate analysis

I combined summary statistics of element representation, surface modification, completeness, size, and shape for each assemblage into an NMDS analysis (Table 11, Fig. 8). I used the scores on the NMDS of element representation to represent differences and similarities in element representation across assemblages. Surface modifications are represented by the percentage of specimens with high abrasion or high weathering (stages 2-3) within each assemblage. The proportion of fragmentary and complete specimens represents the breakage across assemblages. I used the percentage of specimens above the median specimen size across assemblages (6.9 mm) as a proxy for the distribution of size within an assemblage and the percentage of specimens within the flat and columnar categories to represent shape. The surface area to volume ratio was excluded because it overlaps with both shape and element data already included. All variables were log transformed to express values as orders of magnitude. Alike in the analysis of element representation, I used Bray-Curtis distances in a two dimensional NMDS (stress=9.8%). The distances in the ordination represent the pairwise dissimilarities across assemblages (correlation of the fitted values and ordination distances: non-metric fit R^2=0.99, linear fit R^2=0.942). I assessed the significance of each taphonomic characteristic in the observed pattern of similarities between assemblages using permutation tests (1,000 replicates). This analysis demonstrates that abrasion, weathering, completeness, and size are important factors of the observed pattern of taphonomic resemblance between Cabbage Patch assemblages (Table S10). Upper and middle Cabbage Patch assemblages (C0173, C0174, and C1704) are more similar to one another than to any of the lower Cabbage Patch assemblages. Middle and upper Cabbage Patch assemblages are characterized by a higher proportion of more complete specimens as well as fewer highly weathered and abraded specimens. All of the low depositional energy lower Cabbage Patch assemblages (C1721, C1708, and MV6613) cluster together as a consequence of higher specimen breakage. C1707, the high depositional energy assemblage from the lower Cabbage Patch beds, differs from all other assemblages in the large proportion of highly weathered and abraded specimens and the low number of large specimens there.

An NMDS of all specimens (not figured) supports the conclusion that more weathered specimens are also more abraded. More columnar specimens are little abraded and weathered. Flatter specimens, are larger, and have a higher surface area to volume ratio. They are also more broken.

A summary of the significant differences across assemblages (Table 8) shows that only two pairs of assemblages are not significantly different in any taphonomic characteristic: C0173 and C0174 (upper unit and upper part of the middle unit of the Cabbage Patch beds respectively) as well as C0174 and C1704 (both middle Cabbage Patch). The taphonomic characteristics that differ across the other pairs of assemblages are from most to least different: surface area to volume ratio, completeness, size, weathering, and abrasion. C1707 is most different from all other assemblages.

6. COMPARATIVE TAPHONOMY OF CABBAGE PATCH FOSSIL ASSEMBLAGES

My results provide evidence for some differences in specimen preservation between depositional environments. The mean and median size of specimens in the coarse-grained deposit (sandstone: C1707) is smaller than in finer-grained ones (siltstones and mudstones) unlike in the channel-lag deposits studied by Behrensmeyer (1988). The size range of specimens preserved in the coarse-grained assemblage at C1707 is also narrower than in the finer-grained deposits of the Cabbage Patch assemblages, a pattern consistent with other deposits (Wilson 2008). Despite this accordance between specimen size and lithology, two assemblages from mudstones (C0174 and C1704) are not significantly different from C1707 but differ significantly from two other mudstone deposits (MV6613 and C1721). Specimen size in the Cabbage Patch beds seems to be the result of the superimposition of two patterns: one that is driven by lithology where very coarse-grained deposits preserve smaller specimens and a smaller size range, and one where older localities (lower Cabbage Patch beds) do not preserve as many small specimens as younger ones. Blob and Fiorillo (1996) have noted differences in size distribution across assemblages with similar sedimentary facies in the Judith River Formation. They suggested that hydrodynamic sorting could have influenced the size distribution of the fossil assemblage prior to burial. Similarly, it is possible that the size sorting between the lower and middle Cabbage Patch changed as a consequence of changes in hydrological regime.

There are no differences in shape, whether assessed using flatness and columnarity or using shape categories, across assemblages and depositional environments in Cabbage Patch. On the contrary, Wilson (2008) found coarse-grained deposits to preserve a higher proportion of compact (equidimensional) specimens but fewer flat specimens than fine-grained deposits. Blob and Fiorillo (1996), however, found significantly different proportions of compact and flat specimens in two fine-grained sandstone assemblages (Blob and Fiorillo 1996, table 4). Although the measurement thresholds chosen by Wilson (2008), Blob and Fiorillo (1996), and myself to categorize the shape of fossil specimens may be different, it is noteworthy that two assemblages from similar sedimentary facies can differ in the distribution of specimens across shape categories (Blob and Fiorillo 1996). Based on these data and the results from this study, there does not appear to be a clear relationship between lithology (in particular grain size) and the shape of the specimens preserved. It appears that little shape sorting occurred in the Cabbage Patch beds unlike in the assemblages studied by Wilson (2008), Blob and Fiorillo (1996), or Moore and Norman (2009) who found flatness and columnarity to play a role in the composition of two assemblages from the Oligocene-aged Brule Formation of South Dakota.

Weathering has been used by Behrensmeyer (1978), Potts (1986), and Fiorillo (1988) to determine the length of the period of bone accumulation. Lyman and Fox (1989) showed that such inferences could only be made when other factors affecting weathering (e.g., skeletal element, depositional environment, taxon representation) are controlled for. As a consequence, I do not use bone weathering to determine the length of the period of accumulation in Cabbage Patch. Instead, I provide here a relative measure of bone accumulation across assemblages. The similarities in the abundance of specimens across weathering categories support a similar period of accumulation across low energy deposits. The dispersion of fossils throughout the productive horizons in these deposits suggests that this accumulation was slow, possibly attritional. Deposits accumulated by carnivores or catastrophic events would be expected to be more concentrated within the productive horizons.

Nevertheless, some bones show evidence for predator handling and damage. Several specimens from C0173 (e.g., UMPC 13217, KUVP 19859, KUVP 19858, and parts of KUVP 19852) show evidence for acid damage, possibly from digestion. Another specimen from this locality (part of KUVP 19853) shows a possible tooth puncture. Other assemblages include specimens demonstrating possible interactions with predators in the form of acid damage (C1721: UWBM 98804, UWBM 98889; MV6613: parts of UMPC 14036) or tooth punctures (C1708: UWBM 98912). Coprolites are also found throughout the Cabbage Patch beds (e.g., UMPC 13213 from C1708, but also UMPC 14018, KUVP 20713, and KUVP 20653 from C1712). Some contain partials bones or teeth of mammals. Thus, mammalian carnivores probably contributed a portion of the carcasses that accumulated on the land surface and were later buried.

Experimental work has showed that multiple sub-parallel to parallel shallow scratches on fossils may be evidence of trampling (Fiorillo 1988, Domínguez-Rodrigo et al. 2009, Cusimano 2015). This type of marks is present on some fossils recovered from the Cabbage Patch assemblages, possible evidence of the specimens' exposure on the land surface or their shallow burial. These scratches can also be the result of the interaction of the specimens with coarse-grained substrates (Fiorillo 1988). The specimens at C1707, a channel-lag whose depositional energy was high, would likely have contacted the coarse-grained sand deposited at the base of the river bed thus acquiring many of the scratches observed. The high proportion of highly weathered specimens at C1707 may therefore be a consequence of the repeated interaction of the fossils with the substrate in which they were eventually preserved.

The high abrasion of the specimens at C1707 is different from that of other localities. This is consistent with the coarse lithology of these deposits and their interpretation as a high depositional energy channel-lag (Behrensmeyer 1988). Wilson (2008) also found a higher proportion of highly abraded specimens in a coarse-grained deposit and, conversely, more minimally abraded specimens in a fine-grained one. Moore and Norman (2009) found that abrasion did not have an important role in determining the specimen assemblages recovered from two fine-grained deposits. Abrasion has been suggested to be a consequence of transport (Fiorillo 1988) although there is evidence of extensive bone transport without abrasion (Behrensmeyer 1982, Evans 2014). There can also be abrasion with little or no transport as a consequence of interactions with windborne particles, bone oscillation at the base of a river channel, travel of sediment around a motionless bone, water impact on a bone in the absence of sediment particle interaction, and soil movement from freezing, thawing, swelling, and shrinking (Behrensmeyer 1982, Fisher 1995, Evans 2014). Other processes, including trampling, chewing, licking, and digestion, have also been recognized as possibly abrading bones in the absence of transport (Behrensmeyer 1991, Andrews and Nesbit Evans 1993, Fisher 1995). The association of the abraded fossils and the sedimentological evidence for a channel leave little doubt that the specimens from C1707 were transported, likely to a greater extent than the specimens from the other Cabbage Patch assemblages studied. The small size of the specimens preserved suggests, however, that this transport was not extensive. Trampling and acid etching may have contributed, at least in part, to the abrasion of mammalian specimens throughout the beds. The covariation between weathering and abrasion found in the multivariate analysis of all specimens suggests that the same process, such as interactions with sediment, could have been involved in weathering and abrading specimens.

No significant differences in shape were found across assemblages. However, these analyses quantified columnarity, flatness, and shape categories after biostratinomy and diagenesis. The differences in surface area to volume ratio across assemblages support differences in the preservation of elements according to their original (i.e., whole element) shape in the death assemblages. C1707, in particular, appears to include very few flat elements (i.e., high surface area to volume ration, categories 4-5) compared to the other assemblages, a characteristic consistent with the depositional environment inferred from geological characteristics. Indeed, high surface area to volume ratio elements are more susceptible to transport and hydrodynamic sorting (Wolff 1973, Cassiliano 1997, Coard 1999, Schreve 2006, but see Evans 2014) and are therefore unlikely to be preserved in a high depositional energy environment where the flow of water would have carried them away. My analysis of the covariation between specimen characteristics in the Cabbage Patch beds shows indeed that flatter elements, which have a high surface area to volume ratio, are more prone to breakage than more columnar or compact specimens.

The concentration of metapodials and teeth at the base of the channel deposits of C1707 along with coarse grains is evidence of transport sorting (Behrensmeyer 1991, Coard 1999). Conversely, the presence of a high proportion of high surface area to volume ratio elements in the other assemblages, in particular C1708, is evidence for little transport (Cassiliano 1997). Similarly, the presence of the particularly fragile bones of birds at C1704 (UWBM 98777) and MV6613 (UMPC 14020) also suggests little transport or at least transport in a low energy fluid or one carrying fine grained sediments. MV6613 is the assemblage with the highest proportion of high surface area to volume ratio elements after C1708. A small amount of transport in the low depositional energy assemblages is consistent with my interpretation of the sedimentological data as evidence for low depositional energy deposits. Based on the proportion of high surface area to volume ratio specimens, transport across low energy deposits was less important in the lower Cabbage Patch than in the middle and upper Cabbage Patch suggesting a change in hydrodynamic regime between the lower and middle units of the beds.

The similarities in the patterns of the ordinations of skeletal elements and their sorting according to density (see C1704, C1707, C1708, and C1721 in Figs. 7A and 7B) support the hypothesis that the skeletal element composition of the Cabbage Patch assemblages studied was at least in part density mediated. The predator-driven assemblages cluster together in this analysis of element preservation according to density. The high abundance of low-density elements in those assemblages, but not in others (e.g., C1708, Pliocene-aged floodplain deposits from the Palm Springs Formation), suggests that these elements are preferentially selected by predators of small mammals.

The pattern of skeletal element representation across assemblages is broadly compatible with the conclusions about depositional environments from sedimentological data. C1708 is found to be most similar to the Pliocene-aged floodplain deposits from the Palm Springs Formation (Cassiliano 1997) consistent with the interpretation as a low energy deposit from lithological data. A similar conclusion can be made for C1704 and C1721 based on their similarities in skeletal element composition with each other and C1708 as well as the Palm Springs Fm. floodplain assemblage.

The more complex geology of MV6613 with its short episodes of higher energy depositional environments (Table 4) is reflected in its similarities with low depositional energy assemblages (e.g., Palm Springs Fm. floodplain and C1708) as well as its similarities with the channel fill assemblage from the Palm Springs Fm.

The ambiguous pattern of skeletal element representation at C0173 suggests a mix of low depositional energy accumulation evidenced by similarities with the Palm Springs Formation floodplain and Siwalik IV assemblages and a higher energy component evidenced by similarities with Siwalik I. The deposits from Siwalik I and IV, accumulated at least in part by predators, also suggest that predation could have played a role in the accumulation of bones at C0173. C0173 is one of the assemblages where canid remains have been found (Table S11) and evidence of predation recorded.

The skeletal element representation at C0174 similar to that of the Palm Springs Formation floodplain deposits and even, to a lesser extent, C1708 is consistent with the interpretation of the deposits as low energy environment from lithological data. The similarities with C0173, and Siwalik IV, or even the assemblage accumulated by *Canis latrans* and C1707 (see below), suggest a minor influence of predators in the accumulation of the fossil assemblage.

The few small carnivorans recovered from C0174 (Table S11) are consistent with the possibility of such accumulation.

The skeletal element representation at C1707 is most similar to assemblages derived in part or whole from carnivores and low energy deposits. This is a very surprising result in light of the sedimentology of the assemblage. The cross-bedded upward-fining sandstone is indicative of a channel-lag. It is possible that the lack of a skeletal element dataset for such a depositional environment prevented a more accurate classification of C1707. The small number of identifiable elements at C1707 (Table 1) may also hamper a better classification of this assemblage. C1707 is never found to be similar to the Palm Springs channel-fill assemblage (Cassiliano 1997) from which it differs in the proportion of skulls, dentaries, metapodials, and phalanges (Table 3), or the coarser deposits of the Siwalik (Badgley 1986a). The abundance of metapodials and teeth at C1707 may be a consequence of hydrodynamic sorting. Metapodials and teeth have been found to be lag bones in previous studies (Coard 1999), along with elements rare across the assemblages of the Cabbage Patch beds (including limb bones and podials). Dentaries, a common element in lag deposits (Coard 1999), are not particularly abundant at C1707 however. This may be a consequence of the susceptibility to weathering of this element (Behrensmeyer 1991). Dentaries are flat elements that are fragile and more susceptible to breakage as evidenced by the results of the NMDS of all specimens. Flat elements are rarer in coarser-grained deposits (Wilson 2008).

Many have studied the link between skeletal element representation and raptorial agents of accumulation, sometimes linking individual assemblages with specific predators (e.g., Dodson and Wexlar 1979, Hoffman 1988, Andrews 1990). However, this may be difficult in the fossil record as a consequence of the disintegration and reworking of pellets post-regurgitation

(Hoffman 1988, Saavedra and Simonetti 1998, Terry 2004, 2007, Czaplewski 2011). Therefore, although none of the Cabbage Patch assemblages display a skeletal element composition similar to those produced by avian predators (Fig. 7A), I cannot use this evidence to reject the possibility that avian predators played a role in the assembly of the small mammal fossil assemblages. There is in fact evidence from select fossil specimens that raptorial birds participated in the accumulation of skeletal remains in the Cabbage Patch beds. For example, Rasmussen (1977) had suggested that a specimen of sicistine rodent (Dipodidae) from the middle Cabbage Patch (UMPC 2247, Fig. 5B) is the product of a raptorial bird pellet. I find that several characteristics of the specimen do support such origin for these remains:

(1) Sicistine rodents are known to be a prey of raptorial birds in modern and fossil assemblages (e.g., Storch 1969, Cserkész 2007).

(2) The specimen includes several individuals from the same rodent taxon (MNI=3), a pattern consistent with raptorial pellets where the remains include a restricted number of taxa (Kusmer 1990, Lyman et al. 2003).

(3) The specimen includes several partial skulls and dentaries as well as a tibia and a caudal vertebra, elements that can be common in owl pellets (Dodson and Wexlar 1979, Andrews 1990, Terry 2004, Gomez 2005, Rudzik et al. 2015). No other elements are preserved suggesting that the specimens likely did not die in a burrow where a more complete portion of the skeleton would have been preserved (as in KUVP 18400 or UWBM 63273, two gopher skeletons from the middle Cabbage Patch, Fig. 5C).

(4) A few elements of a partial manus or pes are articulated; these elements are common in intact owl pellets (Terry 2004) and often articulated in owl pellets unlike in the products of

mammalian predators’ digestion (Czaplewski 2011). They provide evidence for burial while or quickly after soft tissues where still present around the bones (as in decomposing owl pellets).

(5) The bones of UMPC 2247 are little broken and display only few macroscopic chemical damages that are consistent with the processing of preys by owls. In remains accumulated by diurnal raptors and mammalian predators, elements are heavily fragmented and display heavy to extreme digestive damage (Mayhew 1977, Dodson and Wexlar 1979, Andrews 1990, Montalvo et al. 2008, Lloveras et al. 2009, Czaplewski 2011, but see Rudzik et al. 2015 for geographic variation).

(6) The skulls also display the characteristic damage of raptorial birds in which the posterior and dorsal portion of the animal is removed (Mayhew 1977, Dodson and Wexlar 1979, Kusmer 1990, Terry 2004). Several other rodent specimens (e.g., UMPC 2146, *Pleurolicus* and UMPC 1409, *Gregorymys*) display this skull breakage pattern also noticed by Cassiliano (1997) in the Pliocene deposits of the Palm Springs Formation.

Evidence for a raptorial contribution to the accumulation of bones in Cabbage Patch assemblages can also be found in the composition of the fauna, dominated by small mammals (Table 1, Rasmussen 1977, Rasmussen and Prothero 2003). Damuth (1982) in his study of Oligocene-aged deposits from the Brule Formation of South Dakota found small mammals (<5 kg) to be more abundant in a floodplain assemblage (86.29%) than in a near stream one (42.62%). Although he suggests that small mammals may be underrepresented in both assemblages because of preservation, the relative abundance of small mammals in the Cabbage Patch assemblages is much higher than in the deposits of the Brule Fm. This suggests a bias against large mammals and towards small ones in the accumulation of fossils in the Cabbage Patch beds. One possible agent of accumulation that would favor small mammals and filter out large mammals is predation by raptors (Mayhew 1977, Dodson and Wexlar 1979, Andrews 1990, Cassiliano 1997, Lyman et al. 2003, Czaplewski 2011, Rudzik et al. 2015).

The large proportion of small mammals in some of the Cabbage Patch assemblages may also be explained by the ecology of the taxa present. Thus, the large proportion of gophers (Geomyidae: Entoptychinae) at C0173 (Table S11) may be a consequence of the burrowing ecology of these animals (Rensberger 1971, Gobetz and Martin 2006), which is known to lead to higher preservation rates (Weissbrod and Zaidner 2014). Alternatively, the fragmentary nature of the entoptychine remains at C0173 may suggest that the specimens were not preserved within burrows but represent an accumulation by selective predators providing further evidence for an important role of predators in the accumulation of mammalian remains in the Cabbage Patch beds. Geomyid and heteromyids rodents, close modern relatives of the gophers from C0173 can be common preys of predatory birds (Alvarez-Castañeda et al. 2004).

The abundance of small mammals in the Cabbage Patch beds has important consequences on the taphonomic characteristics of the assemblages. Small animal remains are likely to be degraded by breakage, weathering, and abrasion faster and to a greater extent than the remains of larger mammals as a consequence of higher surface area to volume ratios and their higher likelihood of transportation (Behrensmeyer 1978, Badgley 1986a, Andrews 1990). Indeed, the proportion of highly weathered and abraded specimens in Cabbage Patch is high compared to assemblages of larger mammals (e.g., Fiorillo 1988).

Although rare, large mammals are found throughout the Cabbage Patch beds. At least one of three families of large ungulates (i.e. Equidae, Merycoidodontidae, and Rhinocerotidae) is present in all of the assemblages studied. Large ungulate teeth are only absent from C1704 and C1707. Yet, a rhinocerotid astragalus (*Diceratherium;* UMPC 1462, Prothero and Rasmussen

2008) was recovered from C1704 and several specimens of the largest carnivore known from the Cabbage Patch beds, *Cynodesmus thooides*, have also been found there (e.g., UWBM 98680, UWBM 98730). A taxonomically ambiguous partial rib of a large mammal was also recovered *in situ* from C1707 (UWBM 98781, Fig. 5A). Large mammals are relatively abundant at assemblages where the depositional environment was unfavorable to the preservation of small mammals (e.g., C1709; Douglass 1903, Riel 1964). The presence of some large mammals, mammalian predators, and the taxonomic diversity of the small mammals within the Cabbage Patch assemblages suggest that avian predators could not have been the sole agents of accumulation (Marti 1976, Andrews 1990, Kuzmer 1990). The disarticulation of the vertebrate remains suggests that avian predators' pellets, if produced, would have been broken down and reworked, possibly by fluvial processes. These processes would have incorporated in the deposits larger mammals including carnivorans.

It appears that middle and upper Cabbage Patch assemblages overall preserve a higher percentage of more complete material than lower Cabbage Patch assemblages as evidenced by the ratios of elements to fragments. However, it is difficult to determine if the increased breakage was pre- or post-burial and thus if the increased fragmentation in older assemblages is the product of increased exposure on the surface, higher levels of trampling, longer or rougher transport, increased predator activity, or the result of diagenesis. Moreover, although the ratio of elements to fragments is highly correlated with the ranked age of each assemblage, the relationship is not perfect. The lower Cabbage Patch includes an assemblage with a high ratio of elements to fragments (MV6613) as well as one with a very low ratio (C1721). It is likely that exposure time on the surface as well as mechanical and chemical breakage varied greatly across assemblages irrespective of the age of the deposits. This interpretation is supported by the lack of relationship between the ratio of elements to fragments and the breakage of identifiable elements. Even assemblages with high ratios of elements to fragments (C0173 and MV6613) can be significantly different from one another in their proportions of complete and partial specimens.

The higher energy deposits of C1707 preserve a greater proportion of fragmentary elements than any other assemblage suggesting a higher breakage consistent with the interpretation as a channel-lag (Behrensmeyer 1988). Superimposed on these temporal and depositional patterns, geographical differences are also apparent. The assemblages from the Deer Lodge basin have higher ratios of elements to fragments than those from the Flint Creek basin (Table 1).

The broad agreement between lithologies and patterns of specimen characteristics across the assemblages studied leads to the recognition of three taphofacies within the Cabbage Patch beds: (1) Taphofacies I: the fine-grained deposits of the lower Cabbage Patch beds (C1708, C1721, and MV6613), (2) Taphofacies II: the fine-grained deposits of the middle and upper Cabbage Patch beds (C1704, C0174, and C0173), and (3) Taphofacies III: the coarse-grained deposits (C1707). Taphofacies III is characterized by high proportions of heavily weathered and abraded specimens as well as small specimens. Breakage is also particularly high in this taphofacies. The features of this taphofacies are associated to the relatively high energy fluvial environment that led to the accumulation of the fossils as part of a channel-lag. Taphofacies I and II differ from one another in the more fragmented nature of the material from taphofacies I compared to the more complete specimens found in taphofacies II. The higher completeness in taphofacies II is associated to smaller-sized specimens, a higher percentage of flat specimens, decreased mean and median flatness, and a smaller proportion of high surface area to volume ratio specimens. The covariation of flatness, size, and shape suggests a decrease in hydrodynamic sorting and depositional energy between the lower and middle Cabbage Patch beds. This is consistent with other lines of evidence from the lithology of the Cabbage Patch beds as a whole. Indeed, conglomerates are more common in the lower than in the middle and upper units of the Cabbage Patch beds and no lacustrine intervals have been observed in the lower Cabbage Patch beds in the Flint Creek Basin. They are common in the middle Cabbage Patch beds (Rasmussen 1977). Despite a possibly higher energy fluvial environment in the lower Cabbage Patch beds than in more recent units, there is no consistent lithological difference between the beds' units across basins where they are exposed (Rasmussen 1977); the assemblages studied also do not differ in lithology.

7. CONCLUSIONS

The results of this taphonomic analysis support the conclusion that fossil preservation is broadly similar across low energy deposits of the Cabbage Patch beds. The localities described in this report are preserved in similar lithologies and differ little in the taphonomic characteristics of their specimens. They may be considered broadly isotaphonomic and can be used in future faunal analyses, specifically the investigation of taxonomic and paleoecological change through time and space. The biological patterns that arise from such work would be representative of the consequence of changing biotic, climatic, tectonic, or environmental settings through time. The lithologically and taphonomically distinct channel-lag assemblage of the lower Cabbage Patch (C1707) should likely be excluded from direct comparisons with assemblages from low energy deposits. Despite heavy filtering of the fossil assemblage by taphonomy, it may still however provide critical information such as biostratigraphic data.

Such studies should consider several caveats. Thus, although assemblages from low energy deposits were deposited by the concurrent action of predators that concentrated small mammal remains and little fluvial transport, some assemblages may show higher proportions of certain taxa or ecological guilds as a consequence of the preferential preservation of these animals (e.g., burrowing rodents in C0173).

There is also important variation across taphofacies in skeletal element representation. Comparisons between the lower and middle/upper Cabbage Patch beds should account for the change in hydrodynamic sorting between the units. The Deer Lodge and Flint Creek basins also differ in completeness, element representation, and the ratio of elements to fragments. Such differences may be best overcome by comparing sets of specimens across assemblages that are similar in size, shape, surface area to volume ratio, and completeness such as the cheek teeth of mammals.

The results of my analysis of the depositional environments and specimen preservation of the fossils from the Cabbage Patch beds suggest that, presuming careful sampling, future faunal analyses of vertebrate microfossil assemblages with similar lithologies and specimen preservation will yield biologically informative patterns of faunal change relatively unbiased by the preservation of the fossils and help shed light on the rise of modern mammalian communities during the Arikareean in the northern Rocky Mountains.

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FIGURES

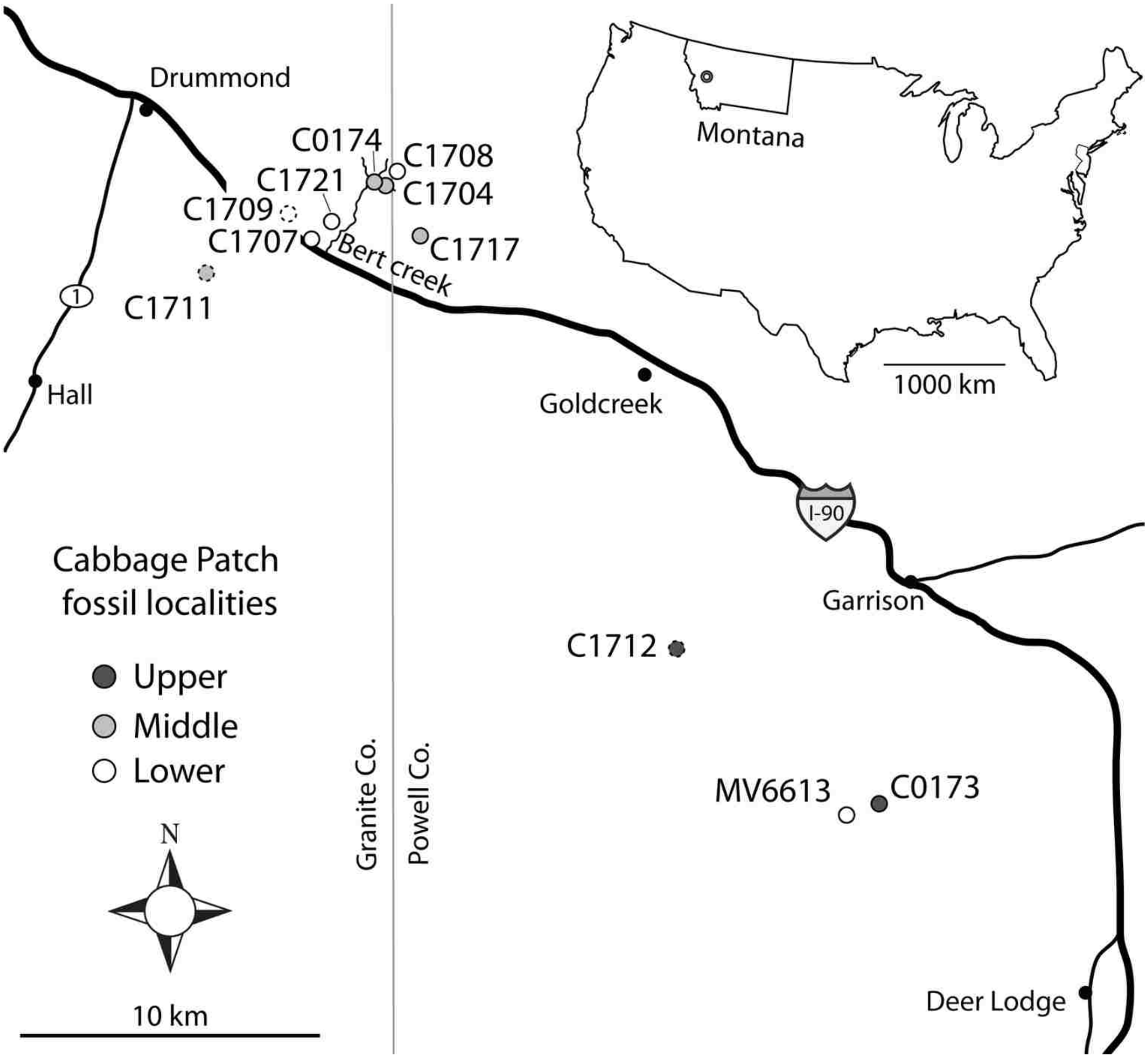

Figure 2.1. Map of the assemblages discussed in the text. Continental map shows the location of the area studied in the United States and the state of Montana. Full circles correspond to the assemblages studied. Dashed circles represent localities mentioned in the text or figures.

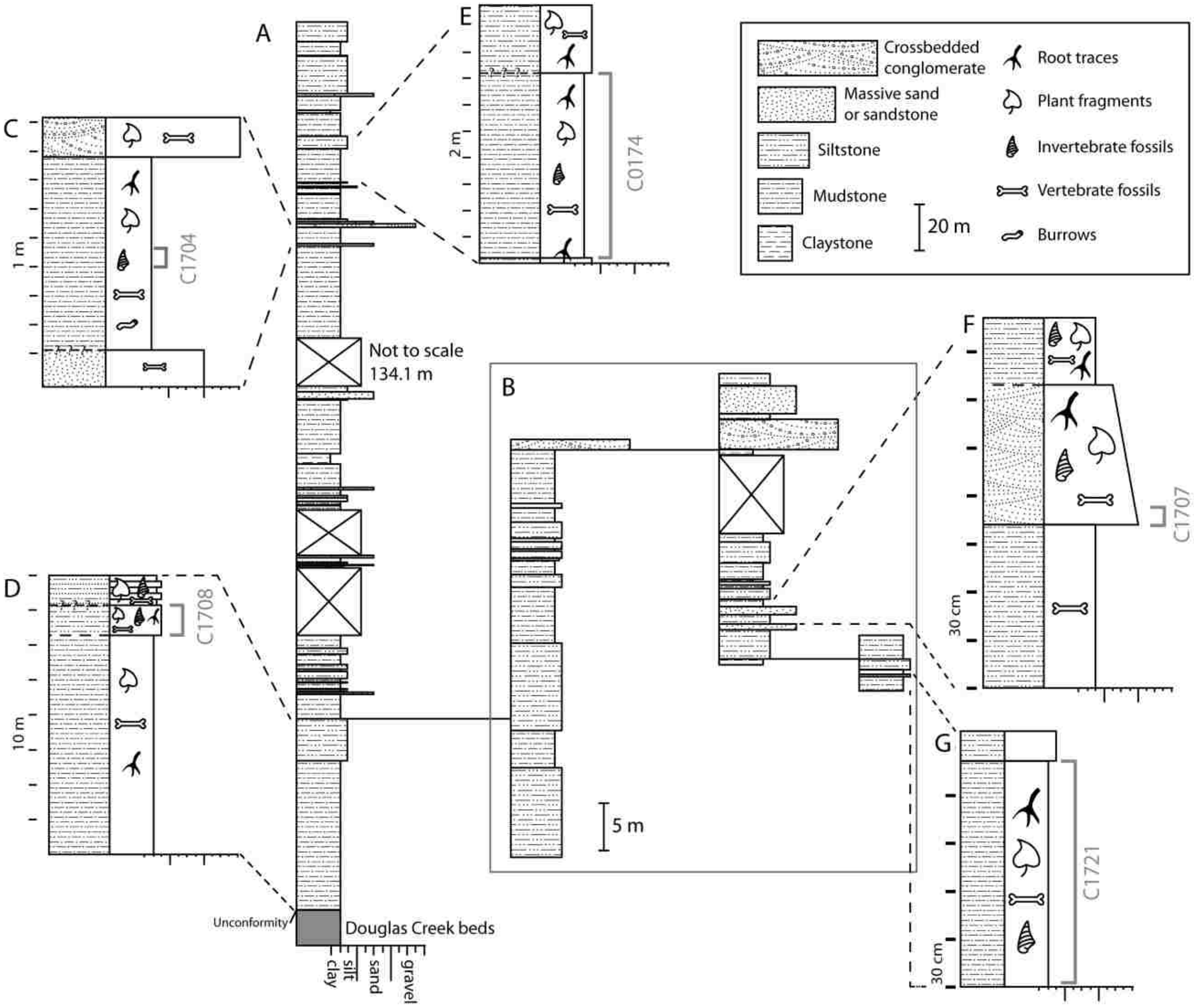

Figure 2.2. Summary of the stratigraphy of the Cabbage Patch beds in the Flint Creek basin (drawn from data modified and updated from Rasmussen 1969, 1977). A-B) Main stratigraphic section through Bert Creek. C) Detailed section for C1704. D) Detailed section for C1708. E) Detailed section for C0174. F) Detailed section for C1707. G) Detailed section for C1721.

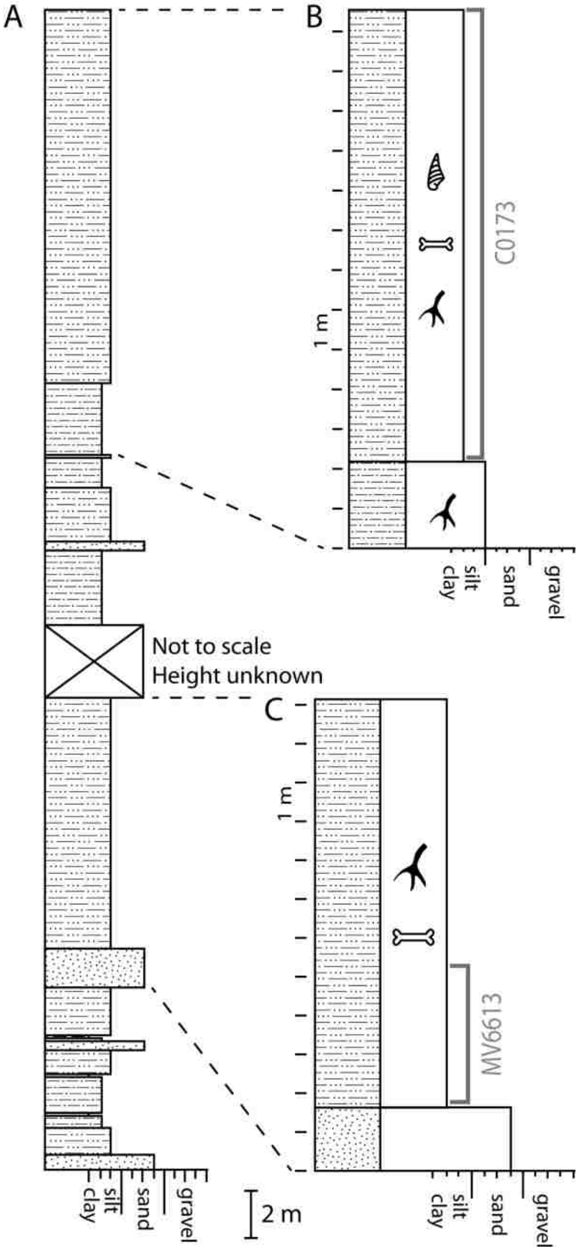

Figure 2.3. Stratigraphy of the Cabbage Patch beds in the Deer Lodge basin (drawn from data modified and updated from Rasmussen 1977). A) Main section through the Tavenner Ranch area. B) Detailed section for C0173. C) Detailed section for MV6613. See Figure 2 for legend.

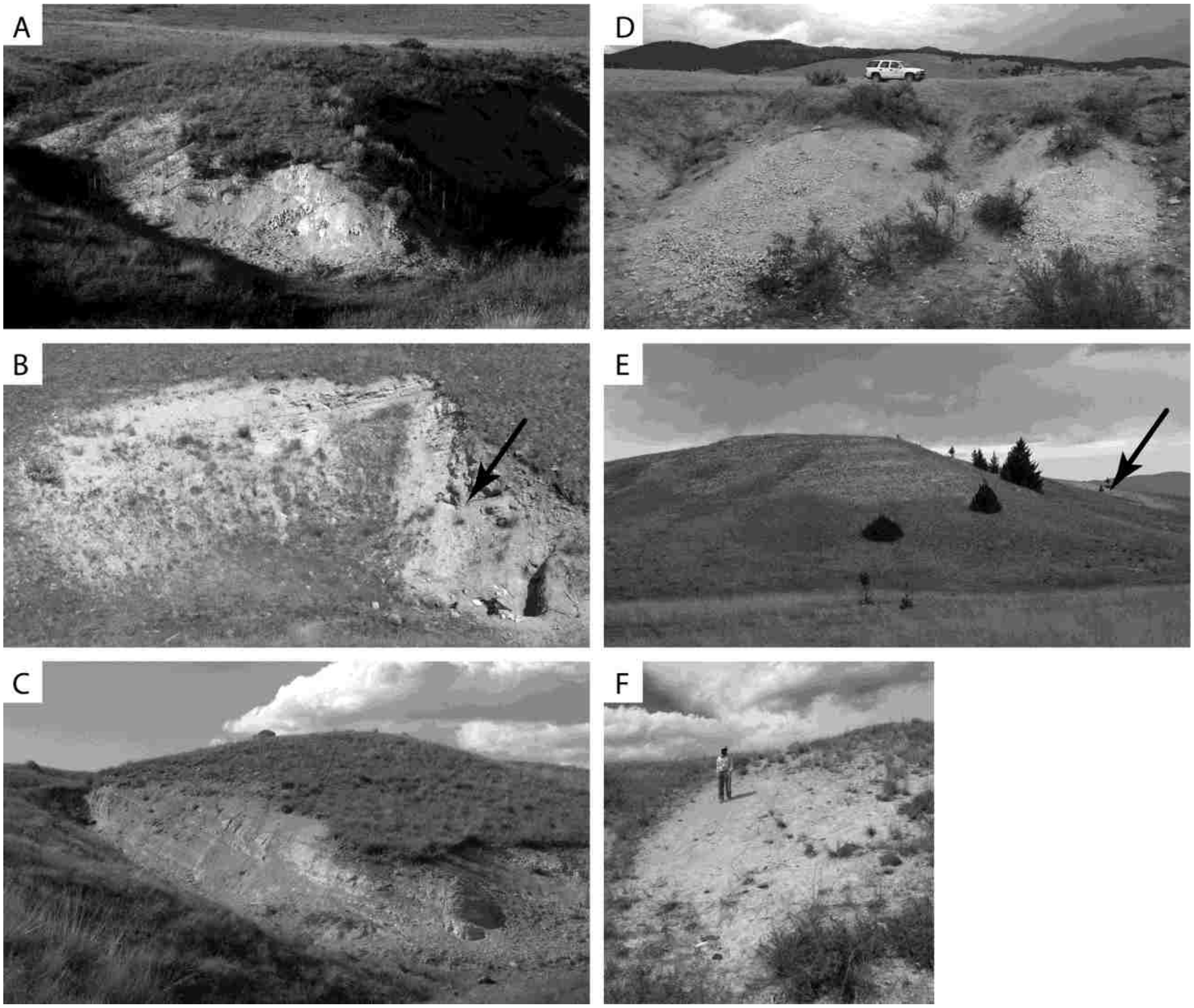

Figure 2.4. Views of the outcrops of the assemblages studied. A) C1708. B) C1707, productive horizon at the arrow. C) C1721. D) C1704. E) C0173, outcrop at the arrow (photo courtesy of A. Barnosky). F) C0174.

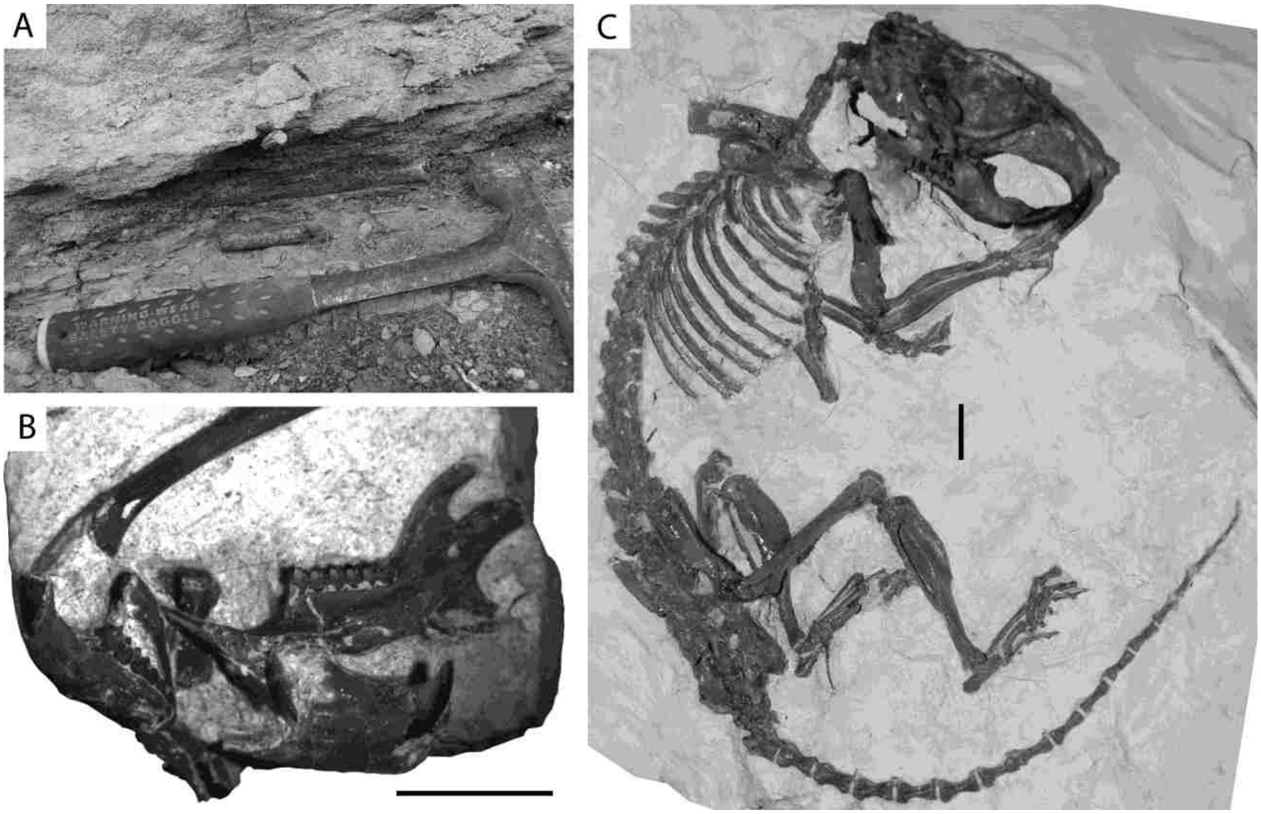

Figure 2.5. Examples of fossils from the Cabbage Patch beds. A) In-situ isolated and fragmented mammalian rib at C1707 (UWBM 98781). B) Possible fossil owl pellet from C1717 (UMPC 2247), scale = 5 mm. C) *Pleurolicus* skeleton found in its burrow at C1711 (KU 18400), scale = 1 cm.

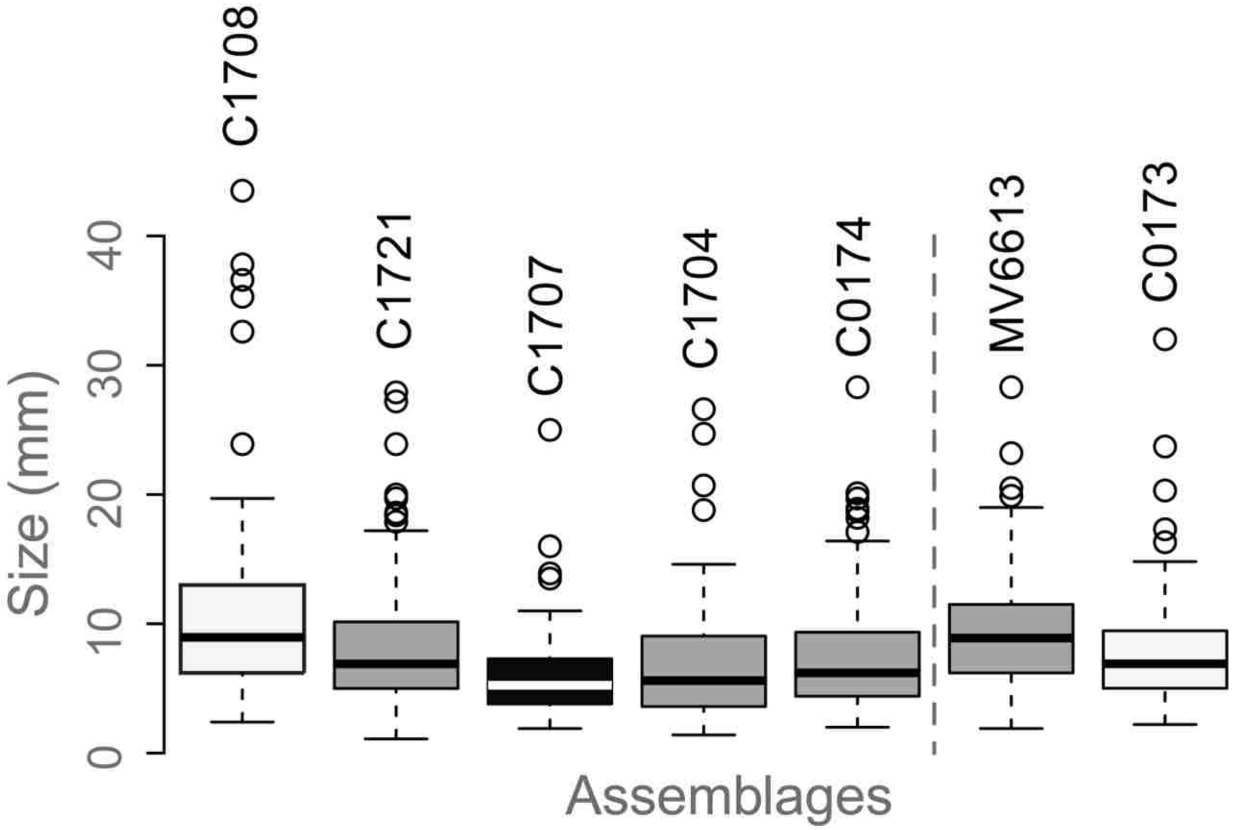

Figure 2.6. Box and whisker plot showing the mean and range of specimen size across assemblages. Assemblages are ordered stratigraphically. The dashed line separates the assemblages from the Flint Creek and Deer Lodge basins. The color of the box corresponds to the lithology of the deposits. White: light grey, dark grey: mudstone, black: sandstone. Outliers are shown with circles.

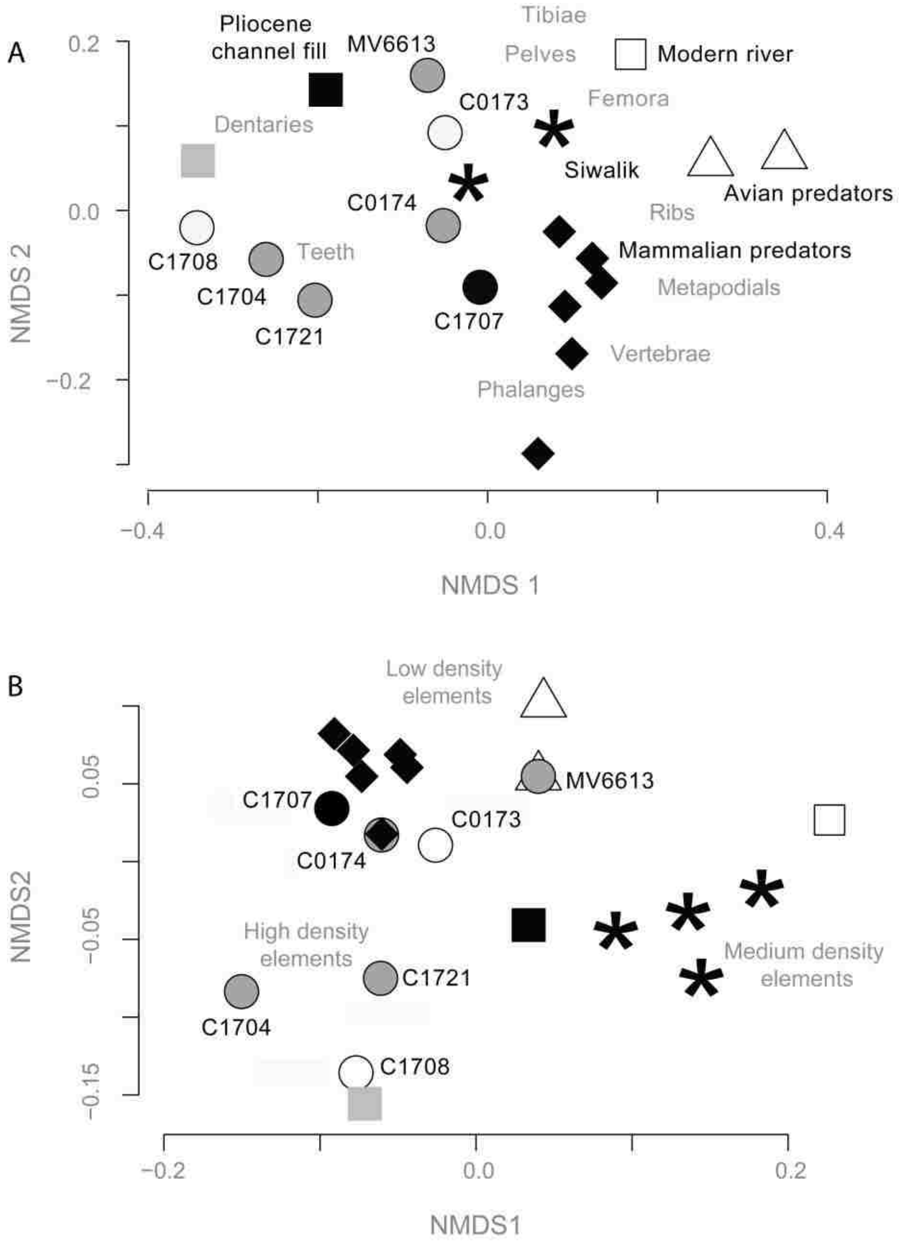

Figure 2.7. Non-metric dimensional scaling plots of Cabbage Patch assemblages and select comparative assemblages. A) NMDS plot of skeletal element representation across Cabbage Patch assemblages and select other assemblages from the literature. The most influential elements are listed in grey. B) NMDS plot of density distribution across categories in Cabbage Patch and select assemblages from the literature. The influential density categories are listed in grey.

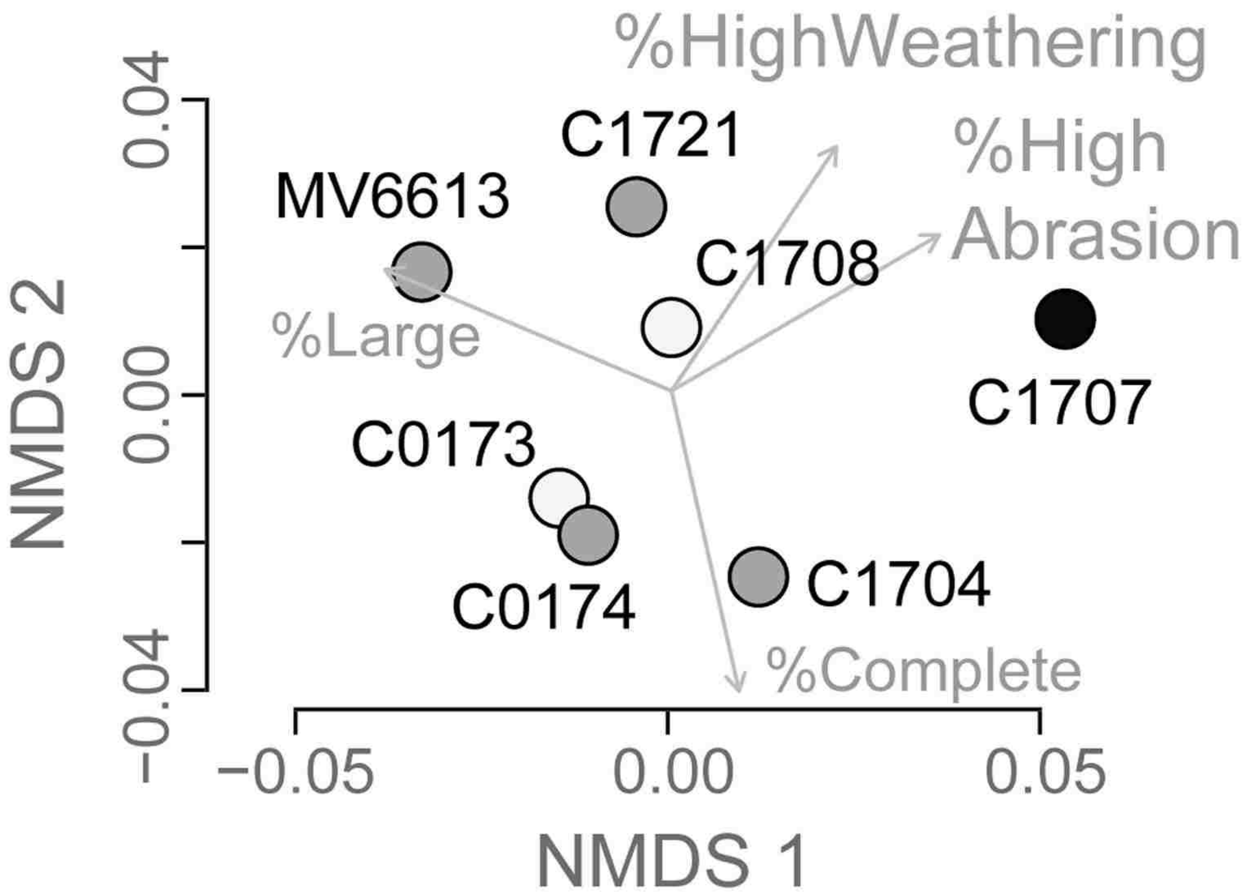

Figure 2.8. NMDS plot of summary characteristics of taphonomy across assemblages. Colors denote lithology of the deposits (see Fig. 15).

TABLES

Table 2.1. Assemblages focused of this study. Abbreviations: Loc.: assemblage, #: number, Els.: Elements, Frags.: Fragments, N: Sample size. For all assemblages except MV6613, the assemblage name is that at the UWBM. For MV6613, it is the name at the UMPC. Ratio is the number of elements / number of fragments recovered for a standardized amount of concentrate.

UWBM Loc. #	Loc. name	UMPC Loc. #	KUVP Loc. #	Unit	N Els.	N Frags.	Ratio	N Dataset	% Small mammals
C0173	Tavenner Ranch	MV6550	Ku-Mt-21	Upper	505	92	0.13	104	97.4
C0174	Cabbage 13	MV6547	Ku-Mt-46	Middle	131	94	0.15	108	96.8
C1704	Strawberry Quarry	MV6504-4	Ku-Mt-12	Middle	104	93	0.12	104	97.2
C1707	Grizzly Den	MV6554 (Unit 7)	Ku-Mt-17 (Unit 7)	Lower	48	91	0.1	102	100
C1708	Sharp Claw Butte	MV6558-2	Ku-Mt-25	Lower	104	92	0.045	103	96.8
C1721	Hops Garden	--	--	Lower	101	91	0.1	102	98
--	Tavenner Ranch 3	MV6613	Ku-Mt-22	Lower	101	95	0.16	106	100

Table 2.2. List of variables collected from specimens for the analysis of bone preservation

References: 1: Moore and Norman (2009), 2: Fiorillo (1988), 3: Hofmann (1994).

Variable name	Description of the variable	Type of variable	Reference
Weathering	Cracking and flacking of the bone surface	Categorical from 0 to 3	1, 2, SI
Abrasion	Rounding of edges and processes of the bone	Categorical from 0 to 3	1, 2, SI
% Completeness	Volume percentage of the original element for this taxon	Estimated to the closest 5%	1, SI
L1	Measurement of the longest axis of the bone	Measured in mm	1
L2	Second longest axis perpendicular to L1	Measured in mm	1
L3	Third longest axis perpendicular to L2	Measured in mm	1
Columnarity	-L3/L1	Unitless	1, 3
Flatness	-L3/L2	Unitless	1, 3
Surface area to Volume Ratio	Ratio of surface area to volume of bone based on element identity	Categorical from 1 to 5	1, SI

Table 2.3. Representation, as a percentage, of skeletal elements across assemblages from the Cabbage Patch beds and comparative assemblages from the literature. References: 1, this study; 2, Lloveras et al. (2012); 3, Aslan and Behrensmeyer (1996); 4, larger mammal assemblages of Badgley (1986a); 5, small mammal assemblages of Cassiliano (1997); 6, Lloveras (2008); 7, Andrews and Nesbit Evans (1983).

Assemblage	Astragali	Calcanea	Dentaries	Femora	Humeri	Pelves	Metapodials	Phalanges	Radii/Ulnae	Ribs	Scapulae	Skulls	Tibiae	Teeth	Vertebrae	Source
C0173	2.4	4.3	9.1	3	5.8	3	10.4	13.2	5.5	0.3	1.3	4.3	5	25	7.7	1
C0174	0.5	0.5	8.7	3.9	2.4	1.5	8.3	17	4.4	0.5	1	5.8	3.4	28.6	13.6	1
C1704	1.7	1.7	5.1	0.7	1.7	0.7	4.4	8.5	1	0.3	0.7	3.4	0.3	60.8	8.9	1
C1707	0	4.5	6.1	7.6	1.5	1.5	12.1	16.7	4.5	1.5	0	1.5	3	28.8	10.6	1
C1721	2.4	3.4	9.6	2.9	2.9	0	3.8	13.5	1.9	1	1	0.5	1	50	6.2	1
C1708	1.2	1.5	12.1	1.5	1.5	0.6	2.4	7.6	0.9	0.3	0	3.3	0.9	61.5	4.5	1
MV6613	1.4	1.4	18.9	10.1	6.8	1.4	8.8	11.5	6.8	0	0	4.1	4.1	16.2	8.8	1
Eagle Owl 1	0	4.7	2.1	8.6	1.3	7.3	13.7	14.6	3.9	11.6	0.4	3.4	10.3	7.3	10.7	2
Eagle Owl 2	2.4	3.9	0.5	11.2	1.9	8.6	18.6	15.1	1.7	8.5	1	1.4	9.6	2.5	13.2	2
Modern Fluvial	1	2.7	5	6.7	8.4	4.7	7.7	5	9.1	9.7	4	7.4	9.4	5.4	13.8	3
Siwalik I	1.5	5.4	4.2	2.9	2.7	2.4	10.1	9.1	5	9.4	1.6	6.2	3.9	27.9	7.7	4
Siwalik II	1.1	1.6	4.4	4.2	2.2	2.2	8.7	2.9	2.2	18.2	2	5.8	3.6	31.3	9.6	4
Siwalik III	1.5	2	2.9	3.9	2.5	2.8	5.9	3.9	3.5	24.7	1.1	7.6	2.8	21.4	13.5	4
Siwalik IV	1.8	1.5	6.8	3	3	1.2	4.7	5	5.3	7.7	2.7	6.8	2.7	36.2	11.6	4
Pliocene Channel Fill	1.6	2.6	18.5	2.6	4.3	2.4	3	4.7	1.4	0	1.2	13.4	3.5	34.3	6.3	5
Pliocene Floodplain	0.8	1	13.4	1.2	2	0.8	1.7	4.7	1.5	0.2	0.6	6.1	1.2	61.7	3.1	5
Lynx	0.5	0.9	3.1	2.5	3	3.4	8.3	24.1	3.4	8	1.5	4	1.8	20.9	14.8	6
Mongoose	1.3	1.5	2.2	2.6	3.2	1	6.5	24.2	2.5	8.9	0.7	2	1.2	15.8	26.4	7
Coyote	0.3	0.7	4.3	4.6	4.6	2	11.8	21.7	6.2	4.3	0.7	2.6	3.9	13.5	18.8	7
Fox	0.6	1.2	2.4	4.7	3.5	1.2	13.5	28.2	2.9	4.7	0.6	1.2	2.9	14.7	17.6	7
ArcticFox	1.5	0	4.4	0.7	2.2	0	13.3	39.3	1.5	3.7	0	3.7	1.5	8.9	19.3	7
Marten	0	0	3.4	1.7	5	0.8	12.6	22.7	4.2	5	1.7	2.5	0.8	20.2	19.3	7

Table 2.4. Summary of the sedimentological characteristics for the assemblages used in this study. (continued on next page)

Assemblage	Grain size	Sorting	Roundness
C0173	Siltstone (minor amounts of clay), rare very fine to very coarse sand, very rare gravel	Poorly sorted	Subrounded to subangular
C0174	Mudstone (mostly clay and silt) with very minor amounts of very fine to fine sand	Poorly sorted	Subrounded to subangular
C1704	Mudstone (mostly clay and silt) with minor amounts of very fine to fine sand	Moderately sorted	Subrounded to subangular
C1707	Very fine to medium sandstone with minor amounts of coarse to very coarse grains	Very poorly sorted	Angular to subrounded
C1708	Siltstone with minor amounts of clay, and rare very fine sand	Moderately sorted	Angular to subangular
C1721	Mudstone (mostly clay and silt) with minor amounts of very fine to fine sand	Moderately sorted	Subrounded to subangular
MV6613	Mudstone with mostly clay, abundant very fine sand and silt, minor silt-sized glass shards, rare granules	Poorly sorted	Glass shards angular to subangular, silt angular to subrounded, and sand subangular to rounded

Table 2.4. continued

Assemblage	Color	Thickness	Sedimentary features	Environmental interpretation
C0173	Olive gray (5Y 5/2)	1,070 cm; top of unit eroded	Massive; no features	Low energy fluvial environment; reworked aeolian ash falls
C0174	Mottled pale brown (2.5Y 8/2) to light gray (2.5Y 7/2)	1,400 cm	Massive; no features	Low energy fluvial environment; lacustrine / lacustrine delta fill
C1704	Light gray (5Y 7/1) in base to pale yellow (5Y 7/3) in top	670 cm; fossils concentrated within the middle 60 cm of the unit	Massive; no features	Low energy fluvial environment
C1707	Very diverse	85 cm; fossils in bottom 15 cm	Cross-bedding; fining-upwards	Channel-lag
C1708	Light olive gray (5Y 6/2)	840 cm; richest concentration of fossils 90 to 180 cm below the top of the unit	Massive; no features	Low energy fluvial environment; reworded aeolian ash falls
C1721	Pale olive (5Y 6/3)	145 cm; fossils dispersed throughout unit	Massive; no features	Low energy fluvial environment; reworked aeolian ash falls
MV6613	Light olive gray (5Y 6/2) to Yellowish brown (10YR 5/3, 10YR 5/4)	350 cm; fossils most abundant in lower 120 cm	Massive; occasional thin lenticular sands containing sedimentary and metamorphic rock fragments; presence of calcareous nodules	Low energy fluvial environment with crevasse splays

Table 2.5. Summary of the paleontological characteristics for the assemblages used in this study.

Locality/Horizon	Plants/Algae	Invertebrates	Vertebrates
C0173	Numerous root traces	Land snails abundant, fresh-water snails rare	Fish bones very rare, turtles and amphibians rare, mammal bones and teeth common
C0174	Numerous carbonaceous plant fragments, rare diatoms, very common root traces	Very abundant fresh-water snails, numerous invertebrate burrows	Fish and amphibians absent, mammal bones and teeth common
C1704	Numerous root burrows, rare diatoms, plant fragments common	Rare ostracods, rare molds and poorly preserved broken shells of fresh-water and land snails, slug shells, insect burrow casts	Fish bones very rare, amphibian bones locally concentrated, mammal bones and teeth locally concentrated
C1707	Few root traces, small plant fragments	Fragments of freshwater snails	Fish bones common, frog bones very abundant, mammal bones and teeth common
C1708	Root traces and plant fragments common	Molds of land and fresh-water snails, ostracod molds	Fish abundant, frog bones common including some partially articulated, mammal bones and teeth common
C1721	Root traces and plant fragments common	Few freshwater snail fragments	Fish absent, Frog bones abundant, mammal bones and teeth very common
MV6613	Root traces abundant	Rare slug shells and fresh-water snail shells	Fish and frog remains absent, Mammal bones and teeth common

Table 2.6. Intra-observer error across variables.

Variable	Mean error	Mean error (as % of measurement)
Length	0.18 mm	2.2
Width	0.16 mm	4.5
Depth	0.11 mm	3.2
Columnarity	0.02	4.5
Flatness	0.03	5.6
Completeness	2.76 %	5.4

Table 2.7. Summary statistics of the size of specimens across assemblages.

Summary statistics	C0173	C0174	C1704	C1707	C1721	C1708	MV6613
Mean	7.7	7.6	6.9	5.9	8.4	10.8	9.4
Median	6.9	6.2	5.6	5.2	6.9	8.9	8.9
Standard Deviation	4.3	4.6	4.6	3.2	5.2	7.6	4.6
Minimum	2.2	2	1.4	1.9	1.1	2.4	1.9
Maximum	32	28.3	26.6	25	27.9	43.5	28.3
Range	29.8	26.3	25.2	23.1	26.8	41.1	26.4
Coefficient of Variation	56.2	60.8	67.5	54.8	62.2	70	48.4

Table 2.8. Summary of the significant differences between Cabbage Patch assemblages. Variables in italics are significantly different at the 0.1 level only. The assemblage in bold is the high depositional energy one. A "/" denotes a lack of significant difference between assemblages.

	C0173	C0174	C1704	**C1707**	C1721	C1708
C0174	/	--	--	--	--	--
C1704	SAV ratio	/	--	--	--	--
C1707	Abrasion Size	Abrasion Weathering	Weathering *Completeness* SAV ratio	--	--	--
C1721	*Completeness* *SAV ratio*	Weathering	Completeness	*Abrasion* Size Weathering *SAV ratio*	--	--
C1708	*Completeness* SAV ratio	Size SAV ratio	Size Weathering Completeness *SAV ratio*	Size SAV ratio	Weathering *SAV ratio*	--
MV6613	Completeness	Size *Completeness*	Size Completeness SAV ratio	*Abrasion* Size *Completeness* *SAV ratio*	SAV ratio	SAV ratio

Table 2.9. Taphonomic characteristics across assemblages including (1) proportions of columnar, compact, and flat specimens, (2) proportions of specimens in weathering categories 0 through 3, (3) proportions of specimens in abrasion categories 0-1 through 3, (4) proportions of specimens in surface area to volume ratio categories 1 through 5, (5) proportions of fragmentary (0-50%), partial (>50-95%<), and complete (95-100%) specimens, and (6) proportions of elements in three density categories (skulls are not included, see text). †: categories grouped in Chi-square tests. Abbreviations: SAV, surface area to volume ratio; Sa, sandstone; Si, siltstone; Mu, mudstone.

	C0173$^{\text{Si}}$	C0174$^{\text{Mu}}$	C1704$^{\text{Mu}}$	C1707$^{\text{Sa}}$	C1721$^{\text{Mu}}$	C1708$^{\text{Mu}}$	MV6613$^{\text{Si}}$
% Columnar	67.3	57.4	52.9	58.8	50.5	54.9	71.7
% Compact	8.7	19.4	14.4	11.8	18.4	13.7	5.7
% Flat	24	23.1	32.7	29.4	31.1	31.4	22.6
Weathering 0	24	18.5	26.9	11.8	35	9.8	20.8
Weathering 1	46.2	62	42.3	42.2	32	52	48.1
Weathering 2	23.1	13.9	26	31.4	24.3	27.5	23.6
Weathering 3	6.7	5.6	4.8	14.7	8.7	10.8	7.5
Abrasion 0-1	15.3	19.4	11.5	4	14.6	11.8	15.1
Abrasion 2	39.4	38	35.6	29.4	34	38.2	34.9
Abrasion 3	45.2	42.6	52.9	66.7	51.5	50	50
SAV: 1†	4.1	0.7	5.2	0	7.3	5.4	4.7
SAV: 2†	33	43.5	48.3	43.8	44	34.6	25
SAV: 3	39	31.3	20.7	39.6	23.9	18.5	42.2
SAV: 4	16.6	15	15.5	14.6	22	33.1	23.4
SAV: 5	7.3	9.5	10.3	2.1	2.8	8.5	4.7
% Fragmentary (0-50)	45.9	45.8	32.7	50	41.6	46.7	41.6
% Partial (>50-95>)	14.3	16.8	15.4	16.7	29.7	27.6	33.7
% Complete (95-100)	39.8	37.4	51.9	33.3	28.7	25.7	24.8
% Low density (<0.41)	28.2	29.2	16.4	31.8	16.8	9.9	34.5
% Mid density (>0.41-0.5>)	16.8	13.1	7.4	10.6	14	14.5	24.4
% High density (>0.5)	51	52	72.7	56	68.8	72.1	37.3

Table 2.10. Results of the pairwise Spearman rank-order correlation tests. R^2 values are shown for a subset of the assemblages included in the analysis (see appendix A2.8 for details and p-values).

	C0173	C0174	C1704	C1707	C1721	C1708	MV6613
C0174	0.86	--	--	--	--	--	--
C1704	0.80	0.76	--	--	--	--	--
C1707	0.82	0.81	0.64	--	--	--	--
C1721	0.78	0.64	0.79	0.80	--	--	--
C1708	0.82	0.81	0.91	0.74	0.80	--	--
MV6613	0.84	0.88	0.69	0.83	0.78	0.85	--
Pliocene Channel Fill	0.78	0.79	0.77	0.58	0.59	0.90	0.76
Pliocene Overbank	0.86	0.89	0.82	0.66	0.63	0.92	0.85
Mongoose	0.59	0.62	0.59	0.71	0.68	0.60	0.59
Coyote	0.76	0.81	0.55	0.82	0.65	0.58	0.75
Fox	0.65	0.67	0.44	0.81	0.63	0.52	0.64

Table 2.11. Taphonomic characteristics of Cabbage Patch assemblages included in the multivariate analysis of similarity. NMDS scores are from Table S10. See text for details.

	C0173	C0174	C1704	C1707	C1721	C1708	MV6613
Element NMDS1	0.949787	0.947745	0.739104	0.991155	0.796576	0.657541	0.92919
Element NMDS2	1.091978	0.982213	0.942215	0.909323	0.89399	0.979574	1.159691
% High abrasion	84.6	80.6	88.5	96.1	85.5	88.2	84.9
% High weathering	29.8	19.5	30.8	46.1	33	38.3	31.1
% Fragmentary	45.9	45.8	32.7	50	46.7	41.6	41.6
% Complete	39.8	37.4	51.9	33.3	25.7	28.7	24.8
% Large	29.8	26.9	26	9.8	33	50	48.1
% Columnar	67.3	57.4	52.9	58.8	50.5	54.9	71.7
% Flat	24	23.1	32.7	29.4	31.1	31.4	22.6

APPENDIX

A2.1 Description of the sedimentology and paleontology of select horizons of the Cabbage Patch beds

C1708 - Sharp Claw Butte: Sharp Claw Butte is an assemblage of the lower Cabbage Patch beds (Fig. 3) within the type area (i.e., the Flint Creek basin, Fig. 1). The unit (840 cm thick) of light olive gray (5Y 6/2) ash-derived siltstone (Fig. 6A) contains clay (~15%) and minor amounts of very fine to fine sand (< 5 %). The grains are moderately sorted and sub-angular to angular. There are no visible sedimentary features in this massive bed in which the richest concentration of fossils is located about 90 to 180 cm from the top of the overlying horizon. This overlying horizon consists of interbedded mudstones and siltstones where a few invertebrate and vertebrate fossils can be found (Rasmussen 1977). The underlying bed is a bedded mudstone where some rare vertebrate fossils can be found (Rasmussen 1977, personal observations 2013). The contact with this underlying horizon is gradual. The contact with the upper horizon is buried. The fossils from Sharp Claw Butte include common small root traces and small plant fragments scattered throughout the unit. There are a few molds and debris of land and freshwater snails but no complete shells. There are a few molds of ostracods. Vertebrate bones are common and scattered throughout the unit but most vertebrate fossils are concentrated in a productive horizon towards the top of the unit. Amphibians are common. There are some local associations of frog bones including articulated specimens such as the type of *Tephrodytes brassicarvalis* (Henrici 1994). Mammal bones and teeth are common but mostly isolated and scattered. Rarely, the teeth of a single individual are recovered associated. A few partial mammal skulls have been recovered as well (e.g., KU 18166). Most mammal fossils are very fragmentary but rarely heavily weathered. Fish bones are particularly abundant (relative to other deposits) at this assemblage.

C1721 - Hops Garden: Hops Garden is an assemblage of the lower Cabbage Patch beds from the Flint Creek basin (Fig. 1). The fossiliferous horizon is a 145 cm thick unit of mudstone (Figs. 3, 6C). The unit includes multiple lenses of ashes, some of which little reworked and pristine. These lenses may be as thick as 15 cm. The pale olive (5Y 6/3) mudstone is moderately sorted. The ash-derived unit contains mostly clay and silt as well as minor amounts of very fine to fine sand (< 5 %). The silt grains are subangular to subrounded grains. The bed is massive with no visible sedimentary features. The fossils are dispersed throughout the unit; there is no concentration of the fossils. The overlying horizon is an aeolian ash fall 19 cm thick. The base of the fossiliferous unit is buried and the underlying unit is not available for description. The contact with the overlying horizon is abrupt. The fossils from Hops Garden include common root traces and small plant fragments scattered throughout the unit. There are some molds and debris of land and freshwater snails but no complete shells. Vertebrate bones are common and scattered throughout the unit. Frog remains are common. Mammal bones and teeth are common but mostly isolated and scattered. The teeth of a single individual are sometimes recovered associated. No fish bones were recovered at this assemblage.

C1707 - Grizzly Den: Grizzly Den is an assemblage of the lower biostratigraphic unit of the Cabbage Patch beds from the Flint Creek basin (Fig. 1). The unit is a fining-upwards 85 cm thick arkosic sandstone (Figs. 3, 6B). The grains of the basal 15 cm of the unit are mostly very fine to medium sized with few (< 10%) coarse and very coarse grains. Some lenses of sand are much coarser (mostly coarse to very coarse sand with less than 5% of smaller grains). The sandstone somewhat coarsens for the next 5 cm up section where it is dominated by fine to very coarse grains. The upper part of the unit is composed mostly of silt-sized to fine sand grains with few medium to very coarse grains (< 2 %). The sandstone is an arkose including grains of mica, quartz, feldspar, and iron oxide. It is very poorly sorted. The arkose is poorly consolidated towards the base of the unit and much better consolidated towards the top. Sediment color varies greatly throughout the beds. The grains are angular to sub-rounded. Cross-bedding is visible throughout the unit (Fig. 6B). The fossils are concentrated in the bottom 15 cm of the unit along with coarser grains of sand (Fig. 7a). The underlying horizon is a siltstone with few grains of sand that contains a few fish bones in its upper half. The overlying horizon is a massive ash-derived siltstone with numerous, sometimes large (> 0.5 cm wide) root casts, few small plant fragments, freshwater snail shells, amphibian and fish bones, mammalian bones and teeth. Rasmussen (1977) also reported the presence of charophytes, diatoms, land snails, and sponge spicules. The contact between C1707 and the underlying unit is an unconformity. The contact with the overlying unit is gradual. The fossils from Grizzly Den include common small root traces towards the top of the unit. A few small plant fragments are scattered throughout the unit. There are a few fragments of freshwater snails but no complete shells. Vertebrate bones and teeth are common at the base of the unit and very rare above. All vertebrate fossils are isolated and scattered. No articulated material was recovered from this unit. Fish bones are present though less common than at C1708. Amphibian bones are very abundant, more so than in any other assemblage considered in this study. Mammal fossils are common and very fragmentary.

MV6613 - Tavenner Ranch3: Tavenner Ranch 3 is an assemblage of the lower Cabbage Patch beds from the Deer Lodge basin (Fig. 1). The fossiliferous horizon is a 350 cm thick unit of sandy mudstone (Fig. 4). The unit includes some calcareous nodules as well as occasional thin lenses of arkosic sand containing sedimentary and metamorphic rock fragments. These lenses are common about 130 cm from the base of the unit. The sandy mudstone is yellowish brown (10YR 5/3 to 5/4) at the base of the fossiliferous unit (lower 120 cm) where most fossils are found. It is light olive gray (5Y 6/2) towards the top of the unit (top 230 cm). The matrix is poorly sorted and contains mostly clay as well as abundant very fine sand and silt. Few silt-sized glass shards can also be found (< 5%). Granules are rare (< 2%). The silt grains are angular to subrounded, the sand grains subangular to rounded. Glass shards are angular to subangular. The bed is massive with no visible sedimentary features. Calcareous nodules are present in the unit. The fossils are dispersed throughout the unit but are most abundant in the bottom 120 cm of the unit. They are not associated with the lenses of arkosic sand. The overlying horizon is a sandy mudstone 60 cm thick very similar in lithology to the unit of MV6613 but displays massive bedding. The contact between the two units is undescribed. The horizon underlying the unit bearing MV6613 is a coarse-grained arkosic sand over 160 cm thick. The contact between the two units is abrupt. The fossils from MV6613 include common root traces scattered throughout the unit but most abundant at the base of the unit. Rare slug shells and fresh-water snail shells are found throughout the unit. Mammal bones and teeth are common but mostly isolated and scattered. No fish or frog bones were recovered at this assemblage. No fossils have been recovered from the unit underlying MV6613.

C1704 - Strawberry Quarry: Strawberry Quarry is a very productive assemblage of the middle Cabbage Patch beds in the Flint Creek basin (Fig. 1). The 670 cm thick unit of mudstone is light gray (5Y 7/1) at the base of the unit and pale yellow (5Y 7/3) towards the top of the unit (Figs. 3, 6D). The ash-derived matrix is dominated by clay and silt; it contains only minor amounts of very fine to fine sand (< 5 %). The silt and sand grains are moderately sorted and sub-rounded to sub-angular. There are some very rare (< 1% of the matrix) burrow casts of insects. The fossils are concentrated in the middle 60 cm of the unit. The overlying horizon is a very coarse-grained, cross-bedded conglomerate. A water-worn tooth fragment was found in this unit (Rasmussen 1977). The underlying bed is a poorly sorted, very-coarse sand. A single water-worn rhinoceros tooth was found in that unit (Rasmussen 1977). The contact between the fossil-bearing unit and the overlying conglomerate is abrupt. The contact with the underlying horizon is buried. The fossils from Strawberry Quarry include rare diatoms (Rasmussen 1977), common plant fragments scattered throughout the unit, and rare ostracods. Root casts are very common and sometimes quite large (> 2 cm in diameter). Invertebrate fossils include molds and fragments of freshwater and land snails (no complete shells). Slug shells are also present, sometimes abundant in screenwashed concentrate. Fish bones are very rare at Strawberry Quarry. A few salamander vertebrae (Plethodontidae: Tihen and Wake 1981, Salamandridae: Tihen 1974, pers. obs.) have been recovered in this horizon. Frogs are also present but not as abundant as they are at Sharp Claw Butte or Hops Garden. Mammal bones and teeth are common but mostly isolated and scattered. Quarrying of the outcrop led to the discovery of several fragmented canid specimens (*Cynodesmus thooides*, UWBM 97346, 97348, 98680, 98730) concentrated in a lens. Most specimens however are found isolated and disarticulated.

C0174 - Cabbage 13: Cabbage 13 is an assemblage of the middle Cabbage Patch beds in the Flint Creek Basin (Figs. 1) correlated to the section measured by Rasmussen (1977). The corresponding measured unit is 1400 cm thick (Fig. 3). Neither the base nor the top of the unit hosting Cabbage 13 are exposed. The unit is a mudstone consisting mostly of clay and silt (Fig. 6E). There are only few very fine to fine sand grains (~5%). The mottled pale brown (2.5Y 8/2) to light gray (2.5Y 7/2) matrix is poorly sorted. The silt and sand grains are sub-rounded to sub-angular. There are no visible sedimentary features in this massive bed. The overlying horizon consists of a massive ash-derived siltstone where few mammal bones and plant fossils (rare diatoms, common plant fragments and root traces) have been found (Rasmussen 1977). The underlying bed is a rooted aeolian ash bed. The contact with the overlying horizon is buried. The contact with the underlying horizon is abrupt. Cabbage 13 was first discovered by Konizeski and colleagues (Konizeski and Donohoe 1958) who found an in-situ *Diceratherium* dentary. Since then, numerous mammalian fossils have been recovered. Most mammalian remains are isolated and scattered partial jaws, teeth, and bone fragments. No articulated material has been discovered at this assemblage yet. The mammalian fossils are most abundant in the middle of the exposed outcrop. No amphibians or fish have been recovered from this horizon to date. Invertebrates are very abundant. In fact, freshwater snails are the most abundant macrofossils in the horizon; they are more abundant than at any other outcrop of the Cabbage Patch beds examined (see Pierce 1993). Complete shells are very commonly recovered in addition to molds and debris. Land snails are also present but rarer. Diatoms are rare but plant fragments and root traces are both very abundant. Some of these root traces are very large (> 1 cm in diameter).

C0173 - Tavenner Ranch: C0173 is a very fossiliferous assemblage of the upper Cabbage Patch beds from the Deer Lodge basin (Fig. 1). The 10.7 m thick ash-derived olive gray (5Y 5/2) siltstone (Figs. 4, 6F) contains minor amounts of clay (< 10%), rare very fine to very coarse sand grains (< 2%) as well as very few granules and pebbles (< 2%). The matrix is poorly sorted. The grains are sub-angular to sub-rounded. There are no visible sedimentary features in this massive bed. The fossils are scattered throughout the beds. The top of the unit is eroded and there is no overlying horizon visible. The underlying horizon is a very poorly sorted massive siltstone with very few sand grains. No fossils have been recovered from this horizon. The fossils found at C0173 include very abundant small to medium sized root casts. Land snails are abundant but freshwater snails are rare. Vertebrate fossils include common mammal bones and teeth, rare amphibian and turtle remains, and some very rare fish remains. Numerous bone fragments are recovered as well as more complete specimens including partial jaws, skulls, and associated bones. Some specimens may be heavily weathered.

A2.2 Supplementary tables

Table S2.1. Weathering stages of Fiorillo (1988). After Moore and Norman (2009, table 4).

Weathering stage	Description
0	Bone surface shows no sign of cracking or flaking
1	Bone surface shows cracking, usually parallel to fibrous grain of bone. Cracking confined to outermost layers of bone.
2	Bone surface shows flaking, as well as cracking, on outer surface. Cracking has started to penetrate bone cavities.
3	Extreme outermost layers are gone; fibrous texture present. Most cracks penetrate into bone cavities.

Table S2.2. Abrasion stages of Fiorillo (1988). After Moore and Norman (2009, table 4).

Abrasion stage	Description
0	The bone is still fresh and unabraded. All process and edges of bone are still very sharp and well defined.
1	Abrasion has been slight. Edges and processes have begun to show some rounding or polish.
2	Abrasion has been moderate. Edges are well rounded. Processes are recognizable as protrusions on bone.
3	All edges extremely well rounded. Processes no longer present or, at best, are merely remnants.

Table S2.3. Element categorization and surface area to volume ratio categories used in this study (after Moore and Norman 2009). Abbreviations: SA = surface area, Vol = volume.

Category	Element
1 (lowest SA:Vol)	Astragalus, sesamoid-patella, podial
2	Calcaneum, phalanx, vertebra
3	Humerus, femur, ulna, radius, tibia, metapodial
4	Dentary, fibula, sacrum, pelvis, rib
5 (highest SA:Vol)	Skull, scapula

Table S2.4. Comparisons of size across assemblages: summary of the p-values of the pairwise Nemenyi test. Significant differences are indicated by *.

	C0173	C0174	C1704	C1707	C1708	C1721
C0174	1.00	--	--	--	--	--
C1704	0.51	0.89	--	--	--	--
C1707	0.04*	0.21	0.93	--	--	--
C1708	0.12	0.01*	0.00*	0.00*	--	--
C1721	1.00	0.96	0.28	0.01*	0.29	--
MV6613	0.21	0.03*	0.00*	0.00*	1.00	0.43

Table S2.5. Comparisons of weathering across assemblages: summary of the p-values of the pairwise Chi-square tests. Significant differences are indicated by *.

	C0173	C0174	C1704	C1707	C1721	C1708
C0174	0.233	--	--	--	--	--
C1704	0.886	0.077	--	--	--	--
C1707	0.082	0.008*	0.036*	--	--	--
C1721	0.249	0.004*	0.37	0.008*	--	--
C1708	0.113	0.065	0.036*	0.654	0.004*	--
MV6613	0.957	0.259	0.665	0.171	0.14	0.249

Table S2.6. Comparisons of abrasion across assemblages: summary of the p-values of the pairwise Chi-square tests. Significant differences are indicated by *.

	C0173	C0174	C1704	C1707	C1721	C1708
C0174	0.8943					
C1704	0.8943	0.603				
C1707	0.0235*	0.0054*	0.1914			
C1721	0.8943	0.8943	0.8943	0.0816		
C1708	0.8943	0.7738	0.961	0.1046	0.8943	
MV6613	0.8943	0.8943	0.8943	0.0666	0.9791	0.8943

Table S2.7. Comparisons of surface area to volume ratio across assemblages: summary of the p-values of the pairwise Chi-square tests. Significant differences are indicated by *.

	C0173	C0174	C1704	C1707	C1721	C1708
C0174	0.5302	--	--	--	--	--
C1704	0.04*	0.3013	--	--	--	--
C1707	0.4947	0.3838	0.04*	--	--	--
C1721	0.0931	0.5302	0.8654	0.0931	--	--
C1708	0.0117*	0.05*	0.0931	0.002*	0.0931	--
MV6613	0.548	0.1414	0.0085*	0.0931	0.0163*	0.0087*

Table S2.8. Summary of the NMDS using skeletal element representation. Scores for each assemblage in rows 1-22, loadings for the different elements in rows 24-38. Significant loadings at the 0.05 level are indicated by *, at the 0.1 level by $^{\bullet}$.

Assemblage/Element	NMDS1	NMDS2
C0173	-0.05027442	0.09188972
C0174	-0.05224435	-0.017791668
C1704	-0.260864738	-0.057764672
C1707	-0.008844301	-0.090701608
C1721	-0.203426138	-0.106086116
C1708	-0.342486136	-0.020440708
MV6613	-0.070855207	0.159641251
Eagle Owl 1	0.262673585	0.056908837
Eagle Owl 2	0.349519431	0.065068169
Modern Fluvial	0.168459003	0.184504533
Siwalik I	0.037840237	0.05176072
Siwalik II	0.054935809	0.089369639
Siwalik III	0.078334894	0.096488259
Siwalik IV	-0.02240311	0.032606949
Pliocene Channel Fill	-0.190675662	0.142671456
Pliocene Floodplain	-0.341246971	0.058554087
Lynx	0.084341349	-0.025055086
Mongoose	0.090990953	-0.11322144
Coyote	0.123321153	-0.056540999
Fox	0.134168413	-0.085619451
ArcticFox	0.059441308	-0.287150531
Marten	0.099294896	-0.16909134
Astragali	-0.51053	0.859861
Calcanea$^{\bullet}$	0.121828	0.992551
Dentaries*	-0.87052	0.49213
Femora*	0.599284	0.800537
Humeri	0.260048	0.965596
Pelves*	0.563112	0.82638
Metapodials*	0.925683	-0.3783
Phalanges*	0.298177	-0.95451
Radii/Ulnae*	0.662872	0.748733

Ribs*****	1	0.000381
Scapulae	0.387193	0.921999
Skulls*****	-0.20987	0.977729
Tibiae*****	0.567365	0.823466
Teeth*****	-0.99581	-0.09144
Vertebrae*****	0.712668	-0.7015

Table S2.9. Summary of the NMDS scores of the assemblages included in the analysis of density.

	MDS1	MDS2
Pliocene Floodplain	-0.070230685	-0.153074176
C1708	-0.077044693	-0.135763594
Pliocene Channel Fill	0.034790441	-0.04084123
Siwalik IV	0.090713695	-0.045820712
Siwalik II	0.140911154	-0.076056806
Siwalik I	0.135456267	-0.031917355
Siwalik III	0.179779268	-0.019571624
C1704	-0.150754009	-0.082065599
C1721	-0.061412675	-0.074345714
C0173	-0.025978482	0.011748782
C0174	-0.060043359	0.017988134
Lynx	-0.058978883	0.01889641
C1707	-0.092026358	0.034100605
MV6613	0.040738782	0.05478986
Eagle Owl 1	0.039459189	0.05476409
ArcticFox	-0.073269414	0.054779052
Mongoose	-0.044279594	0.062077162
Fox	-0.078643193	0.07159083
Marten	-0.090441291	0.082370579
Coyote	-0.048582185	0.068734744
Modern Fluvial	0.226554888	0.026691443
Eagle Owl 2	0.043281139	0.10092512

Table S2.10. Summary of the NMDS using summary characteristics of the taphonomy of Cabbage Patch assemblages. Scores for each assemblage in rows 1-7, loadings for the different elements in rows 9-19. Significant loadings at the 0.1 level by •.

Assemblage/Variable	NMDS1	NMDS2
C0173	-0.01514	-0.01452
C0174	-0.0112	-0.01957
C1704	-0.011711	-0.02517
C1707	0.052985	0.00971
C1721	0.00000391	0.008505
C1708	-0.00474	0.024967
MV6613	-0.03361	0.016081
Elements NMDS1	0.248317	-0.96868
Elements NMDS2	-0.99427	0.106856
% High Abrasion•	0.863901	0.503662
% High Weathering•	0.559061	0.829126
% Fragmentary	0.377484	0.926016
% Complete•	0.219865	-0.97553
% Large Specimens•	-0.92103	0.38949
% Columnar	-0.96211	0.272664
% Flat	0.940237	0.340521

Table S2.11. Representation of mammalian families across the Cabbage Patch assemblages studied as a percentage. Estimates were made strictly from cheek teeth.

Family	Sample size	Aplodontidae	Canidae	Castoridae	Cricetidae	Dipodidae	Eomyidae	Equidae	Erinaceidae	Eutypomyidae	Geomyidae
C0173	195	28.7	1	1.5	4.6	4.1	1	0.5	6.2	0	42.1
C0174	61	4.9	3.3	9.8	14.8	23	0	1.6	1.6	0	14.8
C1704	187	18.7	2.7	3.2	9.6	34.8	0.5	0	1.6	0.5	13.4
C1707	22	9.1	0	13.6	13.6	36.4	0	0	4.5	0	0
C1721	102	20.6	1	7.8	12.7	16.7	0	0	0	0	0
C1708	237	15.6	0.8	4.6	11.8	1.7	14.8	0	4.6	0	0
MV6613	42	54.8	0	9.5	0	4.8	7.1	0	0	2.4	0

Family	Herpetotheriidae	Heteromyidae	Leporidae	Leptomerycidae	Merycoidodontidae	Proscalopidae	Rhinocerotidae	Sciuridae	Soricidae	Talpidae	% Small mammals
C0173	6.2	0.5	0	0.5	1	1	0	0.5	0.5	0	97.4
C0174	9.8	0	11.5	0	0	0	1.6	3.3	0	0	96.8
C1704	8	0	2.7	0	0	0.5	0	0.5	0.5	2.7	97.2
C1707	22.7	0	0	0	0	0	0	0	0	0	100.0
C1721	12.7	0	1	15.7	2	2	0	3.9	3.9	0	98.0
C1708	27.4	0	2.1	3.8	0	0.4	3	0.8	2.1	6.3	96.8
MV6613	4.8	0	4.8	4.8	0	0	0	0	7.1	0	100.0

A2.3 Comment about body mass of mammals from the Cabbage Patch beds.

There are few species of large mammals present in the Cabbage Patch beds. The only large carnivore known from the Cabbage Patch beds is *Cynodesmus thooides* (Douglas 1903, Wang 1994), a ca. 9 kg canid (based on data from Wang 1994 and formula from Van Valkenburgh. 1990). The mass of the only equid known from dental remains in the Cabbage Patch beds, *Miohippus*, has been estimated at ca. 50 kg (MacFadden 1986). Several species of rhinocerotids are known from the Cabbage Patch beds (Prothero and Rasmussen 2008). *Diceratherium* is a very large rhinocerotid that may have been as large as ca. 2.6 tons (Paleobiology Database 2016a). The largest species of Diceratherium, in fact, is known from the Cabbage Patch beds (Prothero and Rasmussen 2008). *Skinneroceras* is a smaller rhinocerotid that may have been about half the size of the largest *Diceratherium* species but similar in size to the smaller *D. annectens* (Prothero and Rasmussen 2008). Though the systematics of the oreodonts (Merycoidodontidae) from the Cabbage Patch beds (Riel 1964, Rensberger 1977) is yet to be updated, the two genera whose presence is confirmed, *Eporeodon* and *Promerycochoerus* (Calede, unpublished data), range in size from ca. 52 to as much as 241 kg (Scott 1990, Paleobiology Database 2016b).

A2.4 Reference cited

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A2.5 Characteristics of elements included in the analyses

Locality Number	Repository	Specimen Number	Element	SAVratio	Completeness
C0173	KU	18033	dentary	4	45
C0173	KU	18037	dentary	4	35
C0173	KU	18038	dentary	4	5
C0173	KU	18041	skull	5	5
C0173	KU	18042	skull	5	5
C0173	KU	18043	skull	5	5
C0173	KU	18097	skull	5	5
C0173	KU	18105	skull	5	5
C0173	KU	18374	dentary	4	5
C0173	KU	18386	dentary	4	25
C0173	KU	18476	dentary	4	60
C0173	KU	18477	skull	5	5
C0173	KU	19828	radius	3	65
C0173	KU	19865	calcaneum	2	65
C0173	KU	19866	calcaneum	2	65
C0173	KU	19867	femur	3	50
C0173	KU	19868	vertebra	2	95
C0173	KU	19872	podial	1	95
C0173	KU	19875	metapodial	3	95
C0173	KU	19876	phalanx	2	100
C0173	KU	19893	sacrum	4	85
C0173	KU	19894	humerus	3	45
C0173	KU	18393-1	vertebra	2	100
C0173	KU	18393-10	vertebra	2	95
C0173	KU	18393-11	innominate	4	35
C0173	KU	18393-12	vertebra	2	100
C0173	KU	18393-13	vertebra	2	50
C0173	KU	18393-14	skull	5	5
C0173	KU	18393-15	tibia	3	15
C0173	KU	18393-16	tibia	3	15
C0173	KU	18393-2	vertebra	2	100
C0173	KU	18393-3	vertebra	2	95
C0173	KU	18393-4	vertebra	2	100
C0173	KU	18393-5	vertebra	2	95

C0173	KU	18393-6	vertebra	2	90
C0173	KU	18393-7	sacrum	4	95
C0173	KU	18393-8	skull	5	5
C0173	KU	18393-9	tibia	3	60
C0173	KU	19852-1	skull	5	5
C0173	KU	19852-2	skull	5	5
C0173	KU	19852-3	dentary	4	20
C0173	KU	19852-4	dentary	4	5
C0173	KU	19852-5	skull	5	5
C0173	KU	19852-6	skull	5	5
C0173	KU	19853-1	vertebra	2	100
C0173	KU	19853-10	vertebra	2	95
C0173	KU	19853-11	vertebra	2	95
C0173	KU	19853-12	vertebra	2	100
C0173	KU	19853-13	vertebra	2	100
C0173	KU	19853-14	vertebra	2	100
C0173	KU	19853-15	vertebra	2	100
C0173	KU	19853-16	vertebra	2	50
C0173	KU	19853-17	vertebra	2	50
C0173	KU	19853-18	vertebra	2	40
C0173	KU	19853-19	vertebra	2	95
C0173	KU	19853-2	vertebra	2	100
C0173	KU	19853-20	vertebra	2	25
C0173	KU	19853-21	vertebra	2	30
C0173	KU	19853-22	vertebra	2	20
C0173	KU	19853-23	vertebra	2	80
C0173	KU	19853-24	vertebra	2	70
C0173	KU	19853-25	vertebra	2	70
C0173	KU	19853-26	vertebra	2	70
C0173	KU	19853-27	vertebra	2	50
C0173	KU	19853-28	vertebra	2	50
C0173	KU	19853-29	vertebra	2	45
C0173	KU	19853-3	vertebra	2	100
C0173	KU	19853-30	vertebra	2	85
C0173	KU	19853-31	vertebra	2	15
C0173	KU	19853-4	vertebra	2	100
C0173	KU	19853-5	vertebra	2	100
C0173	KU	19853-6	vertebra	2	100
C0173	KU	19853-7	vertebra	2	90
C0173	KU	19853-8	vertebra	2	95

C0173	KU	19853-9	vertebra	2	50
C0173	KU	19854-1	scapula	5	15
C0173	KU	19854-2	scapula	5	15
C0173	KU	19854-3	scapula	5	10
C0173	KU	19854-4	scapula	5	5
C0173	KU	19854-5	scapula	5	15
C0173	KU	19854-6	scapula	5	5
C0173	KU	19854-7	scapula	5	10
C0173	KU	19854-8	scapula	5	5
C0173	KU	19855-1	humerus	3	40
C0173	KU	19855-10	humerus	3	5
C0173	KU	19855-11	humerus	3	15
C0173	KU	19855-12	humerus	3	5
C0173	KU	19855-13	humerus	3	5
C0173	KU	19855-14	humerus	3	35
C0173	KU	19855-15	humerus	3	5
C0173	KU	19855-16	humerus	3	10
C0173	KU	19855-17	humerus	3	5
C0173	KU	19855-18	humerus	3	5
C0173	KU	19855-19	humerus	3	15
C0173	KU	19855-2	humerus	3	40
C0173	KU	19855-20	humerus	3	50
C0173	KU	19855-21	humerus	3	50
C0173	KU	19855-22	humerus	3	5
C0173	KU	19855-23	humerus	3	25
C0173	KU	19855-24	humerus	3	30
C0173	KU	19855-25	humerus	3	20
C0173	KU	19855-26	humerus	3	5
C0173	KU	19855-27	humerus	3	5
C0173	KU	19855-28	humerus	3	50
C0173	KU	19855-29	humerus	3	20
C0173	KU	19855-3	humerus	3	40
C0173	KU	19855-30	humerus	3	5
C0173	KU	19855-31	tibia	3	40
C0173	KU	19855-32	humerus	3	50
C0173	KU	19855-33	humerus	3	25
C0173	KU	19855-34	humerus	3	10
C0173	KU	19855-4	humerus	3	30
C0173	KU	19855-5	humerus	3	35
C0173	KU	19855-6	humerus	3	50

C0173	KU	19855-7	humerus	3	40
C0173	KU	19855-8	humerus	3	5
C0173	KU	19855-9	humerus	3	5
C0173	KU	19856-1	radius	3	45
C0173	KU	19856-2	radius	3	45
C0173	KU	19856-3	radius	3	50
C0173	KU	19856-4	radius	3	50
C0173	KU	19856-5	radius	3	50
C0173	KU	19856-6	radius	3	30
C0173	KU	19856-7	radius	3	25
C0173	KU	19856-8	radius	3	40
C0173	KU	19856-9	radius	3	60
C0173	KU	19857-1	ulna	3	45
C0173	KU	19857-10	ulna	3	5
C0173	KU	19857-11	ulna	3	20
C0173	KU	19857-12	ulna	3	10
C0173	KU	19857-13	ulna	3	15
C0173	KU	19857-14	ulna	3	5
C0173	KU	19857-15	ulna	3	5
C0173	KU	19857-16	ulna	3	35
C0173	KU	19857-17	ulna	3	5
C0173	KU	19857-18	ulna	3	10
C0173	KU	19857-19	ulna	3	45
C0173	KU	19857-2	ulna	3	60
C0173	KU	19857-20	ulna	3	55
C0173	KU	19857-21	ulna	3	45
C0173	KU	19857-22	ulna	3	50
C0173	KU	19857-3	ulna	3	45
C0173	KU	19857-4	ulna	3	45
C0173	KU	19857-5	ulna	3	45
C0173	KU	19857-6	ulna	3	20
C0173	KU	19857-7	ulna	3	25
C0173	KU	19857-8	ulna	3	20
C0173	KU	19857-9	ulna	3	50
C0173	KU	19858-1	innominate	4	60
C0173	KU	19858-10	innominate	4	35
C0173	KU	19858-11	innominate	4	35
C0173	KU	19858-12	innominate	4	25
C0173	KU	19858-14	innominate	4	30
C0173	KU	19858-15	innominate	4	30

C0173	KU	19858-16	innominate	4	30
C0173	KU	19858-17	innominate	4	25
C0173	KU	19858-18	innominate	4	10
C0173	KU	19858-2	innominate	4	50
C0173	KU	19858-3	innominate	4	40
C0173	KU	19858-4	innominate	4	30
C0173	KU	19858-5	innominate	4	25
C0173	KU	19858-6	innominate	4	15
C0173	KU	19858-7	innominate	4	25
C0173	KU	19858-8	innominate	4	20
C0173	KU	19858-9	innominate	4	30
C0173	KU	19859-1	femur	3	5
C0173	KU	19859-10	femur	3	35
C0173	KU	19859-11	femur	3	20
C0173	KU	19859-12	femur	3	20
C0173	KU	19859-13	femur	3	70
C0173	KU	19859-14	femur	3	40
C0173	KU	19859-2	femur	3	5
C0173	KU	19859-3	femur	3	5
C0173	KU	19859-4	femur	3	10
C0173	KU	19859-5	femur	3	25
C0173	KU	19859-6	femur	3	30
C0173	KU	19859-7	femur	3	5
C0173	KU	19859-8	femur	3	30
C0173	KU	19859-9	femur	3	5
C0173	KU	19860-1	tibia	3	40
C0173	KU	19860-10	tibia	3	25
C0173	KU	19860-11	tibia	3	50
C0173	KU	19860-12	tibia	3	50
C0173	KU	19860-13	tibia	3	10
C0173	KU	19860-14	tibia	3	20
C0173	KU	19860-15	tibia	3	65
C0173	KU	19860-16	tibia	3	5
C0173	KU	19860-17	tibia	3	5
C0173	KU	19860-18	tibia	3	25
C0173	KU	19860-19	tibia	3	10
C0173	KU	19860-2	tibia	3	30
C0173	KU	19860-20	tibia	3	10
C0173	KU	19860-21	tibia	3	20
C0173	KU	19860-22	tibia	3	55

C0173	KU	19860-3	tibia	3	30
C0173	KU	19860-4	tibia	3	35
C0173	KU	19860-5	tibia	3	35
C0173	KU	19860-6	tibia	3	20
C0173	KU	19860-7	tibia	3	35
C0173	KU	19860-8	tibia	3	20
C0173	KU	19860-9	tibia	3	20
C0173	KU	19861-1	calcaneum	2	95
C0173	KU	19861-10	calcaneum	2	100
C0173	KU	19861-11	calcaneum	2	100
C0173	KU	19861-12	calcaneum	2	80
C0173	KU	19861-13	calcaneum	2	85
C0173	KU	19861-14	calcaneum	2	100
C0173	KU	19861-15	calcaneum	2	100
C0173	KU	19861-16	calcaneum	2	95
C0173	KU	19861-17	calcaneum	2	100
C0173	KU	19861-18	calcaneum	2	60
C0173	KU	19861-19	calcaneum	2	60
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C0173	KU	19861-21	calcaneum	2	30
C0173	KU	19861-22	calcaneum	2	15
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C0173	KU	19861-5	calcaneum	2	95
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C0173	KU	19861-7	calcaneum	2	90
C0173	KU	19861-8	calcaneum	2	95
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C0173	KU	19862-1	astragalus	1	95
C0173	KU	19862-10	astragalus	1	100
C0173	KU	19862-11	astragalus	1	100
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C0173	KU	19862-15	astragalus	1	95
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C0173	KU	19862-8	astragalus	1	100
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C0173	KU	19864-1	metapodial	3	100
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C0173	KU	19864-107	phalanx	2	100
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C0173	KU	19864-113	phalanx	2	100
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C0173	KU	19864-124	phalanx	2	60
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C0173	KU	19864-126	phalanx	2	100
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C0173	KU	19864-15	phalanx	2	100
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C0173	KU	19864-31	phalanx	2	100
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C0173	KU	19864-34	vertebra	2	95

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C0173	KU	19864-36	metapodial	3	100
C0173	KU	19864-37	metapodial	3	100
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C0173	KU	19864-53	tibia	3	25
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C0173	KU	19864-7	phalanx	2	100
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C0173	KU	19864-80	metapodial	3	80
C0173	KU	19864-81	vertebra	2	100
C0173	KU	19864-82	metapodial	3	30
C0173	KU	19864-83	metapodial	3	15
C0173	KU	19864-84	metapodial	3	100
C0173	KU	19864-85	phalanx	2	100
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C0173	KU	19864-89	phalanx	2	100
C0173	KU	19864-9	phalanx	2	100
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C0173	KU	19864-92	phalanx	2	100
C0173	KU	19864-93	phalanx	2	100
C0173	KU	19864-94	phalanx	2	100
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C0173	KU	19869-2	sesamoid	1	100
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C0173	KU	19870-1	dentary	4	10
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C0173	KU	19870-2	dentary	4	10
C0173	KU	19870-3	dentary	4	15
C0173	KU	19870-4	dentary	4	15
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C0173	KU	19870-6	dentary	4	5
C0173	KU	19870-7	dentary	4	5
C0173	KU	19870-8	dentary	4	5
C0173	KU	19870-9	dentary	4	10
C0173	KU	19871-1	skull	5	5
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C0173	KU	19895-82	skull	5	5
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C0173	KU	23711-10	vertebra	2	95
C0173	KU	23711-11	vertebra	2	100
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C0173	KU	23711-14	vertebra	2	100
C0173	KU	23711-15	phalanx	2	100
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C0173	KU	23711-17	phalanx	2	100
C0173	KU	23711-18	phalanx	2	100
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C0173	KU	23711-2	dentary	4	70
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C0173	KU	23711-21	phalanx	2	100
C0173	KU	23711-22	phalanx	2	85
C0173	KU	23711-23	metapodial	3	100
C0173	KU	23711-3	dentary	4	95
C0173	KU	23711-4	metapodial	3	100
C0173	KU	23711-5	tibia	3	90
C0173	KU	23711-6	tibia	3	40
C0173	KU	23711-7	ulna	3	95
C0173	KU	23711-8	radius	3	100
C0173	KU	23711-9	vertebra	2	100
C0173	UMPC	1406	dentary	4	60
C0173	UMPC	1407	dentary	4	55
C0173	UMPC	1408	dentary	4	55
C0173	UMPC	1409	skull	5	45
C0173	UMPC	1413	vertebra	2	15
C0173	UMPC	1414	phalanx	2	65
C0173	UMPC	1415	innominate	4	10
C0173	UMPC	1416	innominate	4	20
C0173	UMPC	1417	humerus	3	40
C0173	UMPC	1418	femur	3	5

C0173	UMPC	2105	dentary	4	75
C0173	UMPC	2106	dentary	4	65
C0173	UMPC	2107	dentary	4	40
C0173	UMPC	2110	phalanx	2	95
C0173	UMPC	2111	dentary	4	80
C0173	UMPC	2112	skull	5	5
C0173	UMPC	2113	skull	5	5
C0173	UMPC	2114	humerus	3	70
C0173	UMPC	2115	calcaneum	2	50
C0173	UMPC	2116	humerus	3	10
C0173	UMPC	2302	skull	5	10
C0173	UMPC	2306	dentary	4	60
C0173	UMPC	2307	dentary	4	40
C0173	UMPC	2308	dentary	4	50
C0173	UMPC	2309	dentary	4	40
C0173	UMPC	13217	phalanx	2	90
C0173	UMPC	13232	dentary	4	65
C0173	UMPC	13249	skull	5	10
C0173	UMPC	13250	dentary	4	35
C0173	UMPC	13251	dentary	4	5
C0173	UMPC	13968	skull	5	15
C0173	UMPC	13969	humerus	3	60
C0173	UMPC	13970	skull	5	5
C0173	UMPC	13972	skull	5	5
C0173	UMPC	13973	dentary	4	45
C0173	UMPC	13974	vertebra	2	90
C0173	UMPC	13975	dentary	4	30
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C0173	UMPC	13977	skull	5	5
C0173	UMPC	13228-1	dentary	4	30
C0173	UMPC	13228-2	tibia	3	55
C0173	UMPC	13228-3	skull	5	5
C0173	UMPC	13233-1	calcaneum	2	25
C0173	UMPC	13233-10	femur	3	25
C0173	UMPC	13233-11	metapodial	3	100
C0173	UMPC	13233-12	calcaneum	2	100
C0173	UMPC	13233-13	femur	3	50
C0173	UMPC	13233-2	ulna	3	25
C0173	UMPC	13233-3	calcaneum	2	100
C0173	UMPC	13233-4	metapodial	3	100

C0173	UMPC	13233-5	calcaneum	2	100
C0173	UMPC	13233-6	femur	3	10
C0173	UMPC	13233-7	calcaneum	2	95
C0173	UMPC	13233-8	metapodial	3	100
C0173	UMPC	13233-9	innominate	4	35
C0173	UMPC	13253-1	femur	3	70
C0173	UMPC	13253-10	rib	4	30
C0173	UMPC	13253-2	phalanx	2	85
C0173	UMPC	13253-3	ulna	3	80
C0173	UMPC	13253-4	ulna	3	80
C0173	UMPC	13253-5	phalanx	2	100
C0173	UMPC	13253-6	tibia	3	50
C0173	UMPC	13253-7	vertebra	2	5
C0173	UMPC	13253-8	vertebra	2	95
C0173	UMPC	13253-9	rib	4	50
C0173	UMPC	13978-5	humerus	3	50
C0173	UMPC	13978-6	ulna	3	45
C0173	UMPC	13978-7	tibia	3	45
C0173	UMPC	13978-8	radius	3	45
C0173	UMPC	13978-9	metapodial	3	70
C0173	UMPC	2117-1	metapodial	3	55
C0173	UMPC	2312-1	humerus	3	65
C0173	UMPC	2312-10	metapodial	3	70
C0173	UMPC	2312-2	vertebra	2	100
C0173	UMPC	2312-3	femur	3	35
C0173	UMPC	2312-4	humerus	3	35
C0173	UMPC	2312-5	tibia	3	45
C0173	UMPC	2312-6	metapodial	3	80
C0173	UMPC	2312-7	metapodial	3	100
C0173	UMPC	2312-8	scapula	5	5
C0173	UMPC	2312-9	metapodial	3	100
C0174	KU	18672	dentary	4	10
C0174	KU	20526	skull	5	5
C0174	KU	20527	dentary	4	5
C0174	KU	20531-1	skull	5	5
C0174	KU	20531-10	metapodial	3	100
C0174	KU	20531-11	phalanx	2	100
C0174	KU	20531-12	phalanx	2	100
C0174	KU	20531-13	phalanx	2	100
C0174	KU	20531-14	phalanx	2	70

C0174	KU	20531-15	metapodial	3	100
C0174	KU	20531-16	phalanx	2	100
C0174	KU	20531-17	phalanx	2	100
C0174	KU	20531-18	phalanx	2	100
C0174	KU	20531-19	phalanx	2	100
C0174	KU	20531-2	dentary	4	30
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C0174	KU	20531-21	phalanx	2	100
C0174	KU	20531-22	phalanx	2	100
C0174	KU	20531-23	phalanx	2	100
C0174	KU	20531-24	phalanx	2	90
C0174	KU	20531-3	ulna	3	35
C0174	KU	20531-4	ulna	3	40
C0174	KU	20531-5	femur	3	35
C0174	KU	20531-6	calcaneum	2	100
C0174	KU	20531-7	vertebra	2	95
C0174	KU	20531-8	tibia	3	50
C0174	KU	20531-9	innominate	4	50
C0174	KU	20536-1	vertebra	2	90
C0174	KU	20536-10	vertebra	2	40
C0174	KU	20536-11	vertebra	2	95
C0174	KU	20536-12	phalanx	2	75
C0174	KU	20536-13	phalanx	2	100
C0174	KU	20536-14	metapodial	3	80
C0174	KU	20536-15	metapodial	3	100
C0174	KU	20536-16	metapodial	3	100
C0174	KU	20536-2	vertebra	2	50
C0174	KU	20536-3	vertebra	2	100
C0174	KU	20536-4	vertebra	2	50
C0174	KU	20536-5	vertebra	2	100
C0174	KU	20536-6	vertebra	2	100
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C0174	KU	20536-8	vertebra	2	70
C0174	KU	20536-9	vertebra	2	45
C0174	UWBM	97316	dentary	4	10
C0174	UWBM	97319	dentary	4	10
C0174	UWBM	97320	phalanx	2	100
C0174	UWBM	97329	dentary	4	25
C0174	UWBM	97330	dentary	4	15
C0174	UWBM	97331	dentary	4	5

C0174	UWBM	97332	metapodial	3	100
C0174	UWBM	97335	metapodial	3	100
C0174	UWBM	97336	metapodial	3	85
C0174	UWBM	97337	femur	3	15
C0174	UWBM	97338	vertebra	2	85
C0174	UWBM	97339	ulna	3	5
C0174	UWBM	97349	phalanx	2	75
C0174	UWBM	97350	skull	5	5
C0174	UWBM	97363	tibia	3	50
C0174	UWBM	97397	skull	5	5
C0174	UWBM	97399	metapodial	3	100
C0174	UWBM	97402	astragalus	1	100
C0174	UWBM	97403	femur	3	10
C0174	UWBM	97502	skull	5	5
C0174	UWBM	97504	phalanx	2	100
C0174	UWBM	97505	dentary	4	60
C0174	UWBM	97506	dentary	4	40
C0174	UWBM	98591	tibia	3	65
C0174	UWBM	98594	humerus	3	50
C0174	UWBM	98595	phalanx	2	100
C0174	UWBM	98596	dentary	4	10
C0174	UWBM	98601	humerus	3	25
C0174	UWBM	98602	vertebra	2	60
C0174	UWBM	98604	skull	5	5
C0174	UWBM	98607	vertebra	2	95
C0174	UWBM	98611	metapodial	3	100
C0174	UWBM	98612	rib	4	50
C0174	UWBM	98617	dentary	4	5
C0174	UWBM	98622	vertebra	2	100
C0174	UWBM	98624	vertebra	2	35
C0174	UWBM	98644	humerus	3	5
C0174	UWBM	98646	femur	3	5
C0174	UWBM	98647	skull	5	5
C0174	UWBM	98648	tibia	3	10
C0174	UWBM	98650	ulna	3	5
C0174	UWBM	98655	femur	3	40
C0174	UWBM	98703	metapodial	3	30
C0174	UWBM	98704	vertebra	2	100
C0174	UWBM	98705	vertebra	2	100
C0174	UWBM	98707	vertebra	2	95

C0174	UWBM	98721	phalanx	2	100
C0174	UWBM	98782	metapodial	3	55
C0174	UWBM	98784	ulna	3	20
C0174	UWBM	98821	phalanx	2	65
C0174	UWBM	98822	phalanx	2	100
C0174	UWBM	98823	phalanx	2	100
C0174	UWBM	98892	femur	3	75
C0174	UWBM	98893	phalanx	2	100
C0174	UWBM	98894	phalanx	2	100
C0174	UWBM	98896	phalanx	2	95
C0174	UWBM	98897	radius	3	15
C0174	UWBM	98898	innominate	4	50
C0174	UWBM	98899	metapodial	3	50
C0174	UWBM	98903	tibia	3	55
C0174	UWBM	98904	metapodial	3	65
C0174	UWBM	98906	phalanx	2	95
C0174	UWBM	98907	phalanx	2	100
C0174	UWBM	98908	ulna	3	20
C0174	UWBM	98909	metapodial	3	55
C0174	UWBM	98910	vertebra	2	100
C0174	UWBM	98911	humerus	3	5
C0174	UWBM	108063	tibia	3	50
C0174	UWBM	108064	vertebra	2	95
C0174	UWBM	101384-1	phalanx	2	100
C0174	UWBM	101384-2	phalanx	2	40
C0174	UWBM	97318-9	humerus	3	5
C0174	UWBM	97326-3	scapula	5	15
C0174	UWBM	97326-4	femur	3	45
C0174	UWBM	97326-5	tibia	3	45
C0174	UWBM	97326-6	innominate	4	10
C0174	UWBM	97401-1	vertebra	2	100
C0174	UWBM	97401-2	vertebra	2	100
C0174	UWBM	97404-12	metapodial	3	80
C0174	UWBM	97404-13	vertebra	2	50
C0174	UWBM	98786-1	metapodial	3	5
C0174	UWBM	98786-2	ulna	3	10
C0174	UWBM	98901-1	vertebra	2	100
C0174	UWBM	98901-2	vertebra	2	50
C0174	UWBM	98905-1	phalanx	2	40
C0174	UWBM	98905-2	phalanx	2	40

C0174	UWBM	98905-3	phalanx	2	70
C0174	UWBM	98905-4	phalanx	2	85
C1704	KU	18677	dentary	4	60
C1704	KU	18680	dentary	4	5
C1704	KU	20545-1	calcaneum	2	100
C1704	KU	20545-2	calcaneum	2	100
C1704	KU	20545-3	skull	5	5
C1704	KU	20545-4	podial	1	95
C1704	KU	20545-5	vertebra	2	95
C1704	KU	20545-6	vertebra	2	100
C1704	KU	20545-7	vertebra	2	100
C1704	KU	20545-8	metapodial	3	75
C1704	KU	20545-9	phalanx	2	100
C1704	KU	20546-1	vertebra	2	95
C1704	KU	20546-10	metapodial	3	100
C1704	KU	20546-11	vertebra	2	40
C1704	KU	20546-12	metapodial	3	50
C1704	KU	20546-13	phalanx	2	100
C1704	KU	20546-14	phalanx	2	100
C1704	KU	20546-15	vertebra	2	100
C1704	KU	20546-16	vertebra	2	80
C1704	KU	20546-17	astragalus	1	100
C1704	KU	20546-18	ulna	3	45
C1704	KU	20546-19	vertebra	2	95
C1704	KU	20546-2	vertebra	2	100
C1704	KU	20546-20	ulna	3	50
C1704	KU	20546-21	calcaneum	2	95
C1704	KU	20546-22	astragalus	1	95
C1704	KU	20546-23	phalanx	2	100
C1704	KU	20546-24	phalanx	2	100
C1704	KU	20546-25	vertebra	2	100
C1704	KU	20546-26	metapodial	3	100
C1704	KU	20546-27	metapodial	3	100
C1704	KU	20546-28	vertebra	2	100
C1704	KU	20546-29	phalanx	2	100
C1704	KU	20546-3	vertebra	2	100
C1704	KU	20546-30	vertebra	2	100
C1704	KU	20546-31	phalanx	2	40
C1704	KU	20546-32	phalanx	2	95
C1704	KU	20546-33	vertebra	2	100

C1704	KU	20546-34	vertebra	2	100
C1704	KU	20546-35	metapodial	3	85
C1704	KU	20546-36	vertebra	2	70
C1704	KU	20546-37	phalanx	2	95
C1704	KU	20546-38	femur	3	5
C1704	KU	20546-39	humerus	3	5
C1704	KU	20546-4	phalanx	2	100
C1704	KU	20546-40	humerus	3	5
C1704	KU	20546-41	humerus	3	5
C1704	KU	20546-42	scapula	5	20
C1704	KU	20546-43	rib	4	25
C1704	KU	20546-44	phalanx	2	100
C1704	KU	20546-45	phalanx	2	100
C1704	KU	20546-46	metapodial	3	100
C1704	KU	20546-47	vertebra	2	50
C1704	KU	20546-48	metapodial	3	95
C1704	KU	20546-49	phalanx	2	100
C1704	KU	20546-5	phalanx	2	100
C1704	KU	20546-50	phalanx	2	100
C1704	KU	20546-6	vertebra	2	50
C1704	KU	20546-7	astragalus	1	100
C1704	KU	20546-8	calcaneum	1	100
C1704	KU	20546-9	phalanx	2	100
C1704	UMPC	1462	astragalus	1	100
C1704	UWBM	97348	skull	5	5
C1704	UWBM	97393	dentary	4	45
C1704	UWBM	97394	vertebra	2	95
C1704	UWBM	97433	vertebra	2	95
C1704	UWBM	97434	scapula	5	35
C1704	UWBM	97435	phalanx	2	80
C1704	UWBM	97437	phalanx	2	95
C1704	UWBM	97438	phalanx	2	35
C1704	UWBM	97439	metapodial	3	5
C1704	UWBM	97440	phalanx	2	100
C1704	UWBM	97446	phalanx	2	95
C1704	UWBM	98680	dentary	4	75
C1704	UWBM	98778	dentary	4	35
C1704	UWBM	98824	dentary	4	25
C1704	UWBM	98825	humerus	3	70
C1704	UWBM	98920	vertebra	2	70

C1704	UWBM	101292	skull	5	5
C1704	UWBM	101361	dentary	4	40
C1704	UWBM	101362	vertebra	2	100
C1704	UWBM	101363	ulna	3	65
C1704	UWBM	101364	tibia	3	20
C1704	UWBM	101365	humerus	3	15
C1704	UWBM	101366	phalanx	2	100
C1704	UWBM	101375	astragalus	1	100
C1704	UWBM	101376	calcaneum	2	100
C1704	UWBM	101377	metapodial	3	5
C1704	UWBM	101378	metapodial	3	50
C1704	UWBM	101379	phalanx	2	100
C1704	UWBM	101383	innominate	4	95
C1704	UWBM	108073	vertebra	2	55
C1704	UWBM	108074	vertebra	2	65
C1704	UWBM	108079	phalanx	2	100
C1704	UWBM	108081	innominate	4	30
C1704	UWBM	108082	vertebra	2	90
C1704	UWBM	108086	vertebra	2	60
C1704	UWBM	108087	femur	3	45
C1704	UWBM	108148	metapodial	3	45
C1704	UWBM	108157	skull	5	5
C1704	UWBM	97447-9	phalanx	2	25
C1704	UWBM	98730-1	skull	5	5
C1704	UWBM	98730-2	dentary	4	90
C1704	UWBM	98921-7	metapodial	3	80
C1707	UWBM	98665	dentary	4	85
C1707	UWBM	98720	skull	5	10
C1707	UWBM	98779	calcaneum	2	80
C1707	UWBM	98781	rib	4	50
C1707	UWBM	98827	phalanx	2	100
C1707	UWBM	98829	metapodial	3	100
C1707	UWBM	98928	metapodial	3	100
C1707	UWBM	98929	humerus	3	5
C1707	UWBM	98930	dentary	4	60
C1707	UWBM	98931	phalanx	2	100
C1707	UWBM	98932	femur	3	5
C1707	UWBM	98933	vertebra	2	40
C1707	UWBM	98934	calcaneum	2	60
C1707	UWBM	98935	calcaneum	2	95

C1707	UWBM	98936	fibula	4	20
C1707	UWBM	101368	femur	3	5
C1707	UWBM	101369	ulna	3	10
C1707	UWBM	108001	phalanx	2	100
C1707	UWBM	108002	radius	3	50
C1707	UWBM	108003	phalanx	2	100
C1707	UWBM	108004	metapodial	3	85
C1707	UWBM	108005	vertebra	2	100
C1707	UWBM	108006	metapodial	3	10
C1707	UWBM	108131	phalanx	2	100
C1707	UWBM	108132	vertebra	2	90
C1707	UWBM	108133	vertebra	2	75
C1707	UWBM	108134	femur	3	5
C1707	UWBM	108135	innominate	4	50
C1707	UWBM	108136	vertebra	2	30
C1707	UWBM	108137	phalanx	2	95
C1707	UWBM	108138	tibia	3	30
C1707	UWBM	108139	femur	3	5
C1707	UWBM	108140	phalanx	2	100
C1707	UWBM	108141	phalanx	2	100
C1707	UWBM	108142	metapodial	3	50
C1707	UWBM	108143	femur	3	40
C1707	UWBM	108144	vertebra	2	100
C1707	UWBM	108145	vertebra	2	100
C1707	UWBM	108146	metapodial	3	40
C1707	UWBM	108147	metapodial	3	100
C1707	UWBM	108149	phalanx	2	50
C1707	UWBM	108150	dentary	4	40
C1707	UWBM	108151	radius	3	5
C1707	UWBM	108152	phalanx	2	100
C1707	UWBM	108153	tibia	3	35
C1707	UWBM	108154	phalanx	2	75
C1707	UWBM	108155	metapodial	3	50
C1707	UWBM	108156	dentary	4	35
C1708	KU	18155	skull	5	5
C1708	KU	18159	dentary	4	70
C1708	KU	18166	skull	5	85
C1708	KU	18501	dentary	4	15
C1708	KU	18668	dentary	4	20
C1708	KU	19935	astragalus	1	95

C1708	KU	19931-1	humerus	3	5
C1708	KU	19931-10	phalanx	2	50
C1708	KU	19931-11	phalanx	2	35
C1708	KU	19931-12	phalanx	2	60
C1708	KU	19931-13	phalanx	2	45
C1708	KU	19931-14	phalanx	2	70
C1708	KU	19931-15	metapodial	3	100
C1708	KU	19931-16	phalanx	2	90
C1708	KU	19931-2	humerus	3	25
C1708	KU	19931-22	humerus	3	80
C1708	KU	19931-23	vertebra	2	95
C1708	KU	19931-24	calcaneum	2	100
C1708	KU	19931-25	calcaneum	2	95
C1708	KU	19931-26	femur	3	55
C1708	KU	19931-27	vertebra	2	100
C1708	KU	19931-28	phalanx	2	50
C1708	KU	19931-29	vertebra	2	95
C1708	KU	19931-3	ulna	3	35
C1708	KU	19931-30	calcaneum	2	95
C1708	KU	19931-31	calcaneum	2	95
C1708	KU	19931-32	dentary	4	5
C1708	KU	19931-33	dentary	4	5
C1708	KU	19931-34	calcaneum	2	90
C1708	KU	19931-35	astragalus	1	100
C1708	KU	19931-36	phalanx	2	100
C1708	KU	19931-37	dentary	4	10
C1708	KU	19931-38	metapodial	3	90
C1708	KU	19931-39	vertebra	2	90
C1708	KU	19931-4	ulna	3	35
C1708	KU	19931-40	dentary	4	35
C1708	KU	19931-41	innominate	4	40
C1708	KU	19931-42	femur	3	60
C1708	KU	19931-43	innominate	4	10
C1708	KU	19931-44	femur	3	70
C1708	KU	19931-45	vertebra	2	90
C1708	KU	19931-47	phalanx	2	70
C1708	KU	19931-48	vertebra	2	95
C1708	KU	19931-49	podial	1	100
C1708	KU	19931-5	metapodial	3	65
C1708	KU	19931-6	metapodial	3	50

C1708	KU	19931-7	phalanx	2	50
C1708	KU	19931-75	rib	4	80
C1708	KU	19931-8	metapodial	3	35
C1708	KU	19931-9	phalanx	2	100
C1708	UMPC	13230	dentary	4	30
C1708	UMPC	14030	dentary	4	90
C1708	UWBM	18070	dentary	4	35
C1708	UWBM	97345	dentary	4	25
C1708	UWBM	98736	astragalus	1	100
C1708	UWBM	98741	skull	5	5
C1708	UWBM	98742	phalanx	2	100
C1708	UWBM	98743	ulna	3	15
C1708	UWBM	98744	dentary	4	5
C1708	UWBM	98749	phalanx	2	100
C1708	UWBM	98759	phalanx	2	100
C1708	UWBM	98761	skull	5	5
C1708	UWBM	98766	dentary	4	10
C1708	UWBM	98767	dentary	4	80
C1708	UWBM	98800	phalanx	2	70
C1708	UWBM	98811	metapodial	3	80
C1708	UWBM	98812	phalanx	2	65
C1708	UWBM	98813	astragalus	1	95
C1708	UWBM	98814	phalanx	2	100
C1708	UWBM	98815	phalanx	2	100
C1708	UWBM	98816	phalanx	2	50
C1708	UWBM	98817	vertebra	2	95
C1708	UWBM	98818	sesamoid	1	95
C1708	UWBM	98819	phalanx	2	50
C1708	UWBM	98820	dentary	4	80
C1708	UWBM	98912	phalanx	2	100
C1708	UWBM	98913	vertebra	2	90
C1708	UWBM	98914	metapodial	3	75
C1708	UWBM	98915	phalanx	2	100
C1708	UWBM	98916	phalanx	2	5
C1708	UWBM	98918	humerus	3	5
C1708	UWBM	98927	dentary	4	10
C1708	UWBM	101291	dentary	4	60
C1708	UWBM	101293	tibia	3	25
C1708	UWBM	101294	metapodial	3	60
C1708	UWBM	101295	vertebra	2	100

C1708	UWBM	101389	dentary	4	15
C1708	UWBM	108071-11	humerus	3	5
C1708	UWBM	19931-17	tibia	3	60
C1708	UWBM	19931-18	tibia	3	5
C1708	UWBM	19931-19	femur	3	5
C1708	UWBM	19931-20	femur	3	5
C1708	UWBM	19931-21	sesamoid	1	100
C1708	UWBM	19931-69	vertebra	2	50
C1708	UWBM	19931-70	vertebra	2	50
C1708	UWBM	19931-71	vertebra	2	80
C1708	UWBM	19931-72	vertebra	2	90
C1708	UWBM	19931-73	vertebra	2	75
C1708	UWBM	19931-74	vertebra	2	50
C1708	UWBM	98917-1	phalanx	2	100
C1708	UWBM	98917-2	phalanx	2	100
C1721	KU	20696	femur	3	50
C1721	UWBM	18039	phalanx	2	100
C1721	UWBM	18041	dentary	4	50
C1721	UWBM	18042	metapodial	3	5
C1721	UWBM	18043	phalanx	2	60
C1721	UWBM	18044	vertebra	2	70
C1721	UWBM	97343	humerus	3	35
C1721	UWBM	97352	humerus	3	5
C1721	UWBM	97354	vertebra	2	5
C1721	UWBM	97358	metapodial	3	5
C1721	UWBM	97361	dentary	4	25
C1721	UWBM	97385	tibia	3	35
C1721	UWBM	97386	phalanx	2	90
C1721	UWBM	97387	astragalus	1	95
C1721	UWBM	97389	ulna	3	25
C1721	UWBM	97452	femur	3	5
C1721	UWBM	97453	humerus	3	5
C1721	UWBM	97457	astragalus	1	100
C1721	UWBM	97460	dentary	4	10
C1721	UWBM	97461	metapodial	3	5
C1721	UWBM	97470	dentary	4	20
C1721	UWBM	97472	ulna	3	20
C1721	UWBM	97476	humerus	3	5
C1721	UWBM	97483	vertebra	2	100
C1721	UWBM	97485	phalanx	2	100

C1721	UWBM	97487	dentary	4	5
C1721	UWBM	97493	rib	4	85
C1721	UWBM	97494	dentary	4	5
C1721	UWBM	97496	humerus	3	10
C1721	UWBM	97500	dentary	4	5
C1721	UWBM	98633	phalanx	2	65
C1721	UWBM	98635	podial	1	90
C1721	UWBM	98637	astragalus	1	100
C1721	UWBM	98640	scapula	5	5
C1721	UWBM	98642	astragalus	1	50
C1721	UWBM	98658	phalanx	2	100
C1721	UWBM	98670	dentary	4	5
C1721	UWBM	98671	femur	3	40
C1721	UWBM	98672	phalanx	2	45
C1721	UWBM	98675	dentary	4	50
C1721	UWBM	98685	dentary	4	60
C1721	UWBM	98686	dentary	4	55
C1721	UWBM	98691	dentary	4	45
C1721	UWBM	98797	phalanx	2	100
C1721	UWBM	98799	phalanx	2	25
C1721	UWBM	98802	femur	3	10
C1721	UWBM	98804	metapodial	3	50
C1721	UWBM	98805	phalanx	2	50
C1721	UWBM	98806	vertebra	2	75
C1721	UWBM	98807	podial	1	95
C1721	UWBM	98808	phalanx	2	70
C1721	UWBM	98809	phalanx	2	55
C1721	UWBM	98810	rib	4	20
C1721	UWBM	98880	skull	5	5
C1721	UWBM	98882	astragalus	1	100
C1721	UWBM	98883	calcaneum	2	95
C1721	UWBM	98884	phalanx	2	65
C1721	UWBM	98885	calcaneum	2	95
C1721	UWBM	98886	ulna	3	55
C1721	UWBM	98887	vertebra	2	65
C1721	UWBM	98888	humerus	3	5
C1721	UWBM	98889	phalanx	2	100
C1721	UWBM	98890	phalanx	2	50
C1721	UWBM	98891	vertebra	2	100
C1721	UWBM	98902	sacrum	4	95

C1721	UWBM	101310	ulna	3	85
C1721	UWBM	101311	vertebra	2	30
C1721	UWBM	101312	calcaneum	2	90
C1721	UWBM	101313	vertebra	2	95
C1721	UWBM	101314	phalanx	2	65
C1721	UWBM	101315	dentary	4	70
C1721	UWBM	101316	podial	1	100
C1721	UWBM	101317	phalanx	2	85
C1721	UWBM	101318	calcaneum	2	90
C1721	UWBM	101319	phalanx	2	90
C1721	UWBM	101320	dentary	4	25
C1721	UWBM	101321	femur	3	65
C1721	UWBM	101322	metapodial	3	100
C1721	UWBM	101323	phalanx	2	50
C1721	UWBM	101324	metapodial	3	95
C1721	UWBM	101325	femur	3	10
C1721	UWBM	101326	vertebra	2	100
C1721	UWBM	101327	vertebra	2	5
C1721	UWBM	101351	phalanx	2	85
C1721	UWBM	101352	metapodial	3	100
C1721	UWBM	101353	phalanx	2	100
C1721	UWBM	101354	phalanx	2	100
C1721	UWBM	101355	vertebra	2	75
C1721	UWBM	101356	phalanx	2	60
C1721	UWBM	101357	fibula	4	20
C1721	UWBM	101358	phalanx	2	70
C1721	UWBM	101391	phalanx	2	100
C1721	UWBM	101392	vertebra	2	35
C1721	UWBM	101393	metapodial	3	100
C1721	UWBM	108045	dentary	4	30
C1721	UWBM	108058	vertebra	2	75
C1721	UWBM	108059	phalanx	2	90
C1721	UWBM	108061	tibia	3	65
C1721	UWBM	108068	scapula	5	5
C1721	UWBM	101359-1	calcaneum	2	95
C1721	UWBM	101359-2	calcaneum	2	100
C1721	UWBM	101359-3	calcaneum	2	40
C1721	UWBM	108069-7	phalanx	2	40
C1721	UWBM	97342-1	dentary	4	5
C1721	UWBM	98696-4	dentary	4	20

MV6613	KU	18145	dentary	4	90
MV6613	KU	18450	skull	5	15
MV6613	KU	18451	dentary	4	60
MV6613	KU	18452	dentary	4	5
MV6613	KU	18456	dentary	4	30
MV6613	KU	20571	metapodial	3	50
MV6613	KU	20572	humerus	3	20
MV6613	KU	20573	podial	1	90
MV6613	KU	20574	astragalus	1	95
MV6613	KU	20575	phalanx	2	100
MV6613	KU	20576	phalanx	2	100
MV6613	KU	20577	metapodial	3	75
MV6613	KU	20578	humerus	3	100
MV6613	KU	20579	ulna	3	80
MV6613	KU	20581	femur	3	60
MV6613	KU	20583	humerus	3	40
MV6613	KU	20584	femur	3	50
MV6613	KU	20590-49	vertebra	2	60
MV6613	UMPC	2118	dentary	4	85
MV6613	UMPC	2315	dentary	4	60
MV6613	UMPC	2316	humerus	3	50
MV6613	UMPC	13271	dentary	4	85
MV6613	UMPC	13273	dentary	4	70
MV6613	UMPC	13980	dentary	4	95
MV6613	UMPC	13987	dentary	4	40
MV6613	UMPC	13990	femur	3	40
MV6613	UMPC	13998	dentary	4	5
MV6613	UMPC	13999	skull	5	5
MV6613	UMPC	14001	skull	5	5
MV6613	UMPC	14002	dentary	4	65
MV6613	UMPC	14016	humerus	3	85
MV6613	UMPC	14017	dentary	4	60
MV6613	UMPC	14021	skull	5	10
MV6613	UMPC	14022	dentary	4	10
MV6613	UMPC	14027	podial	1	95
MV6613	UMPC	14028	dentary	4	70
MV6613	UMPC	14032	dentary	4	65
MV6613	UMPC	13275-1	femur	3	90
MV6613	UMPC	13275-2	humerus	3	35
MV6613	UMPC	13275-3	tibia	3	50

MV6613	UMPC	13275-4	phalanx	2	100
MV6613	UMPC	14014-1	dentary	4	25
MV6613	UMPC	14014-10	vertebra	2	25
MV6613	UMPC	14014-11	astragalus	1	100
MV6613	UMPC	14014-12	phalanx	2	100
MV6613	UMPC	14014-13	femur	3	40
MV6613	UMPC	14014-14	vertebra	2	95
MV6613	UMPC	14014-15	vertebra	2	95
MV6613	UMPC	14014-16	vertebra	2	90
MV6613	UMPC	14014-2	dentary	4	20
MV6613	UMPC	14014-3	metapodial	3	60
MV6613	UMPC	14014-31	ulna	3	45
MV6613	UMPC	14014-32	vertebra	2	55
MV6613	UMPC	14014-33	metapodial	3	50
MV6613	UMPC	14014-4	metapodial	3	100
MV6613	UMPC	14014-5	metapodial	3	100
MV6613	UMPC	14014-6	phalanx	2	100
MV6613	UMPC	14014-7	phalanx	2	100
MV6613	UMPC	14014-8	phalanx	2	100
MV6613	UMPC	14014-9	metapodial	3	50
MV6613	UMPC	14036-105	ulna	3	30
MV6613	UMPC	14036-107	vertebra	2	95
MV6613	UMPC	14036-108	vertebra	2	85
MV6613	UMPC	14036-12	dentary	4	5
MV6613	UMPC	14036-14	sesamoid	1	100
MV6613	UMPC	14036-3	metapodial	3	100
MV6613	UMPC	14036-68	vertebra	2	80
MV6613	UMPC	14036-69	metapodial	3	70
MV6613	UMPC	14036-7	femur	3	65
MV6613	UMPC	14036-70	innominate	4	45
MV6613	UMPC	14036-71	phalanx	2	40
MV6613	UMPC	14036-73	femur	3	45
MV6613	UMPC	14036-74	tibia	3	30
MV6613	UMPC	14036-75	ulna	3	35
MV6613	UMPC	14036-76	ulna	3	35
MV6613	UMPC	14036-78	phalanx	2	65
MV6613	UMPC	14036-82	femur	3	65
MV6613	UMPC	14036-83	phalanx	2	95
MV6613	UMPC	14036-85	phalanx	2	100
MV6613	UMPC	14036-87	phalanx	2	100

MV6613	UMPC	14036-90	humerus	3	20
MV6613	UMPC	14036-91	vertebra	2	90
MV6613	UMPC	14036-93	tibia	3	65
MV6613	UMPC	14036-95	radius	3	65
MV6613	UMPC	14036-99	femur	3	50
MV6613	UMPC	20580-1	humerus	3	20
MV6613	UMPC	20580-2	humerus	3	50
MV6613	UMPC	20580-3	metapodial	3	50
MV6613	UMPC	20580-4	calcaneum	2	100
MV6613	UMPC	20580-5	radius	3	65
MV6613	UMPC	20580-6	tibia	3	50
MV6613	UMPC	20580-7	tibia	3	50
MV6613	UMPC	20580-8	tibia	3	65
MV6613	UMPC	20590-1	vertebra	2	5
MV6613	UMPC	20590-2	metapodial	3	5
MV6613	UMPC	20590-3	femur	3	60
MV6613	UMPC	20590-4	femur	3	65
MV6613	UMPC	20590-5	femur	3	5
MV6613	UMPC	20590-6	podial	1	100
MV6613	UMPC	2317-1	phalanx	2	95
MV6613	UMPC	2317-2	calcaneum	2	70

A2.6 Characteristics of the specimens included in the combined dataset used in the analyses.

Abbreviations: E, Weathering; A, Abrasion; L, Length; W, Width; D, Depth; F, Flatness; C, Columnarity.

Locality Number	Museum	Specimen	Element	E	A	L	W	D	F	C
C0173	KUVP	18393-15	tibia	2	2	9.3	3.1	2.6	-0.84	-0.28
C0173	KUVP	18393-17	fragment	2	2	10.8	2.5	2.1	-0.84	-0.2
C0173	KUVP	18393-18	fragment	2	1	7.5	4	2.7	-0.67	-0.36
C0173	KUVP	18393-19	fragment	2	2	7.2	3.9	2.6	-0.68	-0.36
C0173	KUVP	18393-20	fragment	1	2	10.5	3.1	2.3	-0.73	-0.21
C0173	KUVP	18393-21	fragment	2	3	7.3	5.8	3.1	-0.54	-0.43
C0173	KUVP	18393-22	fragment	0	3	4.9	2.1	1.2	-0.55	-0.24
C0173	KUVP	18393-23	fragment	1	3	11.4	5.1	1.6	-0.32	-0.14
C0173	KUVP	18393-24	fragment	0	1	14.8	7.5	4.6	-0.61	-0.31
C0173	KUVP	19853-15	vertebra	1	2	4.3	1.7	1.4	-0.84	-0.33
C0173	KUVP	19853-32	fragment	1	2	6	5.3	3.4	-0.65	-0.57
C0173	KUVP	19853-33	fragment	1	2	3.2	2.9	1.6	-0.57	-0.5
C0173	KUVP	19853-8	vertebra	1	1	5.4	2.9	2.7	-0.9	-0.49
C0173	KUVP	19853-9	vertebra	1	2	6.7	3.6	2.7	-0.75	-0.4
C0173	KUVP	19857-8	ulna	1	1	8.8	4.1	2.4	-0.57	-0.27
C0173	KUVP	19858-13	fragment	1	2	13	6.3	4.2	-0.66	-0.32
C0173	KUVP	19864-110	phalanx	1	1	4.9	2	1.6	-0.81	-0.32
C0173	KUVP	19864-14	phalanx	0	0	4.2	1.9	1.3	-0.71	-0.31
C0173	KUVP	19864-19	metapodial	2	1	10.3	2.3	2.2	-0.95	-0.22
C0173	KUVP	19864-6	phalanx	0	0	4.6	1.9	1.3	-0.71	-0.29
C0173	KUVP	19895-1	fragment	1	2	32	5.6	2.4	-0.43	-0.08
C0173	KUVP	19895-10	fragment	0	3	6	3.8	3.1	-0.81	-0.51
C0173	KUVP	19895-11	fragment	0	2	7.3	2.1	1.3	-0.62	-0.18
C0173	KUVP	19895-12	fragment	3	3	6	5.7	2.4	-0.42	-0.4
C0173	KUVP	19895-13	fragment	1	3	8.8	4.3	2.9	-0.66	-0.33
C0173	KUVP	19895-14	fragment	0	1	7.1	2.9	2.8	-0.97	-0.39
C0173	KUVP	19895-15	fragment	1	3	8.7	1.6	1.1	-0.69	-0.13
C0173	KUVP	19895-16	fragment	1	3	5.9	1.9	1.5	-0.78	-0.25
C0173	KUVP	19895-17	fragment	1	1	9.9	5.7	5.2	-0.91	-0.52
C0173	KUVP	19895-18	fragment	1	3	7	2.4	1.7	-0.7	-0.24
C0173	KUVP	19895-19	fragment	1	1	6.1	2.3	0.7	-0.31	-0.12
C0173	KUVP	19895-2	fragment	1	2	16.3	5.1	3.5	-0.68	-0.21

C0173	KUVP	19895-20	fragment	0	1	7.7	2.1	1.3	-0.62	-0.17
C0173	KUVP	19895-21	fragment	1	2	6.3	2	1.5	-0.74	-0.23
C0173	KUVP	19895-22	fragment	2	3	9.6	3.8	2.8	-0.74	-0.29
C0173	KUVP	19895-23	fragment	1	2	9.9	4.6	4.1	-0.9	-0.42
C0173	KUVP	19895-24	fragment	1	3	6.8	2.5	2.2	-0.87	-0.32
C0173	KUVP	19895-25	fragment	0	3	4.2	3.3	1.3	-0.38	-0.3
C0173	KUVP	19895-26	fragment	3	3	6	1.6	1.6	-0.99	-0.27
C0173	KUVP	19895-27	fragment	1	2	2.5	2	1.6	-0.81	-0.65
C0173	KUVP	19895-28	fragment	0	3	4.9	1.9	1.6	-0.84	-0.32
C0173	KUVP	19895-29	fragment	1	3	5.8	3	1.4	-0.47	-0.24
C0173	KUVP	19895-3	fragment	2	2	9.2	7	5.8	-0.83	-0.63
C0173	KUVP	19895-30	fragment	0	3	5.9	1.4	1.2	-0.8	-0.19
C0173	KUVP	19895-31	fragment	0	2	5.4	2.5	1.4	-0.56	-0.25
C0173	KUVP	19895-32	fragment	1	2	8.5	2.4	2.3	-0.96	-0.27
C0173	KUVP	19895-33	fragment	2	3	10.4	5.4	1.8	-0.34	-0.18
C0173	KUVP	19895-34	fragment	0	3	6.9	5.5	1.8	-0.33	-0.27
C0173	KUVP	19895-35	fragment	1	3	10.9	6.5	2.3	-0.35	-0.21
C0173	KUVP	19895-36	fragment	1	2	3.9	2.5	1.1	-0.45	-0.29
C0173	KUVP	19895-37	fragment	3	3	10.3	5.1	3.7	-0.73	-0.36
C0173	KUVP	19895-38	fragment	1	3	7.8	3.4	1.4	-0.41	-0.18
C0173	KUVP	19895-39	fragment	1	3	2.9	2.4	0.9	-0.39	-0.33
C0173	KUVP	19895-4	fragment	1	2	14.2	7.7	3.8	-0.49	-0.27
C0173	KUVP	19895-40	fragment	2	2	5.1	2.8	1.9	-0.68	-0.37
C0173	KUVP	19895-41	fragment	0	2	9.9	3.7	2.8	-0.74	-0.28
C0173	KUVP	19895-42	fragment	0	2	8.7	4.7	3	-0.63	-0.34
C0173	KUVP	19895-43	fragment	1	1	7.5	3.1	1.2	-0.39	-0.16
C0173	KUVP	19895-44	fragment	1	2	6.5	3.9	2.8	-0.72	-0.43
C0173	KUVP	19895-45	fragment	1	2	4.1	2	0.7	-0.36	-0.18
C0173	KUVP	19895-46	fragment	1	3	7.9	2.6	1.8	-0.69	-0.22
C0173	KUVP	19895-47	fragment	0	3	5.9	2.4	1	-0.43	-0.17
C0173	KUVP	19895-48	fragment	1	3	4.2	2.9	1	-0.34	-0.23
C0173	KUVP	19895-49	fragment	2	2	6.3	2.4	2.3	-0.97	-0.36
C0173	KUVP	19895-5	fragment	2	2	11	2.8	1.4	-0.49	-0.12
C0173	KUVP	19895-50	fragment	1	3	5.2	2	1	-0.5	-0.19
C0173	KUVP	19895-51	fragment	1	3	4.7	3	0.9	-0.3	-0.19
C0173	KUVP	19895-52	fragment	1	3	5.8	2.8	1.6	-0.56	-0.27
C0173	KUVP	19895-53	fragment	1	2	4.3	2.3	0.9	-0.41	-0.21
C0173	KUVP	19895-54	fragment	0	2	2.2	1.8	1.2	-0.65	-0.53
C0173	KUVP	19895-55	fragment	2	3	17.3	8.8	5.5	-0.62	-0.32
C0173	KUVP	19895-56	fragment	2	2	5.3	3.7	1.4	-0.36	-0.26

C0173	KUVP	19895-57	fragment	2	3	6.8	1.6	1.6	-0.98	-0.24
C0173	KUVP	19895-58	fragment	0	2	4	2	1.7	-0.86	-0.43
C0173	KUVP	19895-59	fragment	1	2	9.9	7.6	3.7	-0.48	-0.37
C0173	KUVP	19895-6	fragment	2	2	9.6	2.9	2.3	-0.8	-0.24
C0173	KUVP	19895-60	fragment	1	3	11.1	2.6	1.6	-0.6	-0.14
C0173	KUVP	19895-61	fragment	0	3	8.8	2.6	2.1	-0.82	-0.24
C0173	KUVP	19895-62	fragment	2	3	6.9	3.2	2	-0.63	-0.29
C0173	KUVP	19895-63	fragment	1	3	3.4	1.9	1.2	-0.64	-0.36
C0173	KUVP	19895-64	fragment	1	3	5.1	2.2	0.9	-0.41	-0.18
C0173	KUVP	19895-65	fragment	3	3	5.7	1.8	1.3	-0.69	-0.22
C0173	KUVP	19895-66	fragment	1	3	5.4	1	1	-0.94	-0.18
C0173	KUVP	19895-67	fragment	3	3	6.8	1.2	0.9	-0.78	-0.14
C0173	KUVP	19895-68	fragment	2	3	3.7	2.4	1.3	-0.54	-0.35
C0173	KUVP	19895-69	fragment	0	3	9.4	6.1	3.9	-0.63	-0.41
C0173	KUVP	19895-7	fragment	0	2	9.4	5.2	2.4	-0.46	-0.25
C0173	KUVP	19895-70	fragment	2	3	7.1	4.6	2.7	-0.6	-0.39
C0173	KUVP	19895-71	fragment	3	3	11.2	2.2	2.2	-0.99	-0.19
C0173	KUVP	19895-72	fragment	1	3	10.1	2.1	2	-0.95	-0.2
C0173	KUVP	19895-73	fragment	1	2	8.2	2.6	1.2	-0.46	-0.15
C0173	KUVP	19895-74	fragment	1	2	4.2	3.1	1.6	-0.52	-0.38
C0173	KUVP	19895-75	fragment	0	2	3	2.9	1.2	-0.42	-0.41
C0173	KUVP	19895-76	fragment	2	3	4.6	2.6	0.9	-0.35	-0.2
C0173	KUVP	19895-77	fragment	2	3	2.5	2.2	1.2	-0.55	-0.48
C0173	KUVP	19895-78	fragment	1	2	2.6	2	1.8	-0.88	-0.67
C0173	KUVP	19895-79	fragment	0	2	8	3	1.5	-0.5	-0.19
C0173	KUVP	19895-8	fragment	2	2	9.5	3.3	2.3	-0.69	-0.24
C0173	KUVP	19895-80	fragment	3	3	3.4	1.5	1	-0.69	-0.3
C0173	KUVP	19895-81	fragment	2	3	3.8	2.4	1.4	-0.57	-0.36
C0173	KUVP	19895-9	fragment	1	2	8.9	7.1	2.3	-0.32	-0.26
C0173	UMPC	2106	dentary	2	0	20.3	11	4.8	-0.44	-0.24
C0173	UMPC	2113	skull	0	1	9	3.6	3.1	-0.85	-0.34
C0173	UMPC	13232	dentary	0	0	23.7	9.7	4.2	-0.43	-0.18
C0174	KUVP	20531-13	phalanx	0	0	3.7	1.7	1.2	-0.69	-0.32
C0174	KUVP	20531-23	phalanx	0	0	4.8	2.1	1.7	-0.8	-0.35
C0174	KUVP	20531-5	femur	1	0	5.3	2.9	2.5	-0.84	-0.47
C0174	KUVP	20531-8	tibia	0	0	8.2	2.5	1.9	-0.76	-0.23
C0174	KUVP	20536-14	metapodial	1	0	7.9	2.4	2.1	-0.84	-0.26
C0174	UWBM	97316	dentary	0	1	7.7	4	2.9	-0.74	-0.38
C0174	UWBM	97336	metapodial	2	3	28.3	5.4	5.3	-0.98	-0.19
C0174	UWBM	98604	skull	2	2	4.2	2.8	2.3	-0.8	-0.54

C0174	UWBM	98645	fragment	1	3	18.9	5.1	3.4	-0.65	-0.18
C0174	UWBM	98652	fragment	2	3	8.5	8.3	6.5	-0.78	-0.77
C0174	UWBM	98823	phalanx	1	2	4.9	2	1.9	-0.94	-0.38
C0174	UWBM	98894	phalanx	1	2	3.4	1.3	1.3	-0.96	-0.38
C0174	UWBM	98897	radius	1	2	2.7	2.5	1.4	-0.56	-0.52
C0174	UWBM	98924	fragment	1	2	7	3.2	1.8	-0.55	-0.25
C0174	UWBM	108065-1	fragment	1	2	9.9	1.9	1.3	-0.68	-0.13
C0174	UWBM	108065-2	fragment	1	3	17.1	4.5	2.5	-0.55	-0.15
C0174	UWBM	108065-3	fragment	1	3	5.4	2.1	1.3	-0.62	-0.24
C0174	UWBM	108065-4	fragment	1	3	3.3	2.3	0.8	-0.37	-0.25
C0174	UWBM	108065-5	fragment	2	2	6.2	4	2.4	-0.61	-0.39
C0174	UWBM	108065-6	fragment	1	3	3.8	3	2.5	-0.81	-0.64
C0174	UWBM	108065-7	fragment	0	2	5.6	1.4	1.3	-0.94	-0.23
C0174	UWBM	108065-8	fragment	1	3	4.5	1.3	0.7	-0.55	-0.16
C0174	UWBM	108065-9	fragment	0	2	3.2	1.4	1	-0.74	-0.33
C0174	UWBM	97316-1	fragment	3	3	16	6.2	4.2	-0.67	-0.26
C0174	UWBM	97316-2	fragment	0	1	12.3	10.4	6.2	-0.6	-0.5
C0174	UWBM	97316-3	fragment	1	1	5.8	2.6	1.1	-0.42	-0.19
C0174	UWBM	97316-4	fragment	1	2	4.3	3.7	2.1	-0.57	-0.49
C0174	UWBM	97316-5	fragment	1	2	3.5	3.1	2.1	-0.67	-0.59
C0174	UWBM	97316-6	fragment	3	2	4.8	2	1.7	-0.83	-0.35
C0174	UWBM	97316-7	fragment	2	3	3.5	2.9	1.7	-0.59	-0.49
C0174	UWBM	97318-1	fragment	0	3	8.7	3.5	2.6	-0.75	-0.3
C0174	UWBM	97318-10	fragment	1	3	3.9	3.8	0.9	-0.24	-0.23
C0174	UWBM	97318-11	fragment	1	3	3.7	2.6	0.9	-0.36	-0.25
C0174	UWBM	97318-12	fragment	1	3	7.4	3	1.3	-0.45	-0.18
C0174	UWBM	97318-13	fragment	1	2	4.5	3.6	1.9	-0.53	-0.42
C0174	UWBM	97318-14	fragment	0	3	3.3	3.1	2.2	-0.71	-0.66
C0174	UWBM	97318-15	fragment	1	3	4	1.3	0.8	-0.59	-0.19
C0174	UWBM	97318-16	fragment	1	3	3	1.5	0.6	-0.4	-0.2
C0174	UWBM	97318-2	fragment	1	3	7.7	5.2	1.7	-0.32	-0.21
C0174	UWBM	97318-3	fragment	1	3	5.5	3	0.9	-0.29	-0.16
C0174	UWBM	97318-4	fragment	1	2	9.5	4.4	2.9	-0.67	-0.31
C0174	UWBM	97318-5	fragment	1	3	7.6	2.2	1.6	-0.71	-0.21
C0174	UWBM	97318-6	fragment	2	3	5.7	3.4	2.7	-0.79	-0.48
C0174	UWBM	97318-7	fragment	1	3	11.5	11.4	3.8	-0.33	-0.33
C0174	UWBM	97318-8	fragment	1	2	7	3.9	2.8	-0.72	-0.39
C0174	UWBM	97322-1	fragment	3	2	18.7	11.6	4.2	-0.36	-0.23
C0174	UWBM	97322-10	fragment	1	2	5.5	1.8	0.7	-0.37	-0.12
C0174	UWBM	97322-11	fragment	1	2	3.1	1.3	1	-0.73	-0.31

C0174	UWBM	97322-2	fragment	2	3	19.7	7.8	3.8	-0.49	-0.19
C0174	UWBM	97322-3	fragment	2	2	6.2	5.8	4.8	-0.82	-0.77
C0174	UWBM	97322-4	fragment	3	3	11.6	3.9	1.8	-0.45	-0.15
C0174	UWBM	97322-5	fragment	1	2	11.1	2.9	1.3	-0.44	-0.11
C0174	UWBM	97322-6	fragment	2	2	7.1	3.8	2.5	-0.64	-0.34
C0174	UWBM	97322-7	fragment	0	3	7.5	3.3	1.6	-0.49	-0.22
C0174	UWBM	97322-8	fragment	1	2	9.2	3.9	1.6	-0.4	-0.17
C0174	UWBM	97322-9	fragment	1	1	6.3	1.3	1	-0.81	-0.16
C0174	UWBM	97326-2	fragment	1	1	13	5.4	2.1	-0.39	-0.16
C0174	UWBM	97336-1	fragment	0	1	10.7	7.3	5	-0.68	-0.47
C0174	UWBM	97336-2	fragment	0	1	6.8	4.5	4.3	-0.95	-0.64
C0174	UWBM	97336-3	fragment	1	3	4.9	2.6	1.7	-0.63	-0.34
C0174	UWBM	97336-4	fragment	1	2	3.6	2.8	1.2	-0.42	-0.33
C0174	UWBM	97336-5	fragment	2	1	4.8	3.6	1.2	-0.34	-0.26
C0174	UWBM	97340-1	fragment	2	2	16.4	11.8	2.7	-0.23	-0.16
C0174	UWBM	97340-10	fragment	0	2	4.1	3	1.9	-0.61	-0.46
C0174	UWBM	97340-11	fragment	1	1	9.1	2.5	0.8	-0.34	-0.09
C0174	UWBM	97340-12	fragment	2	2	5.6	3.8	2.9	-0.76	-0.52
C0174	UWBM	97340-13	fragment	0	2	5.4	2.3	1.5	-0.67	-0.29
C0174	UWBM	97340-14	fragment	1	3	4.3	2.3	1	-0.42	-0.23
C0174	UWBM	97340-15	fragment	1	2	4	2.5	1.9	-0.76	-0.47
C0174	UWBM	97340-16	fragment	3	3	4.7	2.8	1.6	-0.57	-0.34
C0174	UWBM	97340-17	fragment	1	1	7	1.8	1.7	-0.93	-0.24
C0174	UWBM	97340-2	fragment	1	2	7.7	7.7	6.5	-0.85	-0.84
C0174	UWBM	97340-3	fragment	1	3	16.4	6.1	3	-0.5	-0.19
C0174	UWBM	97340-4	fragment	1	3	11.3	9.4	2.7	-0.28	-0.24
C0174	UWBM	97340-5	fragment	1	3	7.5	3.9	2.8	-0.71	-0.38
C0174	UWBM	97340-6	fragment	1	3	5.3	5.1	3.4	-0.66	-0.64
C0174	UWBM	97340-7	fragment	0	1	7.8	7.4	4	-0.54	-0.51
C0174	UWBM	97340-8	fragment	3	3	20.1	3.9	3	-0.77	-0.15
C0174	UWBM	97340-9	fragment	1	2	6.2	3	0.8	-0.27	-0.13
C0174	UWBM	97398-1	fragment	2	3	12.3	10.9	4	-0.37	-0.33
C0174	UWBM	97398-2	fragment	1	2	7.2	6.2	3.6	-0.58	-0.51
C0174	UWBM	97398-3	fragment	1	2	18.2	10.9	5.3	-0.49	-0.29
C0174	UWBM	97398-4	fragment	1	2	5.7	4.6	2.4	-0.51	-0.41
C0174	UWBM	97404-1	fragment	1	3	9.8	2.4	1.2	-0.48	-0.12
C0174	UWBM	97404-10	fragment	0	3	4.2	1.4	0.7	-0.48	-0.16
C0174	UWBM	97404-11	fragment	1	3	2.6	2.6	1.3	-0.48	-0.48
C0174	UWBM	97404-12	metapodial	1	1	7.5	2.1	1.4	-0.67	-0.19
C0174	UWBM	97404-13	vertebra	1	2	4.6	3.1	3	-0.97	-0.64

C0174	UWBM	97404-14	fragment	2	1	3.3	1.4	1.2	-0.9	-0.37
C0174	UWBM	97404-2	fragment	2	3	10.9	3.9	1.8	-0.47	-0.17
C0174	UWBM	97404-3	fragment	1	3	12.5	4.3	1.4	-0.32	-0.11
C0174	UWBM	97404-4	fragment	1	3	14	5.2	2	-0.37	-0.14
C0174	UWBM	97404-5	fragment	1	3	7.4	3	2.3	-0.77	-0.31
C0174	UWBM	97404-6	fragment	1	3	11.1	2.6	1.7	-0.65	-0.15
C0174	UWBM	97404-7	fragment	1	2	5.2	2.1	1.2	-0.59	-0.23
C0174	UWBM	97404-8	fragment	0	1	5.9	2.5	1.2	-0.5	-0.21
C0174	UWBM	97404-9	fragment	1	2	3.4	3.3	1.6	-0.49	-0.47
C0174	UWBM	98650b	fragment	1	1	5.7	4.1	3.9	-0.97	-0.69
C0174	UWBM	98651-1	fragment	0	3	8.5	3	2.1	-0.7	-0.25
C0174	UWBM	98651-2	fragment	1	3	3.8	2.1	1.7	-0.81	-0.45
C0174	UWBM	98651-3	fragment	0	3	3.6	3.4	0.8	-0.24	-0.23
C0174	UWBM	98651-4	fragment	1	3	6.7	1.1	0.8	-0.74	-0.12
C0174	UWBM	98651-5	fragment	0	2	5.2	4	2	-0.5	-0.38
C0174	UWBM	98868-1	fragment	1	2	10.3	5.2	3.3	-0.64	-0.32
C0174	UWBM	98868-2	fragment	1	1	11.8	6.4	2.2	-0.34	-0.19
C0174	UWBM	98868-3	fragment	1	2	5.2	1.3	0.8	-0.59	-0.15
C0174	UWBM	98868-4	fragment	1	2	5	1.2	1	-0.81	-0.19
C0174	UWBM	98905-1	phalanx	1	2	2	1.6	1	-0.64	-0.53
C1704	KUVP	20545-4	podial	2	1	6.7	4.4	3.5	-0.79	-0.51
C1704	KUVP	20545-5	vertebra	2	0	6.2	3.1	2.9	-0.91	-0.46
C1704	KUVP	20546-14	phalanx	0	0	2.8	0.9	0.7	-0.8	-0.25
C1704	KUVP	20546-16	vertebra	2	1	2.3	2.3	1.4	-0.62	-0.6
C1704	KUVP	20546-22	astragalus	0	2	2.1	1.3	1	-0.79	-0.47
C1704	KUVP	20546-26	metapodial	2	2	3.6	0.8	0.8	-0.9	-0.21
C1704	KUVP	20546-28	vertebra	1	3	2	0.7	0.6	-0.91	-0.31
C1704	KUVP	20546-30	vertebra	0	1	3	1.1	1	-0.87	-0.33
C1704	KUVP	20546-37	phalanx	1	1	1.4	1	0.9	-0.88	-0.62
C1704	KUVP	20546-48	metapodial	2	2	2.9	0.8	0.7	-0.97	-0.25
C1704	UWBM	97394	vertebra	2	1	6.4	3.7	3.4	-0.92	-0.54
C1704	UWBM	108076-1	fragment	1	3	9.4	8.1	3.7	-0.46	-0.39
C1704	UWBM	108076-2	fragment	1	3	10.5	3.6	2.6	-0.72	-0.25
C1704	UWBM	108076-3	fragment	2	3	6.4	1.4	1.2	-0.87	-0.19
C1704	UWBM	108076-4	fragment	0	3	7	3	2.3	-0.76	-0.32
C1704	UWBM	108076-5	fragment	0	1	3.7	2.9	1.3	-0.46	-0.36
C1704	UWBM	108076-6	fragment	1	3	5.9	4	2.9	-0.72	-0.48
C1704	UWBM	108078-1	fragment	1	3	12.9	4.4	1.7	-0.4	-0.13
C1704	UWBM	108078-10	fragment	1	2	6.4	4.1	2.3	-0.58	-0.36
C1704	UWBM	108078-11	fragment	2	3	7.1	5.1	2.2	-0.43	-0.31

C1704	UWBM	108078-12	fragment	0	3	4.8	4.1	2.5	-0.61	-0.52
C1704	UWBM	108078-13	fragment	0	2	4.6	2.7	1	-0.38	-0.22
C1704	UWBM	108078-2	fragment	1	3	9.6	3.1	2.5	-0.8	-0.26
C1704	UWBM	108078-3	fragment	0	3	7.7	3.7	1.5	-0.41	-0.19
C1704	UWBM	108078-4	fragment	1	2	8.9	4.2	1.2	-0.29	-0.13
C1704	UWBM	108078-5	fragment	1	3	3.8	3	1	-0.34	-0.27
C1704	UWBM	108078-6	fragment	0	3	6.1	5	1.6	-0.32	-0.26
C1704	UWBM	108078-7	fragment	0	3	7.1	3.1	1.1	-0.36	-0.16
C1704	UWBM	108078-8	fragment	1	3	5.7	2.4	1.8	-0.74	-0.31
C1704	UWBM	108078-9	fragment	0	2	2.9	2.8	1.5	-0.55	-0.52
C1704	UWBM	108083-1	fragment	0	3	5.4	2.8	1.4	-0.52	-0.27
C1704	UWBM	108083-2	fragment	1	2	6.2	2.9	2.8	-0.97	-0.45
C1704	UWBM	108084-1	fragment	2	2	3.4	1.7	0.7	-0.4	-0.2
C1704	UWBM	108084-10	fragment	1	3	2.8	2.2	0.7	-0.32	-0.25
C1704	UWBM	108084-11	fragment	0	2	3.6	1.2	0.7	-0.55	-0.18
C1704	UWBM	108084-12	fragment	0	3	2.7	0.9	0.6	-0.7	-0.24
C1704	UWBM	108084-13	fragment	2	2	3.1	1.6	1.1	-0.66	-0.34
C1704	UWBM	108084-14	fragment	1	3	2.6	1.4	0.9	-0.66	-0.36
C1704	UWBM	108084-15	fragment	1	3	2.7	1.6	0.4	-0.26	-0.16
C1704	UWBM	108084-16	fragment	0	3	2.6	1.4	0.4	-0.26	-0.13
C1704	UWBM	108084-17	fragment	0	2	1.9	1.3	0.8	-0.66	-0.44
C1704	UWBM	108084-18	fragment	0	1	2.1	1.1	0.9	-0.75	-0.41
C1704	UWBM	108084-2	fragment	1	2	2.3	1.4	0.6	-0.44	-0.26
C1704	UWBM	108084-3	fragment	0	3	3.9	1.4	1.1	-0.74	-0.27
C1704	UWBM	108084-4	fragment	1	2	4.5	3.2	1.8	-0.55	-0.4
C1704	UWBM	108084-5	fragment	1	3	3.8	2.6	1.1	-0.43	-0.29
C1704	UWBM	108084-6	fragment	1	3	2.8	1.4	0.6	-0.46	-0.23
C1704	UWBM	108084-7	fragment	0	3	4.9	3.5	1	-0.29	-0.2
C1704	UWBM	108084-8	fragment	0	2	2.9	2.9	0.6	-0.21	-0.21
C1704	UWBM	108084-9	fragment	0	2	3.8	1.4	0.6	-0.46	-0.17
C1704	UWBM	108085-1	fragment	2	2	11.7	5.4	5.4	-0.99	-0.46
C1704	UWBM	108085-2	fragment	1	3	14.6	7.3	3.8	-0.52	-0.26
C1704	UWBM	108085-3	fragment	0	3	7.2	3.8	1	-0.27	-0.14
C1704	UWBM	108085-4	fragment	1	2	3.8	3.4	1.8	-0.53	-0.47
C1704	UWBM	108085-5	fragment	2	3	4	1.3	1	-0.74	-0.24
C1704	UWBM	18075-1	fragment	1	3	11.2	5.8	2.9	-0.5	-0.26
C1704	UWBM	18075-2	fragment	1	2	5.9	4.3	2.9	-0.67	-0.49
C1704	UWBM	18077-1	fragment	1	2	10.9	3.7	1.7	-0.45	-0.15
C1704	UWBM	18077-2	fragment	1	3	9.8	3.6	2.1	-0.57	-0.21
C1704	UWBM	18077-3	fragment	2	2	4.1	2.4	1.8	-0.72	-0.43

C1704	UWBM	97435b	fragment	2	3	20.7	11.5	6	-0.53	-0.29
C1704	UWBM	97437-1	fragment	2	2	26.6	23.9	7.3	-0.31	-0.27
C1704	UWBM	97437-2	fragment	2	3	24.7	6.9	4.3	-0.62	-0.18
C1704	UWBM	97437-3	fragment	3	3	11.5	4.5	4	-0.89	-0.35
C1704	UWBM	97437-4	fragment	2	3	12.8	3.7	2	-0.55	-0.16
C1704	UWBM	97437-5	fragment	0	2	3.1	2.9	2.4	-0.83	-0.77
C1704	UWBM	97441-1	fragment	2	3	12.3	4.7	1.9	-0.4	-0.16
C1704	UWBM	97441-2	fragment	1	2	11.9	2.8	1.3	-0.48	-0.11
C1704	UWBM	97443-1	fragment	3	3	12.3	7.4	3.2	-0.44	-0.26
C1704	UWBM	97443-2	fragment	3	3	8.7	5.6	1.8	-0.32	-0.21
C1704	UWBM	97443-3	fragment	1	3	4.8	3.5	1.3	-0.36	-0.27
C1704	UWBM	97443-4	fragment	1	2	5.5	1.7	1.2	-0.69	-0.21
C1704	UWBM	97443-5	fragment	3	2	5.2	2.4	1.3	-0.54	-0.25
C1704	UWBM	97447-1	fragment	2	2	12.8	4.3	2	-0.46	-0.16
C1704	UWBM	97447-2	fragment	0	3	8.4	5.3	1.8	-0.35	-0.22
C1704	UWBM	97447-3	fragment	1	3	11.4	2.5	1.8	-0.71	-0.16
C1704	UWBM	97447-4	fragment	1	2	9	7.3	2.7	-0.38	-0.3
C1704	UWBM	97447-5	fragment	0	2	6	2.7	1.2	-0.44	-0.2
C1704	UWBM	97447-6	fragment	0	3	5.6	3.3	0.9	-0.28	-0.17
C1704	UWBM	97447-7	fragment	1	2	5.6	1.9	1.1	-0.54	-0.19
C1704	UWBM	97447-8	fragment	1	3	6.2	2.4	1.6	-0.68	-0.26
C1704	UWBM	97448-1	fragment	2	2	11	5.3	1.8	-0.33	-0.16
C1704	UWBM	97448-2	fragment	2	1	11.4	4.9	2.2	-0.45	-0.2
C1704	UWBM	97448-3	fragment	2	2	13.5	3.6	2.8	-0.79	-0.21
C1704	UWBM	97448-4	fragment	3	3	12.5	5.1	2.7	-0.52	-0.21
C1704	UWBM	97448-5	fragment	1	2	13.3	2.8	1.7	-0.58	-0.13
C1704	UWBM	97448-6	fragment	1	3	6.4	5.3	1.1	-0.21	-0.18
C1704	UWBM	98921-1	fragment	2	3	18.8	7.7	5.9	-0.77	-0.32
C1704	UWBM	98921-10	fragment	1	1	5.4	4.7	3.3	-0.71	-0.62
C1704	UWBM	98921-11	fragment	1	3	4.8	2	1.5	-0.74	-0.3
C1704	UWBM	98921-12	fragment	1	3	3.6	2.6	2.2	-0.82	-0.6
C1704	UWBM	98921-13	fragment	0	3	3.5	2.6	1.8	-0.68	-0.51
C1704	UWBM	98921-14	fragment	2	3	4.3	2.1	0.9	-0.46	-0.22
C1704	UWBM	98921-15	fragment	2	2	3.4	2.3	1.5	-0.65	-0.45
C1704	UWBM	98921-16	fragment	2	3	3.5	1.3	1.1	-0.85	-0.31
C1704	UWBM	98921-17	fragment	1	3	3.3	1.8	1.2	-0.65	-0.36
C1704	UWBM	98921-18	fragment	1	2	3.6	1.1	1	-0.97	-0.29
C1704	UWBM	98921-2	fragment	1	2	9.1	3.3	2.4	-0.73	-0.27
C1704	UWBM	98921-3	fragment	0	2	7.8	5.6	5.2	-0.92	-0.66
C1704	UWBM	98921-4	fragment	2	3	5.1	4.5	1.9	-0.42	-0.37

C1704	UWBM	98921-5	fragment	1	3	7	1.8	1	-0.58	-0.15
C1704	UWBM	98921-6	fragment	1	3	4.5	2.6	1.3	-0.51	-0.3
C1704	UWBM	98921-8	fragment	1	3	5.5	3.4	2	-0.57	-0.35
C1704	UWBM	98921-9	fragment	1	1	8.3	3.2	2.9	-0.91	-0.34
C1707	UWBM	98665	dentary	2	0	9.4	3.5	1.5	-0.42	-0.16
C1707	UWBM	98720	skull	1	0	5.7	3.2	2	-0.62	-0.35
C1707	UWBM	98933	vertebra	3	3	6.5	3.8	2.5	-0.67	-0.38
C1707	UWBM	101288	fragment	2	3	7.3	3.9	2.7	-0.69	-0.37
C1707	UWBM	101369	ulna	0	2	2.6	1.6	1.1	-0.73	-0.44
C1707	UWBM	108005	vertebra	2	3	3.5	1.1	0.9	-0.83	-0.26
C1707	UWBM	108137	phalanx	3	3	2.4	2.1	1.3	-0.6	-0.51
C1707	UWBM	108141	phalanx	1	2	2.1	1.1	1	-0.88	-0.46
C1707	UWBM	108143	femur	1	2	13.5	8.4	4.5	-0.53	-0.33
C1707	UWBM	108145	vertebra	0	1	3.4	1.1	0.9	-0.82	-0.26
C1707	UWBM	108150	dentary	1	2	4.2	2.7	1	-0.36	-0.23
C1707	UWBM	108156	dentary	1	2	2.6	1.6	0.8	-0.51	-0.31
C1707	UWBM	101287-1	fragment	3	3	13.9	7.3	5.7	-0.78	-0.41
C1707	UWBM	101287-2	fragment	3	3	8	4.7	3.3	-0.69	-0.41
C1707	UWBM	101287-3	fragment	1	3	9.2	6.4	4.3	-0.67	-0.47
C1707	UWBM	101287-4	fragment	1	3	8.3	3.8	1.9	-0.51	-0.23
C1707	UWBM	101287-5	fragment	2	3	7.8	6.8	4.6	-0.69	-0.59
C1707	UWBM	101287-6	fragment	1	3	9.6	7.6	4.2	-0.55	-0.43
C1707	UWBM	101287-7	fragment	1	3	7.5	5.7	2.1	-0.37	-0.28
C1707	UWBM	101287-8	fragment	2	3	8.8	6.4	1.4	-0.21	-0.16
C1707	UWBM	101289-1	fragment	2	3	7	5.6	5.3	-0.94	-0.75
C1707	UWBM	101289-2	fragment	3	3	7.7	2.5	2	-0.81	-0.26
C1707	UWBM	101367-1	fragment	2	3	25	7.7	4.6	-0.59	-0.18
C1707	UWBM	101367-2	fragment	2	1	6.4	6.3	3.3	-0.52	-0.51
C1707	UWBM	108089-1	fragment	1	3	6.7	2.7	1.5	-0.55	-0.22
C1707	UWBM	108089-10	fragment	1	3	3.7	1.8	0.7	-0.37	-0.18
C1707	UWBM	108089-11	fragment	0	3	5.6	1.6	1.3	-0.84	-0.23
C1707	UWBM	108089-12	fragment	1	3	9.8	3.6	2	-0.54	-0.2
C1707	UWBM	108089-13	fragment	3	3	4.7	2.5	1.3	-0.53	-0.28
C1707	UWBM	108089-14	fragment	1	2	7	2.4	1.2	-0.48	-0.17
C1707	UWBM	108089-15	fragment	2	3	3.1	2.2	1.2	-0.55	-0.4
C1707	UWBM	108089-16	fragment	1	2	3.9	1.5	0.7	-0.48	-0.18
C1707	UWBM	108089-17	fragment	0	2	3.1	1.3	1.2	-0.91	-0.38
C1707	UWBM	108089-18	fragment	2	3	4.5	1.4	0.6	-0.42	-0.13
C1707	UWBM	108089-19	fragment	1	2	4.2	1.3	0.6	-0.48	-0.15
C1707	UWBM	108089-2	fragment	1	3	7.1	4.4	1.6	-0.37	-0.23

C1707	UWBM	108089-20	fragment	1	2	5.4	1.6	0.9	-0.55	-0.16
C1707	UWBM	108089-21	fragment	0	2	3.8	1.9	0.8	-0.44	-0.22
C1707	UWBM	108089-22	fragment	3	3	3	1.1	0.9	-0.84	-0.29
C1707	UWBM	108089-3	fragment	1	3	5.8	1.4	0.6	-0.4	-0.1
C1707	UWBM	108089-4	fragment	3	3	8.8	6.3	2	-0.32	-0.22
C1707	UWBM	108089-5	fragment	3	3	8.8	2.9	1	-0.33	-0.11
C1707	UWBM	108089-6	fragment	3	3	6.7	4.3	2	-0.45	-0.29
C1707	UWBM	108089-7	fragment	2	3	5.2	1.6	1.4	-0.86	-0.27
C1707	UWBM	108089-8	fragment	2	3	5	3.8	1.1	-0.29	-0.22
C1707	UWBM	108089-9	fragment	1	3	4.3	1.6	0.9	-0.53	-0.2
C1707	UWBM	108090-1	fragment	1	3	16	9.2	4.5	-0.49	-0.28
C1707	UWBM	108090-10	fragment	1	3	6.6	3.1	1.5	-0.46	-0.22
C1707	UWBM	108090-11	fragment	0	2	10.6	2.6	1.2	-0.47	-0.12
C1707	UWBM	108090-12	fragment	1	2	8.1	2.1	1.2	-0.59	-0.15
C1707	UWBM	108090-13	fragment	3	3	5.3	2.7	1.2	-0.44	-0.22
C1707	UWBM	108090-14	fragment	2	3	5.4	2.9	1.7	-0.57	-0.31
C1707	UWBM	108090-15	fragment	2	3	3.4	2	0.7	-0.34	-0.2
C1707	UWBM	108090-16	fragment	1	3	6	3.1	1.4	-0.45	-0.23
C1707	UWBM	108090-17	fragment	0	2	4.4	2.4	1.1	-0.46	-0.26
C1707	UWBM	108090-18	fragment	2	2	5.7	4.1	2.1	-0.52	-0.38
C1707	UWBM	108090-19	fragment	1	3	5	2.3	1.3	-0.58	-0.26
C1707	UWBM	108090-2	fragment	3	3	7.7	7.4	1.6	-0.22	-0.21
C1707	UWBM	108090-20	fragment	2	3	6.7	3.2	1.2	-0.39	-0.18
C1707	UWBM	108090-21	fragment	1	2	6.3	4.8	2.4	-0.5	-0.38
C1707	UWBM	108090-22	fragment	1	2	4.4	3.9	2	-0.52	-0.46
C1707	UWBM	108090-23	fragment	2	3	4	2.1	0.8	-0.39	-0.21
C1707	UWBM	108090-24	fragment	2	3	4.3	1.3	0.9	-0.7	-0.21
C1707	UWBM	108090-25	fragment	0	3	5.7	5.6	2.8	-0.5	-0.49
C1707	UWBM	108090-26	fragment	3	3	3.9	1.7	1.2	-0.7	-0.3
C1707	UWBM	108090-27	fragment	2	3	4.2	1.7	1	-0.6	-0.24
C1707	UWBM	108090-28	fragment	2	3	2.5	1.8	0.8	-0.44	-0.32
C1707	UWBM	108090-29	fragment	1	3	3.1	1.7	0.8	-0.47	-0.26
C1707	UWBM	108090-3	fragment	2	3	8.1	6.8	1.8	-0.27	-0.23
C1707	UWBM	108090-30	fragment	1	2	3.7	1.4	0.9	-0.62	-0.24
C1707	UWBM	108090-31	fragment	1	3	5.3	3.8	1.9	-0.48	-0.35
C1707	UWBM	108090-32	fragment	3	2	7.9	3	2	-0.66	-0.25
C1707	UWBM	108090-33	fragment	1	2	5.4	1.8	0.7	-0.37	-0.12
C1707	UWBM	108090-34	fragment	2	3	3	2.9	1.2	-0.42	-0.4
C1707	UWBM	108090-35	fragment	1	3	5.2	1.8	1.3	-0.72	-0.26
C1707	UWBM	108090-36	fragment	0	3	1.9	1.7	0.7	-0.41	-0.37

C1707	UWBM	108090-37	fragment	1	2	5.6	2.4	1.3	-0.53	-0.23
C1707	UWBM	108090-38	fragment	2	3	3.7	2	0.9	-0.44	-0.24
C1707	UWBM	108090-39	fragment	0	2	4.1	2	1.3	-0.67	-0.32
C1707	UWBM	108090-4	fragment	1	3	8.1	6.1	4.6	-0.76	-0.57
C1707	UWBM	108090-40	fragment	1	3	4.4	0.9	0.8	-0.94	-0.18
C1707	UWBM	108090-41	fragment	1	3	4.1	1.3	1	-0.82	-0.25
C1707	UWBM	108090-42	fragment	2	3	3.7	1.1	0.8	-0.74	-0.23
C1707	UWBM	108090-43	fragment	2	3	5.1	1.6	1.4	-0.91	-0.28
C1707	UWBM	108090-44	fragment	1	2	3	1.6	1.2	-0.74	-0.39
C1707	UWBM	108090-45	fragment	2	3	4.6	2.6	2	-0.78	-0.45
C1707	UWBM	108090-46	fragment	2	3	2.9	1.3	0.9	-0.7	-0.31
C1707	UWBM	108090-47	fragment	1	2	2.7	0.8	0.8	-0.96	-0.29
C1707	UWBM	108090-48	fragment	1	2	2.9	1.6	0.9	-0.57	-0.3
C1707	UWBM	108090-49	fragment	1	3	2.8	1.3	0.6	-0.47	-0.22
C1707	UWBM	108090-5	fragment	0	2	7.4	3.5	1.7	-0.48	-0.23
C1707	UWBM	108090-50	fragment	2	3	4.4	1.4	1	-0.74	-0.24
C1707	UWBM	108090-51	fragment	2	2	2.9	1.4	1.2	-0.85	-0.41
C1707	UWBM	108090-6	fragment	1	2	6.7	4.9	3.5	-0.73	-0.53
C1707	UWBM	108090-7	fragment	2	3	6.5	2.6	1.4	-0.53	-0.21
C1707	UWBM	108090-8	fragment	0	3	5.3	3.3	0.9	-0.28	-0.17
C1707	UWBM	108090-9	fragment	1	3	8.1	3.1	1.7	-0.53	-0.2
C1707	UWBM	98937-1	fragment	1	2	11	4.1	1.6	-0.39	-0.14
C1707	UWBM	98937-2	fragment	3	3	5	2.4	1.7	-0.71	-0.34
C1707	UWBM	98937-3	fragment	1	3	3.6	2.9	1.2	-0.42	-0.34
C1707	UWBM	98937-4	fragment	2	2	4.7	3.7	3.2	-0.87	-0.68
C1707	UWBM	98937-5	fragment	2	3	3.8	1.8	1.6	-0.86	-0.42
C1708	KUVP	19931-1	humerus	0	0	7.3	5.1	4.6	-0.89	-0.63
C1708	KUVP	19931-10	phalanx	1	1	8	3.8	2.2	-0.59	-0.28
C1708	KUVP	19931-36	phalanx	1	2	5.8	1.7	1.3	-0.78	-0.22
C1708	KUVP	19931-39	vertebra	2	1	3	3	2.3	-0.79	-0.78
C1708	KUVP	19931-44	femur	1	2	8.3	3.1	1.9	-0.6	-0.22
C1708	KUVP	19931-50	fragment	0	3	18.9	10.4	5.4	-0.52	-0.29
C1708	KUVP	19931-51	fragment	1	3	16.1	4.8	4.2	-0.88	-0.26
C1708	KUVP	19931-52	fragment	1	3	11.9	7.2	3.5	-0.49	-0.3
C1708	KUVP	19931-53	fragment	1	2	7.4	4.3	1.4	-0.33	-0.19
C1708	KUVP	19931-54	fragment	1	2	9.4	4.6	2.3	-0.49	-0.24
C1708	KUVP	19931-55	fragment	3	3	8.9	7.6	3.8	-0.5	-0.43
C1708	KUVP	19931-56	fragment	1	3	13	7.4	3	-0.4	-0.23
C1708	KUVP	19931-57	fragment	2	3	6.6	5	3	-0.59	-0.45
C1708	KUVP	19931-58	fragment	3	3	5.4	5	3.2	-0.64	-0.6

C1708	KUVP	19931-59	fragment	1	2	7.4	2.6	1.1	-0.41	-0.14
C1708	KUVP	19931-60	fragment	1	3	5.7	3	2.2	-0.74	-0.39
C1708	KUVP	19931-61	fragment	1	3	4.5	3.9	1.5	-0.39	-0.34
C1708	KUVP	19931-62	fragment	1	3	7.2	5	1.4	-0.28	-0.19
C1708	KUVP	19931-63	fragment	3	3	12.2	5.5	3.1	-0.56	-0.25
C1708	KUVP	19931-64	fragment	1	2	9.5	6.3	5.2	-0.82	-0.54
C1708	KUVP	19931-65	fragment	3	2	10	2.9	1.8	-0.62	-0.18
C1708	KUVP	19931-66	fragment	1	2	10.6	4.1	2.2	-0.53	-0.21
C1708	KUVP	19931-67	fragment	2	2	4.8	3.3	2.1	-0.63	-0.43
C1708	KUVP	19931-68	fragment	0	3	9	3.6	1.4	-0.39	-0.16
C1708	KUVP	19931-9	phalanx	1	1	5.9	3.1	2.3	-0.74	-0.39
C1708	UWBM	98749	phalanx	1	1	2.4	0.9	0.7	-0.72	-0.28
C1708	UWBM	98767	dentary	2	2	16.9	6.8	3.6	-0.53	-0.21
C1708	UWBM	98814	phalanx	1	2	4.9	2.8	2.4	-0.86	-0.48
C1708	UWBM	98919	fragment	1	2	4.1	2.5	1.3	-0.53	-0.32
C1708	UWBM	108062-1	fragment	2	3	13.2	5.7	4.8	-0.84	-0.36
C1708	UWBM	108062-10	fragment	1	3	9.5	3.5	1.7	-0.48	-0.18
C1708	UWBM	108062-11	fragment	1	2	9.9	3.9	1.1	-0.28	-0.11
C1708	UWBM	108062-12	fragment	1	3	12.1	5	3.3	-0.67	-0.27
C1708	UWBM	108062-13	fragment	2	3	9.5	3.8	2.3	-0.6	-0.24
C1708	UWBM	108062-14	fragment	1	3	9.1	1.9	1.9	-0.98	-0.21
C1708	UWBM	108062-15	fragment	2	3	6.9	2.8	2.7	-0.99	-0.4
C1708	UWBM	108062-16	fragment	1	3	8.7	7.4	2.7	-0.36	-0.3
C1708	UWBM	108062-17	fragment	3	2	5.2	4.9	3.4	-0.68	-0.64
C1708	UWBM	108062-18	fragment	1	3	7.8	1.2	1.1	-0.88	-0.14
C1708	UWBM	108062-19	fragment	1	2	11.2	4.7	2.1	-0.45	-0.19
C1708	UWBM	108062-2	fragment	1	2	11.2	4.5	2	-0.44	-0.17
C1708	UWBM	108062-20	fragment	1	2	8.3	3.6	1	-0.27	-0.12
C1708	UWBM	108062-21	fragment	2	3	10.2	3.1	2.5	-0.81	-0.24
C1708	UWBM	108062-22	fragment	2	2	8	3.8	1.8	-0.47	-0.23
C1708	UWBM	108062-23	fragment	2	1	4.2	2.2	1.6	-0.7	-0.37
C1708	UWBM	108062-24	fragment	1	3	7.9	3.2	1.3	-0.39	-0.16
C1708	UWBM	108062-25	fragment	2	3	6.9	2	1.9	-0.98	-0.28
C1708	UWBM	108062-3	fragment	1	2	17.8	6.9	2.8	-0.41	-0.16
C1708	UWBM	108062-4	fragment	1	2	16.6	4.9	2.8	-0.56	-0.17
C1708	UWBM	108062-5	fragment	1	2	13.7	9.1	5.3	-0.58	-0.39
C1708	UWBM	108062-6	fragment	2	3	9.5	4.1	1	-0.25	-0.11
C1708	UWBM	108062-7	fragment	1	1	8.9	3.4	2.1	-0.62	-0.24
C1708	UWBM	108062-8	fragment	2	3	9.7	3.1	2.1	-0.69	-0.22
C1708	UWBM	108062-9	fragment	1	2	14	5	4.5	-0.89	-0.32

C1708	UWBM	108071-1	fragment	1	3	19.4	19.2	7.4	-0.38	-0.38
C1708	UWBM	108071-2	fragment	1	3	35.3	34	6.9	-0.2	-0.19
C1708	UWBM	108071-3	fragment	1	3	32.6	16	11	-0.69	-0.34
C1708	UWBM	108071-4	fragment	2	3	16.3	10.5	4.3	-0.41	-0.26
C1708	UWBM	108071-5	fragment	2	3	19.7	13.5	7.8	-0.58	-0.4
C1708	UWBM	108071-6	fragment	0	2	5.3	3.5	0.8	-0.24	-0.16
C1708	UWBM	108071-7	fragment	2	3	23.9	20.5	11.5	-0.56	-0.48
C1708	UWBM	108071-8	fragment	0	1	6.7	1.5	0.9	-0.6	-0.13
C1708	UWBM	108071-9	fragment	0	2	8.4	4.6	1.6	-0.34	-0.19
C1708	UWBM	108072-1	fragment	0	2	8.3	3.4	1	-0.29	-0.12
C1708	UWBM	108072-2	fragment	1	3	15.3	8	4.7	-0.58	-0.3
C1708	UWBM	108072-3	fragment	1	3	6.4	4.3	3.3	-0.75	-0.51
C1708	UWBM	108072-4	fragment	0	2	2.7	2.3	1.4	-0.6	-0.5
C1708	UWBM	108072-5	fragment	1	2	3.8	2.4	1.3	-0.53	-0.34
C1708	UWBM	108072-6	fragment	3	3	10	3.2	2.8	-0.89	-0.28
C1708	UWBM	108072-7	fragment	3	2	3.7	3.2	2	-0.6	-0.53
C1708	UWBM	19931-21	sesamoid	1	2	9.2	5.9	3.1	-0.52	-0.33
C1708	UWBM	19931-72	vertebra	1	2	2.9	2.4	1.6	-0.68	-0.56
C1708	UWBM	98925-1	fragment	1	0	36.6	6.4	2.5	-0.4	-0.07
C1708	UWBM	98925-10	fragment	1	2	9	6.4	2.5	-0.39	-0.28
C1708	UWBM	98925-11	fragment	3	3	37.8	15.1	7.2	-0.48	-0.19
C1708	UWBM	98925-12	fragment	1	3	10.8	4.3	2.3	-0.52	-0.21
C1708	UWBM	98925-13	fragment	1	3	8.9	3	2.3	-0.76	-0.25
C1708	UWBM	98925-14	fragment	1	3	6	2.6	1.1	-0.42	-0.18
C1708	UWBM	98925-15	fragment	2	3	6.9	6.5	2.1	-0.32	-0.3
C1708	UWBM	98925-16	fragment	3	3	15.3	10.7	4	-0.38	-0.26
C1708	UWBM	98925-17	fragment	1	3	6.6	3.7	1.2	-0.31	-0.18
C1708	UWBM	98925-18	fragment	2	3	8	4.6	1.5	-0.33	-0.19
C1708	UWBM	98925-19	fragment	2	2	9	3.8	0.8	-0.21	-0.09
C1708	UWBM	98925-2	fragment	0	2	17.5	8	2.5	-0.3	-0.14
C1708	UWBM	98925-20	fragment	2	3	4.9	4.1	3.5	-0.86	-0.71
C1708	UWBM	98925-21	fragment	2	2	4	3.9	2.8	-0.71	-0.69
C1708	UWBM	98925-22	fragment	2	3	5.8	2.5	1.2	-0.48	-0.2
C1708	UWBM	98925-23	fragment	1	3	4.4	2.3	1.2	-0.52	-0.27
C1708	UWBM	98925-3	fragment	1	2	43.5	7.1	2.6	-0.36	-0.06
C1708	UWBM	98925-4	fragment	1	2	8	7.8	3.8	-0.49	-0.48
C1708	UWBM	98925-5	fragment	3	2	15.3	7.4	3.1	-0.42	-0.2
C1708	UWBM	98925-6	fragment	1	3	18.3	10.6	5.8	-0.54	-0.31
C1708	UWBM	98925-7	fragment	2	3	13.9	4.9	2.3	-0.47	-0.17
C1708	UWBM	98925-8	fragment	2	3	11.5	5.3	3	-0.57	-0.26

C1708	UWBM	98925-9	fragment	1	3	9.7	6.6	3.1	-0.47	-0.32
C1708	UWBM	98926-1	fragment	2	3	19.7	5.8	2.6	-0.45	-0.13
C1708	UWBM	98926-2	fragment	2	2	17.7	4.6	4.2	-0.92	-0.24
C1708	UWBM	98926-3	fragment	2	2	6.2	5.2	0.9	-0.17	-0.15
C1708	UWBM	98926-4	fragment	3	3	9.3	6	2.8	-0.47	-0.3
C1708	UWBM	98926-5	fragment	0	1	4.4	3.2	0.9	-0.28	-0.2
C1708	UWBM	98926-6	fragment	2	1	5	2	1	-0.51	-0.2
C1708	UWBM	98926-7	fragment	1	1	2.9	1.3	0.9	-0.68	-0.3
C1721	UWBM	18041	dentary	1	3	3.9	1.9	0.8	-0.42	-0.21
C1721	UWBM	97353	fragment	1	3	17.9	9.9	5.1	-0.52	-0.28
C1721	UWBM	97358	metapodial	1	1	10.2	8.1	6.6	-0.81	-0.64
C1721	UWBM	97453	humerus	0	2	11	10.1	6.6	-0.66	-0.61
C1721	UWBM	97458	fragment	1	3	13.4	12.3	10.1	-0.82	-0.75
C1721	UWBM	97487	dentary	1	0	2.2	1.8	1.4	-0.75	-0.62
C1721	UWBM	97496	humerus	1	1	5.6	5.4	2.6	-0.48	-0.46
C1721	UWBM	98638	fragment	2	3	16.6	7.5	6.4	-0.85	-0.38
C1721	UWBM	101314	phalanx	2	3	9.7	5.2	4.3	-0.84	-0.45
C1721	UWBM	101321	femur	1	2	6.2	3.5	1.9	-0.54	-0.3
C1721	UWBM	101325	femur	1	2	2.6	2.4	1.7	-0.72	-0.67
C1721	UWBM	101358	phalanx	2	1	2.8	1.2	1.2	-0.94	-0.41
C1721	UWBM	101392	vertebra	1	1	2.1	1.8	1.5	-0.85	-0.73
C1721	UWBM	108066-1	fragment	2	3	27.9	8	3.2	-0.39	-0.11
C1721	UWBM	108066-2	fragment	2	2	18.6	4.7	2.6	-0.55	-0.14
C1721	UWBM	108066-3	fragment	3	2	6	2.2	1.3	-0.57	-0.21
C1721	UWBM	108066-4	fragment	3	1	15.6	4.2	1.6	-0.39	-0.1
C1721	UWBM	108066-5	fragment	2	3	8.5	3.3	2.2	-0.66	-0.26
C1721	UWBM	108066-6	fragment	2	3	6.5	1.8	0.6	-0.33	-0.09
C1721	UWBM	108067-1	fragment	1	3	3.7	3.6	2	-0.56	-0.55
C1721	UWBM	108067-10	fragment	0	3	4.4	1.2	1.2	-0.99	-0.28
C1721	UWBM	108067-11	fragment	0	3	13.2	6.8	5	-0.75	-0.38
C1721	UWBM	108067-12	fragment	0	2	4.2	1.1	1.1	-1	-0.26
C1721	UWBM	108067-13	fragment	0	3	4.7	1.1	1.1	-0.99	-0.24
C1721	UWBM	108067-14	fragment	0	2	1.1	0.6	0.2	-0.24	-0.13
C1721	UWBM	108067-2	fragment	0	3	3	2.2	0.6	-0.26	-0.19
C1721	UWBM	108067-3	fragment	0	2	3.8	1.9	1.1	-0.55	-0.28
C1721	UWBM	108067-4	fragment	0	1	6.7	1.4	1.2	-0.85	-0.17
C1721	UWBM	108067-5	fragment	0	2	4.2	1.3	1	-0.8	-0.24
C1721	UWBM	108067-6	fragment	0	3	5.5	1.5	1.3	-0.87	-0.23
C1721	UWBM	108067-7	fragment	0	2	2.8	1	0.9	-0.85	-0.32
C1721	UWBM	108067-8	fragment	1	2	2.1	1.2	0.3	-0.23	-0.13

C1721	UWBM	108067-9	fragment	0	2	4.1	1.2	0.8	-0.72	-0.21
C1721	UWBM	108069-1	fragment	0	3	7.3	5	1.3	-0.27	-0.18
C1721	UWBM	108069-2	fragment	1	2	9.8	6.5	1.8	-0.28	-0.18
C1721	UWBM	108069-3	fragment	2	3	10.8	3.5	2.8	-0.82	-0.26
C1721	UWBM	108069-4	fragment	0	3	8.2	7.7	1.9	-0.25	-0.23
C1721	UWBM	108069-5	fragment	2	3	6.9	4.8	2.9	-0.62	-0.43
C1721	UWBM	108069-6	fragment	1	3	17.2	4.9	2.6	-0.53	-0.15
C1721	UWBM	97455-1	fragment	2	2	27.2	16	10.2	-0.64	-0.38
C1721	UWBM	97455-10	fragment	0	2	4.1	2.6	1.3	-0.48	-0.31
C1721	UWBM	97455-11	fragment	1	1	14.4	5.9	3.1	-0.53	-0.22
C1721	UWBM	97455-2	fragment	2	3	11.4	7	3.1	-0.44	-0.27
C1721	UWBM	97455-3	fragment	2	3	12.7	9.8	3.9	-0.39	-0.3
C1721	UWBM	97455-4	fragment	0	3	4.4	3.2	2.1	-0.68	-0.48
C1721	UWBM	97455-5	fragment	0	2	5.4	4.4	3.4	-0.77	-0.63
C1721	UWBM	97455-6	fragment	0	1	5	2.1	1.1	-0.52	-0.22
C1721	UWBM	97455-7	fragment	0	3	7.8	4.6	1.3	-0.29	-0.17
C1721	UWBM	97455-8	fragment	0	2	5.4	3.1	1.6	-0.5	-0.29
C1721	UWBM	97455-9	fragment	2	3	5.9	3.8	1.4	-0.35	-0.23
C1721	UWBM	98636-1	fragment	3	3	19.7	12.7	4.4	-0.34	-0.22
C1721	UWBM	98636-10	fragment	1	3	6.5	2.7	1.6	-0.61	-0.25
C1721	UWBM	98636-11	fragment	1	3	6.6	4.8	1.6	-0.33	-0.24
C1721	UWBM	98636-12	fragment	2	2	9.3	6.9	4.3	-0.63	-0.47
C1721	UWBM	98636-2	fragment	3	3	23.9	4.1	2.9	-0.71	-0.12
C1721	UWBM	98636-3	fragment	1	2	20	7.6	2.2	-0.29	-0.11
C1721	UWBM	98636-4	fragment	2	2	18.4	7.3	3.2	-0.44	-0.17
C1721	UWBM	98636-5	fragment	2	2	10.2	6.7	2.1	-0.32	-0.21
C1721	UWBM	98636-6	fragment	1	3	10.8	4.6	1.6	-0.35	-0.15
C1721	UWBM	98636-7	fragment	0	3	7.9	5.2	2.2	-0.43	-0.28
C1721	UWBM	98636-8	fragment	2	2	9.5	3	2.6	-0.85	-0.27
C1721	UWBM	98636-9	fragment	1	2	8.4	3	1.2	-0.41	-0.15
C1721	UWBM	98643-1	fragment	1	3	15.8	3.5	1.8	-0.51	-0.11
C1721	UWBM	98643-2	fragment	1	3	7.5	5.6	3.3	-0.59	-0.44
C1721	UWBM	98696-1	fragment	1	1	10.7	6.6	4.1	-0.62	-0.39
C1721	UWBM	98696-10	fragment	0	3	3.2	2.8	1.7	-0.6	-0.52
C1721	UWBM	98696-11	fragment	0	2	7.4	5.8	2.4	-0.41	-0.32
C1721	UWBM	98696-12	fragment	1	3	7	1.8	1.1	-0.58	-0.15
C1721	UWBM	98696-13	fragment	1	2	6.1	5.2	4.3	-0.83	-0.7
C1721	UWBM	98696-14	fragment	2	3	6.8	2.1	0.7	-0.34	-0.1
C1721	UWBM	98696-15	fragment	2	2	7.2	5.1	2.1	-0.41	-0.29
C1721	UWBM	98696-16	fragment	1	3	4.5	3.9	2.7	-0.69	-0.61

C1721	UWBM	98696-17	fragment	1	3	4.5	3.5	1.4	-0.39	-0.31
C1721	UWBM	98696-18	fragment	1	3	8	1.6	1.4	-0.86	-0.17
C1721	UWBM	98696-19	fragment	0	1	5	3.7	1.7	-0.46	-0.34
C1721	UWBM	98696-2	fragment	0	1	12.8	5	2.1	-0.42	-0.16
C1721	UWBM	98696-20	fragment	0	3	7.1	1.9	1.8	-0.93	-0.25
C1721	UWBM	98696-21	fragment	1	2	7	1.3	1	-0.72	-0.14
C1721	UWBM	98696-22	fragment	1	3	4.8	1.4	1.2	-0.9	-0.25
C1721	UWBM	98696-23	fragment	0	3	5.3	2	1	-0.48	-0.18
C1721	UWBM	98696-3	fragment	2	3	10	3.7	3.4	-0.91	-0.34
C1721	UWBM	98696-4	dentary	2	2	6.9	5.7	2.9	-0.5	-0.42
C1721	UWBM	98696-5	fragment	2	3	7.4	3.3	1.8	-0.55	-0.25
C1721	UWBM	98696-6	fragment	0	3	9.7	5.6	2.6	-0.47	-0.27
C1721	UWBM	98696-7	fragment	0	1	10.1	2.5	1	-0.39	-0.1
C1721	UWBM	98696-8	fragment	0	2	9.5	4.1	1.4	-0.33	-0.15
C1721	UWBM	98696-9	fragment	0	2	6.4	3.6	1.1	-0.29	-0.17
C1721	UWBM	98801-1	fragment	0	2	12.6	5.6	1.7	-0.3	-0.13
C1721	UWBM	98801-10	fragment	3	2	5.9	2.9	1.5	-0.52	-0.26
C1721	UWBM	98801-2	fragment	3	3	13.8	7.3	3.2	-0.44	-0.23
C1721	UWBM	98801-3	fragment	3	3	4.3	2.7	1.8	-0.66	-0.41
C1721	UWBM	98801-4	fragment	1	3	5.5	3.9	1.9	-0.48	-0.34
C1721	UWBM	98801-5	fragment	2	3	7.4	7.1	3.9	-0.55	-0.53
C1721	UWBM	98801-6	fragment	1	2	6.7	2.6	1.8	-0.68	-0.26
C1721	UWBM	98801-7	fragment	0	3	6.2	3.1	2.1	-0.68	-0.34
C1721	UWBM	98801-8	fragment	0	2	6.4	4.9	2.7	-0.55	-0.41
C1721	UWBM	98801-9	fragment	0	3	5.7	2.4	1.4	-0.59	-0.25
C1721	UWBM	98803-1	fragment	2	3	8.8	8	3.8	-0.48	-0.43
C1721	UWBM	98803-2	fragment	3	3	7.4	4.7	3	-0.64	-0.41
C1721	UWBM	98803-3	fragment	2	1	5.3	4.6	2.6	-0.56	-0.49
C1721	UWBM	98803-4	fragment	1	1	3.3	1.6	0.6	-0.37	-0.18
C1721	UWBM	98803-5	fragment	1	2	5.6	2.6	1	-0.39	-0.18
C1721	UWBM	98803-6	fragment	3	3	4.6	2.4	2.1	-0.85	-0.44
MV6613	UMPC	13273	dentary	2	2	13.3	3.7	2.1	-0.56	-0.16
MV6613	UMPC	13999	skull	2	2	4	3.4	3.3	-0.98	-0.84
MV6613	UMPC	14021	skull	1	2	14.6	9.9	6	-0.61	-0.41
MV6613	UMPC	14032	dentary	1	2	6.7	2.9	1.7	-0.58	-0.25
MV6613	UMPC	13275-3	tibia	0	1	12	2.8	2.8	-0.98	-0.23
MV6613	UMPC	13275-4	phalanx	0	1	11.3	3.3	2.7	-0.83	-0.24
MV6613	UMPC	13990-1	fragment	3	3	23.2	7.8	5.4	-0.69	-0.23
MV6613	UMPC	13990-2	fragment	1	3	28.3	8.2	3.3	-0.41	-0.12
MV6613	UMPC	13990-3	fragment	2	2	15.1	5.1	2.7	-0.52	-0.18

MV6613	UMPC	14014-17	fragment	1	1	9.6	5.6	2.1	-0.37	-0.21
MV6613	UMPC	14014-18	fragment	0	3	6.7	3.5	1.7	-0.48	-0.25
MV6613	UMPC	14014-19	fragment	1	3	5.5	2.7	1.4	-0.51	-0.25
MV6613	UMPC	14014-20	fragment	1	3	6.2	2.2	2.2	-1	-0.35
MV6613	UMPC	14014-21	fragment	2	2	4.4	3.2	1.5	-0.46	-0.34
MV6613	UMPC	14014-22	fragment	1	2	4.8	2	0.6	-0.32	-0.13
MV6613	UMPC	14014-23	fragment	1	3	9.1	2.7	1.6	-0.59	-0.17
MV6613	UMPC	14014-24	fragment	1	3	4.9	1.8	1.5	-0.8	-0.3
MV6613	UMPC	14014-25	fragment	0	3	6.9	2.1	1.6	-0.77	-0.23
MV6613	UMPC	14014-26	fragment	3	3	4.6	2.4	2	-0.81	-0.42
MV6613	UMPC	14014-27	fragment	1	1	7.3	1.9	1.6	-0.83	-0.21
MV6613	UMPC	14014-28	fragment	2	2	9.5	8.4	5.9	-0.7	-0.62
MV6613	UMPC	14014-29	fragment	0	1	7.9	1.8	1.4	-0.75	-0.17
MV6613	UMPC	14014-3	metapodial	1	1	17.3	4.4	2.9	-0.67	-0.17
MV6613	UMPC	14014-30	fragment	0	3	3.1	3	1	-0.33	-0.31
MV6613	UMPC	14014-34	fragment	1	2	4.1	1.4	1.1	-0.82	-0.28
MV6613	UMPC	14014-9	metapodial	1	2	4.3	1.1	0.9	-0.77	-0.2
MV6613	UMPC	14036-1	fragment	0	3	20.5	13.1	7.6	-0.58	-0.37
MV6613	UMPC	14036-10	fragment	1	3	10	4.4	2.9	-0.66	-0.29
MV6613	UMPC	14036-11	fragment	1	3	8.8	3.2	2.1	-0.66	-0.24
MV6613	UMPC	14036-15	fragment	0	3	6.4	3.6	1.6	-0.44	-0.25
MV6613	UMPC	14036-16	fragment	1	2	12.3	2.2	1.6	-0.74	-0.13
MV6613	UMPC	14036-17	fragment	0	2	6.9	2.9	1.1	-0.38	-0.16
MV6613	UMPC	14036-18	fragment	0	2	9.8	2.9	2.2	-0.75	-0.22
MV6613	UMPC	14036-19	fragment	3	2	12.6	8.3	7.1	-0.85	-0.56
MV6613	UMPC	14036-2	fragment	0	3	15	7.4	3.9	-0.53	-0.26
MV6613	UMPC	14036-4	fragment	3	3	19.9	7	5.2	-0.74	-0.26
MV6613	UMPC	14036-5	fragment	2	2	13.5	8.8	5	-0.57	-0.37
MV6613	UMPC	14036-53	fragment	1	2	13.8	4.7	2.7	-0.57	-0.19
MV6613	UMPC	14036-54	fragment	0	3	7.4	3.7	2.5	-0.67	-0.33
MV6613	UMPC	14036-55	fragment	2	3	7.7	4.4	2.1	-0.48	-0.28
MV6613	UMPC	14036-56	fragment	2	2	5.3	2.4	2.2	-0.91	-0.41
MV6613	UMPC	14036-57	fragment	1	3	5.3	1.5	1.5	-0.97	-0.28
MV6613	UMPC	14036-58	fragment	1	3	8.9	2.9	1.3	-0.46	-0.15
MV6613	UMPC	14036-59	fragment	2	2	6.1	3.3	2.6	-0.79	-0.42
MV6613	UMPC	14036-6	fragment	2	1	9.4	2.9	1.1	-0.39	-0.12
MV6613	UMPC	14036-60	fragment	3	3	8.1	1.1	1	-0.94	-0.12
MV6613	UMPC	14036-61	fragment	1	1	5.8	4	3	-0.75	-0.51
MV6613	UMPC	14036-62	fragment	1	3	10.4	2.7	1.9	-0.73	-0.19
MV6613	UMPC	14036-63	fragment	0	3	8.7	2.4	1.7	-0.69	-0.19

MV6613	UMPC	14036-64	fragment	1	3	8.7	2	1.2	-0.62	-0.14
MV6613	UMPC	14036-65	fragment	1	2	5.5	3.4	1.1	-0.33	-0.21
MV6613	UMPC	14036-66	fragment	1	3	9.9	3	1.7	-0.57	-0.17
MV6613	UMPC	14036-67	fragment	1	3	6.2	1.8	1.4	-0.79	-0.23
MV6613	UMPC	14036-73	femur	2	2	16.5	5.7	2.9	-0.51	-0.18
MV6613	UMPC	14036-77	fragment	2	2	18.1	3.8	3	-0.79	-0.16
MV6613	UMPC	14036-80	fragment	1	3	7.9	3.4	1.3	-0.37	-0.16
MV6613	UMPC	14036-88	fragment	1	2	11.5	4.3	1.7	-0.41	-0.15
MV6613	UMPC	14036-9	fragment	1	1	10.3	3.5	1.5	-0.42	-0.14
MV6613	UMPC	14036-90	humerus	0	2	11.3	11.1	4.2	-0.38	-0.37
MV6613	UMPC	14036-97	fragment	1	2	6.9	2.9	1.1	-0.36	-0.16
MV6613	UMPC	14036-98	fragment	1	1	9.2	4.8	1.9	-0.4	-0.21
MV6613	UMPC	20580-10	fragment	0	1	13.2	4.4	3.6	-0.84	-0.28
MV6613	UMPC	20580-7	tibia	1	1	10	3	2.5	-0.86	-0.25
MV6613	UMPC	20580-9	fragment	1	1	4.2	1.8	1.5	-0.83	-0.36
MV6613	UMPC	20590-10	fragment	1	2	7.4	2.9	2.2	-0.77	-0.3
MV6613	UMPC	20590-11	fragment	2	3	16.5	11.1	3.4	-0.31	-0.21
MV6613	UMPC	20590-12	fragment	2	3	13.1	10.1	2.9	-0.28	-0.22
MV6613	UMPC	20590-13	fragment	1	3	19	5.8	2.5	-0.43	-0.13
MV6613	UMPC	20590-14	fragment	1	3	11.6	6.8	6.4	-0.93	-0.55
MV6613	UMPC	20590-15	fragment	1	3	13.3	7.3	5.8	-0.8	-0.44
MV6613	UMPC	20590-16	fragment	2	3	8.9	6	2.4	-0.41	-0.27
MV6613	UMPC	20590-17	fragment	1	1	9.8	6.9	4	-0.58	-0.4
MV6613	UMPC	20590-18	fragment	0	3	9.9	3.2	1.6	-0.52	-0.17
MV6613	UMPC	20590-19	fragment	1	1	13.4	2.6	2.4	-0.93	-0.18
MV6613	UMPC	20590-20	fragment	1	2	10.4	4	1.8	-0.46	-0.18
MV6613	UMPC	20590-21	fragment	2	3	8.9	7.5	3.7	-0.49	-0.41
MV6613	UMPC	20590-22	fragment	1	3	7.4	5.1	1.2	-0.24	-0.17
MV6613	UMPC	20590-23	fragment	2	3	9.9	3.5	2.7	-0.76	-0.27
MV6613	UMPC	20590-24	fragment	1	2	11.4	4.5	2.6	-0.59	-0.23
MV6613	UMPC	20590-25	fragment	2	2	7.8	2.4	2.2	-0.92	-0.28
MV6613	UMPC	20590-26	fragment	1	3	10.8	3.3	1.5	-0.47	-0.14
MV6613	UMPC	20590-27	fragment	1	3	10.7	3.4	2.8	-0.82	-0.26
MV6613	UMPC	20590-28	fragment	2	2	14.3	6.5	3.3	-0.51	-0.23
MV6613	UMPC	20590-29	fragment	1	3	9.6	3.9	1.6	-0.42	-0.17
MV6613	UMPC	20590-30	fragment	2	3	6.7	3.2	2.2	-0.7	-0.33
MV6613	UMPC	20590-31	fragment	1	3	6.6	4.2	1.5	-0.35	-0.22
MV6613	UMPC	20590-32	fragment	1	3	10.2	2.3	1.3	-0.57	-0.13
MV6613	UMPC	20590-33	fragment	0	3	9.9	2.4	1.8	-0.74	-0.18
MV6613	UMPC	20590-34	fragment	0	3	8.3	1.9	1.9	-0.98	-0.23

MV6613	UMPC	20590-35	fragment	3	3	4.3	3.2	1.2	-0.36	-0.27
MV6613	UMPC	20590-36	fragment	2	2	4.3	1.5	1.2	-0.75	-0.27
MV6613	UMPC	20590-37	fragment	1	2	7.4	2.7	2.2	-0.82	-0.3
MV6613	UMPC	20590-38	fragment	1	2	5.9	2.6	1.5	-0.58	-0.25
MV6613	UMPC	20590-39	fragment	0	2	5.3	2.8	2.6	-0.93	-0.49
MV6613	UMPC	20590-40	fragment	1	2	5	3.4	1.2	-0.37	-0.25
MV6613	UMPC	20590-7	fragment	2	3	12.6	6.3	4.6	-0.73	-0.37
MV6613	UMPC	20590-8	fragment	2	3	13.4	8.2	7.2	-0.88	-0.54
MV6613	UMPC	20590-9	fragment	2	3	11.3	3.9	3.5	-0.89	-0.31
MV6613	UMPC	20950-41	fragment	3	3	8.4	4.9	3.3	-0.67	-0.39
MV6613	UMPC	20950-42	fragment	1	3	6.2	2.1	0.9	-0.4	-0.14
MV6613	UMPC	20950-43	fragment	3	3	4.7	2.6	1.8	-0.7	-0.39
MV6613	UMPC	20950-44	fragment	0	3	4.1	2.8	1.2	-0.42	-0.29
MV6613	UMPC	20950-45	fragment	2	1	1.9	1.7	1.3	-0.74	-0.7
MV6613	UMPC	20950-46	fragment	0	2	3.2	1.8	0.6	-0.3	-0.17
MV6613	UMPC	20950-47	fragment	1	2	5.6	2.1	0.9	-0.45	-0.17
MV6613	UMPC	20950-48	fragment	0	2	2.4	1.8	0.5	-0.3	-0.22

A2.7 Characteristics of the specimens included in the analysis of intra-observer error.

Abbreviations as in A1.6 except Loc., Locality; O, Completeness.

Specimen	Loc.	E 1	A 1	L 1	C 1	F 1	O 1	E 2	A 2	L 2	C 2	F 2	O 2
13969	C0173	1	1	14.1	-0.3	-0.57	50	0	0	14.1	-0.31	-0.57	60
13970	C0173	1	1	6.4	-0.45	-0.46	5	0	1	6.2	-0.45	-0.45	5
18105	C0173	1	1	7.5	-0.63	-0.87	5	0	1	7.5	-0.57	-0.78	5
19868	C0173	0	2	25.1	-0.35	-0.87	95	0	2	25.2	-0.35	-0.85	95
97329	C0174	1	1	18	-0.5	-0.74	30	2	1	17.9	-0.52	-0.82	25
97335	C0174	1	1	9	-0.14	-0.87	100	1	1	9	-0.14	-0.82	100
97336	C0174	2	3	28.2	-0.18	-0.94	85	2	3	28.3	-0.19	-0.98	85
97345	C1708	2	1	7.5	-0.23	-0.45	25	2	1	7.6	-0.2	-0.4	25
97352	C1721	1	2	9	-0.64	-0.97	5	1	2	9	-0.65	-0.98	5
97354	C1721	2	2	8.3	-0.63	-0.72	5	2	2	8.4	-0.62	-0.7	5
97385	C1721	2	1	10.8	-0.3	-0.7	30	2	1	10.7	-0.3	-0.7	35
97386	C1721	1	2	6.3	-0.38	-0.92	90	1	2	6.3	-0.38	-0.92	90
97387	C1721	2	1	18	-0.57	-0.99	95	2	1	17.9	-0.58	-0.94	95
97394	C1704	2	1	6.4	-0.53	-0.87	95	2	1	6.4	-0.54	-0.92	95
97399	C0174	1	2	6	-0.25	-0.88	100	1	1	6	-0.24	-0.87	100
97433	C1704	0	2	9.5	-0.65	-0.83	100	1	2	9.4	-0.67	-0.84	95
97434	C1704	0	1	9	-0.29	-0.59	30	0	0	9.4	-0.28	-0.6	35
97435	C1704	2	3	20.4	-0.3	-0.58		2	3	20.7	-0.29	-0.53	
97438	C1704	0	1	5.9	-0.31	-0.75	45	0	1	6.3	-0.28	-0.8	35
97439	C1704	1	1	8.3	-0.67	-1	5	1	1	8.2	-0.7	-1.01	5
97440	C1704	1	2	4.2	-0.29	-1	100	1	1	4	-0.25	-0.9	100
97446	C1704	1	1	5.2	-0.6	-0.86	95	1	1	4.3	-0.72	-0.86	95
97453	C1721	0	1	11.5	-0.6	-0.71	5	0	2	11	-0.61	-0.66	5
97457	C1721	1	1	11.9	-0.45	-0.55	100	1	1	11.9	-0.42	-0.53	100
97458	C1721	1	3	13.4	-0.75	-0.82		0	3	13.4	-0.75	-0.81	
97483	C1721	0	1	4.7	-0.3	-0.82	95	0	0	4.7	-0.29	-0.98	100
97485	C1721	0	0	7.1	-0.21	-0.75	100	0	0	7	-0.21	-0.71	100
98596	C0174	2	2	9.3	-0.63	-0.64	10	2	2	9.5	-0.64	-0.65	10
98633	C1721	0	1	14.8	-0.31	-0.84	60	0	1	14.7	-0.31	-0.83	65
98635	C1721	1	2	21.5	-0.78	-0.83	95	1	2	21.8	-0.77	-0.84	90
98638	C1721	3	3	16.9	-0.46	-1		2	3	16.6	-0.38	-0.85	
98645	C0174	2	3	19.1	-0.19	-0.68		1	3	18.9	-0.18	-0.65	
98646	C0174	2	1	6.6	-0.62	-0.67	5	1	1	6.7	-0.62	-0.69	5

98647	C0174	2	3	11.7	-0.42	-0.57	5	2	2	11.6	-0.42	-0.58	5
98648	C0174	1	2	5.3	-0.89	-0.9	10	2	2	5.4	-0.89	-0.93	10
98650	C0174	1	2	5.6	-0.71	-0.95		1	1	5.65	-0.69	-0.97	
98652	C0174	2	3	8.4	-0.74	-0.75		2	3	8.5	-0.77	-0.78	
98671	C1721	1	2	8.1	-0.3	-0.46	40	1	2	8.1	-0.3	-0.46	40
98721	C0174	1	2	3.6	-0.36	-0.68	100	1	1	3.4	-0.37	-0.67	100
98736	C1708	1	1	2.5	-0.44	-0.61	100	1	1	2.7	-0.42	-0.64	100
98742	C1708	0	2	5.2	-0.42	-0.85	100	0	2	5.2	-0.43	-0.87	100
98743	C1708	2	2	29.8	-0.36	-0.79	15	2	2	29.8	-0.35	-0.77	15
98749	C1708	1	0	2.4	-0.29	-0.78	100	1	1	2.4	-0.28	-0.72	100
98759	C1708	2	2	3	-0.3	-0.82	100	2	2	3	-0.3	-0.83	100
98761	C1708	1	1	6.6	-0.42	-0.68	5	1	1	6.4	-0.47	-0.7	5
98766	C1708	2	1	17.5	-0.41	-0.87	10	2	1	17	-0.42	-0.87	10
98779	C1707	2	3	14.3	-0.35	-0.82	95	2	2	14.2	-0.36	-0.83	80
98784	C0174	1	2	4.7	-0.43	-0.77	20	1	1	4.8	-0.43	-0.79	20
98800	C1708	2	2	13.8	-0.49	-0.72	65	2	2	13.6	-0.47	-0.69	70
98813	C1708	1	1	14.4	-0.36	-0.62	100	1	1	14.4	-0.41	-0.7	95
98814	C1708	1	2	4.8	-0.48	-0.82	100	1	2	4.9	-0.48	-0.86	100
98817	C1708	2	1	9.7	-0.56	-0.87	95	2	1	9.6	-0.56	-0.9	95
98821	C0174	1	2	5	-0.32	-0.7	60	1	2	5	-0.31	-0.66	65
98822	C0174	0	2	4.4	-0.25	-0.79	100	0	1	4.4	-0.22	-0.71	100
98824	C1704	1	1	6.3	-0.46	-0.76	25	1	1	6.8	-0.41	-0.8	25
98825	C1704	1	0	10.7	-0.19	-0.51	50	1	1	10.4	-0.15	-0.4	70
98827	C1707	3	3	11.9	-0.55	-0.97	100	3	3	11.9	-0.55	-0.96	100
98829	C1707	1	2	5.9	-0.24	-0.82	100	1	2	5.9	-0.24	-0.88	100
98928	C1707	1	2	4.5	-0.22	-0.83	100	1	2	4.4	-0.23	-0.93	100
98929	C1707	2	3	9.2	-0.46	-0.58	5	2	3	8.5	-0.49	-0.56	5
98930	C1707	0	2	6	-0.2	-0.34	55	1	2	6	-0.2	-0.36	60
98931	C1707	1	2	5.6	-0.36	-0.77	100	1	2	5.6	-0.35	-0.77	100
98932	C1707	3	3	6.7	-0.91	-0.97	5	3	2	6.8	-0.91	-0.97	5
98933	C1707	1	3	6.6	-0.38	-0.66	50	3	3	6.5	-0.38	-0.67	40
98934	C1707	2	2	3.4	-0.5	-0.77	75	2	2	3.7	-0.45	-0.72	60
98935	C1707	1	2	3.3	-0.33	-0.73	100	1	2	3.4	-0.37	-0.85	95
98936	C1707	0	3	8.2	-0.43	-0.66	30	1	2	8.4	-0.41	-0.65	20
97437-1	C1704	2	2	26.6	-0.27	-0.31		2	3	29	-0.26	-0.32	
97437-2	C1704	2	3	24.6	-0.18	-0.64		2	3	24.7	-0.18	-0.62	
97437-3	C1704	3	3	11.3	-0.36	-0.91		3	3	11.5	-0.35	-0.89	
97437-4	C1704	2	3	12.7	-0.16	-0.51		2	3	12.8	-0.16	-0.55	
97437-5	C1704	0	2	3.1	-0.77	-0.83		0	2	3.1	-0.77	-0.83	
97441-1	C1704	2	3	12.3	-0.16	-0.4		1	3	12.3	-0.15	-0.46	

97441-2	C1704	1	3	12.1	-0.11	-0.48		1	2	11.9	-0.11	-0.48	
97448-1	C1704	2	2	11	-0.16	-0.35		2	2	11	-0.16	-0.33	
97448-2	C1704	2	1	11.3	-0.19	-0.43		2	1	11.4	-0.2	-0.45	
97448-3	C1704	2	3	13.5	-0.19	-0.68		2	2	13.5	-0.21	-0.79	
97448-4	C1704	3	3	12.7	-0.2	-0.53		3	3	12.5	-0.21	-0.52	
97448-5	C1704	1	3	13.2	-0.13	-0.61		1	2	13.3	-0.13	-0.58	
97448-6	C1704	1	3	5.8	-0.17	-0.43		1	3	6.4	-0.18	-0.21	
98643-1	C1721	1	3	15.8	-0.11	-0.51		0	2	15.9	-0.11	-0.54	
98643-2	C1721	1	3	7.5	-0.44	-0.59		2	2	7.2	-0.46	-0.59	
98868-1	C0174	1	2	10.4	-0.29	-0.59		1	2	10.3	-0.32	-0.64	
98868-2	C0174	1	1	11.8	-0.19	-0.34		0	1	11.9	-0.17	-0.33	
98868-3	C0174	1	2	5.2	-0.15	-0.67		1	2	5.2	-0.15	-0.59	
98868-4	C0174	1	2	5	-0.2	-0.91		1	2	5	-0.19	-0.81	
14036-90	MV6613	0	2	11.3	-0.38	-0.37	20	1	2	11.3	-0.42	-0.4	25
14036-99	MV6613	2	2	10.9	-0.94	-0.26	50	1	1	11	-0.91	-0.25	50
14036-82	MV6613	1	2	7.1	-0.78	-0.23	65	1	2	7.2	-0.74	-0.25	65
14036-12	MV6613	1	1	4.4	-0.92	-0.41	5	1	2	3.8	-0.89	-0.49	5
14036-7	MV6613	1	2	8.8	-0.86	-0.23	65	0	1	9.3	-0.67	-0.21	70
14036-70	MV6613	2	1	7.7	-0.67	-0.33	45	1	1	8.1	-0.89	-0.33	30
14036-3	MV6613	0	1	5.8	-0.89	-0.49	100	0	1	5.4	-0.9	-0.53	100
14036-83	MV6613	2	2	4.5	-0.7	-0.47	95	1	2	4.6	-0.72	-0.47	95
14036-87	MV6613	1	2	4.7	-0.72	-0.44	100	2	1	4.7	-0.73	-0.44	100
14036-78	MV6613	3	3	13.9	-0.88	-0.32	65	2	2	13.5	-0.88	-0.33	75
14036-95	MV6613	1	1	9.4	-0.63	-0.19	65	1	0	9.2	-0.66	-0.17	75
14036-75	MV6613	1	2	7.3	-0.85	-0.3	35	2	1	7.3	-0.85	-0.29	40
14036-76	MV6613	2	2	5.3	-0.53	-0.32	35	1	2	6.2	-0.55	-0.27	30
14036-107	MV6613	1	2	6.5	-0.59	-0.56	95	3	3	6.6	-0.6	-0.56	100
14036-91	MV6613	1	2	12.4	-0.85	-0.65	90	1	2	12	-0.8	-0.66	90

A2.8 Results of the pairwise Spearman correlation coefficient tests.

R^2	C0173	C0174	C1704	C1707	C1721	C1708	MV6613	EagleOwl1	EagleOwl2
C0174	0.86	--	--	--	--	--	--	--	--
C1704	0.80	0.76	--	--	--	--	--	--	--
C1707	0.82	0.81	0.64	--	--	--	--	--	--
C1721	0.78	0.64	0.79	0.80	--	--	--	--	--
C1708	0.82	0.81	0.91	0.74	0.80	--	--	--	--
MV6613	0.84	0.88	0.69	0.83	0.78	0.85	--	--	--
EagleOwl1	0.33	0.38	0.09	0.64	0.26	0.19	0.27	--	--
EagleOwl2	0.24	0.22	0.06	0.53	0.25	0.12	0.19	0.87	--
Modern Fluvial	0.19	0.28	-0.08	0.22	-0.05	0.01	0.15	0.48	0.28
Lynx	0.61	0.75	0.56	0.65	0.40	0.52	0.50	0.66	0.41
Siwalik1	0.57	0.58	0.51	0.71	0.50	0.54	0.41	0.69	0.39
Siwalik2	0.40	0.60	0.34	0.55	0.30	0.47	0.46	0.57	0.29
Siwalik3	0.35	0.57	0.34	0.57	0.26	0.44	0.40	0.65	0.37
Siwalik4	0.47	0.67	0.52	0.50	0.43	0.55	0.52	0.30	-0.04
Pliocene Channel Fill	0.78	0.79	0.77	0.58	0.59	0.90	0.76	0.11	0.02
Pliocene Overbank	0.86	0.89	0.82	0.66	0.63	0.92	0.85	0.09	-0.06
Mongoose	0.59	0.62	0.59	0.71	0.68	0.60	0.59	0.60	0.46
Coyote	0.76	0.81	0.55	0.82	0.65	0.58	0.75	0.63	0.49
Fox	0.65	0.67	0.44	0.81	0.63	0.52	0.64	0.78	0.66
Arctic Fox	0.72	0.76	0.73	0.63	0.63	0.73	0.64	0.50	0.32
Marten	0.68	0.74	0.60	0.65	0.59	0.55	0.59	0.51	0.29

R^2	Modern Fluvial	Lynx	Siwalik1	Siwalik2	Siwalik3	Siwalik4	Pliocene Channel Fill	Pliocene Overbank	Mongoose	Coyote	Fox	Arctic Fox
C0174	--	--	--	--	--	--	--	--	--	--	--	--
C1704	--	--	--	--	--	--	--	--	--	--	--	--
C1707	--	--	--	--	--	--	--	--	--	--	--	--
C1721	--	--	--	--	--	--	--	--	--	--	--	--
C1708	--	--	--	--	--	--	--	--	--	--	--	--
MV6613	--	--	--	--	--	--	--	--	--	--	--	--
EagleOwl1	--	--	--	--	--	--	--	--	--	--	--	--
EagleOwl2	--	--	--	--	--	--	--	--	--	--	--	--
Modern Fluvial	--	--	--	--	--	--	--	--	--	--	--	--
Lynx	0.45	--	--	--	--	--	--	--	--	--	--	--
Siwalik1	0.43	0.80	--	--	--	--	--	--	--	--	--	--
Siwalik2	0.62	0.75	0.77	--	--	--	--	--	--	--	--	--
Siwalik3	0.62	0.83	0.83	0.92	--	--	--	--	--	--	--	--
Siwalik4	0.57	0.73	0.72	0.83	0.84	--	--	--	--	--	--	--
Pliocene Channel Fill	0.11	0.45	0.41	0.48	0.36	0.49	--	--	--	--	--	--
Pliocene Overbank	0.18	0.56	0.48	0.48	0.43	0.62	0.93	--	--	--	--	--
Mongoose	0.52	0.78	0.75	0.67	0.76	0.75	0.41	0.52	--	--	--	--
Coyote	0.55	0.82	0.67	0.61	0.67	0.67	0.47	0.62	0.88	--	--	--
Fox	0.58	0.79	0.72	0.68	0.73	0.62	0.41	0.48	0.92	0.94	--	--

p	C0173	C0174	C1704	C1707	C1721	C1708	MV6613	EagleOwl1	EagleOwl2
C0174	0.00	--	--	--	--	--	--	--	--
C1704	0.00	0.00	--	--	--	--	--	--	--
C1707	0.00	0.00	0.01	--	--	--	--	--	--
C1721	0.00	0.01	0.00	0.00	--	--	--	--	--
C1708	0.00	0.00	0.00	0.00	0.00	--	--	--	--
MV6613	0.00	0.00	0.00	0.00	0.00	0.00	--	--	--
EagleOwl1	0.23	0.16	0.75	0.01	0.34	0.49	0.32	--	--
EagleOwl2	0.39	0.44	0.82	0.04	0.37	0.67	0.50	0.00	--
Modern Fluvial	0.49	0.31	0.77	0.42	0.86	0.98	0.59	0.07	0.30
Lynx	0.02	0.00	0.03	0.01	0.14	0.05	0.06	0.01	0.13
Siwalik1	0.03	0.02	0.05	0.00	0.06	0.04	0.13	0.00	0.15
Siwalik2	0.14	0.02	0.21	0.03	0.27	0.07	0.08	0.03	0.30
Siwalik3	0.20	0.03	0.21	0.03	0.34	0.10	0.13	0.01	0.18
Siwalik4	0.08	0.01	0.04	0.06	0.11	0.03	0.05	0.28	0.89
Pliocene Channel Fill	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.70	0.94
Pliocene Overbank	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.74	0.84
Mongoose	0.02	0.01	0.02	0.00	0.01	0.02	0.02	0.02	0.08
Coyote	0.00	0.00	0.03	0.00	0.01	0.02	0.00	0.01	0.07
Fox	0.01	0.01	0.10	0.00	0.01	0.05	0.01	0.00	0.01
Arctic Fox	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.06	0.24
Marten	0.00	0.00	0.02	0.01	0.02	0.03	0.02	0.05	0.30

p	Modern Fluvial	Lynx	Siwalik1	Siwalik2	Siwalik3	Siwalik4	Pliocene Channel Fill	Pliocene Overbank	Mongoose	Coyote	Fox	Arctic Fox
C0174	--	--	--	--	--	--	--	--	--	--	--	--
C1704	--	--	--	--	--	--	--	--	--	--	--	--
C1707	--	--	--	--	--	--	--	--	--	--	--	--
C1721	--	--	--	--	--	--	--	--	--	--	--	--
C1708	--	--	--	--	--	--	--	--	--	--	--	--
MV6613	--	--	--	--	--	--	--	--	--	--	--	--
EagleOwl1	--	--	--	--	--	--	--	--	--	--	--	--
EagleOwl2	--	--	--	--	--	--	--	--	--	--	--	--
Modern Fluvial	--	--	--	--	--	--	--	--	--	--	--	--
Lynx	0.09	--	--	--	--	--	--	--	--	--	--	--
Siwalik1	0.11	0.00	--	--	--	--	--	--	--	--	--	--
Siwalik2	0.01	0.00	0.00	--	--	--	--	--	--	--	--	--
Siwalik3	0.01	0.00	0.00	0.00	--	--	--	--	--	--	--	--
Siwalik4	0.03	0.00	0.00	0.00	0.00	--	--	--	--	--	--	--
Pliocene Channel Fill	0.69	0.09	0.13	0.07	0.19	0.06	--	--	--	--	--	--
Pliocene Overbank	0.52	0.03	0.07	0.07	0.11	0.01	0.00	--	--	--	--	--
Mongoose	0.05	0.00	0.00	0.01	0.00	0.00	0.13	0.05	--	--	--	--
Coyote	0.03	0.00	0.01	0.02	0.01	0.01	0.08	0.01	0.00	--	--	--
Fox	0.02	0.00	0.00	0.01	0.00	0.01	0.13	0.07	0.00	0.00	--	--
Arctic Fox	0.11	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	--
Marten	0.06	0.00	0.00	0.01	0.00	0.00	0.10	0.02	0.00	0.00	0.00	0.00

Chapter 3. GEOMETRIC MORPHOMETRIC ANALYSES OF WORN CHEEK-TEETH HELP IDENTIFY EXTANT AND EXTINCT GOPHER TAXA (RODENTIA: GEOMYIDAE)

Jonathan J. Calede and Jennifer W. Glusman

ABSTRACT

Entoptychine gophers are a very diverse group of rodents found across the western United States in Oligocene and Miocene deposits of around 30 to 17 million years ago. Because both extant and extinct geomyid gophers are hypsodont, diagnostic characters of the occlusal surface of the teeth are modified with wear, making difficult the identification of the many isolated teeth found in the fossil record. We use geometric morphometrics to test the hypothesis that tooth shape is taxonomically informative and inform expected levels of morphological variation in gophers. Our analysis of 410 specimens of extant gophers demonstrates the usefulness of our approach in identifying specimens to the genus-, subgenus-, and species levels. We apply this method to a sample of over 170 specimens of fossil gophers. Our results confirm that cheek tooth morphology is sufficient to identify entoptychines at the genus- and, in some cases, the species-level. They also cast doubt on the validity of some species within *Entoptychus*. The amounts of morphological divergence observed among fossil and extant genera are similar. Fossil species do not differ greatly from extant ones in that regard either. Further work evaluating the intra- and interspecific morphological variation within entoptychine gophers, including unworn teeth and osteological material, will be necessary to infer the phylogenetic

relationships and evolution of entoptychine gophers, an important member of the Oligocene-Miocene burrowing guild.

1. INTRODUCTION

The family Geomyidae (pocket gophers) is the predominant clade of subterranean rodents in North America today (Cook et al. 2000; Lacey et al. 2000). Geomyids are present across North America (Nowak 1999) and have one of the largest geographic ranges of any clade of subterranean mammals (Belfiore et al. 2008; Spradling et al. 2004; Cook et al. 2000). This incredible diversity in today's ecosystems is mirrored by their rich fossil record. The first geomyids, from the extinct subfamily Entoptychinae, are found in 34 million years old deposits of southern Mexico (Jiménez-Hidalgo et al. 2015). Entoptychines became particularly abundant a few million years later, around 30 million years ago (earliest Arikareean North American Land Mammal 'age'; Tedford et al. 2004; Flynn et al. 2008). In fact, the subfamily Entoptychinae had the greatest species richness of any fossorial rodent group c. 28 to 23.5 Ma (Samuels and Van Valkenburgh 2009). The subfamily includes four genera (*Gregorymys*, *Ziamys*, *Pleurolicus*, and *Entoptychus*) whose remains have been found in Idaho, California, Texas, Montana, New Mexico, Oregon, Wyoming, Nebraska, and South Dakota (Wilson 1949, Hibbard and Keenmon 1950, Hibbard and Wilson 1950, Stevens et al. 1969, Rensberger 1971, McKenna and Love 1972, Rensberger 1973, Gawne 1975, Nichols 1976, 1979, Stevens 1977, McKenna 1980, Stevens and Stevens 1989, Korth et al. 1990, Korth 1992, Korth 1996, Flynn et al. 2008). Ongoing work in the Arikareean-aged Cabbage Patch beds (Renova Formation) of western Montana (initiated by Rasmussen 1977 and Souza 1989) has yielded a rich entoptychine fauna including isolated teeth, jaws, skulls, and partial skeletons across multiple localities. The abundance and taxonomic diversity of this new material provides the opportunity to quantitatively analyze the morphology of Arikareean-aged entoptychines and inform the taxonomy of the very diverse entoptychines.

2. PREVIOUS TAXONOMIC DIAGNOSES OF GOPHER SPECIES

Although often diagnosed by soft tissue features and genetic characteristics (e.g. Connior 2011; Mathis et al. 2014), some geomyine gophers can also be recognized using osteological and dental characteristics (e.g. Russel 1968; Baker and Williams 1974; Jones and Baxter 2004; Hafner et al. 2014; Mathis et al. 2014). Entoptychine gophers are diagnosed by osteological characters of the skull and dentary (e.g. Matthew 1907; Wood 1936) as well as characteristics of the cheek teeth including the size, shape, and height of cusps (Figure 1; e.g. Wood 1936; Rensberger 1971; Korth et al. 1990; Korth 1996). Because entoptychine and geomyines gophers are hypsodont, characters of the occlusal surface of the teeth are modified with wear over the lifetime of the individual. As a consequence, older individuals can be difficult to identify using occlusal morphology. This is particularly problematic when teeth are isolated from diagnostic osteological material (skulls and dentaries) as is often the case in the fossil record. We therefore test the hypothesis that the overall shape of cheek-teeth can help identify gopher taxa. Previous studies of tooth shape in other members of the infraorder Geomorpha, including geomyids and heteromyids, have helped inform the level of morphological variation within populations as well as differences between species (Russel 1968, Carrasco 1998, 2000, Feranec et al. 2005). Rasmussen (1977: figure D) has also found differences in the relative proportions of the upper third molar of three species within the genus *Pleurolicus*. We use a geometric morphometrics approach and a large sample of extant gophers to (1) test whether cheek-tooth shape can be used to accurately identify the taxonomic affinities of these gophers and (2) infer hypotheses of expected levels of morphological differences among fossil taxa. We apply this approach to a large sample of fossil gophers as a quantitative framework for alpha taxonomy in fossil gophers. This work will inform future phylogenetic analyses of Entoptychinae and provide an improved understanding of the evolution of this critical clade of rodents. Entoptychine gophers are potentially biostratigraphically informative (Rensberger 1971, 1973, Rasmussen and Prothero 2003, Calede and Rasmussen 2015). A quantitatively informed taxonomic framework of entoptychine gophers, along with recent developments in radioisotopic dating of gopher-bearing horizons (e.g. Albright et al. 2008; Korth and Samuels 2015; ongoing work by one of us [JJC] in the Cabbage Patch beds of Montana), will enable a revised assessment of this potential.

3. MATERIAL AND METHODS

3.1. Institutional abbreviations

KUVP: University of Kansas Vertebrate Paleontology collections, Lawrence, Kansas, USA; **MVZ**: University of California Museum of Vertebrate Zoology, Berkeley, California, USA; **UCMP**: University of California Museum of Paleontology, Berkeley, California, USA; **UMPC**: University of Montana Paleontology Center, Missoula, Montana, USA; **UNSM**, University of Nebraska State Museum, Lincoln, Nebraska, USA; **UWBM**: University of Washington Burke Museum, Seattle, Washington, USA; **WSUCVM**: Washington State University Charles R. Conner Museum, Pullman, Washington, USA.

3.2. Taxonomic remark

Several taxa used in this analysis are yet to be formally described. Rasmussen (1977) recognized and proposed names for several new species of entoptychine gophers from the Cabbage Patch beds of Montana in his unpublished dissertation. Souza (1989) used one of Rasmussen's (1977) names for a gopher he studied in his unpublished master's thesis. These names have also been used in the MIOMAP database (Carrasco et al. 2007). To limit confusion, we herein use the names of Rasmussen (1977) for the morphotypes (i.e. unpublished species) of entoptychine gophers from the Cabbage Patch beds.

3.3. Sampling

Most specimens included in the geometric morphometric analysis were photographed in occlusal view using a Nikon D80 camera. We also imaged a few specimens using a Clemex LU1376C-CLX camera connected to a Leica MZ9.5 microscope. We only included specimens with a fully erupted adult dentition in our analysis. Both extant and extinct specimens in our sample possess a dentition with fully worn cusps and visible lophs or lophids (wear stage 3 of Czaplewski 2011). We excluded from our dataset very-late-wear specimens in which the shape of the lophs or lophids of the teeth had been obliterated (wear stages 4 and 5 of Czaplewski 2011). By limiting our sample to a single wear stage, we minimized the potential for ontogeny to overwhelm any taxonomic signal. To assess the potential for wear, within wear stage 3, to impact tooth shape, we scanned two specimens of the fossil genus *Pleurolicus* in a Skyscan 1174 X-ray microcomputer tomography scanner. We processed the scans using Skyscan 1.1, NRecon 1.6.9.18, and Mimics Research 18.0 to reveal the internal morphology of the unworn portion of the teeth. We selected several slices throughout the crown of each tooth and included them in a geometric morphometric analysis (see below) to determine variation in tooth shape within an individual through wear. For each of the two teeth, we also selected one of these slices at random to include in our analysis of shape variation in the entire fossil dataset.

We chose to analyze the upper third molar (M3) and lower fourth premolar (p4) because these teeth are often considered to be the most diagnostic in geomyids (e.g. Wood 1936; Russell 1968; Rasmussen 1977; Thaeler 1980; Flynn et al. 2008). The choice of the specific tooth position was also driven by specimen availability.

The extant sample (Table 1) includes 214 M3s and 196 p4s representing four genera and 16 species (67% of the genera and 40% of the species of extant geomyine gophers). Both male and female specimens were included in the analysis to account for the extreme sexual dimorphism of gophers (Connior 2011; Mathis et al. 2014). Our phylogenetic framework for these extant taxa is based on Demastes et al. (2002) for *Cratogeomys*, Chambers et al. (2009) and Sudman et al. (2006) for *Geomys*, Hafner et al. (2014) for *Orthogeomys*, and Belfiore et al. (2008) for *Thomomys*. For all species (except *Thomomys idahoensis* and *Thomomys bulbivorus*) that are present in more than one state or province, we sampled populations in a minimum of two states or provinces across Costa Rica, El Salvador, Honduras, Mexico, and the United States (see Appendix 3.1). We sampled geomyine rodents across a total of 31 states and provinces with the goal of representing the morphological variation of extant geomyines as best as possible.

Of the four entoptychine genera known, only *Pleurolicus* and *Gregorymys* are present in the Cabbage Patch beds (Rasmussen 1977; Rasmussen and Prothero 2003). This material, as well as a large sample of *Entoptychus* material from the John Day Formation, forms the core of our dataset. We also included specimens (see Appendix 3.2) from coeval Arikareean deposits of the western United States (Tedford et al. 2004) including the Harrison Formation (South Dakota), Sharps Formation (South Dakota), McCann Canyon Local Fauna (Nebraska), Fort Logan Formation (Montana), and Peterson Creek Local Fauna (Idaho). The species identification of these specimens follows published identifications (most notably Rensberger 1971, 1973, Wahlert and Souza 1988).We sampled a total of 84 M3s and 90 p4s representing 19 different species and three of the four known genera of entoptychine gophers (Table 2).

To limit potential mistakes in the taxonomic identification of the specimens included in the geometric morphometric analyses, we prioritized the use of specimens identified to the species level and associated with diagnostic osteological material (for fossil and extant specimens) or skins (for extant specimens). For the analysis of M3 shape, we included two specimens that are not identified to the species level. Both are *Gregorymys* specimens from the under-studied Fort Logan Formation of Montana. Three other fossil specimens were not associated with osteological material (KUVP 18028, 18092, and 20517). Only two of those specimens (KUVP 18028 and 20517) are found at localities where more than one species of entoptychine gopher is recovered. However, they can be assigned to species with some confidence on the basis of size. '*Pleurolicus gwinni*' is larger than '*P. nelsoni'* and the two taxa do not overlap in size (Rasmussen 1977). For the analysis of p4 shape, in addition to one of the *Gregorymys* specimens from the Fort Logan Fm., we included in the dataset unidentified specimens of *Gregorymys* (KUVP 18819) and *Pleurolicus* (UWBM 97344) from the Cabbage Patch beds. Only two specimens in this dataset are not associated with other teeth or osteological remains (KUVP 18076 and 18860). KUVP 18076 is from a locality where only one gopher species has been recovered to date. The identification of KUVP 18860 is supported by its size, distinct from that of the one other species of *Gregorymys* known from the area (Rasmussen 1977).

3.4. Landmarking

We used two-dimensional geometric morphometrics to quantify variation in tooth shape across and within taxa. Specifically, we used a series of semilandmarks to represent the outline of the worn teeth of geomyids. In entoptychine gophers, this outline is a continuous band of enamel. In adult geomyine gophers, the enamel band is interrupted by dentine tracts (Russel 1968; Thaeler 1980). One to three traditional landmarks were used in addition to the semilandmarks, depending on the tooth position and subfamily of the specimens (Table 3, Figure 2). Because all homologous features of the occlusal surface of the teeth are erased with wear, we used local maxima and minima on the tooth as type 2 landmarks that represent geometrically equivalent points (Zelditch et al. 2004). Landmarks and semilandmarks were digitized using tpsDig2 v. 2.16 (Rohlf 2013a). We placed the traditional landmarks first, followed by one or several curves (depending on the tooth position and subfamily) along the enamel band of the occlusal surface of the tooth. The curves were resampled to the appropriate number of semilandmarks depending on tooth position and subfamily (Figure 2). The number of semilandmarks used in the analyses was chosen following four different runs of the analyses with a decreasing number of equidistant semilandmarks (84, 43, 29, and 22 respectively). The goal of this sensitivity analysis was to minimize the number of semilandmarks (i.e. variables) and the number of significant axes of the principal component analyses (see below) while maximizing the percentage of the variation in the dataset represented by the axes and the percentage of specimens correctly identified by a canonical variate analysis (see below). We converted the semilandmarks to landmarks using tpsUtil v. 1.58 (Rohlf 2013b). We used the same total number of points (semilandmarks and landmarks combined) in extant and fossil specimens. We used the same number of points for the buccal and the lingual curves in the fossil taxa despite the fact that the sum of the length of the curves on the buccal side of the tooth does not equal that of the lingual side. We made this decision because the lingual side of the tooth does not show as much variation in morphology as the buccal side.

3.5. Analyses

We imported the data from the TPS file produced by tpsUtil into R 3.1.3 (R Development Core Team 2015) using RStudio 0.98.1103 (R Studio 2015) and the package geomorph 2.1.7-1 (Adams and Otárola-Castillo 2013). We performed the analyses using the packages geomorph 2.1.7-1, PMCMR 4.0 (Pohlert 2014), and MASS 7.3-39 (Ripley et al. 2015). We corrected p values with the Bonferonni correction (p = 0.05/number of tests, Shaffer 1995).

Landmarks were rotated, scaled, and translated using generalized Procrustes superimposition (Rohlf and Slice 1990). We used principal component analyses (PCAs) to assess similarities and differences in tooth shape. We then used the scores from the PCAs in canonical variate analyses (CVAs) to determine the utility of tooth shape in classifying specimens according to their taxonomic affinities. We only used the PCA the axes whose eigenvalues were larger than expected by chance (i.e. broken-stick distribution) in our analyses (Table 4). We performed the CVAs on subsets of the data to investigate dental morphology both across genera and across species of geomyine gophers, except within the genera *Geomys* and *Thomomys*. Within *Geomys*, we ran two different geometric morphometric analyses. The first compared tooth shape between the *pinetis* group (*G. pinetis* only) and the *bursarius* group (including *G. bursarius* and *G. arenarius*). These groups represent clades of *Geomys* species identified by phylogenetic analyses of molecular data (Chambers et al. 2009, Sudman et al. 2006). The second analysis explored shape differences across species within the genus. Within *Thomomys*, we performed an analysis to determine shape differences between the two subgenera (i.e. *Megascapheus* vs. *Thomomys*) and another to explore shape differences across species within each subgenus. We also performed a CVA to investigate dental morphology across entoptychine genera (Table 4) and within a subset of the best-sampled fossil species of the genus *Entoptychus*. We used a jackknife in all canonical variate analyses (see Strauss 2010). For each analysis, we calculated the expected percentage of correct identifications based on sample size (Table 4). This number is equivalent to the relative abundance of each taxon in each of the dataset analyzed.

Because the shapes of the teeth of extant and extinct gophers are very different, the two sets of specimens could not be included in a single Procrustes superimposition; we cannot directly compare a measure of variation, such as disparity, between extant and fossil taxa. Instead, we assessed variation within each group (extant or fossil) by (1) performing a Procrustes superimposition of all specimens of one of the two groups (extant or fossil), (2) calculating the variance (i.e. disparity) within each taxon around its mean following Foote (1993), (3) averaging these variances across taxa within the group to obtain a pooled within-group variance, (4) calculating the squared Procrustes distances between the means of the different taxa within the group, (5) dividing the squared distances by the pooled variance to get distances in units of variance, and (6) calculating the square root of this last value to get distances in standard deviation units. These distances have similar properties to Mahalanobis distances and although the landmarking scheme may affect the comparisons, these distances can be compared across groups (extant vs. fossils) despite differing morphologies. We calculated these distances both among genera and among species. We used non-parametric tests (Wilcoxon ranked-sum test, Kolmogorov-Smirnov test, Kruskal-Wallis tests, and post-hoc Nemenyi tests) to compare distances among taxa.

4. RESULTS OF THE GEOMETRIC MORPHOMETRIC ANALYSIS

4.1. Extant genera

The geometric morphometric analysis of geomyine M3s (Figure 3A) shows that the main axis of variation (PC1) represents the degree of mesio-distal folding of the enamel along the buccal edge of the tooth. Teeth of the genus *Orthogeomys* (dark gray circles) are heavily folded (low scores on PC1) whereas teeth of *Thomomys* (white circles) are much flatter along this edge of the tooth (high scores on PC1). PC1 best discriminates the different genera of geomyines. In fact, an ANOVA of the scores along this axis demonstrates a significant difference across genera ($F=229.9$, $p=2.10^{-16}$). Post-hoc comparisons using Tukey Honest Significant Differences show significant differences between all pairs of genera with the exception of *Cratogeomys* and *Geomys* ($p=0.076$; all other comparisons: $p\sim0$). The second axis of the PCA (PC2) differentiates teeth that are bucco-lingually expanded (low scores on PC2) from those that are bucco-lingually compressed (high scores on PC2). The CVA demonstrates that the four genera of gophers can be discriminated based on the shape of the outline of M3 (Figure 3B). Across genera, 93% of specimens were properly assigned to the genus to which they belong. The CVA performed best for *Thomomys* (98.2%) and *Geomys* (96.4%), the best-sampled taxa included in the analysis. Even within *Cratogeomys*, the genus with the lowest percentage of correct identification (66.7%), specimens were accurately assigned to the taxon over nine times more often than expected by chance (Table 4).

The geometric morphometric analysis of geomyine p4s (Figures 4A, 4B) shows that the main axis of variation (PC1) represents the degree of mesio-distal elongation of the tooth, especially that of its anterior lophid (i.e. the metalophid), and the space between the two lophids. The p4 metalophid of *Thomomys* (white circles) is mesio-distally elongated (low scores on PC1), whereas those of *Cratogeomys* (black circles), *Geomys* (light grey circles), and *Orthogeomys* (dark grey circles) are more mesio-distally compressed and bucco-lingually elongated (high scores on PC1). In *Thomomys*, the metalophid and hypolophid are separated by a mesio-distaly expanded re-entrant. In the other geomyines, the two lophids may abut one another. PC1 best discriminates between *Thomomys* and other genera of geomyines (ANOVA: F=128.2, p=2.10^{-16}). The combination of the second and third axes of the PCA (PC2 and PC3) best differentiates teeth of the genus *Cratogeomys* from other geomyine genera. Similarly to PC1, the second axis (PC2) differentiates between teeth that are more mesio-distally compressed (low PC2 scores) and those that are elongated along that direction (high PC2 scores). The third axis separates teeth that have diamond-shaped lophids (low PC3 scores) from those with rounded lophids (high PC3 scores). The CVA demonstrates that the four genera of gophers can be discriminated based on the shape of the outline of p4 (Figures 4C, 4D). Across taxa, the genus of almost 97% of specimens can be accurately identified. The first axis differentiates *Thomomys* from all other genera. CV2 isolates *Orthogeomys* from *Geomys* while CV3 separates *Cratogeomys* from other geomyines genera. In both *Geomys* and *Cratogeomys*, over 90% of specimens were properly classified (Table 4). In *Orthogeomys*, the most poorly classified taxon, over 86% of specimens were accurately classified.

4.2. Cratogeomys

The geometric morphometric analysis of the M3s of two species of *Cratogeomys* (Figure 5A) indicates that they can differentiated by the shape of the lingual and buccal sides of their M3. The two species do not overlap along PC1. A t-test of the scores along that axis demonstrates a highly significant difference between the two species (F=25.51, p=2.2.10^{-4}). In *C.*

castanops, the lingual side of M3 is much flatter than it is in *C. merriami*, in which it is more triangular and comes to an inflection point at the most lingual edge of the tooth. The depth of the buccal curve of the tooth is much shallower in *C. castanops* than in *C. merriami*. PC2 shows the intraspecific variation between specimens with a squarer M3 (high PC2 scores) and those with a more triangular tooth (low PC2 scores). The CVA shows that the two species are successfully differentiated on the basis of the shape of M3 (success rate = 80%, Table 4) although the performance of this analysis is diminished by a low sample size.

The geometric morphometric analysis of p4s of *Cratogeomys* (Figure 5B) shows subtle differences between the two species studied. Specimens of *C. castanops* tend to have lower scores along PC1 than specimens of *C. merriami*. This axis segregates mesio-distally compressed teeth with mesio-distally narrow re-entrants and compressed hypolophids (low PC1 scores) from those that are more expanded in this direction and display a more open re-entrant (high PC1 scores). Although the two species do overlap along PC1 (t-test: F=3.589, p=0.083), the CVA shows that the two species can be reliably differentiated (Table 4). Indeed, over 85% of specimens can be accurately classified by the analysis.

4.3. Geomys

The analysis at the group level shows that the two groups differ in the ratio of length to width of M3 (Figure 6A). The specimens from the *bursarius* group thus tend to display bucco-lingually expanded teeth (low scores on PC1) whereas specimens from the *pinetis* group tend to have teeth that are mesio-distally expanded (high scores on PC1). The two groups are distributed along PC2, an axis that differentiates more triangular teeth (low PC2 scores) from more circular ones (high PC2 scores). The CVA confirms the visual observation that M3 shape is useful in differentiating the two *Geomys* groups studied. 85% of specimens can be assigned to the correct group (Table 4).

When analyzing differences in M3 shape at the species level, the CVA (Figure 6B) does not perform as well as at the group level. Only 56.4% of specimens are properly assigned to the species they belong to. Although this number is as high as 77.8% in *G. pinetis*, many specimens cannot be accurately classified within the *bursarius* group. Thus, over half of *G. bursarius* specimens are incorrectly assigned to *G. arenarius* while one-third of *G. arenarius* specimens were incorrectly classified as *G. bursarius*. Larger sample sizes would likely improve the accuracy rate of specimen classification across *Geomys* species; this is suggested by the proportion of *G. bursarius* specimens correctly classified in the analysis which is almost 1.8 times higher than expected by chance (Table 4).

The results of the geometric morphometric analysis of p4 show that the groups overlap heavily in the morphospace defined by PC1 and PC2 (Figure 6C). Specimens from the *pinetis* group tend to possess teeth that are mesio-distally compressed (low PC2 scores) as opposed to the more mesio-distally expanded teeth of the *bursarius* group (high PC2 scores). The width to length ratio of the metalophid (anterior lophid) decreases along that axis (i.e. low PC2 scores: bucco-lingually expanded metalophids, high PC2 scores: mesio-distally expanded metalophids). The CVA confirms that p4 shape differentiates between the two *Geomys* groups studied (90% of specimens can be correctly classified; Table 4). The CVA of p4 shape at the species level (Figure 6D) accurately classifies over 80% of specimens. The most accurately classified specimens are those of *G. pinetis* (93.3%). However, even within the *bursarius* group, over 75% of specimens are accurately classified into *G. arenarius* and *G. bursarius* (Table 4).

4.4. Orthogeomys

The geometric morphometric analysis of M3 within *Orthogeomys* show that the three species studied (corresponding to three different subgenera) display different tooth morphologies (Figure 7A). The first axis of the PCA shows shape variation from mesio-distally expanded but bucco-lingually compressed teeth (low scores on PC1) to mesio-distally compressed but bucco-lingually expanded teeth (high scores on PC1). Along PC2, tooth morphology varies from rounder teeth with little buccal folding (low scores on PC2) to teeth with a deep folding (high scores on PC2). *O. heterodus* is located in the upper left corner of the morphospace (i.e. the posterior loph of the tooth forms a pronounced, elongated heel) while *O. grandis* is found in the lower right corner (i.e. the posterior loph is relatively short compared to other subgenera of *Orthogeomys*). The location in morphospace of *O. hispidus* is intermediate between the other two taxa. The CVA (Figure 7B) demonstrates that M3 shape can be used to discriminate among the species of the genus *Orthogeomys*. Almost all *O. grandis* specimens are accurately assigned to this species. The percentage of specimens accurately assigned to the a-priori species decreases with smaller sample sizes (Table 4) although overall, almost 86% of specimens of *Orthogeomys* can be accurately identified to the species level based on M3 shape.

The geometric morphometric analysis of the shape of p4 within *Orthogeomys* (Figure 7C) shows variation from teeth with metalophid and hypolophid separated by mesio-distally wide re-entrants (low PC1 scores) to teeth were the two lophids abut each other (high PC1 scores). Along PC2, specimens vary from mesio-distally expanded hypolophids that are wider than the metalophid (low PC2 scores) to subcircular ones that are subequal in size to the metalophid (high PC2 scores). Although *O. grandis* appears to span much of the morphospace defined by PC1 and

PC2, *O. heterodus* is restricted to the upper left corner of the morphospace (i.e. low PC1 and high PC2 scores).

The CVA (Figure 7D) demonstrates that p4 shape can be used to discriminate among the species of the genus *Orthogeomys*. As for the M3, almost all *O. grandis* specimens are accurately assigned to this species based on p4 shape (93.3%). Even if they are more poorly sampled, over 75% of specimens of both *O. heterodus* and *O. hispidus* are accurately classified (Table 4).

4.5. Thomomys

There is much overlap between the two subgenera along the first three axes of the PCA (Figure 8A). There is in fact no significant difference between the two subgenera's mean PC1 score (F=3.038,p=0.084) or variation in scores along that axis (D=0.23, p=0.1). Variation in shape along PC1 reflects changes in the shape of the tooth from a narrower mesio-distally tooth (low scores on PC1) to more expanded ones (high scores on PC1). PC2 represents the bucco-lingual compression of the tooth from more expanded teeth (low scores on PC2) to narrower ones (high scores on PC2). PC3 reflects the overall shape of the teeth, from more rectangular ones with a flatter lingual side (low scores along PC3) to rounder ones with an expanded lingual side (high scores on PC3). Nevertheless, a CVA of M3 shape (Figure 8B) can accurately classify about 77% of the specimens of the subgenus *Thomomys* and 67% of the specimens of *Megascapheus,* over 40% more specimens than expected from chance. Our analysis includes the three best sampled species within the subgenus *Megascapheus*: *T. bulbivorus*, *T. townsendii*, and *T. bottae* (Table 4). Although the CVA suffers from low sample sizes, almost 65% of specimens can be correctly identified to the species level (Figure 8C). The three taxa overlap somewhat in ecomorphospace, but the two better sampled species (*T. bottae* and *T. bulbivorus*) occupy distinct corners of the plot. Therefore, with additional specimens, we would expect a greater accuracy of the CVA in classifying taxa. Within the subgenus *Thomomys*, the specimens from the two best sampled species (*T. mazama* and *T. talpoides*) can be accurately assigned to the a-priori taxon over 86% of the time (Table 4, Figure 8D). Even the most poorly sampled species (*T. monticola*) is properly identified at almost twice the rate of chance and would likely be better identified with additional specimens.

Although there is some overlap in p4 morphology between the two *Thomomys* subgenera, they tend to occupy different parts of the morphospace defined by the first two axes of the first PCA (Figure 9A). Both subgenera span most of the range of values along PC1. Along this axis, the teeth may be mesio-distally compressed with a mesio-distally expanded metalophid (low PC1 scores) or elongated with a bucco-lingually expanded metalophid (high PC1 scores). However, the two subgenera can be differentiated by their location along PC2 (ANOVA: $F=69.78, p=4.2.10^{-13}$). *Thomomys* specimens tend to have low scores along PC2 whereas *Megascapheus* specimens tend to have high scores along that axis (Figure 9B). PC2 reflects the change in shape of the lingual side of the metalophid. It is concave in *Thomomys* and convex in *Megascapheus*. A CVA of p4 shape can accurately classify over 96% of *Megascapheus* specimens and 90% of *Thomomys* specimens (Figures 9C, 9D). Within the subgenus *Megascapheus* (Figure 9C), the CVA can classify accurately over 81% of *Thomomy bulbivorus* specimens. Few specimens of *T. bottae* and *T. townsendii* can be accurately classified by the CVA however (around 43%, Table 4). Within the subgenus *Thomomys* (Figure 9D), the specimens from *T. mazama* and *T. talpoides* can be accurately assigned to the species they belong to over 70% of the time. Only about 36% specimens of *T. monticola* are properly identified by the CVA.

4.6. Fossil genera

The geometric morphometric analysis of M3s of fossil geomyids (*Pleurolicus*, *Gregorymys*, and *Entoptychus*; Figure 10A) shows that these taxa strongly overlap in the morphospace formed by PC1 and PC2. All three genera overlap and span a large range of values along PC1 (ANOVA: F=0.17, p=0.84). This first axis describes the orientation of the transverse sulcus between the protoloph and metaloph. It may either be directed mesially (low PC1 scores) or distally (high PC1 scores). Along PC2, the main shape change is in the orientation of the protoloph and metaloph. These two lophs are either distinct (i.e. the transverse sulcus is wide open) and bucco-lingually straight (high PC2 scores) or come together (i.e. the transverse sulcus is almost closed; low PC2 scores). The CVA (Figure 10B) can accurately classify most specimens of the well-sampled genus *Entoptychus* (94.6%) and many (73.3%) of the *Pleurolicus* specimens, despite its smaller sample size (Table 2). The specimens of *Gregorymys*, which overlap with the other genera in the morphospace defined by PC1 and PC2, are not classified as accurately (Table 4). Nevertheless, they are properly assigned to *Gregorymys* more than twice as much as expected by chance.

The geometric morphometric analysis of p4 fossil specimens shows that *Gregorymys* and *Entoptychus* strongly overlap in the morphospace formed by PC1 and PC2 (Figure 10C). *Pleurolicus* p4s have high scores on PC1 that are distinct from those of the other genera (ANOVA: F=127.2, $p < 2.2.10^{-16}$). In worn specimens, the p4 of *Pleurolicus* differs from those of *Gregorymys* and *Entoptychus* in being bicolumnar; its lophids are connected neither buccally nor lingually, but centrally. The most worn specimens have the highest scores along PC1. In specimens with less wear, the buccal re-entrant is not as pronounced and the teeth more closely resemble those of *Gregorymys* and *Entoptychus*. The p4s of *Gregorymys* and *Entoptychus*, with their lophids connected on the lingual side of the tooth, have low scores on PC1. Along PC2, the shape of the buccal side of the tooth dictates the position of the specimens in the morphospace. The anterior lophid (the metalophid) is either mesio-distally expanded and mesially oriented (low PC2 scores) or more compressed, distally oriented, and contacting the hypolophid (high PC2 scores). The CVA (Figure 10D) discriminates almost all specimens of the well-sampled genus *Entoptychus* (94.7%). The morphologically distinct *Pleurolicus* specimens can also be correctly identified eighty percent of the time despite a very small sample size (Table 2). The specimens of *Gregorymys*, which overlap with *Entoptychus* in the morphospace, are not classified as accurately (Table 4) because of small sample size (Table 2). However, they are properly assigned to *Gregorymys* more than four times as much as expected by chance.

4.7. Entoptychus

Within the best-sampled genus, *Entoptychus*, three species are represented by nine specimens or more (Table 2): *E. cavifrons*, *E. minor*, and *E. wheelerensis*. The geometric morphometric analysis of the M3 of these three species (Figure 11A) shows overlap along PC1 and PC2 of the three species. There is no significant difference in mean PC1 score (ANOVA: F=2.242, p=0.12) or mean PC2 score (ANOVA: F=0.92, p=0.41) across the three species. PC1 and PC2 describe shape changes similar to those identified at the genus level (i.e. orientation and closing of the transverse sulcus respectively). The CVA (Figure 11B) can accurately classify a large number of *E. wheelerensis* specimens (71.4%). Specimens of *E. minor* are not identified as accurately as those of *E. wheelerensis* but are better classified than they would be by chance (Table 4). The small sample size for *E. cavifrons* may prevent a better classification of the specimens (Tables 2, 4).

There are three species of *Entoptychus* represented by enough p4s to be included in a species-level analysis: *E. cavifrons*, *E. minor*, and *E. wheelerensis*. These three species (Figure 11C) overlap in morphospace along both PC1 (ANOVA: F=0.585, p=0.56) and PC2 (ANOVA: F=0.321, p=0.73). The variation in shape along PC1 in this analysis is similar to that described for PC2 in the genus-level analysis (see above) in which the anterior lophid (the metalophid) may be mesio-distally expanded, and mesially oriented (high PC1 scores) or more compressed, distally oriented, and contacting the hypolophid (low PC1 scores). Along PC2, p4 shape varies from teeth with a more distally oriented hypolophid, a compressed metalophid, and a transverse sulcus more open mesio-distally (low PC2 scores) to teeth with a more mesio-distally expanded metalophid, a more bucco-lingually oriented hypolophid, and a transverse sulcus narrower mesio-distally (high PC2 scores). The CVA (Figure 11D) can accurately classify a large number of *E. wheelerensis* specimens (76.2%) but only a few specimens of *E. minor* and *E. cavifrons* (Table 4). There is a large overlap between these latter two taxa. When rerunning the CVA with these two taxa combined into one, over 80 percent of specimens from the composite taxon *E. minor or cavifrons* (N=26) can be accurately classified.

5. DISTANCES AND TAXONOMIC VARIATION

5.1. Distances among genera

There is a wide range of variation in M3 shape divergence (i.e. distances in the M3 morphospace) among geomyine genera; that range is much narrower in fossil gophers (Table 5, Figure 12A). Despite a wide range of intergeneric distances (Table 5), there are no significant differences in distances between any two pairs of gopher genera included in our analyses (posthoc Nemeyi tests p>α=0.001; see Appendix 3.3). The distance between *Entoptychus* and

Pleurolicus falls within the range of distances observed among modern taxa. The distances between *Gregorymys* and *Entoptychus* as well as between *Gregorymys* and *Pleurolicus* are lower than those observed among modern gopher genera. In fact, the distance between *Cratogeomys* and *Geomys* is the only distance within Geomyinae that overlaps with the distribution of distances among fossil gopher genera (Table 5). Nonetheless, the mean variation in M3 shape among fossil genera is not significantly different from that observed among extant genera (Wilcoxon signed-rank test, W=17, p=0.052). The two samples' distributions are also not significantly different from each other (Kolmogorov-Smirnov test, D=0.83, p=0.12).

There is less variation in the distances among geomyine genera in the p4 morphospace than in the M3 morphospace (Figure 12B). Among fossil gophers, the distances in the p4 morphospace are much higher than those in the M3 morphospace; the distances between *Entoptychus* and *Pleurolicus* as well as *Gregorymys* and *Pleurolicus* are particularly large. The distance between *Gregorymys* and *Entoptychus* falls within the range of distances found among extant genera (Table 5). The mean distance among fossil genera in the p4 morphospace is not significantly different from that observed among extant genera (Wilcoxon signed-rank test, W=5, p=0.381) and the two samples' distributions are also not significantly different from each other (Kolmogorov-Smirnov test, D=0.67, p=0.33). There are no significant differences in distances between any two pairs of gopher genera or subgenera included in our analyses (Kruskal-Wallis test, χ^2 =12.06, df=7, p=0.099).

5.2. Distances among species

The smallest distance among extant gophers in the M3 morphospace is observed among *Thomomys* species, particularly within the subgenus *Megascapheus* (Figure 12A, Table 6). The largest distances are found in *Cratogeomys* and *Orthogeomys*. Among fossil genera, the largest distances between species are observed in *Pleurolicus* and the smallest ones in *Entoptychus* (Figure 12A, Table 7). The range of variation in distances among fossil gopher species overlap with that among extant gopher species. Nevertheless, the mean distance among fossil species is significantly different from that of extant ones (Wilcoxon signed-rank test, W=238.5, p=0.0048). The distributions of distances are also significantly different (Kolmogorov-Smirnov test, D=0.48, p=0.0026). The distance between *E. minor* and *E. cavifrons* is in the fourth smallest distance between two fossil species (Table 7). The smallest distance is found between *E. minor* and *E. wheelerensis*, both included in our CVA.

The distances in the p4 morphospace among extant gophers are relatively similar across taxa (Figure 12B). They vary little across species and genera (Figure 12B, Tables 6 and 7). The range of distances among fossil gopher species overlaps with that among extant gopher species. The difference between the mean distances is not significant (Wilcoxon signed-rank test, W=337, p=0.27). The distributions of distances are also not significantly different from each other (Kolmogorov-Smirnov test, D=0.28, p=0.23). The divergence in p4 shape (i.e. distance in the p4 morphospace) between *Entoptychus minor* and *Entoptychus cavifrons* is the smallest observed among gopher species, fossil or extant. Only one distance is smaller in the entire dataset (including divergences in both M3 and p4 shapes), the distance between *T. bottae* and *T. talpoides* in the M3 morphospace.

6. DISCUSSION

6.1. Taxonomic value of isolated geomyid cheek teeth

Our results provide quantitative data to support many of the qualitative observations of Russel (1968) and demonstrate that the shapes of the cheek teeth of both geomyines and entoptychine gophers are taxonomically informative at the genus, subgenus, and sometimes species level. The results of our analyses of M3 shape supports the hypothesis that the degree to which the tooth is bicolumnar helps differentiate genera of geomyines. Thus, the M3 of *Thomomys* is monocolumnar. Among the Geomyini included in our analysis (*Geomys*, *Cratogeomys*, and *Orthogeomys*), *Orthogeomys* displays the most strongly bicolumnar M3. The shape of p4, especially the bucco-lingual elongation of the hypolophid relative to the metalophid is also particularly helpful in differentiating *Thomomys* from the Geomyini. Within the genus *Cratogeomys*, the continuum of tooth morphologies associated with our small sample makes definitive conclusions difficult, but our results are consistent with a more obcordate tooth as a character indicative of *C. merriami*. Within *Geomys*, we do find the M3 to be generally more commonly bicolumnar in the *pinetis* group than in the *bursarius* group. Although Connior (2011) suggested that *G. bursarius* is difficult to identify on the basis of dental morphology, our results indicate that the shapes of M3 and p4 are useful in identifying this taxon. Our analysis of tooth shape within *Orthogeomys* confirms that the morphology of the posterior loph of M3 can be used to distinguish the three subgenera of *Orthogeomys.* Within *Thomomys*, although there is much overlap between the two taxa and large sample sizes are required to distinguish different morphospace occupations, M3 appears useful in distinguishing between the subgenera *Thomomys* and *Megascapheus*. Our analyses indicate that the shape of p4 may be a better characteristic to distinguish the two subgenera. Indeed, our results quantitatively support the observation of Thaeler (1980). In *Megascapheus,* the anterobuccal enamel plate of the p4 is not convex and anteriorly located (as in other geomyids). Instead, it is concave and forms a shallow re-entrant on the buccal side of the tooth. The results of our analysis indicate that the shape of the M3 of *T. bulbivorus* is peculiar. It makes this species easier to classify than any other within *Megascapheus*. Overall, the shapes of M3 and p4 allow the genus identification of over 85% of specimens to be accurately determined. Within *Geomys*, *Orthogeomys,* or *Thomomys,* tooth shape is also a good predictor of supraspecific taxonomic identity. Even at the species-level (within *Geomys* and *Cratogeomys),* tooth shape can be helpful in assigning specimens to a taxonomic category. The usefulness of geometric morphometric analyses of cheek tooth shape in geomyine taxa suggests this approach may also provide important insights when applied to the fossil subfamily Entoptychinae.

Much of the fossil record of Entoptychinae is composed of isolated cheek teeth and partial jaws (e.g., Rensberger 1971, 1973), many of which are worn. Our approach offers the opportunity to identify worn teeth of entoptychines. Our analysis of a large sample of entoptychine teeth confirms that the shapes of p4 and M3 are taxonomically informative. As many as 75% of specimens studied can be accurately assigned to the genus they belong to. These results are particularly encouraging considering the variation in wear of the teeth included in the analysis (within wear stage 3 of Czaplewski 2011). One of the main characteristics of entoptychine cheek teeth changing with wear is the orientation of the lophs and lophids of the teeth relative to the buccal edge of the transverse sulcus. The microCT scans of two specimens of the genus *Pleurolicus* provide insights into the variation in M3 shape within an individual with tooth wear (Figure 13). Despite covering important wear (a thickness of 0.62 and 0.40 mm of tooth, roughly 25% of the total crown height of the tooth, in KUVP 18028 and KUVP 20517 respectively), there is very little change in the shape of the enamel of the occlusal surface through wear in the two specimens of *Pleurolicus* studied. The similarities in shape through wear within an individual suggest that the morphology of the occlusal surface of a specimen may be representative of the morphology of the entire tooth through wear within the wear stage considered in our analysis.

Our analyses are consistent with the observation that, in both *Gregorymys* and *Entoptychus*, the anteroposterior length of the metaloph of M3 is subequal to that of the protoloph (Rensberger 1971); in *Pleurolicus*, the protoloph is anteroposteriorly longer than the metaloph (Calede pers. obs.). We also provide quantitative support for the observation that in the p4 of *Pleurolicus*, the link between the two lophids is made along the middle axis of the tooth between the fused cusps of the metalophid and the hypoconid unlike in *Entoptychus* and *Gregorymys* where the two lophids first join lingually (Rensberger 1971, 1973, Rasmussen 1977, Calede pers. obs.).The similarities in tooth shape between *Entoptychus* and *Gregorymys* we recovered in our analyses may represent derived traits for entoptychines and support a close relationship between these two genera (Rensberger 1971, 1973, Korth 1994).

Within *Entoptychus*, differences between species can sometimes be detected. *E. wheelerensis* is thus reasonably accurately identified (>70%) and distinguished from *E. minor* and *E. cavifrons*. *E. wheelerensis* is diagnosed by a combination of characters of the length of the enamel plates and height of chevrons of its teeth, not characters of the occlusal surface of the crown (Rensberger 1971). It is noteworthy that this taxon could be recovered in our analyses based on aspects of its morphology not used in the original diagnosis. A different situation is found with *E. minor* and *E. cavifrons*. These two taxa are differentiated from one another by three definitive characters: the length of the posterior enamel of m1 and the lengths of the anterior enamel on M1 and M2 (Rensberger 1971). *E. minor* and *E. cavifrons* are suggested to represent a stratigraphic succession (Rensberger 1971:figure 76). In the absence of these dental characteristics mentioned above, even mostly complete skulls cannot be assigned confidently to either one of these taxonomic units (see Rensberger 1971:plate 10-13 and specimens UCMP 72112, 72113, 72120, 73179, 73592). This is a very unique situation in a group of rodents where species can often be diagnosed by cranial and mandibular features as well as characteristics of the unworn or little worn occlusal surface morphology of the teeth (e.g. Munthe 1977; Korth et al. 1990; Korth 1996). Our analyses are consistent with the evidence from cranial morphology: the two taxa overlap heavily in morphospace and cannot be reliably differentiated (success<60%). When combined into a single taxonomic unit, the success rate in identification reaches 80%, suggesting that these two species may in fact represent a single taxon within in which hypsodonty varies through time. Future work evaluating the intra- and interspecific morphological variation within *Entoptychus* in discrete characters of the unworn teeth as well as discrete and continuous characters of the skull and dentary will help shed light on the validity of the different species of *Entoptychus* and help inform a phylogenetic analysis of the Entoptychinae.

6.2. Variation within geomyid taxa

The study of morphological variation within Geomyinae at different taxonomic levels can be used to determine the expected amount of variation in fossil Entoptychinae. Major differences between observed variation in fossil taxa and expected levels of variation based on modern taxa may suggest that further splitting or lumping of species (for example) may better represent the taxonomic diversity of the fossil groups studied. This is a critical analysis for entoptychine gophers in light of their purported biodiversity during the Arikareean (Rensberger 1971; Flynn and Jacobs 2008; Samuels and Van Valkenburgh 2009).

The results of our analyses of variation in M3 and p4 shape show that the amount of variation found in the subfamily Entoptychinae is comparable to that found in the extant Geomyinae. Although the fossil sample represents greater time averaging than the extant one, the modern sample includes a greater taxonomic diversity and a wider geographic sampling (see above). Thus, the morphological variation observed in the extant and the fossil samples, whether in the shape of M3 or that of p4, are comparable.

Our analysis of the variation in p4 and M3 shape across genera demonstrates no significant differences between modern and fossil genera. This suggests that *Gregorymys*, *Pleurolicus*, and *Entoptychus* represent taxonomic units comparable to modern genera of geomyines. This result is consistent with morphological data; the three fossil genera are also well supported by multiple synapomorphies including osteological and dental features (e.g. Wood 1936; Wahlert 1985; Flynn et al. 2008).

Our analyses of the differences in p4 and M3 shape among gopher species demonstrate that the range of morphological divergences between fossil species overlaps that seen in extant species. There are in fact no significant differences between the morphological variation seen in the shape of p4 in extant and that seen in extinct species of gophers. Morphological variation in M3 shape is significantly higher among fossil species than among extant species. This is driven by the high distance values within the fossil genera *Gregorymys* and *Pleurolicus* and the comparably low distances among the extant *Thomomys Megascapheus* species. The small distances within *Megascapheus* are the consequence of the wide range of morphologies found in *T. bottae* and *T. townsendii*. *T. bottae* is a geographically widespread taxon (Belfiore et al. 2008) and, although we only sampled specimens from three states (Arizona, California, and Oregon), this species is known for high karyotypic and genic variation, even within population, as well as variations in sexual dimorphism and soft tissue characteristics such as fur color (see Jones and Baxter 2004). Although restricted to a small area geographically (Belfiore et al. 2008), *T. townsendii* displays a wide range of morphological variation in its skull as well as the shape of its cheek teeth (Davis 1937:figure 4). The large distances within the genus *Pleurolicus* are mostly driven by the diverse *Pleurolicus* fauna from the Cabbage Patch beds of Montana where three morphotypes (i.e. undescribed species) can be identified. Those morphotypes vary widely morphologically (Rasmussen 1977; Calede pers. obs.) but they appear to be supported by multiple characters of the skull and dentary (Rasmussen 1977; Calede pers. obs.). Ongoing work by one of us [JJC] and Rasmussen to formally document the morphology of these animals, including osteological characteristics, will provide the necessary information to confirm this hypothesis. The very low value found for the distance in p4 shape between *E. minor* and *E. cavifrons* support the hypothesis raised by the results of our CVA that these two species may represent a single taxon. The distance between the two taxa in M3 shape is also among the lowest ones observed among fossil species. Only three distances are smaller, although the range of interspecific distances in modern gophers (Table 6) suggests that the difference in M3 shape between *E. minor* and *E. cavifrons* is not outside of the range expected between two gopher species.

7. FUTURE WORK

The morphological distances between extant gophers we determined based on tooth shape could be compared with molecular distances (from Spradling et al. 2004) following the method of Polly (2003) to investigate the potential of tooth shape to be phylogenetically informative. If successful in extant gophers, such an approach could be applied to extinct gophers to inform phylogenetic reconstructions within Entoptychinae. Our results show that the genus *Pleurolicus* is more divergent from *Entoptychus* and *Gregorymys* than these latter two are from one another. These similarities are consistent with the current phylogenetic hypothesis for the relationships of these genera (Korth 1994). Larger datasets of tooth shape may be harvested from microCT scans of gophers as demonstrated herein, including *Ziamys* material and type specimens because of the non-destructive nature of this work, allowing the broader sampling of fossil gophers necessary for such analyses.

Despite demonstrating that the shape of the M3 and p4 of gophers is taxonomically informative at the genus, subgenus, and species levels, our results also support the need for additional research characterizing the morphology of entoptychine gophers, particularly those from the John Day Formation and the Cabbage Patch beds of Montana. In both of these areas, entoptychine gophers are abundant and potentially biostratigraphically informative (Rensberger 1971, 1973, Rasmussen and Prothero 2003, Calede and Rasmussen 2015). A reassessment of the systematics of entoptychines coupled with the development of a phylogenetic framework would help provide more accurate assessments of the biostratigraphic ranges of entoptychine species. Combining this work with recent and ongoing developments in radioisotopic dating of gopher-bearing horizons in the John Day Formation and Cabbage Patch beds (e.g. Albright et al. 2008; Korth and Samuels 2015; ongoing work by one of us [JJC] in the Cabbage Patch beds of Montana) will allow the revision of the value of gophers as biostratigraphic markers during the Arikareean in North America.

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FIGURES

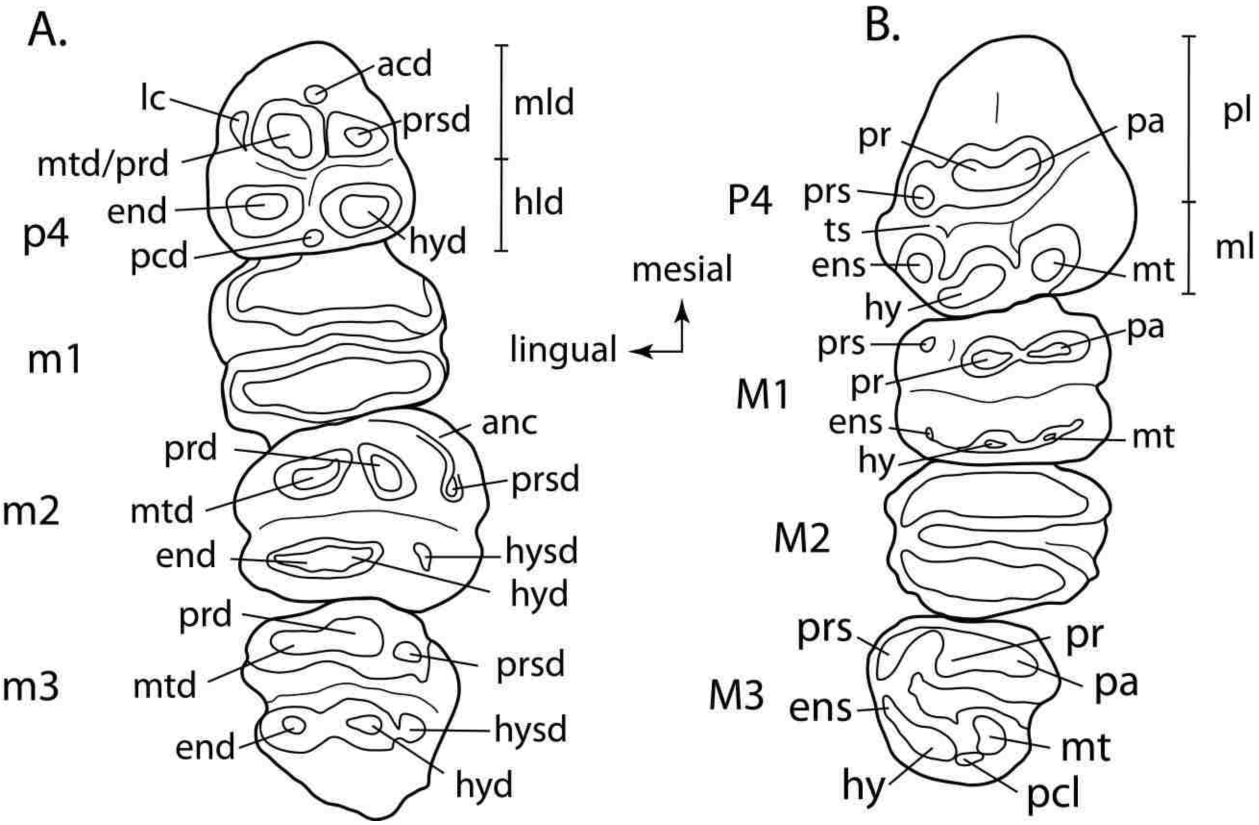

Figure 3.1. Diagramatic drawing of dental features used in this study (redrawn and modified from Souza 1989 and Rensberger 1971). A) Lower tooth row. B) Upper tooth row. Abbreviations: acd, anteroconid; anc, anterobuccal cingulum; end, entoconid; ens, entostyle; hld, hypolophid; hy, hypocone; hyd, hypoconid; hysd, hypostylid; lc, lingual cingulid; ml, metaloph; mld, metalophid; mt, metacone; mtd, metaconid; pa, paracone; pcd, posteroconid; pcl, posterior cingulum; pl, protoloph; pr, protocone; prd, protoconid; prs, protostyle; prsd, protostylid; ts, transverse sulcus.

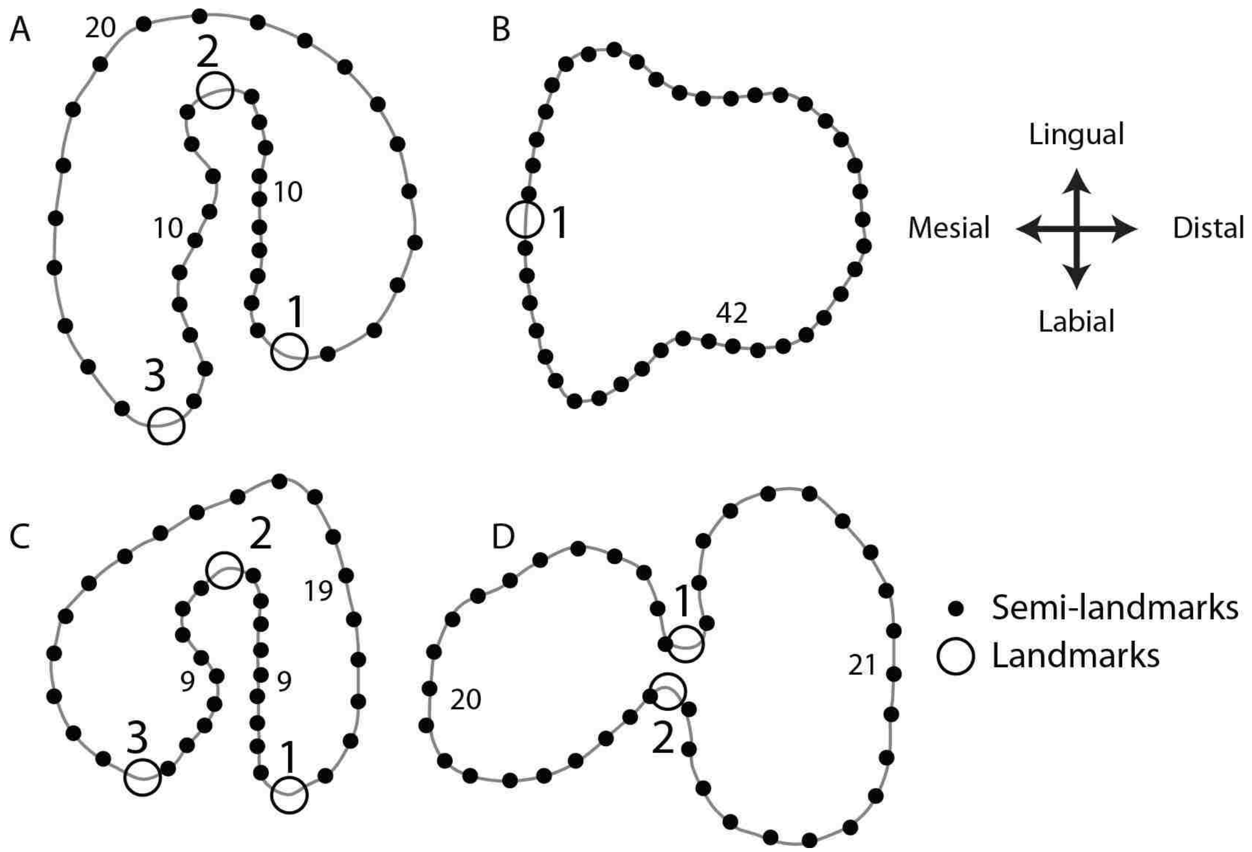

Figure 3.2. Landmark schemes for geomyid specimens. A) M3 of entoptychine gophers. B) M3 of geomyine gophers. C) p4 of entoptychine gophers. D) p4 of geomyine gophers.

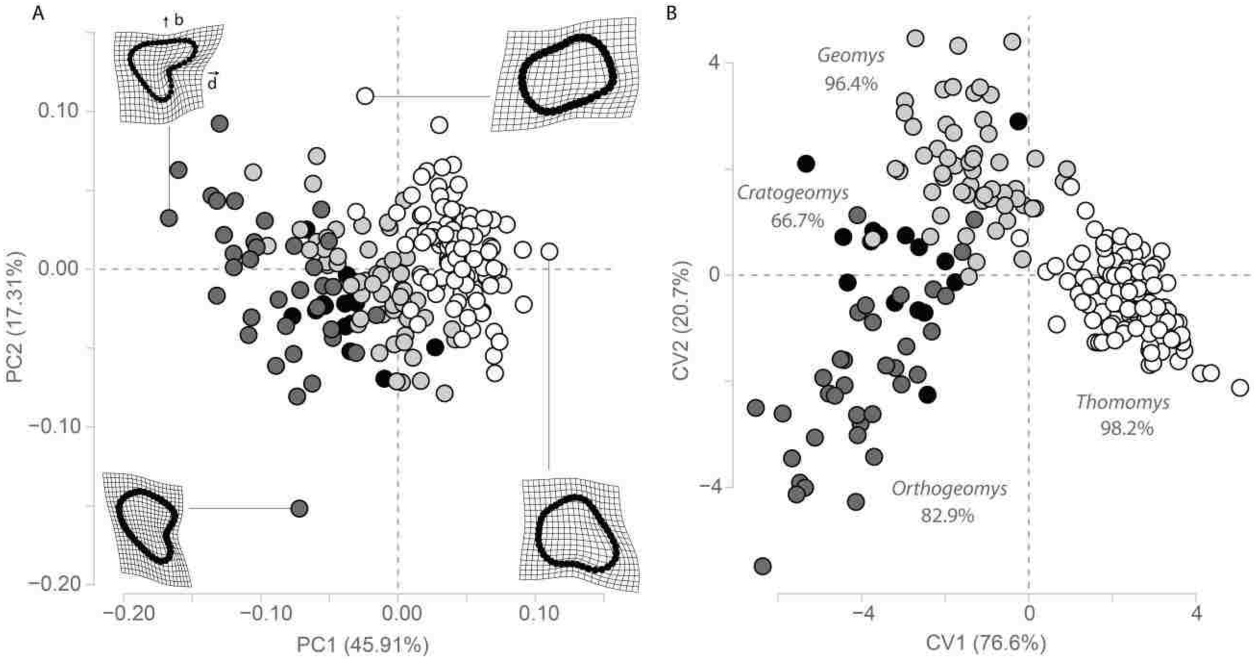

Figure 3.3. Geometric morphometric analysis of the M3 of extant gopher genera. A) First two axes of the PCA and associated deformation grids. The deformation grids show morphologies along the axes. The arrows show the buccal (b) and distal (d) directions. B) Plot of the CVA with percentage of specimens accurately identified by analysis.

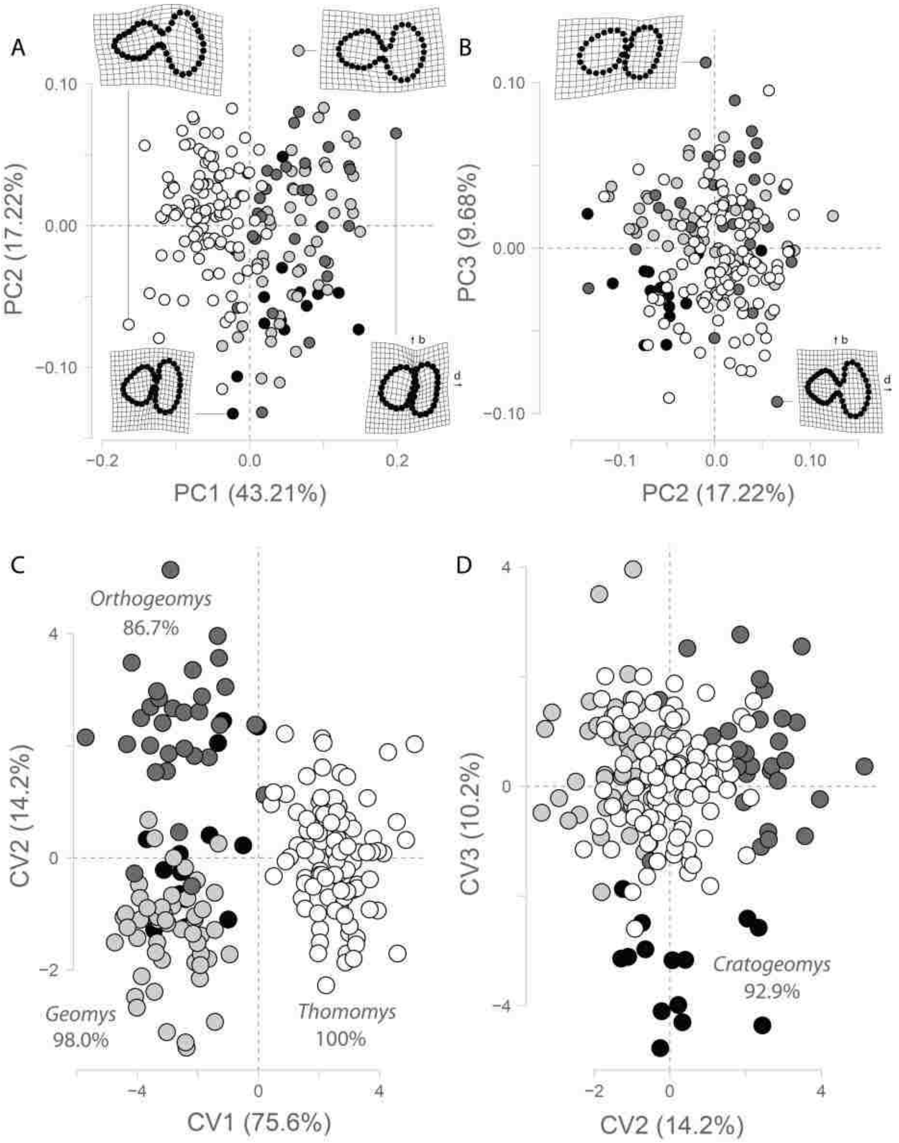

Figure 3.4. Geometric morphometric analysis of the p4 of extant gopher genera. A) First two axes of the PCA and associated deformation grids. The deformation grids show morphologies along the axes. The arrows show the buccal (b) and distal (d) directions. B) Second and third axes of the PCA and deformation grids for the third axis. C) Plot of the first two axes of the CVA with percentage of specimens accurately classified by analysis. D) Second and third axes of the CVA with percentage of specimens of *Cratogeomys* accurately classified by analysis.

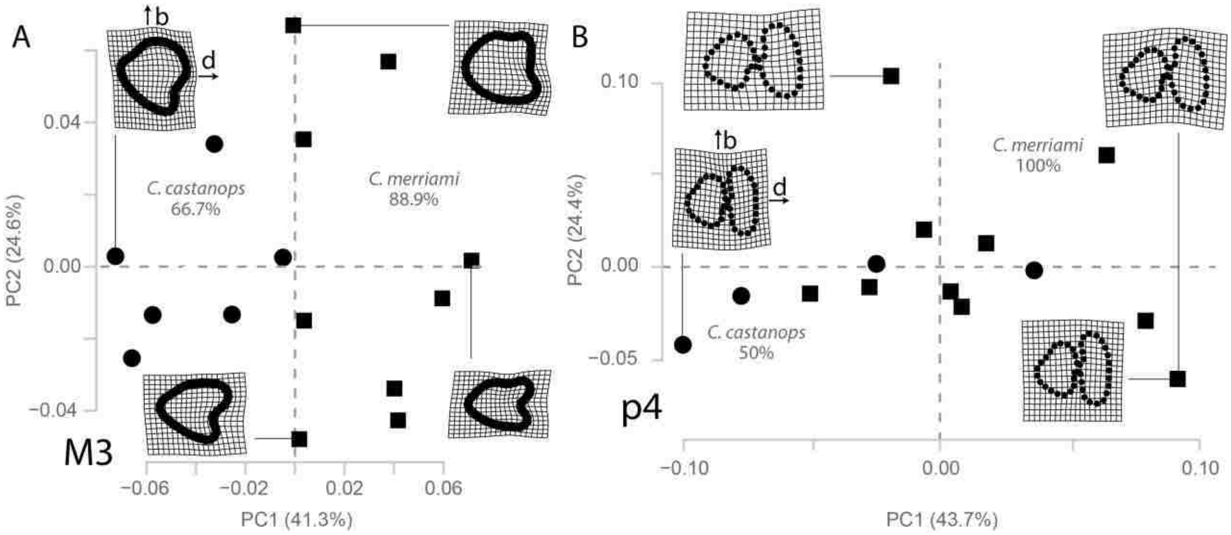

Figure 3.5. Geometric morphometric analysis within *Cratogeomys*. A) First two axes of the PCA of M3 shape and associated deformation grids. B) First two axes of the PCA of p4 shape and associated deformation grids. Percentages of specimens accurately identified by the CVA indicated below each species name. The deformation grids show morphologies along the axes. The arrows show the buccal (b) and distal (d) directions.

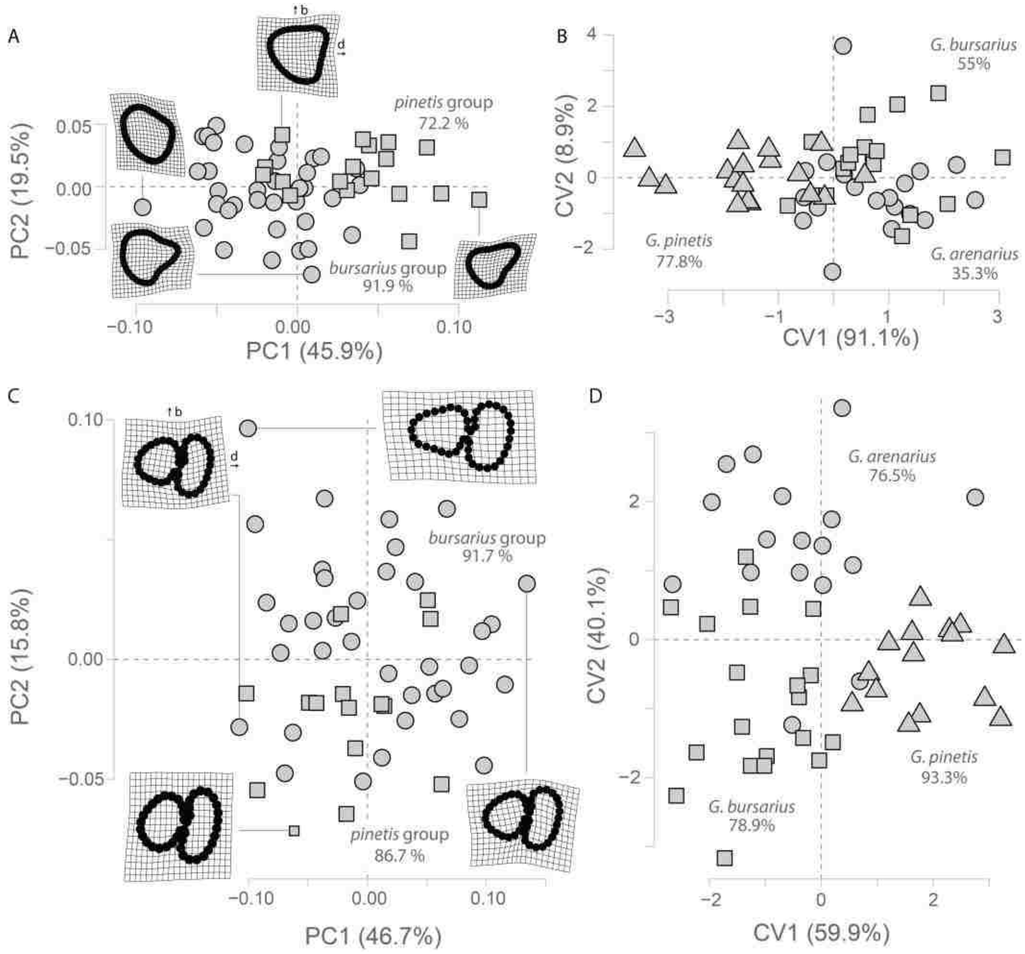

Figure 3.6. Geometric morphometric analysis within *Geomys*. A) First two axes of the PCA of M3 shape and associated deformation grids. The deformation grids show morphologies along the axes. The arrows show the buccal (b) and distal (d) directions. The percentage of specimens accurately identified by the group-level CVA is indicated below each group name. B) Plot of the CVA of M3 shape with percentage of specimens accurately identified for each species below each name. C) First two axes of the PCA of p4 shape and associated deformation grids. The arrows show the buccal and distal directions. The percentage of specimens accurately identified by the group-level CVA is indicated below each group name. D) Plot of the CVA of p4 shape with percentage of specimens accurately identified for each species below each name.

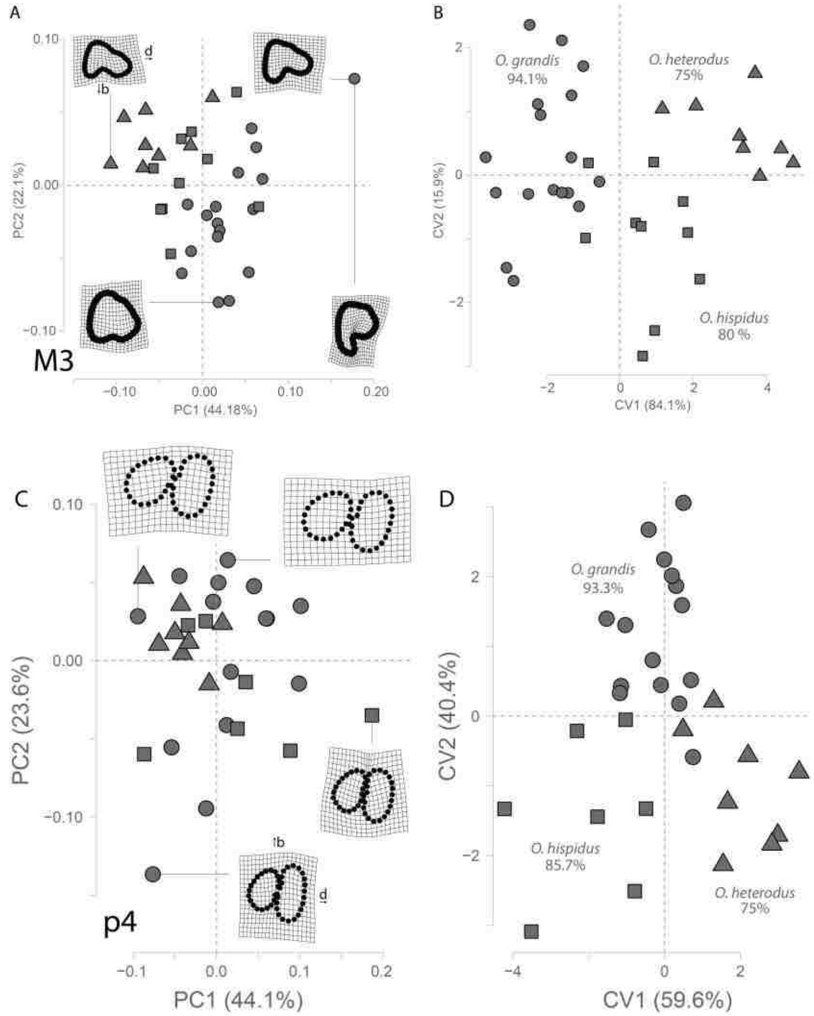

Figure 3.7. Geometric morphometric analysis within *Orthogeomys*. A) First two axes of the PCA of M3 shape and deformation grids along these axes. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. B) Plot of the CVA of M3 shape with percentages of specimens accurately classified below each species' name. C) First two axes of the PCA of p4 shape and deformation grids along these axes. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. D) Plot of the CVA of p4 shape with percentages of specimens accurately classified below each species' name.

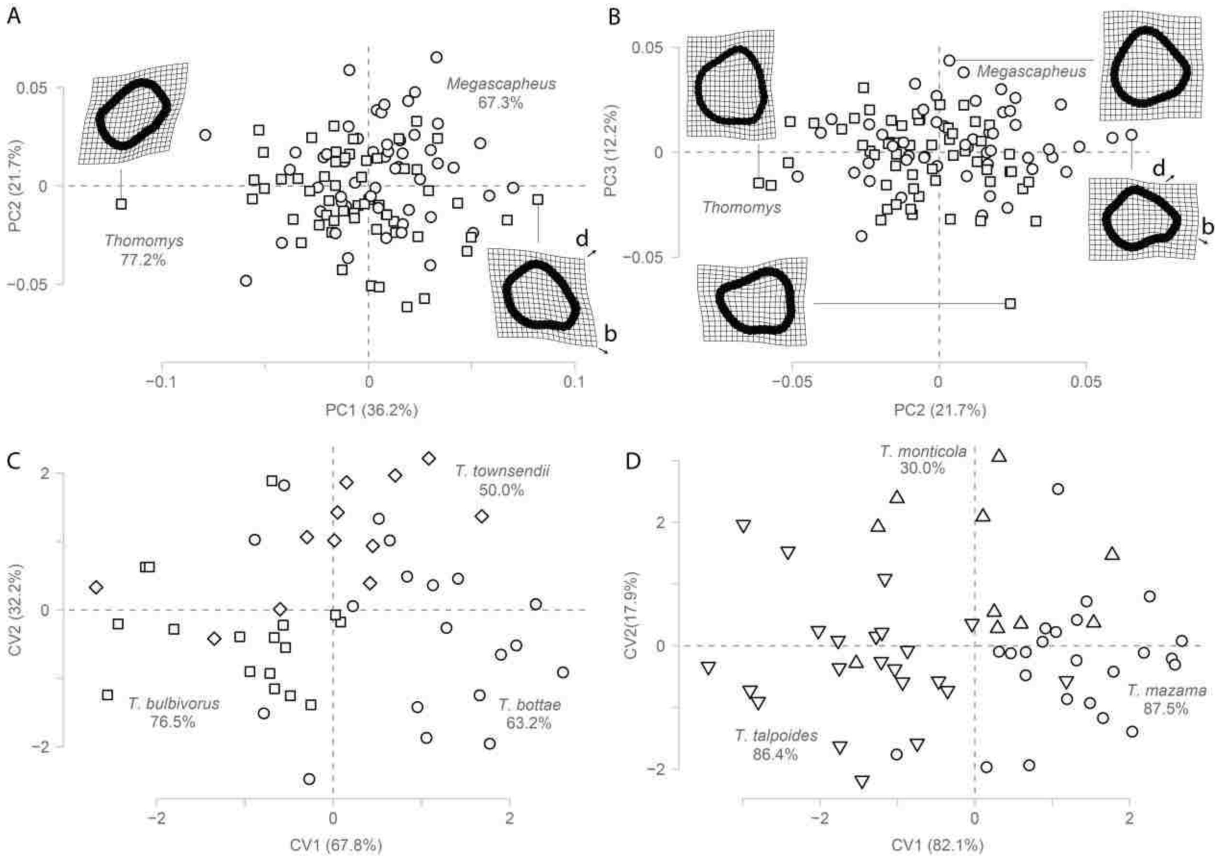

Figure 3.8. Geometric morphometric analysis of M3 shape within the genus *Thomomys*. A) First and second axes of the PCA and deformation grid for PC1. The percentage of specimens accurately classified is indicated under each subgenus' name. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. B) Second and third axes of the PCA and associated deformation grids. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. C) Plot of the CVA within the subgenus *Megascapheus*. The percentage of specimens accurately classified is indicated below each taxon's name. D) Plot of the CVA within the subgenus *Thomomys*. The percentage of specimens accurately classified is indicated below each taxon's name.

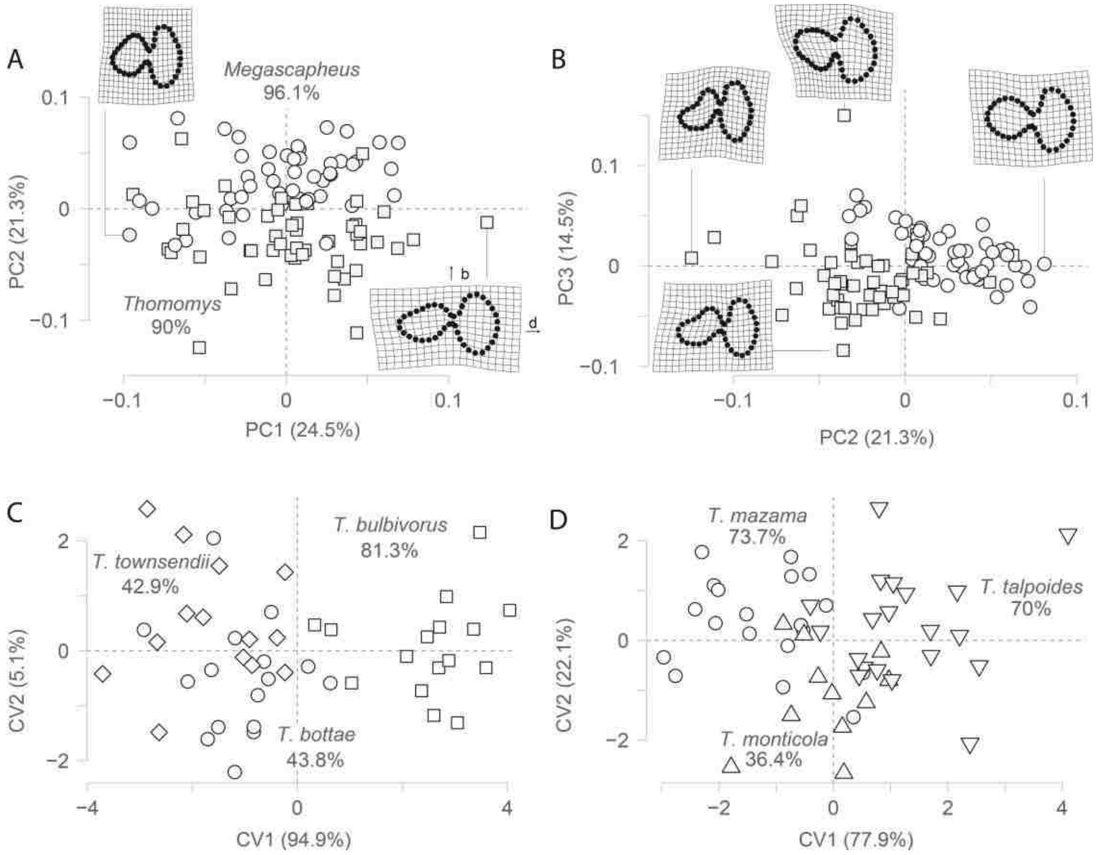

Figure 3.9. Geometric morphometric analysis of p4 shape within the genus *Thomomys*. A) First and second axes of the PCA and deformation grid for PC1. The percentage of specimens accurately classified is indicated under each subgenus' name. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. B) Second and third axes of the PCA and associated deformation grids. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. C) Plot of the CVA within the subgenus *Megascapheus*. The percentage of specimens accurately classified is indicated below each taxon's name. D) Plot of the CVA within the subgenus *Thomomys*. The percentage of specimens accurately classified is indicated below each taxon's name.

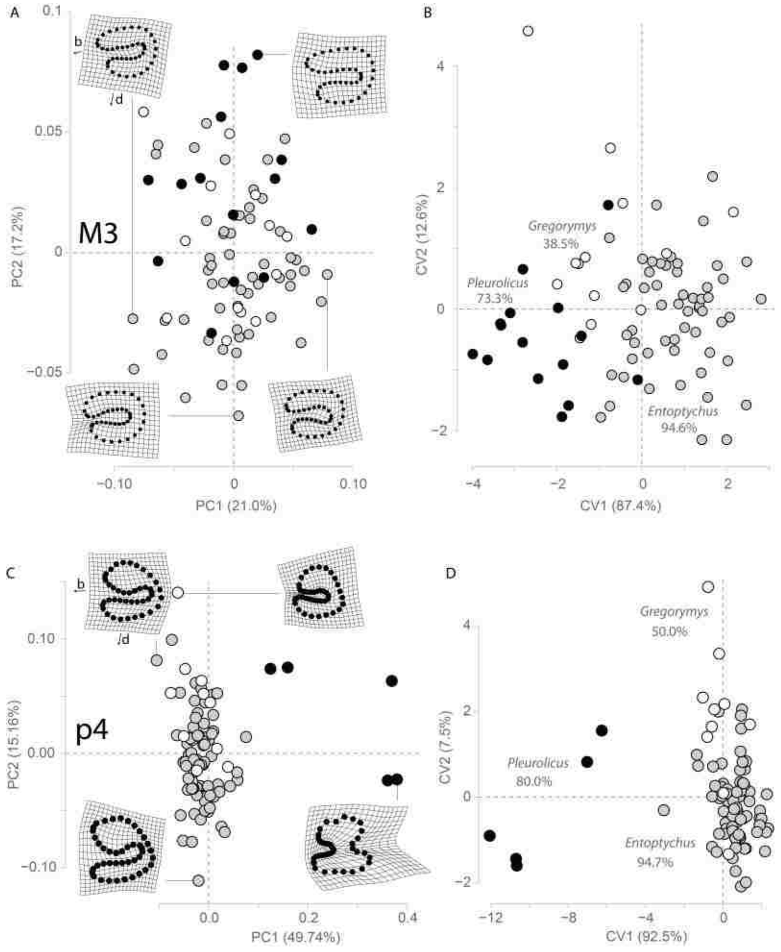

Figure 3.10. Geometric morphometric analysis of entoptychine gophers. A) Analysis of M3: first two axes of the PCA and associated deformation grids. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. B) Analysis of M3: plot of the CVA. The percentage of specimens accurately classified by the analysis is indicated below each taxon name. C) Analysis of p4: first two axes of the PCA and associated deformation grids. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. D) Analysis of p4: plot of the CVA. The percentage of specimens accurately classified by the analysis is indicated below each taxon name.

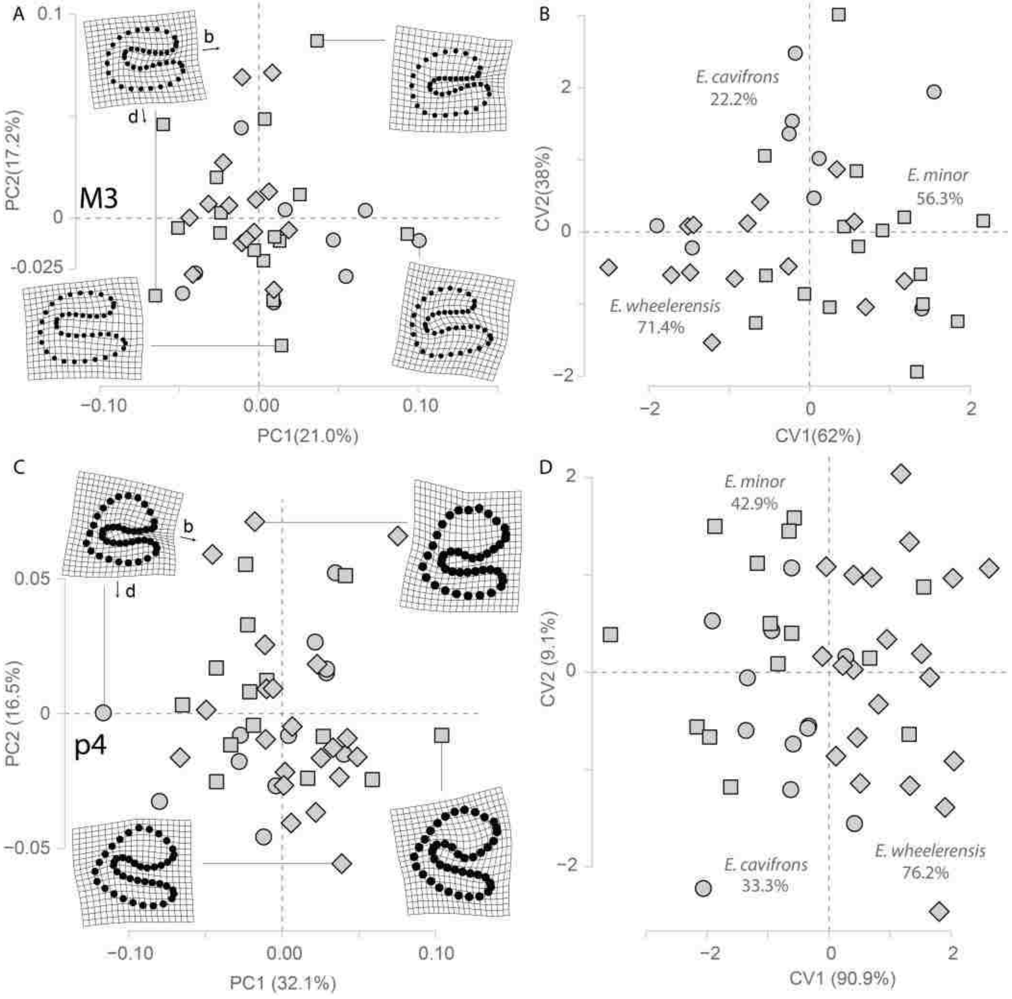

Figure 3.11. Geometric morphometric analysis within *Entoptychus*. A) Analysis of M3: first two axes of the PCA and associated deformation grids. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. B) Analysis of M3: plot of the CVA. The percentage of specimens accurately classified by the analysis is indicated below each taxon name. C) Analysis of p4: first two axes of the PCA and associated deformation grids. The deformation grids show morphologies along the axes. The arrows indicate the buccal (b) and distal (d) directions. D) Analysis of p4: plot of the CVA. The percentage of specimens accurately classified by the analysis is indicated below each taxon name.

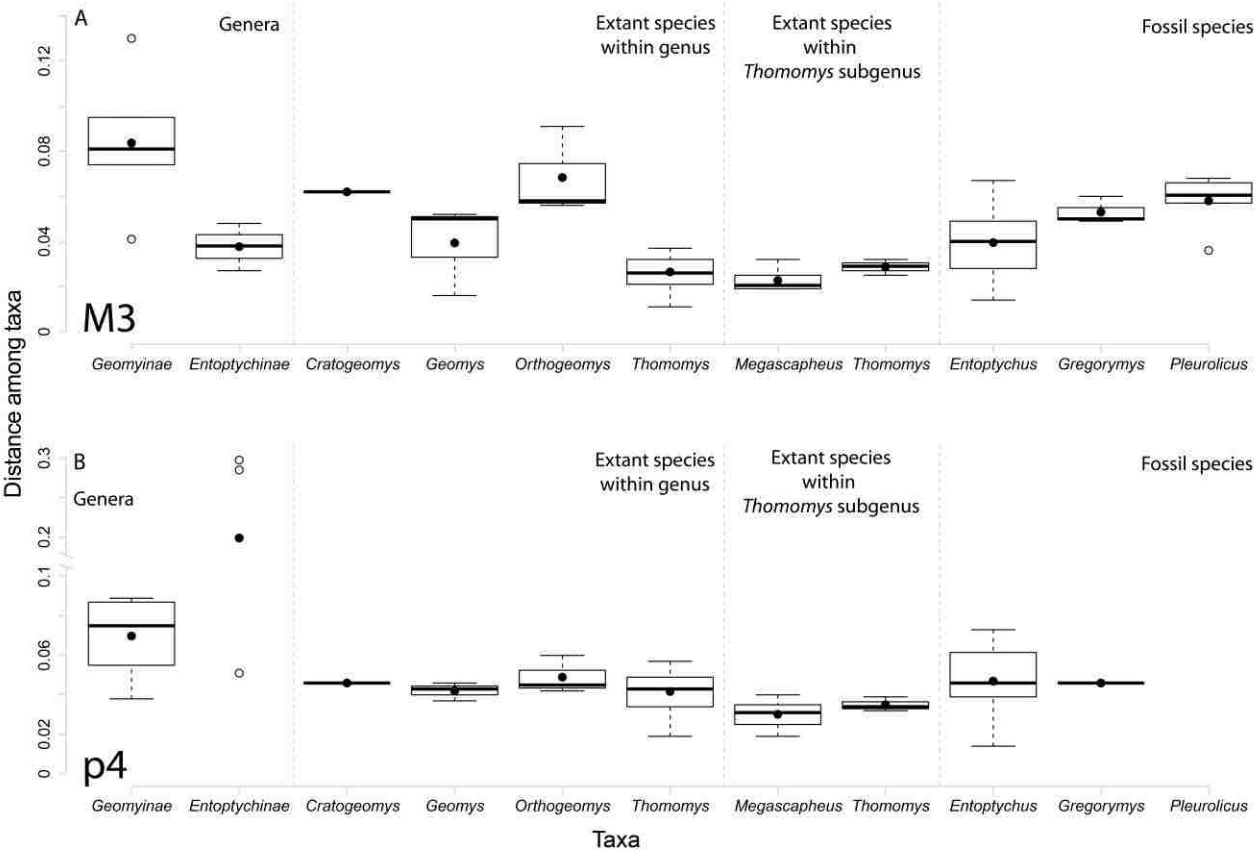

Figure 3.12. Boxplot of variation within taxa. The y axis is the distance among genera or species within the subfamilies and genera studied respectively. The box shows the median and quartiles. The white circles show select values (outliers or unique values in the case of the p4 of Entoptychinae). The black points show the means for each taxon. A) Distances in M3 morphospace. B) Distances in p4 morphospace, note the broken y axis.

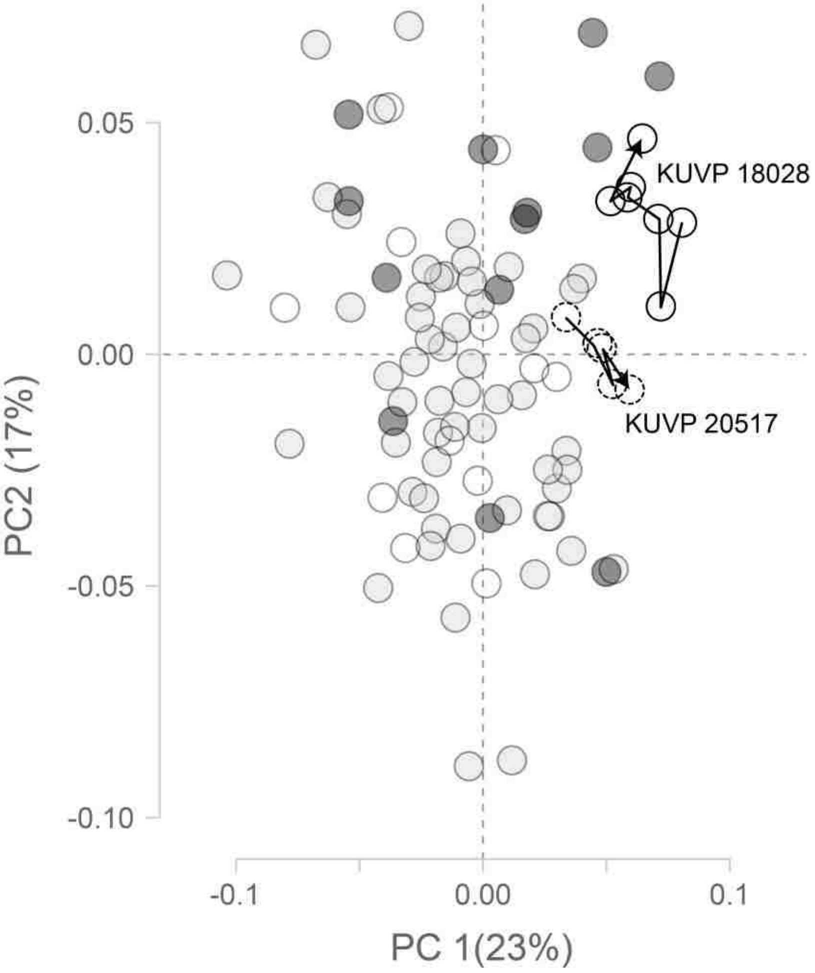

Figure 3.13. Geometric morphometric analysis of the shape of M3 of entoptychine gophers including multiple surfaces from two individuals. The arrows indicate the path in morphospace of the specimen with wear from least to most worn. The transparent points represent other fossil specimens.

TABLES

Table 3.1. Extant gopher (Geomyinae) sampling.

Genus	Subgenus/Group	Species	UM3	Lp4
Cratogeomys	--	*castanops*	6	4
Cratogeomys	--	*merriami*	9	10
Geomys	*bursarius* group	*arenarius*	20	17
Geomys	*bursarius* group	*bursarius*	17	19
Geomys	*pinetis* group	*pinetis*	18	15
Orthogeomys	*Orthogeomys*	*grandis*	17	15
Orthogeomys	*Heterogeomys*	*hispidus*	10	7
Orthogeomys	*Macrogeomys*	*heterodus*	8	8
Thomomys	*Megascapheus*	*bottae*	19	16
Thomomys	*Megascapheus*	*bulbivorus*	17	16
Thomomys	*Megascapheus*	*townsendii*	12	14
Thomomys	*Megascapheus*	*umbrinus*	4	5
Thomomys	*Thomomys*	*idahoensis*	1	0
Thomomys	*Thomomys*	*mazama*	24	19
Thomomys	*Thomomys*	*monticola*	10	11
Thomomys	*Thomomys*	*talpoides*	22	20
	TOTAL		214	196

Table 3.2. Fossil gopher (Entoptychinae) sampling.

Genus	Species	UM3	Lp4
Entoptychus	*basilaris*	4	3
Entoptychus	*cavifrons*	9	12
Entoptychus	*grandiplanus*	3	6
Entoptychus	*individens*	2	5
Entoptychus	*minor*	16	14
Entoptychus	*minor or cavifrons*	6	1
Entoptychus	*planifrons*	2	0
Entoptychus	*productidens*	0	5
Entoptychus	*transitorius*	0	8
Entoptychus	*wheelerensis*	14	21
Gregorymys	sp.	2	2
Gregorymys	*curtus*	1	0
Gregorymys	*douglassi*	2	2
Gregorymys	*formosus*	3	1
Gregorymys	*'tavenneri'*	5	5
Pleurolicus	*dakotensis*	1	0
Pleurolicus	*'gwinni'*	3	0
Pleurolicus	*leptophrys*	0	1
Pleurolicus	*'nelsoni'*	2	0
Pleurolicus	*'rensbergeri'*	2	1
Pleurolicus	*sulcifrons*	7	2
Pleurolicus	sp.	0	1
TOTAL		84	90

Table 3.3. Description of the landmarks used.

Taxon	Tooth	Landmark	Description
Geomyine	M3	1	mesial contact with M2
Entoptychine	M3	1	Labial edge of the metaloph
		2	Lingual end of transverse sulcus
		3	Labial edge of the protoloph
Geomyine	p4	1	labial edge of lingual reentrant
		2	lingual edge of labial reentrant
Entoptychine	p4	1	Labial edge of the hypolophid
		2	Lingual end of transverse sulcus
		3	Labial edge of the metalophid

Table 3.4. Summary of the results of the jackknifed canonical variate analyses. Abbreviation: S, significant axes.

			M3			p4	
Analysis	Taxon	S	Expected %	% correct	S	Expected %	% correct
Extant genera	*Cratogeomys*	7	7.0	66.7	10	7.1	92.9
	Geomys		25.7	96.4		26.0	98.0
	Orthogeomys		16.4	82.9		15.0	86.7
	Thomomys		50.9	98.2		51.5	100
Cratogeomys species	*C. castanops*	4	40.0	83.3	3	28.6	50
	C. merriami		60.0	77.8		71.4	100
Geomys groups	*bursarius* group	6	67.3	91.9	8	70.6	91.7
	pinetis group		32.7	72.2		29.4	86.7
Geomys species	*G. arenarius*		36.4	35.3		33.3	76.5
	G. bursarius		30.9	55		37.3	78.9
	G. pinetis		32.7	77.8		29.4	93.3
Orthogeomys species	*O. grandis*	5	48.6	94.1	5	50.	93.3
	O. heterodus		22.9	75		26.7	75
	O. hispidus		28.6	80		23.3	85.7
Thomomys subgenera	*Thomomys*	9	52.3	77.2	10	49.5	90
	Megascapheus		47.7	67.3		50.5	96.1
T. Megascapheus species	*T. bottae*	7	39.6	63.2	7	34.8	43.8
	T. bulbivorus		35.42	76.5		34.8	81.3
	T. townsendii		25	50.0		30.4	42.9
T. Thomomys species	*T. mazama*	8	42.9	87.5	8	38.0	73.7
	T. monticola		17.9	30.0		22.0	36.4
	T. talpoides		39.3	86.4		40.0	70
Fossil genera	*Entoptychus*	10	66.7	94.6	10	83.3	94.7
	Gregorymys		15.5	38.5		11.1	50.0
	Pleurolicus		17.9	73.3		5.6	80.0
Entoptychus species	*E. cavifrons*	7	23.1	22.2	9	25.5	33.3
	E. minor		41	56.3		29.8	42.9
	E. wheelerensis		35.9	71.4		44.7	76.2

Table 3.5. Divergences of extant and fossil gopher genera.

Taxon1	Taxon2	UM3	Lp4
Cratogeomys	*Geomys*	0.041	0.055
Cratogeomys	*Orthogeomys*	0.074	0.065
Cratogeomys	*Thomomys*	0.095	0.089
Geomys	*Orthogeomys*	0.088	0.038
Geomys	*Thomomys*	0.074	0.087
Orthogeomys	*Thomomys*	0.130	0.086
Entoptychus	*Gregorymys*	0.027	0.051
Entoptychus	*Pleurolicus*	0.048	0.264
Gregorymys	*Pleurolicus*	0.038	0.269

Table 3.6. Intrageneric divergences of extant gopher species. Abbreviations: C, *Cratogeomys*; G, *Geomys*; O, *Orthogeomys*; T, *Thomomys.*

Taxon1	Taxon2	UM3	Lp4
C. castanops	*C. merriami*	0.062	0.046
G. arenarius	*G. bursarius*	0.016	0.043
G. arenarius	*G. pinetis*	0.050	0.046
G. bursarius	*G. pinetis*	0.052	0.037
O. grandis	*O. hispidus*	0.056	0.042
O. grandis	*O. heterodus*	0.091	0.045
O. hispidus	*O. heterodus*	0.058	0.060
T. bottae	*T. bulbivorus*	0.021	0.032
T. bottae	*T. mazama*	0.029	0.052
T. bottae	*T. monticola*	0.026	0.047
T. bottae	*T. talpoides*	0.011	0.042
T. bottae	*T. townsendii*	0.019	0.025
T. bottae	*T. umbrinus*	0.025	0.019
T. bulbivorus	*T. mazama*	0.037	0.046
T. bulbivorus	*T. monticola*	0.036	0.052
T. bulbivorus	*T. talpoides*	0.026	0.056
T. bulbivorus	*T. townsendii*	0.019	0.040
T. bulbivorus	*T. umbrinus*	0.032	0.035
T. mazama	*T. monticola*	0.025	0.032
T. mazama	*T. talpoides*	0.032	0.039
T. mazama	*T. townsendii*	0.029	0.057
T. mazama	*T. umbrinus*	0.024	0.049
T. monticola	*T. talpoides*	0.029	0.034
T. monticola	*T. townsendii*	0.036	0.047
T. monticola	*T. umbrinus*	0.032	0.049
T. talpoides	*T. townsendii*	0.021	0.050
T. talpoides	*T. umbrinus*	0.027	0.043
T. townsendii	*T. umbrinus*	0.020	0.030

Table 3.7. Intrageneric divergences of fossil gopher species. Abbreviations: E, *Entoptychus*; G, *Gregorymys*; P, *Pleurolicus*.

Taxon1	Taxon2	UM3	Lp4
E. basilaris	*E. cavifrons*	0.019	0.048
E. basilaris	*E. grandiplanus*	0.042	0.054
E. basilaris	*E. individens*	0.057	0.070
E. basilaris	*E. minor*	0.028	0.047
E. basilaris	*E. planifrons*	0.056	--
E. basilaris	*E. productidens*	--	0.073
E. basilaris	*E. transitorius*	--	0.068
E. basilaris	*E. wheelerensis*	0.034	0.044
E. cavifrons	*E. grandiplanus*	0.045	0.063
E. cavifrons	*E. individens*	0.052	0.046
E. cavifrons	*E. minor*	0.022	0.014
E. cavifrons	*E. planifrons*	0.049	--
E. cavifrons	*E. productidens*	--	0.039
E. cavifrons	*E. transitorius*	--	0.037
E. cavifrons	*E. wheelerensis*	0.028	0.026
E. grandiplanus	*E. individens*	0.064	0.069
E. grandiplanus	*E. minor*	0.035	0.062
E. grandiplanus	*E. planifrons*	0.067	--
E. grandiplanus	*E. productidens*	--	0.062
E. grandiplanus	*E. transitorius*	--	0.061
E. grandiplanus	*E. wheelerensis*	0.037	0.045
E. individens	*E. minor*	0.040	0.053
E. individens	*E. planifrons*	0.018	--
E. individens	*E. productidens*	--	0.039
E. individens	*E. transitorius*	--	0.046
E. individens	*E. wheelerensis*	0.041	0.047

E. minor	*E. planifrons*	0.040	--
E. minor	*E. productidens*	--	0.043
E. minor	*E. transitorius*	--	0.039
E. minor	*E. wheelerensis*	0.014	0.023
E. planifrons	*E. wheelerensis*	0.041	--
E. productidens	*E. transitorius*	--	0.025
E. productidens	*E. wheelerensis*	--	0.040
E. transitorius	*E. wheelerensis*	--	0.033
G. douglassi	*G. formosus*	0.049	--
G. douglassi	*‘G. tavenneri’*	0.060	0.046
G. formosus	*‘G. tavenneri’*	0.050	--
‘P. gwinni’	*‘P. nelsoni’*	0.057	--
‘P. gwinni’	*‘P. rensbergeri’*	0.066	--
‘P. gwinni’	*P. sulcifrons*	0.058	--
‘P. nelsoni’	*‘P. rensbergeri’*	0.068	--
‘P. nelsoni’	*P. sulcifrons*	0.063	--
‘P. rensbergeri’	*P. sulcifrons*	0.036	--

APPENDIX

A3.1. List of extant specimens included in the analyses. The first dataset includes the specimens included in the analysis of M3. The second includes the specimens included in the analysis of p4. Abbreviations: Spec., specimens; Sub., subgenus or group; Sp., species.

Museum	Spec.	Genus	Sub.	Sp.	Country	State	Sex
WSUCVM	003-3780	*Cratogeomys*		*castanops*	United States	Texas	female
UWBM	33146	*Cratogeomys*		*castanops*	United States	Colorado	male
UWBM	52148	*Cratogeomys*		*castanops*	United States	New Mexico	female
UWBM	33147	*Cratogeomys*		*castanops*	United States	Colorado	female
MVZ	128308	*Cratogeomys*		*castanops*	Mexico	Chihuahua	Female
UWBM	44823	*Cratogeomys*		*castanops*	United States	Texas	female
UWBM	44817	*Cratogeomys*		*merriami*	Mexico	Veracruz	female
UWBM	44812	*Cratogeomys*		*merriami*	Mexico	Veracruz	male
UWBM	44813	*Cratogeomys*		*merriami*	Mexico	Veracruz	male
UWBM	44814	*Cratogeomys*		*merriami*	Mexico	Veracruz	male
UWBM	44815	*Cratogeomys*		*merriami*	Mexico	Veracruz	female
UWBM	44818	*Cratogeomys*		*merriami*	Mexico	Veracruz	male
UWBM	44810	*Cratogeomys*		*merriami*	Mexico	Veracruz	female
UWBM	50728	*Cratogeomys*		*merriami*	Mexico	Puebla	female
UWBM	44809	*Cratogeomys*		*merriami*	Mexico	Veracruz	female
UWBM	44899	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
UWBM	50560	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	male
UWBM	44897	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
UWBM	44898	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	50447	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	50450	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	male
MVZ	50461	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	50463	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	male
MVZ	50465	*Geomys*	*bursarius*	*arenarius*	United States	Texas	female
MVZ	50467	*Geomys*	*bursarius*	*arenarius*	United States	Texas	female
MVZ	50470	*Geomys*	*bursarius*	*arenarius*	United States	Texas	male
MVZ	50473	*Geomys*	*bursarius*	*arenarius*	United States	Texas	male
MVZ	50475	*Geomys*	*bursarius*	*arenarius*	United States	Texas	female

MVZ	50477	*Geomys*	*bursarius*	*arenarius*	United States	Texas	male
MVZ	50949	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	male
MVZ	84228	*Geomys*	*bursarius*	*arenarius*	United States	Texas	male
MVZ	84229	*Geomys*	*bursarius*	*arenarius*	United States	Texas	female
MVZ	90951	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	91278	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	91279	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	male
UWBM	44933	*Geomys*	*bursarius*	*bursarius*	United States	Indiana	female
MVZ	84175	*Geomys*	*bursarius*	*bursarius*	United States	Texas	female
MVZ	97095	*Geomys*	*bursarius*	*bursarius*	United States	Kansas	female
MVZ	31862	*Geomys*	*bursarius*	*bursarius*	United States	Nebraska	female
UWBM	44888	*Geomys*	*bursarius*	*bursarius*	United States	Texas	male
UWBM	44894	*Geomys*	*bursarius*	*bursarius*	United States	Texas	female
UWBM	44895	*Geomys*	*bursarius*	*bursarius*	United States	Texas	female
UWBM	44896	*Geomys*	*bursarius*	*bursarius*	United States	Texas	male
UWBM	44900	*Geomys*	*bursarius*	*bursarius*	United States	Oklahoma	female
UWBM	44901	*Geomys*	*bursarius*	*bursarius*	United States	Texas	female
UWBM	44922	*Geomys*	*bursarius*	*bursarius*	United States	Texas	male
UWBM	44925	*Geomys*	*bursarius*	*bursarius*	United States	Nebraska	male
UWBM	44928	*Geomys*	*bursarius*	*bursarius*	United States	Nebraska	male
UWBM	44931	*Geomys*	*bursarius*	*bursarius*	United States	Kansas	male
MVZ	81061	*Geomys*	*bursarius*	*bursarius*	United States	Texas	male
MVZ	136805	*Geomys*	*bursarius*	*bursarius*	United States	Indiana	female
MVZ	181275	*Geomys*	*bursarius*	*bursarius*	United States	Nebraska	male
UWBM	41609	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41611	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
MVZ	4522	*Geomys*	*pinetis*	*pinetis*	United States	Georgia	male
MVZ	4524	*Geomys*	*pinetis*	*pinetis*	United States	Georgia	male
UWBM	41606	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41607	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41608	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41610	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41612	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41613	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41614	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	44418	*Geomys*	*pinetis*	*pinetis*	United States	Florida	male
MVZ	74432	*Geomys*	*pinetis*	*pinetis*	United States	Georgia	female
MVZ	74544	*Geomys*	*pinetis*	*pinetis*	United States	Florida	male
MVZ	84225	*Geomys*	*pinetis*	*pinetis*	United States	Florida	male
MVZ	84226	*Geomys*	*pinetis*	*pinetis*	United States	Florida	female

MVZ	84227	*Geomys*	*pinetis*	*pinetis*	United States	Florida	male
MVZ	96866	*Geomys*	*pinetis*	*pinetis*	United States	Florida	female
MVZ	131105	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	male
MVZ	98353	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Morazan	female
MVZ	98354	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Morazan	female
MVZ	98357	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	female
MVZ	98359	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	male
MVZ	98361	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Santa Ana	male
MVZ	98362	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Santa Ana	female
MVZ	98363	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Sonsonate	male
MVZ	98364	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Sonsonate	female
MVZ	98366	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Sonsonate	male
MVZ	131106	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	female
MVZ	131107	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	unknown
MVZ	131108	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	female
MVZ	131111	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	female
MVZ	131112	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Sonsonate	female
MVZ	154078	*Orthogeomys*	*Orthogeomys*	*grandis*	Mexico	Michoacan	female
MVZ	154079	*Orthogeomys*	*Orthogeomys*	*grandis*	Mexico	Michoacan	male
MVZ	96842	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	San Luis Potosi	female
UWBM	49934	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	San Luis Potosí	unknown
MVZ	104239	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	San Luis Potosi	female
MVZ	121192	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Veracruz	female
MVZ	141219	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Chiapas	unknown
MVZ	141708	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Chiapas	unknown
MVZ	141709	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Chiapas	unknown
MVZ	153888	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Tamaulipas	female
WSUCVM	60-345	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Chiapas	female
WSUCVM	65-107	*Orthogeomys*	*Heterogeomys*	*hispidus*	Honduras	Atlantida	female
MVZ	167367	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	female
MVZ	155310	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Cartago	male
MVZ	155311	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Cartago	female
MVZ	155312	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Cartago	male
MVZ	167363	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	male
MVZ	167364	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	female
MVZ	167365	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	female
MVZ	167366	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	female
UWBM	44874	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	female
UWBM	44875	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	male
UWBM	44630	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female

UWBM	44659	*Thomomys*	*Megascapheus*	*bottae*	United States	California	male
UWBM	44670	*Thomomys*	*Megascapheus*	*bottae*	United States	California	male
UWBM	44645	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
UWBM	44858	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
UWBM	44883	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
UWBM	44885	*Thomomys*	*Megascapheus*	*bottae*	United States	California	male
WSUCVM	57-185	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	female
WSUCVM	59-388	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
UWBM	44873	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	female
UWBM	44868	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	male
UWBM	44649	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
UWBM	44663	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
WSUCVM	78-239	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
WSUCVM	81-134	*Thomomys*	*Megascapheus*	*bottae*	United States	California	male
WSUCVM	82-237	*Thomomys*	*Megascapheus*	*bottae*	United States	Oregon	female
UWBM	44671	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
WSUCVM	1009	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	unknown
UWBM	32826	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
UWBM	44824	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44829	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44830	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44831	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44834	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44835	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
UWBM	44836	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44838	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44839	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44842	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44843	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
UWBM	44844	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
UWBM	44845	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
UWBM	44847	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
WSUCVM	53-8	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	unknown
WSUCVM	003-3747	*Thomomys*	*Thomomys*	*idahoensis*	United States	Idaho	female
UWBM	77825	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	38567	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	38472	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	38566	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	38569	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	38916	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female

UWBM	77772	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77774	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77779	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77821	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77823	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77824	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77826	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	77827	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	77829	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	77830	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77831	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77833	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	77835	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77837	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
WSUCVM	08-100	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
WSUCVM	62-58	*Thomomys*	*Thomomys*	*mazama*	United States	Oregon	male
WSUCVM	80-730	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
WSUCVM	81-378	*Thomomys*	*Thomomys*	*mazama*	United States	California	female
WSUCVM	59-390	*Thomomys*	*Thomomys*	*monticola*	United States	Oregon	female
UWBM	44607	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
UWBM	44608	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
UWBM	44609	*Thomomys*	*Thomomys*	*monticola*	United States	California	female
UWBM	44610	*Thomomys*	*Thomomys*	*monticola*	United States	California	female
UWBM	44611	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
UWBM	44612	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
UWBM	44613	*Thomomys*	*Thomomys*	*monticola*	United States	California	female
UWBM	44614	*Thomomys*	*Thomomys*	*monticola*	United States	California	female
UWBM	44615	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
WSUCVM	003-3623	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	unknown
WSUCVM	003-3646	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	male
UWBM	45119	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	male
UWBM	45232	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	female
UWBM	45233	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	female
UWBM	45242	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	female
UWBM	45283	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	female
UWBM	45352	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	female
UWBM	45405	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	female
UWBM	45406	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	female
UWBM	45416	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	male
WSUCVM	57-238	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	female

UWBM	8105	*Thomomys*	*Thomomys*	*talpoides*	--	--	male
UWBM	52514	*Thomomys*	*Thomomys*	*talpoides*	United States	Montana	male
UWBM	52512	*Thomomys*	*Thomomys*	*talpoides*	United States	Montana	female
UWBM	45048	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	female
UWBM	58264	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	male
UWBM	45227	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	male
UWBM	45226	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	male
UWBM	45046	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	female
WSUCVM	98-4438	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	unknown
WSUCVM	45438	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	male
WSUCVM	003-3806	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	003-3810	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	003-3811	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	003-3816	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	female
UWBM	41021	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	unknown
UWBM	78696	*Thomomys*	*Megascapheus*	*townsendii*	United States	Oregon	unknown
WSUCVM	53-332	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	53-333	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	54-102	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	female
WSUCVM	93-87	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	unknown
WSUCVM	93-88	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	unknown
WSUCVM	96-90	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	unknown
UWBM	51848	*Thomomys*	*Megascapheus*	*umbrinus*	Mexico	Chihuahua	unknown
UWBM	50738	*Thomomys*	*Megascapheus*	*umbrinus*	Mexico	Durango	unknown
UWBM	50740	*Thomomys*	*Megascapheus*	*umbrinus*	Mexico	Durango	unknown
UWBM	50741	*Thomomys*	*Megascapheus*	*umbrinus*	Mexico	Durango	unknown

Museum	Spec.	Genus	Sub.	Sp.	Country	State	Sex
WSUCVM	03-3780	*Cratogeomys*		*castanops*	United States	Texas	female
UWBM	33146	*Cratogeomys*		*castanops*	United States	Colorado	male
UWBM	33147	*Cratogeomys*		*castanops*	United States	Colorado	female
UWBM	44823	*Cratogeomys*		*castanops*	United States	Texas	female
UWBM	44809	*Cratogeomys*		*merriami*	Mexico	Veracruz	female
UWBM	44810	*Cratogeomys*		*merriami*	Mexico	Veracruz	female
UWBM	44811	*Cratogeomys*		*merriami*	Mexico	Veracruz	female
UWBM	44812	*Cratogeomys*		*merriami*	Mexico	Veracruz	male
UWBM	44813	*Cratogeomys*		*merriami*	Mexico	Veracruz	male
UWBM	44814	*Cratogeomys*		*merriami*	Mexico	Veracruz	male
UWBM	44815	*Cratogeomys*		*merriami*	Mexico	Veracruz	female
UWBM	44818	*Cratogeomys*		*merriami*	Mexico	Veracruz	male
UWBM	44821	*Cratogeomys*		*merriami*	Mexico	Veracruz	male
UWBM	50727	*Cratogeomys*		*merriami*	Mexico	Puebla	female
UWBM	44897	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
UWBM	44898	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
UWBM	44899	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	50447	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	50450	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	male
MVZ	50461	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	50463	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	male
MVZ	50467	*Geomys*	*bursarius*	*arenarius*	United States	Texas	female
MVZ	50470	*Geomys*	*bursarius*	*arenarius*	United States	Texas	male
MVZ	50475	*Geomys*	*bursarius*	*arenarius*	United States	Texas	female
MVZ	50477	*Geomys*	*bursarius*	*arenarius*	United States	Texas	male
MVZ	50949	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	male
MVZ	50951	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	84228	*Geomys*	*bursarius*	*arenarius*	United States	Texas	male
MVZ	84229	*Geomys*	*bursarius*	*arenarius*	United States	Texas	female
MVZ	91278	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	female
MVZ	91279	*Geomys*	*bursarius*	*arenarius*	United States	New Mexico	male
MVZ	181275	*Geomys*	*bursarius*	*bursarius*	United States	Nebraska	male
MVZ	31862	*Geomys*	*bursarius*	*bursarius*	United States	Nebraska	female
UWBM	33145	*Geomys*	*bursarius*	*bursarius*	United States	Colorado	male
UWBM	44893	*Geomys*	*bursarius*	*bursarius*	United States	Texas	male
UWBM	44894	*Geomys*	*bursarius*	*bursarius*	United States	Texas	female
UWBM	44895	*Geomys*	*bursarius*	*bursarius*	United States	Texas	female
UWBM	44896	*Geomys*	*bursarius*	*bursarius*	United States	Texas	male
UWBM	44900	*Geomys*	*bursarius*	*bursarius*	United States	Oklahoma	female

UWBM	44901	*Geomys*	*bursarius*	*bursarius*	United States	Texas	female
UWBM	44908	*Geomys*	*bursarius*	*bursarius*	United States	Indiana	male
UWBM	44910	*Geomys*	*bursarius*	*bursarius*	United States	Indiana	unknown
UWBM	44911	*Geomys*	*bursarius*	*bursarius*	United States	Indiana	unknown
UWBM	44912	*Geomys*	*bursarius*	*bursarius*	United States	Indiana	unknown
UWBM	44922	*Geomys*	*bursarius*	*bursarius*	United States	Texas	male
UWBM	44923	*Geomys*	*bursarius*	*bursarius*	United States	Idaho	female
UWBM	44925	*Geomys*	*bursarius*	*bursarius*	United States	Nebraska	male
MVZ	81601	*Geomys*	*bursarius*	*bursarius*	United States	Texas	male
MVZ	84175	*Geomys*	*bursarius*	*bursarius*	United States	Texas	female
MVZ	97095	*Geomys*	*bursarius*	*bursarius*	United States	Kansas	female
UWBM	41601	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41604	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41606	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41609	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	41612	*Geomys*	*pinetis*	*pinetis*	United States	Florida	unknown
UWBM	44417	*Geomys*	*pinetis*	*pinetis*	United States	Florida	female
UWBM	44418	*Geomys*	*pinetis*	*pinetis*	United States	Florida	male
MVZ	4522	*Geomys*	*pinetis*	*pinetis*	United States	Georgia	male
MVZ	4524	*Geomys*	*pinetis*	*pinetis*	United States	Georgia	male
MVZ	74432	*Geomys*	*pinetis*	*pinetis*	United States	Georgia	female
MVZ	74544	*Geomys*	*pinetis*	*pinetis*	United States	Florida	male
MVZ	84225	*Geomys*	*pinetis*	*pinetis*	United States	Florida	male
MVZ	84226	*Geomys*	*pinetis*	*pinetis*	United States	Florida	female
MVZ	84227	*Geomys*	*pinetis*	*pinetis*	United States	Florida	male
MVZ	96866	*Geomys*	*pinetis*	*pinetis*	United States	Florida	female
MVZ	131105	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	male
MVZ	131106	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	female
MVZ	131107	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	unknown
MVZ	131108	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	female
MVZ	131111	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	female
MVZ	131112	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Sonsonate	female
MVZ	154078	*Orthogeomys*	*Orthogeomys*	*grandis*	Mexico	Michoacan	female
MVZ	154079	*Orthogeomys*	*Orthogeomys*	*grandis*	Mexico	Michoacan	male
MVZ	98356	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	male
MVZ	98357	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	female
MVZ	98359	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Chalatenango	male
MVZ	98361	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Santa Ana	male
MVZ	98362	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Santa Ana	female
MVZ	98363	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Sonsonate	male

MVZ	98366	*Orthogeomys*	*Orthogeomys*	*grandis*	El Salvador	Sonsonate	male
MVZ	121192	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Veracruz	female
MVZ	141708	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Chiapas	unknown
MVZ	141709	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Chiapas	unknown
UWBM	44934	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	San Luis Potosi	female
WSUCVM	60-345	*Orthogeomys*	*Heterogeomys*	*hispidus*	Mexico	Chipapas	female
WSUCVM	65-107	*Orthogeomys*	*Heterogeomys*	*hispidus*	Honduras	Atlantida	female
WSUCVM	88-52	*Orthogeomys*	*Heterogeomys*	*hispidus*	Honduras	Atlantida	female
MVZ	155310	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Cartago	male
MVZ	155311	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Cartago	female
MVZ	155312	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Cartago	male
MVZ	167363	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	male
MVZ	167364	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	female
MVZ	167365	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	female
MVZ	167366	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	female
MVZ	167367	*Orthogeomys*	*Macrogeomys*	*heterodus*	Costa Rica	Heredia	female
UWBM	44624	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
UWBM	44629	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	female
UWBM	44630	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
UWBM	44631	*Thomomys*	*Megascapheus*	*bottae*	United States	California	male
UWBM	44649	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
UWBM	44659	*Thomomys*	*Megascapheus*	*bottae*	United States	California	male
UWBM	44663	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
UWBM	44672	*Thomomys*	*Megascapheus*	*bottae*	United States	California	male
UWBM	44804	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	male
UWBM	44868	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	male
UWBM	44873	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	female
UWBM	44874	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	female
WSUCVM	57-185	*Thomomys*	*Megascapheus*	*bottae*	United States	Arizona	female
WSUCVM	78-239	*Thomomys*	*Megascapheus*	*bottae*	United States	California	female
WSUCVM	81-134	*Thomomys*	*Megascapheus*	*bottae*	United States	California	male
WSUCVM	82-237	*Thomomys*	*Megascapheus*	*bottae*	United States	Oregon	female
WSUCVM	1009	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	unknown
WSUCVM	1011	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	unknown
UWBM	32826	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
UWBM	44824	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44829	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44830	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44834	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44839	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female

UWBM	44840	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44842	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
UWBM	44843	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
UWBM	44844	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
UWBM	44845	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
UWBM	44846	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	male
WSUCVM	53-8	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	unknown
WSUCVM	57-175	*Thomomys*	*Megascapheus*	*bulbivorus*	United States	Oregon	female
WSUCVM	08-100	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	38570	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
WSUCVM	62-58	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	76003	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	76004	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	76005	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	77419	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	77423	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77424	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	77425	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77774	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77831	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77832	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77833	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	77834	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
UWBM	77835	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
UWBM	77837	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	female
WSUCVM	80-730	*Thomomys*	*Thomomys*	*mazama*	United States	Washington	male
WSUCVM	81-378	*Thomomys*	*Thomomys*	*mazama*	United States	California	female
UWBM	44606	*Thomomys*	*Thomomys*	*monticola*	United States	Nevada	female
UWBM	44607	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
UWBM	44608	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
UWBM	44609	*Thomomys*	*Thomomys*	*monticola*	United States	California	female
UWBM	44610	*Thomomys*	*Thomomys*	*monticola*	United States	California	female
UWBM	44611	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
UWBM	44612	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
UWBM	44613	*Thomomys*	*Thomomys*	*monticola*	United States	California	female
UWBM	44614	*Thomomys*	*Thomomys*	*monticola*	United States	California	female
UWBM	44615	*Thomomys*	*Thomomys*	*monticola*	United States	California	male
WSUCVM	59-390	*Thomomys*	*Thomomys*	*monticola*	United States	Oregon	female
WSUCVM	03-3623	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	unknown
UWBM	36483	*Thomomys*	*Thomomys*	*talpoides*	Canda	British Columbia	

UWBM	38589	*Thomomys*	*Thomomys*	*talpoides*	United States	Idaho	male
UWBM	38590	*Thomomys*	*Thomomys*	*talpoides*	United States	Idaho	female
UWBM	44956	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	female
UWBM	45047	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	female
UWBM	45048	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	female
UWBM	45076	*Thomomys*	*Thomomys*	*talpoides*	United States	Idaho	male
UWBM	45226	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	male
UWBM	45227	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	male
UWBM	45276	*Thomomys*	*Thomomys*	*talpoides*	United States	Idaho	male
UWBM	45390	*Thomomys*	*Thomomys*	*talpoides*	United States	Idaho	male
UWBM	45419	*Thomomys*	*Thomomys*	*talpoides*	United States	Idaho	female
UWBM	45438	*Thomomys*	*Thomomys*	*talpoides*	United States	Oregon	male
UWBM	52511	*Thomomys*	*Thomomys*	*talpoides*	United States	Montana	male
UWBM	52512	*Thomomys*	*Thomomys*	*talpoides*	United States	Montana	female
UWBM	52513	*Thomomys*	*Thomomys*	*talpoides*	United States	Montana	female
WSUCVM	55-238	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	female
WSUCVM	57-238	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	female
WSUCVM	98-448	*Thomomys*	*Thomomys*	*talpoides*	United States	Washington	female
WSUCVM	03-3803	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	03-3804	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	female
WSUCVM	03-3806	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	03-3810	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	03-3811	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	female
WSUCVM	03-3816	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	female
UWBM	32827	*Thomomys*	*Megascapheus*	*townsendii*	United States	Oregon	male
WSUCVM	53-332	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	53-333	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
WSUCVM	54-102	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	female
UWBM	78696	*Thomomys*	*Megascapheus*	*townsendii*	United States	Oregon	male
WSUCVM	93-87	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	unknown
WSUCVM	93-88	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	unknown
WSUCVM	96-90	*Thomomys*	*Megascapheus*	*townsendii*	United States	Idaho	male
UWBM	50738	*Thomomys*	*Megascapheus*	*umbrinus*	Mexico	Durango	female
UWBM	50739	*Thomomys*	*Megascapheus*	*umbrinus*	Mexico	Durango	male
UWBM	50740	*Thomomys*	*Megascapheus*	*umbrinus*	Mexico	Durango	female
UWBM	50741	*Thomomys*	*Megascapheus*	*umbrinus*	Mexico	Durango	female
UWBM	51848	*Thomomys*	*Megascapheus*	*umbrinus*	Mexico	Chihuahua	male

A3.2. List of fossil specimens included in the analyses. The first dataset includes the specimens included in the analysis of M3. The second includes the specimens included in the analysis of p4. Abbreviations: Spec., specimens; Sp., species.

Museum	Spec.	Genus	Sp.	State	Rock Unit	Comments
UCMP	69404	*Entoptychus*	*basilaris*	Oregon	John Day Formation	
UCMP	69550	*Entoptychus*	*basilaris*	Oregon	John Day Formation	
UCMP	69551	*Entoptychus*	*basilaris*	Oregon	John Day Formation	
UCMP	69553	*Entoptychus*	*basilaris*	Oregon	John Day Formation	Type
UCMP	648	*Entoptychus*	*cavifrons*	Oregon	John Day Formation	
UCMP	1667	*Entoptychus*	*cavifrons*	Oregon	John Day Formation	
UCMP	67898	*Entoptychus*	*cavifrons*	Oregon	John Day Formation	
UCMP	70973	*Entoptychus*	*cavifrons*	Oregon	John Day Formation	
UCMP	72056	*Entoptychus*	*cavifrons*	Oregon	John Day Formation	
UCMP	72060	*Entoptychus*	*cavifrons*	Oregon	John Day Formation	
UCMP	72065	*Entoptychus*	*cavifrons*	Oregon	John Day Formation	
UCMP	72119	*Entoptychus*	*cavifrons*	Oregon	John Day Formation	
UCMP	72796	*Entoptychus*	*cavifrons*	Oregon	John Day Formation	
UNSM	24058	*Entoptychus*	*grandiplanus*	Nebraska	McCann Canyon Local Fauna	
UNSM	24064	*Entoptychus*	*grandiplanus*	Nebraska	McCann Canyon Local Fauna	
UNSM	24071	*Entoptychus*	*grandiplanus*	Nebraska	McCann Canyon Local Fauna	
UCMP	71003	*Entoptychus*	*individens*	Oregon	John Day Formation	Type
UWBM	33511	*Entoptychus*	*individens*	Oregon	John Day	
UCMP	587	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	65163	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	65165	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	67637	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	67692	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	67697	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	67698	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	67702	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	67912	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	72083	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	72112	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	72115	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	72117	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	72587	*Entoptychus*	*minor*	Oregon	John Day Formation	

UCMP	72589	*Entoptychus*	*minor*	Oregon	John Day Formation	
UCMP	73787	*Entoptychus*	*minor*	Oregon	John Day Formation	
UWBM	33231	*Entoptychus*	*minor or cavifrons*	Oregon	John Day	
UWBM	33241	*Entoptychus*	*minor or cavifrons*	Oregon	John Day	
UWBM	33244	*Entoptychus*	*minor or cavifrons*	Oregon	John Day	
UWBM	33250	*Entoptychus*	*minor or cavifrons*	Oregon	John Day	
UWBM	33624	*Entoptychus*	*minor or cavifrons*	Oregon	John Day	
UWBM	33628	*Entoptychus*	*minor or cavifrons*	Oregon	John Day	
UWBM	27242	*Entoptychus*	*planifrons*	Oregon	John Day	
UWBM	28988	*Entoptychus*	*planifrons*	Oregon	John Day	
UCMP	67342	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	67651	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	67685	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	69125	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	71054	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	71071	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	71073	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	71078	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	71079	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	71180	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	71598	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	71640	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UCMP	86264	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation	
UWBM	58700	*Entoptychus*	*wheelerensis*	Oregon	John Day	
UWBM	89005	*Gregorymys*	*curtus*	South Dakota	Harrison or Rosebud Formation	cast of AMNH 12890 (Type)
KUVP	8928	*Gregorymys*	*douglassi*	--	--	
KUVP	18147	*Gregorymys*	*douglassi*	Montana	Cabbage Patch beds	
KUVP	224	*Gregorymys*	*formosus*	--	--	cast of SDSM 64169
UWBM	89035	*Gregorymys*	*formosus*	South Dakota	Harrison Formation	cast of AMNH 12887 (Type)
UWBM	89064	*Gregorymys*	*formosus*	--	--	cast of SDSM 6257
UWBM	52859	*Gregorymys*	sp.	Montana	Fort Logan Formation	
UWBM	53223	*Gregorymys*	sp.	Montana	Fort Logan Formation	
KUVP	18043	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds	
KUVP	18092	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds	
UMPC	1409	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds	
UMPC	13249	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds	
UMPC	2302	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds	
UNSM	No #	*Pleurolicus*	*dakotensis*	--	--	cast of SDSM 54248

KUVP	18028	*Pleurolicus*	*'gwinni'*	Montana	Cabbage Patch beds	
UMPC	2146	*Pleurolicus*	*'gwinni'*	Montana	Cabbage Patch beds	Type
UMPC	2174	*Pleurolicus*	*'gwinni'*	Montana	Cabbage Patch beds	
KUVP	20517	*Pleurolicus*	*'nelsoni'*	Montana	Cabbage Patch beds	
UMPC	1424	*Pleurolicus*	*'nelsoni'*	Montana	Cabbage Patch beds	
UMPC	2046	*Pleurolicus*	*'rensbergeri'*	Montana	Cabbage Patch beds	
UWBM	63273	*Pleurolicus*	*'rensbergeri'*	Montana	Cabbage Patch	Type
UCMP	86186	*Pleurolicus*	*sulcifrons*	Oregon	John Day Formation	
UCMP	86188	*Pleurolicus*	*sulcifrons*	Oregon	John Day Formation	
UCMP	86191	*Pleurolicus*	*sulcifrons*	Oregon	John Day Formation	
UCMP	86192	*Pleurolicus*	*sulcifrons*	Oregon	John Day Formation	
UCMP	86199	*Pleurolicus*	*sulcifrons*	Oregon	John Day Formation	
UWBM	73465	*Pleurolicus*	*sulcifrons*	Oregon	John Day	
UWBM	89030	*Pleurolicus*	*sulcifrons*	Oregon	John Day	cast of AMNH 7185

Museum	Spec.	Genus	Sp.	State	Rock Unit
UCMP	71095	*Entoptychus*	*basilaris*	Oregon	John Day Formation
UCMP	71098	*Entoptychus*	*basilaris*	Oregon	John Day Formation
UCMP	74032	*Entoptychus*	*basilaris*	Oregon	John Day Formation
UCMP	67555	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	67569	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	67570	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	67575	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	67576	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	67581	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	67583	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	72144	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	73767	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	73796	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	74010	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UCMP	74121	*Entoptychus*	*cavifrons*	Oregon	John Day Formation
UNSM	24041	*Entoptychus*	*grandiplanus*	Nebraska	McCann Canyon Local Fauna
UNSM	24047	*Entoptychus*	*grandiplanus*	Nebraska	McCann Canyon Local Fauna
UNSM	24048	*Entoptychus*	*grandiplanus*	Nebraska	McCann Canyon Local Fauna
UNSM	24051	*Entoptychus*	*grandiplanus*	Nebraska	McCann Canyon Local Fauna
UNSM	24079	*Entoptychus*	*grandiplanus*	Nebraska	McCann Canyon Local Fauna
UNSM	24083	*Entoptychus*	*grandiplanus*	Nebraska	McCann Canyon Local Fauna
UCMP	67893	*Entoptychus*	*individens*	Oregon	John Day Formation
UCMP	71030	*Entoptychus*	*individens*	Oregon	John Day Formation
UCMP	71040	*Entoptychus*	*individens*	Oregon	John Day Formation
UNSM	8072-93	*Entoptychus*	*individens*	Oregon	John Day Formation
UNSM	8075-93	*Entoptychus*	*individens*	Oregon	John Day Formation
UCMP	677	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	1099	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	1469	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	67489	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	67547	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	67548	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	67554	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	67646	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	67789	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	72149	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	73765	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	73768	*Entoptychus*	*minor*	Oregon	John Day Formation
UCMP	74008	*Entoptychus*	*minor*	Oregon	John Day Formation

UCMP	74009	*Entoptychus*	*minor*	Oregon	John Day Formation
UWBM	33233	*Entoptychus*	*minor or cavifrons*	Oregon	John Day Formation
UCMP	70897	*Entoptychus*	*productidens*	Oregon	John Day Formation
UCMP	70948	*Entoptychus*	*productidens*	Oregon	John Day Formation
UCMP	70950	*Entoptychus*	*productidens*	Oregon	John Day Formation
UCMP	74116	*Entoptychus*	*productidens*	Oregon	John Day Formation
UCMP	74120	*Entoptychus*	*productidens*	Oregon	John Day Formation
UCMP	67567	*Entoptychus*	*transitorius*	Oregon	John Day Formation
UCMP	67568	*Entoptychus*	*transitorius*	Oregon	John Day Formation
UCMP	67791	*Entoptychus*	*transitorius*	Oregon	John Day Formation
UCMP	70898	*Entoptychus*	*transitorius*	Oregon	John Day Formation
UCMP	70952	*Entoptychus*	*transitorius*	Oregon	John Day Formation
UCMP	70961	*Entoptychus*	*transitorius*	Oregon	John Day Formation
UCMP	74119	*Entoptychus*	*transitorius*	Oregon	John Day Formation
UCMP	75272	*Entoptychus*	*transitorius*	Oregon	John Day Formation
UCMP	66283	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	66295	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	66379	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67315	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67318	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67323	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67324	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67329	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67342	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67363	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67471	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67479	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67480	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	67779	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	69125	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	69395	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	69560	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	71097	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	71099	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	71100	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
UCMP	74266	*Entoptychus*	*wheelerensis*	Oregon	John Day Formation
KUVP	18820	*Gregorymys*	cf. *G. douglassi*	Montana	Cabbage Patch beds
KUVP	18860	*Gregorymys*	*douglassi*	Montana	Cabbage Patch beds
KUVP	C70	*Gregorymys*	*formosus*	--	--
KUVP	18819	*Gregorymys*	sp.	Montana	Cabbage Patch beds

UWBM	52859	*Gregorymys*	sp.	Montana	Fort Logan Formation
UMPC	2106	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds
UMPC	13228	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds
UMPC	13245	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds
UMPC	13973	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds
KUVP	18076	*Gregorymys*	*'tavenneri'*	Montana	Cabbage Patch beds
UCMP	682	*Pleurolicus*	*leptophrys*	Oregon	John Day Formation
UMPC	2046	*Pleurolicus*	*'rensbergeri'*	Montana	Cabbage Patch beds
UWBM	97344	*Pleurolicus*	sp.	Montana	Cabbage Patch beds
UCMP	86171	*Pleurolicus*	*sulcifrons*	Oregon	John Day Formation
UCMP	86248	*Pleurolicus*	*sulcifrons*	Oregon	John Day Formation

A3.3. Results of the post-hoc Nemenyi tests.

M3 - within subfamilies	Cr	En	Ge	Gr	Or	Pl	Th	TM
Entoptychus (En)	0.965	--	--	--	--	--	--	--
Geomys (Ge)	0.968	1.000	--	--	--	--	--	--
Gregorymys (Gr)	1.000	0.943	0.973	--	--	--	--	--
Orthogeomys (Or)	1.000	0.656	0.831	1.000	--	--	--	--
Pleurolicus (Pl)	1.000	0.422	0.800	1.000	1.000	--	--	--
Thomomys (Th)	0.581	0.181	0.975	0.202	0.044	0.003	--	--
T. Megascapheus (TM)	0.405	0.198	0.856	0.121	0.028	0.004	0.996	--
T. Thomomys	0.829	0.987	1.000	0.749	0.448	0.350	1.000	0.996

Chapter 4. PATTERN AND TEMPO OF FAUNAL TURNOVER IN THE ROCKY MOUNTAINS DURING THE ARIKAREEAN: EVIDENCE FROM THE MAMMALIAN FAUNA OF THE CABBAGE PATCH BEDS OF WESTERN MONTANA (RENOVA FORMATION)

ABSTRACT

The later part of the Oligocene starting 30 million years ago was a time of major faunal change for mammals of North America. It is during this time period, called the Arikareean, that archaic mammalian faunas dominated by extinct families started giving way to more modern faunas including families still around today. I here present a quantitative analysis of series of vertebrate microfossil assemblages from the northern Rocky Mountains that spans much of the early Arikareean to study the time transgressive nature of this faunal transition better studied in Oregon and the Great Plains. Almost 1,000 specimens from the Cabbage Patch beds of western Montana distributed over approximately 4.5 million years provide evidence for a major turnover event between the early early Arikareean and the late early Arikareean in the Rocky Mountains. This turnover corresponds to a major loss of taxa from the White River Chronofauna and the rise to dominance of novel mammals. My results support the presence of three distinguishable biostratigraphic units in the Cabbage Patch beds with distinct faunal compositions. Holdovers from archaic mammalian faunas persist into the youngest of these units, ca. 25.6 Ma. The study of additional fossil assemblages from the region will help further our understanding of the understudied mammals of the Rocky Mountains and provide the data needed to future

biogeographic analyses necessary to assess the endemicity and geographic affinities of the rich mammalian faunas of Montana.

1. INTRODUCTION

The rise of modern mammalian communities at the end of the Paleogene and beginning of the Neogene was the product of a major faunal turnover. Indeed, it is during the late Oligocene and the early- to mid-Miocene (ca. 30–16 million years ago [Ma]) that archaic mammalian taxa of the Eocene and early Oligocene were replaced by modern ones characteristic of the late Cenozoic from the Miocene onwards (Woodburne 2004). This faunal turnover is captured in North America by the transition from the archaic White River Chronofauna to the Runningwater Chronofauna. Although the origination and extinction of a number of individual taxa involved in this transition has been studied (Webb and Opdyke 1995, Tedford et al. 2004, Woodburne 2004, Albright et al. 2008), the pattern of faunal change at the scale of whole faunas has been little investigated (Tedford et al. 2004). The rich fossil record of the Arikareean, 30 to 18.8 Ma, offers the opportunity to quantify the spatial and temporal pattern of the initiation of this faunal transition (Tedford et al. 2004).

The Arikareean, lasting 10.2 million years, consists of four subdivisions (Ar1–4; Tedford et al. 2004). It is the longest North American Land Mammal "Age" (NALMA), overlaps the Oligocene-Miocene boundary, and includes tremendous faunal turnover (Alroy 2000, Tedford et al. 2004). The archaic White River Chronofauna typical of the Orellan and Whitneyan NALMAs (33.7 to 30 Ma; Prothero and Emry 2004, Woodburne 2004) was composed of many taxa now extinct (Table 1). The transition to the Runningwater Chronofauna characteristic of the early Miocene (Webb and Opdyke 1995, Tedford et al. 2004, Woodburne 2004, Albright et al. 2008) involved the origination and diversification of many taxa belonging to extant families or even subfamilies (Table 1). The combination of outgoing taxa of the White River Chronofauna and new taxa, products of cladogenesis in North America and immigration from Eurasia, has been suggested to be the source of the high diversity of mammals of the early Arikareean (Webb 1985, Tedford et al. 2004, see also Albright et al. 2008). Such immigration could have been facilitated by the sea level fall of the middle part of the early Arikareean (ca. 28.3 Ma; Woodburne and Swisher 1995, Hunt 2004, Woodburne 2004). The high mammal biodiversity of the Arikareean may also find its source in the high origination rate of mammals at the time (Webb 1995). In the intermontane west of the United States (including the Rocky Mountains [English and Johnston 2004] and the Cascade Range [Kohn and Fremd 2007]), high topographic complexity could have favored the diversification of mammals as it has been suggested at other times during the Cenozoic (see Davis 2005, Kohn and Fremd 2008, Badgley 2010, Finarelli and Badgley 2010, Badgley et al. 2014).

The faunal transition of the Arikareean is recorded in many rock sequences across the continent (Tedford et al. 2004). Two of those, which have rich fossil records and tight geochronological control, have been extensively studied: the Arikaree Group (Gering, Monroe Creek, and Harrison formations) of the Great Plains, and the John Day Formation of central Oregon (MacDonald 1963, 1970, 1972, Korth 1992, MacFadden and Hunt 1998, Bailey 2004, Tedford et al. 2004, Albright et al. 2008, Fremd 2010, Korth and Samuels 2015). In the tectonically passive Great Plains, White River relict taxa survived into the early Arikareean-aged deposits of the Gering Formation (part of the Arikaree Group) ca. 28.26 to 28.11 Ma (Tedford et al. 2004). Many novel taxa (e.g., the Glires *Archaeolagus*, *Allomys*, and *Pleurolicus*; Tedford et al. 2004) appeared after the extinction of these White River taxa (ca. 28.1 Ma). A few relict taxa (including the shrew *Domnina*) persisted into the McCann Canyon Local Fauna of Nebraska, correlative with the fauna from the Monroe Creek Fm. (ca. 26.5 Ma; Korth 1992; MacFadden and Morgan 2003; Tedford et al. 2004). In the more tectonically active John Day Formation, the transition from the White River Chronofauna to the younger, more modern fauna was initiated earlier than in the Great Plains (at the Picture Gorge Ignimbrite, ca. 28.7 Ma) although several White River relicts were extant in deposits younger than 25 Ma, later than in the Great Plains (Tedford et al. 2004; Albright et al. 2008). The timing of the faunal transition in the Great Plains may appear accelerated relative to Oregon as a consequence of the poor quality of the Ar2-aged mammalian fossil record of the Great Plains (Tedford et al. 2004). Nevertheless, the faunal transition from archaic to modern mammalian communities appears to have been initiated earlier in the more western region, Oregon. I here characterize the timing of the faunal transition of the early Arikareean in the northern Rocky Mountains to test the hypothesis that the geographically intermediate location of the Rocky Mountains was associated with a time transgressive faunal transition that was chronologically intermediate between Oregon and the Great Plains and correlative with the eastward expansion of immigrants from Eurasia and novel taxa from the topographically complex regions of the intermontane west.

2. STUDY SYSTEM AND HYPOTHESES

The Cabbage Patch beds of western Montana offer the rich fossil record necessary to quantify the tempo and pattern of the faunal turnover of the Arikareean in the geographically intermediate Rocky Mountains. Indeed, the Cabbage Patch beds, part of the upper part of the Renova Formation, preserve a series of vertebrate microfossil assemblages placed in stratigraphic context that provide the material necessary to characterize entire fossil mammal communities through the early Arikareean (Rasmussen 1977, Rasmussen and Prothero 2003, Calede and Rasmussen 2015, Calede 2016a). Previous work, based on a qualitative analysis of the presence/absence of mammals and mollusks, divided the Cabbage Patch beds into three biostratigraphic units (Figs. 1 and 2; Rasmussen 1977, Pierce 1993, Rasmussen and Prothero 2003, Calede and Rasmussen 2015). I use a newly assembled dataset of mammalian fossil specimens from these three units and an updated chronostratigraphic framework to test the hypothesis that the transition between the White River and Runningwater chronofaunas was initiated in the Rocky Mountains later than in Oregon but earlier than in the Great Plains. Specifically, I predict that (1) taxa characteristic of the White River Chronofauna were extirpated in western Montana earlier than in the Great Plains but later than in Oregon and that (2) novel taxa arose in the Rocky Mountains later than in Oregon but earlier than in the Great Plains.

3. MATERIAL AND METHODS

3.1. Geographic and chronostratigraphic context

The Cabbage Patch beds crop out in five intermontane basins in western Montana (Rasmussen and Prothero 2003, Calede and Rasmussen 2015, Calede 2016a). In this study, I focused on those with the largest samples of fossil mammals: the Flint Creek and Deer Lodge basins. I also include a locality from the nearby Blackfoot Basin (Fig. 1). There are two sets of assemblages in the Flint Creek Basin. One, south of the Clark Fork River and Interstate 90, includes assemblages from the middle Cabbage Patch without additional stratigraphic information. The other set, north of the interstate and the river and east of the town of Drummond (MT), herein called the Bert Creek area, includes over a dozen localities in close proximity, many of which are placed in a stratigraphic section (Fig. 2A–B). They form the core of the assemblages from the lower and middle units of the Cabbage Patch beds. In the Deer Lodge Basin, all assemblages except that from C1712 are also located in close proximity to one another. This set of assemblages is known as the Tavenner Ranch local fauna (Tedford et al. 2004).

The tuffaceous outcrops of the Cabbage Patch beds are small in both lateral and vertical extent and mostly lack characteristic marker beds helpful in determining stratigraphic correlations across outcrops, and possibly basins (Rasmussen 1977, Calede and Rasmussen 2015, Calede 2016a). However, select localities have been placed in a stratigraphic section by Rasmussen (1977), particularly in the Flint Creek Basin, the proposed type area for the beds (Fig. 2A–B; Table 1; see also Rasmussen 1977, Rasmussen and Prothero 2003, Calede and Rasmussen 2015). The stratigraphy of the beds is not as well resolved in the Deer Lodge Basin but sufficiently so to place localities in relative stratigraphic order (Fig. 2C; Table 2; Rasmussen 1977). The lithostratigraphy of the beds has been supplemented by magnetostratigraphy, although in the absence of radioisotopic dates through the section, the age of the Cabbage Patch beds remains poorly constrained (Rasmussen and Prothero 2003). Recent work yielding radioisotopic dates for select outcrops helps constrain the age of the beds. Thus, the base of the Cabbage Patch beds may be as old as 29.95 Ma ± 0.17 Ma based on a date for a basalt flow underlying the Cabbage Patch beds in the Garnet Range volcanic field (Fig. 1B; Mosolf 2015). Portner et al. (2011) published an age of 26.86 ± 0.26 Ma (^{40}Ar/^{39}Ar) for a tuff correlated across outcrops of the Dunkleberg Creek and Coberly Gulch areas. Fossil localities from these areas (C1706, C1727; Fig. 1) have been assigned to the middle Cabbage Patch but their exact stratigraphic relationship to the dated tuff and assemblages of the middle Cabbage Patch beds of the Bert Creek area is unknown (Rasmussen 1977, Calede 2016a). A tuff from C1712, an isolated outcrop interpreted to include the youngest fossil-bearing deposits of the beds (Rasmussen 1977, Prothero and Rasmussen 2003), was recently dated to 25.6 ± 0.4 Ma ($^{206}Pb/^{238}U$, Constenius and Rasmussen pers. comm. 2015). Ongoing work by myself and colleagues to date five new tuffs through the stratigraphic section will help further resolve the chronology of the Cabbage Patch beds and the tempo of faunal change presented herein. Evidence thus far suggests that the lower Cabbage Patch could be as old as ca. 30 Ma (Ar1); the middle Cabbage Patch is ca. 27 million years old (Ar2); and the upper Cabbage Patch is might be as young asca. 25.6 Ma (Ar2).

3.2. Geological and taphonomic context

The geology of the beds (Rasmussen 1977), particularly in the Flint Creek Basin, is summarized by Calede and Rasmussen (2015) as well as Calede (2016a). The beds are at least 616 m thick and mostly composed of fine-grained tuffaceous sediments rich in volcanic glass reworked by fluvial and lacustrine processes. Fossils have been recovered from over 40 localities (Rasmussen 1977). In this study, I included in my analyses a total of 23 fossil assemblages (Tables 1 and 2). They represent a diversity of depositional environments including lacustrine (C1712), floodplain (e.g., C1701–C1705, C1708, C1721), and channel (C1707) deposits. Differences in taphonomy between assemblages could bias cross-assemblage comparisons of community structure, particularly relative abundances. I therefore included in my analyses of community structure six assemblages from low energy depositional environments (MV6613, C1708, C1721, C1704, C0174, C0173; see below) that display similar taphonomic signatures (Calede 2016a) to limit the impact of preservation on the changes in biodiversity across assemblages. These assemblages represent localized accumulations of vertebrate microfossils little affected by spatial and temporal averaging (Calede 2016a).The seventh locality (MV6554) is similar in lithology and specimen preservation to this well-studied set of localities (yellow-colored [hues of 5Y] poorly sorted massive mudstone to siltstone with bioturbation) and displays little worn specimens alike the other assemblages studied (Rasmussen 1977, Calede 2016a).

3.3. Sampling and database of specimens

The Cabbage Patch beds are the source of a rich vertebrate fossil record (e.g., Douglass 1901, 1903, Konizeski and Donohoe 1958, Riel 1964, Wood and Konizeski 1965, Tihen 1974, Rasmussen 1977, Tihen and Wake 1981, Henrici 1994, Calede and Rasmussen 2015, Calede 2016a). In the late 1960s and early 1970s, Rasmussen initiated an intensive screenwashing protocol and assembled a large collection of vertebrate microfossils and mollusks (Rasmussen 1969, 1977). I resumed this work in 2011 recovering specimens from the surface as they eroded out and quarrying productive horizons. I also used wet screenwashing with medium and fine mesh sizes (0.7 and 0.5 mm wide openings respectively). As a consequence, most fossils from the Cabbage Patch beds have been collected by two investigators following similar methods, limiting the potential for collecting bias. Stratigraphic position for each locality was determined from the data of Rasmussen (1977) as well as additional work by me (Calede 2016a).

I included a total of 988 fossil mammal specimens from 23 assemblages in my dataset (Tables 1 and 2, Appendix 4.1). I included three categories of assemblages in various subsets of my analyses: (1) the seven best sampled assemblages (> 40 specimens, mean ~116 specimens), (2) assemblages with known stratigraphic positions regardless of sample size, and (3) assemblages whose taxonomic composition is reasonably known (> 4 taxa identified) even when the stratigraphic position is limited to the biostratigraphic unit. I limited my dataset to cheek teeth (premolars and molars) because they are taxonomically informative (Janis et al. 1998, 2008) and are more uniform in shape in the context of taphonomy (Calede 2016a). Most specimens were identified as a known species, a species similar to a known species, or a new species yet to be formally described (Appendix 4.1, Calede 2016b:table 2). A few specimens could not be identified to the species level but belong to genera (e.g., *Cormocyon*, *Petauristodon*, *Miohippus*, *Daeodon*) or families (Camelidae, Tayassuidae) that are not known at the species level in the Cabbage Patch beds, and therefore unambiguously represent a valid, unique taxonomic unit for this dataset. Select taxa (*Eutypomys*, *Eporeodon*, and *Promerycochoerus*) are known from specimens identified to the species level as well as specimens only identified to the genus level. Because those taxa are rare and there is no evidence for the presence of two (or more) species within these genera in the Cabbage Patch beds, I included these taxa in my analyses at the genus level. I used the number of identified specimens rather than the minimum number of individuals in all analyses because specimens from the Cabbage Patch beds are found isolated and cannot usually be associated with one another (Badgley 1986, Calede 2016a).

Several mammalian taxa used in this analysis are yet to be formally described. Rasmussen (1977) recognized several new species of mammals in his study of the fauna. He gave them names in his unpublished dissertation. Those names have been used in the MIOMAP database (Carrasco et al. 2007). To limit confusion, we herein use the names of Rasmussen (1977) for the mammal morphotypes (i.e. unpublished species) from the Cabbage Patch beds first identified by Rasmussen (1977).

3.4. Analyses of biodiversity

I used this updated dataset to quantify the tempo and mode of the faunal transition of the Arikareean in the Cabbage Patch beds:

(1) I calculated different measures of richness to assess the correlation of faunal turnover with any possible change in biodiversity through time. I expect the richness of mammalian faunas to decrease through time with the loss of White River taxa.

(2) To determine the link between faunal turnover and faunal stability, I calculated four different estimates of faunal heterogeneity as well as relative abundance distributions (RADs). I predict the different measures of evenness to rise with the immigration of novel taxa as witnessed in an earlier mammalian immigration of the Cenozoic (Clyde and Gingerich 1998). However, it is also possible that evenness would decrease with immigration events if it leads to a higher proportion of rare species (McGill et al. 2007). I expect the RADs of mammalian assemblages that recorded immigration events and faunal perturbations to be more uneven and be better fit by geometric series models. On the contrary, assemblages that reflect later stages of successions (i.e. more stable communities) may display a relative abundance distribution better fit by a lognormal or broken stick model (Magurran 2005, 2009, McGill et al. 2007, Wilson 2014).

(3) I determined the relative abundance of individuals and species belonging to the White River Chronofauna to track their replacement by more novel taxa. I expect the lower Cabbage Patch beds to include many more White River relicts than younger units of the beds, which should include a higher proportion of novel taxa. I expect the relative abundance of individuals within novel taxa to increase over time while that of the White River relicts decreased.

(4) I used a biostratigraphic framework (updated from Rasmussen 1977, Rasmussen and Prothero 2003), multivariate measures of faunal similarity, and calculations of turnover rates to determine the tempo and pattern of faunal change through the Cabbage Patch beds. I predict the turnover rates to be highest at the transitions between the lower and middle units of the beds as well as the middle and upper units of the beds. Similarly, I predict multivariate distances of faunal dissimilarity to be highest at the transitions from the lower to the middle units of the beds and from the middle to the upper unit. I expect the ordination of multivariate similarities to display clusters of assemblages consistent with the *a priori* biostratigraphic units.

3.4.1. Richness—I undertook several analyses to quantify the biodiversity and biostratigraphy of the Cabbage Patch beds and characterize faunal turnover throughout the beds. I calculated the richness of the mammal assemblages in four different ways. I calculated the raw richness as the number of species present in each assemblage with known stratigraphic position. I also calculated standing richness (Foote 2000) by adding the number of species that first appear in an assemblage (FAD: first appearance datum), those that make their last appearance in that assemblage (LAD: last appearance datum), and those that range through (present in an older assemblage, present in a younger assemblage, and may or may not be present in the assemblage of interest) for all assemblages with a known stratigraphic height (all within the Flint Creek Basin). Standing richness provides an estimate of the number of species including taxa that are not present in an assemblage as a consequence of poor sampling (Maas et al. 1995, Wilson 2014, see also Foote 2000). I calculated rarefied richness (Raup 1975) using Analytic Rarefaction 1.3 (by S. Holland). Rarefied richness provides estimates of the number of species that can be compared across assemblages accounting for variation in sampling intensity (Raup 1975); here an estimate of species richness for a sample of 41 specimens (i.e., the sample size of the most poorly-sampled assemblage, MV6613) for each of the seven well-sampled assemblages. I also estimated richness using shareholder quorum subsampling (SQS; Alroy 2010) calculated in R 3.1.3 (R Development Core Team 2015) using RStudio 0.98.1103 (RStudio 2015) with the SQS v.3.3 function (http://bio.mq.edu.au/~jalroy/SQS.html) with 1,000 trials and a shareholder quorum (q) of 0.82 (determined by the minimum coverage corrected for evenness [u] found at MV6613). SQS estimates richness by calculating the expected number of species given a fixed level of coverage of the underlying species abundance distribution of the assemblage. Coverage is the sum of frequencies of the species sampled (Alroy 2010, Cermeño et al. 2013). SQS helps overcome the problem of rarefied richness that more diverse samples require more specimens to detect a similar proportion of the species present in the assemblage.

3.4.2. Relative abundances—I calculated the relative abundances of individuals within taxa at the seven best-sampled localities as percentages of the number of specimens in the assemblage (Appendix 4.2).

I used the relative abundances to calculate four widely used heterogeneity indices: (1) Evenness, which is the ratio of the exponential of Shannon's entropy to the number of species in the assemblage; it ranges from zero to one with the larger values reflecting more even assemblages, (2) Equitability, which is the ratio of Shannon's entropy by the logarithm of the number of taxa present in the assemblage; it measures the evenness among the taxa present in the assemblage ranging from zero to one with the larger values reflecting more even assemblages, (3) Simpson's index (1-D), which measures the evenness of an assemblage from zero to one with higher values indicating greater diversity and zero indicating an assemblage dominated by a single species, and (4) Berger-Parker index, which is the number of specimens in the dominant taxon relative to the total number of specimens in the assemblage. Simpson's and Berger-Parker indices emphasize the abundance of the most common species and are less influenced by species richness than evenness and equitability, which emphasize the richness of the assemblage rather than the abundances of the most common and rarest species (Olszewski 2004, Hammer and Harper 2008, Magurran 2009). For each index, the value for the assemblage and a 95% confidence interval based on bootstrapping (1,000 repetitions) were calculated in R. I calculated Simpson's index using the function of Gardener (2014) available from (http://www.dataanalytics.org.uk). I derived the evenness and equitability from Shannon's entropy, which I calculated using the package vegan 2.3-2 (Oksanen et al. 2015) in R.

I also used the relative abundances to fit curves to the relative abundance distribution (RADs) of each of the seven assemblages. Such curves are most helpful as a relative tool to compare assemblages and I used them to provide a visualization of the relative evenness of the Cabbage Patch assemblages (a shallower slope of the rank versus relative abundance plot indicates a more even assemblage). Although RADs have been difficult to link to ecological processes across ecosystems (Magurran 2005, McGill et al. 2007), they have been used to interpret biodiversity and ecological stability through time and across extant communities or fossil assemblages (Wagner et al. 2006, McGill et al. 2007, Christie et al. 2013, Wilson 2014). I compared the curves fitted to RADs through the beds as an additional estimate of the stability or deterioration of mammalian communities through time in the northern Rockies. I generated the curves using vegan and calculated Akaike weights using qpcR 1.4-0 (Ritz and Spiess 2008). Akaike weights allow the direct comparison of the relative support for different models for a given RAD.

3.4.3. Multivariate similarity across assemblages— I quantified faunal change through time by calculating similarities in relative abundances across assemblages using chord distance in vegan. Chord distance has been showed to help detect faunal turnover (Bobe et al. 2002; Frost 2007; de Ruiter et al. 2008; Calede et al. 2011). I calculated chord distance between all pairs of subsequent assemblages through the beds. Because the stratigraphic position of MV6613 relative to the lower Cabbage Patch assemblages of the Flint Creek Basin is not known, I calculated pairwise distances between MV6613 and all lower Cabbage Patch assemblages as well as MV6613 and the lowest assemblage of the middle unit of the beds included n this analysis (C1704). The chord distance between two assemblages ranges between 0 and √2. Prior to calculating the distance, I transformed the abundances by taking their square root and then converted these values to relative abundances. Such transformation is useful when a high degree of variation is present in a dataset of species counts because it helps better meet the assumptions of statistical tests (including normality and constant variance).

I used a matrix of the presence/absence of 55 taxa known from at least two different assemblages among 18 assemblages with four or more taxa to investigate faunal similarities throughout the beds (Appendix 4.3). Ordinations of faunal similarities can be used to test hypotheses of biostratigraphy (e.g., Ayoub-Hannaa et al. 2013, Székely and Filipescu 2016). Here, I used Sørensen distance (a percentage dissimilarity mathematically equivalent to Bray-Curtis distance calculated using simba 0.3-5, Jurasinski and Retzer 2012) and non-metric multidimensional scaling ordination (NMDS) to visualize dissimilarity in taxonomic composition between assemblages. NMDS does not assume multivariate normality or linear associations and uses the rank order of distances (not the value themselves unlike principal coordinate analysis, Kruskal and Wish 1978). It is therefore less sensitive to numerical differences between assemblages. I used the package vegan to generate the NMDS and the biostats functions (McGarigal 2015) to generate a Monte-Carlo randomization test of the stress value of the NMDS in R. I explored the possible link between faunal dissimilarity and straigraphic distance between assemblages by performing a Mantel test (with Spearman's rank-order correlation coefficient as the correlation method) between pairwise Sørensen distances among assemblages and pairwise differences in stratigraphic position (when known). I used ANOSIM in vegan to test the hypothesis that the biostratigraphic units of the Cabbage Patch beds can be detected in the NMDS analysis (using 10,000 permutations). ANOSIM is a non-parametric test of group differences based on ranked similarities (Clarke 1993).

3.4.4. Biostratigraphy—For each basin, I constructed biostratigraphic ranges for all taxa including every occurrence associated to a known stratigraphic position. In the Flint Creek Basin, this includes 13 localities that are all assigned a stratigraphic height relative to the base of the beds. In the Deer Lodge Basin, these biostratigraphic ranges are not always associated with stratigraphic heights and more often reflect the presence or absence of taxa in the lower, middle, and upper units of the Cabbage Patch beds.

In the Flint Creek Basin, where stratigraphic positions are known, I used "fossil recovery potential functions" (Strauss and Sadler 1989, Wilf and Johnson 2004) to calculate 50% confidence intervals for the observed ranges of each taxon present in more than two assemblages, based on sampling. I used the Adaptive Beta method of Wang et al. (2016), a Bayesian method that does not require the assumption of uniform fossil recovery potential. Using the R code provided by the authors and the stratigraphic positions where fossils have been recovered for a given taxon, I calculated the confidence intervals for the true range of this taxon and estimated the potential for the recovery of additional specimens throughout the section (Table 9). The Adaptive Beta method assumes that a large gap between the last occurrence of a taxon and its disappearance is less probable than a smaller gap is and that the fossil recovery potential function is normal and centered around zero (Wang et al. 2016). I use these confidence intervals to assess uncertainties in the biostratigraphic value of select mammalian taxa from the lower and middle Cabbage Patch present in the Flint Creek Basin.

3.4.5. Turnover rates—I calculated turnover rates using true and range-through occurrences (Foote 2000). Specifically, I calculated the proportional rates of appearance and disappearance throughout the beds for each of the assemblages with a known stratigraphic position in the Flint Creek Basin that includes at least 20 species (standing diversity) and C0173, the only well-sampled assemblage from the upper Cabbage Patch beds (from the Deer Lodge Basin). The assemblages from the lower-most part of the middle Cabbage Patch (C1701–C1703) were combined to mitigate the effects of the poor sampling in this part of the beds (N=28 specimens for all three assemblages combined). Although this prevents the detection of possible turnover events in the lower part of the middle unit of the beds, such events could not be detected because of the poor sampling of the assemblages in this part of the stratigraphic section. These assemblages are not evenly distributed or sampled throughout the section and the turnover rates therefore only offer an indication of relative differences throughout the beds. It cannot be determined with certainty when appearance and disappearance events occurred.

3.5. Institutional abbreviations

KUVP, University of Kansas Museum of Natural History, Lawrence, Kansas, USA; **UMPC**, University of Montana Paleontology Center, Missoula, Montana, USA; **UWBM**, University of Washington Burke Museum, Seattle, Washington, USA.

4. TAXONOMIC UPDATES TO THE CABBAGE PATCH FAUNA

The detailed study of the mammalian fauna from the Cabbage Patch beds presented herein allows the recognition of a number of new taxa, the extension of the geographic ranges of some, and the extension of the temporal ranges of others. These new occurrences are critical to determining the tempo and pattern of the faunal transition of the Arikareean. Among the 95 taxa recognized in the Cabbage Patch beds (see Appendix 4.1), there are at least 30 species new to science (as well as 20 taxa with uncertain affinities that may represent new species). Some of them were recognized by Rasmussen (1977) but all are yet to be formally described. Of these 30 new species, four belong to the order Eulipotyphla and 26 to Rodentia.

Among eulipotyphlans, the new species include two species of shrews within the long-lived genera *Domnina* and *Pseudotrimylus* present in the lower unit of the beds (Rasmussen 1977, Gunnell et al. 2008, Whisler and Calede 2014) and two species of moles ranging through the lower and middle Cabbage Patch, including a new species of the genus *Mystipterus* (Rasmussen 1977). This is the second occurrence of *Domnina* in the Arikareean of the Rocky Mountains (Nichols 1976), the first of *Pseudotrimylus*, and the oldest occurrence of *Mystipterus*, otherwise only known in the Rockies from unpublished occurrences in the Barstovian-aged Hepburn’s Mesa Formation (Carrasco et al. 2007).

Within Rodentia, twelve of the 30 new species belong to the family Aplodontidae. Aplodontids are particularly diverse in the lower Cabbage Patch beds. Such a rich aplodontid fauna is also found in the John Day Formation of Oregon (Rensberger 1975, 1983, Tedford et al. 2004, Hopkins 2006, Fremd 2010), unlike in coeval assemblages of the Great Plains (Tedford et al. 2004). The significance and implications of this new aplodontid fauna will be detailed elsewhere (Hopkins, Calede, and Rasmussen in preparation). There are also five new species of entoptychine geomyids in the Cabbage Patch beds, including three new species within the genus *Pleurolicus* in the middle unit of the beds and two species within *Gregorymys* in the upper unit of the beds (Rasmussen 1977, Souza 1989, Calede 2016c). Ongoing work by me (Calede 2016c) will detail the morphology and stratigraphic significance of these new taxa. Three other families of rodents are represented by new species in the Cabbage Patch beds, including a new species of the cricetid mouse *Leidymys* in the lower unit of the beds (Rasmussen 1977). The new species of *Heosminthus* from the Cabbage Patch beds is particularly important. It is represented by very complete specimens and spans all three units of the beds. It is the first occurrence of this Asian taxon in North America (Daxner-Höck et al. 2014, Calede and Cairns 2015). This new species suggests the immigration of yet another taxon from Asia into North America coeval with that of the sicistine rodent, *Plesiosminthus,* key to the identification of the Arikareean (Tedford et al. 2004). Two other species of sicistine dipodids that are known only from isolated teeth and partial jaws are found in the lower and middle units of the Cabbage Patch beds. A richer input of small mammals from Asia into Arikareean faunas is consistent with the taxonomic composition of the rodent fauna from the John Day Formation (Fremd and Whistler 2009, Korth and Samuels 2015). A diversity of immigrants from Asia into North America during the Arikareean is further supported by the presence of six new species of the beaver *Microtheriomys*. *Microtheriomys*, which ranges through the Cabbage Patch beds, is otherwise only known from the John Day Fm. where a single species of this beaver, *M. brevirhinus*, is found in the Ar1 (Korth and Samuels 2015). This genus is the oldest evidence of anchitheriomyine beavers in North America (Korth and Samuels 2015). Its affinities with *Propalaeocastor* and Anchitheriomyinae suggest an additional faunal link with Asia (Korth and Samuels 2015). The presence of three species of *Microtheriomys* in the lower unit of the beds suggests a diversification of *Microtheriomys* in North America during the Ar1. The presence of this genus in the upper unit of the Cabbage Patch beds is the first occurrence of this genus into the Ar2.

The carnivore fauna of the Cabbage Patch beds, dominated by canids, shows affinities with the carnivore fauna of the Great Plains. Indeed, *Archaeocyon leptodus* and *Cynodesmus thooides*, known from the Whitneyan and Arikareean of the Great Plains, are present in the lower and middle units of the beds (Wang 1994, Wang et al. 1999). The presence of *Leptocyon* cf. *L. delicatus* in the middle Cabbage Patch, albeit represented by a single tooth, is only the second occurrence of this taxon and the first in the Rocky Mountains. It is only otherwise known from coeval deposits of South Dakota (Tedford et al. 2009).

The ungulate fauna from the Cabbage Patch beds has been extensively described (Riel 1964, Rasmussen 1977, Rasmussen and Prothero 2003, Prothero and Rasmussen 2008). The presence of *Pronodens*, mainly in the lower Cabbage Patch, a taxon typical of the Rocky Mountains (Koerner 1940, Tedford et al. 2004) may indicate a relative regional endemicity of the ungulates of the Rocky Mountains while the Rhinocerotidae suggest affinities with the Great Plains (Prothero and Rasmussen 2008). The presence of *Daeodon* in the middle units of the Cabbage Patch beds is the first occurrence of an entelodontid in the Rocky Mountains

(Rasmussen and Prothero 2003). *Daeodon* is also possibly present in the fauna of the Canyon Ferry Reservoir (Hanson 2015).

Herpetotherium, including *H. fugax* and *H. merriami*, is known from the Arikareean (Ar1 and Ar2) of Oregon, Florida, and Nebraska (Korth 1994, Hayes 2005). The specimens from the Cabbage Patch beds are the first occurrence of this genus in the northern Rocky Mountains. A morphotype of *Herpetotherium* from the middle and upper Cabbage Patch beds compares with *H. valens*, a Chadronian-aged species (37–33.7 Ma, Prothero and Emry 2004). This comparison is based on poor material and a larger sample is needed to compare this morphotype to other taxa including *H. youngi* known from the nearby Arikareean-aged Canyon Ferry Reservoir fossil assemblage (Hanson 2015). This is unlikely to be the first occurrence of *H. valens* in the Arikareean. The presence of another marsupialiforme genus, *Nanodelphys*, through the Cabbage Patch beds is the first evidence of this taxon west of the Great Plains.

Several taxa of proscalopid moles are present throughout the Cabbage Patch assemblages. Many proscalopids are already known from Montana including *Proscalops intermedius* from the Arikareean-aged deposits of the Fort Logan Formation (Barnosky 1982). The material from the Cabbage Patch beds does not appear to be referable to this taxon and suggests a greater diversity of proscalopids in the region than previously known.

There are two possible ochotonids present in the Cabbage Patch beds including ?*Desmatolagus* cf. *D. schizopetrus* in the middle unit of the beds and *Gripholagomys* cf. *G. lavocati* in the upper unit. ?*Desmatolagus* is only published from the Hemingfordian of Wyoming (Dawson 1965) although there are reports of possible *Desmatolagus* specimens from the Arikareean of Wyoming (McKenna 1968, reported by Carrasco et al. 2007). This is the first occurrence of an ochotonid in Montana, and the earliest known from the Rocky Mountains (pending description of the material of McKenna 1968). Ochotonids are known from the Ar1 to the Ar3 in the John Day Formation of Oregon (Samuels and Kraatz 2015). *Gripholagomys* is also known from the Ar2 of the Great Plains and the Ar3–4 of the Sespe Formation (Green 1972, Whistler and Lander 2003, Tedford et al. 2004); this is the first occurrence of the genus in the northern Rocky Mountains. *Megalagus turgidus* is already known from the Chadronian to Orellan-aged deposits of the Renova Formation (Fostowicz-Frelik 2013). It goes extinct at the boundary between the Whitneyan and Arikareean, 30 Ma in the Great Plains (Fostowicz-Frelik 2013). The specimens from the lower Cabbage Patch beds are the youngest occurrence yet of this species. *Archaeolagus macrocephalus* is known from the early Hemingfordian of South Dakota and *Archaeolagus* cf. *A. macrocephalus* from the late Arikareean of New Mexico and Oregon (Dawson 1958, Gawne 1976, Samuels and Kraatz 2015). The presence of *Archaeolagus* cf. *A. macrocephalus* in the Ar2-aged middle unit of the Cabbage Patch beds is the oldest occurrence of this taxon and the first one recorded in the Rocky Mountains where only ?*Archaeolagus* sp. has been recorded before (White 1954).

The presence of a few specimens of *Pseudotheridomys,* a Eurasian immigrant, in the lower unit of the Cabbage Patch beds is the first occurrence of this genus in the Rocky Mountains otherwise only known from the late Arikareean of California (Whistler and Lander 2003) and the Ar2 of the Great Plains (Korth 1992, Bailey 2004). *Leptodontomys* is known from the John Day Formation only in the Ar3 (Korth and Samuels 2015). *L. douglassi* is present in the Great Plains during the Ar1 (Korth and Bailey 1992, Bailey 2004, Korth 2008). The presence of *L. douglassi* through the Cabbage Patch beds is the first evidence for this genus in the Rocky Mountains. The Cabbage Patch beds are the only suite of assemblages of the Rocky Mountains where the family Eomyidae is currently known to be present; the eomyid *Paradjidaumo trilophus* is reported from the Arikareean-aged Canyon Ferry Reservoir fauna (Hanson 2015).

Miosciurus ballovianus is present in the John Day Formation starting in the Ar2 (Korth and Samuels 2015); the presence of a squirrel that compares with it in the Cabbage Patch beds starting in the Ar1-aged lower unit of the Cabbage Patch beds may represent the earliest occurrence of *M. ballovianus* or a closely related form in North America. Another species of *Miosciurus*, *M. covensis* is present in the Ar1 of Oregon (Korth and Samuels 2015). The presence of *Petauristodon* in the Ar3 of the John Day Fm. is the earliest record of this genus in North America known to date (Korth and Samuels 2015). The single specimen of *Petauristodon* from the lower unit of the Cabbage Patch beds (Ar1) may therefore represent an even older record of this genus and the oldest one from the Rocky Mountains. *Petauristodon* may also be present in the early Arikareean of the Great Plains (Bailey 2004). *Sciurion* is known from the Orellan through Clarendonian of the Great Plains and Saskatchewan (Skwara 1986, Bell 2004). The presence of *Sciurion* cf. *S. campestre* through the Cabbage Patch beds is the first occurrence of this genus in the Rocky Mountains.

The one species of *Mookomys*, known from a single specimen, present in the upper Cabbage Patch beds may be the earliest occurrence of this taxon otherwise typical of the late Hemingfordian and early Barstovian (Korth 1997, Tedford et al. 2004).

5. RESULTS

5.1. Biodiversity through time and faunal stability

5.1.1. Sampling—The rarefaction curves (Fig. 3) show that the sampling of each assemblage is incomplete. This is particularly true at C1721 for example (Fig. 3B). Taxonomic richness continues to increase with sampling, rather than reaching a plateau, for each assemblage. This suggests that sampling is incomplete, that more species could be identified with additional work, and caution in interpreting the presence/absence and relative abundance of rare taxa through the beds. Despite not fully leveling off, the increase in richness of C1708 appears to decline after 200 specimens and to stabilize around the raw richness of 25 species. A similar raw richness is observed in C1704 as well as C0173 (Fig. 4A).

5.1.2. Taxonomic richness—Overall, it appears that richness decreases through time in the Cabbage Patch beds in both the Flint Creek and the Deer Lodge basins. Thus, although raw richness is very similar between the lower and middle units in the Flint Creek Basin (Fig.4A), the SQS subsampled richness is lower in the middle unit of the beds than in the lower unit (except for C1708, Table 3). So is the rarefied richness (with overlapping confidence intervals, Fig. 4C, Table 3). The standing richness also tends to be lower in assemblages of the middle unit than in those of the lower unit of the beds (Fig. 4D, Table 3). In the Deer Lodge Basin, raw richness varies widely through time (Fig. 5A) but sampling is very unequal across assemblages. The results of subsampling using SQS suggest a decrease in richness through time (Fig. 5B, Table 3). The estimated rarefied species richness is also lowest in the upper unit of the beds in this basin although not significantly so compared to the assemblages from the middle unit of the beds (Fig. 5C, Table 3).

5.1.3. Heterogeneity indices—The heterogeneity indices show a pattern consistent with that observed for richness. There is little difference between assemblages of the lower and middle units of the Cabbage Patch beds but the single well-sampled upper Cabbage Patch assemblage is significantly different from older assemblages (Fig. 6). This is true of both the information theory indices (based on Shannon' entropy: evenness and equitability) and dominance measures (Simpson's and Berger-Parker index). The pattern is more pronounced in the information theory indices that are more sensitive to low sample sizes than dominance measures (Magurran 2009). Evenness is lowest at C0173 and highest in MV6613 (lower Cabbage Patch, Deer Lodge Basin, Fig. 6A). The evenness in C1704 and C1708 are very similar (Table 4). The same pattern is observed for equitability (Fig. 6B) and Simpson's index (Fig. 6C). Each of those heterogeneity indices supports a lower biodiversity in C0173. The Berger-Parker index (Fig. 6D) is significantly higher in C0173 than in all other assemblages supporting a more homogeneous (high dominance) assemblage in C0173 than in older assemblages (Table 4).

5.1.4. RADs—The RADs (Fig. 7) show a difference between the assemblages from the lower and middle units and the single assemblage (C0173) from the upper unit of the Cabbage Patch beds. Amongst the fitted curves, I find the shallowest slope in C1721 (lower Cabbage Patch) and the steepest in C0173 (Upper Cabbage Patch). The slopes of the curves of the other assemblages are similar to one another. Indeed, in C0173, many taxa are rare and few are very abundant. There is a large difference between the first, second, and third most abundant taxa (Fig, 7G). In assemblages of the lower unit, particularly C1708 and C1721, the three most abundant species display very similar abundances (Fig. 7A–B). The models fitted to the RADs vary across localities (Table 5). At the base of the lower unit of the beds (C1708), the best fit is the preemption model. Although the support is more equivocal, this is also the preferred model for MV6613. No better model can clearly be identified for C1721 and MV6554. In C1721, both the Zipf-Mandelbrot and the preemption model are supported. In MV6554, the null, the preemption, and the lognormal models are all equivocally supported. In C1704, the lognormal model is well supported. In C0174, the null and preemption models are both equivocally supported. In C0173, the zipf model is the best-supported model (Table 5).

5.2. Tempo and pattern of faunal replacement

5.2.1. Relative abundances—The relative abundance of White River relicts is larger in the lower than in the middle or upper units of the beds (Fig. 10, Appendix 4.4). In all assemblages of the lower unit, 25% or more of the specimens identified belong to White River relict taxa; almost 50% do in MV6554. More than 30% of the species present in assemblages of the lower Cabbage Patch are White River relicts. In the middle and upper units of the beds, the relative abundance of White River relict specimens drops dramatically below 15%; that of the number of White River relict species does not decrease as dramatically but is consistently lower than in the lower Cabbage Patch. Only one White Rive taxon present in the upper unit of the beds is not recorded (either itself or in the presence of congeneric relatives) in the lower or middle units (Table 11): *Tenudomys*. This taxon is only known from six specimens (<3.5% of the fauna) and may simply be too rare in earlier assemblages to be recorded.

5.2.2. Chord distance—The results of the chord distance analysis (Table 6) show major faunal differences (>1.15) between the lower and middle (between MV6654 and C1704) as well as the middle and upper (between C0174 and C0173) units of the beds respectively. On the contrary, within the lower and middle units (C1708–C1721, C1721–MV6554, C1704–C0174), the differences between assemblages are smaller (<0.9). The differences between MV6613 and other assemblages of the lower Cabbage Patch as well as C1704 are high (0.99–1.19). These may be biased by the sampling at MV6613 (smallest number of specimens) or the cross-basin comparisons (MV6613 is the only locality from the Deer Lodge Basin from the lower Cabbage Patch) that mix temporal and geographic signals. When accounting for differences in stratigraphic thickness among pairs of fossil-producing horizons, the smallest change per meter of the stratigraphic section (i.e. unit time) is found between MV6554 and C1704. This is likely a consequence of the large amount of rock lacking fossils between the two assemblages (Fig. 2), which prevents a more accurate identification of the lower to middle Cabbage Patch transition. The large difference between C1721 and MV6554, two subcoeval assemblages with similar lithologies, suggests relatively large taxonomic differences over small spatial and temporal scales in the Cabbage Patch beds. The differences normalized for time (measured by stratigraphic distance) between C1708 and C1721 as well as C1704 and C0174 are very similar and may provide an estimate of background faunal change through time in the beds.

5.2.3. NMDS—The three-dimensional NMDS (Fig. 8) shows the multivariate similarities between assemblages of the Cabbage Patch beds (stress=6.7%; Monte Carlo randomization test of stress value with k=3 and 100 replicates: p=0.01). The low stress value suggests a good fit between the pattern of the ordination and the dissimilarities between the assemblages (McCune and Grace 2002). The distances in the ordination accurately represent the pairwise dissimilarities across assemblages (correlation of the fitted values and ordination distances: non-metric fit R^2=0.995, linear fit R^2=0.96). The analysis segregates assemblages according to their stratigraphic location (Table 7). The assemblages from the lower unit of the beds in particular are isolated from those of the middle and upper units (Fig. 8A). The two assemblages from the upper unit of the beds (C0173 and C1712) cluster together close to the middle Cabbage Patch units.

Most of the assemblages of the lower unit of the beds placed in stratigraphic context differ little in their faunas in this NMDS. The major differences are found with KU-MT-7 and C1709. The assemblages of the lower unit of the beds cluster together as a result of the presence of several taxa (Table 8, Fig. 8B), including three White River relicts: the leptomerycid *Pronodens transmontanus,* the marsupialiformes *Herpetotherium* indet. A, and a new species of shrew: *Domnina "hutchisoni"* (Whisler and Calede 2014). These taxa, as well as the beaver *Microtheriomys brevirhinus* and the aplodontid rodent *Downsimus "montanus"* are absent from all middle and upper Cabbage Patch assemblages (see Appendix 4.1). The aplodontid *Rudiomys "drummondensis"* is also important in driving the pattern seen in Figure 8. It is known from a single specimen in C1704, a middle Cabbage Patch assemblage, in addition to numerous specimens from assemblages of the lower Cabbage Patch beds (MV6613, C1708, and C1721). The uniqueness of C1709 is linked to the presence of the oreodont *Promerycochoerus* in this assemblage, a taxon absent from all other lower Cabbage Patch assemblages but present in the middle unit of the beds (C0247 and C1701). This uniqueness is most likely a consequence of the taphonomic setting at C1709 (Calede 2016a). Small mammals were not well preserved in this assemblage. Instead, large mammals were better preserved than they are in other assemblages of the beds leading to a relative overabundance of oreodonts (Riel 1964, Rasmussen 1977, Appendix 4.1). The position of KU-MT-7 is linked to the presence of the eomyid rodent *Leptodontomys douglassi* present in three assemblages of the lower unit (MV6613, C1708, and C1721) as well as two of the middle unit (C1704 and C0174) and two (C0173 and C1712) of the upper unit of the beds. KU-MT-7 is the only locality from the Blackfoot Basin I included in my analyses. It is also the locality with the fewest taxa I included in the analysis (S=4; there are also only four taxa in C1703). The clustering of select assemblages from the lower part of the middle

Cabbage Patch assemblages (mostly C1701-C1703), is a consequence of the presence of two species of the gopher *Pleurolicus*: “*P. rensbergeri*” and “*P. nelsoni*” (Fig. 8B). The better sampled assemblages of the upper part of the middle Cabbage Patch (C1704 and C0174) as well as the upper Cabbage Patch assemblages (C1712 and C0173) cluster together because of the presence of the cricetid mouse *Leidymys alicae*, the beaver *Neatocastor hesperus*, and the marsupialiforme *Nanodelphys* B. Among the samples whose exact stratigraphic position is not known, C0247 and KU-MT-53in the Deer Lodge Basin are most similar to assemblages from the lower part of the middle Cabbage Patch beds in the Flint Creek Basin (C1701 and C1703 specifically) mostly because of the presence of “*P. rensbergeri*”. On the other hand, C1711 and C1717 from the Flint Creek Basin are most similar to assemblages of the upper middle Cabbage Patch (C0174 in particular). The ANOSIM ($R=0.4773$, $p=1.10^{-4}$) supports the conclusion that the three biostratigraphic units of the Cabbage Patch beds differ significantly in their faunal composition.

The differences in taxonomic compositions among assemblages are not directly correlated to the stratigraphic distances among them (Mantel test: $r=-0.3213$, $p=0.98$). The faunal similarities observed between assemblages that are distant from one another (>250 m) overlap with those observed in assemblages stratigraphically close to one another (Fig. 9). It is only when assemblages are stratigraphically close (<75 m) that very high Sørensen similarities are observed. These results are consistent with those obtained from the chord distance analysis.

5.2.4. Biostratigraphy and patterns of taxonomic abundance—The Cabbage Patch beds are dominated by small mammals (96.56%; see also Calede 2016a) and specifically by rodents, which represent 68% of the individuals within the fauna (see Appendix 4.1). The mammals from the Cabbage Patch beds are strongly segregated stratigraphically (Figs. 11–12) and therefore help inform the transition to modern faunas of the Arikareean. Although 19 species are shared by the lower and middle units of the beds in the Flint Creek Basin (Fig. 11), there are 13 non-singleton taxa restricted to the lower unit of the beds and 12 to the middle Cabbage Patch. Among the taxa restricted to the lower unit of the beds, there are three artiodactyls including the leptomerycid *Pronodens transmontanus* as well as the rare oreodont *Eporeodon* and a peccary only known from two fragmentary specimens. All are White River Chronofauna relicts. *Pronodens transmontanus* is most abundant in C1721 and MV6554 and unlikely to be present in younger units of the Cabbage Patch beds (Table 9, Fig.13).

Three species of marsupialiformes, which are White River relicts, are also restricted to the lower Cabbage Patch: a large species of *Herpetotherium* that compares with *H. merriami*, a smaller species of *Herpetotherium* yet to be identified, and an unidentified species of the small peradectid *Nanodelphys*. They are particularly abundant in the assemblage from C1708 where they represent over 28% of the fauna (see Appendix 4.2). The confidence intervals confirm that the two species of *Herpetotherium* are indeed unlikely to be found outside of the lower unit of the beds (Table 9). Three different species of marsupialiformes are present in the middle Cabbage Patch; once again with a large species of *Herpetotherium* (*Herpetotherium* cf. *H. valens*), a smaller one (*Herpetotherium* cf. *H. fugax*), and a second unidentified species of the genus *Nanodelphys* (*Nanodelphys* B). The confidence intervals I calculated for *Nanodelphys* species B and *Herpetotherium* cf. *H. valens* support an occurrence limited to the lower unit of the beds (Table 9). A new species of shrew, *Domnina "hutchisoni"*, a White River relict, is also restricted to the lower Cabbage Patch beds (Table 9). It is never really abundant (<5%). A single specimen of *Domnina* (KUVP18353) from the upper unit of the beds (C0173) is very similar to

Domnina “hutchisoni” from the lower Cabbage Patch but it is too worn to be identified to the species level. No specimen of *Domnina* has been recovered from the middle Cabbage Patch (despite a sample of 350 fossil mammal specimens across ten localities).

Five species of rodents are only found in the lower unit of the Cabbage Patch beds. These include a new species of the cricetid mouse *Leidymys*, a genus characteristic of the Ar1. This species is distinct from the rarer *L. alicae*, which is present in all middle and upper Cabbage Patch assemblages but restricted to the middle unit of the beds in the Flint Creek Basin. These two species of *Leidymys* are unlikely to overlap stratigraphically (Table 9). Two species of aplodontid rodents (*Niglarodon “konizeskii”* and *Downsimus “montanus”*) and two species of beavers (*Agnotocastor* species A and *Microtheriomys* new species A) are also restricted to the lower unit of the beds. All but *Niglarodon “konizeskii”* can be confidently assumed to not occur in the middle Cabbage Patch (Table 9). *Microtheriomys* can be very abundant in some assemblages (>20% at MV6554). Other aplodontid and beaver species are present in the middle unit of the beds. Thus, the aplodontid *Niglarodon* new species A and the beaver *Neatocastor hesperus,* a taxon characteristic of the Ar1, are restricted to the middle unit of the beds. Aplodontids are very important members of the Cabbage Patch fauna. They represent over 50% of the fauna at MV6613, almost 15% of the fauna at C1708, and over 22% of the fauna at C0173. They are only rare (<5% of the fauna) at C0174. Three other species of rodents are restricted to the middle unit of the Cabbage Patch beds, the gophers *Pleurolicus “rensbergeri”*, *“P. nelsoni”* (Table 9), and *“P. gwinni”*. *Pleurolicus “nelsoni”* can be abundant (> 12% at C1704 and C0174) whereas another species of *Pleurolicus*, *P. “gwinni”,* is present in low proportions (~4% at C1704 and C0174). A different genus of entoptychine gopher is found in the upper unit of the Cabbage Patch beds, *Gregorymys*.

The middle unit of the Cabbage Patch beds also includes two non-singleton species of lagomorphs ?*Desmatolagus* cf. *D. schizopetrus* and *Archaeolagus* cf. *A. macrocephalus*. ?*Desmatolagus* cf. *D. schizopetrus* is particularly abundant in the assemblage from C0174 where it represents almost 17% of the assemblage, the most of any assemblage (the taxon is otherwise only present in C1702). *Archaeolagus* cf. *A. macrocephalus* unlikely to be present in other units of the Cabbage Patch beds (Table 9). The only equid known from Cabbage Patch, a White River relict, *Miohippus* sp. is restricted to the middle unit of the beds in the Flint Creek Basin (Table 9).

In the Deer Lodge Basin (Fig. 12), the aplodontid *Niglarodon* new species A is present in the lower unit of the beds in addition to the middle one. As in the Flint Creek Basin, *Pronodens transmontanus* is restricted to the lower unit of the Cabbage Patch beds; so is the indeterminate tayassuid. Similarly to the Flint Creek Basin, there are also two species of *Herpetotherium* (*H.* cf. *H. merriami* and *H.* species A) restricted to the lower Cabbage Patch. *Downsimus “montanus”* and *Domnina “hutchisoni”* are restricted to the lower unit of the beds in the Deer Lodge Basin alike in the Flint Creek Basin. Two species of *Pleurolicus*, *“P. rensbergeri”* and *“P. nelsoni”*, are present in the Deer Lodge Basin. They are restricted to the middle unit of the beds like in the Flint Creek Basin. In the Deer Lodge Basin, several species that are restricted to the middle unit of the beds in the Flint Creek Basin extend into the better sampled upper unit of the beds. Those include all three marsupialiformes species *H.* cf. *H. valens*, *H.* cf. *H. fugax*, and *Nanodelphys* B. *Neatocastor hesperus, Miohippus,* and *Leidymys alicae* are also found in the upper unit of the beds in the Deer Lodge Basin. In the Deer Lodge Basin, the upper unit of the beds also includes the genus *Gregorymys* although the species present are different from that identified in the Flint Creek Basin. In C0173, *Gregorymys* represents over 40% of the mammalian assemblage. A new species of *Tenudomys* is also present in both upper Cabbage Patch assemblages of the basin (C0173 and C1712). *Tenudomys* is another White River relict.

5.2.5. Turnover rates—Appearance rates are high in the lower Cabbage Patch beds (Fig. 14). In C1709, the high appearance rate is a consequence of the appearance of many taxa that are absent from C1708 and rare throughout the beds, mostly large mammals (e.g., *Promerycochoerus*, *Eporeodon*, *Niglarodon "konizeskii"*, *Cynodesmus thooides*). At C1721, the high rate is driven by the appearance of many aplodontids and sciurids, some quite rare (e.g., *Allomys magnus*, *Sciurion* cf. *S. campestre*). Appearance rates then decrease throughout the rest of the lower unit of the beds. The appearance rate is very low in the youngest assemblage of the unit (C1707). It spikes again in the lower part of the middle unit of the beds (C1701–C1703) before to decrease in the upper part of the middle Cabbage Patch (C1704 and C0174). The appearance rate is highest in the only assemblage of the upper Cabbage Patch beds included (C0173).

The disappearance rate is high in C1708 but plummets in C1709. It increases in C1721 and remains high in the upper part of the beds (MV6554 and C1707). In C1721, many rare taxa that were present in C1708 or C1709 go extinct (e.g., *Eporeodon, Niglarodon "konizeskii*). The disappearance rate is low in the lower part of the middle Cabbage Patch (C1701–1703) but increases in the upper part of the middle unit of the beds (C1704 and C0174). It is highest in C0174. Although edge effects could play a role in the patterns of appearance and disappearance rates through time in the Cabbage Patch beds, the exclusion of the edge values as well as the consistent appearance rate values across C1709 and C1721 and disappearance rates across C1704 and C0174 suggest that this pattern accurately represents changes in biodiversity through time (Foote 2000).

6. DISCUSSION

The faunal transition of the early Arikareean and the loss of White River taxa were not associated with biodiversity loss. The richness of the Cabbage Patch mammalian fauna is fairly stable through all three units of the Cabbage Patch beds. Richness in the upper unit tends to be lower than in the older units but this decrease is not significant and does not correspond to a loss of Whiter river relicts; many of which are lost at the boundary between the lower and middle Cabbage Patch, not that between the middle and upper units. The loss of White River relicts is compensated by the appearance of taxa typical of the Ar1 (Fig. 10). There is little difference in the composition of the middle and upper units' assemblages with regards to the categories of taxa present (White River relicts, Ar1 taxa, Ar2 taxa). Instead, the loss of species in the upper Cabbage Patch assemblage studied (C0173) may be a consequence of its unique taphonomy. This is further supported by the heterogeneity indices I calculated. Indeed, there is no significant change in evenness throughout the lower and middle Cabbage Patch. However, the only well-sampled assemblage of the upper Cabbage Patch is much more heterogeneous (i.e. evenness is much lower) than older assemblages (Fig. 6). The dominant taxon, the gopher *Gregorymys*, could be overrepresented in this assemblage as a consequence of its burrowing habit (Calede 2016a). Even if the fossil assemblage at C0173 accurately represents the living assemblage (i.e. biocoenosis), it may not represent accurately the general trend across ecosystems of the time but instead a situation unique to the time and place recorded in the assemblage at C0173. There is no major change in evenness associated with the loss of White River relicts and increase in Ar1 species at the boundary between the lower and middle units of the beds.

There is no evidence for a change in faunal stability through the Cabbage Patch beds in association with the faunal transition of the Arikareean. Only three assemblages' RADs can be unequivocally fit by a model. The geometric series fit to the RAD of C1708 suggests that this assemblage was less stable than younger assemblages. C1708 is located at the base of the beds (Fig. 2), which is dated to ca. 30 Ma (Mosolf 2015), the beginning of the Ar1. It is possible that the model fit of the RAD of C1708 reflects the appearance of many Ar1 species (Fig. 11B; Wagner et al. 2006, McGill et al. 2007, Magurran 2009) but testing this hypothesis would require additional fossil assemblages, older than C1708. The lognormal fit for the RAD of C1704 suggests that this assemblage corresponds to a more stable community (McGill et al. 2007). This is consistent with the stratigraphic position of this assemblage in the middle part of the middle unit of the beds (Fig. 2), after the Ar1-Ar2 boundary. The very uneven RAD of C0173 is best fit by a Zipf model, which suggests that species abundance depends on the environment as well as the abundance of other resident species at this locality (Girard-Buttoz et al. 2008, Huang and Zhan 2014). This is likely a reflection of the unique conditions at this locality. The dominant taxon at C0173, *Gregorymys*, is a burrowing gopher (Rensberger 1971, Samuels and Van Valkenburgh 2009, Calede et al. 2016, pers. obs.) whose abundance likely depended greatly on soil conditions, alike that of modern gophers (reviewed in Calede et al. 2011, Marcy et al. 2013).

The faunal turnover through the Cabbage Patch beds suggests several faunal turnover events that correspond to biostratigraphic boundaries. In the absence of lithological parameters throughout the beds, Rasmussen (1977) used a qualitative analysis of the presence and absence of mammalian fossils to divide the Cabbage Patch beds into three units. He suggested that the lower Cabbage Patch is characterized by the presence of eleven taxa absent from the other units of the beds (*Pseudotrimylus*, *Palaeolagus*, *Megalagus*, *Agnotocastor*, *Downsimus*, *Rudiomys*, *Microtheriomys*, *Kukusepasutanka*, *Desmatochoerus*, *Cynodesmus,* and a new species of talpid mole), the middle Cabbage Patch by the presence of six taxa (*Parvericius*, *Archaeolagus*,

?*Desmatolagus*, *Pleurolicus*, *Capatanka*, and *Allomys*), and the upper unit by five (*Entoptychus*, ?*Gripholagomys*, *Gregorymys*, *Mookomys*, and *Euhapsis*) (updated from Rasmussen 1977, Rasmussen and Prothero 2003). Pierce (1992, 1993, Pierce and Rasmussen 1992) recovered similar biostratigraphic units from the study of fossil mollusks. I here present the first quantitative analysis of the biostratigraphy of the Cabbage Patch beds. The results of the chord distance analysis support the division of the beds in these three units; taxonomic dissimilarity is maximal at the transition between the biostratigraphic units of Rasmussen and colleagues. This conclusion is also supported by turnover rates. Indeed, appearance rates are maximal at the base of each of the units of the beds while disappearance rates are high in the upper part of the units (particularly in the middle Cabbage Patch). The combination of these appearance and disappearance rates suggest high turnover at the boundaries between units. The clustering of fossil assemblages according to their a priori assignment of biostratigraphic units and observed stratigraphic position in the NMDS, which is validated by the ANOSIM, further supports the distinction between the three biostratigraphic units of the beds. The taxa important in differentiating the three units of the beds can be determined by looking at the results of the NMDS and the biostratigraphic analysis. Thus, as suggested by Rasmussen (1977), "*Downsimus montanus*", *Agnotocastor*, and two species of *Microtheriomys* (*Microtheriomys brevirhinus* and *Microtheriomys* new species A) can be used to identify assemblages of the lower Cabbage Patch; so can a new species of *Leidymys, Pronodens transmontanus*, *Herpetotherium* indet. A, *Herpetotherium* cf. *H. merriami*, and *Domnina "hutchisoni*." A single taxon appears to be important in characterizing assemblages of the middle unit of the beds, the genus *Pleurolicus*. In the Flint Creek Basin, *Archaeolagus* cf. *A. macrocephalus* may also be used to identify assemblages from the middle Cabbage Patch beds. The presence of the Geomyidae *Tenudomys* *"welchi"* and *Gregorymys* can be used to characterize the upper Cabbage Patch beds. These results suggest that despite the absence of marker beds, deposits can be reliably assigned to a unit of the beds based on the faunal composition of the assemblages they host.

Many taxa present only in the lower Cabbage Patch represent lineages on their way out, holdovers from the White River Chronofauna. In fact, of the 32 taxa representing relict lineages present in the Cabbage Patch beds, 18 are restricted to the lower unit of the beds (Table 10). Six more go extinct in the middle unit, including two very rare taxa absent from the lower unit of the beds (*Daeodon* and *Leptocyon* cf. *L. delicatus*). Eight White River relicts survive into the upper unit of the beds. The presence of *Tenudomys "welchi"* in C1712 confirms the presence of White River relicts in deposits as young as ca. 25.6 Ma in the Rocky Mountains. Thus, it appears that White River relicts persist in younger deposits in the Cabbage Patch beds than in the Great Plains (Tedford et al. 2004). They persist longer in the John Day Formation (Tedford et al. 2004) although future studies of younger fossil assemblages from the northern Rocky Mountains may demonstrate the presence of White River relicts in deposits younger than the Cabbage Patch beds.

The faunal turnover of the Arikareean was initiated earlier but occurred more slowly in the northern Rocky Mountains than in the Great Plains. Ar1 immigrants, including taxa with Eurasian affinities, are found in the oldest assemblage of the Cabbage Patch beds (C1708) suggesting that the transition to modern faunas was already initiated by ca. 30 Ma in the Rocky Mountains, similar to in the John Day Formation but earlier than in the Arikaree Group. Many taxa that are first found in the Ar2 in the Great Plains are present in the Cabbage Patch beds during the Ar1, similar to in the John Day Fm. Nonetheless, White River relicts remain dominant at the base of the beds (C1708) both in the number of taxa and the number of specimens present in the fossil assemblage. The relative abundance of specimens of novel taxa (and to a lesser extent that of species) is variable throughout the lower unit of the beds. It is only in the middle and upper units of the beds that novel taxa are consistently more abundant both in terms of species and specimens than outgoing lineages of the White River Chronofauna (Fig. 10, Appendix 4.4). In all assemblages except C1708, the dominance of novel taxa over relict ones is stronger in the relative abundance of specimens than that of taxa, possibly suggesting an initial invasion dominated by a few very competitive or opportunistic taxa. The most dramatic faunal change is observed between the lower and the middle units of the beds (Table 6, Fig. 8), suggesting a major turnover event locally ca. 28 Ma, coinciding with the Ar1–Ar2 transition and major turnover events in the Great Plains and the John Day Formation (Tedford et al. 2004).

7. CONCLUSIONS

The mammalian fauna of the Arikareean-aged Cabbage Patch beds of western Montana offers a unique window into faunal turnover at a critical time in mammalian evolution: the rise of many modern mammalian clades. The revised chronostratigraphic framework and the detailed study of the taxonomy and biodiversity of the mammalian fauna through time presented herein suggest that the timing of the faunal turnover of the Arikareean in the northern Rocky Mountains was more similar to the timing in the John Day Formation than that in the Great Plains. This pattern supports an eastward spread of the faunal transition and a time transgressive mammalian turnover across the northwestern United States. The presence of taxa with Eurasian affinities among the Ar1 immigrants found in the Cabbage Patch beds suggest a stronger role of transcontinental immigration than previously suggested. Nevertheless ongoing studies by myself and colleagues of the phylogenetic systematics of the Cabbage Patch fauna as well as the ongoing dating of several horizons through the beds will help better resolve the relative roles of immigration and local diversification in the transition away from the White River Chronofauna into modern mammalian communities.

Determining the exact timing of the rise of modern mammalian families will require future studies of older assemblages including the fossil bearing horizons of the lower Renova formation (Black 1965, Rasmussen and Prothero 2003; Tedford et al. 2004) as well as younger assemblages including the Split Rock Local Fauna (Munthe 1988), the Railroad Canyon sequence (Barnosky et al. 2007, Harris 2016), and other Barstovian faunas of Montana (Dorr 1956, Sutton and Korth 1995). Quantitative faunal analyses of other Arikareean mammalian faunas coeval with the Cabbage Patch beds, including the Fort Logan Formation of Montana and the Peterson Creek Local Fauna of Idaho (Scott 1895, Koerner 1940, Black 1961, Nichols 1976, Nichols 1979, Rensberger 1979, Rensberger 1981, Barnosky 1982, Calede 2014), will help assess spatial differences in the timing of faunal change in the Rocky Mountains. Such datasets will provide the necessary information to a biogeographic analysis of Arikareean mammalian faunas throughout the western United States, reveal similarities and differences in the tempo and mode of the rise of modern mammalian families across asynchronous environmental change (Strömberg 2005), and shed light on the processes at play in this critical event in mammalian evolution.

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FIGURES

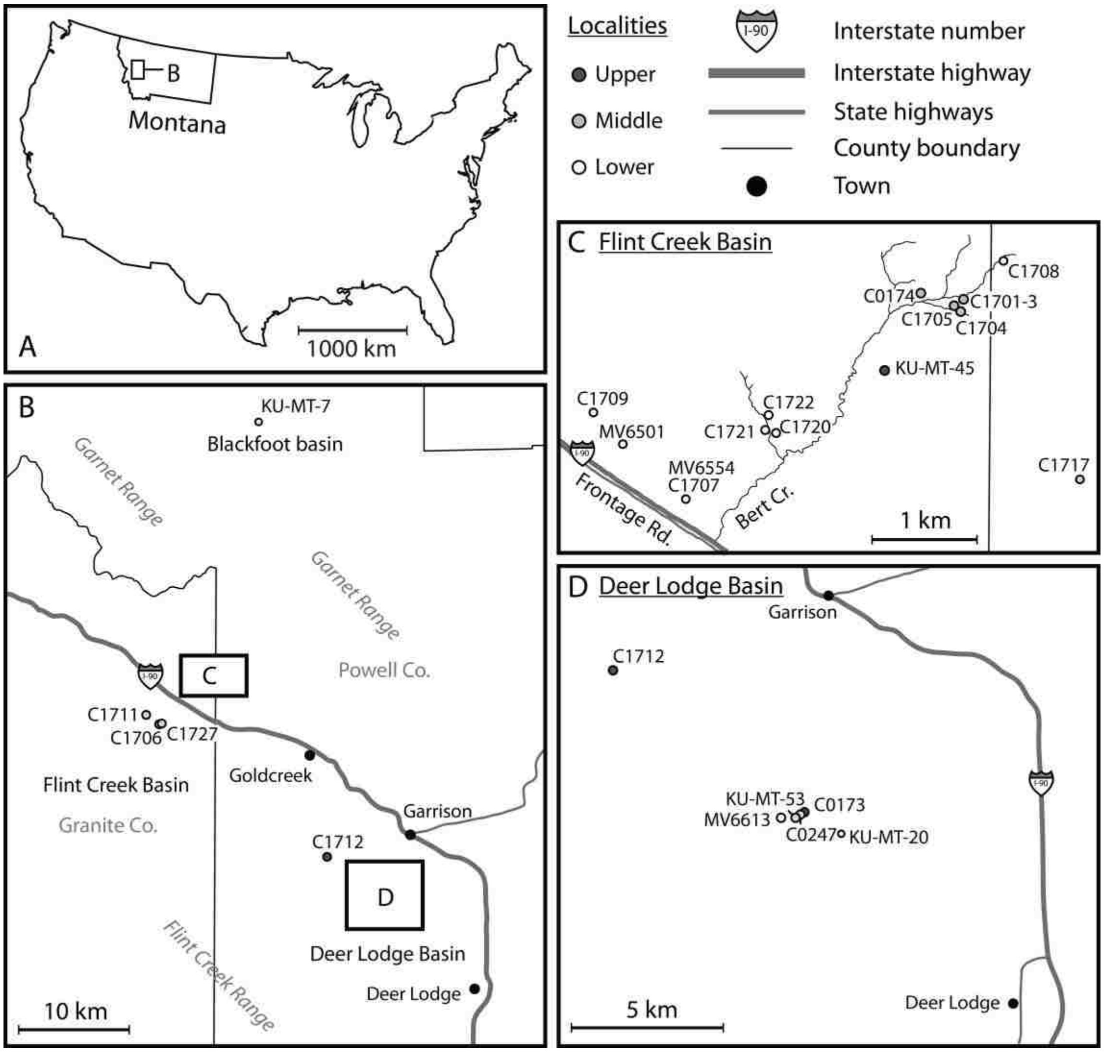

Figure 4.1. Map of the study area. A) Location of the state of Montana and of the study area in the United States. The rectangle labeled B indicates the approximate location of the study area in Montana but is oversized for ease of view. B) Location of the assemblages studied in western Montana (Granite and Powell Counties). The rectangles C and D indicate the location of the two basins studied. C) Detailed view of the location of the assemblages of the Flint Creek Formation in the Bert Creek area. D) Detailed view of the assemblages of the Deer Lodge Basin.

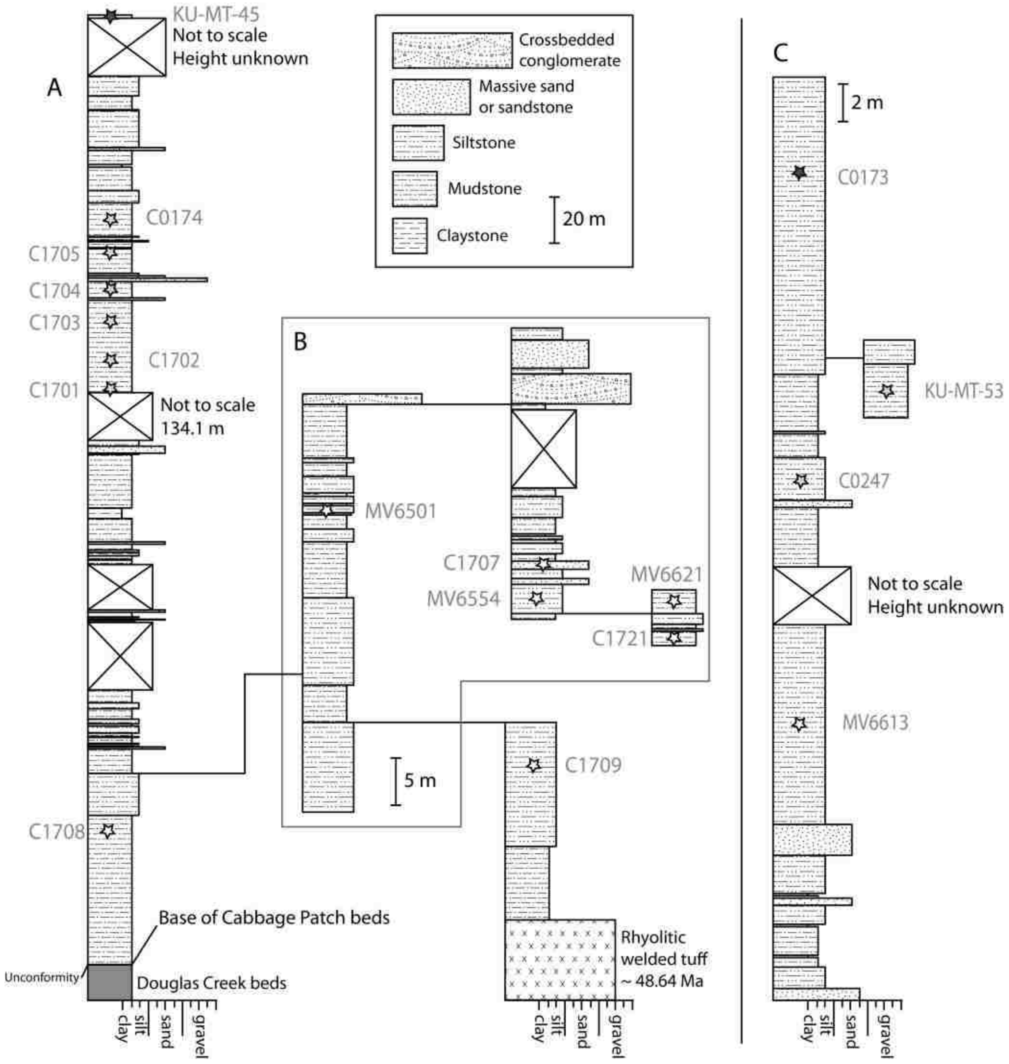

Figure 4.2. Summary of the stratigraphy of the Cabbage Patch beds. A-B) Stratigraphic section through the deposits of the Flint Creek Basin in the Bert Creek area (drawn from data modified and updated from Rasmussen 1969, 1977). C) Stratigraphic section through the deposits of the Deer Lodge Basin in the Tavenner Ranch area (drawn from data modified and updated from Rasmussen 1969, 1977). Note the different units across the three different parts of the figure. The colors of the stars indicate the biostratigraphic units of the assemblages (see Fig. 1 for legend).

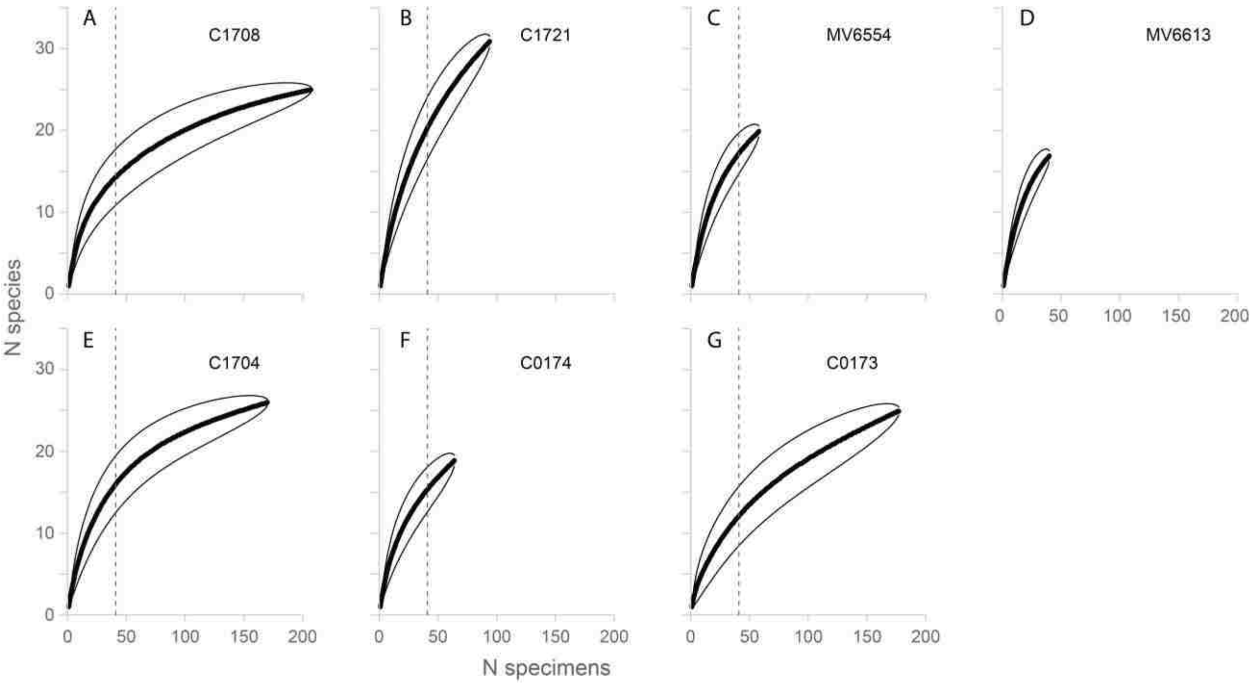

Figure 4.3. Rarefaction curves for the seven best sampled assemblages from the Cabbage Patch beds. The thick line shows the estimated species richness for each subsampled number of specimens (N) in steps of 1. The thinner lines show the upper and lower bounds of the 95% confidence intervals. A) Rarefaction curve for C1708. B) Rarefaction curve for C1721. C) Rarefaction curve for MV6554. D) Rarefaction curve for MV6613. E) Rarefaction curve for C1704. F) Rarefaction curve for C0174. G) Rarefaction curve for C0173. All curves' axes are on the same scale. The dashed line shows the sample size of the most poorly sampled assemblage (N=41), MV6613.

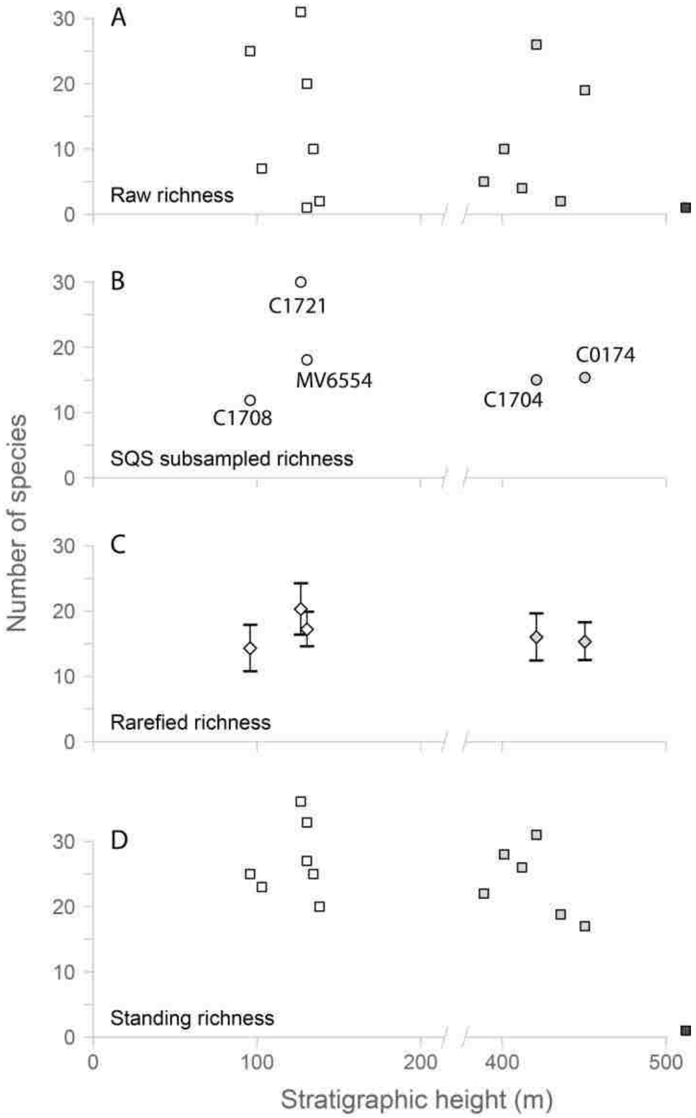

Figure 4.4. Richness of the Cabbage Patch assemblages in the Flint Creek Basin. A) Raw richness. B) Shareholder quorum subsampling (SQS) richness for select labeled assemblages. C) Rarefied richness for the same set of assemblages as B. D) Standing richness for the same assemblages as A. Note the x axis truncated for space. The colors of the symbols reflect the stratigraphic unit of the assemblages (see Fig. 1). Upper and lower bounds of 95% confidence interval are shown for the rarefied richness.

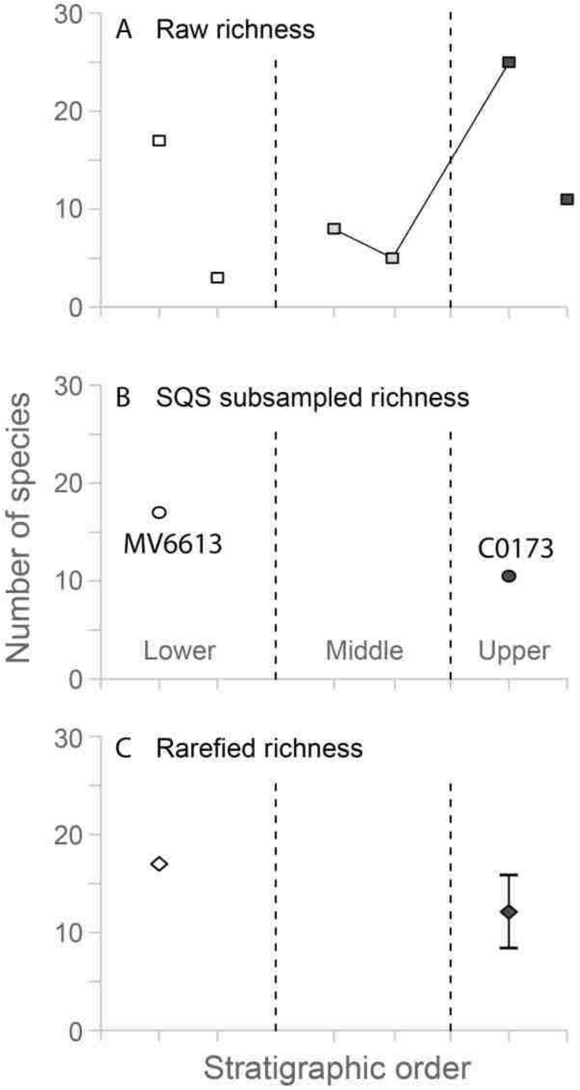

Figure 4.5. Richness of the Cabbage Patch assemblages in the Deer Lodge Basin. Note that the x axis is only meaningful in that it separates the lower, middle, and upper units of the beds (dashed lines; symbols' colors as in Fig. 1). A) Raw richness for all six assemblages of the basin studied. The three basins linked by a line follow one another in the stratigraphic section (not to scale; see Fig. 2C). B) shareholder quorum subsampling (SQS) richness for two labeled assemblages. C) Rarefied richness for the same set of assemblages as B. Upper and lower bounds of 95% confidence interval are shown for the rarefied richness.

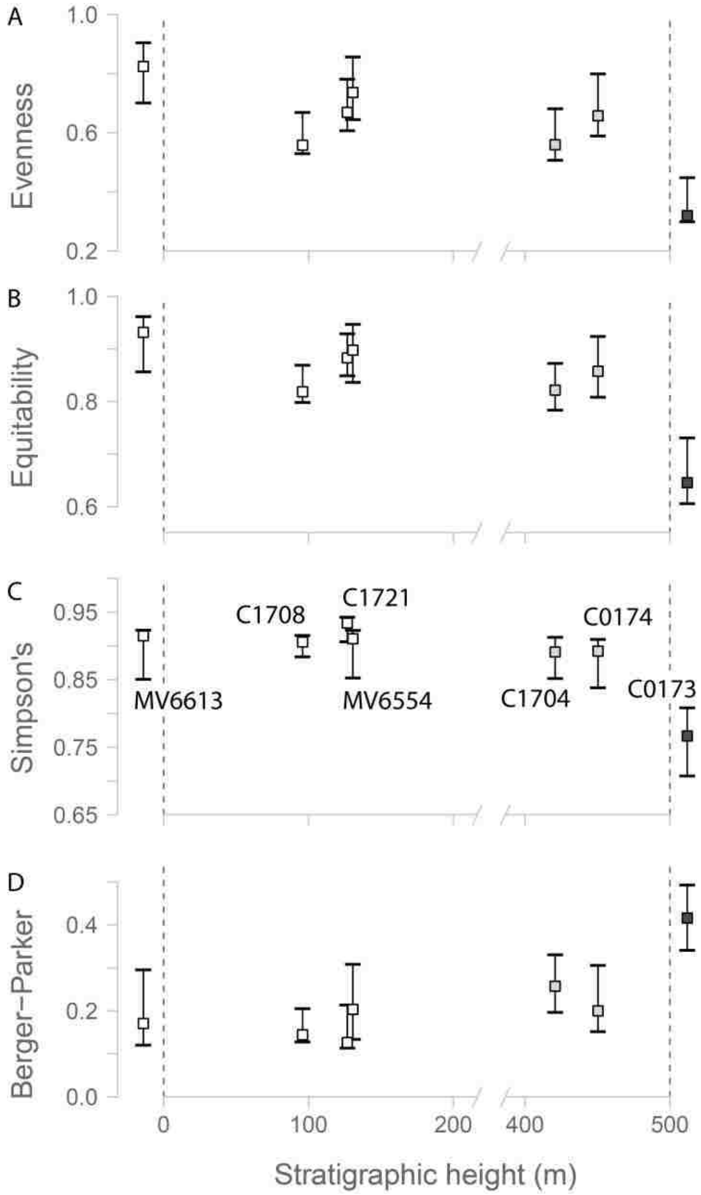

Figure 4.6. Summary of biodiversity indices through the Cabbage Patch beds including upper and lower bounds of 95% confidence intervals. A) Evenness (e^H/S). B) Equitability (J). C) Simpson's index (1-D). D) Berger-Parker index (d). Note the x axis truncated for space. The color of the symbols reflect the stratigraphic unit of the assemblages (see Fig. 1). The assemblages on the outside of the two dashed lines are from the Deer Lodge Basin and lack detailed stratigraphic information. The assemblages in between the dashed lines are from the Flint Creek Basin (x axis indicates stratigraphic position).

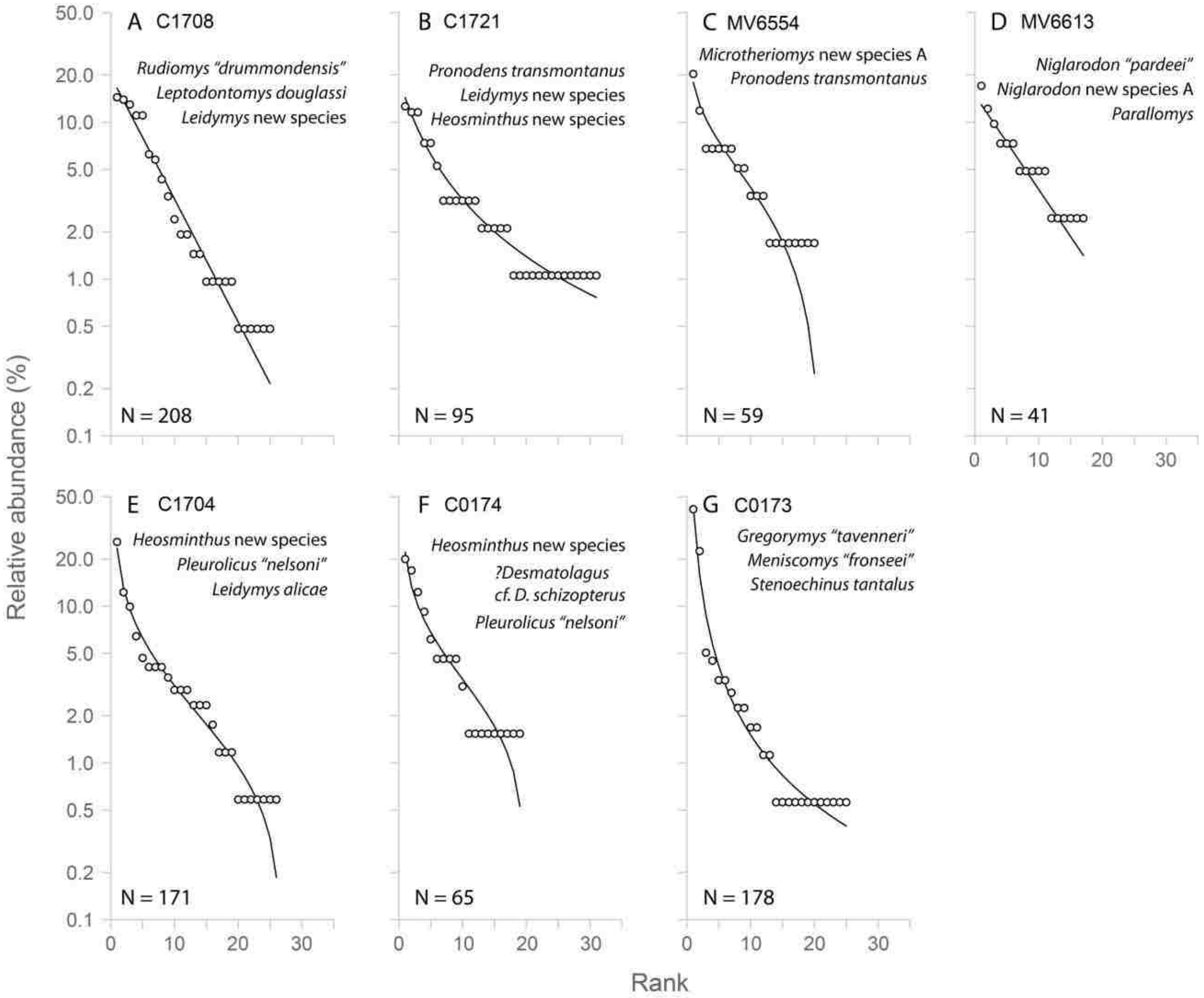

Figure 4.7. Relative abundance distributions for the seven best-sampled assemblages. The curve is that of the best model fit (Table X). The three most abundant taxa within each of the assemblages are also indicated. A0 RAD for C1708. B) RAD for C1721. C) RAD for MV6554. D) RAD for MV6613. E) RAD for C1704. F) RAD for C0174. G) RAD for C0173. Note that all plots are scaled similarly on both the x and y axes.

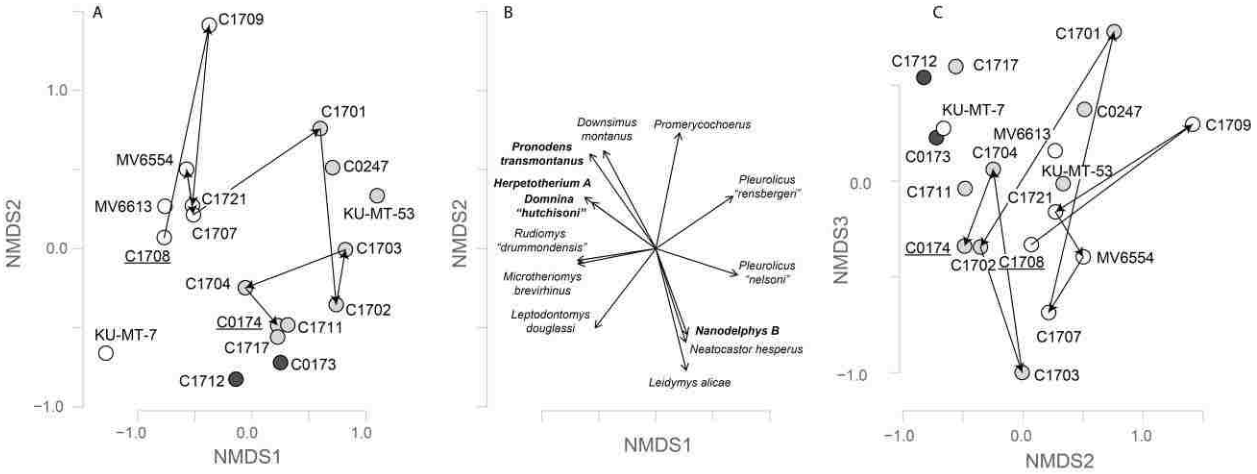

Figure 4.8. Non-metric dimensional scaling plots of Cabbage Patch assemblages. A) First two axes of the NMDS plot showing distance between assemblages. B) Loadings of the species along the first two axes of the NMDS, species in bold are White River relicts. C) Second and third axes of the NMDS plot with distance between assemblages. Color of symbols indicates biostratigraphic unit the assemblage belongs to. The arrows show the trajectory in multivariate space of the Cabbage Patch fauna through the stratigraphic section of the Flint Creek Basin from C1708 to C0174. The first and last assemblages are underlined.

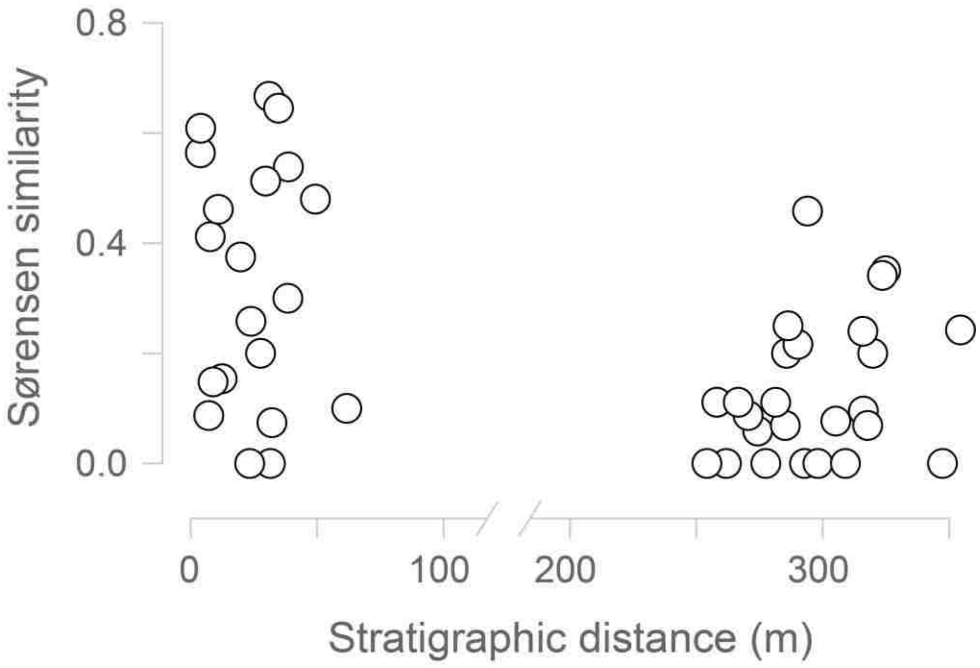

Figure 4.9. Bivariate plot of the pairwise stratigraphic distances between assemblages and Sørensen distance. Note the truncated x axis.

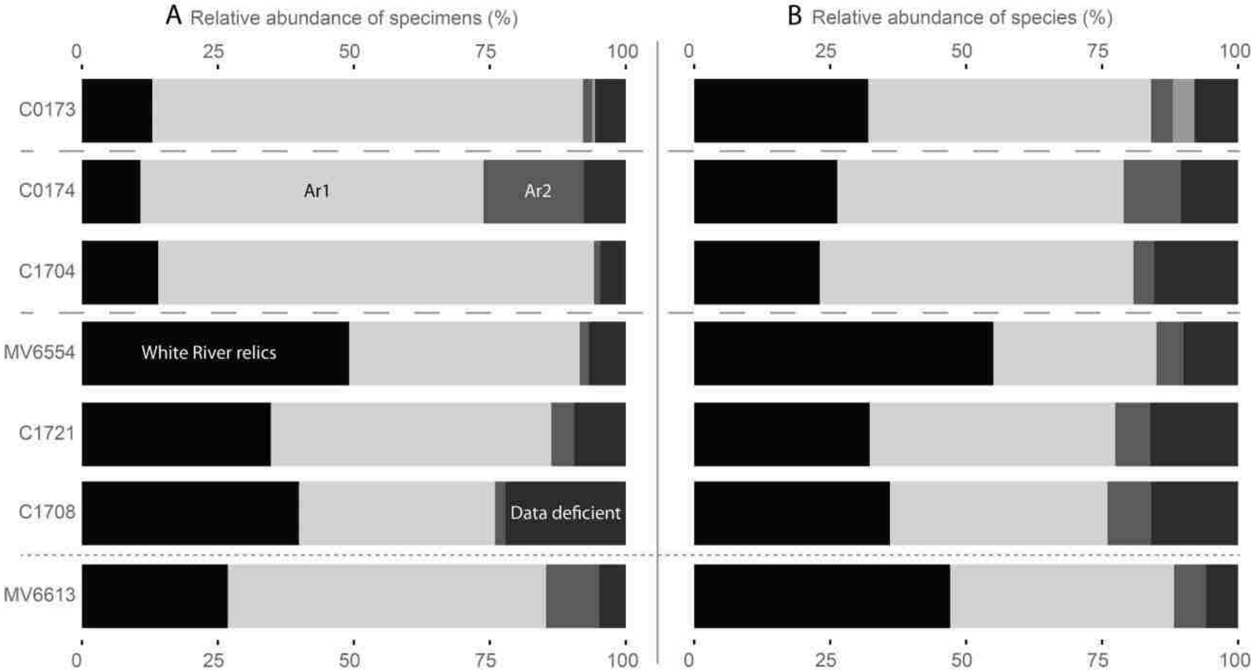

Figure 4.10. Relative abundances of mammalian taxa across the seven best-sampled assemblages of the Cabbage Patch beds. A) Relative abundance of specimens. B) Relative abundance of species. The light gray sliver not labeled in C0173 corresponds to taxa currently known from late Arikareean deposits. The dashed lines separate the three units of the beds (lower, middle, and upper). The dotted line distinguishes the lower assemblage from the Deer Lodge Basin (MV6613) from those of the Flint Creek Basin. See Appendix 4.1 and Table 11 for details.

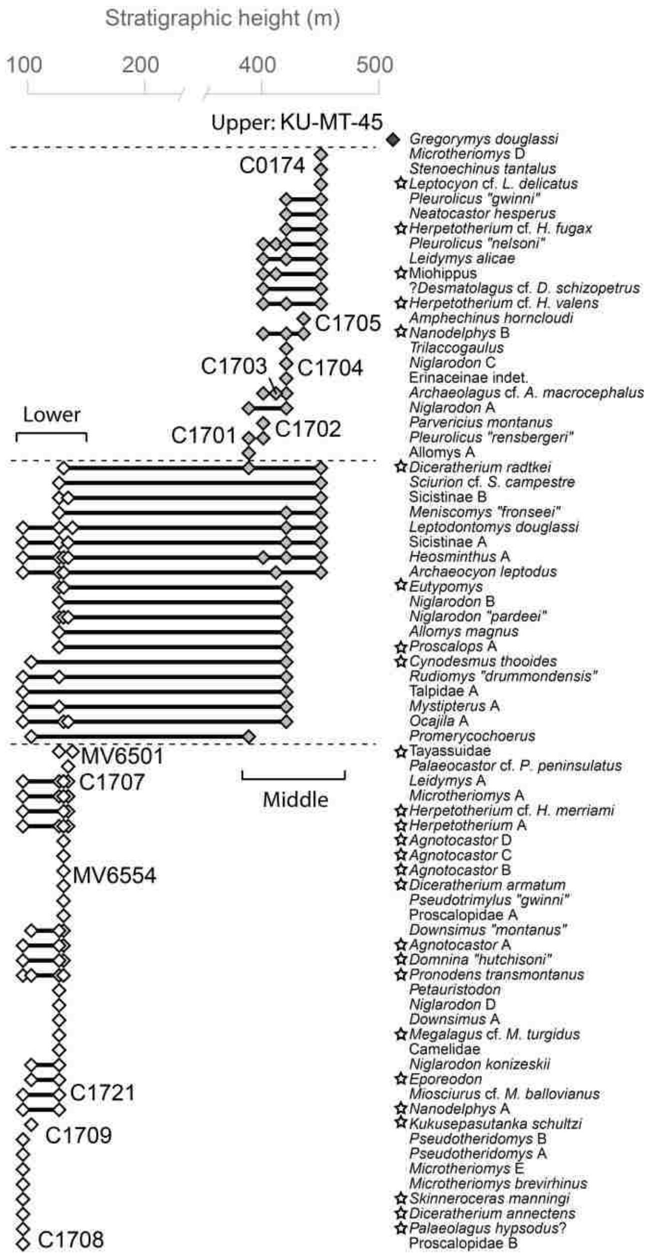

Figure 4.11. Biostratigraphic ranges of mammalian species in the Flint Creek Basin. Note the truncated x axis. The color of the symbols indicates the unit of the beds the assemblages belong to. Dashed lines separate taxa restricted to the lower unit of the Cabbage Patch, shared by the lower and middle units, present only in the middle unit, or present only in the upper unit respectively. Stars indicate White River relicts. See table 11 for family membership of taxa.

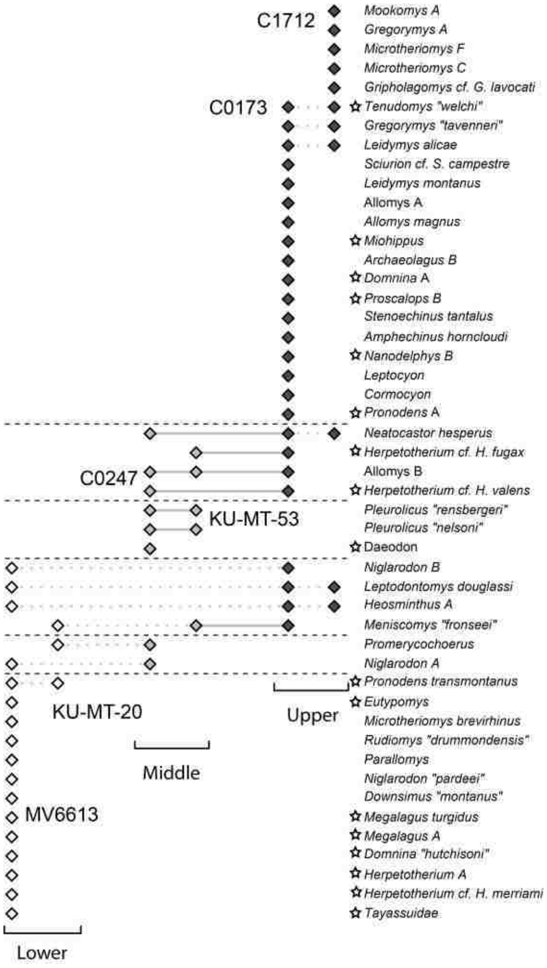

Figure 4.12. Biostratigraphic ranges of mammalian species in the Deer Lodge Basin. Note that the x axis is not informative. The color of the symbols indicates the unit of the beds the assemblages belong to. Assemblages that can be placed in a stratigraphic section are linked by full lines (not to scale; see Fig. 2C). Dotted lines are only provided for ease of reading. Dashed lines separate taxa restricted to the lower unit of the Cabbage Patch, shared by the lower and middle units, shared across all three units of the beds, shared by the middle and upper units, or present only in the upper unit respectively. Stars indicate White River relicts. See table 11 for family membership of taxa.

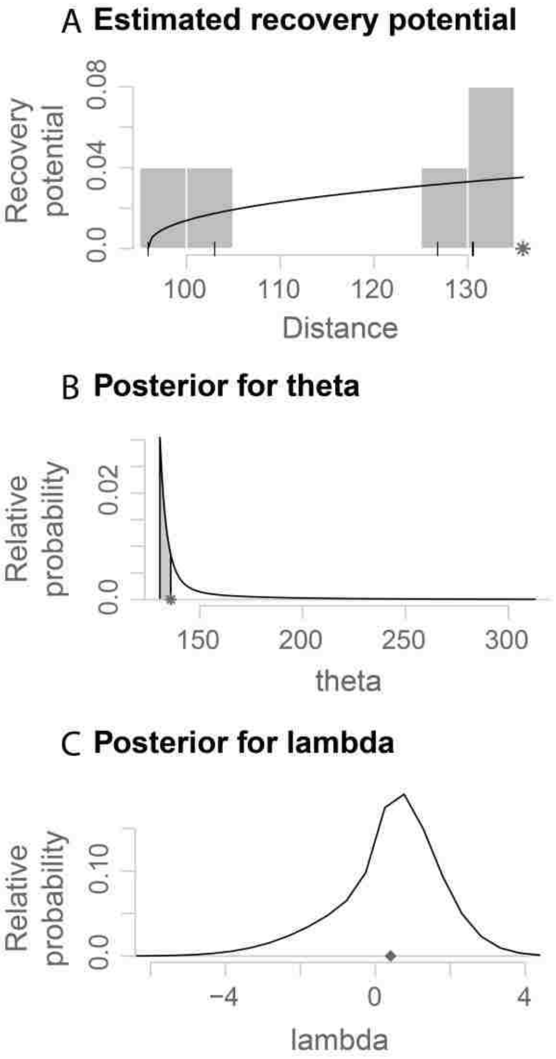

Figure 4.13. Results of the Adaptive Beta method for the disappearance of *Pronodens transmontanus*. A, Recovery potential. The grey bars show the actual occurrences throughout the section. The tick marks indicate the exact values of the stratigraphic position of these occurrences. The line shows the modelled recovery potential function. The star indicates the estimated disappearance of the taxon; B, Posterior distribution for theta (true disappearance, θ); C, Posterior distribution for the recovery function parameter lambda (λ). The confidence intervals are the shaded regions. Point estimates are shown with stars.

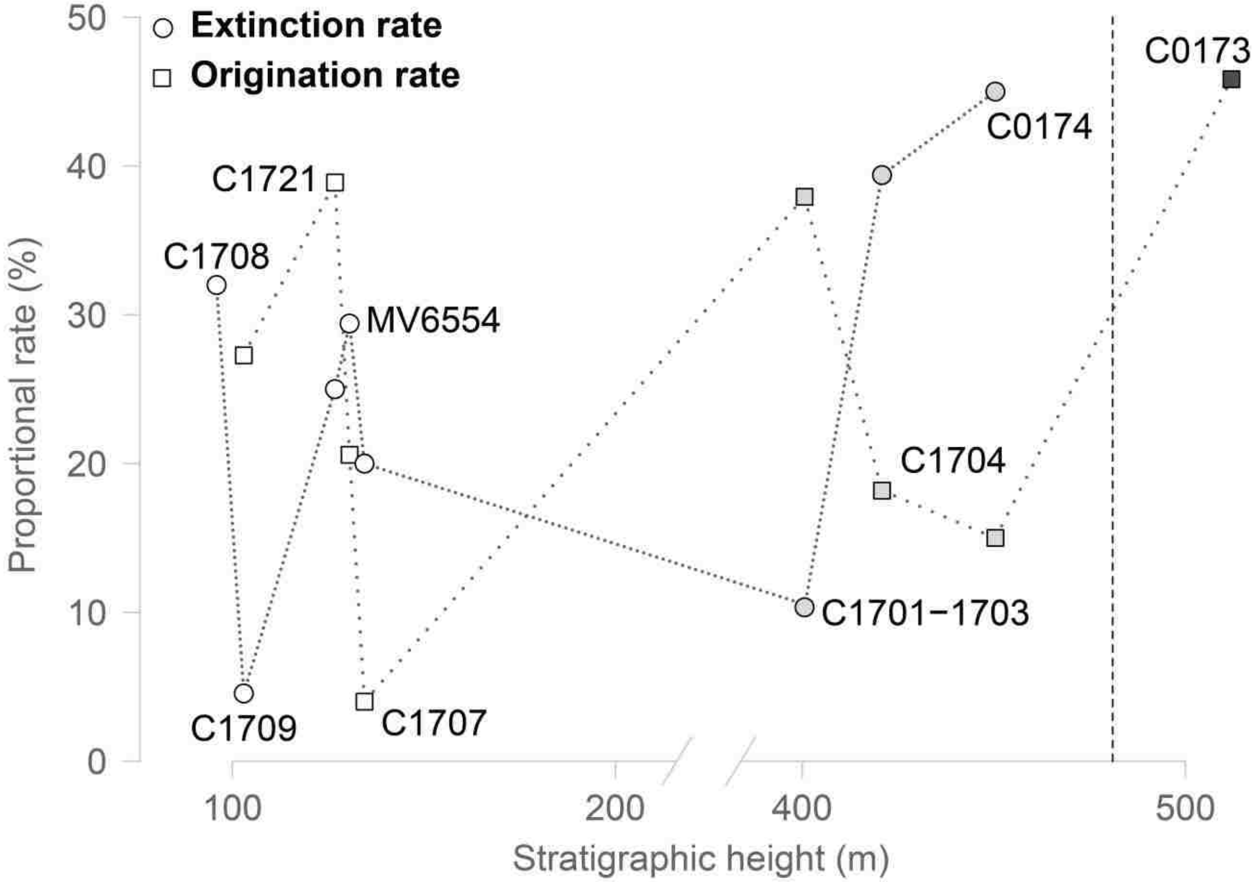

Figure 4.14. Proportional turnover rates through the Cabbage Patch beds. The lines are provided only for ease of reading. Note the truncated x axis. The dashed line indicates a lack of continuous stratigraphy. Squares indicate appearance rate values. Disappearance rate values are shown with circles. The appearance rate at C1708 and the disappearance rate at C0173 are not figured; they are an artefact of the analysis.

TABLES

Table 4.1. Select characteristic taxa of the White River and Runningwater chronofaunas. References: 1, Hunt 2004; 2, Webb 1998; 3, Woodburne 2004; 4, Stevens and Stevens 2007; 5, Dawson 2008; 6, Janis et al. 2008; 7, Honey et al. 1998; 8, Janis et al. 1998; 9, Tedford et al. 2009; 10, Hopkins 2007; 11, Gunnell et al. 2008; 12, Samuels and Van Valkenburgh 2009.

Fauna		White River Chronofauna	Runningwater Chronofauna	References
Typical taxa	Carnivores	Hyaenodontid creodonts, nimravids, daphoenine amphicyonids, hesperocyonine canids	Canine dogs (*Leptocyon*), procyonids, diverse borophagine dogs and mustelids	1, 3, 9
	Ungulates	Hyracodontine and diceratherine rhinocerotids, miohippine horses, poebrodontine camels, hypertragulids and leptomerycid ruminants, entelodonts, antracotheriids, and miniochoerine, merycoidodontine, as well as leptaucheniine oreodonts	Diverse camels and ruminants	2-4, 7-8
	Small mammals	Ischyromyid, cylindrodontid, cedromurine, and sciuravid rodents, aplodontid rodent *Prosciurus*, stem geomyoids, lagomorphs *Megalagus* and *Palaeolagus*	Mylagaulids, marmotines, geomyids, diverse beavers and erinaceine hedgehogs	3, 5-6, 10-12

Table 4.2. Stratigraphic position and number of specimens (N) of assemblages from the Flint Creek Basin placed in stratigraphic section. Abbreviations: DBU, distance from base of formation to base of unit in meters; L, Lower; M, Middle; U, Upper.

Assemblages	C1708	C1709	C1721	MV6621	MV6554	C1707	MV6501	C1711
Unit	L	L	L	L	L	L	L	M
DBU	95.4	90	126.1	129.3	128.7	134	138.2	--
Thickness	0.9	26	1.4	2.4	3.7	0.9	0.3	
Midpoint	95.9	103	126.8	130.5	130.6	134.5	138.3	--
N	208	13	95	1	59	16	2	36
Assemblages	**C1717**	**C1701**	**C1702**	**C1703**	**C1704**	**C1705**	**C0174**	**KU-MT-45**
Unit	M	M	M	M	M	M	M	U
DBU	--	388.1	400.5	410.4	420.5	434.4	443.4	511.3
Thickness		1.2	1.1	3.1	0.6	2.4	14	1.4
Midpoint	--	388.7	401.1	412	420.8	435.6	450.4	512
N	18	6	18	4	171	2	65	1

Table 4.3. Stratigraphic position and number of specimens (N) in the assemblages of the Deer Lodge Basin included in this study. Abbreviations: RSP, Relative Stratigraphic Position; L, Lower; M, Middle; U, Upper.

Unit	Assemblage	Raw Richness	Standing Richness	SQS subsampled richness	Rarefied richness
U	C0173	25	--	10.48	12.1 (8.48-15.73)
M	C0174	19	19	15.35	15.3 (12.6-18.09)
M	C1704	26	32	15.05	16 (12.53-19.48)
L	MV6554	20	34	18.11	17.2 (14.7-19.71)
L	C1721	31	36	30.01	20.3 (16.49-24.06)
L	C1708	25	25	11.84	14.3 (10.88-17.73)
L	MV6613	17	--	--	--

Table 4.4. Measures of richness of select Cabbage Patch assemblages. 95% confidence intervals for rarefied richness are in parentheses. The data for MV6613 are the basis for the shareholder quorum subsampling (SQS) and the rarefaction (see text for details). Abbreviations: U, upper; M, middle; L, lower.

Assemblages	KU-MT-20	MV6613	C0247	KU-MT-53	C0173	C1712
Unit	L	L	M	M	U	U
RSP	--	1	2	3	4	5?
N	5	41	11	19	178	14

Table 4.5. Biodiversity indices for select Cabbage Patch assemblages. 95% confidence intervals are shown in parentheses.

Unit	Assemblage	Evenness	Equitability	Simpson's	Berger-Parker
U	C0173	0.32 (0.31-0.44)	0.65 (0.61-0.73)	0.77 (0.71-0.81)	0.42 (0.34-0.49)
M	C0174	0.66 (0.59-0.80)	0.86 (0.81-0.92)	0.89 (0.84-0.91)	0.20 (0.15-0.31)
M	C1704	0.56 (0.51-0.68)	0.82 (0.78-0.87)	0.89 (0.85-0.91)	0.26 (0.20-0.33)
L	MV6554	0.74 (0.65-0.85)	0.90 (0.84-0.94)	0.91 (0.85-0.92)	0.20 (0.14-0.31)
L	C1721	0.67 (0.61-0.78)	0.88 (0.85-0.93)	0.93 (0.90-0.94)	0.13 (0.12-0.21)
L	C1708	0.56 (0.53-0.66)	0.82 (0.80-0.87)	0.91 (0.89-0.91)	0.14 (0.13-0.20)
L	MV6613	0.82 (0.70-0.90)	0.93 (0.86-0.96)	0.91 (0.85-0.92)	0.17 (0.12-0.29)

Table 4.6. Akaike weights of model fit for relative abundance distributions. Best-supported model indicated in bold when unequivocal. The null model is a broken-stick model. The preemption model is a geometric series.

Assemblage	Null	Preemption	Lognormal	Zipf	Zipf-Mandelbrot
C1708	0.015	**86.04**	0.027	~ 0	13.95
C1721	10.19	25.3	13.57	11.86	39.08
MV6554	29.66	24.02	20.59	17.92	7.81
MV6613	15.94	36.97	20.31	18.53	8.25
C1704	0.19	0.04	**63.71**	22.84	13.22
C0174	30.7	33.09	12.07	10.21	13.93
C0173	~ 0	~ 0	0.058	**72.29**	27.65

Table 4.7. Chord distance between well-sampled assemblages from the Cabbage Patch beds. Transitions between units are marked with an *. Each assemblage is compared with that younger than it in sequence except for MV6613 whose stratigraphic position relative to other lower Cabbage Patch assemblages is unknown. Abbreviation: Loc., Locality; Chord/Strat., ratio of chord distance to thickness of sediments between the two assemblages.

Loc. pair	C1708 MV6613	C1721 MV6613	MV6554 MV6613	C1704 MV6613	C1721 C1708	MV6554 C1721	C1704 MV6554	C0174 C1704	C0173 C0174
Chord distance	1.1	0.99	1.13	1.19	0.87	0.88	1.28*	0.81	1.16*
Chord/Strat.	--	--	--	--	0.028	0.232	0.004	0.027	--

Table 4.8. NMDS scores for all assemblages included in my analysis.

Assemblage	NMDS 1	NMDS 2	NMDS 3
C0173	0.251	-0.721	0.227
C0174	0.227	-0.486	-0.340
C0247	0.708	0.512	0.374
C1701	0.599	0.759	0.780
C1702	0.739	-0.354	-0.344
C1703	0.820	-0.007	-1.000
C1704	-0.057	-0.248	0.061
C1707	-0.512	0.214	-0.686
C1708	-0.768	0.070	-0.332
C1709	-0.373	1.414	0.297
C1711	0.315	-0.483	-0.039
C1712	-0.140	-0.826	0.541
C1717	0.226	-0.559	0.598
C1721	-0.521	0.271	-0.161
KU-MT-53	-1.280	-0.661	0.275
KU-MT-7	1.098	0.334	-0.013
MV6554	-0.572	0.502	-0.396
MV6613	-0.762	0.268	0.158

Table 4.9. Loadings of the taxa included in the NMDS analysis along the first two axes of the ordination. All taxa with $p<0.05$ are displayed in figure 8.

Taxon	NMDS 1	NMDS 2	R^2	p
?Desmatolagus	0.683	-0.730	0.137	0.362
Agnotocastor A	-0.874	0.486	0.235	0.151
Allomys magnus	-0.356	-0.934	0.038	0.746
Allomys A	0.998	0.056	0.055	0.628
Allomys B	0.997	0.075	0.230	0.151
Amphechinus horncloudi	0.290	-0.957	0.171	0.215
Archaeocyon leptodus	-0.884	0.467	0.031	0.782
Archaeolagus cf. *A. macrocephalus*	0.895	-0.446	0.147	0.326
Cynodesmus thooides	-0.288	0.958	0.142	0.351
Diceratherium radtkei	0.258	0.966	0.044	0.698
Domnina "hutchisoni"	-0.887	0.462	0.366	0.026
Downsimus "montanus"	-0.594	0.804	0.539	0.004
Eporeodon	-0.396	0.918	0.327	0.054
Eutypomys	-0.891	0.454	0.193	0.206
Gregorymys "tavenneri"	0.059	-0.998	0.225	0.136
Heosminthus A	-0.478	-0.878	0.314	0.068
Herpetotherium cf. *H. fugax*	0.681	-0.732	0.245	0.133
Herpetotherium cf. *H. merriami*	-0.704	0.711	0.249	0.128
Herpetotherium A	-0.887	0.461	0.450	0.008
Herpetotherium cf. *H. valens*	0.463	-0.887	0.234	0.134
Leidymys alicae	0.327	-0.945	0.603	0.002
Leidymys cf. *L. montanus*	0.357	-0.934	0.160	0.254
Leidymys A	-0.877	0.480	0.305	0.080
Leptocyon large species	0.290	-0.957	0.171	0.215
Leptodontomys douglassi	-0.728	-0.685	0.487	0.007
Megalagus cf. *M. turgidus*	-0.889	0.459	0.153	0.290
Meniscomys "fronseei"	0.691	-0.723	0.071	0.621
Microtheriomys brevirhinus	-0.990	-0.140	0.435	0.016
Microtheriomys A	-0.877	0.480	0.305	0.080
Miohippus	0.726	-0.687	0.313	0.058
Miosciurus cf. *M. ballovianus*	-0.970	-0.245	0.064	0.602
Mystipterus A	-0.907	-0.421	0.054	0.653
Nanodelphys A	-0.951	0.309	0.138	0.356
Nanodelphys B	0.452	-0.892	0.339	0.047

Neatocastor hesperus	0.405	-0.914	0.382	0.030
Talpidae A	-0.898	-0.440	0.287	0.085
Niglarodon "pardeei"	-0.891	0.455	0.267	0.103
Niglarodon "konizeskii"	-0.396	0.918	0.327	0.054
Niglarodon A	0.621	0.784	0.044	0.722
Niglarodon B	-0.568	-0.823	0.061	0.634
Ocajila A	-0.999	0.043	0.096	0.478
Palaeocastor cf. *P. peninsulatus*	-0.512	-0.859	0.010	0.931
Pleurolicus "gwinni"	0.241	-0.970	0.120	0.378
Pleurolicus "nelsoni"	0.974	-0.227	0.490	0.005
Pleurolicus "rensbergeri"	0.898	0.440	0.515	0.004
Promerycochoerus	0.272	0.962	0.528	0.003
Pronodens transmontanus	-0.695	0.719	0.631	0.001
Proscalops A	-0.999	0.049	0.026	0.829
Rudiomys "drummondensis"	-0.994	-0.108	0.435	0.012
Sciurion cf. *S. campestre*	-0.037	-0.999	0.059	0.629
Sicistinae A	-0.991	-0.134	0.101	0.432
Sicistinae B	-0.636	-0.772	0.023	0.829
Stenoechinus tantalus	0.307	-0.952	0.154	0.281
Tayassuidae	-0.889	0.459	0.153	0.290
Tenudomys "welchi"	0.059	-0.998	0.225	0.136

Table 4.10. 50% confidence intervals for the biostratigraphic ranges determined from the Adaptive Beta method.

Taxon	Lower 50%	Upper 50%
Heosminthus A	3.3	beyond
Pronodens transmontanus	68	135.9
Archaeocyon leptodus	beyond	beyond
Sicistinae A	beyond	beyond
Leptodontomys douglassi	beyond	beyond
Herpetotherium A	63.7	138.2
Microtheriomys A	63.7	138.2
Leidymys A	63.7	138.2
Ocajila A	68.3	beyond
Niglarodon "pardeei"	105.1	beyond
Pleurolicus "nelsoni"	393.3	485.4
Domnina "hutchisoni"	61.6	137.6
Agnotocastor A	61.6	137.6
Downsimus "montanus"	76.6	136.3
Mystipterus A	32.5	beyond
Rudiomys "drummondensis"	32.5	beyond
Herpetotherium cf. *H. merriami*	57.5	142
Eutypomys	77.1	beyond
Sicistinae B	72.1	beyond
Diceratherium radtkei	beyond	beyond
Archaeolagus cf. *A. macrocephalus*	389.8	429.4
Miohippus	388.6	492.7
Nanodelphys B	380.7	450
Meniscomys "fronseei"	beyond	beyond
Herpetotherium cf. *H. valens*	381.9	481.5
Leidymys alicae	381.9	481.5

Table 4.11. Biostratigraphic ranges of taxa present in the Cabbage Patch beds. Abbreviations: Hem, Hemingfordian; L, lower; M, middle; U, upper; FAD, First Appearance Datum; WR, White River relicts and members of outgoing lineages. Sources: 1, Hopkins (2008); 2, Tedford et al. (2004); 3. Korth and Samuels (2015); 4, Calede (2014); 5, Lindsay (2008); 6, Calede and Cairns (2015); 7, Flynn (2008); 8, Korth (2008); 9, Flynn et al. (2008); 10, Jiménez-Hidalgo et al. (2015); 11, Woodburne (2004); 12, Munthe (1998); 13, Tedford et al. (2009); 14, Wang et al. (1999); 15, Flynn and Jacobs (2008); 16, Prothero and Emry (2004); 17, Wright (1998).

Family	Genus	Species	L	M	U	FAD	Comment	Source
Sciuridae	*Sciurion*	*cf. S. campestre*	X	X	X	--		--
Sciuridae	*Petauristodon*	indet.	X			--		--
Erinaceidae	*Stenoechinus*	*tantalus*		X	X	--		--
Erinaceidae	Erinaceinae indet.	indet.		X		--		--
Proscalopidae	Genus B	species B	X			--		--
Proscalopidae	Genus A	species A	X			--		--
Soricidae	*Pseudotrimylus*	indet.		X		--		--
Soricidae	*Pseudotrimylus*	*"gwinni"*	X			--		--
Talpidae	New Genus A	new species A	X	X		--		--
Talpidae	*Mystipterus*	new species A	X	X		--		--
Camelidae	indet.	indet.	X			--		--
Aplodontidae	*Rudiomys*	*"drummondensis"*	X	X		Ar1		1
Aplodontidae	*Niglarodon*	species D	X			Ar1		2
Aplodontidae	*Niglarodon*	species C		X		Ar1		2
Aplodontidae	*Niglarodon*	species B	X	X	X	Ar1		2
Aplodontidae	*Niglarodon*	species A	X	X		Ar1		2
Aplodontidae	*Niglarodon*	*"pardeei"*	X	X		Ar1		2
Aplodontidae	*Niglarodon*	*"konizeskii"*	X			Ar1		2
Aplodontidae	*Meniscomys*	*"fronseei"*	X	X	X	Ar1		2
Aplodontidae	*Downsimus*	new species A	X			Ar1		1
Aplodontidae	*Downsimus*	*"montanus"*	X			Ar1		1
Aplodontidae	*Allomys*	species B		X	X	Ar1	FAD Ar2 Great Plains	1-2
Aplodontidae	*Allomys*	new species A		X	X	Ar1	FAD Ar2 Great Plains	1-2

Aplodontidae	*Allomys*	*magnus*	X	X	X	Ar1	FAD Ar2 Great Plains	1-2
Castoridae	*Palaeocastor*	cf. *P. peninsulatus*	X	X		Ar1		3-4
Castoridae	*Neatocastor*	*hesperus*		X	X	Ar1		2
Castoridae	*Microtheriomys*	new species F			X	Ar1	Known from Ar1 only	3
Castoridae	*Microtheriomys*	new species E	X			Ar1	Known from Ar1 only	3
Castoridae	*Microtheriomys*	new species D		X		Ar1	Known from Ar1 only	3
Castoridae	*Microtheriomys*	new species C			X	Ar1	Known from Ar1 only	3
Castoridae	*Microtheriomys*	new species B		X		Ar1	Known from Ar1 only	3
Castoridae	*Microtheriomys*	new species A	X			Ar1	Known from Ar1 only	3
Castoridae	*Microtheriomys*	*brevirhinus*	X			Ar1	Known from Ar1 only	3
Cricetidae	*Leidymys*	new species A	X			Ar1		5
Cricetidae	*Leidymys*	cf. *L. montanus*		X	X	Ar1		5
Cricetidae	*Leidymys*	*alicae*		X	X	Ar1		5
Dipodidae	Sicistinae indet.	species B	X	X		Ar1		6-7
Dipodidae	Sicistinae indet.	species A	X	X		Ar1		6-7
Dipodidae	*Heosminthus*	new species A	X	X	X	Ar1		6
Eomyidae	*Leptodontomys*	*douglassi*	X	X	X	Ar1	Ar3 only John Day	3, 8
Geomyidae	*Pleurolicus*	*"rensbergeri"*		X		Ar1	FAD Ar2 Great Plains	2
Geomyidae	*Pleurolicus*	*"nelsoni"*		X		Ar1	FAD Ar2 Great Plains	2
Geomyidae	*Pleurolicus*	*"gwinni"*		X		Ar1	FAD Ar2 Great Plains	2
Geomyidae	*Gregorymys*	new species A			X	Ar1		9-10
Geomyidae	*Gregorymys*	cf. *G. douglassi*			X	Ar1		9-10
Geomyidae	*Gregorymys*	*"tavenneri"*			X	Ar1		9-10
Heteromyidae	*Mookomys*	species A			X	Ar1		9
Leporidae	*Archaeolagus*	species B			X	Ar1	FAD Ar2 Great Plains	2
Leporidae	*Archaeolagus*	cf. *A. macrocephalus*		X		Ar1	FAD Ar2 Great Plains	2
Erinaceidae	*Ocajila*	species A	X	X		Ar1		2
Canidae	*Leptocyon*	large species		X	X	Ar1	One specimen in Orellan	11-13
Aplodontidae	*Trilaccogaulus*	new species A		X		Ar2		2
Aplodontidae	*Parallomys*	indet.	X			Ar2		1-2
Eomyidae	*Pseudotheridomys*	species B	X			Ar1		8

Eomyidae	*Pseudotheridomys*	species A	X			Ar1		8
Sciuridae	*Miosciurus*	*ballovianus*	X	X		Ar2		3
?Ochotonidae	*Gripholagomys*	cf. *G. lavocati*			X	Ar2	FAD Ar2 Great Plains	2
stem lagomorph	*?Desmatolagus*	cf. *D. schizopetrus*		X		Ar2		2
Erinaceidae	*Parvericius*	*montanus*		X		Ar2		2
Erinaceidae	*Amphechinus*	*horncloudi*		X	X	Ar2	FAD Ar2 Great Plains	2
Canidae	*Archaeocyon*	*leptodus*	X	X		Ar2		14
Merycoidodontidae	*Promerycochoerus*	indet.	X	X		Ar2		2
Canidae	*Cormocyon*	indet.			X	Late	FAD at Ar/Hem boundary	14
Castoridae	*Agnotocastor*	morph. D	X			WR	LAD Ar1 Great Plains	2, 11
Castoridae	*Agnotocastor*	morph. C	X			WR	LAD Ar1 Great Plains	2, 11
Castoridae	*Agnotocastor*	morph. B	X			WR	LAD Ar1 Great Plains	2, 11
Castoridae	*Agnotocastor*	morph. A	X			WR	LAD Ar1 Great Plains	2, 11
Eutypomyidae	*Eutypomys*	*sp.*	X	X		WR		2, 11, 15
Geomyidae	*Tenudomys*	*"welchi"*			X	WR		11
Equidae	*Miohippus*	indet.		X	X	WR		11
Rhinocerotidae	*Skinneroceras*	*manningi*	X			WR		11
Rhinocerotidae	*Diceratherium*	*radtkei*	X	X		WR		11
Rhinocerotidae	*Diceratherium*	*armatum*	X			WR		11
Rhinocerotidae	*Diceratherium*	*annectens*	X			WR		2, 11
Leporidae	*Palaeolagus*	*hypsodus?*	X			WR	LAD Ar1	2, 11
Leporidae	*Megalagus*	species A	X			WR		2, 11
Leporidae	*Megalagus*	cf. *M. turgidus*	X			WR		2, 11
Proscalopidae	*Proscalops*	species B			X	WR	LAD Ar2 Great Plains	2, 11
Proscalopidae	*Proscalops*	species A	X	X		WR	LAD Ar2 Great Plains	2, 11
Soricidae	*Domnina*	indet.			X	WR		11
Soricidae	*Domnina*	*"hutchisoni"*	X			WR		11
Herpetotheriidae	*Herpetotherium*	species A	X			WR		16

Herpetotheriidae	*Herpetotherium*	cf. *H. valens*		X	X	WR	16
Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*	X			WR	16
Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*		X	X	WR	16
Peradectidae	*Nanodelphys*	species B		X	X	WR	16
Peradectidae	*Nanodelphys*	species A	X			WR	16
Canidae	*Cynodesmus*	*thooides*	X	X		WR	2, 11, 16
Canidae	*Leptocyon*	cf. *L. delicatus*		X		Ar2	13
Antracotheriidae	*Kukusepasutanka*	*schultzi*	X			WR	11
Entelodontidae	*Daeodon*	indet.		X		WR	11
Leptomerycidae	*Pronodens*	*transmontanus*	X			WR	11
Leptomerycidae	*Pronodens*	indet.			X	WR	11
Merycoidodontidae	*Eporeodon*	indet.	X			WR	2
Tayassuidae	indet.	indet.	X			WR	17

APPENDIX

A4.1. List of all specimens included in the analyses.

Museum	Specimen	Unit	Locality	Order	Family	Genus	Species
UWBM	98664	L	C1707	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
UWBM	98610	L	C1707	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	98837	L	C1707	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	98714	L	C1707	Eulipotyphla	Erinaceidae	*Ocajila*	species A
UWBM	98716	L	C1707	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
KUVP	18842	L	C1707	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	98700	L	C1707	Rodentia	Castoridae	*Palaeocastor*	cf. *P. peninsulatus*
UWBM	98663	L	C1707	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	98683	L	C1707	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	98737	L	C1707	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	98682	L	C1707	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	98720	L	C1707	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	98838	L	C1707	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	108091	L	C1707	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	98665	L	C1707	Rodentia	Dipodidae	Sicistinae A	
UWBM	98836	L	C1707	Rodentia	Dipodidae	Sicistinae B	
KUVP	18183	L	C1708	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18184	L	C1708	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18527	L	C1708	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18528	L	C1708	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18529	L	C1708	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18530	L	C1708	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18668	L	C1708	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18669	L	C1708	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	98765	L	C1708	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	101389	L	C1708	Carnivora	Canidae	*Archaeocyon*	cf. *A. leptodus*
UWBM	98840	L	C1708	Carnivora	Canidae	*Archaeocyon*	*leptodus*
KUVP	18175	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18507	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18508	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18512	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18515	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18521	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18595	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*

KUVP	18615	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18620	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18633	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18652	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
UWBM	98761	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
UWBM	101290	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
KUVP	18506	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18509	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18510	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18511	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18613	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18618	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18624	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18627	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18631	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18642	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18645	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18648	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18649	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18650	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18655	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18656	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18658	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18661	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18663	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18666	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	98820	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	101296	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	108060	L	C1708	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18513	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18514	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18616	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18619	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18625	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18626	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18632	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18635	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18636	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18637	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18638	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A

KUVP	18639	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18641	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18644	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18646	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18654	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18657	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18660	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18662	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18665	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18667	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
UMPC	3012	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
UWBM	98751	L	C1708	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
KUVP	18155	L	C1708	Eulipotyphla	Erinaceidae	*Ocajila*	species A
KUVP	18157	L	C1708	Eulipotyphla	Erinaceidae	*Ocajila*	species A
KUVP	18499	L	C1708	Eulipotyphla	Erinaceidae	*Ocajila*	species A
KUVP	18523	L	C1708	Eulipotyphla	Erinaceidae	*Ocajila*	species A
KUVP	18600	L	C1708	Eulipotyphla	Erinaceidae	*Ocajila*	species A
KUVP	18605	L	C1708	Eulipotyphla	Erinaceidae	*Ocajila*	species A
KUVP	18611	L	C1708	Eulipotyphla	Erinaceidae	*Ocajila*	species A
KUVP	18604	L	C1708	Eulipotyphla	Proscalopidae	Genus B	species B
KUVP	18166	L	C1708	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
KUVP	18501	L	C1708	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
KUVP	18591	L	C1708	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
KUVP	18606	L	C1708	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
KUVP	18607	L	C1708	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
KUVP	18594	L	C1708	Eulipotyphla	Talpidae	*Mystipterus*	new species A
KUVP	18603	L	C1708	Eulipotyphla	Talpidae	*Mystipterus*	new species A
UWBM	101291	L	C1708	Eulipotyphla	Talpidae	*Mystipterus*	new species A
KUVP	18156	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18158	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18516	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18597	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18598	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18599	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18601	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18602	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18608	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18609	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18612	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	18622	L	C1708	Eulipotyphla	Talpidae	New Genus A	new species A

KUVP	18180	L	C1708	Lagomorpha	Leporidae	*Palaeolagus*	*hypsodus?*
KUVP	18181	L	C1708	Lagomorpha	Leporidae	*Palaeolagus*	*hypsodus?*
KUVP	18182	L	C1708	Lagomorpha	Leporidae	*Palaeolagus*	*hypsodus?*
UWBM	101385	L	C1708	Lagomorpha	Leporidae	*Palaeolagus*	*hypsodus?*
UMPC	13230	L	C1708	Perissodactyla	Rhinocerotidae	*Diceratherium*	*annectens*
KUVP	18670	L	C1708	Perissodactyla	Rhinocerotidae	*Skinneroceras*	*manningi*
KUVP	18678	L	C1708	Perissodactyla	Rhinocerotidae	*Skinneroceras*	*manningi*
UMPC	13231	L	C1708	Perissodactyla	Rhinocerotidae	*Skinneroceras*	*manningi*
KUVP	18152	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18153	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18185	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18397	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18398	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18399	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18407	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18408	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18411	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18412	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18417	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18421	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18429	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18430	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18433	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18502	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18520	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18888	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18889	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18891	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18894	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18895	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18896	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18897	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18898	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	97362	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	98767	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	101387	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	101388	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	108040	L	C1708	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18176	L	C1708	Rodentia	Castoridae	*Agnotocastor*	morph. A
KUVP	18177	L	C1708	Rodentia	Castoridae	*Agnotocastor*	morph. A

KUVP	18532	L	C1708	Rodentia	Castoridae	*Microtheriomys*	*brevirhinus*
KUVP	18534	L	C1708	Rodentia	Castoridae	*Microtheriomys*	*brevirhinus*
UWBM	98756	L	C1708	Rodentia	Castoridae	*Microtheriomys*	*brevirhinus*
UWBM	98763	L	C1708	Rodentia	Castoridae	*Microtheriomys*	*brevirhinus*
UMPC	13212	L	C1708	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	98741	L	C1708	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	98740	L	C1708	Rodentia	Castoridae	*Microtheriomys*	new species E
KUVP	18160	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	18394	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	18395	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	18578	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	18585	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19896	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19897	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19898	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19899	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19900	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19901	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19902	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19903	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19904	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19905	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19908	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19909	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19910	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19911	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19912	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19913	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19914	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19915	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	19916	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	98760	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	101381	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	101386	L	C1708	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	108101	L	C1708	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18159	L	C1708	Rodentia	Dipodidae	Sicistinae A	
KUVP	18536	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	cf. *L. douglassi*
KUVP	18540	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	cf. *L. douglassi*
KUVP	18547	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	cf. *L. douglassi*
KUVP	18569	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	cf. *L. douglassi*

KUVP	18505	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18535	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18537	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18539	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18542	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18544	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18545	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18548	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18549	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18550	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18551	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18552	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18553	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18554	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18555	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18557	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18558	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18560	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18561	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18562	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18563	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18566	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18568	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
UWBM	98662	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
UWBM	108600	L	C1708	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	18543	L	C1708	Rodentia	Eomyidae	*Pseudotheridomys*	species A
KUVP	18538	L	C1708	Rodentia	Eomyidae	*Pseudotheridomys*	species B
KUVP	18565	L	C1708	Rodentia	Eomyidae	*Pseudotheridomys*	species B
KUVP	18575	L	C1708	Rodentia	Sciuridae	*Miosciurus*	cf. *M. ballovianus*
KUVP	18576	L	C1708	Rodentia	Sciuridae	*Miosciurus*	cf. *M. ballovianus*
F:AM	49463	L	C1709	Artiodactyla	Antracotheriidae	*Kukusepasutanka*	*schultzi*
CM	726	L	C1709	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
CM	8938	L	C1709	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
CM	20736	L	C1709	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UMPC	942	L	C1709	Artiodactyla	Merycoidodontidae	*Eporeodon*	indet.
UMPC	940	L	C1709	Artiodactyla	Merycoidodontidae	*Eporeodon*	*occidentalis*
UMPC	941	L	C1709	Artiodactyla	Merycoidodontidae	*Eporeodon*	*occidentalis*
KUVP	18401	L	C1709	Artiodactyla	Merycoidodontidae	*Promerycochoerus*	indet.
KUVP	18402	L	C1709	Artiodactyla	Merycoidodontidae	*Promerycochoerus*	*superbus*
UMPC	1236	L	C1709	Artiodactyla	Merycoidodontidae	*Promerycochoerus*	*superbus*

CM	792	L	C1709	Carnivora	Canidae	*Cynodesmus*	*thooides*
F:AM	65035	L	C1709	Rodentia	Aplodontidae	*Downsimus*	*"montanus"*
FMNH	1125	L	C1709	Rodentia	Aplodontidae	*Niglarodon*	*"konizeskii"*
UWBM	98668	L	C1721	Artiodactyla	Camelidae	indet.	indet.
UWBM	97459	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	97460	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	97462	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	97474	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	97494	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	97501	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	98656	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	98690	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	101308	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	108080	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	108575	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	108588	L	C1721	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	97342	L	C1721	Artiodactyla	Merycoidodontidae	*Eporeodon*	*occidentalis*
UWBM	101299	L	C1721	Artiodactyla	Tayassuidae	indet.	indet.
UWBM	101395	L	C1721	Carnivora	Canidae	*Archaeocyon*	cf. *A. leptodus*
UWBM	97341	L	C1721	Carnivora	Canidae	*Archaeocyon*	*leptodus*
UWBM	97489	L	C1721	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	97490	L	C1721	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	97491	L	C1721	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	98773	L	C1721	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	108016	L	C1721	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	108045	L	C1721	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	108097	L	C1721	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
UWBM	98698	L	C1721	Marsupialiformes	Peradectidae	*Nanodelphys*	species A
UWBM	108010	L	C1721	Eulipotyphla	Proscalopidae	*Proscalops*	cf. species A
UWBM	108098	L	C1721	Eulipotyphla	Proscalopidae	*Proscalops*	cf. species A
UWBM	108570	L	C1721	Eulipotyphla	Proscalopidae	*Proscalops*	cf. species A
UWBM	98792	L	C1721	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
UWBM	98793	L	C1721	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
UWBM	98881	L	C1721	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
UWBM	98676	L	C1721	Eulipotyphla	Talpidae	*Mystipterus*	new species A
UWBM	97467	L	C1721	Lagomorpha	Leporidae	*Megalagus*	cf. *M. turgidus*
UWBM	98657	L	C1721	Rodentia	Aplodontidae	*Allomys*	*magnus*
UWBM	98691	L	C1721	Rodentia	Aplodontidae	*Allomys*	*magnus*
UWBM	98685	L	C1721	Rodentia	Aplodontidae	*Downsimus*	*"montanus"*
UWBM	98872	L	C1721	Rodentia	Aplodontidae	*Downsimus*	*"montanus"*

UWBM	108011	L	C1721	Rodentia	Aplodontidae	*Downsimus*	*"montanus"*
UWBM	98686	L	C1721	Rodentia	Aplodontidae	*Downsimus*	new species A
UWBM	98880	L	C1721	Rodentia	Aplodontidae	*Downsimus*	new species A
UWBM	108094	L	C1721	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UWBM	98675	L	C1721	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
UWBM	101373	L	C1721	Rodentia	Aplodontidae	*Niglarodon*	cf. *"N. konizeskii"*
UWBM	97361	L	C1721	Rodentia	Aplodontidae	*Niglarodon*	species B
UWBM	98693	L	C1721	Rodentia	Aplodontidae	*Niglarodon*	species B
UWBM	108092	L	C1721	Rodentia	Aplodontidae	*Niglarodon*	very large species
UWBM	98842	L	C1721	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	98844	L	C1721	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	98846	L	C1721	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	108088	L	C1721	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	108093	L	C1721	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UWBM	97465	L	C1721	Rodentia	Castoridae	*Agnotocastor*	morph. A
UWBM	98873	L	C1721	Rodentia	Castoridae	*Agnotocastor*	morph. A
UWBM	108582	L	C1721	Rodentia	Castoridae	*Agnotocastor*	morph. A
UMPC	2213	L	C1721	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	97359	L	C1721	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	97500	L	C1721	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	101347	L	C1721	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	101400	L	C1721	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	108103	L	C1721	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	108576	L	C1721	Rodentia	Castoridae	*Microtheriomys*	new species A
UWBM	97477	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	97486	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	97499	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	101297	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	101298	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	101301	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	101394	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	108096	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	108580	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	108585	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
UWBM	108610	L	C1721	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	23502	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	23515	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
UMPC	2215	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	97487	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	98727	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A

UWBM	98747	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	101305	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	101374	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	108048	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	108553	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	108590	L	C1721	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	97466	L	C1721	Rodentia	Dipodidae	Sicistinae A	
UWBM	97488	L	C1721	Rodentia	Dipodidae	Sicistinae A	
UWBM	101315	L	C1721	Rodentia	Dipodidae	Sicistinae A	
UWBM	98746	L	C1721	Rodentia	Dipodidae	Sicistinae B	
UWBM	108047	L	C1721	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
UWBM	108100	L	C1721	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
UWBM	108105	L	C1721	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
UWBM	98874	L	C1721	Rodentia	Eutypomyidae	*Eutypomys*	*montanensis*
UMPC	2214	L	C1721	Rodentia	Sciuridae	*Miosciurus*	cf. *M. ballovianus*
UWBM	101320	L	C1721	Rodentia	Sciuridae	*Miosciurus*	cf. *M. ballovianus*
UWBM	98728	L	C1721	Rodentia	Sciuridae	*Petauristodon*	indet.
UWBM	98684	L	C1721	Rodentia	Sciuridae	*Sciurion*	cf. *S. campestre*
KUVP	18387	L	Ku-Mt-20	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18403	L	Ku-Mt-20	Artiodactyla	Merycoidodontidae	*Promerycochoerus*	*superbus*
KUVP	18769	L	Ku-Mt-20	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18788	L	Ku-Mt-20	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18900	L	Ku-Mt-20	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18848	L	Ku-Mt-7	Eulipotyphla	Talpidae	New genus A	new species A
KUVP	18849	L	Ku-Mt-7	Eulipotyphla	Talpidae	New genus A	new species A
KUVP	18855	L	Ku-Mt-7	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18851	L	Ku-Mt-7	Rodentia	Castoridae	*Microtheriomys*	*brevirhinus*
KUVP	18850	L	Ku-Mt-7	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
UMPC	949	L	MV6501	Artiodactyla	Tayassuidae	indet.	indet.
UMPC	1324	L	MV6501	Rodentia	Eomyidae	*Leptodontomys*	cf. *L. douglassi*
KUVP	18838	L	MV6554	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UMPC	1482	L	MV6554	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UMPC	2240	L	MV6554	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UMPC	2241	L	MV6554	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UMPC	2270	L	MV6554	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UMPC	3030	L	MV6554	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UMPC	23031	L	MV6554	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18812	L	MV6554	Carnivora	Canidae	*Archaeocyon*	*leptodus*
KUVP	18818	L	MV6554	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
UMPC	2237	L	MV6554	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A

UMPC	2194	L	MV6554	Eulipotyphla	Erinaceidae	*Ocajila*	species A
UMPC	2234	L	MV6554	Eulipotyphla	Erinaceidae	*Ocajila*	species A
UMPC	1531	L	MV6554	Eulipotyphla	Proscalopidae	Genus A	species A
UMPC	2235	L	MV6554	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
UMPC	2238	L	MV6554	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
KUVP	18165	L	MV6554	Eulipotyphla	Soricidae	*Pseudotrimylus*	*"gwinni"*
KUVP	18816	L	MV6554	Eulipotyphla	Soricidae	*Pseudotrimylus*	*"gwinni"*
UMPC	2233	L	MV6554	Eulipotyphla	Soricidae	*Pseudotrimylus*	*"gwinni"*
UMPC	2269	L	MV6554	Perissodactyla	Rhinocerotidae	*Diceratherium*	*armatum*
UMPC	1490	L	MV6554	Perissodactyla	Rhinocerotidae	*Diceratherium*	*radtkei*
KUVP	18438	L	MV6554	Rodentia	Aplodontidae	*Downsimus*	*"montanus"*
KUVP	18422	L	MV6554	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
UMPC	1483	L	MV6554	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
KUVP	18807	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. A
KUVP	18809	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. A
UMPC	1491	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. A
UMPC	1496	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. A
KUVP	18173	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. B
KUVP	18806	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. B
KUVP	18810	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. B
KUVP	20676	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. B
KUVP	18808	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. C
KUVP	20677	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. C
UMPC	1494	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. C
UMPC	2262	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. C
KUVP	18841	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. D
UMPC	1530	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. D
UMPC	2261	L	MV6554	Rodentia	Castoridae	*Agnotocastor*	morph. D
KUVP	18171	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	1484	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	1485	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	1487	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	1493	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	1535	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	1544	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	2199	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	2259	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	2260	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	2482	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A
UMPC	3028	L	MV6554	Rodentia	Castoridae	*Microtheriomys*	new species A

KUVP	18813	L	MV6554	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	18814	L	MV6554	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	20605	L	MV6554	Rodentia	Cricetidae	*Leidymys*	new species A
UMPC	1532	L	MV6554	Rodentia	Cricetidae	*Leidymys*	new species A
KUVP	18172	L	MV6554	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18846	L	MV6554	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	23501	L	MV6554	Rodentia	Dipodidae	*Heosminthus*	new species A
UMPC	1537	L	MV6554	Rodentia	Dipodidae	*Heosminthus*	new species A
UMPC	1486	L	MV6554	Rodentia	Eutypomyidae	*Eutypomys*	indet.
CM	31607	L	MV6613	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18452	L	MV6613	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
KUVP	18458	L	MV6613	Artiodactyla	Tayassuidae	indet.	indet.
UMPC	14003	L	MV6613	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. merriami*
UMPC	14032	L	MV6613	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	species A
KUVP	18145	L	MV6613	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
KUVP	18456	L	MV6613	Eulipotyphla	Soricidae	*Domnina*	*"hutchisoni"*
UMPC	14025	L	MV6613	Lagomorpha	Leporidae	*Megalagus*	cf. *M. turgidus*
UMPC	14043	L	MV6613	Lagomorpha	Leporidae	*Megalagus*	cf. *M. turgidus*
KUVP	18454	L	MV6613	Lagomorpha	Leporidae	*Megalagus*	species A
KUVP	20537	L	MV6613	Rodentia	Aplodontidae	*Downsimus*	*"montanus"*
UMPC	13992	L	MV6613	Rodentia	Aplodontidae	*Downsimus*	*"montanus"*
UMPC	13999	L	MV6613	Rodentia	Aplodontidae	*Downsimus*	*"montanus"*
UMPC	13987	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
UMPC	13998	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
UMPC	14009	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
UMPC	14010	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
UMPC	14011	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
UMPC	14012	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
UMPC	14017	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
KUVP	18431	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	2313	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	2314	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	14002	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	14041	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	13271	L	MV6613	Rodentia	Aplodontidae	*Niglarodon*	species B
UMPC	2118	L	MV6613	Rodentia	Aplodontidae	*Parallomys*	indet.
UMPC	13993	L	MV6613	Rodentia	Aplodontidae	*Parallomys*	indet.
UMPC	13994	L	MV6613	Rodentia	Aplodontidae	*Parallomys*	indet.
UMPC	13995	L	MV6613	Rodentia	Aplodontidae	*Parallomys*	indet.
UMPC	14001	L	MV6613	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*

UMPC	14021	L	MV6613	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
KUVP	18450	L	MV6613	Rodentia	Castoridae	*Microtheriomys*	*brevirhinus*
KUVP	18451	L	MV6613	Rodentia	Castoridae	*Microtheriomys*	*brevirhinus*
UMPC	14007	L	MV6613	Rodentia	Castoridae	*Microtheriomys*	*brevirhinus*
KUVP	18457	L	MV6613	Rodentia	Dipodidae	*Heosminthus*	new species A
UMPC	13989	L	MV6613	Rodentia	Dipodidae	*Heosminthus*	new species A
UMPC	14022	L	MV6613	Rodentia	Dipodidae	*Heosminthus*	new species A
UMPC	13980	L	MV6613	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
UMPC	14028	L	MV6613	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
USNM	22819	L	MV6613	Rodentia	Eutypomyidae	*Eutypomys*	*montanensis*
KUVP	18836	L	MV6621	Artiodactyla	Leptomerycidae	*Pronodens*	*transmontanus*
UWBM	98702	M	C0174	Carnivora	Canidae	*Archaeocyon*	cf. *A. leptodus*
UWBM	97319	M	C0174	Carnivora	Canidae	*Leptocyon*	cf. *L. delicatus*
UMPC	13266	M	C0174	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	20524	M	C0174	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
UWBM	97331	M	C0174	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
UWBM	97506	M	C0174	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
KUVP	18406	M	C0174	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
UWBM	97505	M	C0174	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
UWBM	98754	M	C0174	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18672	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
KUVP	18673	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
KUVP	20528	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
KUVP	20529	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UWBM	97324	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UWBM	97334	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UWBM	97405	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UWBM	98592	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UWBM	98597	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UWBM	98598	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UWBM	108562	M	C0174	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UWBM	98603	M	C0174	Perissodactyla	Equidae	*Miohippus*	indet.
PM	3103	M	C0174	Perissodactyla	Rhinocerotidae	*Diceratherium*	*radtkei*
UWBM	98593	M	C0174	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UWBM	98876	M	C0174	Rodentia	Castoridae	*Microtheriomys*	new species D
UWBM	97329	M	C0174	Rodentia	Castoridae	*Neatocastor*	*hesperus*
UWBM	97507	M	C0174	Rodentia	Castoridae	*Neatocastor*	*hesperus*
UWBM	98596	M	C0174	Rodentia	Castoridae	*Neatocastor*	*hesperus*
UWBM	108109	M	C0174	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	20520	M	C0174	Rodentia	Cricetidae	*Leidymys*	*alicae*

KUVP	20521	M	C0174	Rodentia	Cricetidae	*Leidymys*	*alicae*
UWBM	97317	M	C0174	Rodentia	Cricetidae	*Leidymys*	*alicae*
UWBM	98708	M	C0174	Rodentia	Cricetidae	*Leidymys*	*alicae*
UWBM	98791	M	C0174	Rodentia	Cricetidae	*Leidymys*	*alicae*
UWBM	108559	M	C0174	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18674	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18675	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	20507	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	20508	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	20509	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	20510	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	20511	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	20512	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	20513	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	97502	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	98604	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	108561	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	108563	M	C0174	Rodentia	Dipodidae	*Heosminthus*	new species A
UWBM	98617	M	C0174	Rodentia	Dipodidae	Sicistinae A	
UWBM	98826	M	C0174	Rodentia	Dipodidae	Sicistinae A	
UWBM	98870	M	C0174	Rodentia	Dipodidae	Sicistinae A	
UWBM	98871	M	C0174	Rodentia	Dipodidae	Sicistinae B	
UWBM	108558	M	C0174	Rodentia	Eomyidae	*Leptodontomys*	cf. *L. douglassi*
KUVP	20515	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UMPC	13269	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UWBM	108607	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
KUVP	18676	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	20516	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	20517	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UWBM	97330	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UWBM	98878	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UWBM	108605	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UWBM	108606	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UWBM	108619	M	C0174	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	20522	M	C0174	Rodentia	Sciuridae	*Sciurion*	cf. *S. campestre*
UWBM	98877	M	C0174	Rodentia	Sciuridae	*Sciurion*	cf. *S. campestre*
UMPC	14048	M	C0247	Artiodactyla	Entelodontidae	*Daeodon*	indet.
UWBM	63274	M	C0247	Artiodactyla	Merycoidodontidae	*Promerycochoerus*	*superbus*
KUVP	18899	M	C0247	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
CM	18	M	C0247	Rodentia	Aplodontidae	*Allomys*	species B

KUVP	18425	M	C0247	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	13255	M	C0247	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	13259	M	C0247	Rodentia	Castoridae	*Neatocastor*	*hesperus*
UMPC	13260	M	C0247	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	18448	M	C0247	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18449	M	C0247	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UWBM	63273	M	C0247	Rodentia	Geomyidae	*Pleurolicus*	*"rensbergeri"*
UMPC	1365	M	C1701	Artiodactyla	Merycoidodontidae	*Promerycochoerus*	*superbus*
UMPC	1367	M	C1701	Perissodactyla	Rhinocerotidae	*Diceratherium*	*radtkei*
UWBM	97400	M	C1701	Rodentia	Aplodontidae	*Allomys*	new species A
UWBM	108541	M	C1701	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	2046	M	C1701	Rodentia	Geomyidae	*Pleurolicus*	*"rensbergeri"*
UWBM	97344	M	C1701	Rodentia	Geomyidae	*Pleurolicus*	*"rensbergeri"*
UMPC	1374	M	C1702	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
UMPC	1560	M	C1702	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
UWBM	97368	M	C1702	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
UMPC	1551	M	C1702	Eulipotyphla	Erinaceidae	*Parvericius*	*montanus*
UWBM	98613	M	C1702	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UWBM	108556	M	C1702	Lagomorpha	stem lagomorpha	*?Desmatolagus*	cf. *D. schizopetrus*
UMPC	1385	M	C1702	Lagomorpha	stem lagomorpha	*?Desmatolagus*	indet.
UWBM	108554	M	C1702	Lagomorpha	stem lagomorpha	*?Desmatolagus*	indet.
UMPC	1384	M	C1702	Lagomorpha	Leporidae	*Archaeolagus*	cf. *A. macrocephalus*
UWBM	97372	M	C1702	Perissodactyla	Equidae	*Miohippus*	indet.
UWBM	108610	M	C1702	Perissodactyla	Equidae	*Miohippus*	indet.
UWBM	97366	M	C1702	Rodentia	Cricetidae	*Leidymys*	*alicae*
UWBM	108555	M	C1702	Rodentia	Dipodidae	*Heosminthus*	new species A
UMPC	1369	M	C1702	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	1371	M	C1702	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	1372	M	C1702	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UWBM	98660	M	C1702	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	1370	M	C1702	Rodentia	Geomyidae	*Pleurolicus*	*"rensbergeri"*
UMPC	13979	M	C1703	Carnivora	Canidae	*Archaeocyon*	*leptodus*
UMPC	1393	M	C1703	Lagomorpha	Leporidae	*Archaeolagus*	cf. *A. macrocephalus*
UWBM	98860	M	C1703	Perissodactyla	Equidae	*Miohippus*	indet.
UMPC	1424	M	C1703	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UWBM	97346	M	C1704	Carnivora	Canidae	*Cynodesmus*	*thooides*
UWBM	97348	M	C1704	Carnivora	Canidae	*Cynodesmus*	*thooides*
UWBM	98680	M	C1704	Carnivora	Canidae	*Cynodesmus*	*thooides*
UWBM	98730	M	C1704	Carnivora	Canidae	*Cynodesmus*	*thooides*
KUVP	18219	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*

KUVP	18679	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	18686	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	18731	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	18743	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	18759	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
UWBM	97392	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	18683	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
KUVP	18703	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
UMPC	3019	M	C1704	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
KUVP	18334	M	C1704	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18701	M	C1704	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18753	M	C1704	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18757	M	C1704	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18758	M	C1704	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18886	M	C1704	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	23503	M	C1704	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18396	M	C1704	Eulipotyphla	Erinaceidae	Erinaceinae indet.	indet.
KUVP	18241	M	C1704	Eulipotyphla	Erinaceidae	*Ocajila*	species A
UMPC	1807	M	C1704	Eulipotyphla	Erinaceidae	*Ocajila*	species A
UMPC	1805	M	C1704	Eulipotyphla	Proscalopidae	*Proscalops*	species A
KUVP	18704	M	C1704	Eulipotyphla	Proscalopidae	*Proscalops*	species A?
KUVP	18220	M	C1704	Eulipotyphla	Talpidae	*Mystipterus*	new species A
KUVP	18221	M	C1704	Eulipotyphla	Talpidae	*Mystipterus*	new species A
KUVP	18222	M	C1704	Eulipotyphla	Talpidae	*Mystipterus*	new species A
KUVP	18732	M	C1704	Eulipotyphla	Talpidae	*Mystipterus*	new species A
KUVP	18746	M	C1704	Eulipotyphla	Talpidae	*Mystipterus*	new species A
KUVP	18687	M	C1704	Eulipotyphla	Talpidae	New Genus A	new species A
KUVP	23505	M	C1704	Lagomorpha	Leporidae	*Archaeolagus*	cf. *A. macrocephalus*
KUVP	23506	M	C1704	Lagomorpha	Leporidae	*Archaeolagus*	cf. *A. macrocephalus*
KUVP	23507	M	C1704	Lagomorpha	Leporidae	*Archaeolagus*	cf. *A. macrocephalus*
KUVP	23508	M	C1704	Lagomorpha	Leporidae	*Archaeolagus*	cf. *A. macrocephalus*
UWBM	98614	M	C1704	Lagomorpha	Leporidae	*Archaeolagus*	cf. *A. macrocephalus*
KUVP	18016	M	C1704	Rodentia	Aplodontidae	*Allomys*	*magnus*
KUVP	18017	M	C1704	Rodentia	Aplodontidae	*Allomys*	*magnus*
KUVP	18336	M	C1704	Rodentia	Aplodontidae	*Allomys*	*magnus*
KUVP	19801	M	C1704	Rodentia	Aplodontidae	*Allomys*	*magnus*
UMPC	1477	M	C1704	Rodentia	Aplodontidae	*Allomys*	*magnus*
UMPC	1478	M	C1704	Rodentia	Aplodontidae	*Allomys*	*magnus*
UMPC	1828	M	C1704	Rodentia	Aplodontidae	*Allomys*	*magnus*
UMPC	1829	M	C1704	Rodentia	Aplodontidae	*Allomys*	*magnus*

UMPC	1824	M	C1704	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UMPC	1825	M	C1704	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UMPC	1826	M	C1704	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UWBM	98875	M	C1704	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UWBM	101360	M	C1704	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UWBM	98845	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	*"pardeei"*
KUVP	18427	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	species A
KUVP	18434	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	1820	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	species A
UMPC	1822	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	species A
KUVP	18018	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	species B
KUVP	23710	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	species B
UMPC	1823	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	species B
UMPC	1827	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	species B
UWBM	98778	M	C1704	Rodentia	Aplodontidae	*Niglarodon*	species C
UWBM	108616	M	C1704	Rodentia	Aplodontidae	*Rudiomys*	*"drummondensis"*
UMPC	1476	M	C1704	Rodentia	Aplodontidae	*Trilaccogaulus*	new species A
UMPC	1830	M	C1704	Rodentia	Aplodontidae	*Trilaccogaulus*	new species A
KUVP	18006	M	C1704	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	18684	M	C1704	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	18763	M	C1704	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	20540	M	C1704	Rodentia	Castoridae	*Neatocastor*	*hesperus*
UMPC	1809	M	C1704	Rodentia	Castoridae	*Neatocastor*	*hesperus*
UWBM	108560	M	C1704	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	18230	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18231	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18237	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18238	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18239	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18240	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18698	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18882	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	20538	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
UMPC	1808	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
UMPC	1842	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
UMPC	1843	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
UMPC	1844	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
UWBM	98615	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
UWBM	98616	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
UWBM	98863	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*

UWBM	101380	M	C1704	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18007	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18008	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18225	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18226	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18228	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18233	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18677	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18678	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18691	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18692	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18693	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18694	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18695	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18696	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18697	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18707	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18708	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18710	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18712	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18713	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18714	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18715	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18716	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18717	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18718	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18721	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18722	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18723	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18724	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18725	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18726	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18730	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18733	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18737	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18741	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18744	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18745	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18750	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18752	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A

KUVP	18756	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18760	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18883	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18884	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18885	M	C1704	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18227	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18700	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18709	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18728	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18729	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18736	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18739	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18748	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18751	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18762	M	C1704	Rodentia	Dipodidae	Sicistinae A	
UWBM	97393	M	C1704	Rodentia	Dipodidae	Sicistinae A	
KUVP	18234	M	C1704	Rodentia	Eomyidae	*Leptodontomys*	cf. *L. douglassi*
UMPC	1552	M	C1704	Rodentia	Eutypomyidae	*Eutypomys*	indet.
KUVP	18026	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
KUVP	18028	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
KUVP	18680	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UMPC	1474	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UMPC	1813	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UWBM	98862	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UWBM	101382	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
KUVP	18021	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18022	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18023	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18025	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18029	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18030	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18031	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18681	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18682	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18688	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18689	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18706	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18749	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	1810	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	1811	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*

UMPC	1812	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	1814	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	1815	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	1816	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	2015	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UWBM	98861	M	C1704	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18164	M	C1705	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18163	M	C1705	Eulipotyphla	Erinaceidae	*Amphechinus*	*horncloudi*
KUVP	18795	M	C1711	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	18879	M	C1711	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	18775	M	C1711	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18796	M	C1711	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18776	M	C1711	Eulipotyphla	Erinaceidae	*Ocajila*	species A
KUVP	20612	M	C1711	Eulipotyphla	Soricidae	*Pseudotrimylus*	indet.
KUVP	18770	M	C1711	Eulipotyphla	Talpidae	*Mystipterus*	new species A
KUVP	18415	M	C1711	Rodentia	Aplodontidae	*Niglarodon*	species B
KUVP	18428	M	C1711	Rodentia	Aplodontidae	*Niglarodon*	species B
KUVP	18784	M	C1711	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	18786	M	C1711	Rodentia	Castoridae	*Neatocastor*	*hesperus*
UWBM	98600	M	C1711	Rodentia	Castoridae	*Palaeocastor*	cf. *P. peninsulatus*
KUVP	18777	M	C1711	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18867	M	C1711	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18774	M	C1711	Rodentia	Cricetidae	*Leidymys*	cf. *L. montanus*
KUVP	18779	M	C1711	Rodentia	Cricetidae	*Leidymys*	cf. *L. montanus*
KUVP	18783	M	C1711	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18799	M	C1711	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18800	M	C1711	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18801	M	C1711	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18803	M	C1711	Rodentia	Dipodidae	Sicistinae B	
KUVP	18400	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18772	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18773	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18778	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18790	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18791	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18792	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18793	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18804	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18805	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18868	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*

KUVP	18869	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18881	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	20611	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	2045	M	C1711	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
UMPC	2148	M	C1717	Carnivora	Canidae	*Leptocyon*	indet.
UMPC	2173	M	C1717	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
UMPC	2249	M	C1717	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
UMPC	2250	M	C1717	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18162	M	C1717	Eulipotyphla	Erinaceidae	*Amphechinus*	*horncloudi*
UMPC	2252	M	C1717	Rodentia	Aplodontidae	*Niglarodon*	species A
KUVP	18497	M	C1717	Rodentia	Castoridae	*Microtheriomys*	new species B
UMPC	2254	M	C1717	Rodentia	Castoridae	*Microtheriomys*	new species B
UMPC	2253	M	C1717	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	18168	M	C1717	Rodentia	Cricetidae	*Leidymys*	*alicae*
UMPC	2149	M	C1717	Rodentia	Dipodidae	*Heosminthus*	new species A
UMPC	2247	M	C1717	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18167	M	C1717	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UMPC	2146	M	C1717	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UMPC	2147	M	C1717	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UMPC	2150	M	C1717	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
UMPC	2174	M	C1717	Rodentia	Geomyidae	*Pleurolicus*	*"gwinni"*
KUVP	18169	M	C1717	Rodentia	Sciuridae	*Miosciurus*	cf. *M. ballovianus*
KUVP	18409	M	Ku-Mt-53	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	19812	M	Ku-Mt-53	Rodentia	Aplodontidae	*Allomys*	species B
CM	12	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
CM	13	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18414	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18423	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18424	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18437	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	19802	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	19804	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	19806	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	19807	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	19808	M	Ku-Mt-53	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18440	M	Ku-Mt-53	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18441	M	Ku-Mt-53	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18442	M	Ku-Mt-53	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18443	M	Ku-Mt-53	Rodentia	Geomyidae	*Pleurolicus*	*"nelsoni"*
KUVP	18447	M	Ku-Mt-53	Rodentia	Geomyidae	*Pleurolicus*	*"rensbergeri"*

KUVP	19810	M	Ku-Mt-53	Rodentia	Geomyidae	*Pleurolicus*	*"rensbergeri"*
UMPC	1412	U	C0173	Artiodactyla	Leptomerycidae	*Pronodens*	indet.
UMPC	2308	U	C0173	Carnivora	Canidae	*Cormocyon*	indet.
UMPC	2307	U	C0173	Carnivora	Canidae	*Leptocyon*	indet.
KUVP	18095	U	C0173	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. fugax*
KUVP	18096	U	C0173	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
KUVP	18341	U	C0173	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
KUVP	18349	U	C0173	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
KUVP	18352	U	C0173	Marsupialiformes	Herpetotheriidae	*Herpetotherium*	cf. *H. valens*
KUVP	18339	U	C0173	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18343	U	C0173	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18346	U	C0173	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18347	U	C0173	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18350	U	C0173	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18464	U	C0173	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18465	U	C0173	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18466	U	C0173	Marsupialiformes	Peradectidae	*Nanodelphys*	species B
KUVP	18097	U	C0173	Eulipotyphla	Erinaceidae	*Amphechinus*	*horncloudi*
KUVP	18405	U	C0173	Eulipotyphla	Erinaceidae	*Amphechinus*	*horncloudi*
KUVP	23711	U	C0173	Eulipotyphla	Erinaceidae	*Amphechinus*	*horncloudi*
KUVP	18001	U	C0173	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18002	U	C0173	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18003	U	C0173	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18004	U	C0173	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18098	U	C0173	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18354	U	C0173	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18356	U	C0173	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18359	U	C0173	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18404	U	C0173	Eulipotyphla	Erinaceidae	*Stenoechinus*	*tantalus*
KUVP	18351	U	C0173	Eulipotyphla	Proscalopidae	*Proscalops*	species B
KUVP	18353	U	C0173	Eulipotyphla	Soricidae	*Domnina*	indet.
KUVP	18384	U	C0173	Lagomorpha	Leporidae	*Archaeolagus*	species B
UMPC	1411	U	C0173	Perissodactyla	Equidae	*Miohippus*	indet.
KUVP	18101	U	C0173	Rodentia	Aplodontidae	*Allomys*	*magnus*
KUVP	18140	U	C0173	Rodentia	Aplodontidae	*Allomys*	*magnus*
UMPC	13972	U	C0173	Rodentia	Aplodontidae	*Allomys*	new species A
KUVP	18362	U	C0173	Rodentia	Aplodontidae	*Allomys*	species B
KUVP	18367	U	C0173	Rodentia	Aplodontidae	*Allomys*	species B
CM	7	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18104	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*

KUVP	18106	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18110	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18112	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18113	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18114	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18115	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18116	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18117	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18118	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18119	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18120	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18122	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18124	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18126	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18127	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18128	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18129	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18133	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18134	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18135	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18136	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18138	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18139	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18141	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18142	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18143	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18144	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18358	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18361	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18364	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18365	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18413	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18467	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18469	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18470	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UMPC	2306	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UMPC	13975	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
UMPC	14050	U	C0173	Rodentia	Aplodontidae	*Meniscomys*	*"fronseei"*
KUVP	18103	U	C0173	Rodentia	Aplodontidae	*Niglarodon*	species B
KUVP	18131	U	C0173	Rodentia	Aplodontidae	*Niglarodon*	species B

UMPC	1407	U	C0173	Rodentia	Aplodontidae	*Niglarodon*	species B
FMNH	621	U	C0173	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	18376	U	C0173	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18460	U	C0173	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18461	U	C0173	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18492	U	C0173	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	19831	U	C0173	Rodentia	Cricetidae	*Leidymys*	*alicae*
KUVP	18379	U	C0173	Rodentia	Cricetidae	*Leidymys*	cf. *L. montanus*
KUVP	18380	U	C0173	Rodentia	Cricetidae	*Leidymys*	cf. *L. montanus*
KUVP	18381	U	C0173	Rodentia	Cricetidae	*Leidymys*	cf. *L. montanus*
KUVP	18382	U	C0173	Rodentia	Cricetidae	*Leidymys*	cf. *L. montanus*
KUVP	18477	U	C0173	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18482	U	C0173	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18486	U	C0173	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18488	U	C0173	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18491	U	C0173	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18495	U	C0173	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18484	U	C0173	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
FMNH	620	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18027	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18033	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18037	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18038	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18039	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18040	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18041	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18042	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18043	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18044	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18045	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18046	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18047	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18048	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18049	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18050	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18052	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18053	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18054	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18055	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18056	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*

KUVP	18057	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18058	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18059	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18060	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18061	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18062	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18064	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18065	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18066	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18069	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18070	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18071	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18072	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18073	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18074	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18076	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18077	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18078	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18079	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18081	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18082	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18083	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18084	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18086	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18087	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18088	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18090	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18092	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18370	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18371	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18372	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18472	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18473	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18474	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18475	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18476	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18835	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	1408	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	1409	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	2105	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*

UMPC	2106	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	2107	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	2302	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	13228	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	13232	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	13235	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	13249	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	13251	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	13254	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	13973	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	14053	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	14054	U	C0173	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
KUVP	18089	U	C0173	Rodentia	Geomyidae	*Tenudomys*	*"welchi"*
KUVP	18091	U	C0173	Rodentia	Geomyidae	*Tenudomys*	*"welchi"*
KUVP	18093	U	C0173	Rodentia	Geomyidae	*Tenudomys*	*"welchi"*
KUVP	18094	U	C0173	Rodentia	Geomyidae	*Tenudomys*	*"welchi"*
KUVP	18462	U	C0173	Rodentia	Geomyidae	*Tenudomys*	*"welchi"*
KUVP	18463	U	C0173	Rodentia	Geomyidae	*Tenudomys*	*"welchi"*
KUVP	18374	U	C0173	Rodentia	Sciuridae	*Sciurion*	cf. *S. campestre*
KUVP	18832	U	C1712	Lagomorpha	?Ochotonidae	*Gripholagomys*	cf. *G. lavocati*
UMPC	14005	U	C1712	Rodentia	Castoridae	*Microtheriomys*	new species C
UMPC	14006	U	C1712	Rodentia	Castoridae	*Microtheriomys*	new species C
KUVP	18824	U	C1712	Rodentia	Castoridae	*Microtheriomys*	sp.
KUVP	18826	U	C1712	Rodentia	Castoridae	*Microtheriomys*	sp.
KUVP	18825	U	C1712	Rodentia	Castoridae	*Neatocastor*	*hesperus*
KUVP	20652	U	C1712	Rodentia	Cricetidae	*Leidymys*	*alicae*
UMPC	13991	U	C1712	Rodentia	Dipodidae	*Heosminthus*	new species A
KUVP	18834	U	C1712	Rodentia	Eomyidae	*Leptodontomys*	*douglassi*
KUVP	20650	U	C1712	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	3082	U	C1712	Rodentia	Geomyidae	*Gregorymys*	*"tavenneri"*
UMPC	13214	U	C1712	Rodentia	Geomyidae	*Gregorymys*	new species A
KUVP	23499	U	C1712	Rodentia	Geomyidae	*Tenudomys*	*"welchi"*
KUVP	18833	U	C1712	Rodentia	Heteromyidae	*Mookomys*	species A
KUVP	20504	U	Ku-Mt-45	Rodentia	Geomyidae	*Gregorymys*	cf. *G. douglassi*

A4.2. Relative abundances of mammalian taxa at select localities.

Taxa	MV6613	C1708	C1721	MV6554	C1704	C0174	C0173
Niglarodon pardeei	17.07	0.00	1.05	3.39	0.58	0.00	0.00
Niglarodon A	12.20	0.00	0.00	0.00	2.34	0.00	0.00
Parallomys sp.	9.76	0.00	0.00	0.00	0.00	0.00	0.00
Heosminthus A	7.32	0.48	11.58	6.78	25.73	20.00	3.37
Downsimus montanus	7.32	0.00	3.16	1.69	0.00	0.00	0.00
Rudiomys drummondensis	4.88	14.42	5.26	0.00	0.58	0.00	0.00
Leptodontomys douglassi	4.88	13.94	3.16	0.00	0.58	1.54	0.56
Pronodens transmontanus	4.88	4.33	12.63	11.86	0.00	0.00	0.00
Domnina hutchisoni	4.88	2.40	3.16	3.39	0.00	0.00	0.00
Herpetotherium A	2.44	11.06	7.37	1.69	0.00	0.00	0.00
Leidymys A	0.00	12.98	11.58	6.78	0.00	0.00	0.00
Microtheriomys A	0.00	0.96	7.37	20.34	0.00	0.00	0.00
Sicistinae A	0.00	0.48	3.16	0.00	6.43	4.62	0.00
Meniscomys fronseei	0.00	0.00	1.05	0.00	2.92	1.54	22.47
Pleurolicus nelsoni	0.00	0.00	0.00	0.00	12.28	12.31	0.00
Leidymys alicae	0.00	0.00	0.00	0.00	9.94	9.23	2.81
Neatocastor hesperus	0.00	0.00	0.00	0.00	3.51	6.15	0.56
?Desmatolagus	0.00	0.00	0.00	0.00	0.00	16.92	0.00
Stenoechinu stantalus	0.00	0.00	0.00	0.00	0.00	4.62	5.06
Gregorymys tavenneri	0.00	0.00	0.00	0.00	0.00	0.00	41.57
Microtheriomys brevirhinus	7.32	1.92	0.00	0.00	0.00	0.00	0.00
Megalagus cf. *M. turgidus*	4.88	0.00	1.05	0.00	0.00	0.00	0.00
Herpetotherium cf. *H. merriami*	2.44	6.25	0.00	1.69	0.00	0.00	0.00
Niglarodon B	2.44	0.00	2.11	0.00	2.34	0.00	1.69
Eutypomys	2.44	0.00	1.05	1.69	0.58	0.00	0.00
Tayassuidae	2.44	0.00	1.05	0.00	0.00	0.00	0.00
Megalagus A	2.44	0.00	0.00	0.00	0.00	0.00	0.00
Nanodelphys A	0.00	11.06	1.05	0.00	0.00	0.00	0.00
Talpidae A	0.00	5.77	0.00	0.00	0.58	0.00	0.00
Ocajila A	0.00	3.37	0.00	3.39	1.17	0.00	0.00
Palaeolagus hypsodus	0.00	1.92	0.00	0.00	0.00	0.00	0.00
Mystipterus A	0.00	1.44	1.05	0.00	2.92	0.00	0.00
Skinneroceras manningi	0.00	1.44	0.00	0.00	0.00	0.00	0.00
Agnotocastor A	0.00	0.96	3.16	6.78	0.00	0.00	0.00
Archaeocyon leptodus	0.00	0.96	2.11	1.69	0.00	1.54	0.00

Miosciurus cf. *M. ballovianus*	0.00	0.96	2.11	0.00	0.00	0.00	0.00
Pseudotheridomys B	0.00	0.96	0.00	0.00	0.00	0.00	0.00
Diceratherium annectens	0.00	0.48	0.00	0.00	0.00	0.00	0.00
Proscalopidae B	0.00	0.48	0.00	0.00	0.00	0.00	0.00
Microtheriomys E	0.00	0.48	0.00	0.00	0.00	0.00	0.00
Pseudotheridomys A	0.00	0.48	0.00	0.00	0.00	0.00	0.00
Proscalops A	0.00	0.00	3.16	0.00	1.17	0.00	0.00
Allomys magnus	0.00	0.00	2.11	0.00	4.68	0.00	1.12
Downsimus A	0.00	0.00	2.11	0.00	0.00	0.00	0.00
Sciurion cf. *S. campestre*	0.00	0.00	1.05	0.00	0.00	3.08	0.56
Sicistinae B	0.00	0.00	1.05	0.00	0.00	1.54	0.00
Camelidae	0.00	0.00	1.05	0.00	0.00	0.00	0.00
Eporeodon sp.	0.00	0.00	1.05	0.00	0.00	0.00	0.00
Niglarodon konizeskii	0.00	0.00	1.05	0.00	0.00	0.00	0.00
Niglarodon D	0.00	0.00	1.05	0.00	0.00	0.00	0.00
Petauristodon sp.	0.00	0.00	1.05	0.00	0.00	0.00	0.00
Agnotocastor B	0.00	0.00	0.00	6.78	0.00	0.00	0.00
Agnotocastor C	0.00	0.00	0.00	6.78	0.00	0.00	0.00
Agnotocastor D	0.00	0.00	0.00	5.08	0.00	0.00	0.00
Pseudotrimylus gwinni	0.00	0.00	0.00	5.08	0.00	0.00	0.00
Diceratherium radtkei	0.00	0.00	0.00	1.69	0.00	1.54	0.00
Diceratherium armatum	0.00	0.00	0.00	1.69	0.00	0.00	0.00
Proscalopidae A	0.00	0.00	0.00	1.69	0.00	0.00	0.00
Pleurolicus gwinni	0.00	0.00	0.00	0.00	4.09	4.62	0.00
Herpetotherium cf. *H. fugax*	0.00	0.00	0.00	0.00	4.09	1.54	0.56
Nanodelphys B	0.00	0.00	0.00	0.00	4.09	0.00	4.49
Archaeolagus cf. *A. macrocephalus*	0.00	0.00	0.00	0.00	2.92	0.00	0.00
Cynodesmus thooides	0.00	0.00	0.00	0.00	2.34	0.00	0.00
Herpetotherium cf. *H. valens*	0.00	0.00	0.00	0.00	1.75	4.62	2.25
Trilaccogaulus A	0.00	0.00	0.00	0.00	1.17	0.00	0.00
Erinaceinae indet.	0.00	0.00	0.00	0.00	0.58	0.00	0.00
Niglarodon C	0.00	0.00	0.00	0.00	0.58	0.00	0.00
Miohippus sp.	0.00	0.00	0.00	0.00	0.00	1.54	0.56
Microtheriomys D	0.00	0.00	0.00	0.00	0.00	1.54	0.00
Leptocyon cf. *L. delicatus*	0.00	0.00	0.00	0.00	0.00	1.54	0.00
Tenudomy swelchi	0.00	0.00	0.00	0.00	0.00	0.00	3.37
Leidymys cf. *L. montanus*	0.00	0.00	0.00	0.00	0.00	0.00	2.25
Amphechinus horncloudi	0.00	0.00	0.00	0.00	0.00	0.00	1.69
Allomys B	0.00	0.00	0.00	0.00	0.00	0.00	1.12
Allomys A	0.00	0.00	0.00	0.00	0.00	0.00	0.56

Archaeolagus B	0.00	0.00	0.00	0.00	0.00	0.00	0.56
Cormocyon sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.56
Domnina sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.56
Leptocyon	0.00	0.00	0.00	0.00	0.00	0.00	0.56
Pronodens sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.56
Proscalops B	0.00	0.00	0.00	0.00	0.00	0.00	0.56

A4.3. Matrix of presence/absence of taxa for select localities.

Taxon	MV6613	C1708	C1721	MV6554	C1704	C0174	C0173	C1707	C1709	Ku-Mt-7	C0247	C1701	C1702	C1703	C1711	C1717	KuMt53	C1712
?Desmatolagus	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Agnotocastor A	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allomys magnus	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Allomys A	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Allomys B	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Amphechinus horncloudi	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Archaeocyon leptodus	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Archaeolagus cf. A. microcephalus	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
Cynodesmus thooides	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Diceratherium radtkei	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Domnina hutchisoni	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Downsimus montanus	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Eporeodon	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Eutypomys	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Gregorymys tavenneri	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Heosminthus A	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	1	0	1
Herpetotherium cf. H. fugax	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	0
Herpetotherium cf. H. merriami	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Herpetotherium A	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Herpetotherium cf. H. valens	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0
Leidymys alicae	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	0	1
Leidymys cf. L. montanus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Leidymys A	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Large Leptocyon	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Leptodontomys douglassi	1	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1
Megalagus cf. M. turgidus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meniscomys fronseei	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
Microtheriomys brevirhinus	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Microtheriomys A	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Miohippus sp.	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0
Miosciurus cf. M. ballovianus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Mystipterus A	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Nanodelphys A	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nanodelphys B	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0
Neatocastor hesperus	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0	1

Talpidae A	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Niglarodon pardeei	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Niglarodon konizeskii	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Niglarodon A	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0
Niglarodon B	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0
Ocajila A	0	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0
Palaeocastor cf. P. peninsulatus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Pleurolicus gwinni	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0
Pleurolicus nelsoni	0	0	0	0	1	1	0	0	0	0	1	0	1	1	1	0	1	0
Pleurolicus rensbergeri	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0
Promerycochoerus	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Pronodens transmontanus	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Proscalops A	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rudiomys drummondensis	1	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Sciurion cf. S. campestre	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Sicistinae A	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Sicistinae B	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Stenoechinus tantalus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Tayassuidae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tenudomys welchi	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1

A4.4. Number of taxa and specimens per fauna.

Taxa	WR	Ar1	Ar2	Late	Data Deficient
MV6613	8	7	1	0	1
C1708	9	8	4	0	4
C1721	10	14	2	0	5
MV6554	11	6	1	0	2
C1704	6	15	1	0	4
C0174	4	10	3	0	2
C0173	8	13	1	1	2

Specimens	WR	Ar1	Ar2	Late	Data Deficient
MV6613	11	24	4	0	2
C1708	83	72	7	0	46
C1721	33	49	4	0	9
MV6554	29	25	1	0	4
C1704	24	137	2	0	8
C0174	6	41	13	0	5
C0173	23	141	3	1	10

Chapter 5. THE RESPONSE OF MAMMALIAN COMMUNITIES TO THE ENVIRONMENTAL CHANGES OF THE ARIKAREEAN IN WESTERN NORTH AMERICA

ABSTRACT

The early Arikareean, about 30 to 23 Ma, encompasses the transition from the closed forest environments of the Eocene and early Oligocene to the more modern, grass-dominated open habitats of the Miocene. It also includes an important taxonomic turnover coeval with the arrival of immigrant species, many from Asia. I analyzed the change through time in the ecological composition of Arikareean-aged fossil mammal assemblages from Montana (Cabbage Patch beds) and Nebraska (Ridgeview and McCann Canyon local faunas) to investigate if and when mammalian communities responded to these perturbations. Specifically, I looked at the changes in the relative abundances of individuals across dietary, hypsodonty, and locomotory categories through time. I find that the boundary between the Arikareean 1 and the Arikareean 2 ca. 27 million years ago was a time of major change in the ecomorphological composition of mammalian assemblages. It also corresponds to a great taxonomic turnover in these faunas associated to the rise of many novel taxa including many immigrants. Comparisons with modern ecosystems suggest that the ecomorphological composition of Arikareean-aged mammalian faunas initially resembled that found today in closed African forests and then transitioned to compositions more similar to those of shrubland faunas. The loss of individuals and taxa with ecologies associated to forested environments and the rise of novel mammals with affinities for open environments corresponded broadly with the transition to open habitats in Nebraska, while it occurred earlier than current estimates of the spread of open habitats in Montana. Overall, these changes in the mammalian faunas were initiated earlier and were also more profound in Nebraska compared to Montana, implying that these patterns vary spatially. The association between taxonomic and ecological change during the early Arikareean suggests a synergistic effect of environmental change and immigration in initiating the faunal transition to modern mammalian faunas.

1. INTRODUCTION

The challenges of changing environments for taxa and communities are an important focus of conservation biology (Dawson et al. 2011, Naeem et al. 2012). Habitat disturbances, including deforestation, desertification, and vegetational change, have dramatic impacts on the composition of mammalian faunas (e.g., Malcolm and Ray 2000, Jones et al. 2003, Bateman and Ostoja 2004, Pardini 2004, Valone and Sauter 2005). The concern for the consequence on mammal communities of such environmental perturbations has been heightened by the introduction of non-native species into these disturbed ecosystems (e.g., Clout and Lowe 2000, Didham et al. 2007, Nentwig et al. 2009, Gibson et al. 2013, Tompkins et al. 2013). In light of the ongoing climate change experienced by modern ecosystems, understanding the response of mammal communities to environmental change and invasive species has been the focus of many ecological studies (e.g., Manor et al. 2008, Meserve et al. 2011, Elmhagen et al. 2015). Much of this work has investigated changes in mammalian community structure over the course of months, years, decades, or centuries (e.g., Brown et al. 2001, Moritz et al. 2008, Rowe et al. 2011, Supp and Ernest 2014, but see Barnosky et al. 2003, Rowe and Terry 2014, Rull 2014). The fossil record offers the opportunity to simultaneously study the response of mammals to environmental perturbations and novel taxa (through immigration and / or in situ speciation) over millions of years (Blois and Hadly 2009, Dietl and Flessa 2011, Rull 2014), yielding a picture of the evolutionary consequences of ecological change. The Arikareean North American Land Mammal “age” (ca. 30-18.8 million years [Ma]) offers an excellent opportunity to analyze on evolutionary timescales the combined effects of environmental changes and immigration of new species.

The Arikareean represents the beginning of modern mammalian faunas composed of extant families (Webb and Opdyke 1995, Woodburne 2004, Calede 2016a). During the Arikareean, important immigration events, in particular from Asia, contributed novel taxa to faunas composed of archaic lineages with no extant close relatives (see Calede 2016a). These events transformed the taxonomic composition of North American mammalian faunas and heralded the transition to the more modern Miocene fauna achieved during the Hemingfordian and Barstovian. In fact, the Arikareean experienced the largest amount of faunal turnover of any North American Land Mammal Age (Alroy 2000).

This turnover took place at the same time as successive episodes of global warming and global cooling (Zachos et al. 2001a, 2001b, 2008) as well as the shrinking of the forests characteristic of the Eocene in North America, transformed ecosystems. This is the time of the opening of the environment and the spread of the grass-dominated vegetation emblematic of the Miocene (Strömberg 2005, 2011). This environmental transition occurred asynchronously across the North American continent (Strömberg 2005, Fig. 1). Environmental change from forested to open habitats, is recorded in the phytolith fossil record ca. 26 Ma in Nebraska (Strömberg 2005). Paleosol data support an opening of the environment and the presence of sagebrush and bunch grasslands in Nebraska ca. 30 Ma (Retallack 2007, 2013) although phytolith evidence do not corroborate such findings (Strömberg 2004). In Montana, environments have been suggested, based mostly on faunal evidence, to remain more wooded and closed than in the Great Plains during much of the Arikareean (Rasmussen 1977, Rasmussen and Prothero 2003). However, paleosols suggest the presence of open habitats in Montana during the Eocene and the presence of bunch grasslands and sagebrush landscapes ca. 35-34 Ma (Retallack 2007, Sheldon and Hammer 2010, Retallack 2013). Pollen data also support the presence of open habitats by the end of the Eocene in the Rocky Mountains (Leopold et al. 1992). Although phytolith data do not support widespread open environments until the very end of the Arikareean, ca. 19 Ma (Strömberg 2005), they demonstrate the presence of locally grassy, or open, but wet habitats during the Eocene (Miller et al. 2012). Ongoing work by Strömberg and colleagues investigating habitat change throughout the Cabbage Patch beds suggests that grass-dominated vegetation was uncommon in this area through the Arikareean (Strömberg pers. comm. 2016).

It has long been assumed that environmental change drives faunal evolution. Recent work comparing the faunal and floral fossil records (e.g., Strömberg 2006, Hopkins 2007, Dunn et al. 2015), has suggested that vegetational change indeed played a role in mammalian evolution but the association between the two appears more complicated than previously assumed. Nonetheless, the opening of the environment, rather than the spread of grasses, has been put forward as the likely driver of evolutionary changes in the morphology of mammals such as the increased tooth crown height of many ungulate taxa (Janis et al. 2002a, Strömberg 2006, Damuth and Janis 2011, Mihlbachler et al. 2011) and Glires (Jardine et al. 2012). However, few studies (but see Calede et al. 2011) have investigated the link between environmental change and the ecomorphological composition of mammalian communities during the Oligo-Miocene in North

America. Here, I investigate the responses of mammalian communities, including residents and immigrants, to the opening of the environment during the Arikareean.

2. STUDY SYSTEM AND HYPOTHESES

Studies of extant mammalian communities demonstrate that when environmental disturbances alter habitat and vegetation, the composition of mammalian communities changes in concert (Lomolino and Perault 2000, Tabeni and Ojeda 2003, Briani et al. 2004, Ostoja and Schupp 2009). Such changes are a consequence of the habitat specificity of many mammals and the filtering of their distribution and abundance by their ecology. Diet and locomotion in particular have been shown to be very informative in determining the distribution and abundance of mammals across environments (e.g., Andrews et al. 1979, Reid 1997, Assefa et al. 2008, Townsend et al. 2010, Louys et al. 2011, Kovarovic et al. 2013, Lintulaakso and Kovarovic 2016). Thus, arboreal and scansorial mammals are more common in forested environments (Van Valkenburgh 1985, Mares et al. 1986, Reed 1997, Townsend et al. 2010, Kovarovic et al. 2013), and saltatorial mammals are more diverse in open environments (Rosenzweig and Winakur 1969, Kotler and Brown 1988); so are cursorial as well as semifossorial and fossorial mammals (Kappelman et al. 1997, Nevo 1999, Hopkins 2007, Ojeda and Tabeni 2009). Open environments are also characterized by the presence of a high biodiversity of grazers and consumers of underground food storages (i.e. roots and tubers) whereas forested environments are generally typified by the presence of diverse frugivores, folivores, and invertivores (Reed 1997, Yeakel et al. 2007, Townsend et al. 2010, Kovarovic et al. 2013). Because in Glires (rodents and lagomorphs) diet and burrowing behavior are correlated with hypsodonty (i.e. tooth crown height), open environments are also associated with a higher biodiversity of hypsodont Glires (high crowned) that feed on abrasive foods and/or burrow than forested environments where brachydont Glires (i.e. low crowned) are more common (Williams and Kay 2001, Jardine et al. 2012). Comparisons of modern ecosystems also suggest that, overall, open environments and decreased habitat complexity support lower taxonomic and ecological diversities than forested habitats (August 1983, Mares et al. 1986, Fox and Fox 2000, Williams et al. 2002, Tews et al. 2004, García et al. 2013). When taxonomic diversity decreases faster than ecological diversity, functional redundancy (here number of genera divided by the functional richness, Villéger et al. 2011) decreases. Functional redundancy has been positively correlated with community resilience to perturbations and ecosystem stability in modern ecosystems (Naeem 1998, Carmona et al. 2016). Thus, tracking the ecomorphological (i.e. functional) diversity of mammalian communities can inform ecosystem processes (Naeem et al. 2012, Carmona et al. 2016). This method has been broadly applied in modern ecosystems (Stevens et al. 2003, Blackburn et al. 2005, Ahumada et al. 2011, Pool and Olden 2012, Chan et al. 2013). It has also been adopted in the fossil record to better understand the consequences of mass extinctions (Villéger et al. 2011, Christie et al. 2013, Wilson 2013) and reconstruct past environments and environmental change (e.g., Collinson and Hooker 1989, Clyde and Gingerich 1998, Hernandez-Fernandez et al. 2006, White et al. 2009, Kovarovic et al. 2013, Domingo et al. 2014). The locomotion of mammals has been used to investigate environmental changes in the fossil record (e.g., Janis et al. 2002b, Samuels and Van Valkenburgh 2009, Janis et al. 2012, Figueirido et al. 2015). Diet and hypsodonty have also been included in many studies of extant and Cenozoic mammalian community structure across habitats (Townsend et al. 2010, Ahumada et al. 2011, Kovarovic et al. 2013, Domingo et al. 2014). Changes in herbivore diets in particular have been used extensively to infer environmental change (Semprebon and Rivals 2007, Badgley et al. 2008, Jardine et al. 2012, Domingo et al. 2014).

Using ecomorphological composition of mammal paleofaunas to understand consequences of past environmental change on faunal communities requires the examination of well sampled assemblages whose depositional history is well understood and whose age is well constrained. Focusing on small mammals, in particular, provides a more sensitive measure of biotic response to environmental change because these taxa typically have smaller geographic ranges and more likely respond *in situ* to environmental change (Barrett and Peles 1999, Merritt 2010). Few Arikareean-aged deposits offer such opportunity, and many of the best studied localities in Oregon and the Great Plains lack a rich vertebrate microfossil assemblages. Fortunately, a less studied area from the northern Rocky Mountains, the Cabbage Patch beds of western Montana, a series of fossil-bearing horizons of the upper part of the Renova Formation, include numerous well-sampled vertebrate microfossil assemblages whose taphonomy has been studied (Calede 2016b) and stratigraphy is resolved (Rasmussen and Prothero 2003, Calede 2016a). These assemblages provide the necessary data to track small mammal communities over ca. 4.5 million years through the early Arikareean. Because the environmental changes of the Arikareean were asynchronous across the continent (Strömberg 2005, see above), I include in this study data from two of the few vertebrate microfaunas of the Great Plains (Ridgeview, Bailey 2004; McCann Canyon, Korth 1992), coeval with Cabbage Patch, to compare patterns of faunal change across regions.

I track the ecomorphological composition of mammalian assemblages through the early Arikareean in Nebraska and Montana to test the hypotheses that (1) taxonomic and functional richness as well as functional redundancy decreased with the environmental transition of the

Arikareean, (2) this environmental transition was associated with a turnover from mammals with closed habitat affinities (e.g., arboreal and frugivorous mammals, low crowned Glires) to mammals with affinities for open environments (e.g., burrowers and grazers, high crowned Glires), (3) the timing of the faunal turnovers in Montana and Nebraska reflects the asynchrony of environmental transitions known from the plant and paleosol record, (4) the reconstruction of Arikareean environments based on mammalian faunas are consistent with data from the paleobotanical and paleopedological records, and (5) these changes in the ecological composition of Arikareean mammalian assemblages were linked to taxonomic turnover from immigration and in situ evolution.

3. MATERIAL AND METHODS

3.1. Sampling and dataset assembly

I included in this study a total of 4,999 fossil mammal specimens identified to the genus or species level available from 11 assemblages (N>40 specimens) across the two regions studied (Table 1, Fig. 1). All assemblages were screenwashed (Korth 1992, Bailey 2004, Calede 2016a) to recover the smallest members of the vertebrate fauna. I restricted my analyses to cheek teeth (premolars and molars) to limit taxonomic and taphonomic biases (Calede et al. 2011, Calede 2016a). Seven of those assemblages are from the Cabbage Patch beds. A detailed study of their lithology and taphonomy (Calede 2016b, see also Calede 2016a) demonstrates that the depositional histories and preservations of these assemblages are similar enough to validate comparisons of their ecological compositions. They provide snapshots of the composition of the mammalian fauna of western Montana ca. 30 to 26.5 Ma (Calede 2016a), spanning all three biostratigraphic units (lower, middle, and upper) of the Cabbage Patch beds and the early early-late early Arikareean (Ar1-Ar2) boundary. Current radioisotopic ages and correlations (Calede 2016a) suggest that the lower Cabbage Patch may be as old as ca. 30 Ma (Ar1), the middle Cabbage Patch is ca. 26.5 Ma (Ar2), and the upper Cabbage Patch may be as young as ca. 25.6 Ma (Ar2) (Calede 2016a). The four assemblages from Nebraska represent two faunas. The Ridgeview Local Fauna is considered ca. 29 Ma (Bailey 2004), coeval with the lower unit of the Cabbage Patch beds. The McCann Canyon Local Fauna is ca. 26.5 Ma (MacFadden and Morgan 2003, Tedford et al. 2004), coeval with the middle units of the Cabbage Patch beds. The taxonomy of the mammals from all three faunas (Cabbage Patch, Ridgeview, and McCann Canyon) has been extensively studied (Rasmussen 1977, Korth 1992, Korth and Bailey 1992, Bailey 2004, Hayes 2005, Korth and Branciforte 2007, Korth 2008, Calede 2016a). All specimens studied are reposited at the University of Nebraska State Museum (Ridgeview and McCann Canyon local faunas) as well as the University of Montana Paleontology Center, University of Kansas Museum of Natural History, and the University of Washington Burke Museum (Cabbage Patch Beds). The lithology of the deposits from Nebraska (channel-derived bedded sands and gravels; Korth 1992, Bailey 2004) is distinct from that found in the Cabbage Patch beds (which is indicative of low-energy fine-grained floodplain deposits), but it is consistent across all four assemblages from Nebraska included in this dataset. Although depositional environments can influence the preservation of fossil mammals (see Calede 2016b), there is no evidence supporting the differential preservation of different ecomorphological groups through time in Nebraska. In the youngest assemblage from Montana (C0173), one taxon, the burrower *Gregorymys* is likely more abundant than it was in the living community (see Calede 2016b). The pattern at this locality should therefore be interpreted with caution. Although the biodiversity of the assemblages from Montana and Nebraska may not be directly comparable with one another, they provide two independent tests of the temporal correlation between faunal and environmental changes during the Arikareean in North America.

3.2. Ecological assignments

Reconstructing the ecology of the extinct Oligocene mammals included in this study is facilitated by their close phylogenetic affinities with extant taxa. Arikareean-aged mammals have been extensively studied (Janis et al. 1998, 2008) and are known from well-preserved dental, cranial, and postcranial remains (e.g., Rasmussen 1977, Wang et al. 1999, MacFadden and Morgan 2003, Calede 2014, Korth and Samuels 2015) that allow their categorization according to locomotion, diet, and hypsodonty. Because the assemblages studied are biased towards small mammals (Korth 1992, Bailey 2004, Calede 2016b), variance in body mass, another important ecomorphological trait, is very small in this fossil dataset.

I determined diet and locomotion for each genus (total of 94 fossil genera) based on evidence from previous studies, observations and quantitative analyses of the morphology of fossils from the areas studied, as well as inferences based on similarities and phylogenetic affinities with fossil and extant relatives (Table 2). I assigned each taxon to one of eight locomotory categories and one of six dietary categories (unless the locomotion and/or diet is/are unknown). Diet has only been studied in a few of the numerous extinct genera of rodents included in this study. I therefore used hypsodonty, which is correlated to diet in rodents (Williams and Kay 2001), to assign individual genera to dietary categories. Each genus (total of 55 genera) was assigned to one of four categories of hypsodonty. I then classified hypsodont and hypselodont rodents to a diet of abrasive materials. This category includes grasses and forbs as well as roots and tubers. Because hypsodonty is also linked to burrowing behavior in rodents

(Williams and Kay 2001, Jardine et al. 2012), this dietary category also includes animals that ingest a lot of non-food items such as soil. I classified mesodont taxa as fruit and foliage eaters based on studies of extant and extinct Glires (Fraser and Theodor 2010, Jardine et al. 2012). Because brachydont taxa can either be omnivorous or fruit/foliage eaters, I used similarities in tooth morphology (e.g., morphology of cusps and lophs of the occlusal surface) between the fossil taxa and extant relatives or ecological analogues to inform the assignment of individual rodent genera to dietary categories (see Table 2). Tooth morphology is highly correlated to diet in rodents (e.g., Evans et al. 2007, Coillot et al. 2013, Kimura et al. 2013).

3.3. Taxonomic/functional richness and functional redundancy

In each assemblage, I calculated the number of guilds (i.e. groups of mammals belonging to the same diet and locomotion categories) represented (i.e. functional richness), the number of genera present (as a proxy for taxonomic richness), and the functional redundancy. I excluded taxa with an unknown diet or locomotion from these calculations. I expect the taxonomic and functional richness as well as the functional redundancy to be lowest in the youngest assemblages studied, presumably the more open environments (Fig. 2).

3.4. Ecomorphological turnover and environmental change

I analyzed the composition of mammalian communities in both regions by tracking the relative abundance of individuals across locomotory, dietary, and hypsodonty categories through time. I used chord distance to assess the similarities in relative abundances of individuals across ecological categories between subsequent assemblages and detect faunal turnover (Bobe et al. 2002, Frost 2007, de Ruiter et al. 2008, Calede et al. 2011, Calede 2016a) I only calculated these values for select assemblages of the Cabbage Patch beds placed in a stratigraphic context (Calede 2016a). I excluded the proportion of unknown ecologies from these analyses by rescaling the relative abundances of the known ecologies to 100%. I also analyzed the guild representation by combining dietary and locomotory information for each genus thus assigning each genus to a macroguild (following the macroniche terminology of Mares et al. 1986). I tracked the relative abundance of each macroniche across localities. I expect the relative abundance of fruit and foliage consumers to decrease and the relative abundance of mixed-feeders and consumers of abrasive foods to increase with the opening of the environment (Fig. 2). I also predict that habitat openness will be reflected in a decrease in the relative abundance of arboreal and scansorial taxa (more common in forested environments) and an increase in that of fossorial, saltatorial, and cursorial taxa. I predict that the reltive abundance of hypsodont Glires will increase with the transition to open environments whereas that of brachydont individuals will decrease. I expect chord distance values to be highest at times of environmental change such as the transition between the Ridgeview and the McCann Canyon Fauna (ca. 26 Ma) in Nebraska. In Montana, in the absence of published detailed habitat data, I predict that ecological change will be recorded at the Ar1-Ar2 transition, coincident with a taxonomic turnover (Calede 2016a).

3.5. Environmental inference based on Arikareean faunas

I compared changes in ecological composition across Arikareean-aged mammal-bearing assemblages with modern mammal communities associated to known climates and vegetations in order to associate fossil assemblages with environments. I combined two datasets (Reed 1996, Townsend 2004) including a total of 51 mammalian communities from Africa, Central America, and South America. Although the dataset of Reed (1996) is focused on large mammals, the communities compiled by Townsend (2004) include many small mammals (see also Townsend et al. 2010). Both datasets include, in addition to the relative abundances of mammals across ecological categories, independent data on the vegetation and climate of the communities' habitat (see Appendix 5.1). Although both datasets are focused on tropical communities, they include environments ranging from forests to desert as well as bushland, grassland, shrubland, woodland, and plains. Mean annual precipitation ranges across habitats from 125 to 4,000 mm a year, overlapping with estimates of mean annual precipitation during the Arikareean in both Montana and Nebraska (Pierce 1993, Retallack et al. 2000, Retallack 2007, Eronen et al. 2015). Despite the diversity of environments included in this dataset, future iterations of this work will seek to include more temperate communities (including mixed coniferous forests, deciduous forests, and shrublands) more likely to be analogous to those of the North American mid to late Oligocene (Wing 1987, Pierce 1993, Retallack et al. 2000, Woodburne 2004, Retallack 2007).

For each modern community and fossil assemblage, I combined dietary and locomotory categories and deleted the carnivorous dietary category as it was extremely rare in the fossil assemblages (see Appendix 5.2). Unknown ecologies were also excluded from the dataset. The combination of categories allowed the inclusion of a large sample of modern communities along with the fossil assemblages from the Arikareean while preserving important ecological information. The relative abundances of mammals from each community/assemblage were scaled to 100%. I used Bray-Curtis distance calculated using simba 0.3-5 (Jurasinski and Retzer 2012) and non-metric multidimensional scaling ordination (NMDS) to visualize dissimilarity in ecological composition between modern communities and fossil assemblages. NMDS does not assume multivariate normality or linear associations and uses the rank order of distances (not the value themselves unlike principal coordinate analysis, Kruskal and Wish 1978). It is therefore less sensitive to numerical differences between assemblages. I used the vegan package in R to generate the NMDS and the biostats functions (McGarigal 2015) to generate a Monte-Carlo randomization test of the stress value of the NMDS. I predict that the NMDS (i.e. ecospace) will help recover a gradient of open to closed environments consistent with mammalian ecologies (see above). The location in the ecospace of fossil assemblages will be indicative of their likely environment. I predict that older assemblages (Ar1) will cluster with forested extant communities while younger assemblages will cluster with mammalian communities from more open environments (Fig. 2).

3.6. Interactions with taxonomic turnover

To better determine the process by which mammalian communities responded to environmental change during the Arikareean, I also compared the change in the relative abundance of specimens across ecological categories through time with the changes in the relative abundance of genera through time. I assigned each taxon from the Cabbage Patch beds of Montana to one of three environmental affinities: closed/mesic habitats, open habitats, unknown affinities using locomotory and dietary categories associated to the closed to open environment gradient of the NMDS and data from the literature (Table 2). I then calculated the frequency of genera with open and closed/mesic affinities for each of the six best samples assemblages from Montana placed in a stratigraphic context. I also calculated the proportion of new taxa (for all assemblages except the oldest C1708) with open or closed/mesic affinities to determine the ecological affinities of immigrant and newly evolved taxa. Overall, I expect the frequency of genera with affinities for open environments to increase over time alike the relative abundance of individuals although I predict that the changes in taxa will lag behind the changes in relative abundance of individuals (Barnosky et al. 2003). I predict that more taxa with affinities for closed habitats will go extinct among the resident taxa over time. Conversely, I expect a higher proportion of novel taxa will have affinities for open habitats than closed habitats. This proportion should increase through time (Fig. 2).

All analyses were run in in R 3.1.3 (R Development Core Team 2015) using RStudio 0.98.1103 (RStudio 2015), the package vegan 2.3-5 (Oksanen et al. 2015), and the biostats functions (McGarigal 2015).

4. Results

4.1. Taxonomic/functional richness and functional redundancy

The functional richness of mammalian assemblages varies little through time in Montana (Table 1, Fig. 7), with between 10 and 13 ecological guilds identified in each assemblage. These patterns are similar in Nebraska, with between seven and 13 guilds in the assemblages and no trend through time in functional richness. Functional richness, unlike taxonomic richness, is not linked to sampling across regions (Spearman’s rank order correlation; rho=0.31, p=0.35; rho=0.77, p=0.005 respectively). As a consequence of taxonomic richness, functional redundancy is also correlated with sampling (rho=0.77, p=0.005). This correlation disappears (rho=0.58, p=0.1) when I remove the two best sampled assemblages from Nebraska (Dw-121 and Cr-117) from the analysis. In Montana, functional redundancy is around 1.4 in four of the seven assemblages and between 1.1 and 1.2 in the other three assemblages including an assemblage from the middle unit of the beds (C0174) and two from the lower unit of the beds (MV6613 and MV6554). In Nebraska, functional redundancy varies greatly across assemblages but no pattern through time can be detected (Fig. 8).

4.2. Ecomorphological turnover and environmental change

4.2.1. Locomotion— I found changes in locomotory ecology common to Nebraska and Montana (Table 3, Fig. 3). Specifically, the proportion of arboreal individuals was higher overall during the Ar1 than during the Ar2. The proportion of terrestrial individuals (i.e. ambulatory mammals that are not arboreal and do not burrow, swim, jump, or run extensively) also tended to be higher during the Ar1 than during the Ar2. This is particularly evident in Nebraska. Conversely, the proportion of saltatorial, semifossorial, and fossorial individuals was higher during the Ar2 than the Ar1. Once again, the difference between the two time periods was greater in Nebraska than in Montana.

There were also changes in locomotory ecologies that differed between the two regions. Specifically, semiaquatic mammals were present in Montana, particularly during the Ar1. Although there was little change in the abundance of the rare cursorial mammal individuals between the Ar1 and Ar2 in Nebraska, they were more abundant in the Ar1 than the Ar2 in Montana.

There were also changes in locomotory ecology within the Ar2 in Montana between the middle and upper units of the Cabbage Patch beds. In the middle unit, the proportions of fossorial and saltatorial individuals were subequal; semifossorial taxa were not very abundant. In the upper unit of the beds, fossorial and semifossorial individuals dominated the assemblage; saltatorial individuals represented only a small proportion of the mammals in the assemblage. The change in locomotory ecology in the Cabbage Patch beds was greatest at the transitions between the lower and middle units of the beds as well as the middle and upper units of the beds (Fig. 4, Table 4). The smallest difference between subsequent assemblages is observed within the middle unit of the beds.

4.2.2. Diet—I also found changes in dietary ecology common to Nebraska and Montana (Table 3, Fig. 5). There was a greater proportion of individuals eating abrasive foods during the Ar2 than the Ar1. Although this pattern is much stronger in Nebraska where abrasive consumers were absent during the Ar1 and represented over 60% of the fauna during the Ar2, there also was a large increase (~20% of the fauna) in the relative abundance of abrasive consumers between the middle and upper units of the Cabbage Patch beds in Montana. Conversely, fruit and foliage consumers were more abundant overall during the Ar1 than the Ar2. Despite being rare, invertivorous mammals tended to be more abundant during the Ar1 than the Ar2. Carnivores were very rare or absent across the assemblages studied.

There were also changes in dietary ecology that differed between the two regions. In Nebraska, the proportion of omnivorous mammals was very high during the Ar1 (>45%) and dramatically lower during the Ar2 (<15%). In contrast, in Montana, the abundance of omnivores varied across assemblages. No consistent pattern of change through time can be identified.

The pattern of turnover through time in the abundances of dietary categories is very similar to that observed for locomotory categories (rho = 0.9, p=0.08, Spearman's rank order correlation). Indeed, the highest chord-distance value is found between the lower and middle units of the Cabbage Patch beds (Table 4). The second highest value is found at the transition between the middle and upper units. The lowest value is found between the two assemblages from the middle Cabbage Patch beds.

4.2.3. Hypsodonty—Similarly to locomotion and diet, I found changes in the frequency of hypsodonty categories common to Nebraska and Montana (Table 3, Fig. 6). Thus, in Nebraska, brachydont and mesodont individuals dominated Ar1 faunas (>99.7%) whereas hypsodont individuals dominated Ar2 faunas (>75%). Although not very abundant (<3%), hypselodont individuals were only present in the Ar2 assemblages. Likewise, although in Montana, hypsodont Glires were present through the section (from the oldest to the youngest assemblages), they were more abundant in the youngest Ar1 assemblage and the Ar2, and most abundant in the youngest assemblage (~50%); hypselodont Glires, although rare (<4%), were only present in two assemblages from the Ar2.

Turnover in the composition of Glires with regards to hypsodonty categories was maximal in the oldest part of the lower unit of the beds and minimal in the upper part of that same unit. The second highest chord distance value is found at the transition between the Ar1 and Ar2 (Table 4). Turnover between Ar2 assemblages was low.

4.2.4. Macroguilds—Among older assemblages of Montana (C1708 and C1721), terrestrial omnivore individuals are most abundant. At C1708, arboreal omnivores are also very abundant. At C1721, cursorial fruit and foliage eaters are the second most abundant guild. Semiaquatic abrasive food consumers are the most abundant guild of mammals present in the assemblage from MV6554. Among the older Ar2 assemblages, those from the middle unit of the Cabbage Patch beds, terrestrial omnivores remain abundant but saltatorial omnivores and fossorial fruit and foliage consumers become very abundant, more so than they were during the Ar1. In the youngest locality (C0173), one guild, the fossorial abrasive food consumers, dominates the fauna. Other guilds are present in low abundances. Only semifossorial fruit and foliage consumers are also abundant at C0173. In Nebraska, Ar1-aged assemblages are, similar to coeval assemblages from Montana, dominated by terrestrial omnivores. Both Ar2-aged assemblages from Nebraska are dominated by fossorial abrasive food consumers.

4.3. Environmental inference based on Arikareean faunas

The distances in the NMDS produced (Fig. 9; stress= 7.6%; Monte Carlo randomization test of stress value with k=3 and 100 replicates: p=0.01) accurately represent the pairwise dissimilarities across assemblages/communities (correlation of the fitted values and ordination distances: non-metric fit R^2=0.99, linear fit R^2=0.97). An additional analysis not figured (k=2, stress=13.2%) shows a similar pattern. The low stress values of these analyses suggest a good fit between the observed ordination pattern and the dissimilarities between assemblages (McCune and Grace 2002). The mammal communities from South America (Townsend 2004) and Africa (Reed 1996) from similar environments do not cluster together. There are higher proportions of mammal individuals feeding on fruits and foliage, scansorial individuals, and invertivorous individuals in South American communities. However, both the African and South American communities display a gradient from forested (higher NMDS1 and NMDS2 scores) to open environments (low NMDS1 and NMDS2 scores). More closed environments are characterized by higher proportions of arboreal individuals whereas open environments are characterized by higher relative abundances of fossorial individuals as well as mixed-feeders and abrasive food consumers. Fossil assemblages are most similar to the African dataset (lower NMDS1 scores) but most of them include higher proportions of omnivorous and terrestrial individuals than extant communities. All Ar1-aged assemblages from both Montana and Nebraska as well as the oldest Ar2 assemblage from Montana (C1704) are most similar to the forested environments of Africa but are located outside the range of values exhibited by extant communities. Some of them (Dw-122, MV6613, and C1721) cluster with the Kilimanjaro forest community. The youngest assemblage from Montana (C0173) is most similar to the savanna from the Sahel. The Ar2 assemblages from Nebraska display the most negative scores along NMDS1 and NMDS2, beyond the range observed in extant communities. Nonetheless, Cr-125 plots close to the Kalahari Thornveld.

4.4. Interactions with taxonomic turnover

In Montana, the proportion of genera with affinities for forested/mesic environments is high (>50%) throughout the Ar1 (Table 5, Fig. 10) and decreases in the Ar2 but there is little difference between the two time periods. Conversely, the proportion of taxa with affinities for open environments is low (<15%) throughout the Ar1 and increases in the Ar2 although once again, there is only a small difference between the two time periods. The two time series are negatively correlated but the relationship is not quite significant (rho=-0.83, p=0.058; Spearman’s rank order correlation). New appearances during the Ar1 are almost exclusively composed of taxa with affinities for closed/mesic habitats whereas new appearances during the Ar2 are mostly composed of taxa with affinities for open environments. Of the nine taxa with known habitat affinities that go extinct through this series of Cabbage Patch assemblages (excluding last occurrences in C0173, the youngest assemblage), seven (~78%) are taxa with affinities for forested/mesic environments.

5. DISCUSSION

There were no decreases in taxonomic richness, functional richness, or functional redundancy in Nebraska or Montana during the Arikareean. Although in both regions the fauna went from being dominated by mammals with affinities for forested and mesic environments to dominated by mammals with affinities for open environments, this transition was more pronounced in Nebraska than Montana. Despite this difference in magnitude, the timing of the ecological transition is similar across the two regions. Reconstructions of the environments based on the ecological composition of the fossil assemblages suggest that Ar1 faunas inhabited closed forests whereas Ar2 faunas may have been associated to more savanna-like habitats. Differences in ecologies across taxa suggest that these changes in the ecological composition of Arikareean mammalian assemblages were linked to taxonomic turnover from immigration and in situ evolution. I discuss these results in more detail below.

5.1. Taxonomic/functional richness and functional redundancy

There is no evidence for a directional change in the functional richness or functional redundancy of mammalian assemblages during the Arikareean. However, in Montana, the lowest values of functional redundancy are found at assemblages preceding biostratigraphic boundaries (i.e. the youngest assemblages from the lower and middle units of the beds). These lower values may be indicative of environmental perturbations. This interpretation is consistent with the results from the chord distance analyses which show the greatest amounts of change in the ecological composition of mammalian communities in Montana at the transition between the biostratigraphic units of the Cabbage Patch beds. However, they are not associated with low taxonomic evenness or relative abundance distributions associated to disturbed environments (Calede 2016a).

5.2. Ecomorphological turnover and environmental change

Overall, the nature of the changes in ecological composition of Arikareean assemblages is consistent with a response of mammalian communities to an opening of the environment through time. The ecological composition of the Ar1-aged faunas reflected more forested and mesic environments whereas Ar2-aged assemblages were dominated by mammals with ecologies associated to more open environments.

In both Montana and Nebraska, the oldest assemblages are rich in taxa and individuals whose ecology is associated to closed, forested environments. Many taxa consume soft fruits and foliage. Most Glires are brachydont and mesodont, a pattern consistent with the regional pattern of Glires diversity in the Great Plains (Jardine et al. 2012). Consumers of abrasive foods as well as hypsodont Glires are very rare or absent. Arboreal taxa can be abundant but many mammals are terrestrial. Although a few fossorial mammals are present, most are members of the Proscalopidae, a taxon that has been suggested to dig in soft moist soils based on the functional morphology of their forelimb (Reed and Turnbull 1965, Bjork 1975). The others are members of *Scalopoides,* a talpid mole that dug complex burrows in moist, wooded environments (Retallack 2004, Calede et al. 2011, Piras et al. 2012).

A few additional mammals present in Montana display ecologies usually associated to open environments but a close inspection of these taxa only reinforces the conclusion that the Ar1 was rich in forest-dwelling mammals. For example, there is a saltatorial mammal during the Ar1, *Heosminthus*, a dipodid rodent (Daxner-Höck et al. 2014, Calede and Cairns 2015). Although ricochetal rodents have usually been associated with open environments, ancestral character state reconstructions within dipodoids suggest that ricochetal locomotion evolved in mesic forested environments (Wu et al. 2014). In fact, even small mammal cursoriality has been suggested to have evolved in closed habitats (Lovegrove and Mowoe 2014). The high abundance of cursorial mammals in the lower unit of the Cabbage Patch beds is the product of the high abundance of the leptomerycid *Pronodens*, a small mouse-deer that, despite exhibiting cursorial adaptations, was very small and has been interpreted as an analog (Table 2) to modern mouse-deer (genera *Hyemoschus*, *Moschiola*, *Tragulus*), forest specialists that feed on fallen fruits and leaves (Ramesh et al. 2012, Sridhara et al. 2013, Granados et al. 2016).

During the Ar2, faunas became rich in mammals with ecologies associated to open environments. The great abundance of hypsodont taxa during the Ar2, particularly in Nebraska, the presence of some hypselodont taxa, and the presence of open-environment mammals like the cursorial leporid *Archaeolagus* support the interpretation of the Ar2 of both Montana and Nebraska has more open than they were during the Ar1. Although hypsodont mammals are abundant in the youngest assemblage of the lower Cabbage Patch (Ar1), this is a consequence of the large proportion of beavers (*Microtheriomys* specifically) in MV6554 (Table 3, Calede 2016a). Most conspicuously, fossorial rodents became very abundant in both Montana and Nebraska. In Montana, the burrowing niche was occupied by the entoptychine gophers *Pleurolicus* and *Gregorymys*. In Nebraska, the dominant burrowing rodents were the palaeocastorine beaver *Palaeocastor* and the gopher *Entoptychus*. Both *Entoptychus* and *Palaeocastor* were more strongly fossorial than either *Pleurolicus* or *Gregorymys* (Calede 2014, Korth and Samuels 2015, Calede et al. 2016). The evolution of palaeocastorine beavers has been linked to the rise of more open and arid environments (Samuels and Van Valkenburgh 2009, Korth and Samuels 2015). The increased abundance of hypsodont and fossorial rodents in Montana and Nebraska during the Ar2 is consistent with the regional pattern of Glires diversity in the Great Plains (Jardine et al. 2012). Nonetheless, although both Montana and Nebraska supported mammal communities rich in fossorial rodents, the composition of this guild suggests that the environment of Nebraska during the Ar2 was not only more open than it was during the Ar1, but also more open than during the Ar2 in Montana. The presence of a few arboreal taxa, such as the squirrel *Sciurion*, in the Ar2-aged assemblages of the Cabbage Patch beds, further supports the presence of some tree cover in the environment in Montana.

The transition in the ecological composition of mammalian communities is roughly coeval in Montana and Nebraska. In Montana, it takes place between the middle and upper units of the Cabbage Patch beds, ca. 26 Ma. In Nebraska, this transition is recorded only slightly earlier, ca. 26.5 Ma, but the accuracy of the dating of the deposits may obscure the exact timing of the mammals' response to environmental change in this area.

In Montana, this timing is not consistent with evidence from phytoliths. The results of the chord distance analyses suggest a strong, coupled change in locomotory and dietary ecology (e.g., fossoriality and consumption of abrasive foods) in Montana ca. 26 Ma. However, new data indicate that grass-dominated open habitats were not present in the northern Rocky Mountains (Montana/Idaho border) until ca. 23 Ma (Harris 2016), well after the deposition of the Cabbage Patch beds (Calede 2016a), although there is evidence for locally open bunch grasslands and sagebrush landscapes from paleosols (Retallack 2007, Sheldon and Hammer 2010, Retallack 2013). The ecological transition is mainly detected in a single assemblage, the youngest one from the beds, C0173. Calede (Chapters 1, 3) recognized that the unique faunal composition of this assemblage (dominated by a single species of the gopher *Gregorymys*) may be a consequence of its taphonomic setting and thus not representative of the regional pattern of the time. Additionally, the incomplete sampling of the Cabbage Patch beds (Calede 2016a), may affect the apparent timing of the ecological transition of the Arikareean. Because rarefaction analyses demonstrate that not all taxa have been discovered across the Cabbage Patch assemblages, rare taxa may be missing from the samples. Such rare taxa may have represented declining lineages that likely would have had affinities for the disappearing forested habitats (see below). Thus, the transition to mammalian assemblages with affinities for open environments may appear accelerated relative to its actual timing. Therefore, although mammalian faunas may have locally displayed affinities for open environments, the interpretation of a regional response to environmental change ca. 26 Ma should be considered provisional and will be dependent on future work documenting the composition of the phytolith assemblage through the Cabbage Patch beds.

In Nebraska, the transition in the ecological composition of mammalian communities is roughly coincidental with widespread open habitats in Nebraska ca. 26 Ma (Strömberg 2005). Although the assemblages included in this study are ca. 26.5 Ma, the dating of the deposits may obscure the exact timing of the mammals' response to environmental change in this area. Ongoing work by me and my collaborators to provide additional dates through the Cabbage Patch beds will help provide a chronostratigraphic framework for the response of mammalian communities to environmental change during the Arikareean.

5.3. Environmental inference based on Arikareean faunas

A comparison of the guild representation in the fossil assemblages with extant mammalian communities further supports a switch from closed to open environments in Montana ca. 26 Ma, at the transition into the upper unit of the beds. The NMDS analysis suggests that the environments of the lower, and even middle units of the Cabbage Patch beds, were most similar to modern mesic forests (or maybe woodlands for C0174) whereas the environment at C0173 (upper Cabbage Patch) was most similar to the modern shrubland of the Sahel Savanna. This inference, however limited by the taphonomy of C0173 (see above), is consistent with interpretations of the invertebrate fauna that suggests a dry environment at the time of the deposition of the youngest unit of the Cabbage Patch beds following a warm and wet middle Cabbage Patch (Pierce 1993). Calede (2016b) presented evidence from the non-mammalian fauna that the environment of the lower unit of the Cabbage Patch beds was likely wetter than that of the middle and upper units of the beds. For example, frogs are particularly abundant in the assemblage from C1708, a locality of the lower Cabbage Patch beds (Henrici 1994). In contrast, the amphibian fauna of the middle and upper units of the beds includes plethodontid and salamandrid salamanders (Tihen 1974, Tihen and Wake 1981), which can be some of the most terrestrial batrachians (Wake and Deban 2000). Fish are also particularly abundant at C1708 (Calede 2016b). Future work including temperate extant communities may help refine the ecological analysis presented herein but taphonomic biases towards the preservation of burrowing mammals (Calede 2016b) as well as detailed information on the diet and locomotion of both extant and fossil taxa will limit the explanatory power of such comparisons. Such difficulties can be overcome by including the data on the isotopic signature of the deposits, the composition of the phytolith assemblage, and the morphology of these silica structures (Dunn et al. 2015). These data are currently being collected by Strömberg and colleagues (Strömberg pers. comm. 2016) from the same Cabbage Patch horizons as the mammalian assemblages described herein; they will help associate mammalian taxa to likely habitats.

The comparison of Arikareean-aged mammalian assemblages from Nebraska and extant mammalian communities suggests a more dramatic environmental transition between the Ar1and the Ar2 than in Montana. The similarities between the Ar2-aged assemblages from Nebraska and the Kalahari Thornveld, a semiarid savanna (Meyer 2004), suggest the presence of a very open and xeric environment during the Late Oligocene in the Great Plains. Future studies of the phytolith assemblages from the deposits of the Ridgeview and McCann Canyon Local Fauna could help test this hypothesis and further refine the already well known Cenozoic history of the environments of the Great Plains (Strömberg 2005).

5.4. Interactions with taxonomic turnover

To further determine the timing of the changes in the ecological composition of Arikareean-aged mammalian assemblages and detect possible links with the important taxonomic turnover of the time, I investigated the changes in the proportion of genera (as opposed to individuals) according to their environmental affinities through the Cabbage Patch beds. The small difference between the Ar1 and the Ar2-aged assemblages of Montana in the proportions of mammal genera with affinities for closed or open environments suggests that the environment transition, or at least the response of mammals to an environmental change event, was still ongoing 26.5 or even 25.6 Ma. It appears that mammalian faunas first responded to environmental perturbations with changes in the relative abundances of individuals present and only later with changes in taxonomic composition associated with ecological traits. This pattern is consistent with previous results of the response of mammalian communities to warming over time (Barnosky et al. 2003). Yet, the correlation of the high faunal dissimilarities in ecological categories (Figs. 4-6) with biostratigraphic boundaries suggests a link between the taxonomic and ecological turnover. The increasing proportion of novel taxa (including immigrants from Asia and in situ originations) with affinities for open environments over time supports the hypothesis that the appearance of locally new taxa played a major role in the ecological transition of the Late Oligocene. This transition was not the product of competitive replacement. Instead, the association between the extirpation of mammalian taxa through the section and their affinities for mesic forested habitats further supports a link between ecology and extirpation and the possible adaptive nature of open-habitat ecologies (e.g., burrowing). This pattern is consistent with a change in mammalian community structure driven by the changes in the environment (see Calede et al. 2011 for another example). Future analyses of the specific pattern of relative abundance and timing of extirpation or origination for key Arikareean taxa will help resolve the influence of taxonomic turnover on the ecological transition of the Arikareean.

A similar pattern in which novel taxa participate into the ecological transition of mammalian communities has been described before for the Paleocene-Eocene Thermal Maximum (PETM, Clyde and Gingerich 1998). However, the faunal turnover of the PETM took place over 0.08 Ma compared to the possibly ca. 1 Ma represented by the faunal transition in the Cabbage Patch beds (Clyde and Gingerich 1998, Gingerich 2003, Calede Chapter 3). The lasting consequence on Cenozoic mammalian communities of the interaction between faunal immigration and environmental change over evolutionary timescales echoes the concerns of modern terrestrial communities and provide us with a record of the evolutionary consequences of ecological interactions.

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FIGURES

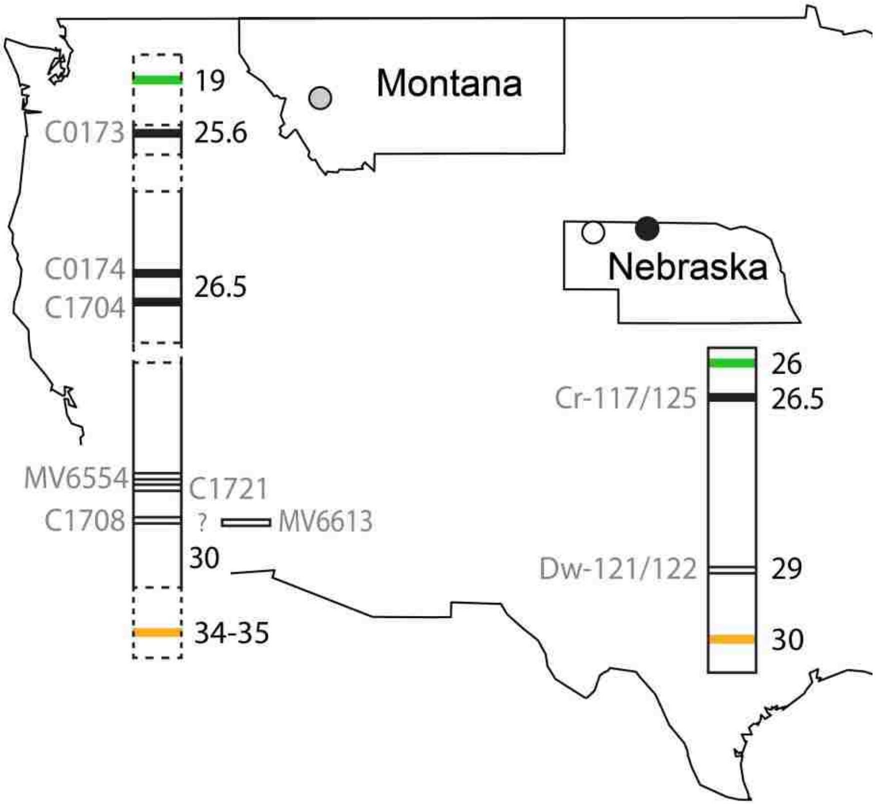

Figure 5.1. Map showing the location of the fossil assemblages studied. The colors of the dots in Nebraska correspond to the ages (black= Ar2, white, Ar1) of the deposits. The stratigraphic columns show the approximate age (in black) of the assemblages (in grey). The column for the deposits from Montana (the Cabbage Patch beds) is scaled to the measured section (see Calede 2016a). Dashed sections indicate sections not to scale. The column for the deposits from Nebraska is not scaled. The rectangles (black= Ar2, white, Ar1) show the location of the horizons that yielded the assemblages studied. The green rectangles show the age of open environments based on phytolith evidence. The orange rectangles show the age of open environments based on paleosol evidence.

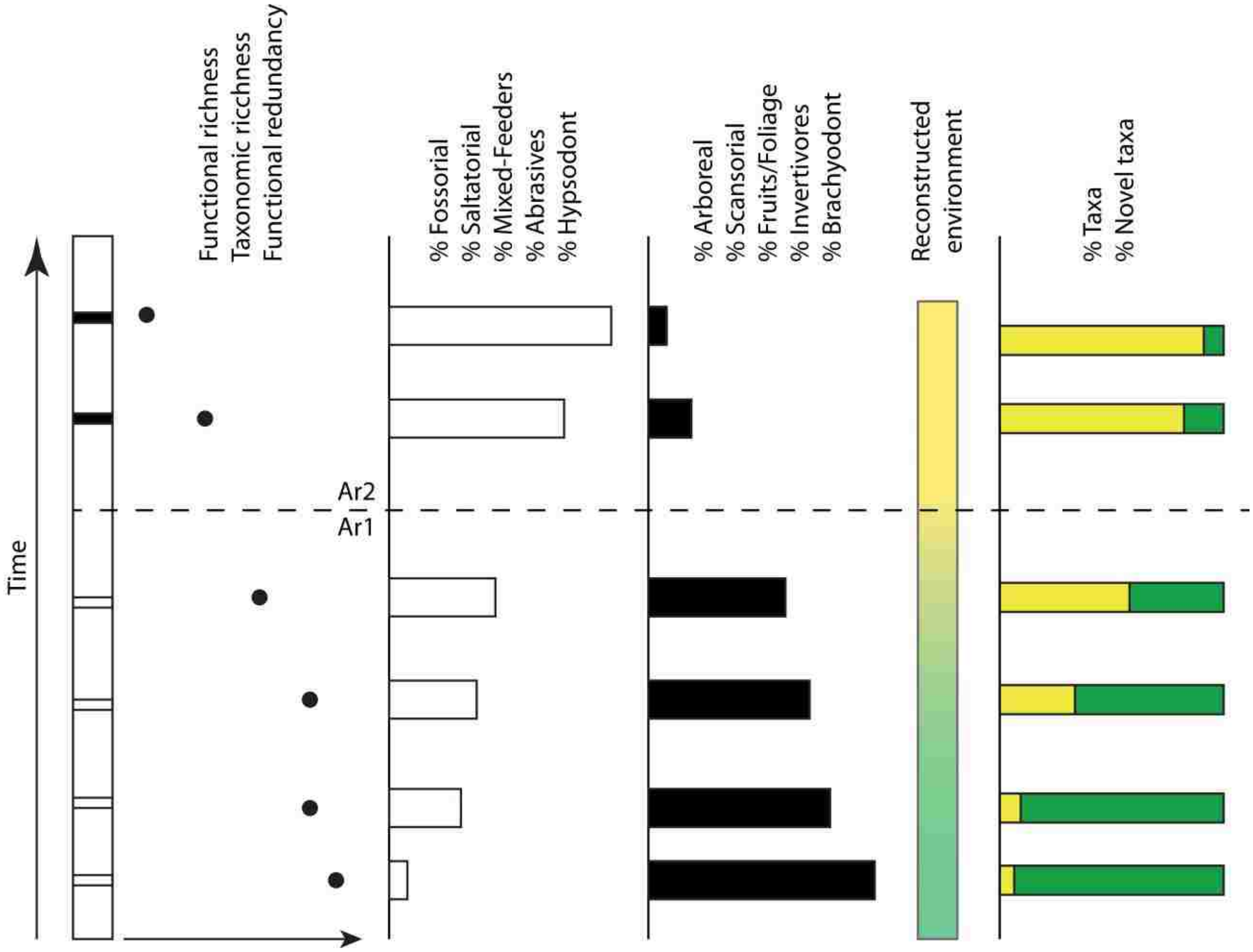

Figure 5.2. Predictions of changes in variables with opening of the environment during the Arikareean. White rectangles: Ar1 assemblages, black rectangles: Ar2 assemblages. Dashed line shows boundary between Ar1 and Ar2. Yellow reflects open habitat affinities while green indicates forested habitat affinities.

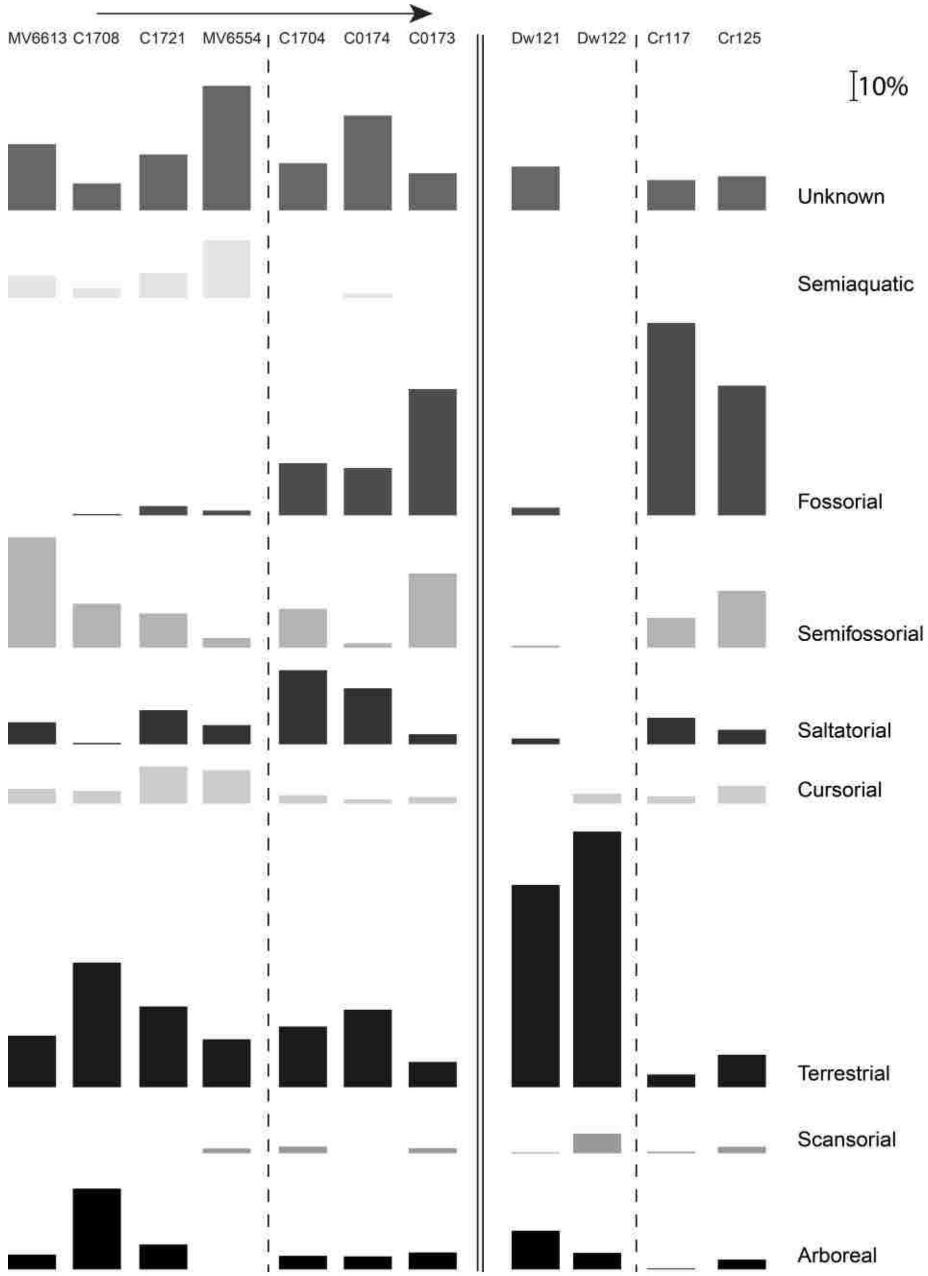

Figure 5.3. Relative abundances of locomotor modes across Arikareean assemblages. Dashed lines divide Ar1 (to the left) and Ar2 (to the right) assemblages. The double line separates assemblages from Montana (to the left) from those from Nebraska (to the right). Note the scale in the upper right corner. With the exception of MV6613, the assemblages from Montana are presented from oldest (C1708) to youngest (C0173) as indicated by the arrow.

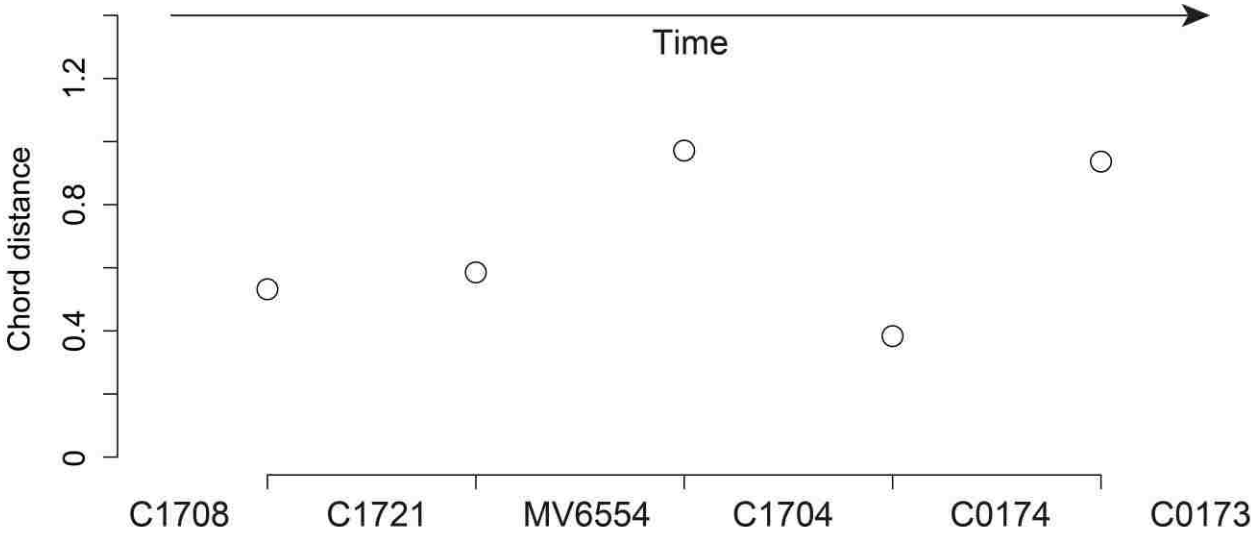

Figure 5.4. Plot of the chord distance values between subsequent assemblages from Montana (Cabbage Patch beds).

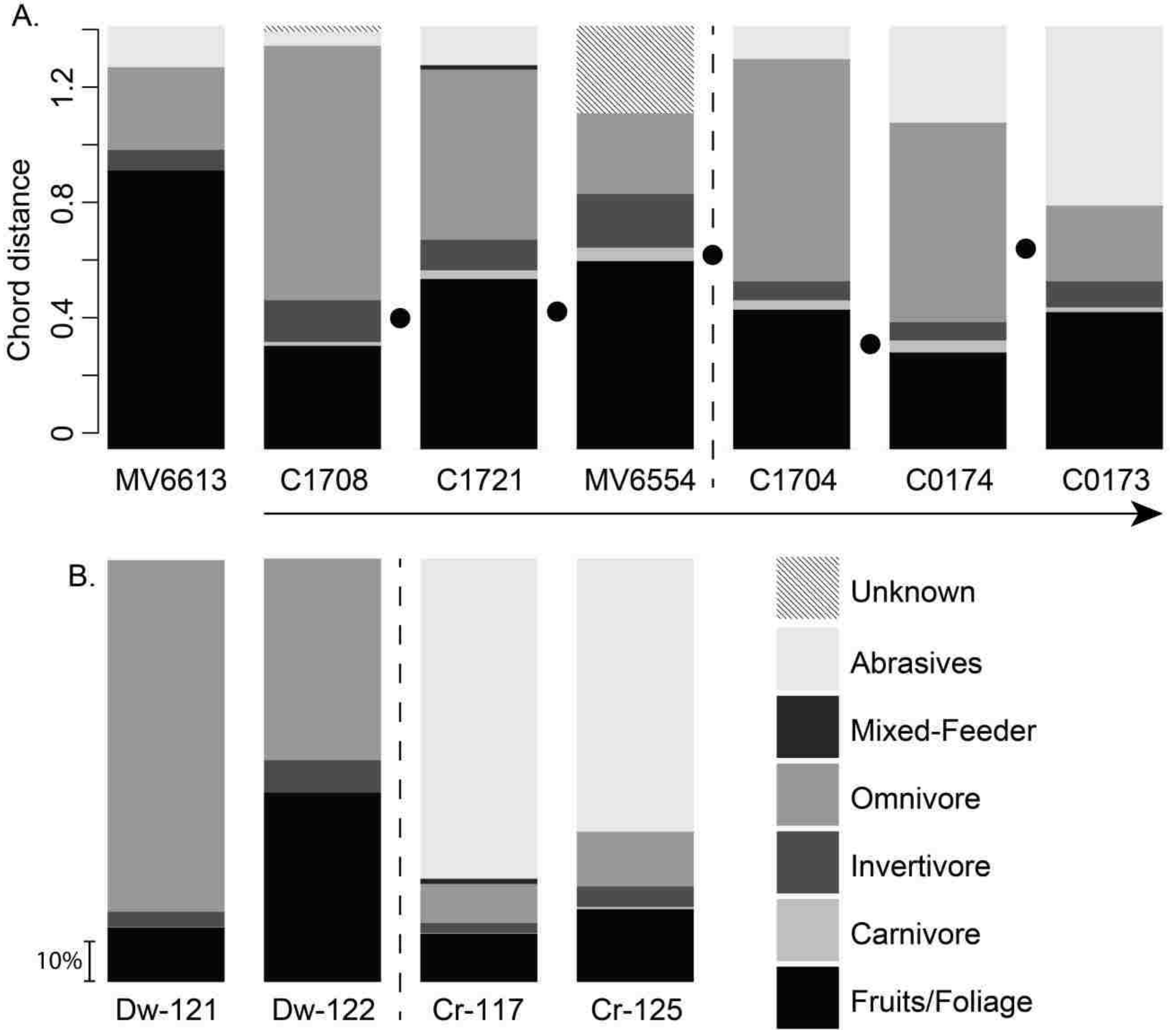

Figure 5.5. Relative abundances of dietary categories across Arikareean assemblages. A. Montana; B. Nebraska. Dashed lines divide Ar1 (on the left) and Ar2 assemblages (on the right). Note the scale in the lower left corner. The black circles indicate chord distance values. With the exception of MV6613, the assemblages from Montana are presented from oldest (C1708) to youngest (C0173) as shown by the arrow.

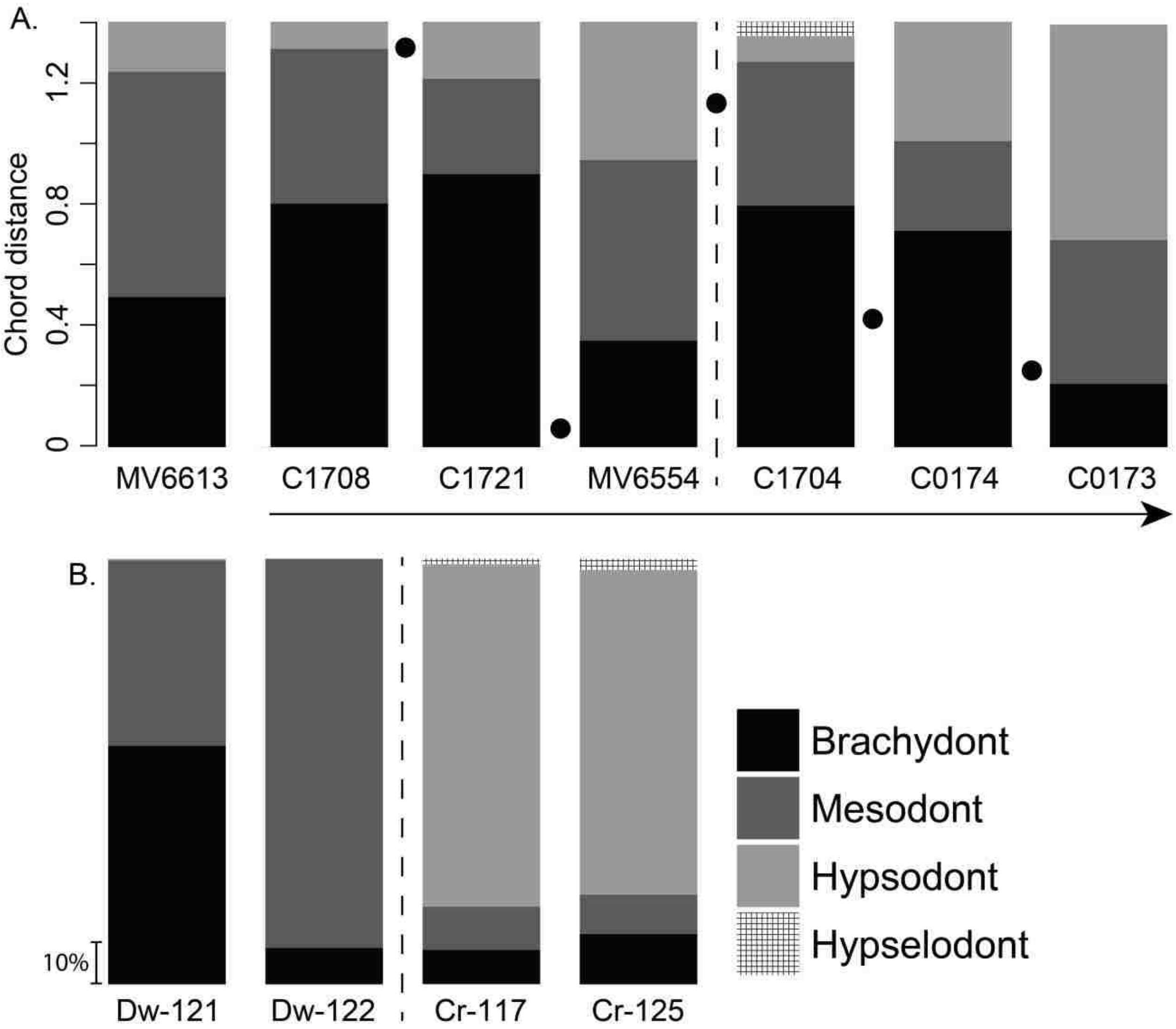

Figure 5.6. Relative abundances of hypsodonty categories of Glires across Arikareean assemblages. A. Montana; B. Nebraska. Dashed lines divide Ar1 (on the left) and Ar2 assemblages (on the right). Note the scale in the lower left corner. The black circles indicate chord distance values. With the exception of MV6613, the assemblages from Montana are presented from oldest (C1708) to youngest (C0173) as shown by the arrow.

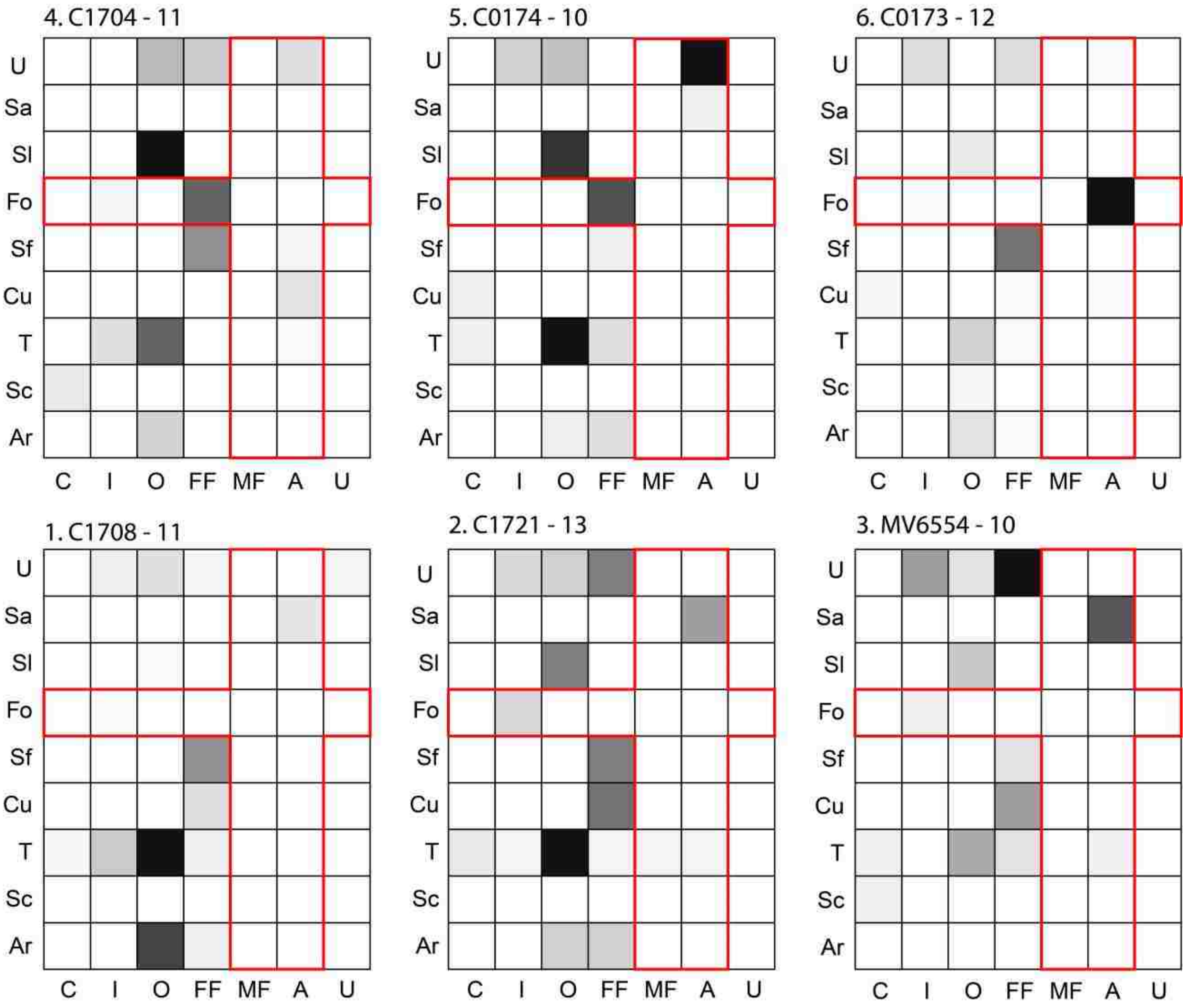

Figure 5.7. Guild representation in the six best sampled assemblages from Montana placed in stratigraphic context. See table 1 for abbreviations. The numbers (1-6) refer to the relative age (from oldest to youngest). The number to the right of the locality name (after the dash) indicates the functional richness. The darker the cell, the higher the percentage of mammals in this guild. Cell darkness is scaled differently across assemblages. See table 3 for values. The cells surrounded by the red polygon correspond to ecologies associated with open environments (see Figure 9).

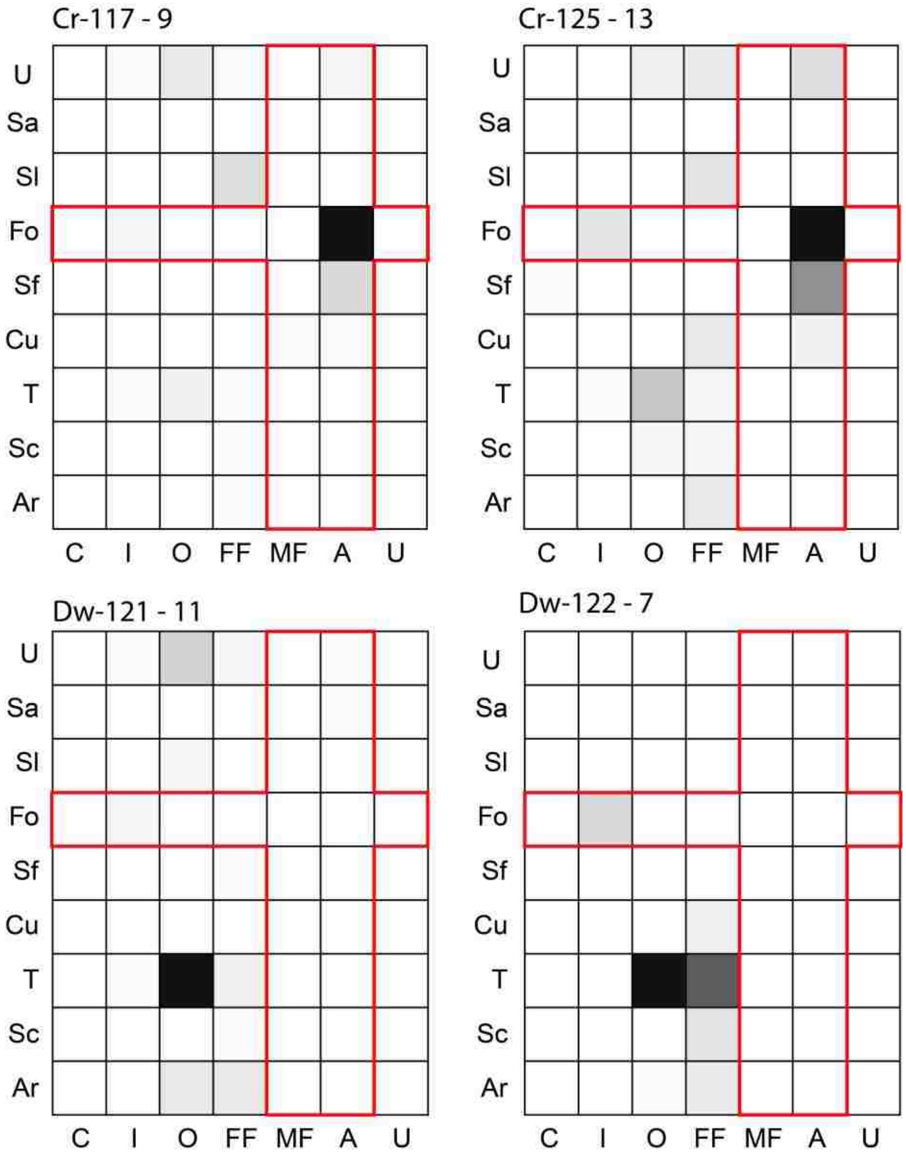

Figure 5.8. Guild representation in the four assemblages from Nebraska. See table 1 for abbreviations. The number to the right of the locality name (after the dash) indicates the functional richness. The darker the cell, the higher the percentage of mammals in this guild. Cell darkness is scaled differently across assemblages. See table 3 for values. The cells surrounded by the red polygon correspond to ecologies associated with open environments (see Figure 8).

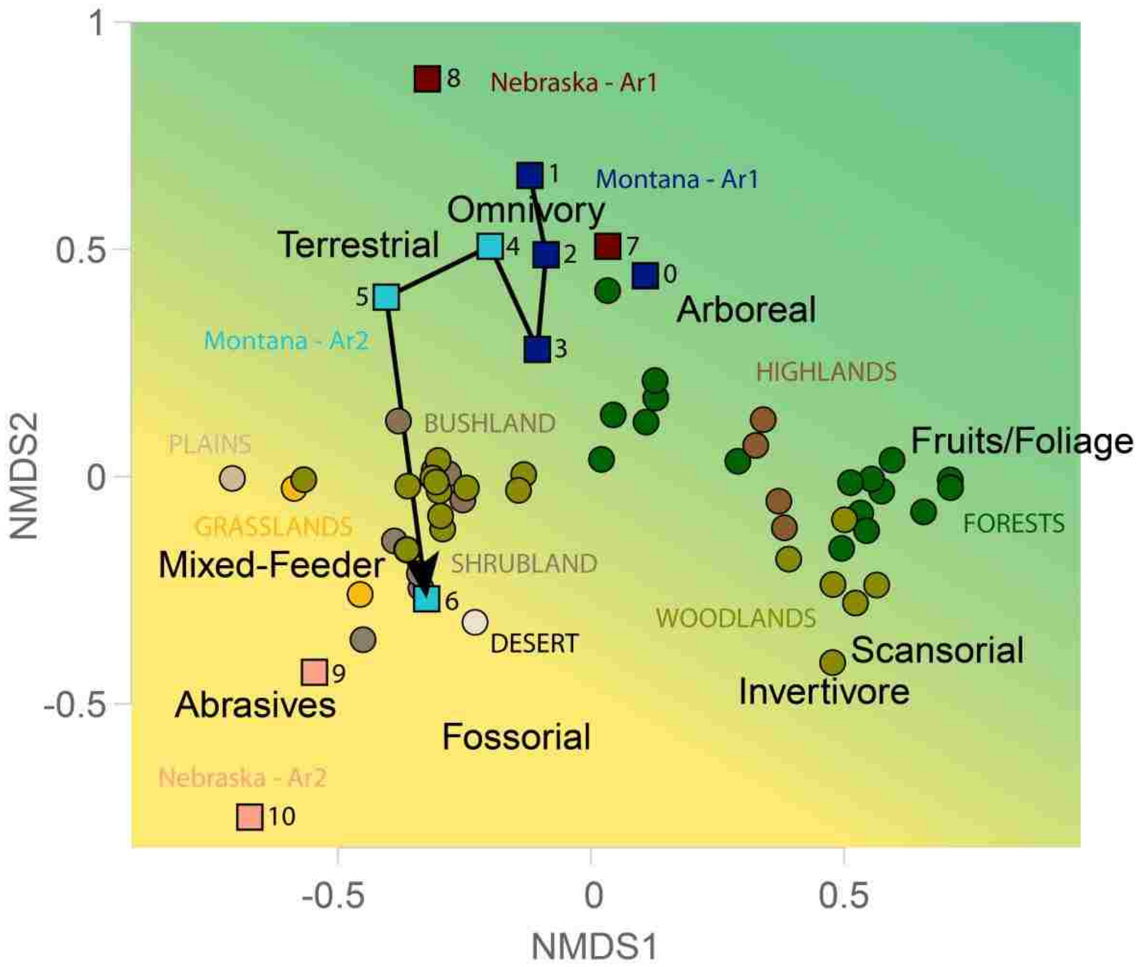

Figure 5.9. NMDS ordination of extant mammalian communities and fossil assemblages. Circles represent modern communities. The color corresponds to the environment the community lives in. Squares represent fossil assemblages. Labels: 0, MV6613; 1, C1708; 2, C1721; 3, MV6554; 4, C1704; 5, C0174; 6, C0173; 7, Dw-122; 8, Dw-121; 9, Cr-125; 10, Cr-117. The loadings of significant ecological categories (α<0.05) are indicated. The color gradient in the background reflects the closed-open environment axis of the modern communities. The colors of the symbols correspond to the environments/fossil assemblages labeled in the same color. The arrow (from 1 to 6) represents the trajectory through time of fossil assemblages from Montana in the ecospace represented by the ordination. See Appendix 5.3 for NMDS scores.

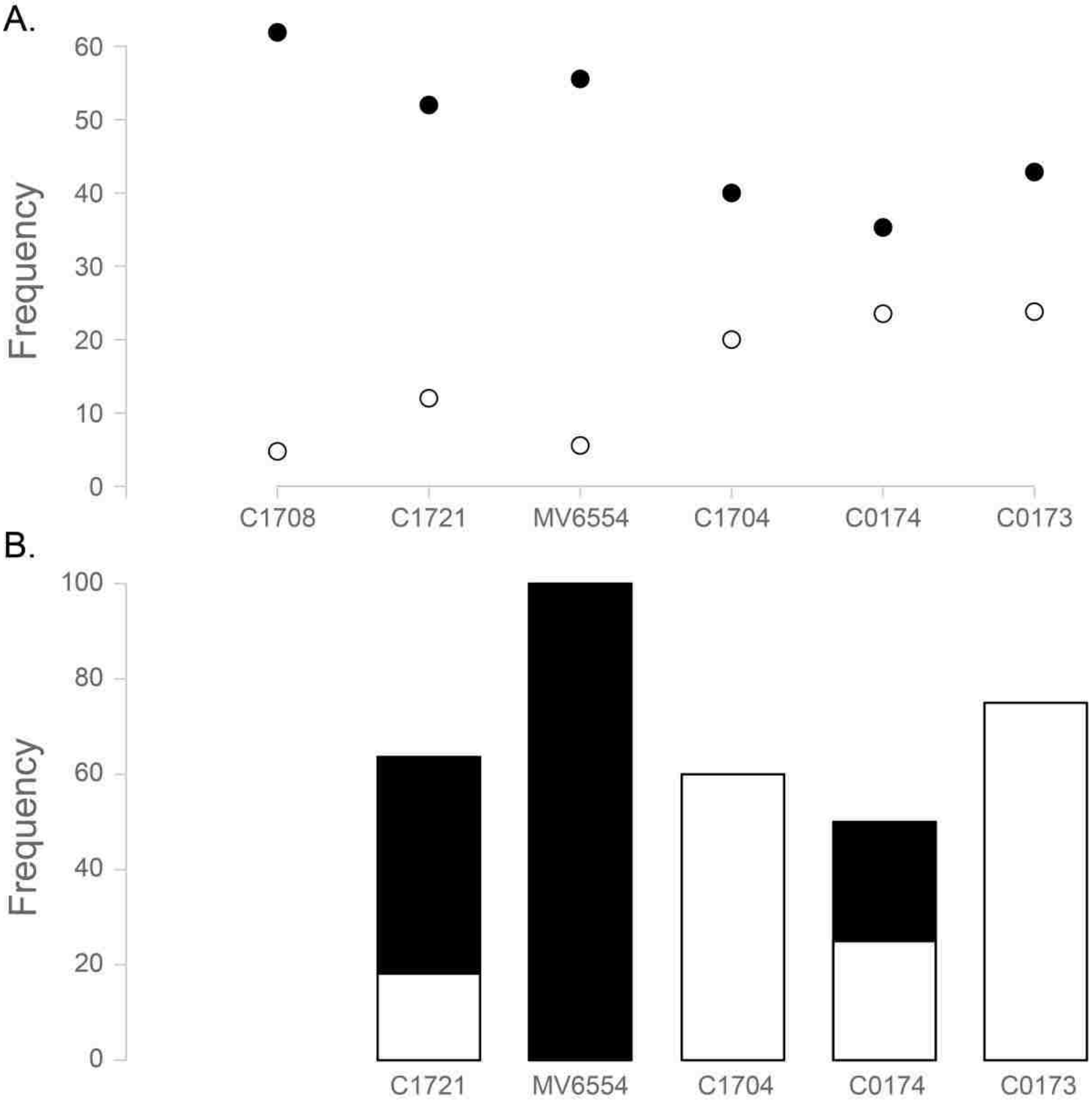

Figure 5.10. Species frequency through time in Montana. A) Frequency of species (not individuals) with closed/mesic habitat affinities (full circle) and open habitat affinities (open circle). B) Frequency of new species (first recorded in this assemblage among those studied) with closed/mesic habitat affinities (full bars) and open habitat affinities (open bar).

TABLES

Table 5.1. Fossil assemblages and functional richness. Abbreviations: Ar, Arikareean; CP, Cabbage Patch beds; LF, Local Fauna; N, number of specimens; S, number of genera.

Name	Unit	Age	N	S	Functional Richness	Redundancy
C0173	Upper CP	Ar2	179	21	12	1.42
C0174	Middle CP	Ar2	70	17	10	1.20
C1704	Middle CP	Ar2	179	20	11	1.45
MV6554	Lower CP	Ar1	63	18	10	1.10
C1721	Lower CP	Ar1	97	25	13	1.46
C1708	Lower CP	Ar1	213	21	11	1.45
MV6113	Lower CP	Ar1	41	12	8	1.13
Cr-125	McCann Canyon LF	Ar2	186	25	13	1.46
Cr-117	McCann Canyon LF	Ar2	738	29	9	2.44
Dw-122	Ridgeview LF	Ar1	105	11	7	0.86
Dw-121	Ridgeview LF	Ar1	3128	45	11	2.91

Table 5.2. Ecological assignment of fossil genera included in the analyses. Abbreviations: A, Abrasive foods; Ar, Arboreal; C, Carnivory; CP, Cabbage Patch; Cu, Cursorial; Dw, dental wear (including mesowear and gross dental wear); Env., Environmental affinity; Fa, faunal affinities in other regions; FF, Fruits and Foliage; Fo, Fossorial; Gm, gross morphology; Hyp., Hypsodonty; I, Invertivory; Loc., Locomotion; MF, Mixed-Feeder; O, Omnivory; Ph, phylogenetic relationships; Qa, quantitative analyses of morphology; RLF, Ridgeview Local Fauna; Sc, Scansorial; Sf, Semifossorial; Sl, Saltatorial; T, Terrestrial; U, Unknown. Sources: 1, Albright 1998; 2, Asher et al. 2005; 3, Barnosky 1982; 4, Benton et al. 2015; 5, Calede 2014; 6, Calede et al. 2016; 7, Casanovas-Vilar and Agusti 2007; 8, Dawson 1958; 9, Daxner-Hock 2004; 10, Daxner-Hock 2005; 11, Daxner-Hock 2010; 12, Emry and Korth 2007; 13, Emry and Thorington 1984; 14, Engler and Martin 2015; 15, Figueirido et al. 2015; 16, Flynn 2008; 17, Flynn and Jacobs 2008; 18, Fraser and Theodor 2010; 19, Gawne 1976; 20, Goin et al. 2016; 21, Goodwin 2008; 22, Gunnell et al. 2008; 23, Hooker 1992; 24, Hopkins 2005A; 25, Hopkins 2005B; 26, Hopkins 2007; 27, Horovitz et al. 2008; 28, Houssaye et al. 2015; 29, Hubbart 2012; 30, Hutchison 1968; 31, Janis and Theodor 2014; 32, Janis et al. 2012; 33, Jardine et al. 2012; 34, Korth 2007; 35, Korth 2008; 36, Korth and Bailey 2006; 37, Korth and Branciforte 2007; 38, Korth and Emry 1991; 39, Korth and Samuels 2015; 40, Levering et al., in review; 41, Lopatin 1996; 42, Martin 1973; 43, Martin 1980; 44, Metais and Vislobokova 2007; 45, Mihlbachler and Solounias 2006; 46, Mihlbachler et al. 2011; 47, Miljutin 2006; 48, Nagel and Morlo 2003; 49, Maridet et al. 2014; 50, Ostrander 1986; 51, Pratt and Morgan 1989; 52, Prieto et al. 2014; 53, Prothero 1998; 54, Prothero 2005; 55, Rose 2012; 56, Rybczynski; 57, Samuels 2009; 58, Samuels et al. 2013; 59, Slater 2015; 60, Specimen observations; 61, Tedford et al. 2004; 62, Thorington et al. 2005; 63, van Dam and Utescher 2016; 64, Vasileiadou et al. 2009; 65, Wang

1993; 66, Wang 1994; 67, Wang et al. 1999; 68, Webb 1977; 69, Webb 1998; 70, Wood 1935; 71, Wood 1936; 72, Gobetz and Martin 2006; 73, Rensberger 1971; 74, Lindsay 2008; 75, Samuels and Van Valkenburgh 2008; 76, Samuels and Van Valkenburgh 2009; 77, Casanovas-Vilar and van Dam 2013; 78, Calede et al. 2011; 79, Korth and Rybczynski 2003; 80, Bjork 1975; 81, Furio et al. 2012; 82, Daxner-Hock et al. in press; 83, Piras et al. 2012.

Genus	Diet	Hyp.	Loc.	Proxies	Env.	Source
Agnotocastor	FF	2	U	Gm, Qa	U	33, 57
Allomys	FF	1	U	Gm	C	24
Amphechinus	O	--	Sc	Gm	O	41, 49, 60
Ankylodon	I	--	U	Gm		60
Archaeocyon	C	--	T	Gm, Qa	O	58-59, 67
Archaeolagus	A	4	Cu	Gm	O	19, 33
Arikareeomys	FF	2	Ar	Gm, Fa		7, 10-11, 14, 33
Brachyerix	O	--	U	Gm		60
Campestrallomys	FF	1	Ar	Gm		24, 26
Cedromus	FF	1	Ar	Gm		33, 38
Centetodon	I	--	U	Gm		2, 60
Cormocyon	C	--	Cu	Gm, Qa	O	15, 59, 67
CP Sicistinae A	O	1	U	Gm, Ph	U	47, 60
CP Sicistinae B	O	1	U	Gm, Ph	U	47, 60
CP Talpidae A	I	--	U	Gm	C	22, 60
Cynodesmus	C	--	Sc	Gm	C	65-66
Desmatolagus	A	3	U	Gm	O	33, 41
Diceratherium	FF	--	T	Gm, Qa	C	1, 28, 53-54
Domnina	I	--	U	Fa, Gm, Ph	C	22, 82
Downsimus	FF	1	U	Gm	U	24, 26
Entoptychus	A	3	Fo	Gm, Qa		6, 33
Eporeodon	MF	--	T	Dw, Qa	O	40, 45
Euroxenomys	A	3	Sa	Gm, Fa		9, 33, 52
Eutypomys	A	3	T	Gm	U	17, 56, 79
Florentiamys	O	1	T	Gm		33, 71
Geringia	O	2	T	Gm, Ph		33, 42-43, 74
Gregorymys	A	3	Fo	Gm, Qa	O	6, 72

Gripholagomys	A	3	U	Gm		33
Haplomys	FF	1	Ar	Gm		24, 26
Heliscomys	O	1	T	Gm		33, 70
Heosminthus	O	1	Sl	Gm, Ph	U	47, 60
Herpetotherium	O	--	T	Fa, Gm, Ph	C	23, 27, 64, 81
Hesperopetes	FF	1	Ar	Gm		12
Hitonkala	O	1	U	Gm		33
Hypisodus	MF	--	Cu	Janis 2008		31, 68
Kirkomys	O	1	U	Gm		33
Leidymys	O	1	T	Gm, Ph	U	33, 42-43, 74
Leptauchenia	FF	--	Sc	Gm, Dw		4, 45
Leptocyon	C	--	Cu	Gm	O	59, 61, 65
Leptodontomys	O	1	Ar	Gm, Fa	C	7, 9-10, 14, 16, 78
Megalagus	FF	2	T	Gm, Dw	C	8, 18, 33
Meniscomys	FF	2	Sf	Gm	O	24-26
Microtheriomys	A	3	Sa	Gm, Ph	C	39
Miohippus	FF	--	T	Qa, Dw	C	32-33, 46
Miosciurus	FF	1	Ar	Gm, Ph	C	39
Miospermophilus	FF	1	Sf	Gm, Ph		13, 21, 29, 33, 77
Mookomys	O	1	Sl	Gm		33, 39
Mystipterus	I	--	T	Gm	C	22, 30
Nanodelphys	O	--	Ar	Gm	C	20, 55
Nanotragulus	FF	--	Cu	Gm		44, 69
Neatocastor	A	3	U	Gm	U	17
Neoadjidaumo	FF	2	Ar	Gm, Fa		7, 10-11, 14
Niglarodon	FF	2	Sf	Gm, Ph	U	24-26
Nototamias	FF	1	Sc	Gm, Ph		33, 51
Ocajila	O	--	U	Gm	U	60
Paciculus	O	2	Sl	Gm		33, 42-43, 74
Palaeocastor	A	3	Fo	Gm, Qa		5, 33, 57, 75-76
Palaeogale	C	--	Sf	Gm, Qa		48
Paleolagus	FF	2	T	Gm, Dw	C	8, 18, 33
Parallomys	FF	1	U	Gm	C	24, 26
Parvericius	O	--	T	Gm		50, 60
Pentabuneomys	O	1	Ar	Gm, Fa		7, 10-11, 14, 35
Petauristodon	FF	1	Ar	Gm, Ph	C	33, 39, 62
Plesiosminthus	O	1	U	Gm, Ph		33

Pleurolicus	FF	2	Fo	Gm, Qa	O	6, 73
Priusaulax	A	2	U	Gm		2006
Proharrymys	O	1	T	Gm, Ph		37, 39
Proheteromys	FF	2	T	Gm		33, 39
Promerycochoerus	MF	--	T	Dw, Qa		40, 45
Promylagaulus	A	3	Sf	Gm, Ph		24-26
Pronodens	FF	--	Cu	Gm	C	31, 44, 69
Proscalopid A	I	--	Fo	Gm, Ph	C	3, 22, 80
Proscalopid B	I	--	Fo	Gm, Ph	C	3, 22, 80
Proscalops	I	--	Fo	Gm, Ph	C	3, 22, 80
Prosciurus	FF	1	Ar	Gm, Ph		24, 26
Protosciurus	FF	1	Ar	Gm, Ph		21, 33, 77
Protospermophilus	FF	1	Sf	Gm, Ph		21, 29, 33, 77
Pseudotheridomys	FF	2	Ar	Fa, Gm, Ph	C	7, 10-11, 14, 33, 63
Pseudotrimylus	I	--	U	Fa, Gm, Ph	C	22, 82
RLF Soricidae	I	--	U	Gm		60
Rudiomys	FF	2	Sf	Gm, Ph	U	24-26
Sanctimus	O	1	U	Gm		33
Scalopoides	I	--	Fo	Gm, Qa		30, 83
Sciurion	FF	1	Ar	Gm, Ph	C	33, 39, 62
Scottimus	O	1	U	Gm		33
Skinneroceras	U	--	U	--		--
Spermophilus	FF	2	Sf	Gm, Ph		21, 29, 33, 77
Stenoechinus	I	--	U	Gm	U	60
Tenudomys	FF	2	U	Gm	U	33
Trilaccogaulus	A	3	Sf	Gm, Ph	O	24-26
Tylionomys	O	1	T	Gm, Fa		34, 37
Zophoapeomys	FF	2	Ar	Gm, Fa		7, 10-11, 14, 35

Table 5.3. Summary of the ecological composition of each fossil assemblage.

Ecological category	MV6613	C1708	C1721	MV6554	C1704	C0174	C0173	Dw121	Dw122	Cr117	Cr125
Fruits/Foliage	65.85	24.41	40.21	44.44	32.96	22.86	32.40	12.88	44.76	11.38	17.20
Carnivore	0.00	0.94	2.06	3.17	2.23	2.86	1.12	0.10	0.00	0.14	0.54
Invertivore	4.88	9.86	7.22	12.70	4.47	4.29	6.15	3.61	7.62	2.44	4.84
Omnivore	19.51	60.09	40.21	19.05	52.51	47.14	17.88	83.02	47.62	9.21	12.90
Mixed-Feeder	0.00	0.00	1.03	0.00	0.00	0.00	0.00	0.00	0.00	1.22	0.00
Abrasives	9.76	3.29	9.28	0.00	7.82	22.86	42.46	0.38	0.00	75.61	64.52
Unknown	0.00	1.41	0.00	20.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brachydont	35.29	57.27	64.18	25.00	56.76	50.88	14.86	56.05	8.54	8.06	11.84
Mesodont	52.94	36.36	22.39	42.50	33.78	21.05	33.78	43.52	91.46	10.12	9.21
Hypsodont	11.76	6.36	13.43	32.50	6.08	28.07	50.68	0.43	0.00	80.50	76.32
Hypselodont	0.00	0.00	0.00	0.00	3.38	0.00	0.68	0.00	0.00	1.32	2.63
Arboreal	4.88	26.76	8.25	0.00	4.47	4.29	5.59	12.79	4.76	0.27	3.23
Scansorial	0.00	0.00	0.00	1.59	2.23	0.00	1.68	0.32	5.71	0.54	2.15
Terrestrial	17.07	41.31	26.80	15.87	20.11	25.71	8.38	67.07	79.05	4.20	10.75
Cursorial	4.88	4.23	12.37	11.11	2.79	1.43	2.23	0.00	2.86	2.44	5.91
Saltatorial	7.32	0.47	11.34	6.35	24.58	18.57	3.35	1.92	0.00	8.81	4.84
Semifossorial	36.59	14.55	11.34	3.17	12.85	1.43	24.58	0.67	0.00	9.89	18.82
Fossorial	0.00	0.47	3.09	1.59	17.32	15.71	41.90	2.56	7.62	63.82	43.01
Semiaquatic	7.32	3.29	8.25	19.05	0.00	1.43	0.00	0.16	0.00	0.00	0.00
Unknown	21.95	8.92	18.56	41.27	15.64	31.43	12.29	14.51	0.00	10.03	11.29

Table 5.4. Chord distance values between subsequent assemblages from Montana.

Assemblage pair	Locomotion	Diet	Hypsodonty
C1708-C1721	0.53	0.41	0.25
C1721-MV6554	0.59	0.42	0.73
MV6554-C1704	0.97	0.62	0.67
C17014-C0174	0.38	0.30	0.40
C0174-C0173	0.94	0.64	0.71

Table 5.5. Frequency of taxa and new taxa with closed/mesic, open, or unknown environmental affinities across assemblages from Montana.

	C1708	C1721	MV6554	C1704	C0174	C0173
Closed/Mesic	61.90	52	55.56	40	35.29	42.86
Open	4.76	12	5.56	20	23.53	23.81
Unknown	33.33	36	38.89	40	41.18	33.33
New Open	--	18.18	0	60	25	75
New Closed	--	45.45	100	0	25	0
New Unknown	--	36.37	0	40	50	25

APPENDIX

A5.1. Locality information for the extant mammalian ecosystems included in the analyses.

Locality	Category	Rainfall	Source
Manu	Forest	2100	Townsend 2004
Sian Ka'an	Forest	1128	Townsend 2004
Beni	Forest	1900	Townsend 2004
Iguazu	Forest	1600	Townsend 2004
La Selva	Forest	3962	Townsend 2004
Yasuni	Forest	3500	Townsend 2004
La Amistad	Forest	2500	Townsend 2004
Rio Platano	Forest	4000	Townsend 2004
Sierra Gorda	Forest	2500	Townsend 2004
Maya Mountains	Forest	1500	Townsend 2004
Caatinga	Open woodland	600	Townsend 2004
Pantanal	Open woodland	1600	Townsend 2004
Banados del Este	Open woodland	1000	Townsend 2004
Cerradão	Open woodland	1270	Townsend 2004
Estancia Toledo	Chaco	865	Townsend 2004
Estancia Zalazar	Chaco	900	Townsend 2004
Ulla Ulla	Highland	635	Townsend 2004
Lauca	Highland	335	Townsend 2004
Huascaran	Highland	884	Townsend 2004
Los Puzuelos	Highland	300	Townsend 2004
W of Niger	Forest	1600	Reed 1996
E of Cross	Forest	1550	Reed 1996
Makakou	Forest	1800	Reed 1996
Kilimanjaro	Forest (Montane)	1050	Reed 1996
E of Niger	Forest	1596	Reed 1996
Congo Basin	Forest	1800	Reed 1996
Knysna	Forest (some Montane)	1016	Reed 1996
Rwenzori NP	Moist woodland	900	Reed 1996
Guinea Woodland	Moist woodland	1000	Reed 1996
W Lunga NP	Moist woodland	875	Reed 1996
Natal Woodland	Moist woodland	875	Reed 1996
Serengeti Bushland	Bushland	803	Reed 1996
Rukwa Valley	Bushland/woodland	700	Reed 1996
Lake Mweru	Bushland/woodland/edaphic grasslands	850	Reed 1996

Kafue NP	Medium woodland	821	Reed 1996
Serengeti	Bushland/woodland	750	Reed 1996
S Savanna Woodland	Open woodland	650	Reed 1996
Sudan Savanna	Open woodland	689	Reed 1996
Kruger NP	Open woodland	675	Reed 1996
Linyanti Swamp	Open woodland/swamp	650	Reed 1996
Amboseli NP	Scrub woodland	600	Reed 1996
Tarangire NP	Scrub woodland	600	Reed 1996
Okavango Delta	Shrubland with floodplain	600	Reed 1996
Chobe NP	Scrub woodland with river	650	Reed 1996
SW Arid Region	Shrubland	400	Reed 1996
Kalahari Thornveld	Shrubland	450	Reed 1996
Sahel Savanna	Shrubland with edaphic grassland	450	Reed 1996
Serengeti Plains	Plains	500	Reed 1996
S Savanna Grasslands	Grasslands with floodPlain	500	Reed 1996
Kafue Flats	Edaphic grasslands	821	Reed 1996
Namib Desert	Desert	125	Reed 1996

A5.2. Ecological composition of extant mammalian communities and fossil assemblages included in the analyses.

Locality	Habitat	Habitat Details	Fruits/Foliage	Invertivore	Omnivory	Mixed Feeder	Abrasives	Arboreal	Scansorial	Terrestrial	Fossorial	Semiaquatic
Serengeti Bushland	Bushland	Bushland	27.3	9.09	11.4	25	27.3	6.25	15.6	59.4	14.1	4.69
Rukwa Valley	Bushland	Bushland Woodland	27.3	5.47	12.6	24.6	30	5.77	13.5	63.5	9.62	7.69
Serengeti	Bushland	Bushland Woodland	26.4	9.44	13.2	24.5	26.4	5.33	13.3	62.7	10.7	8
Lake Mweru	Bushland	Bushland Woodland Edaphic grasslands	36	0	8.01	20	36	5.4	8.11	73	5.4	8.11
Namib Desert	Desert	Desert	25	12.5	0	25	37.5	0	27.8	50	22.2	0
Manu	Forest	Forest	72.6	23.5	3.91	0	0	33.3	31.6	21	5.3	8.8
Sian Ka'an	Forest	Forest	65.9	21.9	12.2	0	0	11.8	47.1	31.4	9.79	0
Beni	Forest	Forest	74.3	20	5.71	0	0	28	28	30	6	8
Iguazu	Forest	Forest	57.6	30.3	12.1	0	0	10.8	37	28.2	10.8	13.1
La Selva	Forest	Forest	72.2	22.2	5.58	0	0	26.8	31.7	22	17.1	2.4
Yasuni	Forest	Forest	74.6	21.2	4.21	0	0	33	31.7	19.5	11	4.87
La Amistad	Forest	Forest	75.7	19.4	4.88	0	0	19.7	31	33.8	11.3	4.26
Rio Platano	Forest	Forest	59.1	31.8	9.09	0	0	18.5	37	37	7.41	0
Sierra Gorda	Forest	Forest	82.6	9.5	7.88	0	0	2.74	45.8	41.7	9.74	0
Maya Mountains	Forest	Forest	66.7	26.7	6.67	0	0	5	45	35	10	5
W of Niger	Forest	Forest	36.7	6.67	30	13.3	13.3	37.5	12.5	28.1	9.38	12.5
E of Cross	Forest	Forest	42.4	6.06	30.3	12.1	9.09	35	10	27.5	10	17.5
Makakou	Forest	Forest	44.4	0	30.6	11.1	13.9	34.2	19.5	36.6	2.44	7.32
E of Niger	Forest	Forest	36.7	13.3	20	16.7	13.3	27.3	12.1	36.4	9.09	15.2
Congo Basin	Forest	Forest	56.4	7.69	18	10.3	7.69	26.4	22.6	28.3	9.43	13.2
Kilimanjaro	Forest	Montane Forest	52.9	0	23.5	17.7	5.88	31.6	5.26	63.2	0	0
Knysna	Forest	Montane Forest	41.7	0	33.3	8.33	16.7	23.5	23.5	35.3	11.8	5.88
Kafue Flats	Grassland	Edaphic Grasslands	18.2	0	9.08	22.7	50	0	14.3	68.6	2.86	14.3

S Savanna Grasslands	Grassland	Grasslands Floodplain	12	16	0	24	48	0	14.6	58.5	17.1	9.76
Ulla Ulla	Highland	Highland	90.1	9.94	0	0	0	0	21.4	71.5	7.1	0
Lauca	Highland	Highland	92.1	7.95	0	0	0	0	25.9	55.5	18.6	0
Huascaran	Highland	Highland	75	12.5	12.5	0	0	0	30.8	61.5	7.69	0
Los Puzuelos	Highland	Highland	88.5	11.5	0	0	0	0	24.1	51.8	24.1	0
Serengeti Plains	Plains	Plains	0	15.4	15.4	30.8	38.5	0	0	84.2	15.8	0
SW Arid Region	Shrubland	Shrubland	20	12.5	5.01	20	42.5	1.67	11.7	61.7	18.3	6.67
Kalahari Thornveld	Shrubland	Shrubland	10	30	0	30	30	0	6.67	60	33.3	0
Sahel Savanna	Shrubland	Shrubland Edaphic Grassland	11.1	11.1	16.7	27.8	33.3	0	22.6	51.6	16.1	9.68
Okavango Delta	Shrubland	Shrubland Floodplain	16.7	13.9	11.1	16.7	41.7	1.85	14.8	53.7	18.5	11.1
Est. Toledo	Woodland	Chaco	57.2	38	4.8	0	0	7.11	35.7	28.6	21.4	7.11
Est. Zalazar	Woodland	Chaco	58.6	31	10.3	0	0	2.63	31.6	42.1	18.4	5.26
Kafue NP	Woodland	Medium Woodland	22.2	8.33	16.7	13.9	38.9	5.45	16.4	52.7	14.6	10.9
Rwenzori NP	Woodland	Moist woodland	31.4	5.71	22.9	14.3	25.7	15.7	17.7	45.1	11.8	9.8
Guinea Woodland	Woodland	Moist woodland	35	7.49	12.5	17.5	27.5	11.9	17	52.6	10.2	8.47
W Lunga NP	Woodland	Moist woodland	29.4	2.94	14.7	23.5	29.4	7.84	13.7	60.8	7.84	9.8
Natal Woodland	Woodland	Moist woodland	29	5.25	13.2	23.7	29	7.5	17.5	57.5	10	7.5
Caatinga	Woodland	Open woodland	60.8	35.7	3.54	0	0	2.77	38.2	41.7	17.3	0
Pantanal	Woodland	Open woodland	63.9	29.7	6.4	0	0	12.3	35.1	38.6	8.79	5.27
Banados del Este	Woodland	Open woodland	57.9	36.8	5.27	0	0	0	20.8	29.2	25	25
Cerradão	Woodland	Open woodland	63.9	33.3	2.8	0	0	16.7	26.2	26.2	23.8	7.1
S Savanna Woodland	Woodland	Open woodland	24.1	8.62	8.62	24.2	34.5	4.82	10.8	66.3	12.1	6.02
Sudan Savanna	Woodland	Open woodland	25.8	6.45	16.1	22.6	29	3.92	13.7	62.7	13.7	5.88
Kruger NP	Woodland	Open woodland	26.8	7.31	12.2	22	31.7	3.17	14.3	61.9	12.7	7.94
Linyanti Swamp	Woodland	Open woodland swamp	20	0	8.01	24	48	2.86	11.4	68.6	2.86	14.3
Amboseli NP	Woodland	Scrub woodland	24.2	9.09	12.1	21.2	33.3	2.17	17.4	60.9	15.2	4.35
Tarangire NP	Woodland	Scrub woodland river	25.7	14.3	11.4	22.9	25.7	2.08	10.4	68.8	16.7	2.08
Chobe NP	Woodland	Scrub woodland river	17.5	12.5	10	20	40	1.79	14.3	57.1	17.9	8.93

Dw121	Fossil	Nebraska - Ar1	12.9	3.61	83.1	0	0.38	15	0.37	81.5	2.99	0.19
Dw122	Fossil	Nebraska - Ar1	44.8	7.62	47.6	0	0	4.76	5.71	81.90	7.62	0
Cr117	Fossil	Nebraska - Ar2	11.4	2.44	9.22	1.22	75.7	0.31	0.62	26.2	72.9	0
Cr125	Fossil	Nebraska - Ar2	17.3	4.87	13	0	64.9	3.64	2.42	45.5	48.5	0
MV6613	Fossil	Montana - Ar1	65.9	4.88	19.5	0	9.76	6.25	0	84.4	0	9.38
C1708	Fossil	Montana - Ar1	25	10.1	61.5	0	3.36	29.4	0	66.5	0.52	3.61
C1721	Fossil	Montana - Ar1	41.1	7.37	41.1	1.05	9.47	10.1	0	76	3.8	10.1
MV6554	Fossil	Montana - Ar1	45.9	13.1	19.7	0	21.3	0	2.7	62.2	2.7	32.4
C1704	Fossil	Montana - Ar2	33.7	4.57	53.7	0	8	5.3	2.65	71.5	20.5	0
C0174	Fossil	Montana - Ar2	23.5	4.42	48.5	0	23.5	6.25	0	68.8	22.9	2.08
C0173	Fossil	Montana - Ar2	32.8	6.22	18.1	0	42.9	6.37	1.91	44	47.8	0

A5.3. NMDS scores for the localities included in the analysis.

Locality	NMDS1	NMDS2	NMDS3
Serengeti Bushland	-0.25334	-0.05147	-0.05324
Rukwa Valley	-0.30985	0.013943	-0.02138
Serengeti	-0.2818	0.00615	-0.04438
Lake Mweru	-0.38041	0.122231	-0.05219
Namib Desert	-0.22917	-0.3207	-0.16473
Manu	0.710147	-0.0075	0.137716
Sian Ka'an	0.574494	-0.03207	-0.06102
Beni	0.59495	0.036154	0.106287
Iguazu	0.495492	-0.15805	0.101621
La Selva	0.657492	-0.0778	0.090632
Yasuni	0.710608	-0.02423	0.110802
La Amistad	0.554773	-0.00542	0.011424
Rio Platano	0.533004	-0.08021	0.024556
Sierra Gorda	0.51304	-0.01334	-0.24831
Maya Mountains	0.544713	-0.11897	-0.08845
W of Niger	0.043972	0.135649	0.459501
E of Cross	0.1279	0.172915	0.474829
Makakou	0.126733	0.211188	0.403068
E of Niger	0.02084	0.03775	0.312234
Congo Basin	0.290413	0.033661	0.278613
Kilimanjaro	0.032793	0.40912	0.216523
Knysna	0.108842	0.119907	0.340656
Kafue Flats	-0.58669	-0.02607	-0.04092
S Savanna Grasslands	-0.45629	-0.25938	-0.16677
Ulla Ulla	0.340351	0.125102	-0.42696
Lauca	0.371275	-0.05417	-0.39855
Huascaran	0.325619	0.068498	-0.24866
Los Puzuelos	0.382253	-0.1127	-0.38597
Serengeti Plains	-0.70887	-0.00406	-0.28676
SW Arid Region	-0.38858	-0.14161	-0.11996
Kalahari Thornveld	-0.45052	-0.35885	-0.34522
Sahel Savanna	-0.33614	-0.24518	-0.09414
Okavango Delta	-0.33911	-0.21304	-0.01521
Est. Toledo	0.522863	-0.27827	-0.00399
Est. Zalazar	0.390831	-0.18165	-0.08076
Kafue NP	-0.29315	-0.11558	0.058879
Rwenzori NP	-0.13295	0.004392	0.183139
Guinea Woodland	-0.1433	-0.03025	0.05959

W Lunga NP	-0.30203	0.035318	0.027083
Natal Woodland	-0.24635	-0.02504	0.012426
Caatinga	0.478301	-0.23751	-0.15627
Pantanal	0.501234	-0.09504	-0.02594
Banados del Este	0.477713	-0.40933	-0.00462
Cerrad?o	0.564726	-0.23864	0.064375
S Savanna Woodland	-0.36197	-0.02097	-0.08425
Sudan Savanna	-0.31279	-0.00307	-0.0322
Kruger NP	-0.30019	-0.03175	-0.04622
Linyanti Swamp	-0.56767	-0.00685	-0.0411
Amboseli NP	-0.29724	-0.08652	-0.07925
Tarangire NP	-0.3057	-0.01209	-0.16163
Chobe NP	-0.36388	-0.16097	-0.07014
Dw121	-0.32341	0.874946	-0.02151
Dw122	0.033248	0.506632	-0.10851
Cr117	-0.67433	-0.74923	0.426247
Cr125	-0.54648	-0.4306	0.288651
MV6613	0.107498	0.441931	-0.22137
C1708	-0.12055	0.662372	0.189701
C1721	-0.08862	0.488096	0.024775
MV6554	-0.10601	0.279825	-0.28005
C1704	-0.19919	0.50654	-0.07321
C0174	-0.40472	0.394774	0.002903
C0173	-0.32481	-0.26895	0.347625

Chapter 6. CONCLUSIONS

The detailed study of the taphonomy, systematics, biodiversity, and ecology of the mammalian fauna from the Cabbage Patch beds offers critical insights in the Oligocene paleontology of the Rocky Mountains, Arikareean mammals, and Cenozoic mammalian evolution.

The results of the taphonomic analysis of the Cabbage Patch beds demonstrate that the majority of the most productive localities are derived from low-energy deposits accumulated by predators and attrition and reworked by fluvial processes. Avian predators in particular may have played an important role in the accumulation of the fossil assemblages, leading to the overrepresentation of small mammals in the record. The combined study of the sedimentology of the fossil-bearing horizons and the mammalian remains supports the recognition of taphofacies, bodies of rocks defined by a specific set of taphonomic characteristics. Thus, there is an association between a number of specimen characteristics (including size, breakage, shape, weathering, and abrasion) and the lithology of the deposits that they come from. Nonetheless, many assemblages from the Cabbage Patch beds are similar enough in their preservation to allow comparisons of mammalian diversity through the beds. This taphonomic analysis demonstrates that with careful sampling, faunal analyses of select isotaphonomic vertebrate microfossil assemblages can yield biologically informative patterns of faunal change through the Cabbage Patch beds.

The geometric morphometric analysis of the teeth of modern gophers demonstrates that the shapes of the cheek teeth of extant geomyine gophers are taxonomically informative at the genus, subgenus, and sometimes species level. These results suggest that the geometric morphometric analysis of the shape of cheek teeth may provide important insights when applied to the fossil subfamily Entoptychinae. Much of the fossil record of Entoptychinae is composed of worn and isolated cheek teeth and partial jaws. Our analysis shows that despite lacking the diagnostic characters of the occlusal surface or associated osteological remains, isolated teeth can be taxonomically informative. The teeth of entoptychines can be identified to the genus level, sometimes the species level, and even help inform diagnoses and species boundaries. For example, we suspect that *Entoptychus minor* and *E. cavifrons* from the John Day Formation of Oregon may represent a single taxon. Future analyses of the osteology, ontogeny, and variation within and across entoptychine taxa will provide the necessary data to test such hypotheses. Our quantitative analysis of cheek tooth shape in entoptychines broadly supports previous analyses of the cranial morphology of the gophers from the Cabbage Patch beds where three undescribed species of *Pleurolicus* and at least one of *Gregorymys* are present. The detailed study of the morphology of entoptychine gophers, particularly those from the John Day Formation and the Cabbage Patch beds of Montana, coupled with the development of a phylogenetic framework would help provide more accurate assessments of the biostratigraphic ranges of entoptychine species and, combined with recent and ongoing developments in radioisotopic dating of gopher-bearing horizons in these areas, will allow a revised assessment of the value of gophers as biostratigraphic markers during the Arikareean in North America.

The mammalian fauna of the Cabbage Patch beds offers a unique window into faunal turnover during the rise of many modern mammalian clades. The revised chronostratigraphic framework and the detailed study of the taxonomy and diversity of the mammalian fauna through the beds suggest that the timing of the faunal turnover of the Arikareean in the northern Rocky Mountains was more similar to the timing in the John Day Formation of Oregon than the timing in the Arikaree Group of the Great Plains. The most substantial faunal turnover event through the beds occurs between the two oldest biostratigraphic units of the Cabbage Patch beds, likely coeval with the boundary between the early early and late early Arikareean, ca. 28 Ma. This pattern supports an eastward spread of the faunal transition of the Arikareean and a time transgressive mammalian turnover across the western United States. The presence of taxa with Eurasian affinities in the Cabbage Patch beds suggests a stronger role of transcontinental immigration in the faunal turnover of the Arikareean than previously suggested. Establishing the pattern of faunal turnover through the Cabbage Patch beds is a critical step to determining the role of environmental change in the rise of modern mammalian communities initiated during the Arikareean. Future studies of faunas coeval with the Cabbage Patch beds but also older and younger assemblages, will help assess spatial differences in the timing of faunal change in the Rocky Mountains and provide the necessary information to a biogeographic analysis of Arikareean mammalian faunas throughout the western United States.

My ecomorphological categorization of the fossil mammals from the Cabbage Patch beds enables an analysis of the changes in dietary and locomotory ecologies through time at the scale of communities. I conducted a similar analysis of a comparative dataset from Nebraska that provides the opportunity to contrast patterns of faunal change across regions with asynchronous environmental changes. Although in both regions the fauna went from being dominated by mammals with affinities for forested and mesic environments (e.g., fruit and foliage consumers, arboreal mammals) to dominated by mammals with affinities for open environments (e.g, consumers of abrasive grass and roots or tubers, burrowers) through the early Arikareean, this transition was more pronounced in Nebraska than Montana. Despite this difference in magnitude, the timing of the ecological transition is similar across the two regions. Reconstructions of the environments based on the ecological composition of the fossil assemblages suggest that faunas of the earliest Arikareean inhabited closed forests whereas younger faunas may have been associated to more savanna-like habitats. Differences in ecologies across taxa suggest that these changes in the ecological composition of Arikareean mammalian assemblages were linked to taxonomic turnover from immigration and in situ evolution. These results suggest that the link between environmental change, ecological filtering, and taxonomic turnover acting over evolutionary timescales led to the rise of modern mammalian faunas.